Università degli Studi di Torino



Doctoral School of Sciences and Innovative Technologies

PhD program in Earth Science (XXX Cycle)

Neogene and Quaternary palaeodiversity of the European lizards (Reptilia, Squamata)

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"Ich probiere."

Paul Ehrlich

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1. Introduction

Non-snake squamates (i.e., lizards and worm lizards) are an important component of the extant European herpetofauna, with nearly 80 species living in the continent nowadays (Sillero et al. 2014; Speybroeck et al. 2016). In addition, a number of extinct taxa and fossil representatives of extant ones have been reported to inhabit Europe since at least the middle Jurassic (Rage 2013, but see also the now dated account of Estes, 1983, and Böhme and Ilg 2003), including members of families that are now locally or globally extinct.

Because of this very long presence in the continent and a high taxonomical diversity, the study of the evolutionary history of this group of reptiles in the European territory, aimed at the understanding of the events that might have influenced their past and current distribution, figures as a very interesting topic.

Within this research context, this thesis is a contribution to our knowledge of the Neogene and Quaternary palaeontological record of European non-snake squamates. The fossil record of lizards and amphisbaenians will be summarized and discussed, including a revision of previously described material coming from different European localities, as well as descriptions of new material that has remained undescribed to date. The work is focused on the Neogene and Quaternary, roughly the last 23 millions of years, because this is the period of time during which the modern lizard fauna of Europe settled, with the first representatives of taxa closely related to modern ones appearing in the lower Miocene (Čerňanský 2010a; Rage 2013).

Before starting to consider the fossil record, however, a comparative osteological study of the skull bones of the extant European lizards and worm lizards is carried out. This analysis was needed because of the poor knowledge of the comparative osteology of these reptiles, which hampered our capability to identify fossil bones and to better understand the evolutionary history of the group. The analysis is

focused on the skull bones, because they are considered to be the most diagnostic elements in the lizard skeleton (Bell & Mead 2014).

The body of this thesis is therefore composed by different parts:

- The first part (chapter 2) is dedicated to the comparative study of lizard skull bones. This part includes also a diagnostic key created to ease the identification of isolated bones and a comment on the degree of recognisability of extant European lizards.

- The second part (chapters 3 and 4) consists of the description and identification of the fossil material directly studied in this work and of the summary of the fossil record of the Neogene and Quaternary non-snake squamates in Europe.

- The third part (chapter 5) contains some examples of informations that can be obtained from the study of remains of non-snake squamates, together with the rest of the herpetofauna. Here, case studies dealing with palaeoenvironmental and palaeobiogeographical reconstructions are presented.

1.1. Subject matter of the research: lizards and worm lizards

Squamates are considered to include three different groups, lizards ("Lacertilia" or "Sauria"; see chapter 1.2), amphisbaenians (Amphisbaenia) and snakes (Serpentes), together forming a clade that is the sister group to rhynchocephalians (see e.g., Conrad 2008; Hedges & Vidal 2009). However, even though the monophyly of both amphisbaenians and snakes has been largely confirmed (among others, Conrad 2008; Hedges & Vidal 2009; Gauthier et al. 2012), this is not true for the lizard group, which is in fact paraphyletic. As stated above, this thesis is focused only on the lizard and amphisbaenian (= worm lizard) taxa of the squamate clade.

In contrast with the generally accepted above-mentioned framework of the higher level relations of the three squamates vernacular groups, different hypotheses have been proposed to show how the various lizard (and squamate in general) taxa are related to one another. As clearly presented by Gauthier et al. (2012), one of the main causes of this uncertainty is linked to the kind of dataset used, with molecular data and morphology sometimes leading to strikingly different topologies. One of the

prime examples of this is the position of Iguania (i.e., Iguanidae, Agamidae and Chamaeleonidae): this clade is usually placed at the base of the squamate tree, sister to all other squamates, in morphological analyses (e.g., Estes et al. 1988; Gauthier et al. 1988, 2012; Conrad 2008; Fig. 1.1), but it has a far more derived position, grouped in a clade called Toxicofera with Anguimorpha and Serpentes, when molecules are considered (e.g., Hedges & Vidal 2009; Reeder et al. 2015; Fig. 1.2). The recent analysis by Reeder et al. (2015) seems to have made an important step in the resolution of this issue, combining both large morphological and molecular datasets: their results strongly support the molecular hypothesis and suggest that the



Figure 1.1) Morphology-based phylogenetic tree of Squamata, showing Iguania by the base of the tree (modified from Gauthier et al. 2012).



Figure 1.2) Molecular-based pylogenetic tree of Squamata, showing Iguania included in Toxicofera (modified from Reeder et al. 2015).

morphology-based analyses might be deeply influenced by convergent features leading to erroneous results. As stated also by the same authors, however, morphological, and in particular osteological, data still play an important role in phylogenetic analyses, because they provide the only possible way to include extinct taxa.

Regardless of their inner relations, lizards are a very diverse group of reptiles, including more than 6000 extant species worldwide grouped in more than 30 families (Uetz et al. 2017). Some suprafamiliar clades are commonly recognized, though the validity of some of these groups has been questioned by the recent molecular phylogenies.

Although being the subject of one of the most debated issues in squamate phylogeny (see above), Iguania is commonly considered to be monophyletic (Conrad 2008; Hedges & Vidal 2009; Gauthier et al. 2012; Reeder et al. 2015). Being either the most basal squamate group or a member of the Toxicofera, this clade includes iguanids, agamids and chamaeleonids. Among iguanians, iguanids are the only clade having a completely pleurodont dentition and so they are often referred to as Pleurodonta (Evans 2008; Gauthier et al. 2012; Reeder et al. 2015, even if the latter authors include in the clade also some fossil taxa that have been considered as a stem member of the group by Gauthier et al. 2012). Eight subfamilies, sometimes elevated to family level, are recognised (Evans 2008; Vitt & Caldwell 2009). Iguanids are a very diverse clade composed by species that display a large number of ecological requirements and life styles (Vitt & Caldwell 2009). Today they are mostly confined to the New World, with some exceptions living in Madagascar and in the Fiji Islands (Vitt & Caldwell 2009), but they are reported in the Cretaceous and the Paleogene of Europe and, at least for what stem members of the group are concerned, in the Cretaceous of Mongolia (Augé 1987; Gao & Norell 2000; Böhme & Ilg 2003; Smith 2009; Rage 2013; Blanco et al. 2016). Agamids and chamaeleonids compose the Acrodonta clade, distinguished by having acrodont marginal teeth among other things. In agamids, a small number of subpleurodont teeth is retained by the anterior end of both maxillae and dentaries, as well as on the premaxilla, whereas chamaeleons display only acrodont teeth (Evans 2008). Agamids are diurnal lizards, mostly terrestrial or semiarboreal, currently living in Africa, Asia, Australia and Europe (Vitt & Caldwell 2009). They have a long evolutionary history, which can be traced back to the Late Cretaceous of Asia (Borsuk-Bialynicka & Moody 1984). In Europe, they are currently represented by Laudakia stellio, which occurs on the Balkan Peninsula, but five other Asian species of the genera Laudakia, Phrynocephalus and Trapelus reach the Southern part of the European Russia (Sillero et al. 2014). Chamaeleons are mostly forest dwellers, with species living at different levels from the ground to the canopy (Vitt & Caldwell 2009). This is reflected on their morphology, which is highly specialized for an arboreal life and for their particular way of prey capture. Extant representatives live in Africa, Madagascar, Arabian Peninsula, Turkey, India and Mediterranean Europe (Vitt & Caldwell 2009), but it is known that their past range reached further North, as chamaeleon fossils are reported from the Miocene of Central Europe (Moody & Roček 1980; Roček 1984; Fejfar & Schleich 1994; Böhme & Ilg 2003; Čerňanský 2010b; Čerňanský et al. 2016c; Georgalis et al. 2016a). In any case, their fossil record is rather poor and, despite a suggested origin based on molecular data dated back to the Cretaceous (Raxworthy et al. 2002; Wiens et al. 2006; Townsend et al. 2011; Bolet & Evans 2013; Dollion et al. 2015), no fossil older than Miocene in age is known, hampering a more complete knowledge of their evolutionary history (Bolet & Evans 2013; Georgalis et al. 2016a). Nowadays, only Chamaeleo chamaeleon is considered native in Europe, whereas populations of Chamaeleo africanus are considered to have been recently introduced by man (Sillero et al. 2014; Speybroeck et al. 2016).

When not included in the Toxicofera, Iguania is considered the sister taxon of a clade including all other squamates named Scleroglossa, in which the most basal taxon is represented by Gekkota, the geckos (Gauthier et al. 1988, 2012; Conrad 2008; Fig. 1.1). Geckos are a largely distributed group, with representatives on every continent but Antarctica (Vitt & Caldwell 2009). They are mostly nocturnal (but diurnal forms exist) and live in a huge variety of different habitats (Vitt & Caldwell 2009). Undisputed gekkotans are known since the Cretaceous (*Cretaceogekko*,

Hoburogekko, Gobekko and an unnamed form, all from Asia), but in general pre-Quaternary fossils are mostly fragmentary and not easy to identify (see Daza et al. 2014 for an updated review). Europe currently hosts only seven species of geckos, mostly confined to Mediterranean countries (Harris et al. 2009; Sillero et al. 2014); however, three of them (Alsophylax pipiens, Cyrtopodion caspium and Tarentola fascicularis) occur only in very small areas of the southwestern part of the continent. In morphological analyses, non-gekkotan scleroglossans are included into two main groups (Conrad 2008; Gauthier et al. 2012; Fig. 1.1): Scincomorpha and Anguimorpha, which together compose a clade named Autarchoglossa. Again, some problems with these clades are raised in molecular analyses, given that Scincomorpha results paraphyletic and Anguimorpha is part of Toxicofera together with Iguania (among others, Reeder et al. 2015; Fig. 1.2). When considered monophyletic (as e.g., in Gauthier et al. 2012), scincomorphs usually consists of Scincoidea (i.e., scincids, cordyliforms and probably also xantusiids) and Lacertoidea (i.e., lacertids and teioids). These two clades are often recovered in molecular analyses too, even if as successive sister taxa to Toxicofera (Reeder et al. 2015). Some morphological analyses, on the other hand, have found different relationships among scincomorphan families (see for example Conrad 2008). In terms of distribution, lacertids and especially scincids are the most widespread among scincomorphs (Vitt & Caldwell 2009): the former are widely distributed in the Old World, reaching far more North than any other lizard, whereas the latter are present roughly worldwide. Other scincomorphs are less common, being confined to the New World (Xantusiidae and Teioidea) or Sub-Saharan Africa and Madagascar (Cordyliformes). Fossil scincomorphs are widely known all over the world, and possibly include some of the oldest known squamates (Paramacellodus and Saurillodon from the late Bathonian of Britain; Evans 2003; Kosma 2004; Rage 2013). Currently, only lacertids and scincids are present in Europe, with the former being by far the most diverse and widespread group of European lizards (Sillero et al. 2014; Speybroeck et al. 2016).

Anguimorphs are another widespread group of lizards. It usually includes anguids, shinisaurids, xenosaurids, varanoids and mosasaurs (Conrad 2008; Conrad et al. 2010; Gauthier et al. 2012; Reeder et al. 2015). Within anguimorphs, some have a very limited range (Vitt & Caldwell 2009): the semiaquatic Shinisaurus, for example, lives only in a small area of Southern China and Northern Vietnam, whereas the terrestrial and crevice-dwelling *Xenosaurus* is found in moist or dry habitat in the Eastern coast of Central America. The helodermatid component of varanoids is also not very widespread, being confined to North and Central America. Anguids and varanids are far more distributed (Vitt & Caldwell 2009), with the former living in almost all continents except Antarctica and Oceania (but their range is restricted in Africa) and the latter currently present in all the Old World but Europe. Like that of the scincomorphs, the fossil record of anguimorphs is also substantial and include some very charismatic species, such as the giant varanid lizard Varanus priscus from Australia (Molnar 2004). Currently, anguimorphs are represented in Europe only by two anguid genera, Anguis and Pseudopus (Sillero et al. 2014; Speybroeck et al. 2016), but other families such as helodermatids and varanids were also present in the past (Hoffstetter 1957; Böhme & Ilg 2003; Augé 2005; Conrad et al. 2012; Delfino et al. 2013 among others).

Finally, amphisbaenians are almost always recovered as a monophyletic group in phylogenetic analyses (among others, Conrad 2008; Gauthier et al. 2012; Reeder et al. 2015). However, there is far less consensus when dealing with their relations with other squamates. Very different positions have been suggested for worm lizards in the squamate tree: nested within Scincoidea and sister group of Serpentes (Conrad 2008), within anguimorphs and strongly related with snakes (Gauthier et al. 2012; Fig. 1.1) or sister to lacertids within Lacertoidea (Müller et al. 2011; Reeder et al. 2015; Fig. 1.2). It has to be noted, however, that the positions recovered in the former two hypotheses might be the result of converging traits linked to fossorial habits, such as loss of limbs and trunk elongation. Amphisbaenians are usually grouped together with or considered related to the Mexican and Australasian family

Dibamidae in morphological analyses, even if Reeder et al. (2015) place dibamids as sister to gekkotans (Fig. 1.2). Again, this might be related to convergence related to loss of limbs. Worm lizards share a very peculiar morphology, strongly adapted to a burrowing lifestyle. Members of Amphisbaenidae and Blanidae live in Central and South America, Africa, Middle East and Mediterranean Europe (Vitt & Caldwell 2009), whereas the other families are limited to Mexico (Bipedidae), Florida (Rhineuridae) and Africa and Arabian Peninsula (Trogonophidae). In Europe, only three species of the genus *Blanus* can be found in the Iberian Peninsula or in the Greek islands off the coast of Turkey today (Sillero et al. 2014; Speybroeck et al. 2016). Amphisbaenians are documented in the fossil record at least since the Danian of Belgium and the U.S.A. (Sullivan 1985; Böhme & Ilg 2003; Folie et al. 2013; Longrich et al. 2015).

1.2. "Lacertilia", "Sauria" or none of these terms?

As already stated in the previous section, lizards are not monophyletic. Nevertheless, their bones are strongly different from those of Amphisbaenia and Serpentes, even when they do not bear diagnostic features allowing a more precise identification. Therefore, it is not uncommon to find remains clearly attributable to undetermined lizards when studying herpetological fossil material. Now, how can we call those remains? They are certainly squamates, but we also know that they are neither snakes nor amphisbaenians (i.e., they are lizards). Some authors use the term non-snake squamates, but again this is not completely correct, since it keeps amphisbaenians as a possibility. Two names have been used in the past to identify lizards only: "Lacertilia" and "Sauria". Despite not representing monophyletic group anymore, they can still be useful when referring to skeletal remains in order to quickly provide some more information on the original owners of such bones. But which one should we use?

"Lacertilia" was firstly used by Owen (1842) in his *Report on British fossil reptiles*, whereas "Sauria" was coined by Macartney (1802) as a translation in latin for the

french word sauriens used some years before by Brongniart (1800). Then, following the rules of priority, "Sauria" should be the solution. However, in the original works of both Brongniart and Macartney, "Sauria" is intended as a clade containing lizards and crocodilians. Following this, Gauthier et al. (1988) later used this name for a more inclusive taxon consisting of archosaurs, lepidosaurs and their most recent common ancestor. It appears clear, then, that "Sauria" is not a valid option to refer to lizards alone. In Owen's work, "Lacertilia" includes two mosasaurs (Mosasaurus hoffmanni and Leiodon anceps, now named Liodon anceps), a supposed lizard later re-described as a fish (Raphiosaurus subulidens, now Pachyrhizodus subulidens after Woodward 1901), a rhynchosaur (Rhynchosaurus articeps), four species he interpreted as thecodonts (the prosauropod Thecodontosaurus antiquus, the pseudosuchian Cladvodon llovdii and the phytosaurs Palaeosaurus cylindrodon and *Palaeosaurus platyodon*) and two other indeterminate lizards. Even though we can now state that misplacements are indeed present in Owen's classification, all these taxa shared true lizard affinities according to his view: therefore, his term "Lacertilia" actually refers to this group of reptiles, in contrast with "Sauria" which, as previously shown, refers to lizards plus something else. Owen himself used "Sauria" in a wider sense (Owen 1842: p. 60). Given that, "Lacertilia" can be used as an operative taxon to name fossil remains that clearly represent lizards (and not snakes or amphisbaenians), but cannot be identified at species, genus or even family level. Such view is followed in this thesis.

2. Comparative skull osteology of extant european lizards

This chapter explores the cranial anatomy of the extant European lizards and worm lizards in a comparative way, in order to pinpoint significant differences that can be used to identify each single bone of the skull of these animals. The differences, if present, are then used to build a diagnostic key, which is an easy-to-use tool to identify fossil remains or at least to better understand their affinities with modern species.

2.1. Material & Methods

Extant European non-snake squamates consist of 75 species of lizards and 3 worm lizards. The included species correspond to the European species reported by Sillero et al. (2014), plus the lizards and worm lizards living on the Greek islands along the coast of Asiatic Turkey as reported by Speybroeck et al. (2016). Recently introduced taxa have been excluded (as e.g., *Chamaeleo africanus*). The definition of Europe largely follows Arnold and Ovenden (2002), but with the exclusion of Madeira and the Canary islands in the west, because they do not belong to the continent in geological terms.

The following comparative analysis is based on both personal observations and existing bibliography. A large number of disarticulated or mounted skeletonized specimens stored in the collections of different institutions and representing as much species as possible has been directly studied, as well as CT-scans of wet-preserved specimens (see Appendix 1 for a list of all studied specimens). *Anguis* specimens considered for this analysis were collected before the split of *Anguis fragilis* into five different species (*Anguis cephallonica*, *Anguis colchica*, *A. fragilis*, *Anguis graeca* and *Anguis veronensis*; Gvoždík et al., 2010, 2013) mostly based on molecular data. Because of this, it has not been possible to clearly understand whether the herein studied specimens belong to a species different from *A. fragilis* or not and they have

been considered simply as member of the Anguis gr. A. fragilis species complex. During the reviewing process of this thesis, Ceríaco & Bauer (2018) demonstated that the nomenclatural and taxonomic status of the Iberian species of Blanus is problematic. Based on a misidentification of the type locality of *Blanus cinereus* by Albert and Fernández (2009), they proposed the synonymization of *Blanus mariae* with Blanus cinereus, with the latter becoming the valid name for the "southern" Iberian Blanus clade of Albert and Fernández (2009). The "central" Iberian clade (Blanus cinereus sensu Albert and Fernández 2009) is referred to the new species Blanus vandellii Ceríaco & Bauer, 2018. Due to late access to the recent work of Ceríaco & Bauer (2018), and above all for congruence with the papers stemming from this thesis and already published (see Appendix 9), the old names are used in this thesis. Nevertheless, it has to be noted that, after a check of the locality of provenance, the extant specimens herein attributed to *B. mariae* are referrable to *B.* cinereus sensu Ceríaco & Bauer (2018), whereas specimens herein attributed to B. cinereus represent B. vandellii according to Ceríaco & Bauer (2018). The single studied specimen of Chalcides bedriagai, an unnumbered specimen from the personal collection of Salvador Bailon, is a partially preserved articulated skull still largely covered by osteoderms. Because of this, it has been possible to obtain only few data on the precise morphology of its bones. A similar problem comes up with Trachylepis aurata MNHN 1887-863, which is represented only by an isolated left lower jaw. Some species are not represented as prepared skeletons in the visited institutions and therefore they have not been directly studied. The missing species are: Anatololacerta anatolica, Anatololacerta pelasgiana, Darevskia armeniaca, Darevskia lindholmi, Darevskia praticola, Darevskia saxicola, Dinarolacerta montenegrina, Iberolacerta aranica, Iberolacerta aurelioi, Iberolacerta galani, Iberolacerta martinezricai, Podarcis carbonelli, Podarcis cretensis, Podarcis erhardii, Podarcis gaigeae, Podarcis levendis, Podarcis liolepis, Podarcis peloponnesiacus, Podarcis raffonei, Podarcis vaucheri and Psammodromus hispanicus. When available, osteological data related to these species have been

obtained from the bibliography. Details about the osteology of European lizards and worm lizards have been mentioned in more than 100 papers, either dealing directly with comparative osteology (e.g., Evans, 2008) or simply reporting features in the remarks of the identification of fossil material of extant taxa (e.g., Blain, 2009). For a complete list of these works, see Appendix 2.

The terminology used in the description of the skull bones comes mainly from Evans (2008), but terms have been also taken from Barahona (1996), Bell et al. (2003), Daza et al. (2008), Gans & Montero (2008) and Klembara et al. (2010, 2014) when they were lacking in the above mentioned work. The bones have been described following the order of Evans (2008). Four bones, namely the palpebral, the lacrimal, the supratemporal and the orbitosphenoid, are not included in the analysis because they are often lost in disarticulated specimens and so it is difficult to have a satisfactory understanding of their morphological variation. It has to be noted, however, that these bones are rarely if ever found as fossils.

Bones have been photographed with the following sets:

- Leica M205 microscope equipped with the Leica application suite V 3.3.0 at the University of Torino;

- Leica M205 microscope equipped with the Leica application suite V 4.10 at the University of Torino;

- Canon EOS 50D camera mounted on a Leica M420 microscope at the Natural History Museum Wien;

- Samsung WB252F Digital Camera.

Blanus specimens from the Museo Civico di storia naturale di Carmagnola and the Zoologische Staatssammlung München have been scanned at the 'Abdus Salam' International Centre for Theoretical Physics in Trieste and at the Museum für Naturkunde Berlin using a microCT scan. Pictures of teeth of selected specimens have been taken with a Jeol JSM-IT300LV at the University of Torino.

2.2. Results

2.2.1. "Lacertilia"

Nasal

The nasal (Fig. A3.1) is a thin and anteroposteriorly elongated paired bone. It is ventrally concave and has a concave anterior margin. The lateral and medial margins of the bone are straight and parallel, whereas the posterior one can be straight, concave or convex. By the anterior corners of the bone, two anteriorly developed processes are present: the anteromedial one medially and the anterolateral one laterally. The posterior end forms a wide posterior process, which contacts the frontal. The articulation surface with the ascending nasal process of the premaxilla is visible on the anterior half of the medial margin.

Agamidae (Fig. A3.1A-C)

In *L. stellio*, the nasal is subrectangular but tends to shrink posteriorly, since its medial margin is slightly convex and not completely straight. Its posterior margin is rounded, whereas the concavity on the anterior margin is shallow. The anteromedial process is slender and well developed, whereas the anterolateral one is very short (slightly longer in MDHC 245; Fig. A3.1C). The articulation surface with the maxilla is visible along the anterior half of the lateral margin and a small and subquadrangular lappet extends laterally from its anterior end (Fig. A3.1A). The lappet, however, is not distinctly developed in MDHC 245 (Fig. A3.1C). The dorsal surface is smooth, whereas the ventral one can show a large articulation surface with the frontal covering the posterior process and a low longitudinal ridge running anteroposteriorly near the middle of the bone (slightly shifted laterally). In the studied specimens, however, these latter features can be either present (e.g., MDHC 245; Fig. A3.1C) or absent (e.g., HUJ.OST-Z-424; Fig. A3.1B) and it is therefore possible that they are susceptible to some kind of variation.

Chamaeleonidae (Fig. A3.1D-E)

Chamaeleo chamaeleon has small, straight and slender nasals, with smooth dorsal and ventral surfaces. The articulation surface housing the ascending nasal process of the premaxilla runs along the two anteriormost thirds of the straight medial margin of the bone (Fig. A3.1D). The anterior end displays a moderately wide, moderately long and pointed anteromedial process. The anterolateral process is not clearly recognizable, being represented only by a very little developed expansion of the anterior corner of the lateral margin. The dorsal surface of the anterior end is covered by the articulation surface with the medial branch of the anterior dorsal process of the maxilla. The posterior end is pointed and the lateral margin is slightly wavy.

Gekkota (Fig. A3.1F-M)

Nasals of European gekkotans are trapezoidal in shape, with the ventral concavity only present in their anterior portion and a straight posterior part. Those of E. europaea (Fig. A3.1F-G), T. mauritanica (Fig. A3.1L-M) and of some specimens of H. turcicus (Fig. A3.1H-I) tend to be slightly narrower anteriorly. Hemidactylus turcicus and T. mauritanica have a slightly concave posterior margin, whereas, in the other species, the posterior margin is straight. The anterior concavity is deep. The anterolateral process is short and anteroventrally bending, whereas the anteromedial one is long and straight. Both dorsal and ventral surface are smooth. A sharp and ventrally directed osseous expansion is present along the medial margin of the nasals of E. europaea and T. mauritanica, except for their posterior end. In E. europaea, this ridge-like expansion curves laterally by its posterior end, marking the medial half of the anterior margin of the articular surface with the frontal (Fig. A3.1G). The latter structure cannot be recognized in *M. kotschyi* (Fig. A3.1K) and *T. mauritanica*, but it is clearly visible by the posterior end of the ventral surface in *E. europaea* and H. turcicus: the surface is narrow and subrectangular in the former and wide and triangular in the latter. Only in MDHC 119 and 194, the nasals are fused to each other, but this could be due to pathological reasons (Fig. 2.1).

Lacertidae (Fig. A3.1N-U)

In lacertids, the nasal is subrectangular in shape, with a convex posterior margin. The anteromedial process is very long, whereas the anterolateral one is short or very short. The dorsal surface of the bone is almost completely covered by a welldeveloped dermal ornamentation (Fig. A3.1P, R), at least in adults. The ornamentation is less marked in A. erythrurus (Fig. A3.1N), D.



Figure 2.1) Fused nasals of T. mauritanica (*MDHC 194*) *in dorsal (A) and ventral (B) views.*

oxycephala, I. bonnali and I. horvathi, almost absent in O. elegans (Fig. A3.1T) and restricted to the posterior half in Algyroides (Fig. A3.1P) and Ps. hispanicus. In the largest specimens of A. nigropuctatus (e.g., MDHC 243), however, the ornamentation can reach also the anterior margin on the lateral side of the bone. Barahona (1996) reports that the dermal cover can overstep the anterior margin of the bone in adults of I. monticola, L. schreiberi, L. viridis (= L. bilineata), P. muralis and T. lepidus, hiding also the anteromedial process in the largest species. This holds true also for other medium- or large-sized species, such as L. trilineata and P. tiliguerta. A sulcus separating the areas covered by prefrontal and internasal scales is visible in the middle of the surface, with the exception of A. erythrurus, D. oxycephala, D. mosorensis, I. bonnali (according to Barahona 1996, but UAM.R.Lm28A shows it), I. cyreni, I. horvathi, I. monticola cantabrica, O. elegans, P. bocagei, P. carbonelli and Po. hispanicus.

Scincidae (Fig. A3.1V-Z)

The anterior margin of the nasal of scincids is usually oblique and straight, since no anterolateral process is present. On the other hand, the anteromedial one is long (shorter in *T. aurata*; Fig. A3.1Y-Z), moderately wide and strongly ventrally curved;

its dorsal surface is completely covered by the articulation surface with the ascending nasal process of the premaxilla. The posterior margin of the bone is also oblique and roughly straight, with low irregularities, in *C. chalcides* (Fig. A3.1V-W), *C. striatus* and *O. punctatissimus*, whereas it is slightly irregular and rounded in *A. kitaibelii, C. ocellatus* (Fig. A3.1X) and *T. aurata* (Fig. A3.1W-Z). Roughly in the middle of the lateral margin of the bone, a short laminar expansion develops laterally. In ventral view, a low ridge separates this expansion from the rest of the nasal (Fig A3.1W-X). In *A. kitaibelii, C. ocellatus* (Fig. A3.1X), *C. striatus* and *O. punctatissimus*, the expansion is very short and poorly individualized from the laminar body of the bone. A dermal ornamentation, weak in *C. chalcides* (Fig. A3.1V) and *C. striatus* and more developed in *C. ocellatus*, covers a small area in the middle of the dorsal surface. The ornamentation is not present in *A. kitaibelii, O. punctatissimus* and in the single examined specimen of *T. aurata* (Fig. A3.1Y).

Anguidae (Fig. A3.1AA-AD)

The nasal is subtrapezoidal in European anguids. The concavity on its anterior margin is very poorly developed because of the presence of a short, moderately wide and ventrally curved anterolateral process that do not projects anteriorly. The anteromedial process, on the other hand, is rather long and slender in *Anguis* gr. *A. fragilis* (Fig. A3.1AA-AB) and moderately short and wide in *P. apodus* (Fig. A3.1AC-AD). The articulation surface with the premaxilla covers only the dorsal surface of the latter process (Fig. A3.1AA). The posterior margin can be straight and oblique (in both *Anguis* gr. *A. fragilis* and *P. apodus*; Fig. A3.1AD) or present a small and roughly V-shaped notch in the middle (only in *Anguis* gr. *A. fragilis*; Fig. A3.1AA-AB). In *P. apodus*, the posterolateral corner is strongly developed, forming a long and pointed process (Fig. A3.1AC). A dermal ornamentation is visible on the dorsal surface, showing a sulcus separating the areas covered by prefrontal and internasal scales in the middle (Fig. A3.1AC). The degree of development of the

dermal ornamentation is highly variable, with no ornamentation on smaller specimens of *Anguis* gr. *A. fragilis* and stronger ornamentation in larger ones of all species. In the latter cases, the ornamentation can also develop beyond the margins of the bone, hiding its shape in dorsal view (Fig. A3.1AC). As a rule, the ornamentation is stronger in *P. apodus* than in *Anguis* gr. *A. fragilis*. In any case, even when the ornamentation is strongly developed, the anterior end of the bone is smooth.

Frontal

Frontals (Fig. A3.2, A3.3) can be either paired or fused in a single element. This bone is more or less constricted in the middle, with the posterior end that is wider than the anterior one. The anterior end can present a medial process in the middle and lateral processes on the anterolateral corners, whereas the posterior one expands laterally forming the posterolateral processes. By the anterior margin, the articulation surfaces with the nasals are present on the dorsal surface, whereas laterally one can see those with the facial process of the maxilla and the dorsal process of the prefrontals. The articulation surfaces with the posterior margin. Each lateral margin of the frontals develops in ventral direction forming a crista cranii that borders laterally the olfactory lobes of the brain. The anterior processes develop in anteroventral direction from the anterior end of each crista.

Agamidae (Fig. A3.2A-D, A3.3G)

Laudakia stellio has an unpaired, T-shaped and flat frontal, with a posterior end that is roughly twice as large as the anterior one. The constriction at mid-length is weakly developed in adults, but strong in juveniles. The lateral margins are strongly concave and the posterior one can be straight, with only a slightly wavy morphology in the middle, or convex, with a posterior expansion. In HUJ.OST-Z-423, this expansion lodges the subcircular parietal foramen (Fig. A3.2C-D). The anterior margin shows two lateral processes and a medial process. Each lateral process is separated from the medial one by a moderately deep concavity. All processes are pointed, moderately large and equally long. Posterolateral processes are long and slightly dorsoventrally expanded (Fig. A3.3G). The dorsal surface is smooth and distinctly sunken along midline. Articulation surfaces with the nasals are large, deep and U-shaped in dorsal view (Fig. A3.2A, C). A well-developed ridge separates them medially and lower ridges separate each one from the corresponding articulation surface with the maxilla and the prefrontal. No articulation surface with the postfrontal can be seen (Fig. A3.3G). Cristae cranii are not developed and are represented only by weak ventral swellings along the lateral margins (Fig. A3.2B, D, A3.3G). The swelling are slightly more developed in the anterior half of the bone, but actual anterior processes are not present. The anterior half of the ventral surface is strongly sunken.

Maximum length of the frontal varies from 5 mm to 10 mm.

Chamaeleonidae (Fig. A3.2E-F)

The unpaired frontal of C. chamaeleon is strongly different from the above-described morphology. The bone can be divided into a subpentagonal posterior portion and a subtriangular anterior one, of which the former is twice as long as the latter. The anterior portion is strongly sunken dorsally and inclined anteroventrally; it also ends anteriorly with a pointed medial process that inserts through the nasals. The development of the ornamentation on the dorsal surface is variable. A series of small irregular tubercles runs along the midline of the bone for almost its entire length and is usually followed by a low ridge by the posterior end (except for NHMW 611 and 717, in which the tubercles reach the contact with the parietals; Fig. A3.2E). In MNHN 2002-24 only, the tubercles continue posteriorly on the ridge. The rest of the dorsal surface is only slightly irregular (with an ornamentation made mostly by ossification rays) in MNHN 241 and 1942-103 and NHMW 611 (Fig. A3.2E) and 721, but it shows other tubercles in MNHN 2002-24 and NHMW 717. On the other hand, no tubercles on the midline and no ornamentation are present on the dorsal surface of MNHN1887-875. All margins of the frontal are represented by slightly irregular sutures with small interdigitations; the one with the parietal is not straight and is wavy in ventral view. Cristae cranii are low as in *L. stellio*; in ventral view, they converge anteriorly, forming a V-shaped structure (Fig. A3.2F). The dorsal surface of the bone expands laterally by each side of the structure, giving the subpentagonal shape to the posterior portion. The parietal foramen is present posteriorly to the structure and opens both on the dorsal and on the ventral surface of the bone. There are no anterior processes. The wide articulation surfaces with the parietal tabs are visible by the corners of the posterior end on the ventral surface (Fig. A3.2F). Some specimens (e.g., NHMW 611; Fig. A3.2F) display also those with the posterior process of the nasals on the same surface anteriorly, by the sides of the medial process.

Maximum length of the frontal goes from 11 mm to 15 mm.

Gekkota (Fig. A3.2G-N, A3.3H-K)

Gekkotans have a tubular and unpaired frontal. It has an approximately T-like shape in dorsal view and a posterior end that is roughly twice as large as the anterior one. In dorsal view, the lateral margins are constricted in the interorbital region, and the posterior one is slightly concave (in H. turcicus and M. kotschyi; Fig. A3.2I-L) or straight (in E. europaea and T. mauritanica; Fig. A3.2G-H, M-N). The anterior margin is W-shaped in *E. europaea* (Fig. A3.2G-H), V-shaped in *H. turcicus* (Fig. A3.2I-J) and convex or nearly straight in *M. kotschyi* (Fig. A3.2K-L). In *T.* mauritanica, this margin is highly variable, maybe also as an artifact of disarticulation. As a matter of fact, it can be either straight or slightly convex, truncated and slightly irregular. In the middle of the anterior margin of M. kotschyi (except for MDHC 201) and of T. mauritanica, there is a small and pointed medial process. A more developed one is present in E. europaea. Lateral processes are present in E. europaea (moderately developed and pointed), H. turcicus (wide, triangular and well developed) and some specimens of M. kotschvi (very little developed and pointed). Posterolateral processes are long and slightly dorsoventrally expanded. The dorsal surface is smooth and dorsally flattened in *E. europaea*, depressed medially in the anterior third with deep furrows, flattened in the two



Figure 2.2) Partial skull of H. turcicus (MDHC 26) in dorsal view, showing the light ornamentation on frontal, parietals, maxillae and prefrontals. Scale bar = 1 mm.

posterior thirds and covered with a faint ornamentation made up by grooves in H. turcicus (Fig. 2.2, A3.2I), smooth and sometimes slightly concave along the median axis of the bone in *M. kotschvi* and T. mauritanica. The articulation surfaces with the nasals are not bordered by ridges; they are triangular and correspond to the dorsal surface of the lateral processes in H. turcicus (Fig. A3.2I), whereas they are subrectangular and placed along the anterior margin in E. europaea (Fig. A3.2G), M. kotschyi (Fig. A3.2K) and T. mauritanica (Fig. A3.2M). Two shallow but distinct grooves are visible on the dorsal

surface of the frontal of *E. europaea*, running along the lateral margin in the posterior third of the bone (Fig. A3.2G). The articulation surfaces with maxillae and prefrontals are wider in *H. turcicus* (Fig. A3.3I) and *T. mauritanica* (Fig. A3.3K) than in *E. europaea* (Fig. A3.3H) and *M. kotschyi* (Fig. A3.3J). The articulation surface with the anterior process of the postorbitofrontal is not clearly defined on the lateral margins of the posterior portion in *E. europaea* and some specimens of *M. kotschyi* (although these are well-defined in MDHC 418 and 419). The articulation surface for the postorbitofrontal is on the other hand visible in *H. turcicus* (Fig. A3.3I) and *T. mauritanica* (Fig. A3.3K). When both articulation surfaces with pre-frontals and postorbitofrontals are visible, they are distinctly distant from each other.

In the central portion of the bone, the cristae cranii fuse, forming a tubular structure with a slightly flattened ventral surface. The tube is subelliptical in anterior view and subcircular in posterior view. Anterior processes are moderately developed and define, together with the anterior margin of the crista, two anteriorly concave (slightly concave in *T. mauritanica*) surfaces with a roughly dewdrop-like shape in anterior view and a slight inclination in ventromedial direction. Those of E. europaea are slightly more developed and roughly pointed in ventral view (Fig. A3.3H). Moreover, in *H. turcicus* the anterior processes are developed by the anterior margin and so they do not originate the concave surfaces, although their anterodorsal surface takes anyhow a drop-like shape in anterior view. In *H. turcicus*, a low ridge separates the areas corresponding to the articulation surfaces with the nasals from the rest of the ventral surface of the shelf of the frontal (Fig. A3.2J). In M. kotschyi, in place of this low ridge there is a slight osseous swelling and a very low ridge runs medially behind it without continuing inside the tube (Fig. A3.2L). In T. mauritanica, the median ridge is slightly more developed and a stocky osseous swelling is present medially between the ridge and the medial process (Fig. A3.2N). Euleptes europaea can show a condition similar to either that of *H. turcicus* (MDHC 388 and 389; Fig. A3.2H) or to that of *T. mauritanica* (MDHC 384, the largest specimen).

In the examined specimens, maximum length of the frontal goes from 4 mm to 4.5 mm in *E. europaea*, from 5 mm to 6 mm in *H. turcicus*, from 5 mm to 6 mm in *M. kotschyi* and from 7 mm to 9.1 mm in *T. mauritanica*.

Lacertidae (Fig. A3.2O-Y, A3.3L)

Frontals of lacertids are paired, but they can fuse during ontogeny. Only in *A. erythrurus*, *E. arguta* and *O. elegans*, they fuse very early in the postnatal ontogeny and compose therefore an unpaired bone for most of the life of the animal (Fig. A3.2O-P); in this case, the suture line is not visible on the ventral surface. The medial constriction, which is always well evident in juveniles (Fig. 2.3), varies within species in the adults: frontals of *A. erythrurus*, *E. arguta* and *O. elegans* are very strongly constricted (Fig. A3.2O-P), those of *A. bedriagae*, *Algyroides*, *D.*

oxycephala, D. mosorensis, H. graeca, I. bonnali, I. cyreni, I. horvathi, I. monticola. Р. Р. carbonelli, Р. bocagei. filfolensis, Po. hispanicus, P. lilfordi, P. melisellensis, Р. milensis. Р. muralis, Р. pityusensis, *P*. Р. siculus. tauricus. Р. tiliguerta, Р. waglerianus, Psammodromus, T. lepidus and Z. vivipara are slightly constricted (Fig. A3.2S-Y) and those of *Lacerta* have roughly parallel margins (Fig. A3.2Q.R). As a rule. the posterior end is twice as large as



Figure 2.3) Right frontal of a juvenile of T. lepidus (*NHMW 625*) *in dorsal (A) and ventral (B) views. Scale bar = 1 mm.*

the anterior one, giving a shape that roughly resembles an L for the unfused bone and a T for the fused one. In adults of *H. graeca, L. bilineata, L. trilineata, L. viridis* and *T. lepidus*, however, the difference in width between the anterior and posterior ends is lower (Fig. A3.2Q-R, U-V). Both medial and lateral processes are present and moderately developed, even if the medial one may be less distinguishable in some specimens. Even though in juveniles and in adults of most species they could also appear as single processes (Fig. 2.3; see also Barahona 1996), lateral processes are usually bifurcated (always in *Psammodromus*): their medial branch is usually longer than the medial process, whereas the lateral one is slightly shorter than the latter. Low ridges are present on the dorsal surface of the two branches, separating the articulation surface with the nasal from that with the maxilla (ridge on the medial branch) and the latter from the one with the prefrontal (ridge on the lateral branch). All the articulation surfaces, those with the postfrontal included, are large and well

distinct, even though the ones with the facial process of the maxilla are reduced or even absent in some species (A. marchi, A. moreoticus, I. bonnali, I. cyreni, I. horvathi, I. monticola, Lacerta, T. lepidus and Z. vivipara; Fig. A3.2Q, U, X). Articulation surfaces with the prefrontal and the postfrontal are distinctly far from each other (Fig. A3.3L). Posterolateral processes are well developed and can be roughly pointed or more rounded. The posterior margin is strongly irregular and can be wavy (in A. erythrurus and O. elegans, whose margin shows a moderately large posterior expansion in the middle; Fig. A3.2O-P); except for A. erythrurus and O. elegans, it also shows little (A. marchi, A. moreoticus, I. bonnali, I. horvathi, P. filfolensis, P. lilfordi and Z. vivipara; Fig. A3.2X-Y) or strongly (other species; Fig. A3.2Q-V) developed interdigitations, which are less marked in very young individuals (Fig. 2.3). Cristae cranii are moderately low in their posterior portion, whereas the anterior one is more developed and forms a long and thin anterior process with an irregular ventral margin. Arnold et al. (2007) stated that the anterior process is often absent in Z. vivipara. The ventral surface is smooth, with only two very shallow symmetrical sunken areas in its anterior half and by its posterior end. A subtriangular articulation surface housing the parietal tabs of the parietal is also visible by the posterolateral corner of the bone. A dermal ornamentation, on the other hand, is present dorsally. This ornamentation usually becomes more marked with increasing size and age, being very well developed in large animals but significantly less distinguishable in small ones. Roughly at the beginning of the posterior third of the bone, the sulcus separating frontal and frontoparietal shields is visible (Fig. A3.2O, S). In some specimens of *T. lepidus*, this sulcus is located at mid-length (Fig. A3.2W; see also Čerňanský 2010a), whereas in adults of *Lacerta* and in other individuals of *T. lepidus* it is usually placed at 3/5 of the length of the frontal from the anterior end (Fig. A3.2Q). The ornamentation is very poorly developed (sometimes almost absent, particularly in O. elegans) in A. erythrurus, E. arguta and O. elegans, being visible mostly on the posterior half of the bone (Fig. A3.2O). This condition approaches the one seen in juveniles of other, small-sized species.

Measurements of the frontal of lacertid species are given in the following table:

Species	Maximum length
	of the frontal
A. erythrurus	8 mm - 8.8 mm
A. moreoticus	4.6 mm - 4.7 mm
A. nigropuctatus	6.1 mm - 8 mm
A. bedriagae	7 mm - 9.2 mm
D. oxycephala	4.6 mm - 7 mm
D. mosorensis	5.2 mm - 6 mm
E. arguta	9 mm
H. graeca	5.2 mm - 7.6 mm
I. bonnali	6.8 mm
I. cyreni	8 mm
I. horvathi	5.1 mm
I. monticola	6.6 mm - 8 mm
L. agilis	7.1 mm - 8.1 mm
L. bilineata	5.8 mm - 11.1 mm
L. schreiberi	10.4 mm - 10.6 mm
L. trilineata	11.7 mm - 13.7 mm
L. viridis	11 mm - 14 mm
O. elegans	5 mm - 5.7 mm
P. bocagei	5.7 mm - 5.9 mm
P. filfolensis	6.3 m - 6.4 mm
Po. hispanicus	5.5 mm - 7.2 mm
P. lilfordi	7 mm - 7.4 mm
P. melisellensis	4.2 mm - 7 mm
P. milensis	6.8 mm - 7 mm
P. muralis	5.4 mm - 8.5 mm
P. pityusensis	9 mm - 9.2 mm

P. siculus	5.5mm - 8.9 mm
P. tauricus	7 mm - 7.5 mm
P. tiliguerta	6.6 mm - 6.8 mm
P. waglerianus	8 mm - 8.2 mm
P. algirus	9.5 mm
T. lepidus	6.2 mm - 21 mm
Z. vivipara	4.4 mm - 5.4 mm

Scincidae (Fig. A3.2Z-AG, A3.3A-B, M-P)

In European scincids, the frontal can be either unfused, showing no clear constriction in the middle (Chalcides and O. punctatissimus; Fig. A3.2AB-AG) or fused, with a low (T. aurata; Fig. A3.3A-B) or stronger (A. kitaibelii; Fig. A3.2Z-AA) middle constriction. In all species but O. punctatissimus, however, the posterior end is about twice as large as the rest of the bone and so, when paired, the latter is roughly Lshaped in dorsal view. Because of the poor development of the posterolateral process, the frontal of *O. punctatissimus* widens only slightly posteriorly (Fig. A3.2AF-AG). When fused, the suture line is still visible in ventral view on the anterior half of the resulting bone (Fig. A3.3A). As in lacertids, short medial and lateral processes are present on the anterior end and are separated by a moderately shallow concavity, but, in contrast with them, the lateral one is not bifurcated. The only exception is T. aurata, whose lateral processes are represented by short and wide flanges, with an irregular anterior margin made by more or less pointed expansions (Fig. A3.3A-B). In A. kitaibelii and O. punctatissimus, the lateral processes are very little developed, in contrast with distinctly developed medial ones (Fig. A3.2Z-AA, AF-AG). Very low (strongly more distinct in *T. aurata*; Fig. A3.3A) ridges mark the margins of the articulation surface with the nasal, which is subtrapezoidal (A. kitaibelii, C. chalcides and O. punctatissimus; Fig. A3.2Z, AF) or rounded (C. ocellatus, C. striatus and T. aurata; Fig. A3.2AB, AD, A3.3A) in shape. The articulation surface with the prefrontal is long and large; it reaches half the length of the bone (the posterior third in O. punctatissimus; Fig. A3.3P), but it does

not touch the smaller and shorter (very short in A. kitaibelii; Fig. A3.3M) articulation surface with the postfrontal. In C. ocellatus and O. punctatissimus, however, these two articulation surfaces are very close to each other (Fig. A3.3O-P); they can also contact each other in the latter species (e.g., MDHC 427; Fig. A3.3P). The posterolateral process is moderately short (shorter in *O. punctatissimus*; Fig. A3.2AF-AG) and wide, with a rounded or pointed distal end (in dorsal view); it is slightly longer and more slender in A. kitaibelii (Fig. A3.2Z-AA) and T. aurata (Fig. A3.3A-B). The posterior margin is straight or slightly concave. The crista cranii and the anterior process are morphologically similar to those of lacertids, even though the latter is larger (in lateral view) and distally pointed. The frontal of A. kitaibelii and *T. aurata*, however, lacks the anterior process and the former species shows also poorly developed cristae cranii (Fig. A3.2AA, A3.3A, M). The ventral surface is smooth, whereas a weak (C. chalcides and C. striatus; Fig. A3.2AD) or well developed (C. ocellatus; Fig. A3.2AB) cover of dermal ornamentation is present in the middle of the dorsal surface; the ornamentation is lacking by the anterior and posterior ends and along the lateral margin. No sulci are visible on it. In this case also, T. aurata is an exception, since it has a moderately developed ornamentation that reaches the posterior margin (Fig. A3.3A). Moreover, the grooves separating frontal, frontoparietal and interfrontal shields are visible in this species. The two frontoparietal shields contact each other medially, separating the frontal and interfrontal ones (Fig. A3.3A). The ornamentation is usually totally absent in smaller specimens and in A. kitaibelii and O. punctatissimus (except for some weak grooves visible in some specimens of the former and in all specimens of the latter).

The following table summarizes the maximum lengths of the frontal in European species.

Species	Maximum length of the frontal
A. kitaibelii	2.6 mm - 3.1 mm

C. bedriagai	Not measured
C. chalcides	4 mm - 5.5 mm
C. ocellatus	7 mm - 8.3 mm
C. striatus	4.5 mm - 4.8 mm
O. punctatissimus	2.6 mm - 2.7 mm
T. aurata	8 mm

Anguidae (Fig. A3.3C-F, Q-R)

European anguids have a paired frontal, with a posterior end that is slightly less than twice as large as the anterior one. Usually, the constriction in the middle is not present and the lateral margin is straight or convex in dorsal view. Only one very small specimen of Anguis gr. A. fragilis, MDHC 49, shows a very poorly developed hint of constriction and a roughly sigmoid-shaped lateral margin; this could be due to ontogenetic variation, since this specimen is much smaller than the others and could therefore be a juvenile. A similar ontogenetic change is present in *P. apodus*, according to Klembara et al. (2017). The anterior end of the frontal is pointed, because the medial process is well developed and moderately wide, whereas there is no lateral process. The articulation surface with the posterior process of the nasal is barely recognizable in Anguis gr. A. fragilis (Fig. A3.3C), but more clearly visible in P. apodus (Fig. A3.3E). Both the articulation surfaces with the prefrontal and the postfrontal are visible: the latter develops along the posterior third (Anguis gr. A. fragilis; Fig. A3.3Q) or fifth (P. apodus; Fig. A3.3R) of the lateral margin, whereas the former covers the rest of it. In Anguis gr. A. fragilis, they usually contact each other, but in MDHC 49 they are distinctly far from one another. *Pseudopus apodus*, on the other hand, shows a variable condition, with the contact that can be both present or absent, even though the articulation surfaces are close to each other also when they do not touch each other. The posterolateral process is moderately short and pointed; it develops a small (very poorly developed in *P. apodus*) and posteriorly directed ventral lappet that underlies the anterolateral corner of the parietal (Fig.

A3.3D, F). The posterior margin is roughly straight, but slightly irregular; in ventral view, a small articulation surface for the ventral lappet of the parietal is recognizable medially to the lappet of the posterolateral process (Fig. A3.3D, F). The crista cranii is laminar and well developed in ventral direction; an anterior process is not clearly distinguishable from the rest of the crista (Fig. A3.3Q-R). A moderately low ridge starts from the anterior end of the crista and runs towards the tip of the medial process on the ventral surface of the frontal, which is otherwise smooth (Fig. A3.3D, F). The dorsal surface, on the other hand, is covered by a well-developed dermal ornamentation, which is less marked in smaller specimens and, in Anguis gr. A. fragilis, near the posterior end of larger ones also (Fig. A3.3C). Moreover, the ornamentation reaches the lateral margin of the bone in adults of *P. apodus* (Fig. A3.3E), but not in Anguis gr. A. fragilis (Fig. A3.3C). The frontal is almost entirely covered by the frontal shield, except for its posterior end. In both Anguis gr. A. fragilis and P. apodus, the small frontoparietal shield can be recognized by the posterolateral half of the latter end, whereas a small interfrontal shield contacting the frontal one is present on the medial half only in Anguis gr. A. fragilis (Fig. A3.3C). This latter shield is absent in the frontals of all observed specimens of *P. apodus*, because the contact between the frontal and the interparietal scales is located by the frontoparietal suture (Fig. A3.3E). Anyway, Klembara et al. (2017) show that sometimes a very small interfrontal shield might be present in the latter species also. The maximum length of the frontal goes from 4 mm to 6.8 mm in Anguis gr. A. fragilis and from 15.2 mm to 17 mm in P. apodus.

Parietal

Parietals (Fig. A3.4, A3.5) are quadrangular bones that can be either paired or fused in a single element. They are composed by a straight shelf, with anterolaterally directed anterolateral processes by the anterolateral corners and posterolaterally directed and ventrally curved postparietal processes by the posterolateral ones. The shelf can be pierced by the parietal foramen.

Agamidae (Fig. A3.4A-B, A3.5D)

Laudakia stellio has an unpaired parietal with a short and wide quadrangular shelf. This bone has a smooth dorsal surface and is strongly concave in ventral direction, since the lateral margins are markedly ventrally developed. A wide and very deep notch is present in the middle of the anterior margin (Fig. A3.4A-B), being even larger in juveniles. The parietal foramen is located inside this notch (Evans 2008), as proved by the fact that, in one of the specimens (HUJ.OST-Z-423), it is visible on the expansion developed from the middle of the posterior margin of the frontal (Fig. A3.2C-D). Laterally to the notch, the anterior margin is dorsoventrally-expanded and forms a moderately deep, anteriorly concave surface (Fig. A3.5D). The anterolateral processes are large and pointed; they are strongly laterally projected, but they do not develop in anterior direction. The postparietal processes are very long and large; they have a truncated posterior end and show a distinct ventrolateral concavity. In adults, a moderately developed ridge runs in anterior direction on the dorsal surface of each postparietal process, starting from the middle of the medial margin (Fig. A3.4A). By the base of the process, the ridge curves laterally, reaching the posterolateral margin of each anterolateral process. This ridge is distinctly less developed in juveniles. Another very low ridge marks the posterior margin of the shelf. The ventral surface is smooth and a very small parietal fossa is present in the middle of the posterior margin (Fig. A3.4B). No parietal notch is, however, clearly visible in dorsal view. Maximum length of the parietal goes from 3 mm to 5.5 mm, whereas its maximum width varies from 5.8 mm to 11.8 mm.

Chamaeleonidae (Fig. A3.4C-D, A3.5E)

The parietal of *C. chamaeleon* is an unpaired bone that differs from the abovedescribed morphology. It is composed by a small laminar body, subtriangular in shape, and by a long and posteriorly rounded parietal crest, which is narrow (without lateral expansions) in dorsal view (Fig. A3.4C) and large in lateral view (Fig. A3-5E). The crest contacts the processus ascendens of the supraoccipital anteroventrally, with a well-developed, ventrally expanded median crest (processus parietalis inferior
in Čerňanský et al. 2014; Fig. A3.5E), and the squamosals by its posterior end. Each lateral side of the crest is slightly concave. The parietal crest continues anteriorly on the dorsal surface of the laminar body, contacting the ridge located on the posterior end of the dorsal surface of the frontal. This surface of the laminar body is smooth, but in MNHN 241 and 2002-24 and in NHMW 611, 717 and 721 the dorsal margin of the crest is covered by numerous tubercles (Fig. A3.4C, A3.5E). The ventral surface of the laminar portion shows a deep sunken area in the middle, which is the area of articulation with the processus ascendens of the supraoccipital (a remnant of the parietal fossa; Fig. A3.4D). This area continues posteriorly in a groove along the ventral margin of the median crest, which represents the articulation surface with the dorsal expansion of the processus ascendens. On both sides of the sunken area there is a small ridge-like process, slightly developed in ventral direction. Postparietal processes are not present, not it is the opening of the parietal foramen. Anterior and anterolateral margins of the laminar body are represented by interdigitated sutures (Fig. A3.4C). Two wide and anteriorly rounded parietal tabs develop from each lateral corner of the anterior margin (Fig. A3.4C-D); their anterior margin can also be interdigitated.

Maximum length of the parietal goes from 13.3 mm to 21.5 mm and its maximum width varies from 6 mm to 11 mm.

Gekkota (Fig. A3.4E-L, A3.5F-I)

Parietals of gekkotans are paired, except for those of MDHC 119 (but this could be a pathological trait). It has to be noted, however, that Wellborn (1933) states that this bone tends to fuse in old specimens of *T. mauritanica*. In *E. europaea* and *T. mauritanica*, the posteromedial corner of the bone ends on a squared end (Fig. A3.4E-F, K-L), whereas in *M. kotschyi* and *H. turcicus* the parietal ends either with a pointed or squared end (Fig. A3.4G-J). Anterolateral processes are little developed and do not project anteriorly; they are slightly expanded ventrally (strongly expanded in *T. mauritanica*). Medially to those of *H. turcicus* and *M. kotschyi* there is a small notch, which is moderately wide and shallow in *H. turcicus* (Fig. A3.4G-H) and more

developed in *M. kotschvi* (Fig. A3.4I-J). A thin osseous lamina forms the lateral margin of the bone from the base of the anterolateral process to the beginning of the postparietal process. This lamina provides attachment for the jaw adductor muscles. It is developed laterally and, in *M. kotschyi*, also slightly dorsally (Fig. A3.5H). The lamina is very narrow in E. europaea (Fig. A3.4F), moderately developed in M. kotschyi (Fig. A3.4J), moderately to well developed in T. mauritanica (Fig. A3.4L) and prominent in *H. turcicus* (Fig. A3.4H). The medial margin of the parietals is generally straight and shows some interlocking wedges in T. mauritanica (Fig. A3.4K-L); in one specimen, MDHC 302, the parietal experience the fusion of these wedges in the posterior portion. The postparietal process is thin and distally pointed. It shows different degrees of posteroventral curvature, ranging from having a mild curvature (nearly horizontal) in two specimens of *M. kotschyi* (MDHC 201 and 285; Fig. A3.5H) to be strongly curved in *T. mauritanica* (Fig. A3.5I). An oblique ridge runs on the posterior margin of the parietal, by the base of the postparietal process, marking the attachment surface for the longissimus capitis neck muscles (Al Hassawi 2007). This ridge is well marked in all the species except E. europaea. Around the mid-length of the lateral margin, the triangular and very small epipterygoid process develops in ventral direction. The process of E. europaea and T. mauritanica is moderately developed and continues with a lamina that reaches the anterior margin (Fig. A3.5F, I). The one of *E. europaea* is rounded and not triangular. Medially to the process, one can see a shallow groove, which continues also anteriorly and posteriorly along the lateral margin. In E. europaea and H. turcicus, only a short portion of this groove is clearly recognizable by the anterior margin of the shelf. The dorsal surface of the shelf is smooth, except for that of *H. turcicus*, which shows a faint ornamentation made up of shallow grooves (Fig. 2.2, A3.4G). The ventral surface shows two shallow concavities: a larger and subcircular one placed anteriorly and a smaller and subtriangular one placed posteriorly. The anterior concavity is twice as large as the posterior one. The concavities are poorly distinguishable in E. europaea. There are no traces of the parietal foramen.

Maximum length goes from 3 mm to 3.2 mm in *E. europaea*, from 3.5 mm to 4.5 mm in *H. turcicus*, from 3.5 mm to 4 mm in *M. kotschyi* and from 3.9 mm to 5.1 mm in *T. mauritanica*. Maximum width is 2 mm in *E. europaea* and goes from 2.4 mm to 2.9 mm in *H. turcicus*, from 2 mm to 2.9 mm in *M. kotschyi* and from 2.9 mm to 4 mm in *T. mauritanica*.

Lacertidae (Fig. A3.4M-V, A3.5J)

Lacertids have an unpaired parietal, with a weakly- (A. marchi, I. bonnali, I. horvathi, P. filfolensis and Z. vivipara; Fig. A3.4U-V) or strongly-interdigitated (other species; Fig. A3.4O-P, S-T) anterior margin. The interdigitations are absent in A. erythrurus and generally O. elegans, whose anterior margin is wavy and presents a concavity in the middle (Fig. A3.4M-N, Q-R). The shelf is larger than it is long in A. erythrurus, E. arguta, I. horvathi, O. elegans and Z. vivipara (Fig. A3.4M-N, Q-R, U-V), whereas it is longer in the other species (Fig. A3.4O-P, S-T). Anterolateral processes are anteriorly pointed, usually bifurcated (Barahona 1996) and distinctly developed in anterior direction to form parietal tabs. The degree of development of the tabs is linked to age and size, with adults and larger species having more developed ones. In A. erythrurus, E. arguta and O. elegans, moreover, they are also expanded laterally (Fig. A3.4M-N, Q-R). The morphology of the long postparietal processes varies: they are thin in A. erythrurus, A. marchi, A. moreoticus, D. mosorensis, E. arguta, I. bonnali, O. elegans, P. siculus, Ps. hispanicus and Z. vivipara (Fig. A3.4M-N, Q-R, U-V), whereas they widen proximally in A. fitzingeri, A. nigropunctatus, A. bedriagae, D. oxycephala, H. graeca, I. cyreni, I. horvathi, I. monticola, Lacerta, P. bocagei, P. filfolensis, Po. hispanicus, P. lilfordi, P. melisellensis, P. milensis, P. muralis, P. pityusensis, P. tauricus, P. tiliguerta, P. waglerianus, P. algirus and T. lepidus (Fig. A3.4O-P, S-T). A well-developed dermal ornamentation, whose development increases in older individuals and larger species, is present on the dorsal surface of the shelf, but not on the processes. The two frontoparietal (anteriorly), the interparietal (in the middle of the shelf), the two lateral (laterally) and the occipital (posteriorly) shields are recognizable because of the presence of the grooves marking their borders on the ornamentation. *Acanthodactylus erythrurus, E. arguta* and *O. elegans* show a less-developed ornamentation (Fig. A3.4M, Q); the two former species lack the occipital shield, whereas a very small one is present in *O. elegans* (Fig. A3.4Q). In *T. lepidus*, on the other hand, the latter shield is very large (Fig. 2.4, A3.4S). An area levis devoid of ornamentation is present on the parietal shelf of *A*.



Figure 2.4) Articulated parietal of T. lepidus (MNHN 1991.4242) in dorsal view. Scale bar = 1 mm.

erythrurus, I. horvathi, O. elegans, Ps. hispanicus and *Z. vivipara* (Fig. A3.4M, Q, U), whereas in other species the ornamentation reaches the posterior margin (at least in adults). Five ventral crests are present on the ventral surface: a medial one in the middle of the shelf, two anterolateral ones running posteromedially from each anterolateral corner of the shelf and two posterolateral ones running anteromedially along the ventral surface of the postparietal processes. The crests are moderately low in small species (Fig. A3.4N, R, V) and in juveniles of the largest ones, but they can grow to become sharp and very well developed in adults of the latter (Fig. A3.4P, T). The deep (shallower in juveniles) parietal fossa is visible posteriorly to the medial ventral crest. Anterolateral ventral crests always touch the medial one, whereas a contact between the former and the posterolateral ones is absent in adults of *A. fitzingeri, A. nigropunctatus, H. graeca, Lacerta, P. filfolensis, P. melisellensis, P. milensis, P. muralis* (in contrast with what stated by Barahona 1996 and Barahona & Barbadillo 1997), *P. pityusensis, P. siculus, P. tauricus, P. tiliguerta, P.*

waglerianus, P. algirus and T. lepidus (Fig. A3.4P, T) and present in juveniles of the previously cited species as well as in both adults and juveniles of other ones (Fig. A3.4N, R, V). It has to be noted, however, that the contact is also present in a some adult specimen of L. agilis (MDHC 178) and P. melisellensis (MDHC 217, 218 and NHMW 650), suggesting that variation may rarely be present, at least in these species. The fossa is wide and U-shaped in A. erythrurus, Algyroides, A. bedriagae, D. oxycephala, H. graeca, I. bonnali, I. cyreni, I. monticola cantabrica, O. elegans, P. bocagei, P. carbonelli, P. filfolensis, Po. hispanicus, P. lilfordi, P. melisellensis, P. milensis, P. siculus, P. tauricus, P. tiliguerta, P. waglerianus, Ps. hispanicus and Z. vivipara (Fig. A3.4N, R, V), narrow and U-shaped in I. monticola monticola, L. schreiberi, L. viridis, P. pityusensis, P. algirus and juveniles of P. muralis, triangular in L. bilineata, L. trilineata, T. lepidus and adults of P. muralis (Fig. A3.4P, T). Lacerta agilis can show either a narrow or a wide U-shaped fossa. A parietal notch is present in juveniles of all species and is retained in adults of A. erythrurus, A. marchi, O. elegans, Ps. hispanicus and Z. vivipara (Fig. A3.4M, Q, U), whereas in adults of the other species the posterior margin is straight (Fig. A3.4O, S). A wide and either subcircular or subelliptical parietal foramen is present in the middle of the shelf.

Spagios	Maximum length	Maximum width	
Species	of the parietal	of the parietal	
A. erythrurus	3.9 mm - 4 mm	4.5 mm - 5.1 mm	
A. fitzingeri	3.2 mm	2.9 mm	
A. moreoticus	3.5 mm	3.3 mm	
A. nigropunctatus	4.4 mm - 6.6 mm	4 mm - 4.6 mm	
A. bedriagae	5 mm - 9 mm	4.7 mm - 7 mm	
D. oxycephala	3.5 mm - 5.2 mm	3.4 mm - 5 mm	
D. mosorensis	4.3 mm - 5.5 mm	4.1 mm - 5 mm	

Measurements are given in the following table:

E. arguta	4.5 m	5 mm	
H. graeca	4.3 mm - 6 mm	4 mm - 5 mm	
I. bonnali	4.9 mm	3.7 mm	
I. cyreni	5.6 mm	4.6 mm	
I. horvathi	4 mm	5 mm	
I. monticola	4.3 mm - 5.5 mm	4 mm - 5 mm	
L. agilis	4 mm - 5.4 mm	4 mm - 5 mm	
L. bilineata	3.7 mm - 10 mm	4.3 mm - 8 mm	
L. schreiberi	7 mm	5.4 mm	
L. trilineata	8.5 mm - 11 mm	6.6 mm - 8.4 mm	
L. viridis	8.4 mm - 9.3 mm	8 mm - 9 mm	
O. elegans	2.9 mm - 3.4 mm	3.2 mm - 4.1 mm	
P. bocagei	4.4 mm	3.7 mm	
P. filfolensis	4.8 mm	4 mm	
Po. hispanicus	3.6 mm - 5.9 mm	3.5 mm - 4 mm	
P. lilfordi	5.8 mm	4.5 mm - 4.8 mm	
P. melisellensis	3 mm - 4.9 mm 3 mm - 4.4 m		
P. milensis	4.5 mm	4 mm	
P. muralis	4 mm - 6 mm	3.6 mm - 5 mm	
P. pityusensis	6.5 mm	5 mm	
P. siculus	3.5 mm - 7.4 mm 3.4 mm - 5.5 m		
P. tauricus	5 mm	4 mm - 4.2 mm	
P. tiliguerta	4.6 mm - 4.9 mm	4 mm - 4.2 mm	
P. waglerianus	5.7 mm	4.1 mm	
P. algirus	5.5 mm	5 mm	
T. lepidus	3.5 mm - 20 mm	4.7 mm - 16 mm	
Z. vivipara	2.6 mm - 3.4 mm	3.2 mm - 4.1 mm	

Scincidae (Fig. A3.4W-AF, A3.5K-M)

The unpaired parietal of scincids has a straight anterior margin and poorly developed anterolateral processes, forming very small, rounded and anteriorly directed parietal tabs. Those of *C. ocellatus*, however, are very strongly developed in lateral direction, giving a concave shape to the lateral margins of the bone (Fig. A3.4AA-AB). A moderate lateral development is visible in *T. aurata* too (Fig. A3.4AE-AF). A small and triangular process, whose development is strongly variable within different individuals, can be present in the middle of the anterior margin of C. ocellatus and C. striatus (Fig. A3.4AA-AB). The postparietal processes are long, thin and pointed in C. chalcides, C. striatus and T. aurata (Fig. A3.4Y-Z, AE-AF, A3.5M), long, slender and posteriorly rounded in O. punctatissimus (Fig. A3.4AC-AD, A3.5L) and long, robust and posteriorly rounded in C. ocellatus (Fig. A3.4AA-AB, A3.5K). In the latter species, moreover, they show a distinct angle at mid-length in dorsal view. Ablepharus kitaibelii, on the other hand, presents short, slender and pointed postparietal processes (Fig. A3.4W-X). On the dorsal surface, a weak dermal ornamentation is present in the middle of the anterior half of the shelf, whereas the rest of it is smooth. The ornamentation is clearly divided into three portions by two sulci: the central portion is the interparietal shield, whereas the smaller lateral ones are the lateral shields (Fig. A3.4Y). In C. ocellatus, the ornamentation covering the lateral areas is very poorly developed (barely recognizable), but it reaches the lateral margins of the shelf (Fig. A3.4AA). On the other hand, the ornamentation is slightly more developed and reaches both the lateral and the anterior margins in T. aurata (Fig. A3.4AE), whereas in A. kitaibelii and O. punctatissimus it is represented only by very light grooves (sometimes completely absent in the former; Fig. A3.4W, AC). The ventral surface is also smooth, except for the presence of the ventral crests (as in lacertids). Those of A. kitaibelii, C. chalcides, C. striatus, O. punctatissimus and T. aurata are less developed and only the anterolateral and posterolateral ones touch each other (Fig. A3.4X, Z, AD, AF). Chalcides ocellatus, on the other hand, shows robust ventral crests, all of which are always in contact (Fig. A3.4AB). The parietal fossa is very narrow and shallow in C. chalcides (Fig. A3.4Z), larger and deeper in C. ocellatus (Fig. A3.4AB) and T. aurata (Fig. A3.4AF) and moderately large and shallow in A. kitaibelii (Fig. A3.4X) and C. striatus. The fossa of O. punctatissimus is narrow, but its depth cannot be defined since it is completely covered by a laminar extension of the median ventral crest (Fig. A3.4AD). A suture line is distinctly visible longitudinally in the middle of the ventral surface of the parietal of O. punctatissimus MDHC 427 (Fig. A3.4AD). The posterior margin of the parietal is characterized by the presence of two pointed processes (forked in MDHC 398; Fig. A3.4Y-Z), which develop posteriorly and define a wide (narrow in O. punctatissimus; Fig. A3.4AC-AD) parietal notch. These processes are wide and moderately short in C. chalcides and C. striatus (Fig. A3.4Y-Z), very long and wide in O. punctatissimus (Fig. A3.4AC-AD), long and thin in C. ocellatus (Fig. A3.4AA-AB). Ablepharus kitaibelii and T. aurata show only two wide and posteriorly rounded tabs, which are very short in the latter (Fig. A3.4AE-AF) and slightly longer in the former (Fig. A3.4W-X). The notch is U-shaped or, exceptionally (MDHC 398 and 404), V-shaped, but can show an irregular margin. Except for A. kitaibelii and T. aurata, a long and thin (moderately wide in O. punctatissimus) epipterygoid process is present in the middle of each lateral margin, developing in ventral direction (Fig. A3.5K-L). In the two aforementioned species the same process is short and triangular (Fig. A3.5M). The parietal foramen is wide, subcircular and located in the middle of the shelf; it can be partially or completely obliterated by the dermal ornamentation (e.g., in T. aurata MDHC 208; Fig. A3.4AE-AF). Measurements are given in the following table:

Snecies	Maximum length	Maximum width	
opecies	of the parietal	of the parietal	
A. kitaibelii	2 mm - 2.5 mm	2.4 mm - 2.5 mm	
C. chalcides	3.2 mm - 4.1 mm	3.7 mm - 4 mm	
C. ocellatus	4.7 mm - 5.1 mm	5.3 mm - 6.5 mm	
C. striatus	2.7 mm - 2.8 mm	2.7 mm - 3.1 mm	
O. punctatissimus	2.8 mm	2 mm	
T. aurata	5 mm	6 mm	

Anguidae (Fig. A3.4AG-AH, A3.5A-C, N-O)

The parietal of anguids is unpaired and presents a rectangular shelf, which is longer than it is large. The anterior margin is slightly irregular, with very small interdigitations in adults, whereas the lateral ones are roughly straight. In ventral view, a small articulation surface for the ventral lappet of the posterolateral process of the frontal is visible near each anterolateral corner of the shelf and a similar small and anteriorly developed ventral lappet is present medially to this surface. The anterolateral processes are poorly developed. The long postparietal processes are strongly medially expanded in their proximal half, but they narrow distally, ending with a moderately robust and posteriorly rounded distal end. The ventral curve is little developed (Fig. A3.5N-O). A well-developed dermal ornamentation is present on the dorsal surface of the shelf and the frontoparietal, interparietal, lateral and occipital shields are recognizable (Fig. A3.4AG, A3.5A, C). The interparietal shield is very large and reaches the anterior margin of the shelf, limiting the frontoparietal ones to the anterolateral corners of the bone. By the anterior margin, the interparietal shield is distinctly wider in Anguis gr. A. fragilis (Fig. A3.4AG) than in P. apodus (Fig. A3.5A). In Anguis gr. A. fragilis, moreover, the dermal ornamentation is usually less marked on the frontoparietal shields compared to the rest of the shelf (Fig. A3.4AG). The occipital shield is small in Anguis gr. A. fragilis (Fig. A3.4AG) and large in P. apodus (Fig. A3.5A). Posteriorly, the ornamentation does not reach the posterior margin of the shelf, because of the presence of a large and smooth area levis (Fig. A3.4AG, A3.5A, C). As in lacertids and scincids, the ventral crests are visible on the otherwise smooth ventral surface. Anterolateral and posterolateral crests contact each other in both Anguis gr. A. fragilis and Pseudopus, whereas the contact between the anterolateral and the medial ones is present only in the latter genus (Fig. A3.5B), since in Anguis gr. A. fragilis the posterior ends of the anterolateral ventral crests is shifted towards the posterior margin of the bone (Fig. A3.4AH). The medial ventral crest (lamina medialis in Klembara et al. 2010) is moderately wide, the posterolateral ones (ventrolateral ridge in Klembara et al. 2010)

can be robust or sharp and the anterolateral ones (cristae cranii parietalis in Klembara et al. 2010) are sharp; the latter are subdivided in two sections: a well-developed anterior one and a low posterior one. In adults of Anguis gr. A. fragilis, the medial ventral crest covers completely the parietal fossa and therefore only the very wide and U-shaped parietal notch is visible posteriorly to it (Fig. A3.4AH); in juveniles and in *P. apodus*, on the other hand, the posterior portion of the wide fossa is visible in ventral view (Fig. A3.5B). Moreover, in the latter species, a carina arcuata extends posteriorly covering most of the notch, which appears only as a wide but shallow concavity in dorsal view (fig. A3.5A). The carina is not developed posteriorly in Anguis gr. A. fragilis (Fig. A3.4AG-AH). The development of the parietal notch undergoes ontogenetic variation in Anguis gr. A. fragilis, since its depth seems to increase during growth. A little or moderately developed epipterygoid process is present in P. apodus (Fig. A3.5O), by the contact of the anterolateral and posterolateral ventral crests, but not in Anguis gr. A. fragilis (Fig. A3.5N). A wide and elliptical (Anguis gr. A. fragilis; Fig. A3.4AG-AH) or circular (P. apodus; Fig. A3.5A-B) parietal foramen is present in the middle of the shelf, even though sometimens it can be obliterated by the dermal ornamentation (Fig. A3.5C). Maximum length of the parietal varies from 3.2 mm to 5.8 mm in Anguis gr. A.

fragilis and from 11 mm to 11.5 mm in *P. apodus*, whereas its maximum width goes from 3 mm to 4.4 mm in the former and from 10.5 mm to 11 mm in the latter.

Premaxilla

The unpaired premaxilla (Fig. A3.6, A3.7) is composed of a ventral alveolar plate, from which the medially located ascending nasal process projects posterodorsally. The dorsal margin of the alveolar plate extends posteriorly forming the two thin and triangular palatal processes, divided medially by a wide notch. Between the bases of these processes, the small and ventrally directed incisive process is present. The alveolar margin of the alveolar plate bears the teeth. The two foramina of the longitudinal canals open by the sides of the ascending nasal process, by its junction

with the alveolar plate. A septonasal crest runs medially along the posterior surface of the nasal process.

Agamidae (Fig. A3.6A-C)

The premaxilla of *L. stellio* is moderately slender, with a narrow alveolar plate in anterior view. The dorsal margin of the alveolar plate does not form two palatal processes, but a single, short and roughly subquadrangular lamina. The incisive process is present in the middle of the posterior margin of this lamina (Fig. A3.6B-C). Teeth are subpleurodont, monocuspid, roughly conical, large and stocky. The usual tooth number is two, but HUJ.OST-Z-5 bears only a single tooth. Teeth are smaller and more numerous in juveniles (e.g., 4 in NHMW 570). Moreover, NHMW 570 displays a toothless area in the middle of the alveolar margin.

The ascending nasal process is stocky, moderately long and pointed. Its base is almost as large as the alveolar plate, but it shrinks dorsally, taking a roughly subtriangular shape in anterior view (Fig. A3.6A). The septonasal crest is robust and well developed (Fig. A3.6C); it runs along the entire height of the process.

The maximum width of the alveolar plate ranges from 1.5 mm to 2.5 mm.

Chamaeleonidae (Fig. A3.6D)

Chamaeleo chamaeleon has a very small and slender premaxilla, with a very slender, long and pointed ascending nasal process. The alveolar plate has concave lateral margins in anterior view and is larger at its dorsal end. Palatal processes are not developed and there is no incisive process. Teeth are very small, acrodont, triangular and monocuspid. The number of tooth positions is 2 or 3. Maximum width of the alveolar plate varies from 0.5 mm to 1 mm.

Gekkota (Fig. A3.6E-X)

In gekkotans, the notch between the palatal processes can be moderately shallow and rounded and so the latter form a subtrapezoidal lamina rather than two triangular extensions; the triangular portion of the processes is short and mainly limited to the posterolateral corners. The lamina is very short in *E. europaea* (Fig. A3.6G-I), but longer in the other species. The incisive process is absent, but a very small and thin

notch is visible where it should be located. In some specimens of *T. mauritanica* (MDHC 119, 194 and 302), a foramen can be seen in ventral view anteriorly to the notch. Teeth are pleurodont, cylindrical, slender and bicuspid, with a labial and a lingual cusp (morphotype F sensu Kosma 2004; see also Sumida & Murphy 1987). The ascending nasal process is long, narrow (very narrow in *T. mauritanica*; Fig. A3.6T-U) and pointed; in *H. turcicus* it is wider proximally (Fig. A3.6J-K), whereas in most specimens of *M. kotschyi* (except for MDHC 418) it tends to slightly widen at the end, forming a small pointed lobe (Fig. A3.6O-P). The only exception is the one of *E. europaea*, which is moderately robust, wider and shows a slight constriction by the basis, taking an arrow-like shape in anterior view (Fig A3.6E-F). *Hemidactylus turcicus* and *M. kotschyi* have a very small septonasal crest, which is not extending into the end of the nasal process (Fig. A3.6K, P). In *E. europaea* and *T. mauritanica*, on the other hand, the crest runs along the entire length of the process; it is very low in the former (Fig. A3.6F) and moderately developed in the latter (Fig. A3.6U).

The maximum width of the alveolar plate goes from 1.4 mm to 1.5 mm in *E. europaea*, from 1.9 mm to 2 mm in *H. turcicus* and *M. kotschyi* and from 2.7 mm to 3.5 mm in *T. mauritanica*. Premaxillae of *E. europaea* show 8 to 9 tooth positions, those of *H. turcicus* 10 to 11, whereas in those of *M. kotschyi* and *T. mauritanica* they go from 9 to 11.

Lacertidae (Fig. A3.6Y-AO)

Premaxilla of lacertids present a long (ususally shorter in *Lacerta*, *T. lepidus* and *Z. vivipara*; Fig. A3.6AG-AH, AO) and pointed ascending nasal process, which could be narrow with parallel lateral margins (*Algyroides*, *A. anatolica*, *A. bedriagae*, *D. oxycephala*, *Darevskia*, *D. mosorensis*, *H. graeca*, *I. aranica*, *I. aurelioi*, *I. bonnali*, *I. horvathi*, *I. martinezricai*, *O. elegans*, *Podarcis* and *Psammodromus*; Fig. A3.6AK-AL), arrow-shaped (*E. arguta*, *I. cyreni*, *I. galani* and *I. monticola*; Fig. A3.6AC-AD), stocky and leaf-shaped (*Lacerta*, *T. lepidus* and *Z. vivipara*; Fig. A3.6AG-AH, AO) or moderately narrow and slightly leaf-shaped at the dorsal end

(A. erythrurus; Fig. A3.6Y-Z) in adults. Juveniles of all species show the first morphology and then develop the other ones during ontogeny. Some degree of variability is present in Α. nigropunctatus, D. oxycephala, D. mosorensis and P. muralis, since (e.g., A. nigropunctatus MDHC (white arrows). Scale bar = 1 mm.



some adult or subadult specimens Figure 2.5) Detail of the premaxillary dentition of T. lepidus MRAC 92-050-R-1, showing bicuspid teeth

242, D. oxycephala NHMW 629, D. mosorensis NHMW 660 and P. muralis MDHC 6) develop a more triangular or rather arrow-shaped morphology. Similarly, MDHC 311, a large and probably old specimen of *P. muralis*, displays a more leaf-shaped nasal process. The septonasal crest is moderately developed and covers almost the entire length of the process, except for some specimens of A. moreoticus, A. nigropunctatus, L. trilineata and Z. vivipara, in which the crest is less developed in its distal half (Fig. A3.6AO). In adults of A. nigropunctatus, I. cyreni, I. monticola, Lacerta, P. melisellensis, P. muralis, P. siculus, P. tauricus, P. tiliguerta, P. waglerianus, P. algirus, T. lepidus and maybe also P. filfolensis, a dermal ornamentation can be present on the dorsal half of the external surface of the nasal process (Fig. A3.6AG, AJ-AK). The notch between the palatal processes is deep, wide and V-shaped (Fig. A3.6AB). Teeth are pleurodont, cylindrical, slender and monocuspid (morphotype B sensu Kosma 2004), but adults of Lacerta, P. siculus and T. lepidus show some bicuspid teeth (morphotype G sensu Kosma 2004) also (Fig. 2.5, A3.6AG-AH). Some specimens of I. monticola can present a second pair of foramina of the longitudinal canals (Barahona 1996; Fig. A3.6AC). Acanthodactylus erythrurus UAM.R.ACVII (Fig. A3.6Y) and P. muralis MDHC 6 show two accessory foramina on the base of the ascending nasal process too.

Number of tooth positions, together with measurements of the width of the alveolar plate, is given in the following table:

	Number of teeth	Maximum width	
Species	number of tooth	of the alveolar	
	positions	plate	
A. erythrurus	7	2 mm - 2.1 mm	
A. fitzingeri	7 - 10	1.4 mm	
A. marchi	9	1.3 mm	
A. moreoticus	7	1.2 mm	
A. nigropunctatus	9 - 11	2 mm - 2.1 mm	
A. anatolica	7	Not measured	
A. bedriagae	8 - 9	2 mm - 2.5 mm	
D. oxycephala	7	1.4 mm - 1.8 mm	
D. armeniaca	7	Not measured	
D. lindholmi	7	Not measured	
D. praticola	7	Not measured	
D. saxicola	7	Not measured	
D. mosorensis	8 - 9	1.7 mm - 2 mm	
E. arguta	7	2.7 mm	
H. graeca	8 - 9	1.5 mm - 2.1 mm	
I. aranica	7	Not measured	
I. aurelioi	7	Not measured	
I. bonnali	7	1.8 mm	
I. cyreni	8 - 9 (rarely 7)	2 mm	
I. horvathi	7 - 8	1.7 mm	
I. martinezricai	9	Not measured	
I. monticola	7 or more	1.8 mm - 2 mm	
L. agilis	7 - 9	1.9 mm - 2.4 mm	
L. bilineata	9 - 11	1.9 mm - 3.3 mm	

L. schreiberi	8	3 mm
L. trilineata	9 - 12	3.8 mm - 4 mm
L. viridis	8 - 11	3.3 mm - 4 mm
O. elegans	7	1.3 mm - 1.4 mm
P. bocagei	7	1.7 mm
P. carbonelli	7	Not measured
P. filfolensis	5	1.8 mm
Po. hispanicus	7	1.3 mm - 1.6 mm
P. lilfordi	6 - 8	2 mm
P. melisellensis	6 - 8	1.1 mm - 2 mm
P. milensis	7	1.8 mm
P. muralis	7	1.4 mm - 2 mm
P. pityusensis	Not counted	2.1 mm
P. siculus	7	1.5 mm - 2.7 mm
P. tauricus	7 - 8	1.9 mm - 2 mm
P. tiliguerta	7	2 mm
P. waglerianus	7	2.2 mm
P. algirus	9	1.9 mm - 2.4 mm
Ps. hispanicus	> 8	Not measured
T. lepidus	7 - 11	1.6 mm - 6.5 mm
Z. vivipara	7 - 8	1.4 mm - 1.7 mm

Scincidae (Fig. A3.6AP-AS, A3.7A-D)

European scincids differ from other European lizards in having paired premaxillae, both provided with a laminar and subquadrangular palatal process (Fig. A3.6AS, A3.7C). In *C. chalcides* MDHC 398 and *O. punctatissimus* MDHC 427, however, the two paired premaxillae join together by their ventral margin, suggesting that a possible fusion may be present in old individuals. Together, the palatal processes compose a structure similar to the subtrapezoidal lamina seen in gekkotans. Except maybe for *C. bedriagai*, an incisive process can be present: it can be either split into

two halves by the separation of the paired premaxillae or developed as a single process. Teeth are morphologically similar to those of gekkotans, but their crown is slightly curved posteriorly and shows a light striation on the lingual surface. Those of *C. ocellatus* differ from those of the other species because they are robust and provided with a blunt and mediolaterally enlarged crown (Fig. A3.7A-B). Each premaxilla bears half of the ascending nasal process, which is long, moderately narrow and pointed in its entirety. Larger species have a proportionally longer and more slender ascending nasal process. In *O. punctatissimus* MCZ 38517, the process displays a light constriction by its base and therefore assumes an arrow-shaped appearance in anterior view. Since the process is split by its medial line, a septonasal crest is not recognizable. The external surface of the premaxillae is smooth, with no traces of dermal ornamentation (Fig. A3.6AP, A3.7A).

Species	Number of tooth positions	Maximum width of the alveolar plate
A. kitaibelii	4 - 5	0.5 mm - 0.8 mm
C. bedriagai	3 - 4	0.7 mm - 0.8 mm
C. chalcides	3 - 4	1 mm
C. ocellatus	3 - 4	1.1 mm - 1.9 mm
C. striatus	3 - 4	0.9 mm - 1 mm
O. punctatissimus	3 (5 on the whole in MDHC 427)	Roughly 0.5 mm
T. aurata	4 - 5	1.6 mm - 1.7 mm

Measurements and number of tooth positions are given in the following table:

Anguidae (Fig. A3.7E-J)

In European anguids, the premaxilla has a wide and low alveolar plate. In *Anguis* gr. *A. fragilis*, the ascending nasal process is short and very narrow by its base, but it presents a wide and lobe-shaped dorsal half, provided with a pointed end (Fig.

A3.7E-F). In *P. apodus*, on the other hand, it is moderately wide, with straight and parallel lateral margins and a rounded dorsal end (Fig. A3.7I-J). According to Klembara et al. (2017), however, the process of young *P. apodus* is slightly widened at mid-length. The anterior surface of the process is smooth (Fig. A3.7E, I), whereas only in Anguis gr. A. fragilis a low but distinct septonasal crest runs along he posterior one (Fig. A3.7F); the development of the crest increases during growth, being unrecognizable in juveniles. Each palatal process is split into two portions by a deep notch (Fig. A3.7H): laterally there is the narrow maxillary process, provided with a roughly rounded end, whereas the pointed and slightly wider vomerine process is present medially. The two vomerine processes are not fused medially, but they are flanked and present a wide notch between them. The ventral end of the septonasal crest splits into two prominent ridges, which merge into the dorsal surface of the vomerine processes (Fig. A3.7F). These ridges are present also in *P. apodus*, even if the crest is not present in this species (Fig. A3.7J). A well-developed incisive process is present: it is composed by two lobe-shaped and ventrally concave portions located on the ventral surface of the vomerine processes (Fig. A3.7H). Teeth are subpleurodont, slender (slightly thicker in *P. apodus*), monocuspid and slightly posteriorly curved by their tip; they are roughly subcylindrical, but the pointed tip gave them a more trenchant shape (morphotype A sensu Kosma 2004) in Anguis gr. A. fragilis (Fig. A3.7E-F). Teeth of P. apodus have a blunter tip (Fig. A3.7I-J). No striation is visible on the crown of the teeth of Anguis gr. A. fragilis, whereas distinct striae are visible on both the labial and the lingual sides in *P. apodus*.

The number of tooth positions is 9 in *Anguis* gr. *A. fragilis* and goes from 6 to 7 (7 to 9 following Roček, 1980b, and Klembara et al., 2017) in *P. apodus*, whereas the maximum width of the alveolar plate varies from 1.4 mm to 2.9 mm in *Anguis* gr. *A. fragilis* and from 5 mm to 5.5 mm in *P. apodus*.

Maxilla

The paired maxillae (Fig. A3.8, A3.9) consist of an alveolar portion and a dorsomedially developed facial process. The alveolar portion is composed by a tooth-bearing alveolar border and by a palatal shelf developed medially. The anterior end (anterior premaxillary process) has a concave anterior margin because of the presence of the anteromedial and anterolateral processes. The posterior end corresponds to an elongated posterior process. The superior alveolar canal passes through the base of the facial process. It opens anteriorly on the dorsal surface of the premaxillary process, with the vomeronasal foramen. Posteriorly, it opens on the dorsal surface of the palatal shelf, by the posterior end of the facial process, with the wide superior dental foramen (infraorbital foramen in Barahona 1996). The canal opens also on the lateral surface of the maxilla, with a variable number of ventrolateral (labial) foramina; the number of these foramina can be different in the two maxillae of the same specimen.

Agamidae (Fig. A3.8A-C)

Laudakia stellio has a slightly medially curved anterior premaxillary process, provided with a roughly straight (slightly concave in juveniles) anterior margin. Adults lack an anterolateral process, whereas a very little developed one can be seen in juveniles. The pointed anteromedial process, on the other hand, is distinctly developed in dorsal direction (Fig. A3.8A-B). The posterior process is long and pointed, showing a moderately deep groove for the articulation of the jugal on its dorsal surface. A strong spur is present on its dorsal margin; the step can be posteriorly rounded or pointed and projects in posterior direction. The maxilla carries two large, subpleurodont, stocky, conical and monocuspid teeth by its anterior end (Fig. A3.8C), whereas acrodont and triangular teeth are present posteriorly. Acrodont teeth are closely spaced and extend towards the medial surface of the alveolar shelf (Fig. A3.8B). They can also present small accessory cusps located anteriorly and posteriorly to the main one. The size of the acrodont teeth increases posteriorly, with the anteriormost ones being very small. In juveniles, however, there is only one

smaller subpleurodont tooth anteriorly and the acrodont teeth are very large for the entire length of the tooth row. Only the posterior fourth (fifth in juveniles) of the alveolar border does not bear teeth. The anterior and posterior openings of the superior alveolar canal are moderately wide and subcircular. Four or 5 ventrolateral foramina can be present on the otherwise smooth lateral surface.

The facial process is triangular in lateral view. The anterior margin is roughly straight, whereas the posterior one is strongly concave. The dorsal end is bifid, with two wide and rounded projections. The anterior one is longer than the posterior one. The whole anterior margin of the process, anterior projection included, bends medially (Fig. A3.8B). Both the lateral and the medial surface of the process are smooth.

Including the subpleurodont ones, a number of 9 to 18 tooth positions is present (10 to 15, according to Siebenrock 1895). The alveolar border can measure from 5.5 mm to 15 mm in maximum length.

Chamaeleonidae (Fig. A3.8D-E)

The anterior premaxillary process of the maxilla of *C. chamaeleon* is strongly curved medially (Fig. A3.8E), contacting the other maxilla with a straight anteromedial margin. There are neither anteromedial nor anterolateral processes, although a small notch for the insertion of the very small premaxilla is present. The palatal shelf develops a moderately large medial expansion in the middle, which is the contact surface with the palatine; the articulation surface is recognizable in dorsal view. The posterior process is not stepped and shows a moderately deep groove on the dorsal surface. Teeth are carried on the ventral margin of the bone and are present on its whole length, but in MNHN 241 and 2002-24 and NHMW 611 they lack on the posterior end (Fig. A3.8E); they are acrodont, triangular and tricuspid. They are well spaced (though exceptions may occur; e.g., NHMW 611, Fig. A3.8E, but see also Čerňanský 2011) and larger in the posterior portion of the alveolar border. The lateral surface of the bone is smooth (Fig. A3.8D). Usually only 1 ventrolateral foramen is

present (Fig. A3.8E), but rarely 2 of them can be present (e.g., the right maxilla of MNHN 1942-103 and the left ones of NHMW 611 and 721).

Two dorsally developed processes are present: a first one anteriorly to the external nares and a second one (facial process) posteriorly to it. The anterior dorsal process is dorsally bifid: the lateral portion contacts the anterior end of the prefrontal posterodorsally, whereas the medial portion contacts the nasal dorsally and the ascending nasal process of the premaxilla medially. On the dorsal surface of this process, two large and rounded tubercles are present along its lateral margin (three in the left maxilla of NHMW 611). The facial process is slightly larger than the anterior dorsal one in lateral view and touches the lateral process of the prefrontal dorsally. Ventrolateral foramina are located by the base of this second process (Fig. A3.8D).

The maximum length of the alveolar border goes from 15.1 mm to 19 mm, whereas the number of tooth positions varies from 14 to 21.

Gekkota (Fig. A3.8F-M, A3.9Q-T)

In the maxillae of gekkotans, the anteromedial process is well developed and pointed in *E. europaea* (Fig. A3.8F-G, A3.9Q), small and roughly subtriangular in dorsal view in *H. turcicus* (Fig. A3.8H-I, A3.9R) and *M. kotschyi* (Fig. A3.8J-K, A3.9S) and moderately developed and anteriorly truncated or pointed in *T. mauritanica* (Fig. A3.8L-M, A3.9T). The anterolateral process, on the other hand is almost absent in *E. europaea* (Fig. A3.8F-G, A3.9Q), small and subtriangular in *H. turcicus* (Fig. A3.8H-I, A3.9R) and *T. mauritanica* (Fig. A3.8L-M, A3.9T) and very little developed or absent in *M. kotschyi* (Fig. A3.8J-K, A3.9S). The vomeronasal foramen is moderately wide, except for *E. europaea* in which it is smaller. The posterior process is pointed (rounded in *E. europaea*; Fig. A3.8F-G) and show no step on the dorsal margin. On its dorsal surface, a wide but shallow groove runs in posteromedial direction starting from the superior dental foramen. Such groove is not clearly visible in *H. turcicus*, but this species presents another moderately shallow groove posteriorly to the facial process, representing the position of the ventral margin of the lacrimal foramen (Fig. 2.6). In *M. kotschyi*, another shallow groove, bordered dorsally by a low ridge, can be present by the base of the facial process, dorsally to the superior dental foramen; in MDHC 418, this groove is medially closed and represented only by a posteriorly open foramen. Teeth are pleurodont, cylindrical, slender and bicuspid, with a labial and a lingual cusp (morpho-type F sensu Kosma 2004; see also Sumida & Murphy 1987); they are present on the whole length of the bone.

The facial process is tall and subtrapezoidal in lateral view; its length is equivalent to half the length of the entire maxilla. Its posterodorsal end is rounded in *E. europaea* (Fig. A3.8F-G) and presents a pointed posterodorsal projection in the other species (Fig. A3.8H-M). The posterior and dorsal margins of the process are straight, whereas the anterior margin is more variable between species: it is very steep and inclined anteriorly in *E. europaea* (Fig. A3.8F-G) and *H. turcicus* (Fig. A3.8H-I), very steep and roughly vertical in *M. kotschyi* (Fig. A3.8J-K) and displays a V-shaped notch in *T. mauritanica* (Fig. A3.8L-M). In *E. europaea*, *M. kotschyi* and *T. mauritanica*, both medial and lateral surfaces are smooth, with only a highly variable number of flanked foramina by the base of the process, whereas in *H. turcicus* the lateral surface is covered by a very faint ornamentation made up of grooves (Fig. 2.2) and the medial one presents a wide foramen by its base and a low sigmoid-

shaped ridge running near the anterior margin (Fig. 2.6). A small foramen is visible near the anterodorsal corner of the facial process in *europaea* and *T*. *E*. *mauritanica*: it passes through the process, opening in ventral



Figure 2.6) Left maxilla of H. turcicus (MDHC 238) in medial view, showing the sigmoid medial ridge (mr) on the medial surface and the groove of the lacrimal foramen (marked by an arrow). Scale bar = 1 mm.

direction on the lateral surface and in dorsal direction on the medial one. A similar foramen seems to be present also in some specimen of *M. kotschyi* (e.g., MDHC 201 or the right maxilla of MDHC 419), but it is shifted ventrally.

The maximum length of the alveolar border goes from 4.3 mm to 5 mm in *E. europaea*, from 5 mm to 6.6 mm in *H. turcicus*, from 5.2 mm to 6.8 mm in *M. kotschyi* and from 7.9 mm to 10.5 mm in *T. mauritanica*. Maxillae of *E. europaea* show 25 to 30 tooth positions, those of *H. turcicus* 25 to 29, those of *M. kotschyi* 22 to 30 and those of *T. mauritanica* 27 to 32. Ventrolateral foramina goes from 6 to 9 in in *E. europaea*, from 6 to 7 in *H. turcicus*, from 4 to 7 in *M. kotschyi* and from 4 to 7 in *T. mauritanica*.

Lacertidae (Fig. A3.8N-X, A3.9A-B, U-V)

The anterior premaxillary process of the maxilla of lacertids shows a deep anterior concavity, since both anteromedial and anterolateral processes are well developed (Fig. A3.9U-V). The two processes are similar in size, but the anteromedial one can develop a lappet on its dorsal surface (Fig. A3.9P-W, A3.9A-B, V): the latter is present in all species but A. erythrurus (Fig. A3.8N-O, A3.9U), A. fitzingeri, A. marchi, E. arguta, H. graeca and O. elegans. Barahona (1996) reported a lappet in juveniles of L. viridis (probably L. bilineata, since her specimens were collected in the Iberian Peninsula), but not in adults and, therefore, at least in this species, this could be a feature linked to ontogenetic variation. It has to be noted, however, that all adult specimens of *Lacerta* included in this study present a lappet (Fig. A3.8P-R, A3.9V). In lateral view, the posterior process is large and pointed. In I. monticola monticola, Lacerta, P. bocagei, P. carbonelli, P. filfolensis, Po. hispanicus, P. lilfordi, P. melisellensis, P. milensis, P. muralis, P. pityusensis, P. siculus, P. tauricus, P. tiliguerta and P. waglerianus, the dorsal margin of this process presents a step, which develops a posteriorly projecting spur in L. agilis, P. melisellensis, P. milensis, P. tauricus and sometimes also L. bilineata, L. viridis and P. muralis. The spur is always strongly developed in *P. melisellensis* (Fig. A3.8S-T), but it can be short or even almost absent in L. agilis, P. milensis and P. tauricus. Lacerta bilineata,

L. viridis and *P. muralis* can either display a short spur (Fig. A3.8R) or a simple step (Fig. A3.8P-Q). The wide vomeronasal foramen opens on the base of the anterior margin of the dorsal process, in an anteriorly directed concavity bordered laterally and medially by two low ridges. The superior dental foramen is very wide and is followed by a very wide posteriorly directed groove. The tooth row does not reach the posterior end of the bone, leaving a small posterior toothless portion which is shorter in large-sized species. Teeth are cylindrical, pleurodont, slender, mono- and bicuspid (morphotype B and G sensu Kosma 2004, respectively). Tricuspid teeth (morphotype H sensu Kosma 2004) can be also present, mostly in large-sized species. *Hellenolacerta graeca*, *P. filfolensis*, *P. lilfordi*, *P. melisellensis*, *P. milensis*, *P. pityusensis*, *T. lepidus* and some specimens of *P. tauricus* and *L. trilineata* can present a low number of hypertrophied maxillary teeth (Fig. A3.8S-T, W-X). Hypertrophied teeth are present also on the maxillae of MDHC 48 and 73, two very young individuals of *L. bilineata*.

The facial process is roughly subtriangular in shape, with slightly irregular anterior and posterodorsal margins and two projections developing posterodorsally from its dorsal end. The two projections can be narrow (*A. erythrurus* and *O. elegans*; Fig. A3.8N-O) or large (other species; Fig. A3.8P-W, A3.9A-B) in lateral view and the anterior one is more developed than the posterior one. They are scarcely developed in *A. fitzingeri*, *A. marchi*, *A. bedriagae*, *Z. vivipara* (Fig. A3.9A-B) and in some specimens of *L. schreiberi* and *T. lepidus*. A well-developed dermal ornamentation is present on the lateral surface of the process (Fig. A3.8P, R, S, U), except for *A. erythrurus*, *Algyroides*, *D. oxycephala*, *D. mosorensis*, *E. arguta*, *H. graeca*, *I. bonnali*, *I. horvathi*, *O. elegans* and *Z. vivipara* in which the ornamentation is absent or less developed (Fig. A3.8N, A3.9A). The sulcus between the areas covered by internasal and prefrontal scales can be visible in *Lacerta*, *T. lepidus* and sometimes *Podarcis* (e.g., *P. muralis*, *P. tauricus* and *P. waglerianus*). The medial surface shows a low and arched ridge roughly at mid-length, starting on the dorsal surface of the palatal shelf and running posterodorsally. The ridge appears to be slightly more developed in *A. nigropunctatus*, *A. bedriagae*, *H. graeca*, *L. agilis*, *L. bilineata* (Fig. A3.8Q), *L. schreiberi* and *Z. vivipara* (Fig. A3.9B) and is not visible in *A. erythrurus* (Fig. A3.8O). In *O. elegans* and *P. algirus*, there is also a low ridge running dorsoventrally from the middle of the anterior margin to the palatal shelf (Fig. A3.8V).

Measurements, number of tooth positions and of ventrolateral foramina are given in the following table:

Species	Maximum length of the alveolar border	Number of tooth positions	Number of ventrolateral foramina
A. erythrurus	6 mm - 7.2 mm	16 - 19	3 - 4
A. fitzingeri	3.2 mm	18 - 19	5
A. marchi	4.3 mm	20	5 - 6
A. moreoticus	4 mm	16 - 17	6
A. nigropunctatus	5.7 mm - 7 mm	20 - 22	6 - 8
A. bedriagae	6.8 mm - 9 mm	16 - 21	6 - 7
D. oxycephala	5.9 mm - 6.1 mm	19	6 - 8
D. mosorensis	5.4 mm - 6.9 mm	18 - 21	5 - 7
E. arguta	9 mm	16 - 20	5 - 7
H. graeca	5.1 mm - 7.5 mm	20	6 - 8
I. aranica	Not measured	14 - 17	Not counted
I. aurelioi	Not measured	15 - 17	Not counted
I. bonnali	Not measured	15 - 18	Not counted
I. cyreni	Not measured	16 - 20	Not counted
I. horvathi	5.3 mm - 5.5 mm	17 - 18	5
I. martinezricai	Not measured	15 - 17	Not counted
I. monticola	5.9 mm	15 - 18	5 - 6
L. agilis	6.4 mm - 6.9 mm	15 - 18	4 - 8
L. bilineata	5 mm - 11.7 mm	16 - 21	5 - 8

L. schreiberi	8.3 mm - 8.4 mm	17	6
L. trilineata	11 mm - 13 mm	18 - 21	5 - 6
L. viridis	11.5 mm - 13.7 mm	18 - 22	4 - 7
O. elegans	3.8 mm - 4.4 mm	17 - 21	4 - 6
P. bocagei	5 mm	17 - 19	7
P. filfolensis	6 mm - 6.2 mm	14 - 16	7
Po. hispanicus	4.5 mm - 6.1 mm	18 - 19	6 - 7
P. lilfordi	6.6 mm - 7 mm	15 - 16	5 - 8
P. melisellensis	4 mm - 7 mm	16 - 19	4 - 7
P. milensis	6 mm	17 - 18	6 - 7
P. muralis	5 mm - 6.9 mm	14 - 21	4 - 8
P. pityusensis	7.8 mm	15	6 - 7
P. siculus	4.9 mm - 8.7 mm	17 - 20	4 - 7
P. tauricus	6 mm - 6.4 mm	19 - 20	6 - 8
P. tiliguerta	6 mm - 6.5 mm	19	5 - 6
P. waglerianus	7 mm	17	6
P. algirus	6.3 mm - 7 mm	19 - 21	5
T. lepidus	5.1 mm - 22 mm	13 - 24	5 - 10
Z. vivipara	4.5 mm - 5.2 mm	17 - 21	4 - 6

Scincidae (Fig. A3.9C-L, W-Y)

Scincids show a very deep, U-shaped concavity on the anterior margin of the anterior premaxillary process, due to the presence of well-developed and pointed anterolateral and anteromedial processes (Fig. A3.9W-Y). The two processes are roughly similar in size. The posterior process is long and usually pointed and does not present steps; except for *O. punctatissimus* (Fig. A3.9I-J), its posterior tip is slightly shifted in dorsal direction (Fig. A3.9C-H, K-L). The location of the small vomeronasal foramen is similar to the condition seen in lacertids, but in scincids the concavity is shallower because of the absence of a clearly developed lateral ridge. The medial ridge, on the other hand, is present but low in *C. ocellatus* (Fig. A3.9G-

H) and T. aurata (Fig. A3.9K-L) and well developed in A. kitaibelii (Fig. A3.9C-D), C. chalcides (Fig. A3.9E-F), C. striatus and O. punctatissimus (Fig. A3.9I-J); in the latter four species, moreover, it continues on the dorsal surface of the anteromedial process in a distinct lappet. In O. punctatissimus, the lappet bends strongly in medial direction, giving a forked aspect to the anterior end of the anteromedial process in dorsal view (Fig. A3.9Y). The opening of the superior dental foramen is medially oriented. A moderately deep groove is present on the dorsal surface of the posterior process, posteriorly to the latter foramen, though it seems not to be in continuity with it (as it is, for example, in lacertids). As in the premaxillae, teeth are similar to those of gekkotans, but they have a slightly posterolingually curved crown provided with light striae on the lingual surface. They are absent only on the tip of the posterior process. The ones of *C. ocellatus* are robust and have a blunt and very enlarged crown (Fig. A3.9G-H). Even if not as much as in C. ocellatus, more robust teeth are present in O. punctatissimus too (Fig. A3.9I-J). In the latter species, the increase in robustness is less marked in the anteriormost teeth, but becomes more evident towards the posterior end of the tooth row. Anyway, the last tooth is slightly smaller than the preceding one.

The facial process is roughly pentagonal in lateral view. The anterior and posterior margins are concave, whereas the anterodorsal and posterodorsal ones are roughly straight, though slightly irregular. *Trachylepis aurata* differs from the other species in having a strongly concave posterodorsal margin (Fig. A3.9K-L). *Ophiomorus punctatissimus*, on the other hand, does not display a clear distinction between an anterodorsal and a posterodorsal segment of the dorsal margin, which is rather convex in this species (Fig. A3.9I-J). In *C. chalcides*, *C. striatus* and *T. aurata*, the dorsal margins are similar in length (Fig. A3.9E-F, K-L), whereas in *A. kitaibelii* and *C. ocellatus* the anterodorsal one is longer than the posterodorsal one (Fig. A3.9C-D), G-H). In *A. kitaibelii*, this difference in length is very strongly marked, since the posterodorsal margin is less than one third of the anterodorsal one (Fig. A3.9C-D). The anterior, dorsal and posterior corners of the process are pointed in *Chalcides*.

(Fig. A3.9E-H), but they do not develop projections. *Trachylepis aurata* shares a similar morphology, but the dorsal corner is rounded (Fig. A3.9K-L), whereas all corners are rounded in *A. kitaibelii* and *O. punctatissimus* (Fig. A3.9C-D, I-J). The lateral surface is smooth, whereas a very low arched ridge is visible on the medial one. This latter ridge is similar to the one present in some lacertids, but much lower (almost not recognizable in *A. kitaibelii*, *C. ocellatus*, *O. punctatissimus* and *T. aurata*).

Species	Maximum length of the alveolar border	Number of tooth positions	Number of ventrolateral foramina
A. kitaibelii	1.7 mm - 2.1 mm	12 - 14	3 - 5
C. bedriagai	3.4 mm - 3.5 mm	13 - 14	4 - 5
C. chalcides	4.6 mm - 5 mm	16 - 17	4 - 6
C. ocellatus	6 mm - 7.5 mm	11 - 13	5 - 7
C. striatus	3.8 mm - 4 mm	16 - 18	3
O. punctatissimus	2.4 mm - 2.5 mm	10 - 11	3 - 4
T. aurata	7.1 mm - 7.3 mm	22	5 - 6

The following table shows measurements, number of tooth positions and number of ventrolateral foramina:

Anguidae (Fig. A3.9M-P, Z)

In European anguids, both anteromedial and anterolateral processes are pointed and very well developed, defining a very deep and U-shaped anterior concavity, which is also moderately narrow in dorsal view (Fig. A3.9Z). The two processes are slender and roughly similar in size in *Anguis* gr. *A. fragilis*, but the anteromedial process is slightly shorter than the anterolateral one in *P. apodus*. A well-developed lappet is present on the dorsal surface of the anteromedial process; in *Anguis* gr. *A. fragilis*, this lappet projects anteriorly beyond the end of the process with a pointed tip and bends slightly in medial direction (Fig. A3.9Z). The posterior process is long, slender

and pointed in lateral view, lacking any step. The vomeron as al foramen is small (very small in *P. apodus*) and opens in a shallow anteriorly concave area, bordered laterally and medially by two very low ridges. The superior dental foramen is wide and continues posteriorly in a wide groove that runs along the dorsal surface of the posterior process. Teeth are large (maximum size is reached in the middle of the tooth row in Anguis gr. A. fragilis and by its posterior end in P. apodus) and subpleurodont, lacking only on the posterior end of the maxilla. In Anguis gr. A. *fragilis*, they are monocuspid, trenchant, well spaced and distinctly posterolingually bent by their tip (Fig. A3.9M-N). Maxillae of *P. apodus*, on the other hand, show two different tooth morphologies: anteriorly, they have monocuspid, cylindrical and slightly robust teeth, provided with a pointed and not curved tip, whereas on the posterior end there are very large, cylindrical and stout teeth, provided with a blunt and rounded crown (Fig. A3.9O-P). Teeth of P. apodus are closely spaced and increase gradually in size posteriorly, but the last ones are smaller than the preceding ones. Striae are not present in Anguis gr. A. fragilis, but visible on both the lingual and the labial sides in *P. apodus*.

The facial process is subtrapezoidal in lateral view, with a slightly convex dorsal margin and slightly concave anterior and posterior margins; the latter is almost vertical in *Anguis* gr. *A. fragilis* (Fig. A3.9M-N) and slightly oblique in *P. apodus* (Fig. A3.9O-P). The width of the process is smaller than half the length of the bone in *Anguis* gr. *A. fragilis* and roughly half the length in *P. apodus*. Both its anterodorsal and posterodorsal corners are rounded and a variable number of small foramina can be present near the former one. No dermal ornamentation is present on the lateral surface of the facial process in *Anguis* gr. *A. fragilis* (Fig. A3.9O), whereas a very light one is visible in *P. apodus* (Fig. A3.9O). The medial surface shows a thicken area by the anterior margin and a low (sometimes more distinct in *Anguis* gr. *A. fragilis*) arched ridge similar to the one present in lacertids and scincids.

The maximum length of the alveolar border goes from 3.3 mm to 7 mm in *Anguis* gr. *A. fragilis* and from 12.5 mm to 16.6 mm in *P. apodus*, whereas the number of

tooth positions is 9 in *Anguis* gr. *A. fragilis* and goes from 9 to 14 in *P. apodus*. 3 or 4 ventrolateral foramina are present in *Anguis* gr. *A. fragilis*, 3, 4 or 5 in *P. apodus*.

Prefrontal

The prefrontal (Fig. A3.10) is a paired bone composed of an anteriorly concave body, the orbitonasal flange, and a large and pointed dorsal process developed in posterodorsal direction from the medial side of its dorsal margin. A laminar structure, the anterodorsal process, develops in anterior direction from the dorsal margin of the orbitonasal flange and a posteroventral process develops ventrolaterally from its ventrolateral corner. A small posterolaterally directed projection is present by the tip of the posteroventral process. A wide notch located between the anterodorsal and the posteroventral processes marks the dorsal and the medial margins of the lacrimal foramen.

Agamidae (Fig. A3.10A-B)

In posterior view, the prefrontal of *L. stellio* has a subrectangular orbitonasal flange. The posteroventral process is poorly developed and not clearly individualized, and a similarly small and subtrapezoidal orbitonasal flange projection is recognizable on the ventromedial corner of the flange (Fig. A3.10B). The projection and the posteroventral process are separated by a wide but very shallow ventral concavity. Both the dorsal and the posterior surface of the flange are smooth, except for a low but distinct ridge that marks posteriorly the articulation surface with the maxilla on the former. Moreover, a very robust tubercle develops in lateral direction from the dorsolateral corner of the bone (Fig. A3.10B). The notch of the lacrimal foramen is very wide and deep (Fig. A3.10B). The dorsal process is robust and long (longer than the moderately short anterodorsal process). On its lateral surface, there is a distinct and sharp palpebral crest, running anteroposteriorly from the lateral tubercle to the posterior tip (Fig. A3.10B).

Chamaeleonidae (Fig. A3.10C-E)

Prefrontals of *C. chamaeleon* have a subrectangular orbitonasal flange, with a moderately shallow ventral concavity (Fig. A3.10C). They are anteroposteriorly elongated in dorsal view (Fig. A3.10E), with an anterior end that is strongly narrower than the posterior one. The anterodorsal process is long and thick and contacts the anterior dorsal process of the maxilla, forming the dorsal margin of the external nares. A subtriangular or subrectangular orbitonasal flange projection is present by the ventromedial corner of the flange (Fig. A3.10C): it is strongly longer than the moderately small posteroventral process and does not display projections by its tip. Another (lateral) process develops form the anterior margin, just ventrally to the posterior end of the anterodorsal process (Fig. 2.7): this process is short and moderately large in lateral view and contacts the facial process of the maxilla. The

lateral process marks the lateral margin of the large lacrimal foramen, whose medial margin is composed by a wide notch on margin of the lateral the orbitonasal flange. The dorsal process is laminar, posteriorly rounded and strongly mediolaterally expanded (Fig. A3.10D-E). Its posterior end contacts the postorbital with a slightly interdigitated suture. A series of tubercles with an irregular dorsal margin (but rather rounded) runs along the dorsolateral margin of the bone (i.e. on the anterodorsal process and on the dorsal process; Fig.



Figure 2.7) Articulated skull of C. chamaeleon (NHMW 721) in lateral view, showing the lateral process of the prefrontal (lp) and the lacrimal foramen (lf). Scale bar = 1 mm.

A3.10D-E), forming a continuous ridge that starts on the anterior dorsal process of the maxilla and ends posteriorly on the squamosal (passing also through the postorbital). The dorsal surface of the bone shows an ornamentation made of small tubercles (Fig. A3.10E).

Gekkota (Fig. A3.10F-Q)

Prefrontals of gekkotans have a crescent shape in posterior view because of the presence of a ventromedially directed orbitonasal flange projection (Fig. A3.10F, J, M, P). This projection is wider and more developed than the posteroventral process and has a subtrapezoidal shape (subtriangular in *E. europaea*, Fig. A3.10F, and MDHC 97, Fig. A3.10P, and more rounded in MDHC 98). The anterodorsal process is thin and smooth, whereas the posteroventral one is pointed. The posterolateral surface of the orbitonasal flange is smooth in all species except for *H. turcicus*, in which it can present a faint ornamentation made up of grooves (Fig. 2.2). The notch of the lacrimal foramen is deep in *H. turcicus* (Fig. A3.10I-J) and shallow in other species. The dorsal process is slender in *E. europaea* and *M. kotschyi* (Fig. A3.10F-H, L-N), stouter in *H. turcicus* and *T. mauritanica* (Fig. A3.10I-K, O-Q).

Lacertidae (Fig. A3.10R-Z)

In lacertids, the prefrontal shows a distinct and size-linked dermal ornamentation on the dorsal surface (Fig. A3.10R, X), with larger species provided with a stronger cover. *Acanthodactylus erythrurus*, *A. fitzingeri*, *E. arguta* and *O. elegans*, in particular, have a very poorly marked ornamentation (Fig. A3.10U). The anterodorsal process is covered by this ornamentation on its posterior half, whereas the anterior one is smooth. The lacrimal foramen is represented by a deep and wide notch. A long, slender and laterally-directed projection is present dorsally to the notch in *O. elegans* (Fig. A3.10U-V). A similar, but proportionally smaller process can be present in *T. lepidus* too (Fig. A3.10X-Y). The dorsal process is robust; in lateral view, it is slightly longer than the orbitonasal flange in *A. erythrurus*, *A. marchi*, *A. moreoticus*, *O. elegans* and *Psammodromus* (Fig. A3.10W), but it is shorter (roughly as long as the flange or even shorter than it) in the other species

(Fig. A3.10S, Z). At least in *A. nigropunctatus*, this character could be subject to individual variation, since the dorsal process is longer than the flange in MDHC 242, an adult male, but distinctly shorter than it in MDHC 171 and 243, a possible juvenile female and an adult male respectively. A well distinct palpebral crest runs along the entire lateral surface of the process; it is more developed in large-sized species. *Scincidae (Fig. A3.10AA-AF)*

A subquadrangular orbitonasal flange projection is present also in the prefrontal of scincids (Fig. A3.10AB, AE). As in gekkotans, it is distinctly wider than the posteroventral process, but, in contrast with them, it is shorter than the latter (these differences are less marked in the largest specimens of *C. chalcides* and *C. ocellatus*). Both the dorsal surface of the thin anterodorsal process and the posterolateral surface of the orbitonasal flange are smooth. The posteroventral process is thin and truncated by the end. Its posterolateral projection is moderately large and not clearly individualized (Fig. A3.10AA-AC), except for C. striatus and T. aurata in which it is more easily recognizable (Fig. A3.10AD-AF). A deep notch for the lacrimal foramen is present; it is particularly deep in A. kitaibelii, in which, moreover, it is partially covered dorsolaterally by an osseous projection of the bone (Fig. A3.10AA-AC). The dorsal process is slender and slightly shorter than the rest of the bone in lateral view in all species (Fig. A3.10AD, AF) but A. kitaibelii, in which it can be slightly longer (Fig. A3.10AA, AC). A low (A. kitaibelii, Chalcides and O. punctatissimus; Fig. A3.10AA, AC) or sharp (T. aurata; Fig. A3.10AD, AF) palpebral crest is visible on its base, except maybe for the prefrontals of C. bedriagai. Anguidae (Fig. A3.10AG-AL)

Anguids have a subtriangular orbitonasal flange projection, which is wider but very slightly shorter than the slender and truncated posteroventral process (Fig. A3.10AH, AK). There is no ornamentation in *Anguis* gr. *A. fragilis* (Fig. A3.10AG), whereas very mild rugosities are visible dorsally in *P. apodus*, on the base of the dorsal process (Fig. A3.10AJ). A distinct posterolateral projection is absent and the notch for the lacrimal foramen is very wide and moderately (*Anguis* gr. *A. fragilis*, Fig.

A3.10AG-AI) or very (*P. apodus*; Fig. A3.10AJ-AL) deep. The dorsal process is slender and moderately long, being as long as or slightly longer than the rest of the prefrontal in lateral view. The palpebral crest is low; in adults of *Anguis* gr. *A. fragilis*, it is not clearly recognizable.

Jugal

Jugals (Fig. A3.11) are curved and paired bones, roughly L-shaped in lateral view, with an anterior and a posterodorsal processes. The anterior process can present a medially developed shelf, the palatal process, whose posterior end can develop a triangular medial process of the jugal. Between the anterior and the posterodorsal process, a quadratojugal process can develop in ventral direction. A row of small foramina pierces the lateral surface of the bone.

Agamidae (Fig. A3.11A-B)

Laudakia stellio shows a distinctly triradiate jugal, because of the presence of a moderately long and triangular quadratojugal process. The anterior process is robust, but narrows towards the pointed anterior end. The lateral surface of the anterior half of the process is completely covered by the articulation surface with the spur of the maxilla (Fig. A3.11A). A short palatal process is present, but it lacks any sign of a medial one (Fig. A3.11B). The posterodorsal process is very massive and slightly shorter than the anterior one. It bends posteriorly in its posterior portion, originating a distinct angle at mid-length. Its distal end is rounded. On the medial surface of the bone, the articulation surface with the postorbital is visible all along the anterodorsal margin of the posterodorsal process (Fig. A3.11B). Large foramina are present on the lateral surface.

Chamaeleonidae (Fig. A3.11C-D)

Jugals of *C. chamaeleon* have a thin and pointed anterior process and a dorsoventrally expanded posterodorsal process. A number of very small tubercles is present on the lateral surface of the latter (Fig. A3.11C): they are aligned and run parallel to the concave dorsal margin. The length of the two processes is similar. The

palatal process is represented by a low and sharp ridge running longitudinally on the medial surface of the anterior process (Fig. A3.11D), whereas a developed quadratojugal one is not present. The anterior end of the jugal forms part of the lateral margin of the lacrimal foramen.

Gekkota (Fig. A3.11E-K)

In gekkotans, the jugal is very different from the above-described morphology. In this group of squamates, this bone is straight in lateral view and slightly sigmoid shaped in dorsal view. The anterior end is dorsoventrally flattened, pointed and wider than the posterior one, whereas the latter is narrower and more robust. In *E. europaea*, the difference between the two ends is less marked (Fig. A3.11E-F). In *H. turcicus*, the lateral margin of the posterior end is folded in ventral direction and

gives a subcylindrical shape to the end (Fig. A3.11H).

Lacertidae (Fig. A3.11L-S)

In the jugal of lacertids, the anterior process can be narrow and pointed (most species; Fig. A3.11P-S), moderately large, flattened and more rounded anteriorly (A. erythrurus; Fig. A3.11L-M) or moderately large, flattened and anteriorly forked (O. elegans; Fig. A3.11N-O). The lateral surface of the anterior portion of this process is largely covered by the articulation surface with the posterior process of the maxilla (Fig. A3.11P, R), except for A.



Figure 2.8) Dorsal view of the right jugal of P. algirus (UAM.R.Ps9; A), T. lepidus (MDHC 216; B) and Anguis gr. A. fragilis (MDHC 102; C), displaying different developments of the medial process (white arrows): well developed (A), poorly developed/almost indistinct (B) and absent (C). Scale bars = 1 mm.

erythrurus and O. elegans in which this surface is narrow and the bone is more laterally exposed (Fig. A3.11L, N). In those species in which either a step or a spur are present on the dorsal margin of the posterior process of the maxilla (see above), the articulation surface on the jugal recalls the stepped and spurred morphology respectively. The palatal process is present: it is low developed in A. erythrurus (Fig. A3.11M), E. arguta and O. elegans (Fig. A3.11O) and moderately to well developed in other species (Fig. A3.11Q, S). A distinct medial process is present in O. elegans (Fig. A3.110) and *Psammodromus* (Fig. 2.8A, A3.11Q), but a little developed one (Fig. 2.8B) can be also present in other genera (e.g., *Podarcis*, as also reported by Blain et al. 2007). The posterodorsal process is narrow and pointed. Proportions of the anterior and posterodorsal processes differs within species: the anterior one is the longest in Algyroides, D. oxycephala, D. mosorensis, L. agilis, L. bilineata, L. schreiberi, L. viridis, O. elegans, P. siculus, P. tauricus, P. tiliguerta, P. waglerianus, P. algirus, Z. vivipara and some specimen of P. muralis (Fig. A3.11N-Q), the posterodorsal one is the longest in A. erythrurus and E. arguta (Fig. A3.11L-M), whereas they have roughly the same length in A. bedriagae, H. graeca, I. bonnali. I. cyreni, I. horvathi, I. monticola, L. trilineata, P. bocagei, P. filfolensis, Po. hispanicus, P. lilfordi, P. melisellensis, P. milensis, P. pityusensis, T. lepidus and some specimen of *P. muralis* (Fig. A3.11R-S). A certain degree of ontogenetic variation can, however, be present, as demonstrated by T. lepidus NHMW 625, a very young individual whose anterior process is clearly longer than the posterodorsal one (Fig. 2.9). The quadratojugal process can be absent (A. erythrurus and O. elegans; Fig. A3.11L-O), weakly developed (I. horvathi, P. pityusensis, P. tiliguerta and *P. algirus*; Fig. A3.11P-Q) or well developed (other species; Fig. A3.11R-S). Its development may vary during ontogeny, being more developed in juveniles and less developed in adults (e.g., *P. algirus*; Barahona & Barbadillo 1997). The lateral surface of the ventral portion of the bone can be covered, at least in large specimens, by a moderately to well-developed dermal ornamentation (absent in A. erythrurus,

Algyroides, *D. oxycephala*, *D. mosorensis*, *E. arguta*, *H. graeca*, *I. bonnali*, *I. cyreni*, *I. horvathi*, *I. monticola* and *O. elegans*). A moderately large foramen opens on the medial surface of the jugal, at the meeting point of the anterior and the posterodorsal processes

Scincidae (Fig. A3.11T-Y)

Scincids have very slender jugals. The anterior process is very thin and pointed, lacking a palatal process; its lateral surface is completely covered by the articulation surface with the posterior process of the maxilla. The posterodorsal process is more robust and has a truncated (*C. chalcides*, *C. striatus* and *T. aurata*; Fig. A3.11V-W), pointed (*C. bedriagai*) or rounded (*A. kitaibelii*, *C. ocellatus* and *O. punctatissimus*; Fig. A3.11T-U, X-Y) dorsal end. The length of the two processes is similar in *C. chalcides* (Fig. A3.11V-W), whereas in *C. ocellatus* and *O. punctatissimus* the posterodorsal process is roughly twice as long as the anterior one (Fig. A3.11X-Y) and in *A. kitaibelii*, *C. striatus* and *T. aurata* the former is slightly longer than the latter (Fig. A3.11T-U). There is no quadratojugal process. The row of foramina on the lateral surface is absent, but a single one pierces the bone at the meeting point of the two processes, opening both laterally and medially. In *O. puncatissimus*, the



Figure 2.9) Right jugal of NHMW 625, a young individual of T. lepidus, in medial view. Note the anterior process, which is longer than the posterodorsal one. Scale bar = 1 mm.
medial opening of this foramen is located more dorsally, roughly at mid-length of the posterodorsal process (Fig. A3.11Y).

Anguidae (Fig. A3.11Z-AC)

The jugals of European anguids are slender, similar in this regard to those of scincids. The thin anterior process has a narrow and laminar anterior end and bears a poorly developed palatal process. No medial process is present in Anguis gr. A. fragilis (Fig. 2.8C, A3.11AA), but a small hint of it is visible in *P. apodus* (Fig. A3.11AC). The articulation surface with the maxilla is twisted in ventral direction. The posterodorsal process is slender (but more robust than the anterior one) and has a rounded (Anguis gr. A. fragilis; Fig. A3.11Z-AA) or pointed (P. apodus; Fig. A3.11AB-AC) end; in Anguis gr. A. fragilis, it is very slightly shorter than the anterior process, whereas in *P. apodus* it is slightly longer than the latter. The quadratojugal process is present and distinctly developed in Anguis gr. A. fragilis (Fig. A3.11Z-AA), though it can be less marked in juveniles. *Pseudopus apodus*, on the other hand, shows a very little developed (almost absent) quadratojugal process (Fig. A3.11AB-AC). As in scincids, the row of foramina is replaced by a single foramen, opening by the meeting point of the processes. The lateral surface is smooth in Anguis gr. A. fragilis (Fig. A3.11Z), but presents an ornamentation made up by mild rugosities in *P. apodus* (Fig. A3.11AB).

Postfrontal and postorbital

Postfrontal and postorbital (Fig. A3.12) are paired bones that show a high variation in morphology throughout the groups of squamates here considered. They can be separate during the entire life of the animal, fuse during ontogeny or be present as a single element called postorbitofrontal. The latter can origin from early fusion of postfrontal and postorbital, but can also be the result of the loss of one of the two bones, as in many cases is not known if such loss occurs and which bone remains (see e.g., Jollie 1960, Evans 2008 and Daza & Bauer 2010).

Agamidae (Fig. A3.12A-B)

Laudakia stellio lacks a postfrontal (Jollie 1960; Evans 2008), but the postorbital is large and well developed. The latter has a subtriangular shape and is flattened, with only a very poorly developed concavity in ventral direction. The anterior margin of the bone is slightly concave, the medial one is moderately concave and the lateral one is roughly straight. All vertices are pointed. The anteromedial vertex shows the articulation surface with the anterolateral process of the parietal on its posterior surface (Fig. A3.12B) and that with the posterolateral process of the frontal on the anterior one (Fig. A3.12A). The lateral margin contacts the jugal and squamosal and articulation surfaces are visible by its anterior (Fig. A3.12A) and posterior (Fig. A3.12B) ends. No articulation surface with the ectopterygoid is recognizable on the anterior surface of the ventrolateral apex, suggesting the lack of a contact with this bone in contrast with other agamids (Evans 2008). Both dorsal and ventral surface are smooth, but the anterior margin is moderately swollen dorsally.

Chamaeleonidae (Fig. A3.12C-E)

As in agamids, chamaeleonids lack a postfrontal too, retaining only a large postorbital (Jollie 1960; Evans 2008). That of *C. chamaeleon* is composed of a roughly triangular, dorsoventrally developed and laminar posterior portion (Fig. A3.12C-D) and by a strongly mediolaterally expanded and laminar anterior process (Fig. A3.12E) developing from the anterodorsal corner of the triangle. In lateral view, the anterior margin is strongly concave, whereas the dorsal and the posteroventral ones are roughly straight. The anterior process contacts the parietal and the frontal medially and the prefrontal anteriorly through interdigitated sutures (Fig. A3.12E). The posterodorsal and the ventral corner of the triangular posterior portion (posterior and ventral processes, respectively) are pointed (Fig. A3.12C-D). The former contacts the squamosal posteroventrally, whereas the latter contacts the squamosal posteriorly and the jugal ventrally. A series of tubercles runs along the dorsolateral margin of the bone. An ornamentation consisting on smaller tubercles can be present also on the lateral and dorsal surfaces (Fig. A3.12C, E), but it is lacking in MNHN 1942-103 and 1887-875. The medial surface is smooth.

Gekkota (Fig. A3.12F-M)

A paired postorbitofrontal is present in gekkotans: this bone has been interpreted as the postfrontal by some authors (e.g. Jollie 1960, Evans 2008 and references therein), but Daza & Bauer (2010) recommended maintaining the term postorbitofrontal since there are no conclusive evidences about its origin. In E. europaea (Fig. A3.12F-G), H. turcicus (Fig. A3.12H-I) and M. kotschyi (Fig. A3.12J-K), it is a small V-shaped bone composed by two processes developed in anteromedial (anterior process) and posteromedial (posterior process) direction. That of T. mauritanica differs from this morphology because of the presence of a U-shaped medial margin and of a third laterally developed process, which gives it a shape that resembles a Y (Fig. A3.12L-M). The anterior and posterior processes have the same length in M. kotschvi, whereas the anterior one is longer than the posterior one in *E. europaea* and shorter than the posterior one in *H. turcicus* and in *T. mauritanica*. The anterior process is the narrowest in dorsal view and has a pointed end; its anterior (orbital) margin is slightly concave. The posterior process, which is wider in dorsal view, has a straight lateral margin (concave in T. mauritanica; Fig. A3.12L-M); its end is pointed in E. europaea (Fig. A3.12F-G), H. turcicus (Fig. A3.12H-I) and most specimens of M. kotschyi, more squared in MDHC 285 (Fig. A3.12J-K), and rounded in all specimens of T. mauritanica (Fig. A3.12L-M). In lateral view, the more robust process is the anterior one. Differences in width and thickness of the two processes are less marked in *E. europaea* (Fig. A3.12F-G). The lateral process of *T. mauritanica* is shorter than the other two processes (Fig. A3.12L-M); it is wide and has a pointed end. The lateral corner of the bone (the vertex of the V) is rounded in *E. europaea* (Fig. A3.12F-G) and H. turcicus (Fig. A3.12H-I) and pointed in M. kotschyi (Fig. A3.12J-K). Both ventral and dorsal surfaces are smooth; the dorsal one is also flattened. There is no postorbitofrontal lateral notch.

Lacertidae (Fig. A3.12N-X)

In lacertids, postfrontal and postorbital usually remain separated, but they fuse in older individuals in *A. nigropunctatus*, most species of *Lacerta*, *P. siculus* and *T*.

lepidus and form a postorbitofrontal (Fig. A3.12W-X) in *E. arguta*, *L. schreiberi*, Psammodromus and Z. vivipara. When free, the postfrontal is long, large and laminar, with two processes at the concave anterior end (Fig. A3.12N-S). The anteromedial process is long and pointed, its medial surface being the concave articulation surface with the frontal, whereas the anterolateral process is short (longer in L. agilis; Fig. A3.12N-O) and pointed. The anteromedial process is expanded in Lacerta (Fig. A3.12N-Q) and T. lepidus, at least in adults, whereas the anterolateral one is lacking in A. bedriagae, I. aurelioi, I. bonnali (present, however, in UAM.R.Lm28A), I. horvathi and O. elegans (Fig. A3.12R-S). On the ventral surface, a low ridge runs for the entire length of the bone near its lateral margin: the area located laterally to this ridge is the articulation surface with the postorbital (Fig. A3.12Q). The anterior end of the ridge curves medially and then again laterally, forming a V-shaped notch that houses the anteromedial process of the postorbital. The posterior end of the postfrontal can be poorly ossified. A dermal ornamentation is present on the dorsal surface of the bone (Fig. A3.12N, P). This ornamentation is moderately or well developed in all species, except for A. erythrurus, A. marchi, I. bonnali, I. horvathi and O. elegans (Fig. A3.12R). Traces left by supraocular scales can be visible. The free postorbital is L-shaped and narrow (Fig. A3.12T-V). It is composed by three pointed processes: the very short anteromedial process, the anterolateral process (usually the largest one) and the narrow posterior process (the longest one). The postorbital of D. oxycephala, I. aurelioi, I. bonnali, P. filfolensis and *P. pityusensis* lacks the anteromedial process (Fig. A3.12T). Barahona (1996) stated that this process is lacking in adults of L. bilineata (L. viridis in her text) too, but a moderately to well-developed one has been identified in all the herein-studied specimens, either juveniles or adults. It has to be noted that she incorrectly names the missing process as the anterolateral one in the main text, but then marks the anteromedial one in the figures. The anteromedial process can either be present and well developed or absent in L. trilineata. Both dorsal and ventral surfaces of the postorbital are usually smooth, but a dermal ornamentation can be sometimes present externally (e.g., *P. bocagei* UAM.R.PB48; Fig. A3.12U).

Scincidae (Fig. A3.12Y-AL)

Scincids have usually separate postfrontal and postorbital too, but Evans (2008) states that the postorbital may be reduced or lacking. The postorbital is present in Chalcides and O. punctatissimus, but it appears to be absent in A. kitaibelii and it has not been possible to to find it in the studied specimens of *T. aurata*; however, in the latter case, this may be also due to a loss during preparation rather than to an actual absence of the bone. The postfrontal is Y-shaped, with a laminar body, two pointed (rounded in O. punctatissimus; Fig. A3.12AE-AF) processes on the anterior corners and a concave anterior margin (Fig. A3.12Y-AH). In dorsal view, the body is slender and triangular in A. kitaibelii (Fig. A3.12Y-Z), slender and subrectangular in C. chalcides, C. striatus and O. punctatissimus (Fig. A3.12AA-AB, AE-AF), wider and laterally expanded in the posterior half in C. ocellatus (Fig. A3.12AC-AD), wider and provided with a moderately developed and pointed posterior projection by the posterolateral corner in T. aurata (Fig. A3.12AG-AH). A similar projection is present in O. punctatissimus too (Fig. A3.12AE-AF). Both the dorsal and the ventral surfaces are smooth, but a variable number of foramina can pierce the laminar body of the bone. In C. chalcides, the anterolateral process is moderately developed, similar in size and length to the anteromedial one and slightly curved posteriorly by its distal end (Fig. A3.12AA-AB). The anteromedial process is also moderately developed, but it is straight. Chalcides ocellatus and T. aurata, on the other hand, show a moderately large and long anteromedial process, which is longer than the anterolateral one (Fig. A3.12AC-AD, AG-AH). Moreover, in the latter species both processes are straight. Ablepharus kitaibelii, C. striatus and O. punctatissimus show a longer anteromedial process too, but it is more slender (Fig. A3.12Y-Z, AE-AF). The medial margin of the bone is distinctly dorsoventrally enlarged, forming a concave articulation surface for the contact with both the frontal and parietal, whereas the lateral one shows only a narrow articular surface housing the postorbital (or the posterodorsal process of the jugal, when the postorbital is absent). In *A. kitaibelii*, the concavity for the articulation with the frontal and parietal is very little developed and therefore the medial margin is not so much expanded. The posterior end of the bone can be irregular because of a lower degree of ossification. The postorbital (Fig. A3.12AI-AL) is an L-shaped and slender rod, with a short anterolateral process and a long posterior process. The distal end of both processes is pointed. In *C. ocellatus*, this bone is more robust than in the other species (Fig. A3.12AK-AL). The articulation surfaces with the postfrontal and the squamosal are recognizable in *C. ocellatus* and *O. punctatissimus*, on the medial side of the ventral surface and on the lateral side of the dorsal surface respectively.

Anguidae (Fig. A3.12AM-AQ)

Free postfrontal and postorbital are present in anguids. The former is roughly Tshaped in dorsal view, with a slightly concave anterior margin and a straight and slender body (Fig. A3.12AM-AP). In Anguis gr. A. fragilis, the body is roughly subrectangular, but its posterior end is usually poorly ossified and therefore it can appear more pointed (Fig. A3.12AM-AN). Pseudopus apodus, on the other hand, shows a triangular body with a pointed end in dorsal view (Fig. A3.12AO-AP). A long anteromedial process develops from the medial corner of the anterior margin: it is moderately (Anguis gr. A. fragilis; Fig. A3.12AM-AN) or distinctly (P. apodus; Fig. A3.12AO-AP) robust and roughly three times longer than the very short anterolateral process. A concave articulation surface is visible on both the medial and the lateral margins, continuing also on the posterior margin of the processes; the surfaces contact the frontal/parietal complex and the postorbital, respectively, and are less expanded in juveniles. Both the dorsal and ventral surfaces are smooth, but foramina can pierce the body of the bone. The postorbital (Fig. A3.12Q) is reduced to a medially concave and blade-like bone in anguids. It has smooth outer and inner surfaces and a laminar and pointed posterior process. The anterior end is more thickened and presents a small hint of the strongly reduced anterolateral process, bending anterolaterally. The development and the thickness of this latter process are

higher in *P. apodus* than in *Anguis* gr. *A. fragilis*. The concave medial surface articulates with the postfrontal, whereas a shallow concavity lodging the anterior end of the squamosal is barely visible laterally. As reported by Klembara et al. (2017), the postorbital can expand medially with a variably developed and laminar ossification in adults and subadults of *P. apodus* (Fig. A3.12Q).

Squamosal

The squamosal (Fig. A3.13) is a paired and anteroposteriorly elongated bone. An anterior process forms the anterior end, whereas the posterior portion can be composed by a single posterior process or by a ventrally developed quadrate process and a posterodorsally developed dorsal parietal process. The morphology of this bone is largely variable between different groups.

Agamidae (Fig. A3.13A-B)

The squamosal of *L. stellio* is large, roughly straight in lateral view and slightly medially concave. The anterior process is large and has a rounded tip. The dorsal margin of this process shows a large and concave articulation surface for the contact with jugal and postorbital (Fig. A3.13A). The posterior portion consists of a strongly dorsoventrally expanded dorsal parietal process, which forms a subtriangular structure whose posterior margin, the contact surface with the postparietal process of the parietal, is straight. A quadrate process is situated between the anterior and dorsal parietal processes. This third process is large and rounded and contacts the quadrate with a flattened articulation surface visible in medial view. A straight ridge is visible on the medial surface (Fig. A3.13B), which is otherwise smooth; it runs from the base of the dorsal parietal process to the tip of the quadrate process. A small and dorsomedially directed triangular expansion is present on the ridge, near the parietal process. The lateral surface is smooth.

Chamaeleonidae (Fig. A3.13C-D)

In *C. chamaeleon*, the squamosal presents a dorsal parietal process and a quadrate process as in agamids, but they are more distinct, giving a Y-like shape to the bone.

The anterior process is laminar and dorsoventrally expanded in lateral view; it contacts the postorbital anterodorsally and the jugal anteriorly. The quadrate process is rod-like and shows a medial expansion by its ventral end (Fig. A3.13D); this is the shortest branch of the bone and contacts the paroccipital process of the otooccipital medially and the quadrate ventrally. The slender dorsal parietal process is the longest branch; it is slightly curved in dorsal direction and has a rounded end contacting the posterior end of the parietal crest. The lateral surface of the bone is smooth, except for a few tubercles present on the dorsal margin of the anterior end of the dorsal parietal process (Fig. A3.13C). However, no tubercles are present on MNHN 1887-875.

Gekkota and Lacertidae (Fig. A3.13E-J)

The squamosal is small and morphologically similar in both European gekkotans and lacertids, resembling a small rod ventrally curved at the posterior end, which is represented by a single posterior process. The anterior process is pointed, whereas the posterior one is wider. The anterior process is shorter in gekkotans (Fig. A3.13E-F) than it is in lacertids (Fig. A3.13G-J). The posterior process is expanded in *Lacerta* (Fig. A3.13I-J), O. elegans, P. tauricus, P. tiliguerta, Psammodromus, some individuals of T. lepidus and a single specimen of P. muralis (namely, the large and probably old MDHC 311). It can present a dermal ornamentation on its dorsal surface in large individuals of L. bilineata, L. schreiberi and T. lepidus. Arribas and Odierna (2004) describe a triangular medial process that may frequently occur on the squamosal of *I. martinezricai*. Jollie (1960) states that the squamosal is absent in most gekkotans, but he writes also that the shape of their supratemporal is very similar to the squamosal of other lizards. This strong morphological similarity (which is also recognizable in the specimens herein studied) suggests that this bone is indeed the squamosal, as supported also by other authors (see Evans 2008, Daza & Bauer 2012 and references therein). Pygopodidae and Carphodactylidae share an expanded squamosal with a medially directed process posteriorly that differs significantly from the one of other gekkotans, but this is considered a putative synapomorphy of the clade including them (Daza & Bauer 2012).

Scincidae and Anguidae (Fig. A3.13K-P)

The squamosal of scincids and anguids is similar to that of gekkotans and lacertids in shape, but it is larger and its anterior process is very long. In scincids (Fig. A3.13K-L), the anterior end is pointed, whereas in anguids it is a flattened lamina (Fig. A3.13M-P). *Anguis* gr. *A. fragilis* has a rounded and subhorizontal end (Fig. A3.13M-N), whereas in *P. apodus* it is pointed and more dorsally concave (Fig. A3.13O-P).

Quadrate

The paired quadrate (Fig. A3.14) is composed of a posteriorly curved pillar structure and a strongly posteriorly concave osseous lamina, which develops laterally from the anterior margin of the pillar forming a large and deep conch. The lateral margin of the conch is defined by the tympanic crest, a slightly expanded portion of the lamina. Another similar but much smaller lamina can be present on the medial side of the pillar, developing in anteromedial direction. The ends of the pillar are represented by the cephalic condyle dorsally and by the mandibular condyle ventrally. The cephalic condyle is dorsally flattened, whereas the mandibular one is divided into two portions by a concavity. Laterally to the cephalic condyle, a foramen for the chorda tympani nerve can be visible in dorsal view; in many cases, however, this portion of the lateral lamina is poorly ossified and presents a more or less developed squamosal notch. The quadrate foramen pierces the lateral lamina dorsally to the mandibular condyle; sometimes the foramina are two, whereas in some cases no opening is visible.

Agamidae (Fig. A3.14A-B)

The quadrate of *L. stellio* is quadrangular and mediolaterally expanded in anterior view. The conch is not strongly concave (Fig. A3.14B), since the well-developed lateral lamina bends posteriorly only in its dorsal part. A very well-developed medial

lamina is present, but it is more expanded in its dorsal portion. In juveniles, only the latter portion of the medial lamina is visible. In posterior view, the mandibular condyle is strongly larger than the cephalic one and so the pillar resembles an elongated triangle (Fig. A3.14B). The cephalic condyle is strongly expanded in an anteromedial to posterolateral direction and presents a rectangular, elongated and flattened articular surface dorsally (Fig. A3.14B). The medial portion of the mandibular condyle is more developed than the lateral one. A large and deep squamosal notch is present laterally to the cephalic condyle and so the foramen for the chorda tympani nerve is not visible.

The maximum length of the quadrate ranges from 2 mm to 6 mm.

Chamaeleonidae (Fig. A3.14C-D)

No conch and no medial lamina are present in the quadrate of *C. chamaeleon*, which consists only of a straight pillar. Therefore, the bone turns up to be roughly rod-like in shape, with an anteroposteriorly compressed appearance and a dorsal end that is larger than the ventral one. The cephalic condyle is subdivided into three portions: an oval-shaped (in dorsal view) and dorsally flat articular surface contacting the quadrate process of the squamosal, a small lateral head embracing laterally the same process and a larger and thicker medial head contacting the paroccipital process of the otooccipital. The mandibular condyle is rather flattened, since its concavity is poorly developed. The anterior surface of the bone is flat or concave (Fig. A3.14C), whereas the posterior one is slightly convex (Fig. A3.14D). A foramen can be present on the posterior surface, on the base of the medial head of the cephalic condyle. The maximum length of the bone ranges from 6.9 mm to 10 mm.

Gekkota (Fig. A3.14E-L)

In gekkotans, there is no lamina medially to the narrow pillar and so the latter forms the straight medial margin of the bone. In anterior view, the general outline of the bone is strongly rounded laterally, giving it a roughly bean-like shape. The only exception is *E. europaea* (Fig. A3.14E-F), in which the bone is rather straight (anterodorsally elongated) in anterior view, forming a narrower conch than in other

species. Nevertheless, Paluh et al. (2018) recently demonstrated that the shape of this bone is significantly dependent on ontogeny in at least *H. turcicus*, with younger individuals showing a narrower and shallower conch. The bone is also rounded anteriorly in lateral view. In *M. kotschyi*, the tympanic crest is slightly thicker near the ventral end of the bone (Fig. A3.14J), whereas in the other species there are no clear differences in thickness. The cephalic condyle is not significantly expanded to the sides. Laterally to it, the lateral lamina is scarcely ossified and presents a variably wide and deep squamosal notch; the foramen for the chorda tympani nerve is therefore not visible in these lizards. The lateral portion of the mandibular condyle is more developed than the medial one.

The maximum length of the quadrate ranges from 2.5 mm to 3 mm in *E. europaea*, from 2.9 mm to 4 mm in *H. turcicus*, from 3 mm to 3.9 mm in *M. kotschyi* and from 4.6 mm to 6.3 mm in *T. mauritanica*.

Lacertidae (Fig. A3.14M-U)

The quadrate of lacertids is roughly straight and rectangular in anterior view. In medial view, its outline is rounded (Fig. A3.14R, U), except for *A. erythrurus, E. arguta* and *O. elegans*, in which it is more angular (Fig. A3.14O). The medial lamina is present and moderately developed; it shows an alar expansion (the pterygoid flange) near the ventral end of the bone. The flange is usually poorly developed in juveniles and more developed in adults. Nevertheless, adults of *A. erythrurus* and *Ps. hispanicus* (and sometimes of *I. bonnali*, *I. cyreni* and *I. monticola* too) retain a little developed flange (Fig. A3.14M-N), whereas the latter is well developed in both juveniles and adults in some members of the genus *Podarcis* (e.g., *P. bocagei*, *P. carbonelli*, *Po. hispanicus* and *P. muralis*; Fig. A3.14P-Q). On the dorsal half of the anterior surface of the lateral lamina there is a flat platform, which is distinctly concave in adults of *T. lepidus* (Fig. A3.14S). The margins of the platform are often marked by low ridges, which can be absent in juveniles. The cephalic condyle is posteroventrally expanded and subelliptical in dorsal view. A variably developed squamosal notch is present in juveniles, but in adults this portion of the lamina can

be more ossified and the foramen for the chorda tympani nerve is recognizable. The medial portion of the mandibular condyle is slightly more ventrally developed than the lateral one.

Species	Maximum length
	of the quadrate
A. erythrurus	3.2 mm - 3.6 mm
A. fitzingeri	1.8 mm - 1.9 mm
A. marchi	2 mm
A. moreoticus	2.3 mm
A. nigropunctatus	2.9 mm - 3.7 mm
A. bedriagae	3 mm - 4 mm
D. oxycephala	2.5 mm - 3.5 mm
D. mosorensis	3 mm - 3.3 mm
E. arguta	5 mm
H. graeca	2.9 mm - 3.7 mm
I. bonnali	2.5 mm - 2.6 mm
I. cyreni	3.3 mm - 3.4 mm
I. horvathi	2.5 mm
I. monticola	3 mm - 3.1 mm
L. agilis	3.5 mm - 3.9 mm
L. bilineata	2.8 mm - 5.8 mm
L. schreiberi	4.6 mm - 4.8 mm
L. trilineata	5.8 mm - 7.4 mm
L. viridis	6 mm - 6.6 mm
O. elegans	2 mm - 2.4 mm
P. bocagei	2.8 mm - 2.9 mm
P. filfolensis	3 mm
Po. hispanicus	2.4 mm - 2.8 mm

Maximum length is given in the following table:

P. lilfordi	3 mm - 3.3 mm
P. melisellensis	2.1 mm - 3.3 mm
P. muralis	2.2 mm - 3.3 mm
P. milensis	3.1 mm
P. pityusensis	Not measured
P. siculus	2.6 mm - 3.9 mm
P. tauricus	3 mm - 3.1 mm
P. tiliguerta	2.8 mm - 3 mm
P. waglerianus	3.5 mm - 4 mm
P. algirus	3.5 mm - 4 mm
T. lepidus	2.6 mm - 11 mm
Z. vivipara	2.3 mm - 2.6 mm

Scincidae (Fig. A3.14V-AG)

In scincids, the general shape of the quadrate resembles that of the ones of lacertids, with a straight and subrectangular aspect in anterior view and a rounded outline in medial view. The quadrates of A. kitaibelii, C. chalcides, C. striatus and O. punctatissimus are narrow in anterior view (Fig. A3.14V-W, AB-AC), whereas those of C. ocellatus and T. aurata are wider (Fig. A3.14Y-Z, AE-AF). The former species show a hint of the medial lamina, but the pterygoid flange is absent. The medial lamina, on the other hand, is moderately developed in T. aurata (Fig. A3.14AE-AF) and well developed in C. ocellatus (Fig. A3.14Y-Z), but still without a pterygoid flange. Ophiomorus punctatissimus displays a low lateral lamina, which is less developed than in other species and does not originate a deep conch (Fig. A3.14AB-AC). An anterodorsally convex osseous swelling is present on the dorsal half of the lateral lamina in C. ocellatus and O. punctatissimus (Fig. A3.14Y, AA-AB, AD). In the former species, a low ridge runs in dorsoventral direction medially to the swelling (Fig. A3.14Y), ending by the middle of the height of the bone. Both the swelling and the ridge are less developed in smaller specimens of C. ocellatus. When it is well developed, the ventral margin of the swelling overhangs anteriorly. These structures

are absent in the other species, whose anterior surface is smooth. Except for *O*. *punctatissimus*, the cephalic condyle is slightly expanded to the sides. In *O*. *punctatissimus*, on the other hand, the condyle is strongly expanded posteroventrally, giving a strongly posteriorly concave shape to the quadrate (Fig. A3.14AD). The mandibular condyle presents similar-sized portions in all species. The presence of a squamosal notch and the degree of completeness of the foramen for the chorda tympani nerve are similar to the lacertid scheme, with a very large and deep squamosal notch present in juveniles and adults of smaller species (e.g., *C. chalcides* and *C. striatus*) and a completely recognizable foramen in adults of larger ones (e.g., *C. ocellatus*). *Ablepharus kitabelii* and *O. punctatissimus*, however, are exceptions, since they can show a closed foramen despite representing very small species.

Species	Maximum length of the quadrate
A. kitaibelii	1.5 mm - 1.7 mm
C. chalcides	2.9 mm - 3.1 mm
C. ocellatus	4 mm - 5 mm
C. striatus	2.9 mm - 3 mm
O. punctatissimus	1.6 mm
T. aurata	4.5 mm - 4.6 mm

Anguidae (Fig. A3.14AH-AM)

The quadrate of European anguids is a straight and subrectangular bone in anterior view. It lacks a real conch, since only a very low to moderately developed lamina is present along the lateral margin of the pillar; its degree of development is higher in *P. apodus* (Fig. A3.14AK-AL) than in *Anguis* gr. *A. fragilis* (Fig. A3.14AH-AI). A similar-sized or slightly more developed lamina is present on the medial side of the bone, developing a small pterygoid flange near its ventral end (less recognizable in

P. apodus and in juveniles of *Anguis* gr. *A. fragilis*). The cephalic condyle is very strongly expanded both posteriorly and anteriorly and so the bone appears very wide in its dorsal portion in lateral view. In *Anguis* gr. *A. fragilis*, the anterior expansion tends to bend ventrally, creating an anterodorsally directed articulation surface with a rounded outline in lateral view (Fig. A3.14AJ). In *P. apodus*, the same expansion does not bend ventrally and the anterior outline of the bone appears angular in lateral view (Fig. A3.14AM). The posterior expansion is straighter, in lateral view, and slightly wider in dorsal view. A ridge runs ventrally from the expansion along the posterior surface of the pillar body of the bone. The mandibular condyle is moderately wide in posterior view and its portions are poorly ventrally developed and similar in size. Even if the lateral lamina is not much developed, a small (*Anguis* gr. *A. fragilis*) or deep (*P. apodus*) notch on the lateral side of the cephalic condyle is still recognizable in dorsal view: this can be a remnant of the foramen for the chorda tympani nerve.

The maximum length varies from 1.9 mm to 2.7 mm in *Anguis* gr. *A. fragilis* and from 6.5 mm to 7.8 mm in *P. apodus*.

Epipterygoid

The epipterygoid (Fig. A3.15) is a rod-like paired bone.

Agamidae (Fig. A3.15A)

The ventral end of the epipterygoid of *L. stellio* is strongly larger than the dorsal one. In lateral view, this bone is distinctly concave in anterior direction, since the dorsal end bends anteriorly.

Chamaeleonidae

The epipterygoid is not present in chamaeleonids (Evans 2008).

Gekkota (Fig. A3.15B)

In gekkotans, this bone is straight. Its dorsal end is slightly larger than the ventral one.

Lacertidae (Fig. A3.15C)

The epipterygoid of lacertids curves posteriorly in its dorsal portion. The ventral end is rounded and slightly larger than the dorsal one.

Scincidae (Fig. A3.15D-E)

Scincids have a short and straight epipterygoid, with a rounded ventral end that is distinctly larger than the dorsal one. The dorsal end of the epipterygoid of *O*. *punctatissimus* curves very slightly in posterior direction (Fig. A3.15E).

Anguidae (Fig. A3.15F)

This bone is slightly arched, moderately robust and slightly twisted in anguids, with similar-sized dorsal and ventral ends. The one of *P. apodus* can display a small posterior process and a low posteroventral crest on the posterior surface (see Klembara et al. 2017).

Vomer

The paired vomers (Fig. A3.16) are laminar and dorsally concave bones, with an anteroposteriorly elongated shape. Their anterior end is pointed, whereas the posterior one is wider. The lateral margin of the anterior half bears a notch, marking the medial margin of the vomeronasal fenestra.

Agamidae (Fig. A3.16A-B)

Laudakia stellio has small and laminar vomers, with a short flange-like expansion in the middle of its lateral margin. The anterior end is rounded, whereas the posterior border is irregular and bears laterally a pointed posterior process that fits in the vomerine process of the palatine (Fig. A3.16B).

Chamaeleonidae (Fig. A3.16C-E)

Vomers of *C. chamaeleon* are fused in an unpaired, laminar and slender bone, which is subrectangular in shape and can be pierced by foramina. The notch of the vomeronasal fenestra is wide but shallow (Fig. A3.16C-D). Posteriorly to it, the lateral margins of the vomer are straight. The anterior end is rounded in ventral view and displays the concave articulation surface with the maxilla anteriorly. The posterior end is forked, provided with either two divergent and pointed posterior

projections separated by a wide V-shaped notch (Fig. A3.16E) or two laminar tabs with a wavy posterior margin and a small U-shaped notch between them (Fig. A3.16C-D). Its ventral surface is distinctly concave, whereas the dorsal one is convex.

Gekkota (Fig. A3.16F-M)

The posterior end of the vomers of gekkotans is only slightly wider than the anterior one and it can be rounded or more squared. The notch of the vomeronasal fenestra is very poorly developed and so the lateral margin is convex. The articulation surface with the palatal process of the premaxilla is clearly visible on the anterolateral margin of the anterior end. The anterior end of the vomers of *E. europaea*, moreover, can be pierced by a teardrop-shaped notch (Fig. A3.16F-G). A well developed, pointed, posterodorsally directed process as long as two thirds of the vomer is present in the middle of the lateral margin. In E. europaea and M. kotschyi, the process is concave in medial direction (Fig. A3.16G, K), whereas the concavity cannot be clearly seen in *H. turcicus* and *T. mauritanica*, in which the process is notably thicker in the distal portion (Fig. A3.16I, M). The process of E. europaea is also very wide (Fig. A3.16F-G). In dorsal view, the articulation surface with the vomerine process of the palatine is visible ventrally to the process, bordered by low ridges both ventrally and dorsally in E. europaea (Fig. A3.16G) and H. turcicus (Fig. A3.16I) and only ventrally in T. mauritanica (Fig. A3.16M). The articulation surface is not clearly recognizable in M. kotschyi (Fig. A3.16K), in which only the dorsal ridge is visible, marking the ventral margin of the posterodorsal process. A transverse septum (barely visible in T. mauritanica; Fig. A3.16M) divides the dorsal surface into two sunken regions: the smaller vomeronasal region anteriorly and the nasal one, twice as long as the former, posteriorly. The septum corresponds on the ventral surface to a slightly sunken transverse area (barely recognizable in T. mauritanica; Fig. A3.16L). A very low longitudinal ridge is present on the dorsal surface of the vomers of *E. europaea*, running from the septum up to the articulation surface with the vomerine process of the palatine.

Lacertidae (Fig. A3.16N-Q)

Vomers of lacertids are very much larger in their posterior half (which is laterally rounded in dorsal view) than in the anterior one (which is straight). Acanthodactylus erythrurus, O. elegans and Psammodromus show a lower difference in width between the two portions; the two former species have also a more angular lateral margin of the posterior half (Fig. A3.16N-O). A wide and deep notch for the vomeronasal fenestra separates the two portions. The posterior end is usually bifurcated, because of the presence of two posteriorly developed and pointed processes: the medial one is usually the longest one, but variation may occur. The dorsal surface of this end is the articulation surface with the vomerine process of the palatine, whose anterior margin can be marked by a very low and arched ridge (Fig. A3.16P). A well-developed longitudinal ridge runs along the medial margin of the dorsal surface of the bone. A deep lacrimal groove runs longitudinally along the ventral surface of the anterior half of the bone, otherwise smooth. By the posterior end of such groove there is a large foramen, which opens on the dorsal surface in a moderately wide and posteriorly directed cavity. Another groove, bending medially by its anterior end, is present on the dorsal surface, roughly in the middle of the anterior half. A very small foramen connects this second groove with the cavity in which the former foramen opens.

Scincidae (Fig. A3.16R-Y)

In European scincids, the vomers are usually fused in a single, unpaired element, which reaches its maximum width at mid-length (Fig. A3.16R-U). Only *T. aurata* and *O. punctatissimus* show separate vomers (Fig. A3.16V-Y). The posterior end has roughly the same width as the anterior one. In dorsal view, the lateral margin of the posterior half is straight, whereas the notch on that of the anterior one is moderately deep. Each lateral margin of the anterior end clearly shows a concave articulation surface for the contact with the palatal process of the premaxilla (very little developed in *A. kitaibelii*), whereas the contact surface with the incisive process is recognizable on the anterior tip of the bone. A posterodorsally directed process is

present, as in gekkotans, but, because of the narrowing of the posterior end (which develops a pointed or rounded medial tip, similar to the medial posterior process of lacertids), this process is slightly shifted medially compared to the one of gekkotans and tends to partially cover the latter in dorsal view. The process is moderately wide, laminar and posteriorly truncated; its ridge-like ventral margin marks dorsally the surface that houses the vomerine process of the palatine. It is very little developed, almost absent, in A. kitaibelii (Fig. A3.16R). A small and narrow notch separates the posterior tips of the two fused vomers. Three well-developed ridges are present on the dorsal surface of the fused complex of bones: a longitudinal one running along its midline and two transverse ones located at mid-length. The latter start from each lateral margin, but reaches the former only in T. aurata (Fig. A3.16X), in which the channel separating them appears as an anteroposteriorly directed foramen. The transverse ridges are well developed in A. kitaibelii, C. chalcides, C. striatus and T. aurata (Fig. A3.16R, X), low in C. ocellatus (Fig. A3.16T) and almost indistinct in O. punctatissimus (Fig. A3.16V). Dorsally, the two portions of the longitudinal ridge (one for each vomer) may remain unfused. With the exception of A. kitaibelii and O. punctatissimus (Fig. A3.16R, V), two other low (very low in C. striatus) and transverse ridges are visible roughly by the middle of the notch of the vomeronasal foramen, located on both sides of the longitudinal one and touching them medially (Fig. A3.16T, X). The ventral surface is smooth, except for a wide groove located along the midline and two symmetrical foramina located near the anterior end. The ventral groove can house some other foramina too. Ablepharus kitaibelii lacks the two foramina and the posterior end of its groove is closed ventrally by osseous expansions of the margins (Fig. A3.16S). Ophiomorus punctatissimus lacks any sign of ventral groove (Fig. A3.16W), but some foramina are present near the anterior end.

Anguidae (Fig. A3.16Z-AB)

In European anguids, the anterior end of the vomer is squared in dorsal view and it is wider than the rounded posterior one. The notch of the vomeronasal fenestra is

shallow. Posteriorly to it, the lateral margin is convex, whereas the medial one is straight in dorsal view. The convexity of the lateral margin is more marked in Anguis gr. A. fragilis (Fig. A3.16Z) than in P. apodus (Fig. A3.16AB). Anteriorly, a groovelike structure contacting the vomerine process of the premaxilla is present on the anterior margin. A small osseous expansion is also present on the dorsal surface of the bone, near the anterior end (Fig. A3.16Z, AB), marking another, anterolaterally directed groove. As in gekkotans and scincids, there is a wide posterodorsally directed process on the lateral side of the posterior end, marking the deep articulation surface for the vomerine process of the palatine with a ridge-like ventral margin. In anguids, this process is shifted medially as in scincids and presents a well-developed notch by its posterior end. The strongly concave dorsal surface of the vomer is crossed near the middle by a complex of ridges and grooves. In Anguis gr. A. fragilis, a well-developed ridge extends from the lateral surface of the concavity, almost reaching another low ridge developed from the medial one (Fig. A3.16Z); these ridges are separated by a groove and a second one is visible dorsomedially to the medial ridge, running anterolaterally. A foramen pierces the bone by the base of the lateral ridge, sometimes continuing posteriorly in a groove. In P. apodus, the medial ridge is absent, leaving only a well-developed and posterodorsally concave lateral one (Fig. A3.16AB). A flattened surface visible in medial view on the anterior half of the bone is the contact surface with the other vomer. The ventral surface is smooth, except for a low longitudinal ridge in the middle. Some vomerine teeth can be present on the ventral surface of the posterior portion in *P. apodus* (see Klembara et al. 2017)

Septomaxilla

The septomaxilla (Fig. A3.17) is a small, laminar and paired bone, whose morphology varies within the different groups.

Agamidae

In *L. stellio*, the septomaxilla is rectangular and anteroposteriorly elongated in dorsal view. All margins are rather straight, but a shallow concavity is present on the

posterior one. Small and pointed processes are present at the four corners of the bone: two are directed anteriorly and the other two posteriorly.

Chamaeleonidae

The septomaxilla is lacking in chamaeleons (Jollie 1960; Evans 2008; Anderson & Higham 2013).

Gekkota (Fig. A3.17A-P)

The septomaxilla of European gekkotans is rectangular in dorsal view, elongated anteroposteriorly and ventrally concave. Two low ridges with irregular dorsal margins run on the dorsal surface, along the lateral and medial margins. In E. *europaea* and *T. mauritanica*, the morphology of one of the two ridges (the lateral and the medial one, respectively) is different, being very high at the posterior end and tending to sharply lower anteriorly (Fig. A3.17C-D, O-P); in the latter species, moreover, both ridges have a regular dorsal margin (Fig. A3.17O-P). In T. mauritanica, the medial ridge is fused with the lamina only in the posterior half and a moderately deep groove is visible on the base of its medial surface, continuing anteriorly in the space between the unfused half of the ridge and the lamina (Fig. A3.17P). Such a groove is visible also in some specimen of *H. turcicus* (Fig. A3.17H) but not in E. europaea (Fig. A3.17D), whereas in M. kotschyi the medial surface of the medial ridge is only concave and does not show clear grooves (Fig. A3.17L). On the ventral surface, an arched ridge starts from the posteromedial corner and develops in anterolateral direction, continuing on the anterior margin of a short and laterally directed triangular process placed in the posterior third of the bone. This process is posteriorly concave. From the posterolateral corner, a thin (moderately robust in T. *mauritanica*; Fig. A3.17M-P) lateral process develops in posterior direction; it is roughly as long as the lamina in E. europaea, H. turcicus and M. kotschyi (Fig. A3.17A-L) and longer than it in T. mauritanica (Fig. A3.17M-P). In E. europaea and *M. kotschyi*, this process is clearly hook-shaped, since its posterior end curves dorsally and laterally (Fig. A3.17A-D, I-L); in the other two species, the hook-shape is less recognizable (Fig. A3.17E-H, M-P). By the posteromedial corner, one can see

another thin, pointed and posteriorly directed process, which is roughly two thirds (*H. turcicus*; Fig. A3.17E-F) or one half (*E. europaea* and *T. mauritanica*; Fig. A3.17A-B, M-N) as long as the lateral process. Only a very small hint of the medial process can be seen in *M. kotschyi* (Fig. A3.17I-J).

Lacertidae (Fig. A3.17R-W)

In lacertids, the septomaxilla is short and ventrally concave, with a roughly squared shape in dorsal view. The anterior end develops an anteroventrally directed and subtriangular expansion, whereas a pointed posteromedial process develops in posterior direction from the medial corner of the posterior end. The posteromedial process is lacking in A. erythrurus and O. elegans (Fig. A3.17V-W), short in A. marchi, A. moreoticus, A. bedriagae and I. bonnali (Fig. A3.17R-S) and moderately long in the other species (Fig. A3.17T-U). The lateral margin of the bone is characterized by two processes: the anterolateral one is narrow and roughly pointed, whereas the posterolateral one is wide and roughly quadrangular. The former develops dorsally (anterodorsally in A. erythrurus, O. elegans and Psammodromus; Fig. A3.17V), whereas the latter is directed laterally. The tip of the posterolateral process is more angular in A. erythrurus and O. elegans (Fig. A3.17V-W) than in other species (Fig. A3.17R-U). A small and irregular ridge is present on the anterior half of the medial margin of the septomaxilla, developing in dorsal direction. The base of this ridge can be pierced by an anteroposteriorly directed canal. Both the dorsal and the ventral surface of the bone are smooth.

Scincidae (Fig. A3.17X-AA)

Scincids have a septomaxilla that is morphologically similar to the one of lacertids, but lacks the anteroventral expansion of the anterior end. A small ventral expansion, however, is present on the posterior margin in *Chalcides* (Fig. A3.17Z-AA). Moreover, in scincids, the posterolateral process is usually more rounded than in lacertids. The same process is more developed in *C. ocellatus* (Fig. A3.17Z-AA) than in *A. kitaibelii, C. chalcides, C. striatus* and *O. punctatissimus* (Fig. A3.17X-Y). Another difference with the septomaxilla of lacertids is the greater development in

posterior direction of the dorsally developed ridge of the medial margin, which reaches the long posteromedial process in *C. ocellatus* (Fig. A3.17Z). This is not true, however, for *A. kitaibelii* (Fig. A3.17X). On the ventral surface, a low and arched ridge runs along the anterior and lateral margins of the bone. Near the anteromedial corner of the bone, this ridge forks.

Anguidae (Fig. A3.17AB-AE)

The general morphology of the septomaxilla of anguids is similar to the one showed by lacertids. The posteromedial process is very short in adults of *Anguis* gr. *A. fragilis* (Fig. A3.17AB-AC; slightly longer in juveniles), but distinctly longer in *P. apodus* (Fig. A3.17AD-AE). The anterolateral one is not distinctly developed, in particular in *P. apodus*, whose septomaxilla has a subtriangular aspect in dorsal view (Fig. A3.17AD-AE). The posterolateral process bends dorsally and, in *P. apodus*, gains a pointed shape in dorsal view. In some features, however, this bone resembles scincids: these features are the greater posterior development of the ridge on the medial margin and the presence of the arched ridge on the ventral surface (which appears to be more developed in anguids).

Palatine

The paired palatine (Fig. A3.18) is an anteroposteriorly elongated bone composed of three processes: the vomerine, maxillary and pterygoid processes, developed in anterior, lateral and posterior direction respectively. The pterygoid process is always the longest one. On the dorsal surface of the bone, a palatine ridge runs transversely between the vomerine and maxillary processes, separating them, whereas the ventral surface of the palatine is characterized by the presence of the choanal duct. The maxillary process is pierced by the wide infraorbital foramen. Palatine teeth can be present on the ventral surface of the pterygoid process.

Agamidae (Fig. A3.18A-B)

In *L. stellio*, the palatine has a rectangular shape and a massive, dorsally concave and subtrapezoidal vomerine process, whose margins are highly irregular. A triangular

notch is present on the anterior margin of the latter process. The maxillary process is robust, moderately developed and subrectangular. Its posterolateral corner strongly extends posterolaterally, with a long and slender projection, and its lateral surface is the articulation surface with the maxilla. A moderately deep notch marking the medial margin of the infraorbital foramen is visible on the distal end of the maxillary process. The pterygoid process is wide and has a straight lateral margin and a slightly convex medial one. The posterior margin, on the other hand, shows a shallow concavity. The choanal duct is moderately narrow and reduced to the anterior part of the bone (Fig. A3.18B). There are no palatine teeth.

Chamaeleonidae (Fig. A3.18C-D)

Palatines of *C. chamaeleon* are roughly subtrapezoidal in shape. The roughly subrectangular and thin vomerine process is longer and narrower than the maxillary one. The articulation surface with the vomer is recognizable anteroventrally, whereas the one with the vomerine process of the other palatine is visible medially. This latter suture is strongly interdigitated. The maxillary process is short and wide; the articulation surface with the maxillary shelf is clearly visible in ventral view (Fig. A3.18D). The pterygoid process is large and has smooth dorsal and ventral surfaces, without palatine teeth. A foramen is visible at mid-length, near the medial margin of the process. The contact surface with the pterygoid is located posteromedially and is represented by a long and oblique suture. The palatine ridge is short and stocky and shows a large articulation surface with some low interdigitations dorsally (Fig. A3.18C; this is the articulation surface with the prefrontal). The choanal duct is moderately narrow, roughly covering a third of the ventral surface of the bone (Fig. A3.18D). The infraorbital foramen is not present since the palatine is excluded from its formation by the prefrontal and the jugal.

Gekkota (Fig. A3.18E-L)

The morphology of the palatine of European gekkotans is different from the standard one described above. In these animals, the pterygoid process is represented by a subquadrangular (more rounded in *E. europaea*; Fig. A3.18E-F) and thin lamina,

whereas the vomerine and maxillary processes are slender, pointed and anteroventrally developed. These two processes develop from the anteromedial and the anterolateral corners of the lamina respectively and they define the lateral walls of the choanal duct, which is continued on the ventral surface of the lamina by a very shallow trough. The vomerine process is more robust and slightly longer than the maxillary one. On the lateral surface of the maxillary process of *H. turcicus* and *T. mauritanica*, one can recognize the articulation surface with the maxilla (Fig. A3.18G-H, K-L). In *E. europaea* and *H. turcicus*, a small osseous expansion projects near the base the maxillary process, forming a small, subtriangular and thin process (Fig. A3.18E-H). Usually, *M. kotschyi* does not display this expansion (Fig. A3.18I-J), but sometimes a very small hint of it can be present. Roughly in the same position, the palatines of *T. mauritanica* show a wide foramen not closed laterally, the margins of which are formed by osseous expansions of the lateral margin (Fig. A3.18K-L); this foramen could represent the interorbital foramen, otherwise not recognizable in the palatines of gekkotans. No palatine ridge or palatine teeth are present.

Lacertidae (Fig. A3.18M-P)

The vomerine process of the palatine of lacertids is dorsally concave, moderately long, moderately large and shows a pointed anterior projection. The projection is well developed in *Algyroides*, *A. bedriagae*, *D. oxycephala*, *D. mosorensis*, *H. graeca*, *I. bonnali*, *I. cyreni*, *I. monticola*, *O. elegans*, *P. bocagei*, *P. carbonelli*, *Po. hispanicus*, *P. lilfordi*, *P. melisellensis*, *P. muralis*, *P. pityusensis*, *P. siculus*, *P. tiliguerta* and *Z. vivipara* (Fig. A3.18O-P) and poorly developed in other species (Fig. A3.18M-N); according to Barahona (1996), it is absent in *L. bilineata* (*L. viridis* in her text), but a well-developed one was present in at least some of the herein studied specimens. The maxillary process is moderately long, wide, laminar and subtrapezoidal, with a pointed corner that develops posterolaterally; its anterolateral margin is strongly oblique in all species (Fig. A3.18O-P), except for *A. erythrurus* and *O. elegans*, in which the inclination is distinctly less marked (Fig. A3.18M-N). The infraorbital foramen is wide and is flanked medially by an anteriorly directed

and moderately developed lappet, which is located on the ventral surface of the bone. The pterygoid process is long, moderately wide and subrectangular, with slightly convergent lateral and medial margins. The posterior end, contacting the pterygoid, shows a V-shaped notch in the middle, flanked by two pointed projections. The size of these projections is usually similar, but they can undergo a significant individual variation. The palatine ridge is well developed and projects anterodorsally with a short laminar expansion. The choanal duct is very wide, occupying almost the entire ventral surface of the bone. There are no palatine teeth.

Scincidae (Fig. A3.18Q-X)

The most distinctive feature of the palatine of scincids is a strongly gutter-like shape in ventral view, due to the fact that both medial and lateral margins can develop laminar expansions that envelop the choanal duct (incipient secondary palate sensu Caputo 1991). The latter appears therefore very deep. The expansion of the medial margin is absent in A. kitaibelii snd T. aurata (Fig. A3.18Q-R, W-X) and poorly developed and ventrolaterally directed in Chalcides and O. punctatissimus (Fig. A3.18S-V); its medial surface is the articulation surface with the opposite palatine. This expansion continues anteriorly in the dorsally concave (less concave in O. *punctatissimus*) vomerine process, which is short and small in C. chalcides, C. striatus and O. punctatissimus (Fig. A3.18S-V), long and narrow in A. kitaibelii and C. ocellatus (Fig. A3.18Q-R) and long and wider in *T.aurata* (Fig. A3.18W-X). The anterior projection is not well individualized in *Chalcides* (Fig. A3.18S-T), slightly more recognisable in A. kitaibelii and T. aurata (Fig. A3.18Q-R, W-X) and distinctly recognisable in O. punctatissimus (Fig. A3.18U-V). The expansion of the lateral margin is directed ventromedially and very well developed, approaching the opposite one. Ablepharus kitaibelii and T. aurata show the maximum development of this lamina, which almost touches the medial margin of the bone in these two species (Fig. A3.18Q-R, W-X). The ventral surface of the expansion is smooth and its anterior end projects beyond the anterior margin of the bone and the anterior end of the vomerine process, being therefore visible in dorsal view too as a triangular projection. The anterolateral margin of this projection bears an articulation surface with the maxilla. The very short maxillary process is not clearly distinguishable from the rest of the bone; its lateral margin shows a notch that represent the medial margin of the infraorbital foramen. The notch is deeper in A. kitaibelii and T. aurata than it is in *Chalcides* and the one of the former species is almost closed laterally. Only O. punctatissimus displays a complete and moderately wide infraorbital foramen (Fig. A3.18U-V). The pterygoid process is wide and subtrapezoidal, except for A. *kitaibelii* in which it is very narrow and anteroposteriorly elongated. Because of the narrowing of the pterygoid process, a large portion of the posterior part of the expansion of the lateral margin of A. kitaibelii is visible in dorsal view (Fig. A3.18Q). A long and pointed process, slender in C. chalcides and C. striatus (Fig. A3.18S-T) and wider in A. kitaibelii, C. ocellatus, O. punctatissimus and T. aurata (Fig. A3.18Q-R, U-X), develops posteriorly from its posterior margin, splitting the latter into two portions: the medial portion is oblique and regular, whereas the lateral one is straight and slightly irregular. The latter represents the contact with the pterygoid, whose palatine process is housed in an articulation surface recognizable on the ventral surface (marked anteromedially by a low and arched ridge in C. chalcides; Fig. A3.18T). The palatine ridge is moderately developed. The dorsal surface of the bone is smooth and no palatine teeth are present on the ventral one.

Anguidae (Fig. A3.18Y-AB)

In anguids, the palatine has a long, slender and pointed vomerine process, which is very slightly concave in dorsal direction. The maxillary process is slender and well developed too. It has a T-like shape in dorsal view, because of the presence on its distal end of a short, triangular and posteriorly developed expansion connected to a similarly-shaped and anteriorly directed ventral lappet (probably homologous to that of lacertids). The lateral surface of the process, composed by both the expansion and the lappet, presents the concave maxillary facet (Fig. A3.18Z). The infraorbital foramen is very wide. The pterygoid process is long, slender and subrectangular. In *Anguis* gr. *A. fragilis*, a very deep and narrow V-shaped notch is visible in the middle

of its posterior end (Fig. A3.18Y-Z), which is therefore split into two pointed and equally long portions. In contrast, the notch is very small or absent in *P. apodus* (Fig. A3.18AA-AB). The articulation surface with the palatine process of the pterygoid covers the entire medial half of the ventral surface of the bone (Fig. A3.18Z, AB), being marked medially by an oblique ridge running from the anteromedial to the posterolateral corner of the bone. The dorsal surface of the palatine is smooth, except for a narrow groove (sulcus dorsalis in Klembara et al. 2010) running posterolaterally from the anteromedial corner (Fig. A3.18Y, AA). A moderately developed palatine ridge composes the anterior margin of the bone. The choanal groove is wide. *Anguis* gr. *A. fragilis* has no palatine teeth (Fig. A3.18Z), but a single row of them is present on the lateral half of the ventral surface of the pterygoid process in *P. apodus* (Fig. A3.18AB).

Pterygoid

The pterygoid (Fig. A3.19, A3.20) is a paired bone with a triradiate structure, with three branches developing anteromedially (palatine process), anterolaterally (pterygoid flange) and posterolaterally (quadrate process). The palatine process is composed by a laminar portion and by a more robust medial margin. The pterygoid flange is usually pointed and slender; it is separated by the laminar portion of the palatine process by a notch, the pterygoid recess. Two ridges run along the flange, one on its dorsal and one on its ventral surfaces. These ridges represent the insertion points of the superficial pseudotemporal muscle and of the pterigomandibular muscle, respectively (Barahona 1996). The quadrate process is characterized by the presence of the subcircular fossa columellae on the dorsal surface and of the basipterygoid fossa on the medial one. Posteriorly to the former, a pterygoid ridge runs along the dorsolateral surface of the bone, whereas the latter continues posteriorly in a concave surface for the insertion of the palatine process.

Agamidae (Fig. A3.19A-B, AC-AD)

The palatine process of L. stellio is long and subtriangular in dorsal view. It has a straight medial margin and an oblique and wavy lateral one. The pterygoid flange is peculiar in being laterally directed, instead of anterolaterally. It is represented by a straight process, whose distal end is strongly dorsoventrally expanded. In lateral view, the expanded surface, which articulates with the ectopterygoid and can be poorly ossified, has an elongated elliptical shape (Fig. A3.19AC). On the dorsal surface, a robust and well-developed dorsal ridge is visible (Fig. A3.19A), but the ventral one is not developed on the opposed side (Fig. A3.19B). Because of the unique shape of the pterygoid flange, a real pterygoid recess is not distinctly recognizable. The quadrate process is long, straight in dorsal view and dorsoventrally expanded, adopting a flange-like appearance in lateral view. In adults, a clear step is present on its ventral margin and therefore the rounded posterior end is half as wide as the rest of the process (Fig. A3.19AC-AD). A very narrow notch can be visible by the step, cutting the flange longitudinally. Both the basipterygoid fossa and the concave surface for the pterygoideus muscle are wide (Fig. A3.19AD). Neither a pterygoid ridge nor pterygoid teeth are present.

Maximum length varies from 5.6 mm to 14 mm.

Chamaeleonidae (Fig. A3.19AE-AF)

In *C. chamaeleon*, the main feature of the pterygoid is the wing-like quadrate process, which is laminar and very dorsoventrally expanded, forming a posteriorly rounded flange. The medial surface of the flange presents a well-developed ridge in the middle, marking the deep basipterygoid fossa (Fig. A3.19AF). Ventrally to this ridge, the quadrate process expands to form another large and laminar flange guiding the coronoid. This latter flange has a roughly subtriangular shape in medial view and a rounded ventral end. Moreover, the pterygoid of *C. chamaeleon* loses its triradiate shape, since the pterygoid flange is reduced to a ridge located on the anterior margin of the ventral flange of the quadrate process (Fig. A3.19AE). The ridge is more developed in its dorsal portion and the articulation surface with the ectopterygoid is recognizable on its anterolateral surface. The slender palatine process is straight and

triangular shaped in ventral view; the oblique suture with the palatine is present anterolaterally. There are neither pterygoid teeth nor fossa columellae.

Maximum length goes from 7 mm to 12.9 mm.

Gekkota (Fig. A3.19C-J)

In the pterygoid of European gekkotans, the palatine process has a strongly concave medial margin and wide laminar portion. The ventral ridge of the pterygoid flange is well developed, whereas the dorsal one is very poorly distinguishable. The pterygoid recess is moderately deep and reduced in width compare to lacertids. The quadrate process is long, curved and strongly concave in lateral direction. In dorsal view, this process has a rounded end (truncated in T. mauritanica; Fig. A3.19I-J). The basipterygoid fossa is moderately small and is bordered dorsally by a thin and rounded ridge that develops in dorsomedial direction. In *H. turcicus*, the fossa is very shallow and is defined mostly by the ridge. The insertion surface of the pterygoideus muscle is rather flat and ventrally oriented. A moderately to well-developed ridge is visible on the dorsal surface of the quadrate process. It is not clear if this ridge is the pterygoid ridge since apparently it does not start from the fossa columellae. The ridge is more developed in T. mauritanica (Fig. A3.19I) than in other species, whereas it is not clearly recognisable in E. europaea (Fig. A3.19C). Moreover, a very small hint of a real pterygoid ridge seems to be present in T. mauritanica, posteriorly to the fossa columellae. There are no pterygoid teeth.

The maximum length goes from 4 mm to 4.3 mm in *E. europaea*, 5 mm to 6 mm in *H. turcicus*, from 5 mm to 6.5 mm in *M. kotschyi* and from 7.2 mm to 10 mm in *T. mauritanica*.

Lacertidae (Fig. A3.19K-N, A3.20A-D)

The pterygoid of lacertids has a pointed, wide and roughly straight palatine process, whose ventral surface can present pterygoid teeth: teeth are present in *A. erythrurus*, *A. moreoticus*, *A. nigropunctatus*, *E. arguta*, *Lacerta*, *P. milensis*, *P. peloponnesiacus*, *P. tauricus*, *P. algirus*, *T. lepidus* (Fig. A3.19N, A3.20D) and some specimens of *D. oxycephala*, *P. melisellensis* and *P. siculus*; they can be absent or

present in low number in juveniles, but their number increases during ontogeny. The development of the ridges of the pterygoid flange varies within species: the dorsal one is moderately developed in A. moreoticus, H. graeca, I. bonnali, I. cyreni, I. monticola cantabrica, P. filfolensis, P. milensis, P. pityusensis and T. lepidus (Fig. A3.19M) and well developed in A. erythrurus, A. fitzingeri, A. marchi, A. nigropunctatus, A. bedriagae, D. oxycephala, D. mosorensis, E. arguta, I. horvathi, I. monticola monticola, Lacerta, O. elegans, P. bocagei, Po. hispanicus, P. lilfordi, P. melisellensis, P. muralis, P. siculus, P. tauricus, P. tiliguerta, P. waglerianus, P. algirus and Z. vivipara (Fig. A3.19K); the ventral one is low developed in A. erythrurus, A. fitzingeri (Fig. A3.19L), A. marchi, A. moreoticus, A. bedriagae, D. oxycephala, E. arguta, H. graeca, I. cyreni, I. horvathi, I. monticola, Lacerta (except for L. agilis MDHC 178, in which it is more developed), O. elegans, P. melisellensis (except for MDHC 218, in which it is well developed), P. milensis, P. muralis (rarely more developed), P. algirus and Z. vivipara (except for SMNS 06795) and well developed in A. nigropunctatus, D. mosorensis, I. bonnali, P. bocagei, P. filfolensis, Po. hispanicus, P. lilfordi, P. pityusensis, P. siculus, P. tiliguerta, P. wagleriauns and T. lepidus (however, less developed in MDHC 216 and MRAC 92-050-R-1). The ventral ridge can be either well or poorly developed in *P. tauricus*. Roček (1984: p. 29) stated that the ridges are completely lacking in small individuals of T. lepidus and well developed in large ones. The pterygoid recess is wide; it can be moderately shallow (A. erythrurus, T. lepidus; Fig. A3.19M-N) or deeper (other species; Fig. A3.19K-L). Juveniles of *T. lepidus* show a deeper recess, but its depth reduces during growth. The long quadrate process is straight in dorsal view and has a roughly pointed posterior end. It presents a wide fossa columellae and a pterygoid ridge that goes from moderately developed (A. erythrurus, A. moreoticus, D. oxycephala, D. mosorensis, I. monticola, P. filfolensis, P. milensis, P. muralis and T. lepidus; Fig. A3.19M, A3.20C) to well developed (A. fitzingeri, A. marchi, A. nigropunctatus, A. bedriagae, E. arguta, H. graeca, I. bonnali, I. cyreni, I. horvathi, Lacerta, O. elegans, P. bocagei, Po. hispanicus, P. lilfordi, P. melisellensis, P. pityusensis, P.

siculus, P. tauricus, P. tiliguerta, P. waglerianus, P. algirus and Z. vivipara; Fig. A3.19K, A3.20A). Sometimes, the ridge of large individuals displays a dorsally directed expansion in its posterior half (e.g., A. nigropunctatus MDHC 242 and L. schreiberi UAM.R.S-6). The basipterygoid fossa is large and shallow. Maximum length is given in the following table:

Species	Maximum length	
	of the pterygoid	
A. erythrurus	7 mm - 8.5 mm	
A. fitzingeri	5.2 mm	
A. moreoticus	5 mm	
A. nigropunctatus	6.7 mm - 8.6 mm	
A. bedriagae	8 mm - 12.5 mm	
D. oxycephala	7 mm - 9 mm	
D. mosorensis	7 mm - 8 mm	
E. arguta	11.8 mm	
H. graeca	6.1 mm - 8.9 mm	
I. bonnali	6.5 mm - 6.7 mm	
I. cyreni	9 mm - 9.3 mm	
I. horvathi	6.3 mm	
I. monticola	7.1 mm - 9 mm	
L. agilis	7.9 mm - 9 mm	
L. bilineata	6.3 mm - 15.6 mm	
L. schreiberi	12 mm	
L. trilineata	13.5 mm - 15.4 mm	
L. viridis	16 mm - 19 mm	
O. elegans	4.5 mm - 5.6 mm	
P. bocagei	6.3 mm	
P. filfolensis	7.3 mm - 7.4 mm	
Po. hispanicus	4.8 mm - 6.7 mm	

P. lilfordi	7 mm - 8.7 mm
P. melisellensis	7 mm - 8.4 mm
P. milensis	7.9 mm
P. muralis	5.6 mm - 8.5 mm
P. siculus	8.9 mm - 10.2 mm
P. tauricus	7.9 mm - 8.2 mm
P. tiliguerta	7.3 mm - 7.6 mm
P. waglerianus	8.6 mm - 8.8 mm
P. algirus	6.5 mm - 9 mm
T. lepidus	6.5 mm - 32 mm
Z. vivipara	4.6 mm - 5.7 mm

Scincidae (Fig. A3.19O-X, A3.20E-N)

The palatine process of the pterygoid of European scincids is a laminar structure provided with a thicker area in the middle rather than a robust medial margin. It is long and subtriangular in A. kitaibelii (Fig. A3.19O-P), long and subrectangular in C. chalcides, C. striatus and T. aurata (Fig. A3.19Q-R, W-X), short and subtriangular in C. ocellatus and O. punctatissimus (Fig. A3.19S-V). The medial margin of the process can be straight (T. aurata; Fig. A3.19W-X), slightly convex (A. kitaibelii, C. chalcides, C. striatus and O. punctatissimus; Fig. A3.19O-R, U-V) or strongly convex (C. ocellatus; Fig. A3.19S-T). This morphology fits with the "alpha" type scincid pterygoid described by Greer & Parker (1968) and Greer (1974; see also Evans 2008). In *Chalcides*, the anterior end of the process is bifurcate: it has a V-shaped (most specimens of C. chalcides; Fig. A3.19Q-R) or U-shaped (C. ocellatus, C. striatus and C. chalcides MDHC 398; Fig. A3.19S-T) notch in the middle, flanked by two small and pointed processes. The one of T. aurata, on the other hand, has a straight but slightly interdigitated anterior margin and a long and slender anterior projection by the medial corner (Fig. A3.19W-X). Ablepharus kitaibelii has an anteriorly pointed palatine process (Fig. A3.19O-P), whereas that of O. punctatissimus has a wavy anterior margin (Fig. A3.19U-V). Pterygoid teeth are

absent in A. kitaibelii and Chalcides (Fig. A3.19P, R, T), but present in very low number (just 1 or 2 in MDHC 280, 3 in all specimens of O. punctatissimus) in T. aurata and O. punctatissimus (Fig. A3.19V, X). The moderately wide pterygoid recess is very deep and roughly V- or U-shaped in C. chalcides (Fig. A3.19O-R), shallow and U-shaped in C. ocellatus and O. punctatissimus (Fig. A3.19S-V) and deep and U-shaped in A. kitaibelii, C. striatus and T. aurata (Fig. A3.19O-P, W-X). As for the ridges of the pterygoid flange, the dorsal one is moderately developed, whereas the ventral one is very well developed. The development of the ridges decreases in the small species A. kitaibelii (Fig. A3.19O-P), but their proportions are the same. In O. punctatissimus, on the other hand, both the dorsal and the ventral ones are well developed (Fig. A3.19U-V). The quadrate process is long and straight; its posterior end is narrow in dorsal view and finger-shaped in lateral view. The fossa columellae is slightly anteroposteriorly elongated. In C. bedriagai, C. chalcides, C. striatus and T. aurata, the fossa is followed by a pterygoid ridge that is sharp in its anterior portion, whereas posteriorly tends to lower and to shift in ventral direction towards the lateral surface (Fig. A3.19Q, W, A3.20G, M). The ridge is completely absent in C. ocellatus and O. punctatissimus (Fig. A3.19S, U, A3.20I, K), whereas only a hint at the fossa is present in A. kitaibelii (Fig. A3.19O, A3.20E). The basipterygoid fossa is a flattened surface, but the wide surface for the insertion of the pterygoideus muscle is strongly concave. With the exception of A. kitaibelii and C. striatus MNCN 16508, a foramen opens in ventral direction on the ventral portion of the lateral surface of the bone, at the joint of the three branches.

Measurements of the maximum length are given in th	he following table:
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Species	Maximum length
	of the pterygoid
A. kitaibelii	3 mm
C. bedriagai	Not measured
C. chalcides	5.4 mm - 6.5 mm

C. ocellatus	8.4 mm - 10 mm
C. striatus	4.8 mm - 5.1 mm
O. punctatissimus	3.7 mm
T. aurata	8.1 mm - 8.3 mm

Anguidae (Fig. A3.19Y-AB, A3.20O-R)

In European anguids, the pterygoid has a very long, slender and pointed palatine process. Both margins of this process are straight, but the lateral one can show some irregularities. The pterygoid flange is distinctly shorter (roughly half the length of the palatine process) and very slender, with a very prominent dorsal ridge. The ventral ridge, on the other hand, is poorly developed in *Anguis* gr. *A. fragilis* (Fig. A3.19Z), but well developed in *P. apodus* (Fig. A3.19AB). The pterygoid recess is wide, deep and U-shaped in dorsal view. The long and straight quadrate process is pointed in both dorsal and lateral views. The fossa columellae is wide and deep, whereas the basipterygoid fossa is flattened, but marked by flanges both dorsally and ventrally. The flanges are moderately developed and rounded, except for the ventral one of *P. apodus* (the basisphenoid process of Klembara et al. 2010), which is longer and thumb-like (Fig. A3.19AA-AB). The pterygoid ridge can be low or moderately developed. Pterygoid teeth are absent in *Anguis* gr. *A. fragilis* (Fig. A3.19Z), but present in *P. apodus* (Fig. A3.19AB).

The maximum length of the pterygoid of *Anguis* gr. *A. fragilis* ranges from 6 mm to 10.6 mm, whereas it varies from 13 mm to more than 20 mm in *P. apodus*.

Ectopterygoid

The ectopterygoid (Fig. A3.21) is a small and paired bone, the morphology of which varies greatly among different groups.

Agamidae (Fig. A3.21A-E)

Ectopterygoids of *L*. *stellio* have a thick body, a triradiate lateral end and a moderately large and roughly kidney-shaped (in medial view) medial end. The lateral end contacts the maxilla and jugal, whereas there is no contact with the postorbital

(in contrast with other agamids; see Evans 2008). It is composed by an anteriorly developed anterolateral process, a posteriorly developed posterolateral process and a ventrally developed ventral process (Fig. A3.21E). The posterolateral and the ventral processes are similar in size and length, whereas the anterolateral one is slightly longer; all three processes are pointed. The medial end (posteromedial process) contacts the pterygoid flange of the pterygoid with a slightly anteriorly inclined and flattened surface (Fig. A3.21D). A short medial expansion is present by the dorsal end of this surface (Fig. A3.21B), covering dorsally the pterygoid flange. *Chamaeleonidae (Fig. A3.21F-J)*

Chamaeleo chamaeleon has an ectopterygoid which is morphologically similar to the one of *L. stellio*. The main differences among them are in the proportions of the three processes of the lateral end and in the morphology of the articulation surface with the pterygoid flange. In *C. chamaeleon*, the ventral process is short and moderately wide, whereas the anterolateral and posterolateral ones are slightly longer, slender and more pointed (Fig. A3.21J). Moreover, the medial surface of the posteromedial process is narrow and subrectangular and shows a concave and rough articulation surface (Fig. A3.21I).

Gekkota (Fig. A3.21K-R)

Ectopterygoids of European gekkotans are crescent-shaped, with two pointed ends and a medial concavity. In medial view, the posterior end (posteromedial process) is divided into two pointed lappets, which embrace the pterygoid flange of the pterygoid. The dorsal lappet is longer than the ventral one. In ventral view, the lateral margin of the anterior half of the bone (anterolateral process) is composed by the articulation surface with the maxilla. In the ectopterygoid of *E. europaea*, the ventral lappet is very little developed and the articulation surface with the maxilla is very scarcely distinguishable (Fig. A3.21K). The dorsal surface of the bone is smooth.

Lacertidae (Fig. A3.21S-X)

In lacertids, the ectopterygoid is L-shaped and is composed of three processes. The anterolateral process is laminar and pointed; its ventral surface is covered by the
articulation surface with the maxilla. The posterolateral process is short or very short and pointed. The posteromedial process shows a V-shaped concavity at its end in which the pterygoid flange of the pterygoid inserts: the concavity is defined by three lappets, among which the anteromedial one is the longest one. The ventral lappet is more developed than the dorsal one. Usually, the longest process is the posteromedial one, even though this feature can be variable among different individuals (Barahona 1996). This is not true, however, for *A. erythrurus*, *A. marchi*, *O. elegans* and *P. muralis*, in which this process is usually as long as the anterolateral one (Fig. A3.21S-T), and for *Z. vivipara*, in which they can be similar in length or the longest process may even be the anterolateral one (Fig. A3.21W-X). The dorsal surface of the bone is smooth.

Scincidae (Fig. A3.21Y-AF)

The ectopterygoid of European scincids resembles morphologically that of lacertids, but it lacks the posterolateral process. Because of the absence of the latter, in scincids this bone is crescent-shaped rather than L-shaped. Only T. aurata retains an L-shape because of the presence of a very small and triangular hint of posterolateral process (Fig. A3.21AE-AF). The articulation surface with the maxilla is limited to the lateral margin of the anterior end of the anterolateral process. The ventral lappet is usually the most developed one, whereas the smallest one is the dorsal one. Ophiomorus punctatissimus is an exception in having similar-sized ventral and anteromedial lappets (Fig. A3.21AC-AD). Moreover, a distinct anteromedial lappet seems not to be developed in A. kitaibelii (Fig. A3.21Y-Z). The ventral lappet of the posteromedial process of C. ocellatus shows a small anteromedially-developed projection (Fig. A3.21AA-AB), which contacts the palatine process of the pterygoid. Anterolateral and posteromedial processes are similar in length in A. kitaibelii, Chalcides and O. punctatissimus (Fig. A3.21Y-AD), whereas the latter is longer than the former in T. aurata (Fig. A3.21AE-AF). Both dorsal and ventral surfaces are smooth.

Anguidae (Fig. A3.21AG-AJ)

Anguids have a crescent-shaped and medially concave ectopterygoid, like gekkotans. The lateral surface of the bone shows two concave articulation surfaces: one for the posterior process of the maxilla on the anterior end and a larger one (roughly twice as large as the former) for the pterygoid flange posteriorly. The two articulation surfaces come nearly in contact with each other. In lateral view, the posterior end appears bifurcated, because of the presence of two pointed projections (lappets) clasping the pterygoid flange. The dorsal projection is longer and larger than the ventral one. In *P. apodus*, the anterior end appears slightly forked too, because of the presence of a small and anterolaterally directed expansion clasping ventrally the posterior process of the maxilla (Fig. A3.21AI). The mediodorsal surface of the bone is smooth.

General features of the otooccipital region

The otooccipital region (Fig. A3.21, A3.22, A3.23, A3.24, A3.25, A3.26, A3.27, A3.28) is the portion of the braincase composed by the fusion of sphenoid, basioccipital, prootics, supraoccipital and otooccipitals. These bones are separated in juveniles but generally fuse during growth. Posteriorly, supraoccipital, otooccipitals and basioccipital define the foramen magnum, whereas otooccipitals and basioccipital compose the occipital condyle. Between the basioccipital and each otooccipital, there is the recessus scalae tympani. It opens externally with a ventrolaterally directed lateral opening and internally with a medial opening into the cranial cavity and a dorsomedial opening (the perilymphatic foramen) into the cochlear cavity. The cochlear cavity opens externally with the wide fenestra ovalis, which is located between the prootics and otooccipitals. Each side of the otooccipital region shows three semicircular canals: the anterior one develops between the prootic and the supraoccipital, the horizontal one runs between the dorsal portion of the prootic and the base of the paraoccipital process of the otooccipital, whereas the posterior one is located between the supraoccipital and the otooccipital.

Agamidae

The otooccipital region of *L. stellio* is roughly as long as it is wide and does not show evident compression. Bones composing the region usually remain separated also in older individuals. The foramen magnum is wide and subcircular. The portion of the occipital condyle made up by each otooccipital appears to be slightly reduced compared to the one made by the basioccipital. Moreover, the condyle shows a very little developed posterior notch in ventral view. The large recessus scalae tympani opens laterally with a large, narrow and dorsoventrally elongated lateral opening, whereas both the medial opening of the recessus and the perilymphatic foramen are very large and suboval. Semicircular canals are narrow and poorly prominent.

Chamaeleonidae

Bones of the otooccipital region of C. chamaeleon do not fuse. The region is roughly

as long as it is wide. The foramen magnum is suboval and slightly laterally compressed and the basioccipital does not participate in its formation (Fig. 2.10). The occipital condyle is mainly composed by otooccipitals, but a small portion of the posterior end of the basioccipital is also part of it (Fig. 2.10). The three portions of the condyle, however, remain separated, without fusing together. The recessus scalae tympani is strongly reduced, being visible only with a foramen on the otooccipital, and so the basioccipital forms the



Figure 2.10) Posterior view of an articulated skull of C. chamaeleon (MNHN 1887-875), showing the otooccipital portions (oc) of the occipital condyle excluding the basioccipital portion (b) from the margin of the foramen magnum. Scale bar = 1 mm.

ventral wall of the cochlear cavity. The ventral margin of the very wide fenestra ovalis is consequently composed by the sphenooccipital tubercles. The portion of margin made by the latter, however, is small because of the presence of two expansions of the prootic and the otooccipital that almost exclude them. The medial wall of the cochlear cavity is very poorly ossified and so the cavity is open on the medial side. Semicircular canals are moderately narrow and poorly recognizable.

Gekkota (Fig. A3.22, A3.23)

The otooccipital region is roughly as long as it is wide and slightly dorsoventrally compressed in gekkotans (more compressed in *E. europaea*; Fig. A3.22A-C). The foramen magnum is wide and subcircular (subelliptical in MDHC 201, 388 and 389) and the occipital condyle is composed equally by the basioccipital and the two otooccipitals. The occipital condyle appears as paired in gekkotans (Daza et al. 2008), having a clear U-shaped notch that is visible in ventral view. The recessus scalae tympani and its lateral opening are moderately wide (very wide in *E. europaea*; Fig. A3.22B). The latter is roughly subelliptical. The medial opening of the recessus scalae tympani is narrow and elongated, whereas the perilymphatic foramen is smaller (larger in *E. europaea*; Fig. A3.22E) and rounded. In *T. mauritanica*, the medial opening is divided into two subcircular portions, both smaller than the perilymphatic foramen. The semicircular canals are moderately narrow.

Lacertidae (Fig. A3.24, A3.25A-E)

The general features of the otooccipital region of lacertids are similar to those of the one of gekkotans, but the U-shaped notch on the occipital condyle is wider and shallower or even absent, the lateral opening of the recessus scalae tympani is wide and suboval, its medial opening is usually subcircular or anteroposteriorly elongated and the perilymphatic foramen is wide. Semicircular canals are moderately narrow in medium and large-sized species, but they are wider in small-sized taxa. *Scincidae (Fig. A3.25F-J, A3.26, A3.27)*

In scincids, the otooccipital region is roughly as long as it is wide and not compressed. The foramen magnum is wide and subelliptical. The occipital condyle is similar to the one of lacertids. The lateral opening of the recessus scalae tympani is wide, subelliptical and elongated. In *O. punctatissimus*, this opening has poorly developed margins, largely exposing the recessus scalae tympani in lateral view (Fig. A3.27B). The medial opening of the recessus scalae tympani is reduced because of the presence of expansions of its dorsal margin, whereas the perilymphatic foramen is wide and subcircular. The semicircular canals are narrow and poorly prominent.

Anguidae (Fig. A3.28)

Anguids have an otooccipital region that is slightly longer than it is wide and is provided with a wide and subcircular or subelliptical foramen magnum. The portions of occipital condyle composed by the otooccipitals are reduced compared to the portion composed by the basioccipital. The posterior margin of the condyle is not notched, but convex (*Anguis* gr. *A. fragilis*; Fig. A3.28D-E) or rather straight (*P. apodus*; Fig. A3.28I-J), in dorsal and ventral view. The recessus scalae tympani is moderately reduced in *Anguis* gr. *A. fragilis* (Fig. A3.28B), but larger in *P. apodus* (Fig. A3.28G). It opens externally with an anteroposteriorly elongated lateral opening, which is narrow in *Anguis* gr. *A. fragilis* (Fig. A3.28B). The medial opening of the recessus scalae tympani is wide and, in *Anguis* gr. *A. fragilis*, also anteroposteriorly elongated, whereas the perilymphatic foramen can be either moderately small or large. As in scincids, the semicircular canals are narrow and poorly prominent.

Basioccipital

The unpaired basioccipital (Fig. A3.29) is roughly as long as it is wide and has a subhexagonal shape. Its body is dorsally concave, bearing a central cranial depression, and shows two moderately developed lateral wings. The anterior margin can be roughly straight or concave and the posterior one forms the medial portion of the occipital condyle. Both the ventral and the dorsal surfaces are smooth. The

sphenooccipital tubercles are present by the ends of the two lateral wings, constituting the ventral wall of the recessus scalae tympani. The posterior wall of the recessus, on the other hand, is marked by the crista tuberalis.

The basioccipital contacts and fuses with the sphenoid anteriorly, with the prootics anterolaterally and with the otooccipitals posterolaterally.

Agamidae (Fig. A3.29A-B)

In *L. stellio*, the posterior portion of the basioccipital composes more than a third of the occipital condyle. The sphenooccipital tubercles are very well developed and strongly built. They are roughly rounded and moderately narrow in lateral view. However, the development of the tubercles is weaker in juveniles.

Chamaeleonidae (Fig. A3.29C-D)

The small basioccipital of *C. chamaeleon* is wider than it is long. Its posterior end only slightly participates in the formation of the occipital condyle. Sphenooccipital tubercles are very well developed and rounded in lateral view.

Gekkota (Fig. A3.22, A3.23, A3.29E)

In gekkotans, the basioccipital forms the medial third of the occipital condyle. Sphenooccipital tubercles are poorly developed in ventral direction in *E. europaea* (Fig. A3.22B-C), moderately developed in *H. turcicus* (Fig. A3.22G-H) and *M. kotschyi* (Fig. A3.23B-C) and well developed in *T. mauritanica* (Fig. A3.23G-H). When developed, they are subtriangular in lateral view.

Lacertidae (Fig. A3.24, A3.35A-E, A3.29F)

The basioccipital of lacertids is similar to that of gekkotans. In large species, however, it becomes wider than it is long. Sphenooccipital tubercles are moderately developed in small-sized species and well developed in large-sized ones. The degree of development increases during ontogeny. In lateral view, they are ventrally pointed.

Scincidae (Fig. A3.25F-J, A3.26, A3.27, A3.29G)

In scincids, the basioccipital is longer than it is wide. As in lacertids, it composes the medial third of the occipital condyle and has pointed sphenooccipital tubercles. The

latter are poorly developed in *A. kitaibelii*, *C. bedriagai*, *C. chalcides*, *C. striatus* and *O. punctatissimus* (Fig. A3.25G-H, A3.26A-C, A3.27A-C) and very well developed in *C. ocellatus* and *T. aurata* (Fig. A3.26F-H). The developed ones become subtriangular in lateral view.

Anguidae (Fig. A3.28, A3.29H)

The basioccipital is slightly longer than it is wide in *Anguis* gr. *A. fragilis* too (Fig. A3.28E, A.29H). In *P. apodus*, on the other hand, length and width are roughly similar (Fig. A3.28J). Posteriorly, it composes more than one third of the occipital condyle. Sphenooccipital tubercles are moderately or well developed in *Anguis* gr. *A. fragilis* (Fig. A3.28B-C) and always well developed in *P. apodus* (Fig. A3.28F-H); they are subtriangular (but with a rather rounded ventral end) in lateral view and almost entirely excluded from the recessus scalae tympani by two expansions of the otooccipital. The degree of development of the tubercles seems to increase with growth, but they are as a rule larger in *P. apodus* than in *Anguis* gr. *A. fragilis*.

Sphenoid

The sphenoid (Fig. A3.30) is an unpaired bone made up by the complete fusion of parasphenoid and basisphenoid. The body of the bone has a roughly quadrangular shape, with two anterolaterally directed basipterygoid processes starting from the anterolateral corners. Two posterolaterally directed cristae ventrolaterales (parasphenoid wings in Daza et al. 2008) can be also present by the posterolateral corners. Two cylindrical trabeculae cranii are located between the basipterygoid processes, continuing posteriorly in two low cristae trabeculares. These cristae border laterally the sella turcica, which includes the hypophysial fossa. A parasphenoid rostrum (cultriform process in Daza et al. 2008) can be present between the trabeculae, on the anterior margin of the bone. In dorsal view, the sphenoid is crossed transversely by the dorsally developed crista sellaris, which marks the posterior margin of the sella turcica and continues laterally contacting the prootics with the alar processes. The crista is pierced anteroposteriorly by two abducens

foramina and can develop anterodorsally, covering the sella turcica with a dorsum sellae. Posteriorly to the crista, the dorsal surface of the sphenoid is smooth. The ventral surface is also smooth, but can present a sunken area in the middle. In anterior view, medially to the base of the basipterygoid processes, one can see the anterior openings of the vidian canals, which open also medially in the sella turcica (with the internal carotid foramina) and posterolaterally in direction of the contact with the prootics. From the latter openings, the recessus vena jugularis extends posterodorsally on both sides of the sphenoid, continuing along the anterior inferior process of the prootics.

The sphenoid contacts and fuses with the basioccipital posteriorly and prootics posterolaterally.

Agamidae (Fig. A3.30A-D)

The sphenoid of *L. stellio* has moderately short and large basipterygoid processes. The processes are roughly rectangular, with an enlarged and horizontal distal end. The trabeculae cranii are well developed and well-spaced, but they do not continue posteriorly in the cristae trabeculares (Fig. A3.30A-B). The rostrum is well developed, wide and thin. A hint of dorsum sellae is present on the moderately developed crista sellaris, covering the posterior portion of the narrow sella turcica (Fig. A3.30A). The medial openings of the vidian canals are located close to each other in adults (Fig. A3.30B), but they are more spaced in juveniles. The ventral surface is only slightly sunken (Fig. A3.30D), whereas the recessus vena jugularis is deep (Fig. A3.30C). The supravenous processes (and therefore the grooves for the lateral head veins) are absent. Two well-developed cristae ventrolaterales are present in adults.

Chamaeleonidae (Fig. A3.30E-H)

In *C. chamaeleon* the sphenoid is larger than the basioccipital and has a subtrapezoidal body in ventral view. Well-developed cristae ventrolaterales are present and basipterygoid processes are moderately long, moderately thick and roughly triangular shaped. The latter enlarge distally and are tilted mediolaterally at

about 45°. There are no supravenous processes and distinct grooves for the lateral head veins are not present. A very well developed and thick parasphenoid rostrum is present, whereas there are no trabeculae cranii (Fig. A3.30E). The crista sellaris is well developed and projects slightly anteriorly, creating a short dorsum sellae (Fig. A3.30E). The sella turcica is narrow and therefore the medial openings of the vidian canals are close to each other. A very small foramen opens in the sella dorsomedially to the openings of the canals. The ventral surface of the bone is strongly concave and is bordered laterally by two well-developed ridges (Fig. A3.30H). The recessus vena jugularis is very shallow (Fig. A3.30G).

Gekkota (Fig. A3.22, A3.23, A3.30I)

European gekkotans have elongated triangle-shaped basipterygoid processes, which are narrow proximally and enlarge distally. Their distal end is tilted mediolaterally at about 30° (45° in *E. europaea*; Fig. A3.22A) and is slightly dorsolaterally concave. No well-developed cristae ventrolaterales can be seen posteriorly in *E. europaea*, *H.* turcicus and M. kotschyi, whereas two small and pointed ones are present in T. mauritanica (Fig. A3.23J, A3.30I). A laminar, horizontal and anteriorly directed supravenous process is present dorsally to each basipterygoid process: it is low developed in M. kotschyi and H. turcicus MDHC 26, moderately developed in T. mauritanica and well developed in E. europaea and H. turcicus MDHC 238. Laterally, each supravenous process is connected with the continuation of the crista prootica. In lateral view, supravenous and basipterygoid processes are separated by the narrow groove of the lateral head vein, which starts posteriorly from a very small foramen. In *H. turcicus*, this groove is closed laterally and is represented only by an anteriorly opened foramen, whereas the posterior foramen is not visible in E. europaea. The small trabeculae are very close in H. turcicus (fused medially in MDHC 26; Fig. A3.22I) and in most specimens of T. mauritanica (Fig. A3.23I, A3.30I), whereas a small hint of parasphenoid rostrum is present between them in MDHC 194 and 285. The cristae trabeculares are not visible in *M. kotschyi* (Fig. A3.23D); in other species, they are very low and arched, curving laterally and merging with the anterior margin of the supravenous processes. The sella turcica is not covered dorsally, as the crista sellaris does not develop a dorsum sellae. Its dorsal surface shows a high degree of variation: in *E. europaea*, it is always smooth; in *H. turcicus*, the only visible structures are a foramen in MDHC 26 and a low ridge encircling a circular area in MDHC 238, both placed anteriorly to the center of the crista sellaris; in *M. kotschyi*, the surface is smooth and not separated in MDHC 201, 418 and 419, whereas in MDHC 285 the anterior half is occupied by the shallow hypophysial fossa and the posterior one is divided into two portions by a low median ridge; in *T. mauritanica*, it is smooth (MDHC 302) or it can present a very low median ridge running from the trabeculae to the crista sellaris (in MDHC 194) or only a hint of a portion of such ridge (anterior portion in MDHC 119 and posterior portion in MDHC 97 and 98). The sunken area on the ventral surface is present: it is little developed in *E. europaea*, *H. turcicus* and *M. kotschyi* (Fig. A3.22E, J, A3.23E), but strongly deepened in *T. mauritanica* (Fig. A3.23J).

Lacertidae (Fig. A3.24, A3.25A-E, A3.30J-N)

In lacertids, basipterygoid processes of the sphenoid are moderately short; they can be moderately narrow proximally and strongly enlarged by the distal end (*A. erythrurus*, *O. elegans* and juveniles of other species; Fig. A3.24D-E) or enlarged for their entire length (adults of other species; Fig. A3.24I-J, A3.25D-E, A3.30J-K, M). In proportion, larger species have larger processes than smaller ones. The distal end of the processes is strongly dorsolaterally concave and not distinctly tilted mediolaterally; moreover, its medial portion is expanded in anterior view. Welldeveloped (shorter in *A. marchi*, *A. moreoticus* and *A. nigropunctatus*; Fig. A3.30K) cristae ventrolaterales and a long, narrow and laminar parasphenoid rostrum are present. The former reach the sphenooccipital tubercles. Trabeculae cranii are dorsoventrally flattened; they are small and well separated from one another in smallsized animals (e.g., *A. erythrurus*; Fig. A3.24D), but they grow bigger and tend to come in contact in adults of larger ones (e.g., *L. bilineata* and *T. lepidus*; Fig. A3.24I). Cristae trabeculares merge posteriorly with the well-developed crista

sellaris, which does not develop a dorsum sellae. The alar processes of the crista sellaris expand anteriorly, forming vertical and subquadrangular supravenous processes. It is not clear if they are homologous to those of gekkotans. Supravenous processes of lacertids are moderately long and moderately wide and they may be connected to the distal end of the basipterygoid processes by a ventral osseous expansion. The anterior openings of the abducens foramina are visible on the medial surfaces of these processes and a deep and a wide groove for the lateral head vein separates each of them from the related basipterygoid process. A low transverse ridge is present on the dorsolateral surface of the latter and marks the ventral margin of this groove. In some individuals, posterolateral openings of the vidian canals can be located posteriorly, by the contact with the prootics. In adults of A. erythrurus, A. bedriagae, E. arguta, O. elegans, P. tiliguerta, P. algirus and T. lepidus as well as in both adults and juveniles of D. oxycephala, H. graeca and P. siculus, the ventral surface of the bone shows a moderately to strongly sunken area in the middle (Fig. A3.24E). A distinctly less developed concavity, however, can be also visible on the ventral surface of other species, such as I. cyreni, P. melisellensis and P. muralis. In adults of Lacerta and in P. tauricus, either a deeply sunken or a not sunken ventral surface can be present. In the observed specimens of D. oxycephala, the concavity is deep in NHMW 629 and shallow in the other specimens: this suggest that this feature is variable within the species, but since NHMW 629 is probably a subadult and the shallow morphology is present in both juveniles (NHMW 695-1) and adults (NHMW 651 and 695-1), this variation is most probably not strictly linked to ontogeny. This variation is present in *P. siculus* too, since MDHC 91, an adult, displays an unsunken surface.

Scincidae (Fig. A3.25F-J, A3.26, A3.27, A3.300-R)

The sphenoid of scincids has axe-shaped and moderately short basipterygoid processes; the proximal half is narrower than the distal one and the difference in width is stronger in *A. kitaibelii*, *O. punctatissimus* and the largest species. Their distal end is narrow, very slightly dorsolaterally concave and mediolaterally tilted at

about 30° in anterior view and slightly convex in dorsal view. Except for A. kitaibelii (Fig. A3.25J), each posterolateral corner of the sphenoid shows a short and pointed crista ventrolateralis (Fig. A3.26E, J, A3.27E). The trabeculae cranii (very poorly developed in A. kitaibelii, T. aurata and O. punctatissimus; Fig. A3.25I, A3.27D, A3.300) are not in contact (the only exceptions are C. bedriagai and O. punctatissimus; Fig. A3.27D) and, except for O. punctatissimus, continue posteriorly with low but distinct cristae trabeculares. There is no parasphenoid rostrum. The sella turcica is smooth, but it is covered dorsally by a short (A. kitaibelii, C. chalcides, C. striatus and O. punctatissimus; Fig. A3.25I, A3.26D, A3.27D) or well developed (C. ocellatus and T. aurata; Fig. A3.26I, A3.30Q) dorsum sellae. In C. bedriagai, however, the dorsum sellae is not developed. Vertical and laminar supravenous processes are present, as in lacertids. In scincids, they are well developed, but those of A. kitaibelii are very narrow (Fig. A3.25G). The crista prootica seems to merge into them and the anterior openings of the abducens foramina are located on their medial surfaces, together with the posterodorsal end of the cristae trabeculares. The groove for the lateral head vein is shallow and moderately wide. The ridge marking its ventral margin is very poorly recognizable in C. chalcides (except for the largest specimen, MDHC 398, in which this feature is more similar to C. ocellatus), C. striatus and T. aurata, whereas in C. ocellatus it is low developed and extends very slightly beyond the posterior margin of the process. Ablepharus kitaibelii and O. *punctatissimus* show no clear sign of such a ridge. A shallow sunken area is visible in the middle of the ventral surface of the bone in C. chalcides, C. ocellatus and T. aurata (Fig. A3.26E, J).

Anguidae (Fig. A3.28, A3.30S-T)

The basipterygoid processes are axe-shaped and very short in the sphenoid of anguids. Their proximal half is strongly enlarged, almost reaching the width of the distal end. The latter is expanded, almost flattened and almost horizontal in anterior view, whereas it is slightly convex in dorsal view. Very long cristae ventrolaterales are present by the posterolateral corners of the bone. The trabeculae are well

developed and robust, projecting beyond the anterior margin of the bone; the midline contact between them is a very variable feature both in Anguis gr. A. fragilis and P. *apodus*. The cristae trabeculares are also well developed. A well-developed rostrum develops between the trabeculae. The sella turcica is very wide and smooth; it is covered by a well-developed dorsum sellae. The ventral surface of the sphenoid is rather flattened, with only a very slightly sunken area in the middle. In European anguids, the vidian canals continue posteriorly and their posterior opening is located on the prootics. The lateral wall of this posterior portion of the canals, however, is still composed by the sphenoid, since they are covered by the cristae ventrolaterales. A laminar supravenous process similar to the one of lacertids and scincids develops anteriorly from each alar process of the crista sellaris; as in the latter families, it is not clear if one can consider this process to be homologous with that of gekkotans, but the merging of the crista prootica into them seems to suggest so. These processes are narrower and more rounded anteriorly in Anguis gr. A. fragilis (Fig. A3.28B), whereas they are larger and more squared in P. apodus (Fig. A3.28G). A wide and moderately deep groove for the lateral head vein is visible ventrally to them, being marked ventrally by a low ridge located on the dorsal surface of the proximal end of the basipterygoid processes. Sometimes, the anterior part of this ridge can form a dorsally directed expansion that comes close to the related supravenous process.

Supraoccipital

The unpaired supraoccipital (Fig. A3.31)), which includes the epiotic of Jollie (1960), has a transversely elongated shape and is posteriorly inclined. It consists of a thin medial portion and two wide lateral portions that form the roof of the cavum capsularis. The posterior margin of the bone defines dorsally the foramen magnum, whereas the anterior one can carry an anterodorsally developed processus ascendens or other different structures. The dorsal portions of the anterior semicircular canals are located along the anterior margin of the bone, whereas those of the posterior ones run from the posterolateral corners to the middle of the dorsal surface. On each side,

the canals merge in the common crus, which opens in the cavum capsularis. On the medial surface of the lateral portions of the bone, near the contact with the prootic, one can see the moderately wide and posterodorsally opened endolymphatic foramen.

This bone is fused with the prootics anterolaterally and the otooccipitals posterolaterally.

Agamidae (Fig. A3.31A)

Laudakia stellio has a large supraoccipital, provided with a short and subcylindrical processus ascendens. In dorsal view, both the posterior portion of the latter and the semicircular canals are poorly distinguishable. The dorsal surface of the bone is otherwise smooth. The anterior margin carries two laminar, moderately developed and anteriorly directed expansions, located on both sides of the processus ascendens. In ventral view, a very narrow notch separates each ventral opening of the anterior semicircular canals from the cavum capsularis; this is the dorsal portion of the sphenoccipital foramen (Fig. 2.11).

Chamaeleonidae (Fig. A3.31B-C)

The supraoccipital is the largest bone of the otooccipital region of C. chamaeleon. In

the middle of the dorsal surface of the bone, there is the very well developed processus developed ascendens. in direction anterodorsal and strongly expanded dorsally to form a tall median crest (Fig. A3.31B). The dorsal expansion of the processus contacts the parietal crest of the parietal. On both sides of the processus ascendens, two well-developed



Figure 2.11) Posterodorsal view of an articulated skull of L. stellio (NHMW 570), showing the position of the sphenoccipital foramen. Abbreviations: f, sphenoccipital foramen; ot, otooccipital; pa, parietal; pr, prootic; so, supraoccipital; sq, squamosal. Scale bar = 1 mm.

and anteriorly projecting cylindrical processes are present. The common crus is absent and the semicircular canals enter directly the cavum capsularis.

Gekkota (Fig. A3.22, A3.23, A3.31D)

No processus ascendens is present on the supraoccipital of gekkotans. Those of *H. turcicus* and *M. kotschyi* have a pointed tubercle with a posteriorly directed point in the middle of the dorsal surface (Fig. A3.22I, A3.23D). In *H. turcicus*, the dorsal surface of this tubercle is flattened (Fig. A3.22I). In *T. mauritanica*, in the place of the tubercle there is a robust ridge, with the shape of an anteroposteriorly compressed W in dorsal view (Fig. A3.23I). The anterior surface of this ridge is smooth, whereas its dorsal margin is slightly irregular in anterior view. A very low midline crest runs posteriorly from the midpoint of the ridge. The dorsal surface of the supraoccipital of *E. europaea*, on the other hand, is smooth (Fig. A3.22D). The common crus is recognizable externally as an osseous swelling whose lateral margin can develop a slightly laterally developed lamina. The lamina is absent in *E. europaea*, *H. turcicus* and in MDHC 97 and 302.

Lacertidae (Fig. A3.24, A3.25A-D, A3.31E)

In lacertids, the supraoccipital bears a cylindrical and stocky processus ascendens, which continues posteriorly on the dorsal surface of the bone with a low supraoccipital crest (sometimes sharper in adults of large species). The degree of ossification of the processus varies with growth and within species: in juveniles and small-sized species it is ossified only by its base, whereas in adults and larger species the ossification is more developed. Two lateral crests are present by the sides of the processus, running along the anterior margin of the bone and merging in the short marginal processes by the contact with the prootics. In most species, the anterolateral margins are convergent in dorsal view, giving a hexagonal shape to the bone (Fig. A324I, A3.25D, A3.31E), but in *A. erythrurus* they are roughly parallel (Fig. A3.24D).

Scincidae (Fig. A3.25F-I, A3.26, A3.27, A3.31F)

A cylindrical processus ascendens is present also in *Chalcides* and its degree of development recalls the same interspecific differences present in lacertids. The processus of C. ocellatus is stocky, moderately ossified and continues posteriorly with a well-developed supraoccipital crest (Fig. A3.26F-I), whereas C. chalcides and C. striatus have a short and more slender processus, which does not produce a crest posteriorly (Fig. A3.26A-D). Because of this and of the very low development of the semicircular canals, the dorsal surface of the bone is smooth in the latter species. Ablepharus kitaibelii, O. punctatissimus and T. aurata, on the other hand, have a dorsoventrally compressed processus (Fig. A3.25F-I, A3.27A-D, A3.31F), which is very short in the former and longer in the two latter species. A distinct supraoccipital crest is lacking in these species also. Two small and pointed processes are present by the sides of the processus ascendens in C. chalcides (Fig. A3.26A-D); these processes are not recognizable in C. ocellatus and C. striatus, but the more expanded processus ascendens of the former could suggest that they are fused with it (Fig. A3.26F-I). The processus of T. aurata is flanked by two well-developed ridges, running along the anterior margin of the supraoccipital (Fig. A3.31F). Similar, but less developed ridges are visible in C. striatus too. Small marginal processes are recognizable by the anterior end of the contact with the prootics in *Chalcides* and O. punctatissimus.

Anguidae (Fig. A3.28)

The supraoccipital of anguids shows a well-developed, cylindrical and slightly dorsoventrally compressed processus ascendens, whose degree of ossification increases with growth. A low supraoccipital crest is present, but less developed in juveniles. The rest of the dorsal surface of the bone is smooth because of the very poor development of the semicircular canals. Lateral crests similar to those present in lacertids run along the anterior margin of the supraoccipital in anguids too, flanking the processus ascendens; these crests are well developed in adults (sometimes reaching the distal end of the processus), but lower in juveniles. A distinct, roughly V-shaped and rounded notch is clearly visible in the middle of the posterior margin in dorsal view.

Prootic

The prootic (Fig. A3.32) is a paired bone composed by a posterior process posteriorly, an alar process anterodorsally and an anterior inferior process ventrally. The posterior process is almost entirely occupied by the horizontal semicircular canal and, anterodorsally to the latter, by the anterior semicircular canal. A projection of the posterior end of this process covers the anterior surface of the paroccipital process of the otooccipital. From the anterodorsal end of the anterior semicircular canal, the alar process develops in anterodorsal direction; its anterior margin, the crista alaris, bears the articulation surface with the epipterygoid. The incisura prootica, the facial foramen and the laminar crista prootica stand out on the anterior inferior process. The incisura prootica is wide and located medioventrally to the alar process. The facial foramen opens both on the lateral and medial surfaces, ventrally to the horizontal semicircular canal and the crista prootica. The crista prootica runs anteroventrally starting from the ventral end of the anterior semicircular canal. It continues also on the posterior process, curving posteriorly and becoming a ridge that runs ventrally to the horizontal semicircular canal. The posterior portion of the recessus vena jugularis runs ventrally to the crista prootica. In medial view, two other large foramina are visible, opening in a concave acoustic recess: the smaller anterior acoustic foramen is located dorsally to the facial foramen and opens in the ampullary recess, whereas the very large posterior acoustic foramen is placed slightly posteriorly and opens internally between the cochlear cavity and the cavum capsularis. These two foramina carry the branches of the vestibulocochlear nerve.

The inner structures of the prootic, which encloses the anterior portion of the inner ear, include the anterior portions of the cavum capsularis dorsally, that of the cochlear cavity ventrally and the cochlear crest between them. The cavum capsularis is flanked by the opening of the anterior semicircular canal dorsally and by that of the horizontal semicircular canal laterally. By its medioventral corner, there is the opening of the ampullary recess. The dorsal half of the anterior wall of the cochlear cavity houses the wide groove for the perilymphatic duct.

This bone fuses with the sphenoid anteroventrally, the basioccipital posteroventrally, the supraoccipital posterodorsally and the otooccipital posteriorly.

Agamidae (Fig. A3.32A-C)

In *L. stellio*, the prootic has a very long and strong paroccipital projection, whereas the alar process is absent. The incisura prootica is very wide, whereas the recessus vena jugularis is not distinguishable. The facial foramen is also wide. The crista prootica is a strong lamina that becomes very much developed in its posterior portion (Fig. A3.32A). Both the length of the paroccipital projection and the development of the crista prootica are linked to ontogeny, with juveniles having shorter projections and less developed cristae. By the meeting point of the crista and the anterior semicircular canal, a low and arched ridge runs from the former to the dorsal surface of the latter in adults. On the medial surface, a variably developed, thin and pointed superior trabecular process extends forward from the anterior margin of the swelling representing the cavum capsularis (Fig. A3.32B).

The groove for the perilymphatic duct is very shallow. Similarly to the supraoccipital, a very narrow notch marking the ventral portion of the sphenoccipital foramen is present between the opening of the anterior semicircular canal and the cavum capsularis (Fig. 2.11, A3.32B-C).

Chamaeleonidae (Fig. A3.32D-E)

Prootics of *C. chamaeleon* lack an alar process. The paroccipital projection is moderately long. The incisura prootica and the recessus vena jugularis are not clearly distinguishable and the facial foramen is small. Only the (low) posterior portion of the crista prootica is present (Fig. A3.32D). The inner structures are poorly ossified and therefore they are not closed medially (Fig. A3.32E). There is not a distinct groove for the perilymphatic duct and the cochlear crest is very poorly defined. *Gekkota (Fig. A3.22, A3.23, A3.32F-G)*

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The paroccipital projection of the posterior process of gekkotans is short and covers only the proximal half of the paroccipital process. The alar process, on the other hand, is well developed. In lateral view, the latter is triangular (H. turcicus and T. mauritanica; Fig. A3.22G, A3.23G, A3.32F) or subtrapezoidal (E. europaea and M. kotschyi; Fig. A3.22B, A3.23B) in shape and has a pointed (H. turcicus; Fig. A3.22G) or rounded (other species; A3.22B, A3.23B, G) distal end. The crista alaris is mediolaterally expanded. Except for MDHC 98, the incisura prootica is dorsally closed by an osseous expansion. The well-developed crista prootica continues on the sphenoid in the supravenous process. In *H. turcicus* and *M. kotschyi*, the anterior and posterior portions of the crista are separated by a small notch (Fig. A3.22G, A3.23B). The posterior portion of the recessus vena jugularis is directed posterodorsally and reaches the facial foramen in M. kotschyi (Fig. A3.23B), whereas in E. europaea, H. turcicus and T. mauritanica it ends ventrally to the foramen without contacting it. In the latter species, the foramen is housed in a separated entocarotid fossa (not distinguishable in *M. kotschyi*), which is very distinct in *E. europaea* (Fig. A3.22B), mainly because of the presence of a laterally directed osseous expansion marking its ventral margin. In some specimens, this expansion can touch the ventral surface of the crista prootica. The prootic portion of the recessus is shallower than that of the sphenoid. The posterior acoustic foramen of European gekkotans is slightly more anteroposteriorly elongated than that of other lizards and, in contrast with the latter (which is completely defined by the prootic), its posterior margin is marked by the otooccipital (Fig. A3.32F).

Lacertidae (Fig. A3.24, A3.25A-E, A3.32H-K)

In the prootic of lacertids the paroccipital projection of the posterior process can be short (A. fitzingeri, A. marchi, A. moreoticus, A. bedriagae, I. cyreni, I. horvathi, I. monticola cantabrica, O. elegans, P. bocagei, P. carbonelli, P. filfolensis, Po. hispanicus, P. lilfordi, P. melisellensis, P. milensis, P. muralis, P. tauricus, P. tiliguerta, Ps. hispanicus and Z. vivipara; Fig. A3.25B, A3.32H) or long (A. erythrurus, A. nigropunctatus, D. oxycephala, D. mosorensis, E. arguta, H. graeca,

I. bonnali, I. monticola monticola, Lacerta, P. siculus, P. waglerianus, P. algirus and *T. lepidus*; Fig. A3.24B, G, A3.32J). The alar process is wide, wing-like-shaped and anteriorly rounded; it is moderately short in *A. erythrurus, A. fitzingeri, A. marchi, A. moreoticus, D. mosorensis, I. horvathi* and *O. elegans* (Fig. A3.24B) and longer in other species (Fig. A3.24G, A3.25B, A3.32H, J). The length of both the projection and the alar process, however, are linked to the ontogeny, being always shorter in juveniles. The incisura prootica is deep and the facial foramen is moderately or very wide. The crista prootica is well developed and continues on the sphenoid. In *A. erythrurus, A. fitzingeri, A. marchi, A. nigropunctatus, L. agilis, P. filfolensis, P. muralis, P. siculus, P. tiliguerta* and *P. waglerianus*, it has no posterior portion (Fig. A3.24B), whereas a low one is present in other species. Usually, neither a clearly distinguishable recessus vena jugularis nor an entocarotid fossa are recognizable.

Scincidae (Fig. A3.25F-J, A3.26, A3.27, A3.32L-M)

The prootics of scincids have a short paroccipital projection and an anteriorly rounded alar process, which is very short in *A. kitaibelii* (Fig. A3.25G), moderately short in *C. bedriagai*, *C. chalcides*, *C. striatus* and *T. aurata* (Fig. A3.26B, A3.32L) and long in *C. ocellatus* and *O. punctatissimus* (Fig. A3.26G, A3.27B). The incisura prootica is deep (very deep in *C. ocellatus*; Fig. A3.26G) and moderately wide (wider in *A. kitaibelii*; Fig. A3.25G). The facial foramen is also moderately wide, except for the one of *A. kitaibelii*; in *Chalcides* and *T. aurata*, its margins are raised compared to the external surface of the bone. The foramen is located at the posterodorsal end of a shallow and very wide posterior portion of the recessus vena jugularis. The crista prootica is low developed (sometimes even absent) in *A. kitaibelii* and *O. punctatissimus* (Fig. A3.25G, A3.27B) and well developed in the other species (Fig. A3.26B, G). In *Chalcides* and *O. punctatissimus*, it does not continue on the entire posterior process of the prootic: that of *C. bedriagai*, *C. chalcides*, *C. striatus* and *O. punctatissimus* ends by the facial foramen, whereas the one of *C. ocellatus* extends only slightly beyond it. By the anterior end of the contact with the supraoccipital, a

small marginal process is present in all species of *Chalcides* and in *O*. *punctatissimus*.

Anguidae (Fig. A3.28, A3.32N-O)

In anguids, the alar process is long and wide, with a rounded anterior end. The paroccipital projection is moderately long. The incisura prootica is U-shaped, very deep and wide and the facial foramen, which opens laterally in a shallow entocarotid fossa, is also wide. The crista prootica is low (*Anguis* gr. *A. fragilis*; Fig. A3.28B) or moderately developed (*P. apodus*; Fig. A3.28G) and moderately robust; it can also be slightly irregular. The anteriormost and posteriormost portions of the crista are almost unrecognizable. The posterior opening of the vidian canal opens on the ventral surface of the anterior inferior process of the prootic, ventrally to the facial foramen or slightly anteriorly. Only a reduced portion of the recessus vena jugularis is therefore visible posteriorly to it. In disarticulated specimens, the canal appears as a groove, since its lateral wall is composed by the crista ventrolateralis of the sphenoid.

Otooccipital

The otooccipital (Fig. A3.33) is a paired bone made up by the fusion of exoccipital and opisthotic, which are not recognizable as separate elements. Each otooccipital participates in the composition of the occipital condyle. In posterior view, the vertically oriented posterior semicircular canal stands out on the posterior surface of the bone, continuing dorsally on the supraoccipital. Between the ventral portion of the canal and the occipital condyle, there are some foramina: the largest and most dorsally placed one is the vagus foramen, whereas the others can be interpreted as the hypoglossal foramina, which may be highly variable in number. The welldeveloped paroccipital process is present laterally; it is roughly rectangular in posterior view. By the base of this process, one can see the posterior portion of the horizontal semicircular canal. On the lateral surface of the bone, the crista interfenestralis develops in anteroventral direction starting from the paroccipital process; this crista marks the dorsal margin of the lateral opening of the recessus scalae tympani.

The otooccipital encloses the posterior portion of the inner ear, housing the posterior walls of the cavum capsularis dorsally and of the cochlear cavity ventrally. The two cavities are not separated by ridges or grooves. The cavum capsularis is flanked by the opening of the horizontal semicircular canal laterally and by that of the posterior semicircular canal dorsally; its inner surface shows the openings of the ampullary recess ventrally and of the utricular recess dorsally. The cochlear cavity presents the perilymphatic foramen, which opens in the recessus scalae tympani.

This bone contacts the basioccipital ventrally, the prootic anteriorly and the supraoccipital dorsally, fusing with them.

Agamidae (Fig. A3.33A-D)

Each otooccipital of *L. stellio* composes less than a third of the occipital condyle. Two moderately wide hypoglossal foramina are present. The paroccipital process is very long and a very well developed and a laminar ridge is present on the proximal half of its ventral surface (Fig. A3.33A, D). Other lower ridges are visible on the anterior and dorsal surfaces, running along the entire process and lowering distally. A medium-sized foramen for the posterior portion of the vestibulocochlear nerve is visible in anterior view, between the opening of the ampullary recess and the perilymphatic foramen (Fig. A3.33A); it opens posteriorly on the ventromedial wall of the cavum capsularis.

Chamaeleonidae (Fig. A3.33E-H)

In *C. chamaeleon*, the portion of the occipital condyle composed by each otooccipital corresponds to almost its half (Fig. 2.10, A3.33G-H). A very large vagus foramen and, medially to it, a very small hypoglossal foramen are present between the posterior semicircular canal and the condyle (Fig. A3.33F). Another foramen is present between the vagus foramen and the contact with the sphenooccipital tubercles of the basioccipital; this latter foramen is small and completely encircled by the otooccipital and it is the only remain of the lateral opening of the recessus

scalae tympani (Fig. A3.33F). The paroccipital process (Fig. A3.33H) is straight, subrectangular in shape in posterior view and moderately thin in dorsal view. Low ridges are present along the dorsal half and near the ventral margin of its anterior surface. The inner structures are more ossified in the otooccipitals than in the prootics (Fig. A3.33E). Because of the reduction of the recessus scalae tympani, the perilymphatic foramen opens on the medial surface of the bone.

Gekkota (Fig. A3.22, A3.23, A3.33I-J)

Otooccipitals of European gekkotans compose a third of the occipital condyle. In the specimen examined, the number of hypoglossal foramina is highly variable, even among the otooccipitals of a same specimen (see the following table). In MDHC 119, 194, 384 (only on the right side) and 388, another foramen is visible, in posterior view, dorsally to the vagus foramen, placed medially to the posterior semicircular canal. The paroccipital process does not enlarge distally; it is short in *E. europaea* (Fig. A3.22A-E), but longer in all other species (Fig. A3.22F-J, A3.23; A3.33I). In *M. kotschyi* and *T. mauritanica*, a ridge (well developed in MDHC 97, 119 and 194, low in the other specimens) starts from the dorsal end of the semicircular canal and runs along the dorsal half of the anterior surface of the process, ending around the middle of its length; the proximal half of this ridge marks the contact between otooccipital and prootic. Another low ridge can be seen near the ventral margin of the same surface in all species, running along the entire process. This second ridge is only a hint in *E. europaea* and in most specimens of *T. mauritanica*, except for MDHC 119.

In *T. mauritanica*, a low ridge divides in two the lateral half of the cavum capsularis, starting medially between the two recesses housed in it. The medial wall of the cochlear cavity of gekkotans shows also the posterior margin of the posterior acoustic foramen.

	Number of
Species	hypoglossal
	foramina
E. europaea	2 or 3
H. turcicus	1, 5 or 6
M. kotschyi	2 or 3
T. mauritanica	2, 3 or 4

Lacertidae (Fig. A3.24, A3.25A-E, A3.33K-L)

As in gekkotans, the otooccipital of lacertids composes a third of the occipital condyle and the number of hypoglossal foramina is variable (see the following table). The paroccipital process is short in juveniles but well developed in adults of all species, except for *A. fitzingeri*, *A. marchi*, *A. moreoticus*, *I. cyreni*, *I. monticola cantabrica*, *O. elegans*, *P. bocagei*, *P. carbonelli*, *P. filfolensis*, *Po. hispanicus*, *P. melisellensis*, *P. muralis*, *P. tauricus*, *P. tiliguerta*, *P. waglerianus*, *Ps. hispanicus* and *Z. vivipara*, in which it remains rather short (Fig. A3.25A-E, A3.33K). The process is slightly dorsoventrally enlarged by its distal end.

Species	Number of hypoglossal foramina
A. erythrurus	1 or 2
A. fitzingeri	3
A. moreoticus	3
A. nigropunctatus	3
A. bedriagae	3
D. oxycephala	2 or 3
D. mosorensis	2 or 3
E. arguta	1
H. graeca	1, 2 or 3

I. bonnali	3
I. cyreni	3
I. horvathi	Not counted
I. monticola	3
L. agilis	3 or 4
L. bilineata	2, 3 or 4
L. schreiberi	2 or 3
L. trilineata	2, 3 or 4
L. viridis	2, 3 or 4
O. elegans	1, 2 or 3
P. bocagei	3
P. filfolensis	2
Po. hispanicus	2 or 3
P. melisellensis	2 or 3
P. milensis	3
P. muralis	2 or 3
P. siculus	3 or 4
P. tauricus	2 or 3
P. tiliguerta	2 or 3
P. waglerianus	3
P. algirus	3
T. lepidus	3 or 4
Z. vivipara	3

Scincidae (Fig. A3.25F-J, A3.26, A3.27, A3.33M-N)

In scincids, the participation of the otooccipital in the formation of the condyle is the same as in gekkotans and lacertids. Hypoglossal foramina are usually 2, but there can also be 3 or 4 of them. The paroccipital process is very short (*A. kitaibelii* and *O. punctatissimus*; Fig. A3.25F-J, A3.27), short (*C. chalcides, C. striatus* and *T. aurata*; Fig. A3.26A-E, A3.33M) or moderately long (*C. ocellatus*; Fig. A3.26F.J)

and roughly axe-shaped in posterior view. A low (*A. kitaibelii* and *Chalcides*) or moderately developed (*O. punctatissimus* and *T. aurata*) ridge runs along its ventral margin, on the anterior surface.

Anguidae (Fig. A3.28, A3.33O-P)

Each otooccipital of anguids composes less than one third of the occipital condyle. Two hypoglossal foramina are usually present, but rarely there can be a third one. In *P. apodus*, the external opening of one of the foramina is merged with that of the vagus foramen, but they are still recognizable as different foramina because of the presence of a septum between them. The paroccipital process is subrectangular, with only a weak widening by the distal end. It is moderately short in *Anguis* gr. *A. fragilis* (Fig. A3.28A-E, A3.33O) and long in *P. apodus* (Fig. A3.28F-J). Both the anterior and the posterior surfaces of the process are smooth. Ventrally, the otooccipital develops a projection that encloses posteriorly the lateral opening of the recessus scalae tympani, even if the basioccipital is not completely excluded from its formation.

Stapes

The paired stapes (Fig. A3.33Q-U) is a small bone composed by a slender shaft and by an enlarged medial footplate.

Agamidae

Laudakia stellio has short stapes provided with an elliptical footplate. There is no stapedial foramen.

Chamaeleonidae (Fig. A3.33Q)

Stapes of *C. chamaeleon* has a subelliptical footplate, no stapedial foramen and a very narrow and pointed distal end.

Gekkota (Fig. A3.33R)

In European gekkotans, the footplate is elliptical, except for *H. turcicus* in which it is subcircular. Near the footplate, the shaft is pierced by the moderately wide stapedial foramen.

Lacertidae (Fig. A3.33S)

The footplate of the stapes of lacertids is subcircular. No stapedial foramen is present. *Scincidae (Fig. A3.33T)*

The stapes of scincids has an elliptical footplate and no stapedial foramen.

Anguidae (Fig. A3.33U)

In anguids, the stapes has a short shaft with no stapedial foramen and a large and elliptical footplate.

Dentary

The dentary (Fig. A3.34) is a long paired bone, straight in both dorsal and medial view; only the anterior end bends moderately in medial direction. The medial surface of the anterior end is covered by the mandibular symphysis. A channel, the Meckelian fossa, is present on the medial surface of the bone and houses the anterior portion of the Meckel's cartilage. Dorsally to the fossa, an alveolar shelf bears the teeth. The sulcus dentalis (sensu Roček 1984) runs longitudinally between the ridge and the alveolar shelf. The medially developed subdental ridge separates the fossa from the shelf. Another channel, the alveolar canal, is present between the Meckelian fossa and the subdental ridge, housing the inferior alveolar nerve. This canal is visible only as a foramen opening in posterior direction, since the intramandibular septum closes it medioventrally. The posterior end of the bone shows two laminar and posteriorly directed processes: the inferior one ventrally and the superior one dorsally. A variable number of anteroposteriorly aligned mental foramina is present lizards.

Agamidae (Fig. A3.34A-B)

The dentary of *L. stellio* is stocky and its mandibular symphysis is large and subcircular or subelliptical in medial view (Fig. A3.34A). The Meckelian fossa is narrow, but widens slightly in its posterior half (Fig. A3.34A). The subdental ridge is high in medial view and develops a low ventral expansion in its posterior portion

(Fig. A3.34A). The posterior end of the intramandibular septum is located roughly by the middle of the tooth-row (by the 13th/14th tooth position in adults and between the 7th and 8th tooth positions in juveniles). Two different tooth morphologies are present: the two anteriormost teeth are large, subpleurodont, stocky, conical and monocuspid, whereas posteriorly there are acrodont and triangular teeth. The latter are closely spaced and can present small accessory cusps located anteriorly and posteriorly to the main one; their base is slightly extended towards the medial surface of the alveolar shelf. Anteriormost acrodont teeth are very small, but their size tends to increase posteriorly; the largest acrodont teeth, however, are located in the second third of the tooth row, since the posteriormost ones are slightly smaller. In juveniles, the two subpleurodont teeth are smaller, whereas all acrodont ones are large (though an increasing trend is still recognizable towards the posterior end of the bone). Posterior processes are well developed, wide and moderately robust. They are roughly pointed and similar in both width and length. In medial and lateral views, only a small U-shaped notch separates them. In posterior view, a recess similar to the one present in C. chamaeleon (see below) is present (Fig. A3.34B), but in L. stellio it is very narrow. The ventral margin of the dentary is very slightly convex in medial view and slightly expanded in medial direction. On the lateral surface of larger individuals, moderately deep and ventrally directed interdental grooves separate each tooth from the adjacent ones (Fig. A3.34B).

The maximum length of the alveolar shelf ranges from 5.7 mm to 17.5 mm and the number of tooth positions varies from 10 to 19 (including the two subpleurodont ones). The number of mental foramina ranges from 4 to 8.

Chamaeleonidae (Fig. A3.34C-D)

In *C. chamaeleon*, the dentary is stocky and presents a moderately wide mandibular symphysis (Fig. A3.34C), which is almost vertical (it shows only a low inclination of less than 25° in anteroposterior direction). The Meckelian fossa and the subdental ridge are similar to the ones of *L. stellio*, but the anterior half of the former opens in ventral direction (Fig. A3.34C). The posterior end of the intramandibular septum is

visible in the second half of the tooth row, between the 14th and the last tooth position (Fig. A3.34C). Teeth are acrodont and are morphologically similar to the acrodont ones of *L. stellio*. However, they differ from them in being well spaced and carried on the dorsal margin of the bone (not expanding on the medial surface). In articulated specimens, one can see that they continue posteriorly to the anterior margin of the coronoid. Inferior and superior processes are pointed and have roughly the same width, even though the inferior one can be either as long as or longer than the other one. In posterior view, a large recess, deeply developed inside the dentary, is visible between the posterior processes (Fig. A3.34C). As in *L. stellio*, the ventral margin of the bone is very slightly convex in medial view and slightly expanded in medial direction. Interdental grooves are present on the lateral surface (Fig. A3.34D).

The maximum length of the alveolar shelf varies from 15 mm to 18 mm, whereas the number of tooth positions ranges from 17 to 21. The number of mental foramina can be 3, 4 or 5.

Gekkota (Fig. A3.34E-L)

The mandibular symphysis of the dentaries of gekkotans is narrow and inclined anteriorly at an angle of about 45°. The Meckelian fossa is closed in a tubular structure composed by completely fused osseous expansions of the ventral margin and the subdental ridge. The tube is moderately narrow and tends to shrink anteriorly. The fossa is opened only by the anterior end with a small foramen, which continues anteriorly in a groove in all species except for *T. mauritanica*, and by the posterior one with a V-shaped (U-shaped in *T. mauritanica*; Fig. A3.34K) notch. The notch extends along the posterior third (*E. europaea*; Fig. A3.34E), fourth (*H. turcicus*; Fig. A3.34G), fifth (*T. mauritanica*; Fig. A3.34K) or sixth (*M. kotschyi*; Fig. A3.34I) of the alveolar shelf. Teeth are pleurodont, cylindrical, slender and bicuspid, with a labial and a lingual cusp (morphotype F sensu Kosma 2004, Fig. 2.12; see also Sumida & Murphy 1987). The inferior process is long and pointed, whereas the superior one is smaller and divided into two pointed projections separated by a deep V-shaped notch. The size of the two projections is subject to individual variation, but



Figure 2.12) Dentary teeth of European gekkotans in lingual view. A: E. europaea (*MDHC 384*). *B:* H. turcicus (*MDHC 26*). *C:* M. kotschyi (*MDHC 201*). *D:* T. mauritanica (*MDHC 119*). as a rule the dorsal one is the shortest one. The ventral margin of the bone is straight in medial view.

The maximum length of the alveolar shelf ranges from 4.2 mm to 4.8 mm in *E. europaea*, from 6 mm to 7 mm in *H. turcicus*, from 5.3 mm to 7 mm in *M. kotschyi* and from 8.5 mm to 10.6 mm in *T. mauritanica*. Dentaries of *E. europaea* show 28 to 32 tooth positions and 5 to 8 mental foramina, those of *H. turcicus* 28 to 31 of the former and 5 to 6 of the latter, those of *M. kotschyi* 27 to 37 and 4 to 5 and those of *T. mauritanica* 29 to 33 and 3 to 5.

Lacertidae (Fig. A3.34M-P)

Lacertids have a narrow and almost horizontal mandibular symphysis. The Meckelian fossa is wide, but narrows towards the anterior end of the bone. The subdental ridge is narrow in medial view and can display a very little ventral

expansions towards its anterior end. Teeth are slender, cylindrical, pleurodont, mono- and bicuspid (morphotype B and G sensu Kosma 2004, respectively); as in the maxillae, there can be also tricuspid teeth (morphotype H sensu Kosma 2004), mostly in large-sized species. A distinct increase in the robustness of the teeth is visible in the posterior part of the tooth row of Algyroides, A. bedriagae, D. oxycephala, D. mosorensis, E. arguta, H. graeca, I. monticola, Lacerta, P. filfolensis, Po. hispanicus, P. lilfordi, P. melisellensis, P. milensis, P. muralis, P. pityusensis, P. tauricus, P. waglerianus, T. lepidus, Z. vivipara and some specimens of *P. siculus*. Size and proportions of the pointed posterior processes varies within species: they are similar in length in A. erythrurus, E. arguta, L. viridis, T. lepidus and in adults of I. bonnali, L. agilis, L. schreiberi, L. trilineata, P. bocagei, P. carbonelli, Po. hispanicus, P. muralis and P. algirus, whereas the inferior one is longer than the superior one in Algyroides, A. bedriagae, D. oxycephala, D. mosorensis, H. graeca, I. cyreni, I. horvathi, I. monticola, O. elegans, P. filfolensis, P. melisellensis, P. milensis, P. pityusensis, P. siculus, P. tauricus, P. tiliguerta, P. waglerianus, Ps. hispanicus, Z. vivipara (Fig. A3.34O-P) and in juveniles of I. bonnali, L. agilis, L. schreiberi, P. bocagei, P. carbonelli, Po. hispanicus, P. muralis and P. algirus. According to Barahona (1996) and Barahona & Barbadillo (1997), the superior process should be always the longest one in L. bilineata (= L. viridis in Barahona 1996). In all the herein considered specimens of this species, however, the degree of development of the posterior processes follows the standard pattern of most other *Lacerta* species (i.e., equally long in adults, but inferior one longer in juveniles and subadults; Fig. A3.34M-N). The ventral margin is distinctly convex in medial view.

Measurements, number of tooth positions and of mental foramina and the position of the posterior end of the intramandibular septum are given in the following table:

	Maximum	Number of	Position of the	Number of
Species	length of the	tooth	intramandibular	mental
	alveolar shelf	positions	septum	foramina
A amithematic	7.5 mm - 8.2	21 24	18 th tooth position	5 6
A. erymrurus	mm	21 - 24		5-0
A fitzingari	5	23	Between 19th and	5
A. Juzingen	5 11111		20 th tooth position	5
A. marchi	5 mm	21 - 25	Not checked	6
A. moreoticus	4.8 mm - 4.9	21	17 th tooth position	6 - 7
	111111		D (1 10th	
А.	6.5 mm - 8	24 25	Between the 19 th	
nigropunctatus	mm	24 - 27	and the 22 nd tooth	5 - 7
			position	
			Between the 20 th	
A. bedriagae	8 mm - 11 mm	20 - 26	and the 21 st tooth	5 - 7
			position	
			Between the 20 th	
D. oxycephala	6 mm - 8 mm	22 - 26	and the 22 nd tooth	5 - 6
			position	
D. mosorensis	6.4 mm - 8.2	23 - 27	Not checked	4 - 7
E. arguta	10.6 mm -	20 - 23	Not checked	5 - 6
	10.7 mm			
H. graeca	6.5 mm - 8.5	22 - 27	Between 18 th and	4 - 6
	mm	22 2,	20 th tooth position	
I. aranica	Not measured	16 - 20	Not checked	Not counted
I. aurelioi	Not measured	16 - 22	Not checked	Not counted
I. bonnali	Not measured	17 - 21	Not checked	Not counted
I. cyreni	7.7 mm	20 - 24	18 th tooth position	6

I. horvathi	6.2 mm - 6.3 mm	22 - 23	Not checked	6
I. martinezricai	Not measured	19 - 21	Not checked	Not counted
I. monticola	6.7 mm - 6.8 mm	17 - 23	15 th or 16 th tooth position	5
L. agilis	5.6 - 8 mm	18 - 22	Between 14 th and 16 th tooth position	4 - 8
L. bilineata	6.4 mm - 13.2 mm	19 - 27	Between 15 th and 19 th tooth position	5 - 7
L. schreiberi	10.7 mm - 11 mm	23 - 24	17 th tooth position	6 - 8
L. trilineata	12.7 mm - 14.5 mm	23 - 28	Between 16 th and 22 nd tooth position	4 - 6
L. viridis	10.5 mm - 18.1 mm	21 - 30	Between 18 th and 20 th tooth position	4 - 7
O. elegans	4.6 mm - 5.4 mm	22 - 27	Between 20 th and 24 th tooth position	4 - 5
P. bocagei	5.9 mm	23	20 th tooth position	6 - 7
P. erhardii	Not measured	22	Not checked	Not counted
P. filfolensis	6.8 mm - 7 mm	18 - 21	Between 15 th and 16 th tooth positon	6 - 7
Po. hispanicus	5.6 mm - 7.2 mm	21 - 24	18 th tooth position	5 - 6
P. lilfordi	7.2 mm - 8.4 mm	18 - 21	Not checked	6
P. melisellensis	5.2 mm - 8 mm	20 - 25	Between 18 th and 20 th tooth position	4 - 7
P. milensis	6.6 mm - 6.9 mm	22	18 th tooth position	6

P. muralis	5.7 mm - 7.9 mm	19 - 25	Between 16 th and 20 th tooth position	5 - 7
P. pityusensis	9 mm	18 - 23	16 th tooth position	Not counted
P. siculus	5.1 mm - 10 mm	19 - 26	Between 19 th and 22 nd tooth position	4 - 7
P. tauricus	7 mm - 7.4 mm	21 - 24	Between 19 th and 21 st tooth positon	5 - 7
P. tiliguerta	7 mm - 7.5 mm	24 - 26	Between 20 th and 21 st tooth position	6 - 7
P. waglerianus	8 mm - 10 mm	22 - 24	Between 18 th and 19 th tooth position	5 - 6
P. algirus	8.5 mm	21 - 26	17 th tooth position	7
T. lepidus	6 mm - 24.3 mm	16 - 31	Between 12 th and 20 th tooth position	5 - 7
Z. vivipara	5 mm - 5.8 mm	18 - 22	Between 16 th and 18 th tooth position	4 - 7

Scincidae (Fig. A3.34Q-X)

The mandibular symphysis is narrow and almost horizontal in European the dentaries of scincids too. The Meckelian fossa is wide in its posterior half and very narrow in the anterior one. Moreover, the anterior half of the fossa opens in ventral direction, since a ventral expansion of the subdental ridge it medially. The covers



Figure 2.13) Dentary tooth of C. chalcides (*MDHC 94*) *in lingual view. The arrow marks a stria on the lingual side of the tooth.*

remaining portion of the ridge is narrow, as in lacertids. Caputo (2004) states that some specimens of C. ocellatus can present a partly closed fossa, probably because of a very strong development of the subdental ridge. This happens also in T. aurata (e.g., MDHC 280; Fig. A3.34W). Ablepharus kitaibelii, on the other hand, shows an almost entirely closed Meckelian fossa, which opens only by the anterior and posterior ends of the tooth row with narrow notches (Fig. A3.34Q). As in other toothbearing bones of this family, teeth are morphologically similar to those of gekkotans, except for a slightly posteriorly curved crown provided with a light striation on the lingual surface (Fig. 2.13). The exception are C. ocellatus, whose teeth are robust and provided with a blunt and enlarged crown (Fig. A3.34S-T), and O. *punctatissimus*, in which teeth are increasingly more robust towards the posterior end of the tooth row (but the last tooth position is smaller than the preceding ones; Fig. A3.34U-V). The morphology of the posterior processes is usually similar to the one presented by gekkotans, but the notch separating the projections of the superior one is very shallow and roughly U-shaped. Moreover, the largest projection is usually the dorsal one, whereas the ventral one is very small. In A. kitaibelii, the latter is not recognisable and a rounded expansion can be present on the dorsal margin of the inferior posterior process (Fig. A3.34Q-R). Ophiomorus *punctatissimus*, on the other hand, displays three posterior processes by its posterior end, since a central posterior process is located between the dorsal and the ventral ones (Fig. A3.34U-V). The superior posterior process of O. punctatissimus differs from that of other European scincids because it is distinctly directed posterodorsally and not composed by separated projections (Fig. A3.34U-V). In the same species, the three processes can be either roughly similar in size (e.g., in MDHC 427) or the central one can be smaller than the others (e.g., in MCZ 38517). In medial view, the ventral margin of the dentary is straight.

Measurements, number of tooth positions and of mental foramina and the position of the posterior end of the intramandibular septum are given in the following table:

	Maximum	Number of	Position of the	Number of
Species	length of the	tooth	intramandibular	mental
	alveolar shelf	positions	septum	foramina
A. kitaibelii	2.2 mm - 2.8 mm	16 - 19	Not visible	4 - 7
C. bedriagai	5 mm	15 - 18	Not checked	5
C. chalcides	5.2 - 5.9 mm	18 - 22	16 th or 18 th tooth position	4 - 5
C. ocellatus	7.3 - 9 mm	16 - 18	12 th or 14 th tooth position	4 - 7
C. striatus	4.8 mm	18 - 21	Between the 15 th and the 16 th tooth position	4 - 5
O. punctatissimus	2.9 mm	13 - 14	Last tooth position	4 - 6
T. aurata	8.5 mm - 10.9 mm	25 - 31	Between the 20 th and the 21 st tooth position	6 - 8

Anguidae (Fig. A3.34Y-AB)

Dentaries of anguids have a narrow and horizontal mandibular symphysis, like lacertids and scincids. In dorsal view, a small medially developed expansion of the posterior end of the symphysis is recognizable (Fig. 2.14). A real subdental ridge is not present, being replaced by a smooth subdental shelf. The sulcus dentalis is also absent. The subdental shelf is distinctly developed in ventral direction and covers almost entirely the narrow Meckelian fossa. The fossa, therefore, opens ventrally and only its wider posterior end is visible in medial view. Roughly by the beginning of the posterior fourth (*Anguis* gr. *A. fragilis*; Fig. A3.34Y) or third (*P. apodus*; Fig. A3.34AA) of the tooth row, the subdental shelf presents a posteriorly developed and pointed splenial spine, which is moderately long in *Anguis* gr. *A. fragilis* and short
in *P. apodus*. The intramandibular septum develops posteriorly with a pointed portion, which reaches the notch between the posterior processes. This portion is free (i.e., unfused to the wall of the fossa) in Anguis gr. A. fragilis (Fig. A3.34Y), but fused with the wall of the bone in *P. apodus* (Fig. A3.34AA). The opening of the alveolar canal is located by the end of the 9th tooth position in Anguis gr. A. fragilis (near the last tooth position, as stated by Klembara et al. 2014; Fig. A3.34Y) and between the 9th and the 11th tooth position in *P. apodus* (Fig. A3.34AA). Like in the maxilla, teeth are large and subpleurodont, with the maximum size that is reached in the middle of the tooth row in Anguis gr. A. fragilis and by its third quarter in P. apodus. In the former, they are monocuspid, trenchant, well spaced, unstriated and distinctly posterolingually bent by their tip (Fig. A3.34Y-Z), whereas the latter shows monocuspid, cylindrical and slightly robust teeth, provided with a pointed and not curved tip, anteriorly and large, cylindrical and stout teeth, provided with a blunt and rounded crown, posteriorly (Fig. A3.34AA-AB). Moreover, teeth of P. apodus are closely spaced and their change in size is gradual. Weak striae are visible both labially and lingually on the crowns of the teeth of *P. apodus*, but not in those of Anguis gr. A. fragilis. The inferior posterior process (angular process in Klembara et

al. 2014) is short and pointed, whereas the superior one is very long and large (more than twice the former in length). The two posterior projections of the superior process (named, from the dorsal one to the ventral one, coronoid and surangular processes in Klembara et al. 2014) are separated by а moderately wide and deep Ushaped notch (coronoid incisure



Figure 2.14) Anterior end of the dentaries of P. siculus (MDHC 125; A) and Anguis gr. A. fragilis (MDHC 102; B) in dorsal view. The arrow marks the expansion of the anguid symphysis. Scale bar = 1 mm.

in Klembara et al. 2014). They are similar in size in *Anguis* gr. *A. fragilis* (Fig. A3.34Y-Z), but the dorsal one is distinctly shorter than the ventral one in *P. apodus* (Fig. A3.34AA-AB). The surangular process of *P. apodus* bears an opening for the anterior surangular foramen (Fig. A3.34AB), since this process covers the surangular opening of this foramen in this species. In medial view, the bone has a rather convex ventral margin, whose posterior end bends distinctly in dorsal direction. The flexure of the posterior end appears to be stronger in *Anguis* gr. *A. fragilis* than in *P. apodus*. The maximum length of the alveolar shelf goes from 3.8 mm to 6.5 mm in *Anguis* gr. *A. fragilis* and from 17 mm to 20 mm in *P. apodus*. *Anguis* gr. *A. fragilis* shows 10 or 11 tooth positions (8 or 9 in the specimens studied in Edmund 1969) and 3 or 4 mental foramina, whereas in *P. apodus* they range from 12 to 18 and from 4 to 7 respectively.

Splenial

The paired splenial (Fig. A3.35) is a blade-like bone, pierced by two foramina: the anterior inferior foramen anterodorsally and the anterior mylohyoid foramen posteroventrally.

Agamidae and Chamaeleonidae

The splenial is absent in both *L. stellio* and *C. chamaeleon*, as previously reported for some agamids and chamaeleons in general by some authors (Jollie 1960; Evans 2008). The same authors state that the condition seen in agamids is very variable,

including also species in which this bone is either present but reduced or fused to the other portions of the lower jaw. However, even though Baig et al. (2012) reported a small splenial in *Laudakia*, the presence of articulated material



Figure 2.15) Median portion of the right lower jaw of L. stellio (HUJ.OST-Z-5) in medial view, showing the absence of the splenial. Scale bar = 1 mm.

in the herein-studied material (HUJ.OST-Z-5) allows to point out its absence in the European species (Fig. 2.15).

Gekkota (Fig. A3.35A-H)

The splenial of gekkotans is very reduced and thin. The foramina are located on the anterior portion of the bone; they are both wide, but, in *M. kotschyi* and *T. mauritanica* (except for NHMW 31945), the anterior mylohyoid one is represented only by a notch on the ventral margin of the bone (Fig. A3.35E-H). The posterior corner of the splenial of *E. europaea* and *H. turcicus* expands posteriorly and bends laterally, forming a long and thin pointed process (Fig. A3.35A-D), which contributes to form the ventral surface of the lower jaw. In *M. kotschyi*, this bone takes part only in the formation of the medial surface (Fig. A3.35E-F), whereas in *T. mauritanica* only a small triangular process originated by the lateral bending of the posterior end is present (Fig. A3.35G-H). Both medial and lateral surfaces are otherwise smooth.

Lacertidae (Fig. A3.35I-N)

Lacertids have a large and long splenial, with pointed anterior and posterior ends. *Lacerta agilis*, *L. bilineata*, *L. schreiberi*, *L. viridis* and *T. lepidus* can frequently have a forked anterior end (Fig. A3.35M-N). This feature can be present sometimes in *I. cyreni* and *Z. vivipara* also. The foramina are located roughly in the middle of the bone and they are very close to each other. The anterior inferior foramen is large, whereas the anterior mylohyoid one is small. The medial surface of the bone is smooth and slightly concave, whereas two ridges are present on the lateral one: the dorsal crest runs along the dorsal margin, whereas the medial one extends longitudinally in the middle of the surface. The splenial of *A. erythrurus* is expanded ventrally (Fig. A3.35I-J).

Scincidae (Fig. A3.350-V)

The general shape of the splenial of European scincids is similar to that of lacertids, but some differences are present. The two foramina are shifted towards the anterior end of the bone and the anterior inferior one is not closed anteriorly, forming a narrow (wide in *O. punctatissimus*; Fig. A3.35S-T) and very deep notch. The dorsal crest runs ventrally to, and not by, the dorsal margin, whereas the medial one is shifted towards the ventral margin. In *O. punctatissimus*, the dorsal crest is reduced to a small hint located dorsally to the anterior notch (Fig. A3.35S). The ventral margin is straighter in medial view than the one of lacertids (which is rather convex) and the posterior portion of the dorsal one is wavy in *Chalcides* (Fig. A3.35Q-R), straight in *O. punctatissimus* (Fig. A3.35S-T) and convex in *T. aurata* (Fig. A3.35U-V); the same margin is concave in lacertids. *Ablepharus kitaibelii*, however, has a reduced, thin and blade-like splenial, with pointed anterior and posterior ends (Fig. A3.35O-P). A deep and wide notch, representing the anterior inferior foramen, is visible on the dorsal margin of its anterior end, whereas the anterior mylohyoid foramen is represented by a small notch located roughly at mid-length of the ventral margin. Both the medial and the lateral surfaces of the splenial of *A. kitaibelii* are smooth.

Anguidae (Fig. A3.35W-Z)

In anguids, the splenial is composed by a slender and pointed anterior half and by a wide and laminar posterior half. The anterior half is mediolaterally developed, covering ventrally the Meckelian fossa of the dentary. The posterior end of the bone is irregular, with three processes: a wider and posteriorly truncated dorsal one and two longer, slender and pointed ventral ones. Only the small anterior mylohyoid foramen is clearly visible at mid-length, whereas a wide notch located on the anterodorsal margin of the bone marks the ventral margin of the anterior inferior foramen, lying between the splenial and the dentary. This notch is usually very shallow, but it can be very deep in some large specimens of *P. apodus*, because of the presence of a slender and pointed process dorsally (Fig. A3.35Y-Z). A medial crest (prearticular crest in Klembara et al. 2014) runs along the entire length of the bone on its lateral surface, whereas only a short hint of the dorsal crest is present on the anterodorsal margin, by the notch of the anterior inferior foramen. The medial surface is smooth.

Coronoid

The paired coronoid (Fig. A3.36) has an irregular shape, with five processes. In the middle, it shows the dorsally developed coronoid process, which is subtriangular in lateral view. The other processes are the labial process (anterolaterally), the anteromedial process (anteromedially), the posterior process (posteriorly) and the posteromedial process (posteromedially). The anteromedial process is always larger and longer than the labial process and both are pointed. The morphology of other processes varies among different groups.

Agamidae (Fig. A3.36A-B)

In *L. stellio*, the coronoid is robust and roughly straight in dorsal view. It has a welldeveloped, stocky and dorsally rounded coronoid process. There is no labial process and the anteromedial one is well developed, laminar and provided with an expanded (not pointed) anterior end. The posterior process is moderately short and pointed; a groove for the articulation with the dorsal margin of the surangular is present on its ventrolateral surface (Fig. A3.36A). The coronoid and the posterior processes are connected by a low and thin osseous lamina. The posteromedial process is long, thick and straight in medial view; it has a roughly rounded ventral end. On the medial surface of the bone, a very thick coronoid ridge runs from the coronoid process to the ventral end of the posteromedial process (Fig. A3.36B). The ridge is less developed in juveniles.

Chamaeleonidae (Fig. A3.36C-D)

Coronoids of *C. chamaeleon* are robust and straight in dorsal view. The coronoid process is well developed and stocky, provided with a rounded dorsal end. The labial process is absent, whereas the anteromedial one is straight and well developed. The posterior process is well developed, straight and pointed. The posteromedial process is moderately small and triangular; it is connected to the anteromedial process by a moderately developed thin osseous lamina and to the posterior process by a lower thin lamina that marks the anterior margin of the adductor fossa. A low coronoid

ridge runs dorsoventrally on the medial surface of the posteromedial process, starting from the coronoid one (Fig. A3.36D).

Gekkota (Fig. A3.36E-L)

In this group, this bone is strongly crescent-shaped in dorsal view (Fig. 2.16A). The thin and roughly pointed (dorsally rounded in E.



Figure 2.16) Coronoids of T. mauritanica (MDHC 302; A), I. monticola cantabrica (UAM.R.Lm92; B), C. ocellatus (MDHC 250; C) and Anguis gr. A. fragilis (MDHC 102; D) in dorsal view, showing the difference in the degree of medial concavity of the bones. Scale bars = 1 mm.

europaea; Fig. A3.36E-F) coronoid process develops a well-developed osseous lamina posteriorly, running along the medial margin of the posteromedial process. This lamina seems to be homologous to the coronoid ridge of the other groups. The anteromedial process is composed by two laminae split by a groove in dorsal view; the dorsomedial lamina is smaller than the ventrolateral one. The splitting is almost not recognizable in *E. europaea* (Fig. A3.36E-F). A foramen pierces the center of the lateral lamina of the process. The posteromedial process is moderately long, thin and pointed (in *H. turcicus* and *M. kotschyi*; Fig. A3.36G-J) or rounded (in *E. europaea* and *T. mauritanica*; Fig. A3.36E-F, K-L) in dorsal view. It is posteriorly directed, curving only slightly in ventral direction. There is no posterior process. *Lacertidae (Fig. A3.36M-P)*

In lacertids, the coronoid is only moderately concave in medial direction (Fig. 2.16B). The coronoid process is robust and has a rounded dorsal end, which is slightly posteriorly directed in *A. erythrurus*, *A. fitzingeri*, *A. marchi*, *O. elegans* and in juveniles of other species (Fig. A3.36M-N). The anteromedial process is ventrally expanded and the pointed anterior end is represented by a small projection, which is more developed in adults of *A. marchi*, *I. cyreni*, *I. monticola*, *P. bocagei*, *P. carbonelli*, *Po. hispanicus*, *P. muralis* and *Z. vivipara* than in juveniles and in other

species. The posterior process is short and rounded and therefore the posterior portion of the coronoid has the shape of a lappet with a wavy posterior margin. A shallow concavity on this latter margin represents the anterior margin of the adductor fossa. Sometimes, the posterior process is slightly more developed and therefore the concavity is moderately deeper. The posteromedial process is moderately large, roughly rounded and distinctly ventrally directed; a moderately to well-developed coronoid ridge runs on its medial surface, starting from the coronoid process. A second moderately developed ridge connects the posterior surface of the coronoid process with the dorsal surface of the posterior one.

Scincidae (Fig. A3.36Q-V)

Scincids have a moderately crescent-shape coronoid (Fig. 2.16C), provided with an anteromedial process that is morphologically similar to the one of gekkotans. However, in contrast with the latter group, this process does not show foramina. The labial process is strongly reduced in O. punctatissimus (Fig. A3.36U). The coronoid process is dorsally rounded; its thickness is variable, with smaller species (e.g., C. chalcides) having a thin process and larger species (e.g., C. ocellatus) having a more robust one. The posterior process is usually not distinguishable, but a moderately large, rounded, ventrally-directed and lappet-like posteromedial process is present. Only O. punctatissimus can display a small posterior process in some specimen (e.g., MCZ 38517). A well-developed coronoid ridge connects the dorsal end of the coronoid process with the ventral end of the posteromedial process, running along the posterior margin of the former and the anterior margin of the latter. In the smallest species (e.g., C. chalcides), the ridge is very similar to the osseous lamina found in gekkotans. In C. ocellatus, similarly to lacertids, a second, low ridge runs on the posterior surface of the coronoid process, continuing posteriorly on the dorsal portion of the posteromedial one (Fig. A3.36S-T).

Anguidae (Fig. A3.36W-Z)

The coronoid of anguids is rather straight (very slightly medially concave) in dorsal view (Fig. 2.16D). The coronoid process is moderately thin (*Anguis* gr. *A. fragilis*;

Fig. A3.36W-X) or distinctly robust (*P. apodus*; Fig. A3.36Y-Z), dorsally rounded and posteriorly directed. The anteromedial process is represented by a roughly horizontal and slender lamina, lacking any foramina and, at least in Anguis gr. A. *fragilis*, provided with a pointed and moderately developed projection by its anterior end (Fig. A3.36W-X). The posterior process is very short (often lacking in smaller individuals) and is represented only by a small projection on the dorsal margin of the posteromedial process, defining a small and shallow notch on the posterior end of the coronoid. The degree of development of the posterior process is higher in P. apodus (Fig. A3.36Y-Z) than in Anguis gr. A. fragilis (Fig. A3.36W-X). The posteromedial process is very long, slender and can be lobe-shaped or pointed; in anguids, this process develops more posteriorly than ventromedially. A welldeveloped and laminar coronoid ridge, very similar to the lamina of gekkotans, is present between the coronoid and the posteromedial processes. The laminar ridge of P. apodus (Fig. A3.36Y-Z) is thicker and slightly less developed than the one of Anguis gr. A. fragilis (Fig. A3.36W-X), being also less distinguishable from the coronoid process.

Angular, surangular, prearticular and articular

These four bones (Fig. A3.37, A3.38) compose the posterior portion of the mandible, enclosing the posterior portion of the Meckel's cartilage. They can fuse completely or partially to form a compound bone.

The angular is a laminar and elongated bone, composing the ventrolateral wall of this portion of the mandible.

The elongate surangular is located dorsally and contributes to the formation of the dorsal and lateral walls of the mandible. By the middle of its length, there is an expanded area with a slightly irregular and slightly sunken dorsomedial surface. Another laminar expansion is present near the posterior end; this second expansion is arched and encircles the articular condyle of the articular. Two foramina can be seen in lateral view: the anterior surangular foramen, located near the dorsal margin

by the anterior expanded area, and the posterior surangular foramen, located near the ventral margin by the posterior expansion.

Prearticular and articular are always fused in a single and straight bone composing the ventral wall of the mandible. This bone has a pointed anterior end and expands dorsally by the second fourth of its length, forming a projection that contacts the surangular. The posterior end of the bone presents the articular condyle with the quadrate dorsally and the retroarticular process posteriorly. The condyle is wide and subcircular; the articulation surface is directed posteromedially and bears two slightly sunken areas separated by a low median ridge. The retroarticular process is usually long and wide; it is dorsomedially concave and bears a foramen for the chorda tympani on the medial surface, near its anteroventral corner. An angular process can develop in medial direction ventrally to the condyle.

In medial view, the broad adductor fossa stands out anteriorly to the articular condyle. It is defined by the surangular dorsally and by the prearticular/articular complex ventrally.

Agamidae (Fig. A3.37A-B, A3.38A-D, AE)

In *L. stellio*, only the prearticular and the articular are fused together, whereas angular and surangular remain free.

The angular (Fig. A3.37A-B) is slender and very elongated, with a strong dorsolateral concavity and pointed anterior and posterior ends. It is rather straight, but bends slightly in dorsal direction posteriorly. A small foramen is visible in ventral view, at mid-length; it continues in a shallow groove on the medial concave surface of the bone, but does not open dorsally. The lateral surface of the bone is smooth, except for a sharp and sigmoid-shaped ridge running along its entire length.

The surangular of *L. stellio* (Fig. A3.38A-B) is dorsoventrally enlarged and straight in dorsal view; it is moderately thin in its anterior half, but gets thicker in the posterior one. In medial view, it has a pointed posterior end and a truncated anterior one, provided with two anteriorly directed and pointed projections (a very short ventral one and a longer dorsal one). On the medial surface, two very low ridges run in posterior direction from these two projections (Fig. A3.38A); the dorsal one is less developed than the other and marks the ventral margin of the anterior expanded area, whereas the more developed ventral one touches the prearticular/articular complex and marks the dorsal margin of the articulation surface with the angular. The anterior expanded area is less developed than in other lizards and a sharp ridge marks its dorsal margin. The posterior expanded area is short and very poorly arched, but it is moderately thick. The posterior half of the lateral surface of the bone is smooth, whereas the anterior one is covered by the deep articulation surface with the posterior end of the dentary (Fig. A3.38B). The imprints of the posterior processes of the latter bone are recognizable by the posterior portion on this articulation surface. Both the anterior and the posterior surangular foramina are shifted towards the middle of the height of the bone.

The anterior end of the prearticular/articular complex (Fig. A3.38C-D) is truncated and the expansion contacting the surangular is reduced. By this expansion, a rounded tubercle is present on the medial surface of the bone (Fig. A3.38C). The articular condyle is subquadrangular in dorsal view and roughly flat (Fig. A3.38AE). The retroarticular process is very long, robust and slightly dorsally curved in the posterior portion. Its dorsomedial concavity is very deep and bordered dorsally and ventrally by sharp ridges (of which the ventral one is the well-developed tympanic ridge) and its posterior end is rod-like and truncated. The lateral surface of the process is smooth, but a distinct and sharp ridge-like expansion runs along the ventral margin. A thick, well-developed and thumb-like angular process is present, developing in anteroventral direction. The lateral surface of the complex is smooth, except for a low ridge marking the ventral margin of the articulation surface with the angular. The adductor fossa is anteroposteriorly elongated and a sharp ridge connects its

medioventral margin to the ventral corner of the articular condyle.

Chamaeleonidae (Fig. A3.37C-D, A3.38E-F)

Chamaeleo chamaeleon presents a stocky compound bone made up by completely fused surangular, prearticular and articular, whereas the angular is unfused. The latter

(Fig. A3.37C-D) has a pointed anterior end and enlarges posteriorly, bending in dorsolateral direction. It is concave in dorsal direction in its anterior portion, whereas it is straighter in the posterior one. A foramen opens in anterior direction on the dorsomedial surface of the bone, roughly at mid-length.

The surangular and prearticular portions of the compound bone are clearly recognizable as distinct branches separated by a notch where the inferior posterior process of the dentary inserts (Fig. A3.38E-F). Because of the presence of this notch, the latter process contributes to the formation of the lateral wall of the adductor fossa. No expansions are present neither on the surangular branch nor on the prearticular one. The surangular branch is the shortest one and shows a large recess that can be seen in anterior view: this is the posterior continuation of the recess of the dentary. Both the medial and lateral surfaces of this branch are smooth, except for the anterior portion of the latter, which shows the articulation surface with both the superior posterior process of the dentary and the posterior process of the coronoid. The anterior surangular foramen is not visible in lateral view. The prearticular branch is twice as long as the surangular one. It is straight and houses the posterior portion of the Meckel's cartilage in a deep dorsal channel; it also presents a wide groove for the articulation with the angular on the ventrolateral surface. The articular condyle is strongly dorsally concave (Fig. A3.38E). The retroarticular process is not present, but the medial surface of the bone can present a moderately small tubercle in the position of the angular process (Fig. A3.38E).

Gekkota (Fig. A3.38G-N, AF-AI)

A fused compound bone is present in adults gekkotans. Only in young individuals, it can be still separated in two portions (angular/surangular and prearticular/articular). The presence of an angular in the mandible of most gekkotans was doubted by Jollie (1960), but the same author also said that it could be fused with prearticular and surangular.

The compound bone is straight in medial view. An arched ridge borders posterodorsally the sunken surface of the anterior expanded area. The development

of the ridge is highly variable in *T. mauritanica*: it is absent in MDHC 98, barely visible in MDHC 97 and 194 and well developed in MDHC 119 and 302. The retroarticular process is thin, wide and posteriorly truncated. In *M. kotschyi*, the posterior portion of the lamina tends to expand, forming a lobe in medial view (Fig. A3.38K-L). In *E. europaea*, *H. turcicus* and *T. mauritanica*, the process is only slightly larger posteriorly and so it adopt a subrectangular shape rather than a lobed one (Fig. A3.38G-J, M-N). A very low longitudinal lateral crest is present in the middle of the lateral surface of the process, except for *E. europaea* (Fig. A3.38H). The lateral surface of the compound bone is smooth. In *E. europaea* and *T. mauritanica*, the posterior surangular foramen is shifted towards the dorsal margin of the bone and opens in dorsal direction, rather than laterally as in the other species (Fig. A3.38H, N). In the latter species, moreover, a short ridge is present on the dorsal margin, between the foramen and the condyle (Fig. A3.38N). There is no angular process and the adductor fossa is narrow and anteroposteriorly elongated.

Lacertidae (Fig. A3.37E-H, A3.38O-R, AJ)

The angular of lacertids (Fig. A3.37E-H) is unfused and dorsoventrally enlarged. Its anterior end is narrower than the posterior one, which is lobe-shaped (sometimes forked, e.g., *P. bocagei* UAM.R.PB48 and *P. algirus* UAM.R.Ps9; Fig. A3.37E). A moderately developed angular ridge is present on the medial surface, starting roughly in the middle of the ventral margin and running anterodorsally up to the tip of the anterior end. Ventrally to the ridge, the bone is thickened. The posterior alveolar foramen pierces the angular with a dorsomedial to ventrolateral direction (Fig. A3.37H). The lateral surface is smooth, except for the articulation surface with the dentary, which covers its anterior half (Fig. A3.37E-F).

The other bones fuse to form a compound bone (Fig. A3.38O-R, AJ) that can be separated in two portions in juveniles as in gekkotans. The articular condyle is subquadrangular in dorsal view and rather flattened; a stocky tubercle develops in medial direction from its anteromedial corner (Fig. A3.38AJ). The retroarticular process is straight and subtriangular in medial view, since it narrows posteriorly. Its



Figure 2.17) Posterior end of the left compound bone of L. viridis NHMW 663 in medial view, showing the strong expansion of the ventral margin. Scale bar = 1 mm.

posterior end is truncated. A well-developed tympanic ridge is visible on its medial surface, running longitudinally from the posteroventral corner of the articular condyle to the posterior end of the process. This ridge marks the ventral margin of the concave portion of the process,

whereas ventrally to it there is a ridge-like ventral expansion. The expansion is well developed in A. erythrurus and E. arguta, giving a curved ventral margin to the compound bone of these species (Fig. A3.38O). In other European lacertids, the margin is usually straight in medial view (Fig. A3.38P-Q), but a strong ventral development is visible also in both compound bones of MRAC 91-077-R-76 (Fig. A3.38R) and in the left one of NHMW 663 (Fig. 2.17), both large individuals of L. viridis, suggesting some degree of individual variation maybe linked to size in this species (but some kind of pathological condition cannot be excluded a priori). The angular process is not present. The lateral surface of the compound bone is smooth, except for the presence of the wide articulation surface with the angular (Fig. A3.38Q). In L. agilis, L. bilineata, L. viridis and T. lepidus, a distinct and rather sharp longitudinal ridge runs dorsally to the articulation surface (Fig. A3.38Q). Anyway, this ridge undergoes a rather significant degree of individual variation, which might either be linked to the age or the size of the animal. A similar ridge is present also in some large specimen of A. nigropunctatus (MDHC 243), P. muralis (MDHC 6), P. siculus (MDHC 91 and 229) and P. tiliguerta (a very little developed one in both the herein considered specimens). The adductor fossa is very wide.

Scincidae (Fig. A3.37I-J, A3.38S-Z, AK)

In scincids, all the bones but the angular fuse to form a compound bone. The latter (Fig. A3.37I-J) is similar to the one of lacertids in morphology, even if it is more

slender. Moreover, the angular ridge begins closer to the posterior end of the bone compared to the latter group and the external opening of the posterior alveolar foramen is shifted dorsally compared to them, being visible in lateral view. The lateral surface is smooth, but its anterior half is covered by the articulation surface with the dentary, which is more marked in larger species.

The compound bone (Fig. A3.38S-Z, AK) has a ventrally concave aspect in lateral view, since the retroarticular process bends in ventral direction. The concavity is size-linked, being less marked in smaller species (e.g., A. kitaibelii; Fig. A3.38S-T). Nevertheless, the concavity is well distinct in the small O. punctatissimus (Fig. A3.38W-X). As in lacertids, the articular condyle is subquadrangular and shows a medially developed and stocky tubercle on its anteromedial corner. The tubercle is poorly developed in A. kitaibelii and very well developed in C. ocellatus (Fig. A3.38AK) and O. punctatissimus. The retroarticular process is lobe-shaped in medial view, with a well-developed tympanic ridge running along its ventral margin. The only exceptions are A. kitaibelii and O. punctatissimus, the process of which is subrectangular and has a less developed ridge (Fig. A3.38S-T, W-X). The process is more anteroposteriorly elongated in A. kitaibelii, C. chalcides and C. striatus (Fig. A3.38S-T) and more dorsoventrally expanded in C. ocellatus, O. punctatissimus and T. aurata (Fig. A3.38U-Z). There is no angular process. The lateral surface of the compound bone presents the articulation surfaces housing the narrow angular and the posterior end of the dentary, but it is otherwise smooth. The posterior surangular foramen is slightly shifted towards the dorsal margin of the bone. It is replaced by two smaller foramina in the left compound bone of a single specimen of O. punctatissimus, MCZ 38517. Ophiomorus punctatissimus and T. aurata show a very large anterior surangular foramen. The adductor fossa is narrow and anteroposteriorly elongated, as in gekkotans.

Anguidae (Fig. A3.37K-N, A3.38AA-AD, AL-AM)

Anguids have a free angular, whereas the other bones are fused in a compound bone. The angular (Fig. A3.37K-N) is very slender, with pointed anterior and posterior ends. The latter is very slightly larger than the former and a clear constriction is visible by the beginning of the posterior half of the bone in lateral view. The constriction is slightly more evident in *Anguis* gr. *A. fragilis* (Fig. A3.37K-L) than in *P. apodus* (Fig. A3.37M-N). The angular ridge runs along the ventral margin, showing a thickening roughly at mid-length. The dorsoventrally directed posterior alveolar foramen pierces this expansion in the middle. The anterior half of the lateral surface is covered by the articulation surface with the dentary, whereas the posterior one is smooth.

The compound bone (Fig. A3.38AA-AD, AL-AM) can be split into two portions in young individuals, but in adults only the anterior expansions of the surangular and the prearticular remain unfused. The articular condyle is subquadrangular and slightly mediolaterally elongated in dorsal view (Fig. A3.38AL-AM). A robust but short tubercle is present by its anteromedial corner. The retroarticular process is short, stocky and quadrangular in medial view. It expands in ventromedial direction and therefore the posterior portion of the compound bone appears concave in medial view. A low or very low longitudinal lateral crest is visible on the lateral surface of the process (Fig. A3.38AB, AD). The articulation surface with the angular is visible on the lateral surface of the bone, reaching roughly mid-length (Fig. A3.38AB, AD). The posterior surangular foramen is shifted dorsally, near the dorsal margin, and, in *P. apodus*, the anterior one is shifted anteriorly, lying in the articulation surface with the dentary. Because of this latter shift, the anterior surangular foramen of *P. apodus* is not visible in lateral view. By the base of the retroarticular process, a ridge-like ventral expansion is present on the ventral surface of the bone: this expansion is very low in Anguis gr. A. fragilis (Fig. A3.38AA), but can be moderately or well developed in P. apodus (Fig. A3.38AC).

The adductor fossa is strongly reduced, very narrow and anteroposteriorly elongated; in *Anguis* gr. *A. fragilis*, it is slightly longer than it is in *P. apodus*.

2.2.2. Amphisbaenia

The skull of European amphisbaenians (Fig. A3.39, A3.40) lacks a number of bones present in the standard lacertilian model, and it shows also a couple of elements that are distinctive of this group compared to lizards. The missing bones are the palpebral, the lacrimal, the jugal, the postfrontal, the postorbital, the supratemporal and the orbitosphenoid, whereas the tabulosphenoid is a peculiar feature of the amphisbaenians (Jollie 1960; Gans & Montero 2008). Elements-X were also considered to be present only in amphisbaenians among squamates, but they have recently been reported in other squamates also (Gauthier et al. 2012; Montero et al. 2017).

Nasal

Nasals of *Blanus cinereus*, *Blanus mariae* and *Blanus strauchi* (Fig. A3.41A-B) are thin, short and subquadrangular paired bones, with roughly straight lateral and medial margins, a strongly concave anterior margin and a convex posterior margin. They are concave in ventral direction. At the corners of the anterior margin there are the anteromedial and the anterolateral processes, both pointed. The former is longer (roughly twice or three times in length) than the latter, which is very short. The wide and posteriorly rounded posterior process contacts the concave anterior margin of the related frontal. Both the ventral and the dorsal surface of the nasal are smooth, but the articulation surface with the ascending nasal process of the premaxilla is visible in dorsal view along the entire medial margin (Fig. A3.41A). Another articulation surface, the one with the facial process of the maxilla, is present along the lateral one (Fig. A3.41A).

Frontal

In *B. cinereus*, *B. mariae* and *B. strauchi*, the frontals (Fig. A3.41C-E) are short and rectangular paired bones, with subparallel lateral and medial margins. The former is very slightly concave, whereas the latter bears the wavy interfrontal suture. The width of the anterior end is equal to the one of the posterior end. Both a medial and

a lateral process are present by the anterior corners of the bone; they are moderately developed, defining a distinctly concave anterior margin. The articulation surface with the facial process of the maxilla is visible on the lateral side of the anteromedial process, whereas the articulation surface with the ascending nasal process of the premaxilla covers the medial side of the anteromedial one (Fig. A3.41C). A clearly developed posterolateral process is absent. The dorsal surface is smooth and almost flat (Fig. A3.41C), with only a weak ventral bending of the lateral process. On the ventral surface, the laminar crista cranii is well developed (Fig. A3.41D-E). In contrast with the standard morphology it has in lizards, in B. cinereus, B. mariae and B. strauchi this structure runs from the midpoint of the medial margin to the posterolateral corner of the bone, originating a posteromedially concave, ventrally directed and wide ventral process. The rounded posteroventral margin of this process contacts the tabulosphenoid. Its anterolateral surface is split into two portions by a ridge-like anterior process, which contacts the palatine ventrally. The anterior portion of the surface is smooth, whereas the posterior one shows the articulation surface with the dorsal process of the prefrontal by the anterodorsal corner and that with the anterolateral process of the parietal by the posterodorsal one (Fig. A3.41E). The posterior margin of the frontals is strongly interdigitated, carrying long and slender digits. Five digits are usually present, but sometimes there are 4, 6 or even 7 of them.

Parietal

The parietal of *B. cinereus*, *B. mariae* and *B. strauchi* (Fig. A3.41F-H) is unpaired and strongly anteroposteriorly elongated. In dorsal view, the posterior portion is wider than the anterior one, with the more constricted part placed close to the anterior end. The lateral margins of the bone bend strongly in ventral direction, covering laterally the anterior portion of the braincase (Fig. A3.41H). Because of this, the parietal appears strongly ventrally concave and takes a dorsally rounded vaulted shape. Very deep and narrow interdigitations are present on the anterior margin: there

are usually 8 digits, but some specimens can show 7, 9 or even 11 of them. Moderately wide and pointed anterolateral processes are recognizable by the anterolateral corners, flanking the interdigitations and not projecting beyond them. In place of the postparietal processes, a couple of large and rounded posterior plates develop posteriorly from the posterior margin. They cover dorsally the supraoccipital and are separated by a long and narrow parietal notch. The supraoccipital crest of the supraoccipital fits within this notch. Anteriorly to the notch, a sagittal crest runs shortly on the dorsal surface, ending with a moderately developed dorsal knob (Fig. A3.41F). The knob does not reach the middle of the length of the bone. In ZMS 175-1993-1 and 175-1993-2, the crest and the knob are not developed and there is a very large and U-shaped parietal notch; all these features, however, can be due to a juvenile condition, implied also by a lower degree of fusion of the braincase. In ventral view, the notch is preceded by a very small but moderately deep parietal fossa (Fig. A3.41G). Both the dorsal and the ventral surface of the parietal are smooth. However, on the ventral one, two shallow and flanked concave areas are visible on the anterior margin and two low and transverse ridges mark the bases of the posterior plates. There is no parietal foramen.

Premaxilla

In European amphisbaenians, the unpaired premaxilla (Fig. A3.41I-K) has a long and moderately wide ascending nasal process, provided with slightly convex lateral margins and a smooth anterior surface. The process narrows towards the truncated or pointed dorsal end. In a single specimen of *B. strauchi* (MDHC 286), the nasal process is arrow-shaped in anterior view. The alveolar portion of the bone bears 7 pleurodont, cylindrical and monocuspid teeth, among which the middle one is the largest one. Dorsally to the teeth, the moderately developed palatal processes extend posteriorly. These processes are separated from one another by a small and U-shaped notch. By the junction of the nasal process with the alveolar plate, a very large foramen of the longitudinal canal opens anterolaterally on each side of the former. A second foramen can be present, sometimes only on one side of the bone (*B. cinereus* MDHC 156, ZMS 175-1993-1, 227-1975, 548-2003, 652-0-1, 652-0-2, 653-0-1 and 653-0-2, both specimens of *B. mariae* and *B. strauchi* MCCI R-1668; Fig. A3.39E, J; see also Bolet et al. 2014b). Another large foramen is visible on the posterior surface, by each side of the distinctly developed septonasal crest (Fig. A3.41J). In lateral view, the anterior outline of the premaxilla is flat, not overhanging beyond the central tooth position in *B. cinereus* and *B. mariae* (Fig. A3.39C-D, H-I) and overhangs anteriorly in *B. strauchi* (Fig. A3.40C-D, A3.41K).

Maxilla

Blanus cinereus, B. mariae and B. strauchi have short maxillae (Fig. A3.41L-N), provided with a well-developed palatal shelf, which narrows posteriorly. On the anterior half of the medial margin of the shelf, there is a wide and deep notch, marking the lateral margin of the foramen for the Jacobson's organ (Fig. A3.41L). Posteriorly to this notch, a groove is visible on the dorsal surface of the shelf, running posterolaterally to anteromedially. The anterior premaxillary process shows a very well developed, wide and squared anteromedial process by the medial corner, whereas the anterolateral process is completely lacking. The anteromedial process is ventrally concave and overlaps the related palatal process of the premaxilla. The posterior process is very short and pointed. A very distinct and high step is present on its dorsal margin (Fig. A3.41M-N). The wide facial process is subtriangular in lateral view (Fig. A3.41N); its anterior margin is slightly convex, whereas the posterior one is wavy. A moderately long, slender and pointed projection develops posterodorsally from the dorsal end of the process; a second very short (more developed in B. strauchi; Fig. A3.41M-N), moderately wide and rounded one is present on the posterior margin, ventrally to the former. The basis of the facial process is pierced anteroposteriorly by the superior alveolar canal, whose anterior and posterior openings are located on the medial surface of the process. The anterior opening, the vomeronasal foramen, is small and located posteriorly to the anterior margin of the process, whereas the posterior one, the superior dental foramen, is very large and situated near the step on the posterior process (Fig. A3.41M). No groove is present posteriorly to the latter foramen. Two (3 in ZSM 27-1988-2, in the left maxillae of ZSM 27-1988-1 and ZMS 652-0-1 and in the right ones of ZMS 548-2003 and 653-0-1) large ventrolateral foramina represent the lateral openings of the canal (Fig. A3.41N). The lateral surface of the bone is smooth. The alveolar border of the maxilla bears subpleurodont and trenchant teeth, whose crown bends posteriorly. However, maxillae of *B. cinereus* provided with 5 teeth, the anteriormost of which is less developed, are mentioned by Bailon (1991). The teeth are not present at the level of the posterior process.

Prefrontal

The prefrontal of European amphisbaenians (Fig. A3.41O-P) has a small and anteromedially concave body, the orbitonasal flange, whose external surface is smooth. From the dorsal margin of the flange, a short and laminar anterodorsal process develops anteriorly. The dorsal surface of this process is divided into two halves by a low transverse ridge. By the ventrolateral corner of the orbitonasal flange, there is a very short and roughly squared posteroventral process. A shallow but wide notch marking the medial margin of the lacrimal foramen is present on the lateral margin, dorsally to the posteroventral process. The ventromedial corner of the bone does not developed an orbitonasal flange projection. The posterodorsally developed dorsal process is located at the posterodorsal corner of the flange: it is very short, triangular and has a truncated or pointed distal end. There is no palpebral crest.

Squamosal

Due to its varying position related to the quadrate in different species and to its presence in not-closely phylogenetically related taxa, there is a certain degree of uncertainty on the real homology of the so-called squamosal in amphisbaenians and the corresponding bone in lizards (Gans & Montero 2008). However, we here follow



Figure 2.18) Right quadrate of B. cinereus (ZSM 175-1993-1; A), B. mariae (ZSM 27-1988-1; B) and B. strauchi (MCCI R-1635; C) in ventromedial view, showing the different development of the posteromedial ridge. Not to scale.

Gans & Montero (2008) in naming this bone as such. The squamosal of *Blanus* (Fig. A3.39C-D, A3.40C-D) is a very small and slender bone. It is has two pointed ends and a very slightly sigmoid shape in lateral view.

Quadrate

The paired quadrate (Fig. A3.41Q-X) has a triangular shape in lateral view. The body of the bone is a slightly posteriorly curved pillar structure provided with the cephalic condyle on its dorsal end and with the mandibular condyle on the ventral one. The former is anteroposteriorly elongated and slender in dorsal view, whereas the latter is expanded mediolaterally and shows two very poorly developed and similar sized portions. A well-developed and wing-like osseous lamina projects anteriorly from the lateral surface of the pillar, bending medially to follow the lateral wall of the braincase. The conch is therefore not present. The medial lamina is also absent. In *B. strauchi*, a moderately developed ridge is present on the posteromedial side of the pillar (Fig. 2.18C). This ridge is lower in *B. mariae* (Fig. 2.18B) and very poorly developed or not clearly recognizable in *B. cinereus* (Fig. 2.18A). Near the cephalic condyle, a large foramen, maybe the one for the chorda tympani nerve, pierces the lateral lamina.

Epipterygoid

The epipterygoid is usually not present in amphisbaenians, but it is retained in some species of *Blanus* (Gans & Montero 2008). In *B. cinereus* and *B. mariae*, this rod-like bone is distinctly curved, with a posterior concavity, and mediolaterally

compressed (Fig. A3.39D, E-I). Both the dorsal and the ventral end are rounded. The epipterygoids appear to be lacking in ZMS 652-0-1 and can be both present or absent in *B. strauchi*. According to Gans & Montero (2008), the latter species should lack these bones, but it was possible to detect it in at least some of the studied specimens (Fig. A3.40C-D).

Vomer

The paired vomers of European amphisbaenians (Fig. A3.41Y-Z) are very slender, thin and strongly anteroposteriorly elongated. Their laminar body is poorly concave in dorsal direction and presents a well-developed lateral wing roughly at mid-length. The lateral wing is slender, finger-like and presents an anteriorly directed concavity. Anteriorly to the wing, the lateral margin of the bone shows two wide notches, the anteriormost and widest of which is the medial margin of the vomeronasal fenestra (Fig. A3.41Y). Posteriorly to the wing, the vomer shows a very long, slender and pointed posterior process. The dorsal surface of this process is covered by the articulation surface with the vomerine process of the palatine, whose lateral margin is marked by a low ridge by the base of the lateral wing. The anterior end of the vomer is also narrow and roughly pointed. A well-developed ridge runs along the entire medial margin of the bone, projecting dorsally and lowering posteriorly. The anterior end of this ridge is forked, showing two short and slender processes flanking a deep notch. Roughly at one third of the length of the bone, the ridge is connected to the laminar body of the vomer by a moderately stocky osseous expansion, anteroposteriorly pierced by a foramen. The ventral surface of the vomer is smooth.

Septomaxilla

Blanus cinereus, *B. mariae* and *B. strauchi* have small, thin, ventrally concave and subquadrangular septomaxillae (Fig. A3.41AA-AB). This bone shows four short processes, situated at its four corners. A very small anteromedial process and a small posteromedial one are present by the two ends of the medial margin, whereas the anterolateral and the posterolateral ones are located by the ends of the lateral margin.

Both lateral processes are triangular and wider than the medial ones. The anterior processes are directed anteriorly, the posteromedial one is directed posteriorly and the posterolateral one develops in posterolateral direction, slightly bending dorsally. A ventrally directed osseous expansion is present by the anteromedial corner, continuing posteriorly in a ridge running along the medial margin and laterally with a very low and arched ridge that borders laterally the ventral surface (Fig. A3.41AB). A moderately developed ridge, anteroposteriorly pierced by a canal, is present along the medial margin also on the dorsal surface (Fig. A3.41AA).

Palatine

In B. cinereus, B. mariae and B. strauchi, the palatines (Fig. A3.42A-B) are anteroposteriorly elongated and blade-like bones, with straight and posteriorly convergent lateral and medial margins. They are strongly ventrally concave, because of the presence of a very deep and wide choanal duct along the ventral surface (Fig. A3.42B). The anterior half of the medial margin bends very slightly in lateral direction, covering a small part of the duct. The dorsal surface is smooth (Fig. A3.42A). Long, pointed and slender vomerine and maxillary processes develop in anterior direction from the anteromedial and the anterolateral corners of the bone respectively; the vomerine process is slightly longer than the maxillary one. A welldeveloped palatine ridge runs on the dorsal surface of the bone along the anterior margin (Fig. A3.42A), lowering towards its medial side. This ridge projects beyond the lateral margin of the palatine, originating a small and triangular lateral expansion. There is no infraorbital foramen. The pterygoid process is very long and wide and has a pointed posterior end. The articulation surface with the palatine process of the pterygoid is recognizable on the ventral surface of the process. In the middle of the lateral margin of the bone, a small and finger-like laminar expansion is present, projecting posterolaterally and contacting a similar structure on the pterygoid.

Pterygoid

The anterior half of the pterygoid of European amphisbaenians (Fig. A3.42C-D) is dorsally concave and made up by a small, pointed and laminar palatine process and by a long and pointed pterygoid flange. These two processes are separated by a very shallow pterygoid recess. The large and triangular articulation surface with the pterygoid process of the palatine is visible on the dorsal surface of the palatine process (Fig. A3.42C). Dorsally, a moderately developed ridge for the insertion of the superficial pseudotemporal muscle runs along the entire lateral margin of the pterygoid flange (Fig. A3.42C). On its ventral surface, on the other hand, only a small hint of a ridge is recognizable by the anterior tip (Fig. A3.42D). The articulation surfaces with the posterodorsal and the posteroventral processes of the ectopterygoid are present on the dorsal and the ventral surfaces of the flange respectively; the latter is small and limited to the anterior tip (Fig. A3.42D), whereas the former is longer (twice as long as the other; Fig. A3.42C). A small and anteriorly directed expansion, contacting the lateral expansion of the palatine, is present on the medial margin of the pterygoid flange. There are no pterygoid teeth on the ventral surface (Fig. A3.42D). The quadrate process is slender, moderately long and slightly sigmoid-shaped, with a lateral concavity; its posterior end is flattened and can be rounded or pointed, whereas its joint with the anterior portion of the bone is mediolaterally enlarged. The fossa columellae is moderately shallow, but the pterygoid ridge is not clearly developed posteriorly to it. The basipterygoid fossa is very large, flattened and posteromedially directed and continues posteriorly in a large and distinctly concave surface for the insertion of the pterygoideus muscle.

Ectopterygoid

European amphisbaenians have small and subtriangular ectopterygoids (Fig. A3.42E-F). The anterior end of these bones is represented by a moderately wide and anteriorly truncated anteromedial process, whose lateral surface is completely covered by the articulation surface with the posterior process of the maxilla (Fig.

A3.42F). The anterior margin of this process shows a small notch in the middle. The posterior end of the ectopterygoid is forked, because it is composed by two processes: a rounded posteroventral and a pointed posterodorsal one. The former is smaller and shorter than the latter. The pterygoid flange of the pterygoid is lodged between these two processes. A moderately wide and lappet-like anterolateral process develops anterodorsally from the middle of the dorsal margin of the bone. The dorsal margin of the posteroventral process and the ventral margin of the anterolateral one define a low ridge that runs on the lateral surface of the bone (Fig. A3.42F). A very small and anteroposteriorly directed foramen (visible in lateral view) is present in the middle of the bone. The medial surface of the ectopterygoid is smooth and medially concave.

Tabulosphenoid

The tabulosphenoid (Fig. A3.42G-J) is an unpaired (but split longitudinally into two halves in juveniles; e.g., ZMS 175-1993-2 and ZSM 27-1988-2), laminar and quadrangular shaped bone. It is dorsally concave, very slightly longer than it is wide and has subparallel and straight lateral margins. The anterior margin is also straight, except for a small expansion in the middle. The posterior margin, on the other hand, shows two moderately wide and long posterior processes flanking a deep and Ushaped notch, which continues in a V-shaped articulation surface on the ventral surface of the bone (Fig. A3.42H, J). This V-shaped surface, which lodges the parasphenoid rostrum of the sphenoid, is bordered laterally by two robust ridges, which continue anteriorly in low ridges running along the midline towards the anterior margin. The latter ridges usually remain well separated (Fig. A3.42J), but they can fuse medially (at least in B. cinereus, MDHC 156; Fig. A3.42H). A small foramen pierces the tabulosphenoid by both sides of this low ridge, roughly near mid-length. On the ventral surface, a shallow groove runs anterolaterally from each foramen (Fig. A3.42H, J). The dorsal surface of the bone is smooth, except for a moderate swelling by the V-shaped ventral surface (Fig. A3.42G, I).

General features of the otooccipital region

Nine bones compose the otooccipital region of *Blanus* (Fig. A3.42K-O), namely the basioccipital, the sphenoid, the two elements-X, the two prootics, the supraoccipital and the two otooccipitals. These bones are fused in adults, but separate in juveniles. There is a strong variation in the fusion of the elements-X, in particular (Gans & Montero 2008). The region is distinctly dorsoventrally compressed. The foramen magnum is wide and subcircular and the occipital condyle is also wide. The latter is composed by the basioccipital and both the otooccipitals, but the suture between them is not visible and therefore it is impossible to define how much they contribute to its formation (Jollie 1960). In dorsal view, the condyle presents a deep notch in the middle (Fig. A3.42N), whereas in posterior view it is strongly U-shaped (Fig. A3.42L). The very wide and circular fenestra ovalis is the only visible opening on the lateral side of the braincase, since the lateral opening of the recessus scalae tympani is lacking in amphisbaenians (Jollie 1960). The fenestra is shifted anteroventrally compared to lizards (Fig. A3.42M) and is defined by the sphenoid anteroventrally, by the basioccipital posteroventrally, by the prootic anterodorsally and by the otooccipital posterodorsally; it does not open directly in the cochlear cavity, but in a concave area connected posteriorly with the latter. The semicircular canals are very poorly distinguishable, but the otic capsule (the structure which encloses the inner ear) is strongly enlarged, forming an ellipsoidal bulge.

Basioccipital

The unpaired basioccipital of European amphisbaenians (Fig. A3.42O) is subhexagonal, roughly as long as it is wide and dorsally concave. Both the dorsal and ventral surfaces are smooth, but there is a shallow concave area in the middle of the anterior half of the latter, continuing anteriorly on the sphenoid. The lateral wings of the bone are poorly developed and no sphenooccipital tubercle is present (Fig. A3.42L-M, O). When unfused, the anterior margin shows a wide but shallow concavity in the middle, whereas the posterior one forms the medial portion of the occipital condyle.

This bone fuses with the sphenoid and the elements-X anteriorly, the prootics anterolaterally and with the otooccipitals posterolaterally.

Sphenoid

The unpaired sphenoid of B. cinereus, B. mariae and B. strauchi (Fig. A3.42K, M-O) is a subquadrangular and flattened bone, devoid of cristae ventrolaterales. The anterolaterally developed basipterygoid processes are very short, moderately wide, flattened and subrectangular in ventral view; their distal end is slightly dorsoventrally enlarged and tilted of 30° in anterior view (Fig. A3.42K). Together with the lateral margins of the sphenoid, the processes define a laterally directed concavity along both lateral side of the bone (Fig. A3.42O). The middle of the dorsal surface is smooth and flattened, because of the absence of the crista sellaris, of a deep sella turcica and of the trabeculae cranii (Fig. A3.42N). A well-developed, wide, laminar and triangular parasphenoid rostrum, however, is present, projecting anteriorly between the basipterygoid processes. The vidian canals pass through the lateral sides of the bone, opening anteriorly by the medial side of the basipterygoid processes (Fig. A3.42K), medially with a very anteroposteriorly elongated inner opening (Fig. A3.42N) and posterolaterally by the contact with the prootics (Fig. A3.42M). The recessus vena jugularis is not recognizable. The smooth ventral surface is crossed longitudinally by a large sunken area (Fig. A3.42N).

The posterior margin of the sphenoid fuses with the basioccipital medially and the prootics laterally; the elements-X cover ventrally the posterior half of the lateral margins if the bone.

Element-X

This paired bone contacts the anterolateral corner of the basioccipital and covers the posterolateral corner of the sphenoid. It has been interpreted as an epiphysis for muscular attachment (Gans & Montero 2008), but Montero et al. (2017) recently

considered them to be basicranial sesamoids. Montero et al. (2017) also relate this bones with ossifications present on the sphenooccipital tubercles other squamates. In *B*. in cinereus, B. mariae and *B*. strauchi, each element-X is represented by a laminar and subovoid small bone (Fig. 2.19).

Supraoccipital

In European amphisbaenians, (ex). Not to scale.

Figure 2.19) Ventral view of the otooccipital region of B. cinereus ZSM 175-1993-1, showing the unfused elements-X (ex). Not to scale.

the unpaired supraoccipital (Fig. A3.42K-N) is composed by a thin middle portion, almost completely overlapped by the parietal, and by two expanded lateral portions, which fuse with the prootic and the otooccipital. The bone appears rather flattened in general aspect. In dorsal view, the posterior margin of the bone is characterized by the presence of a deep and wide U-shaped notch (Fig. A3.42N). A slightly dorsoventrally compressed processus ascendens is present: it projects shortly beyond the anterior margin, but it continues posteriorly on the dorsal surface with a robust supraoccipital crest, reaching the posterior notch (Fig. A3.42N). The crest is not developed in juveniles.

Prootic

The paired prootics (Fig. A3.42K, M-O) compose the anterior portions of the bulgelike otic capsules. They are usually completely fused with the otooccipitals and the supraoccipital and so their limits are not clearly recognizable. The alar process is long and triangular (Fig. A3.42M); it is wide by its base, but it narrows and tends to bend ventrally by its anterior end. The anterior inferior process is reduced and it almost entirely occupied by the fenestra ovalis, whose anterior margin is marked by



Figure 2.20) Close-up (A) of the right stapes in the skull of B. cinereus (ZSM 653-0-2) and its interpretative drawing (B). Abbreviations: b, basioccipital; cb, compound bone; ff, facial foramen; pt, pterygoid; pr, prootic; q, quadrate; sp, sphenoid; st, stapes. Scale bar = 1 mm.

a moderately developed ridge. On the external surface of the bone, a large facial foramen is visible anteriorly to the fenestra (Fig. A3.42M). A distinct crista prootica is absent. The alar and the anterior inferior processes define a very wide and U-shaped incisura prootica (Fig. A3.42M).

Ventrally, the prootics contact also the sphenoid and the basioccipital.

Otooccipital

The posterior portion of the otic capsule is represented by the otooccipital (Fig. A3.42L-O), which is usually completely fused with the other part of the complex (namely, the prootic and the supraoccipital). This bone fuses also with the basioccipital ventrally, taking part in the formation of the occipital condyle. In posterior view, the wide vagus foramen is visible inside a large concavity (Fig. A3.42L), the jugular foramen of Gans & Montero (2008); a variable number of small hypoglossal foramina flank the vagus one inside the concavity. The anterolaterally oriented paroccipital process is very poorly developed, present only as a robust and ridge-like structure on the lateral surface of the otooccipital.

Stapes

The stapes is made up by a circular and very large footplate and by a very short shaft (Fig. 2.20).

Dentary

In European amphisbaenians, the dentary (Fig. A3.42P-Q) has a moderately wide mandibular symphysis, anteroposteriorly inclined at an angle of about 45°. On the medial surface, the Meckelian fossa is represented by a very narrow groove running along the straight ventral margin of the bone (Fig. A3.42P). Dorsally, a moderately high subdental ridge separates the fossa from the alveolar shelf, which bears subpleurodont, robust and fang-like teeth (Fig. A3.42P). The crown of the teeth curves posteromedially. The tooth number is usually 8, but Bailon (1991) and Gans & Montero (2008) state that sometimes there can be 7 of them (e.g., *B. cinereus* ZMS 175-1993-1 and 175-1993-2, the right dentaries of B. cinereus ZMS 652-0-1 and 653-0-1 and the left ones of B. cinereus ZMS 652-0-2 and 653-0-2). Seven is also the number of mandibular tooth positions reported by Boulenger (1885) for B. cinereus. A small ninth tooth position is reported by Bolet et al (2014) for a single specimen of *B. strauchi*. The alveolar canal, which houses the inferior alveolar nerve, is enclosed in the subdental ridge. This canal is narrow anteriorly, but strongly widens posteriorly, opening near the posterior end of the dentary (posteriorly to the last tooth position) with a very wide posterior cavity (Fig. A3.42P). The intramandibular septum, which close the canal ventrally, extends posteriorly with a pointed and slender portion, which is fused to the wall of the dentary (i.e., not free; Fig. A3.42P). Because of the presence of the projection of the septum, the posterior end of the subdental ridge shows a large V-shaped notch in medial view (Fig. A3.42P). Three processes are located by the posterior end of the bone. The superior and inferior posterior processes are well developed, wide and pointed; the former projects posterodorsally, covering the lateral surface of the coronoid process of the coronoid, whereas the latter is developed in posterior direction, covering ventrolaterally the anterior half of the compound bone. Between them, there is a posteriorly directed, small and pointed central posterior process. The lateral surface



Figure 2.21) Lower jaw of B. mariae (ZSM 27-1988-1) in ventromedial view. Abbreviations: a, angular; c, coronoid; mcf, mandibular central foramen; s, splenial. Not to scale.

of the dentary is smooth, except for the presence of 3 large mental foramina (5 in the right dentary of *B. mariae* ZSM 27-1988-2, 4 in *B. cinereus* ZMS 175-1993-1 and 227-1975 and in the left dentary of *B. mariae* ZSM 27-1988-1).

Splenial

The splenial (Fig. 2.21) is an anteroposteriorly elongated, thin and very slender blade-like bone. The anterior portion is slightly wider than the posterior one. A single foramen pierces the bone in the middle of its posterior half. It is not clear if this foramen is the anterior inferior one or the anterior mylohyoid one.

Coronoid

The coronoid (Fig. A3.42R-S) is thin and straight in dorsal view. In medial view, it is triradiate, with an anteromedial, a coronoid and a posteromedial process. The anteroventrally developed anteromedial process is slender and pointed. A wide notch is present on its ventral margin, marking dorsally the mandibular central foramen (Fig. 2.21). The dorsally developed coronoid process is moderately wide, subtriangular in shape and has a rounded dorsal end. The wide articulation surface with the superior posterior process of the dentary stands out on its lateral surface, bordered by a well-developed and arched ridge (Fig. A3.42S). The posteroventrally developed posteromedial process is wide, roughly leaf-shaped and has a pointed distal end. On the medial surface of the bone, a moderately developed coronoid ridge runs vertically from the tip of the coronoid process to the ventral margin of the bone (Fig. A3.42R).

Angular

Angulars of *B. cinereus*, *B. mariae* and *B. strauchi* are thin, laminar, very narrow and anteroposteriorly elongated (Fig. 2.21). They have a pointed anterior end, but widen posteriorly, ending with a rounded posterior end. Their posterior half is tilted at about 90° compared to the anterior one. This bone is pierced by a large foramen at mid-length.

Compound bone

Articular, prearticular and surangular fuse in European amphisbaenians to form a compound bone (Fig. A3.42T-U). This bone is moderately short and encloses the posterior portion of the Meckel's cartilage in a tubular structure. The dorsal margin is sharpened and slightly convex, whereas the ventral one is straight in the anterior portion but becomes concave posteriorly because of the ventral bending of the retroarticular process. By the anterior end, the surangular (laterally) and the prearticular (medially) portions are still recognizable, since they are not completely fused to one another. Both portions are pointed anteriorly, but the surangular projects beyond the prearticular in medial view (with the dentary process sensu Gans & Montero 2008). The surangular portion presents a mediodorsally directed flattened area, which is covered by a dorsal laminar expansion of the prearticular portion (Fig. A3.42U). A wide, almost vertical and strongly concave articular condyle is present by the posterior end of the bone. Ventrally to it, the stocky, short and lobe-shaped retroarticular process projects posteroventrally. The process is slightly dorsomedially concave and shows a moderately large foramen for the chorda tympani on the medial surface, near its base (Fig. A3.42U). Its lateral surface is smooth. The lateral surface of the compound bone is also smooth, with only two large foramina (Fig. A3.42T): the anterior surangular foramen, anterolaterally directed and located by the base of the dental process, and the posterior surangular one, laterally directed and located near the articular condyle. The ventral surface is covered by the narrow articulation surface with the angular, which reaches the retroarticular process (Fig. A3.42T). In medial view, a moderately small adductor fossa stands out on the posterior half of the bone, anteriorly to the mandibular condyle (Fig. A3.42U).

2.3. Diagnostic key

Because of it being a variable feature that can lead to wrong conclusions (for example, to identify bones of juveniles of larger species as those of adults of smaller ones), size is not considered in the key. However, it can still be a useful tool in case of absence of diagnostic differences (e.g., quadrates of *H. turcicus* and *T. mauritanica*), taking also into account that a juvenile condition may be recognised in some skeletal elements due to the possible presence of juvenile features (see, for example, Evans 2008). When a feature is still considered useful for the identification despite being variable within a taxon, the variability is signaled with an asterisk marking the taxon.

Nasal

1. Nasal short	, B. strauchi
- Nasal anteroposteriorly elongated	2
2. Nasal slender in dorsal view	chamaeleon
- Nasal wider in dorsal view	3
3. Nasal shrinking towards the posterior end; well-defined articular surface	ace with the
maxilla covering the anterior half of the lateral margin	L. stellio
- Nasal not distinctly shrinking posteriorly; articular surface with the	maxilla less
defined	4
4. Dorsal surface smooth, without dermal ornamentation	5
- Dorsal surface ornamented, at least in adults	11
5. Anterolateral process present; lateral laminar expansion absent	6 (Gekkota)
- Anterolateral process absent; lateral laminar expansion present	9
6. Articulation surface with the frontal recognisable	7
- Articulation surface with the frontal not recognisable	8

7. Articulation surface with the frontal narrow and subrectangularE. europaea
- Articulation surface with the frontal wide and triangular
8. Presence of a ventral osseous expansion along the medial marginT. mauritanica
- Absence of the ventral osseous expansion
9. Lateral expansion clearly recognisable
- Lateral expansion very short and poorly individualized10
10. Posterior margin rounded
- Posterior margin oblique and roughly straight
11. Ornamentation restricted to the posterior half of the dorsal
surface
- Ornamentation located in the middle of the dorsal surface12
- Ornamentation largely occupying the dorsal surface14
12. Lateral laminar expansion clearly recognisable
- Lateral laminar expansion poorly individualized13
13. Weak ornamentation; posterior margin oblique and roughly straightC. striatus
- Stronger ornamentation; posterior margin roundedC. ocellatus
14. Posterior margin straight and oblique, sometimes provided with a small, V-
shaped notch in the middle15 (Anguidae)
- Posterior margin convex16
15. Anteromedial process long and slender; posterolateral corner not developed in a
pointed process
- Anteromedial process short and wide; posterolateral corner developing a long and
pointed processP. apodus
16. In adults, ornamentation almost absentO. elegans
- In adults, ornamentation poorly developedA. erythrurus,
D. oxycephala, I. bonnali, I. horvathi
- In adults, ornamentation strongly developed17
17. Sulcus not visible on the ornamented surfaceD. mosorensis,
I. cyreni, I. monticola cantabrica, P. bocagei, P. carbonelli, Po. hispanicus

- Sulcus visible in the middle of the ornamented surface......Other lacertids

Frontal

1. Frontal unpaired2
- Frontal paired and, if fused in a single element, fusion occurs only in old individuals
and the suture line is visible in ventral view10
2. Frontal composed of a subtriangular anterior portion and a subpentagonal posterior
portion; all margins represented by interdigitated suturesC. chamaeleon
- Frontal T-shaped; interdigitated sutures, if present, located by the posterior margin
only
3. Cristae cranii forming a tubular structure
- Cristae cranii not fused in a tubular structure
4. Presence of a faint ornamentation made up by grooves on the dorsal surface and
of large and triangular lateral processes
- Dorsal surface not ornamented and lateral processes absent or less
developed5
5. Presence of a well-developed medial process and of lateral grooves on the
posterior portion of the dorsal surface
- Absence of lateral grooves; medial process absent or little
developedM. kotschyi, T. mauritanica
6. Cristae cranii poorly or not developed; anterior processes absent7
- Cristae cranii more developed and originating well-developed anterior processes
anteriorly9
7. Lateral processes moderately large; dorsal surface sunken along midline; articular
surfaces with the nasals large, deep and U-shapedL. stellio
- Lateral processes short or very short; dorsal surface unsunken; articular surfaces
with the nasals less deep and less distinct

8. Strong middle constriction; pointed and very little developed lateral processes; articular surface with the nasals subtrapezoidal; no distinct ornamentation on the - Weak middle constriction; lateral processes represented by short and wide flanges, with an irregular anterior margin; articular surfaces with the nasals rounded; moderately developed dermal ornamentation on the dorsal surface......T. aurata - Posterior margin wavy, with a posterior expansion in the middle and no 10. Frontal short and rectangular; posterolateral process not clearly developed; articular surface with the ascending nasal process of the premaxilla visible on the dorsal surface; crista cranii running from the medial margin to the posterolateral of the bone: articular surface with corner the postfrontal not present.....B. cinereus, B. mariae, B. strauchi - Frontal anteroposteriorly elongated; posterolateral process present; articular surface with the premaxilla not present; crista cranii running along the lateral margin; 11. Lateral process absent; presence of a ventral lappet of the posterolateral process; crista cranii laminar and well developed, without a distinct anterior - Lateral process present; ventral lappet of the posterolateral process absent; crista 12. Articular surface with the nasal barely recognisable; articular surface with the postfrontal covering the posterior third of the lateral surface; dermal ornamentation never reaching the lateral margin of the dorsal surface; interfrontal shield - Articular surface with the nasal clearly visible; articular surface with the postfrontal covering the posterior fifth of the lateral surface; dermal ornamentation reaching the
lateral margin of the dorsal surface in adults; interfrontal shield absent or very 13. Lateral process never bifurcated; posterior margin without interdigitations; anterior process large in lateral view and distally pointed......14 - Lateral process usually bifurcated; posterior margin interdigitated; anterior process thin, with an irregular ventral margin.....17 14. Posterior end of the frontal only slightly wider than the anterior one; lateral process very little developed; articular surface with the prefrontal reaching the posterior third of the lateral surface; dermal ornamentation not developed, except for - Posterior end twice as large as the anterior one; lateral process short but distinct; articular surface with the prefrontal reaching mid-length; dermal ornamentation 15. Articular surfaces with prefrontal and postfrontal very close to each other; dermal ornamentation well developed......C. ocellatus Articular surfaces with prefrontal and postfrontal well-spaced; dermal ornamentation lightly developed......16 18. Posterior end twice as large as the anterior one.....L. agilis, L. schreiberi - Posterior end less than twice as large as the anterior one, at least in adults......L. bilineata, L. trilineata, L. viridis 20. Posterior end less than twice as large as the anterior one, at least in adults; sulcus between frontal and frontoparietal shields located at mid-length or at 3/5 of the total length......T. lepidus

21. Interdigitations on the posterior margin little developed......A. marchi, A. moreoticus, I. bonnali, I. horvathi, Z. vivipara

Parietal

1. Parietal paired2 (Gekkota)
- Parietal unpaired
2. Lateral lamina very well developed; dorsal surface ornamented
- Lateral lamina less developed; dorsal surface not ornamented
3. Lateral lamina very narrow; groove near the lateral margin visible only by the
anterior marginE. europaea
- Lateral lamina moderately or well developed; groove near the lateral margin clearly
visible both anteriorly and posteriorly to the epipterygoid process4
4. Presence of an anterior laminar development of the epipterygoid process;
postparietal process strongly curved in ventral directionT. mauritanica
- Absence of anterior laminar development of the epipterygoid process; postparietal
process less curved ventrally, sometimes straight in lateral viewM. kotschyi
5. Postparietal processes absent
- Postparietal processes present

6. Main body of the parietal small, laminar and subtriangular; presence of a long parietal crest; presence of a deep sunken area in place of a real parietal fossa; anterior and lateral margins interdigitated......C. chamaeleon - Main body of the parietal large and strongly anteroposteriorly elongated, with a vaulted and ventrally concave shape; interdigitations only on the anterior margin; of parietal small and posterior plates; fossa moderately presence deep......B. cinereus, B. mariae, B. strauchi 7. Presence of a wide and deep anterior notch; parietal foramen located in the notch......L. stellio - Anterior margin devoid of wide notch: parietal foramen located in the middle of 8. When present, dermal ornamentation covering only the anterior half of the parietal - Dermal ornamentation covering most of or entirely the dorsal surface of the shelf; 9. Anterolateral processes strongly developed laterally; postparietal processes robust and provided with a distinct angle at mid-length; contact between anterolateral and medial ventral crests present; processes on the posterior margin thin.....C. ocellatus - Anterolateral processes moderately or not developed in lateral direction; postparietal processes slender and straight; medial ventral crest not in contact with the lateral ones; processes on the posterior margin wide......10 10. Processes on the posterior margin reduced to rounded tabs; epiptervgoid - Processes on the posterior margin pointed and not reduced; epipterygoid processes long......12 11. Postparietal processes short; dermal ornamentation absent or represented only by light grooves; parietal fossa shallow; posterior tabs very short......A. kitaibelii - Postparietal processes long; dermal ornamentation distinctly developed; parietal

12. Postparietal processes with a rounded end; dermal ornamentation represented only by light grooves; parietal notch narrow; processes on the posterior margin very long.....O. punctatissimus - Postparietal processes pointed; light dermal ornamentation present; parietal notch 13. Parietal fossa very narrow.....C. chalcides 14. Articular surface for the ventral lappet of the posterolateral process of the frontal present on the ventral surface; interparietal shield very large, reaching the anterior - Articular surface for the ventral lappet of the posterolateral process of the frontal 15. Occipital shield small; anterolateral ventral crest not in contact with the medial one; medial ventral crest completely covering the parietal fossa in adults; carina arcuata not extending posteriorly to cover parietal notch; epipterygoid process - Occipital shield large; anterolateral ventral crest touching medial one; parietal fossa not completely covered by the medial ventral crest both in juveniles and adults; carina arcuata well developed, covering most of the parietal notch; epipterygoid process little or moderately developed.....P. apodus 16. Dermal ornamentation poorly developed; parietal tabs laterally expanded......17 - Dermal ornamentation well developed; parietal tabs not expanded laterally......19 18. Anterior margin without interdigitations, wavy and provided with a concavity in - Anterior margin with well-developed interdigitations; ornamentation reaching

Premaxilla

1. Premaxillae paired and, if fused, fusion present only in old individuals by the ventral margin of the bones......Scincidae 2. Premaxilla very small and slender; palatal processes absent......C. chamaeleon 3. Alveolar plate narrow, as wide as the base of the ascending nasal process in anterior view; presence of a moderately short and subquadrangular lamina in place - Alveolar plate wider than the base of the ascending nasal process; palatal processes 5. Ascending nasal process short, very narrow by the base and with a lobe-shaped dorsal half; low septonasal crest present in adults......Anguis gr. A. fragilis - Ascending nasal process moderately wide, with straight and parallel or moderately widened at mid-length lateral margins; septonasal crest never developed...P. apodus 6. Notch between the palatal processes shallow and more or less rounded......7 - Second pair of foramina by the base of the ascending nasal process 8. In lateral view, anterior outline of the premaxilla flat......B. cinereus, B. mariae In lateral view, anterior outline of the premaxilla anteriorly overhanging.....B. strauchi 9. Ascending nasal process robust and arrow-shaped......E. europaea 10. Septonasal crest moderately developed for the entire length of the ascending

- Septonasal crest low developed, not reaching the distal tip of the ascending nasal 11. Ascending nasal process proximally wider and with a pointed distal tip......H. turcicus - Ascending nasal process not proximally wider and usually displaying a slightly 12. In adults, ascending nasal process long, moderately narrow and slightly leaf-In adults. ascending nasal process shorter, stocky and leafshaped......Lacerta, T. lepidus, Z. vivipara - In adults, ascending nasal process long and arrow-shaped......E. arguta, I. cyreni, I. galani, I. monticola - In adults, ascending nasal process long and narrow, with parallel lateral

margins......Other lacertids (variable in *A. nigropunctatus*, *D. oxycephala*, *D. mosorensis* and *P. muralis*)

Maxilla

10. Posterior tip of the posterior process not shifted in dorsal direction; presence of a strongly medially bending lappet on the anteromedial process; dorsal margin of the facial process convex, not clearly separated into anterodorsal and posterodorsal portions.....O. punctatissimus - Posterior tip of the posterior process slightly shifted in dorsal direction; if present, lappet on the anteromedial process straight; anterodorsal and posterodorsal margins 11. Medial ridge of the anteriorly concave area well developed, originating a distinct 12. Dorsal margins similar in length; corners of the facial process pointed.....C. chalcides, C. striatus - Posterodorsal margin strongly shorter than the anterodorsal one; corners of the 13. Posterodorsal margin roughly straight and shorter than the anterodorsal one; all - Posterodorsal margin strongly concave and as long as the anterodorsal one; dorsal corner of the facial process rounded......T. aurata 15. Presence of a well-developed spur projecting posteriorly from the step.....P. melisellensis - Spur either shorter or absent......I. monticola monticola, Lacerta, P. bocagei, P. carbonelli, P. filfolensis, Po. hispanicus, P. lilfordi, P. milensis, P. muralis, P. pityusensis, P. siculus, P. tauricus, P. tiliguerta, P. waglerianus 17. Projections of the facial process scarcely developed......A. fitzingeri, A. marchi

18. Projections of the facial process largeE. arguta, H. graeca
- Projections of the facial process narrow
19. Dorsoventral ridge on the medial surface absentA. erythrurus
- Dorsoventral ridge on the medial surface present
20. In adults, dermal ornamentation on the lateral surface absent or poorly
developed21
- In adults, dermal ornamentation on the lateral surface well developed22
21. Projections of the facial process scarcely developedZ. vivipara
- Projections of the facial process more developedA. moreoticus,
A. nigropunctatus, D. oxycephala, D. mosorensis, I. bonnali, I. horvathi
22. Projections of the facial process scarcely developedA. bedriagae, T. lepidus*
- Projections of the facial process more developedOther lacertids

Prefrontal

 1. Dorsal process laminar, posteriorly rounded and strongly mediolaterally expanded; interdigitated suture present by the posterior end of the process; presence of tubercular ornamentation along the lateral margin and on the dorsal surface.

 c. chamaeleon o Dorsal process pointed and not mediolaterally expanded; suture not present by the posterior end of the process; tubercular ornamentation not present.

 c. chamaeleon o Dorsal process pointed and not mediolaterally expanded; suture not present by the posterior end of the process; tubercular ornamentation not present.

 c. chamaeleon o Presence of a very robust tubercle on the dorsolateral corner.

 L. stellio c Tubercle on the dorsolateral corner not present.

 d o Orbitonasal flange projection present.

 d o Orbitonasal flange projection absent.

 d o Orbitonasal flange projection shorter than the posteroventral process.

 o Orbitonasal flange projection shorter than the posteroventral process.

 s o Posterolateral surface of the orbitonasal flange possibly provided with a faint ornamentation made up of grooves; notch of the lacrimal foramen deep....*H. turcicus*

- Posterolateral surface of the orbitonasal flange smooth; notch of the lacrimal
foramen shallow
6. Dorsal process stocky
- Dorsal process slenderE. europaea, M. kotschyi
7. Orbitonasal flange projection subtriangular
- Orbitonasal flange projection subquadrangular
8. Ornamentation not present; notch of the lacrimal foramen
deepAnguis gr. A. fragilis
- Ornamentation made up of mild rugosities; notch of the lacrimal foramen very
deepP. apodus
9. Osseous projection covering the notch of the lacrimal foramen dorsolaterally;
dorsal process slightly longer than the orbitonasal flangeA. kitaibelii
- Notch of the lacrimal foramen not covered dorsolaterally; dorsal process slightly
shorter than the flange10
10. Palpebral crest sharpT. aurata
- Palpebral crest lowChalcides, O. punctatissimus
11. Dorsal process very short; palpebral crest absentB. cinereus,
B. mariae, B. strauchi
- Dorsal process longer; palpebral crest well distinct12 (Lacertidae)
12. Dorsal process as long as or shorter than the orbitonasal flange in lateral
viewOther lacertids (variable in A. nigropunctatus)
- Dorsal process slightly longer than the orbitonasal flange in lateral view13
13. Presence of a projection dorsally to the notch of the lacrimal
foramenO. elegans
- Projection dorsally to the notch of the lacrimal foramen not
presentA. erythrurus, A. marchi, A. moreoticus, Psammodromus

Jugal

1. Jugal absent	. <i>B</i> .	. cinereus,	B	. mariae,	В.	. strauchi
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- Jugal present2
2. Jugal reduced to a small and straight bone
- Jugal L-shaped, composed of an anterior and a posterior processes
3. Posterior end folded
- Posterior end not folded
4. Anterior end distinctly wider than the posterior oneM. kotschyi, T. mauritanica
- Difference in width between anterior and posterior ends less markedE. europaea
5. Posterodorsal process massive or expanded
- Posterodorsal process narrow or slender7
6. Quadratojugal process well developed; articular surface with the posterior spur of
the maxilla visible on the lateral surface; posterodorsal process very massive and
originating a distinct angle at mid-length; tubercles not presentL. stellio
- Quadratojugal process absent; articular surface with the spur of the maxilla absent;
posterodorsal process more laminar and without distinct angles; small tubercles
present on the lateral surface
7. Jugal very slender
- Jugal less slender
8. Palatal process poorly developed; articular surface with the maxilla twisted in
ventral direction
- Palatal process absent; articular surface with the maxilla not twisted
ventrally10 (Scincidae)
9. Medial process absent; posterior end of the posterodorsal process rounded;
posterodorsal process slightly shorter than the anterior one; quadratojugal process
distinctly developed; lateral surface smoothAnguis gr. A. fragilis
- Small hint of medial process visible; posterior end of the posterodorsal process
pointed; posterodorsal process slightly longer than the anterior one; quadratojugal
process very little developed; lateral surface displaying mild rugositiesP. apodus
10. Medial opening of the canal passing through the middle of the bone located at
mid-length of the posterodorsal processO. punctatissimus

- Medial opening of the canal passing through the middle of the bone not shifted
dorsally11
11. Posterodorsal process as long as the anterior oneC. chalcides
- Posterodorsal process roughly twice as long as the anterior one
- Posterodorsal process slightly longer than the anterior one
12. Dorsal end of the posterodorsal process roundedA. kitaibelii
- Dorsal end of the posterodorsal process truncatedC. striatus, T. aurata
13. Palatal process poorly developed14
- Palatal process moderately or well developed16
14. Quadratojugal process well developed; anterior process narrow and pointed;
articular surface with the maxilla largely covering the lateral surfaceE. arguta
- Quadratojugal process absent; anterior process large and flattened; lateral surface
more exposed laterally15
15. Anterior process rounded anteriorly; medial process absent; posterodorsal
process longer than the anterior one
- Anterior process forked anteriorly; medial process distinct; anterior process longer
than the posterodorsal oneO. elegans
16. Quadratojugal process weakly developed17
- Quadratojugal process well developed20
17. Medial process distinctP. algirus
- Medial process absent or little developed
18. Articular surface with the maxilla not steppedI. horvathi
- Articular surface with the maxilla stepped19
19. Anterior and posterodorsal processes similar in lengthP. pityusensis
- Anterior process longer than the posterodorsal oneP. tiliguerta
20. Medial process distinctPs. hispanicus
- Medial process absent or little developed21
21. Articular surface with the maxilla stepped or spurred
- Articular surface with the maxilla not stepped/spurred24 187

23. Anterior process longer than posterodorsal one.....L. agilis, L. bilineata, L. schreiberi, L. viridis, P. siculus, P. tauricus, P. muralis^{*}, P. waglerianus

- Anterior and posterodorsal processes roughly similar in length...I. monticola monticola, L. trilineata, P. bocagei, P. filfolensis, Po. hispanicus, P. lilfordi, P. milensis, P. muralis*

- Anterior and posterodorsal processes roughly similar in length......A. bedriagae, H. graeca, I. bonnali, I. cyreni, I. monticola cantabrica, T. lepidus

Postfrontal and postorbital

Postfrontal

1. Postfrontal absent....L. stellio, C. chamaeleon, B. cinereus, B. mariae, B. strauchi 3. Postfrontal T-shaped; anterior margin poorly concave; anteromedial process - Postfrontal Y-shaped; anterior concavity more developed; difference in length anteromedial and anterolateral between processes absent less or 4. Body roughly subrectangular; anteromedial process moderately robust......Anguis gr. A. fragilis - Body subtriangular; anteromedial process distinctly robust......P. apodus 6. Posterior end of the bone laterally expanded......C. ocellatus

- Posterior end of the bone provided with a pointed projection <i>T. aurata</i>
7. Body subtriangular; medial margin not expandedA. kitaibelii
- Body subrectangular; medial margin distinctly enlarged
8. Anterolateral process similar in length to the anteromedial one and slightly curved
in posterior direction distallyC. chalcides
- Anterolateral process shorter than the anteromedial one and straight9
9. Anterior processes pointed; projection on the posterior end absentC. striatus
- Anterior processes rounded; pointed projection present on the posterior
endO. punctatissimus
10. Anterolateral process absent
I. aurelioi, I. bonnali*, I. horvathi, O. elegans
- Anterolateral process present
11. Anteromedial process expanded (at least in adults)12
- Anteromedial process not expandedOther lacertids
12. Anterolateral process shortL. bilineata,
L. schreiberi, L. trilineata, L. viridis, T. lepidus
- Anterolateral process longerL. agilis
Postorbital
1. Postorbital absent
B. cinereus, B. mariae, B. strauchi and maybe also T. aurata
- Postorbital present
2. Postorbital large
- Postorbital small and slender
3. Presence of a laminar anterior process and of tubercular
ornamentationC. chamaeleon
- Anterior process and tubercular ornamentation absentL. stellio
4. Anteromedial process absentScincidae, Anguidae,
D. oxycephala, I. aurelioi, I. bonnali, P. filfolensis, P. pityusensis, L. trilineata*
- Anteromedial process presentOther lacertids
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Postorbitofrontal

Sauamosal	
- Anterior process shorter than the posterior one	H. turcicus
4. Anterior process longer than the posterior one	E. europaea
- Lateral corner rounded	4
3. Lateral corner pointed	M. kotschyi
- Postorbitofrontal V-shaped, without lateral process	3
2. Postorbitofrontal Y-shaped, with a lateral process	T. mauritanica
clearly recognisable	2 (Gekkota)
- Postorbitofrontal small and V- or Y-shaped; postfrontal and	d postorbital portions not
of Lacerta, P. siculus and T. lepidus	
L. schreiberi, Psammodromus, older individuals of A. nigra	opunctatus, other species
postorbital portions clearly recognisable	E. arguta,
1. Postorbitofrontal anteroposteriorly elongated and la	aminar; postfrontal and

Squamosal

1. Squamosal strongly reducedB. cinereus, B. mariae, B. strauchi
- Squamosal not reduced
2. Squamosal large; posterior end composed by quadrate process and dorsal parietal
process
- Squamosal small; posterior end composed by a single posterior process4
3. Anterior process dorsally concave; dorsal parietal process subtriangular; lateral
surface smoothL. stellio
- Anterior process laminar and dorsoventrally expanded; dorsal parietal process very
long and slender; tubercles usually present on the lateral surfaceC. chamaeleon
4. Anterior process very long
- Anterior process short or moderately long7
5. Anterior end provided with a pointed tipScincidae
- Anterior end represented by a flattened lamina
6. Anterior end rounded and subhorizontal

- Anterior end pointed and more dorsally concave	P. apodus
7. Anterior process short	Gekkota
- Anterior process moderately long	8 (Lacertidae)
8. Medial process present	.I. martinezricai*
- Medial process absent	9
9. Posterior process expanded	Lacerta,
O. elegans, P. tauricus, P. tiliguerta, Psammodromus, T. lepidus*	
- Posterior process not expanded	Other lacertids

Quadrate

1. Lateral lamina absent (quadrate rod-like); cephalic condyle composed by three
portionsC. chamaeleon
- Lateral lamina present; cephalic condyle single2
2. Lateral lamina projecting anteriorly
- Lateral lamina not projecting anteriorly4
3. Ridge on the posteromedial side of the pillar moderately developedB. strauchi
- Ridge on the posteromedial side of the pillar lowB. mariae
- Ridge on the posteromedial side of the pillar very poorly developed, almost not
recognisableB. cinereus
4. Quadrate mediolaterally expanded in anterior view; medial lamina very well
developed, which is more developed in its dorsal portion; cephalic condyle strongly
expanded in anteromedial to posterolateral direction; mandibular condyle very
distinctly enlarged in posterior viewL. stellio
- Quadrate not mediolaterally expanded; medial lamina either absent or less
developed, never reaching its maximum development in the dorsal part; cephalic
condyle never developing anteromedially to posterolaterally; mandibular condyle
less enlarged in posterior view
5. Rounded outline (bean-like shape) in anterior view; medial lamina
absent

- Quadrate subrectangular in anterior view; medial lamina present
6. Quadrate rather straight in anterior view
- Strongly laterally rounded in anterior view7
7. Tympanic crest slightly thicker ventrally
- No clear differences in the thickness of the tympanic
crestH. turcicus, T. mauritanica
8. Well-developed conch present (lateral lamina distinctly developed)9
- Well-developed conch absent (lateral lamina less developed)14
9. Cephalic condyle expanded posteroventrally; pterygoid flange
present10 (Lacertidae)
- Cephalic condyle slightly expanded to the sides; pterygoid flange absent12
10. Anterior outline angular in medial viewA. erythrurus, E. arguta, O. elegans
- Anterior outline rounded in medial view11
11. Anterior platform concave
- Anterior platform flatOther lacertids
12. Quadrate narrow in anterior view; medial lamina reduced to a
hintA. kitaibelii, C. chalcides, C. striatus
- Quadrate wider in anterior view; medial lamina more developed13
13. Medial lamina well developedC. ocellatus
- Medial lamina moderately developedT. aurata
14. Quadrate narrow in anterior view; medial lamina reduced to a
hintO. punctatissimus
- Quadrate wider in anterior view; medial lamina more developed15 (Anguidae)
15. Anterior outline rounded; notch on the cephalic condyle
small
- Anterior outline angular; notch on the cephalic condyle deepP. apodus

Epipterygoid

1. Epipterygoid absent.....C. chamaeleon

- Epipterygoid present	2
2. Epipterygoid small and mediolaterally compressed	B. cinereus,
B. mariae, B. strauchi	
- Epipterygoid larger and not compressed	3
3. Epipterygoid slightly twisted	Anguidae
- Epipterygoid not twisted	4
4. Epipterygoid curved in lateral view	5
- Epipterygoid straight in lateral view	7
5. Dorsal end bending anteriorly; ventral end strongly larger the	han the dorsal
one	L. stellio
- Dorsal end bending posteriorly; ventral end less large than the dorsa	l one6
6. Epipterygoid short; posterior curve poorly marked	punctatissimus
- Epipterygoid long; posterior curve distinctly marked	Lacertidae
7. Dorsal end slightly larger than the ventral one	Gekkota
- Ventral end distinctly larger than the dorsal one	Other scincids

Vomer

5. Finger-like lateral wing presentB. cinereus, B. mariae, B. strauchi
- Finger-like lateral wing absent
6. Posterodorsal process absent
- Posterodorsal process present
7. Vomer small; anterior portion roughly as large as the rest of the bone; presence of
a short flange-like expansion on the lateral margin; single pointed process present by
the posterior endL. stellio
- Vomer proportionally more developed; anterior half narrower than the posterior
one; lateral flange-like expansion not present; posterior end provided with two
processes
8. Difference in width between anterior and posterior portions low9
- Difference in width between anterior and posterior portions strongOther lacertids
9. Lateral margin of the posterior half roundedPsammodromus
- Lateral margin of the posterior half angularA. erythrurus, O. elegans
10. Posterodorsal process shifted medially, covering partially the posterior end11
- Posterodorsal process not shifted medially14 (Gekkota)
11. Notch of the vomeronasal fenestra moderately deep; lateral margin of the
posterior half straight; posterodorsal process posteriorly truncated12
- Notch of the vomeronasal fenestra shallow; lateral margin of the posterior half
convex; posterodorsal process displaying a notch on the posterior
end13 (Anguidae)
12. Transverse ridge almost indistinct; ventral groove absentO. punctatissimus
- Transverse ridge well developed, reaching the longitudinal medial ridge; ventral
groove presentT. aurata
13. Medial ridge present; vomerine teeth never presentAnguis gr. A. fragilis
- Medial ridge absent; vomerine teeth sometimes presentP. apodus
14. Posterolateral process medially concave
- Posterolateral process not concave and strongly thickened distally16

15. Posterolateral process very wide	; articulation surface with	vomerine process of
the palatine visible		E. europaea
- Posterolateral process narrow; articu	ulation surface with the von	nerine process of the
palatine not recognisable		M. kotschyi
16. Articulation surface with the vom	erine process of the palatin	e bordered by ridges
both dorsally and ventrally		H. turcicus
- Articulation surface with th	e palatine bordered b	y a ridge only
ventrally		T. mauritanica

Septomaxilla

1. Septomaxilla absent	C. chamaeleon
- Septomaxilla present	2
2. Septomaxilla subtriangular in dorsal view	P. apodus
- Septomaxilla subquadrangular/subrectangular in dorsal view	3
3. Septomaxilla anteroposteriorly elongated (rectangular)	4
- Septomaxilla anteroposteriorly short (subquadrangular)	8
4. Process by the posterolateral corner short; laterally directed	triangular process
absent	L. stellio
- Process by the posterolateral corner long; presence of a laterally	v directed triangular
process	5 (Gekkota)
5. Lateral process not hook-shaped	6
- Lateral process hook-shaped	7
6. Posterior portion of the medial ridge low	H. turcicus
- Posterior portion of the medial ridge high	T. mauritanica
7. Medial process long	E. europaea
- Medial process short	M. kotschyi
8. Ventral expansion by the anterior end not present	9
- Ventral expansion by the anterior end present	11
9. Posterolateral process bending dorsally	nguis gr. A. fragilis

- Posterolateral process not bending dorsally10 (Scincidae)
10. Small ventral expansion by the posterior margin presentChalcides
- Small ventral expansion by the posterior margin not presentOther scincids
11. Anterolateral process anteriorly developedB. cinereus, B. mariae, B. strauchi
- Anterolateral process dorsally or anterodorsally developed12 (Lacertidae)
12. Posteromedial process lacking; tip of the posterolateral process
angular
- Posteromedial process present; tip of the posterolateral process quadrangular13
13. Anterolateral process anterodorsally directedPsammodromus
- Anterolateral process dorsally directed14
14. Posteromedial process shortA. marchi, A. moreoticus, A. bedriagae, I. bonnali
- Posteromedial process moderately longOther lacertids

Palatine

1. Pterygoid process laminar; on the ventral surface of the pterygoid process, choanal duct represented by a very shallow trough; distinct palatine ridge not - Pterygoid process more robust; on the ventral surface of the pterygoid process, choanal duct deep and distinct; palatine ridge present......5 2. Articulation surface with the maxilla on the maxillary process not recognisable...3 - Articulation surface with the maxilla on the maxillary process recognisable.......4 Presence of a small triangular osseous expansion on the lateral 3. margin......E. europaea - Lateral margin without osseous expansions or, if present, expansion reduced to a 4. Lateral margin with a simple triangular osseous expansion......H. turcicus - Lateral margin with a wide and laterally open foramen......T. mauritanica 5. Palatine gutter-shaped; presence of a pointed process in the middle of the posterior end......6 (Scincidae)

- Palatine not gutter-shaped; posterior pointed process not present10
6. Expansion of the medial margin absent; expansion of the lateral margin very well
developed7
- Expansion of the medial margin present; expansion of the lateral margin less
developed8
7. Vomerine process narrow; pterygoid process very narrowA. kitaibelii
- Vomerine process wider; pterygoid process wide
8. Anterior projection of the vomerine process distinctly recognisable; infraorbital
foramen completeO. punctatissimus
- Anterior projection of the vomerine process not well individualized; infraorbital
foramen represented by a notch
9. Vomerine process short and small; process on the posterior end
slenderC. chalcides, C. striatus
- Vomerine process long and narrow; process on the posterior end
widerC. ocellatus
10. Infraorbital foramen absent or represented by a notch11
- Infraorbital foramen complete
11. Vomerine process massive; posterolateral corner of the maxillary process
provided with a long projection; infraorbital foramen represented by a moderately
deep notchL. stellio
- Vomerine process slender; posterolateral corner of the maxillary process not
projecting posterolaterally; no signs of infraorbital foramen12
12. Interdigitated articular surface with the opposite palatine on the vomerine
process; maxillary process short and wide; palatine ridge short and stocky, with low
interdigitations; choanal duct moderately narrow; finger-like expansion
absentC. chamaeleon
 absent

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choanal duct very deep and wide; presence of a finger-like expansion on the lateral margin.....B. cinereus, B. mariae, B. strauchi 13. Vomerine process slender; maxillary process slender and T-shaped in dorsal view; palatine ridge moderately developed; sulcus dorsalis present on the dorsal - Vomerine process moderately wide; maxillary process wide and subtrapezoidal in dorsal view; palatine ridge well developed; sulcus dorsalis absent.....15 (Lacertidae) 14. Notch the posterior end deep; palatine teeth on verv - Notch on the posterior end very small or absent; palatine teeth present.....P. apodus 15. Anterolateral margin of process the maxillary poorly - Anterolateral margin of the maxillary process strongly oblique......Other lacertids

Pterygoid

 1. Quadrate process wing-like; presence of a ventral flange; pterygoid flange reduced to a ridge; fossa columellae absent.
 C. chamaeleon

 - Quadrate process not wing-like; ventral flange absent; pterygoid flange not reduced; fossa columellae present.
 2

 2. Presence of an expansion on the medial margin of the pterygoid flange; quadrate process slightly sigmoid in dorsal view.
 B. cinereus, B. mariae, B. strauchi

 - Expansion of the medial margin of the pterygoid flange not present; quadrate process straight or curved, not sigmoid, in dorsal view.
 3

 3. Quadrate process curved, laterally concave; medial margin of the palatine process straight or curved, not sigmoid, in dorsal view.
 4 (Gekkota)

 - Quadrate process straight; medial margin of the palatine process straight or convex.
 7

 4. Posterior end of the quadrate process truncated in dorsal view.
 5

5. Basipterygoid fossa very shallow
- Basipterygoid fossa moderately deep
6. Dorsal ridge on the quadrate process recognisable
- Dorsal ridge on the quadrate process not recognisable
7. Pterygoid flange laterally directed and ending with an expanded surface; in adults,
presence of a step on the dorsal margin of the quadrate processL. stellio
- Pterygoid flange anterolaterally directed and pointed; no step on the dorsal margin
of the quadrate process
8. Basipterygoid fossa marked by flanges both dorsally and ventrally9 (Anguidae)
- Basipterygoid fossa not marked by flanges10
9. Ventral ridge on the pterygoid flange poorly developed; ventral flange moderately
developed and rounded; pterygoid teeth absentAnguis gr. A. fragilis
- Ventral ridge on the pterygoid flange well developed; ventral flange longer and
thumb-like; pterygoid teeth presentP. apodus
10. Palatine process provided with a thicker area in the middle11 (Scincidae)
- Palatine process provided with a robust medial margin15 (Lacertidae)
11. Palatine process short; pterygoid recess shallow; pterygoid ridge absent12
- Palatine process long; pterygoid recess deep; pterygoid ridge present13
12. Medial margin of the palatine process strongly convex; anterior end of the
palatine process bifurcated; pterygoid teeth absent; dorsal ridge on the pterygoid
flange moderately developed
- Medial margin of the palatine process slightly convex; anterior end of the palatine
process wavy; pterygoid teeth present; dorsal ridge on the pterygoid flange well
developedO. punctatissimus
13. Medial margin of the palatine process straight; pterygoid teeth
presentT. aurata
- Medial margin of the palatine process slightly convex; pterygoid teeth absent14
14. Palatine process subtriangular; anterior end of the palatine process pointed;
pterygoid ridge reduced to a hintA. kitaibelii

- Palatine process subrectangular; anterior end of the palatine process bifurcated;
pterygoid ridge distinctly developedC. chalcides, C. striatus
15. Pterygoid ridge moderately developed16
- Pterygoid ridge well developed
16. Pterygoid recess moderately shallow (at least in adults)A. erythrurus,
T. lepidus
- Pterygoid recess deep17
17. Pterygoid teeth present (at least in adults)A. moreoticus,
D. oxycephala*, P. milensis
- Pterygoid teeth absentD. oxycephala*, D. mosorensis, I. monticola, P. filfolensis,
P. muralis
18. Pterygoid teeth present (at least in adults)A. nigropunctatus,
E. arguta, Lacerta, P. melisellensis*, P. siculus*, P. tauricus, P. algirus
- Pterygoid teeth absentA. fitzingeri, A. marchi, A. bedriagae, H. graeca,
I. bonnali, I. cyreni, I. horvathi, O. elegans, P. bocagei, Po. hispanicus, P. lilfordi,
P. melisellensis*, P. pityusensis, P. siculus*, P. tiliguerta, P. waglerianus, Z.
vivipara

Ectopterygoid

1. Ectopterygoid small and subtriangular in dorsal viewB. cinereus,
B. mariae, B. strauchi
- Ectopterygoid thick and rod-like in dorsal view2
- Ectopterygoid crescent- or L-shaped, with a medial concavity in dorsal view3
2. Medial end kidney-shaped in lateral view; posterolateral process slightly longer
than the similar-sized anterolateral and ventral processesL. stellio
- Medial end narrow and subrectangular in lateral view; ventral process shorter than
the similar-sized anterolateral and posterolateral processesC. chamaeleon
3. Ectopterygoid L-shaped4
- Ectopterygoid crescent-shaped

4. Articular surface with the maxilla covering the ventral surface of the anterolateral
processLacertidae
- Articular surface with the maxilla limited to the lateral margin of the anterolateral
processT. aurata
5. Posterior end provided with three lappets
- Posterior end forked in lateral view, with two projections/lappets7
6. Anteromedial projection of the ventral lappet present
- Anteromedial projection of the ventral lappet absentC. chalcides,
C. striatus, O. punctatissimus
7. Articular surface with the maxilla limited to the lateral margin of the anterolateral
process
- Articular surface with the maxilla covering the lateral margin of the ventral surface
of the anterolateral process
- Articular surface with the maxilla represented by a concave area on the lateral
surface
8. Ventral lappet of the posteromedial process very little developed; articulation
surface with the maxilla very scarcely distinguishableE. europaea
- Ventral lappet moderately developed; articulation surface with the maxilla
distinctOther gekkotans
9. Anterior end not forked
- Anterior end slightly forkedP. apodus

Tabulosphenoid

1. Tabulosphenoid present	B. cinereus, B. mariae, B. strauchi
- Tabulosphenoid absent	"Lacertilia"

General features of the otooccipital region

1. Presence of the elements-X; region distinctly dorsoventrally compressed; fenestra ovalis very wide, shifted ventrally to touch sphenoid and basioccipital and opening

2. Basioccipital excluded from the formation of the foramen magnum; occipital condyle composed mainly by the otooccipitals; recessus scalae tympani strongly reduced, opening externally with a very small lateral opening reduced to a foramen; sphenooccipital tubercles composing a small part of the ventral margin of the - Basioccipital participating in the formation of the foramen magnum; portion of the occipital condyle made by the basioccipital larger; recessus scalae tympani not reduced, with a real lateral opening; ventral margin of the fenestra ovalis not 3. Portion of the occipital condyle made by each otooccipital reduced compared to - Portion of the occipital condyle made by each otooccipital equal to the basioccipital 5. Posterior margin of the condyle convex; lateral opening of the recessus scalae tympani narrow; medial opening of the recessus scalae tympani anteroposteriorly - Posterior margin of the condyle straight; lateral opening of the recessus scalae tympani wider; medial opening of the recessus scalae tympani not elongated.....P. apodus

7. Medial opening of the recessus scalae tympani divided into two 8. Recessus scalae tympani and related lateral opening very wide......E. europaea _ Recessus scalae tympani and related lateral opening narrow......H. turcicus, M. kotschyi 9. Medial opening of the recessus scalae tympani subcircular or anteroposteriorly elongated.....Lacertidae - Medial opening of the recessus scalae tympani reduced by expansions of its dorsal 10. Margins of the lateral opening of the recessus scalae tympani poorly developed......O. punctatissimus - Margins of the lateral opening of the recessus scalae tympani more developed......Other scincids

Basioccipital

1. Sphenooccipital tubercles absent	t		B. cir	nereus, B.	mariae, B	. strauchi
- Sphenooccipital tubercles present	t	• • • • • • • • • • •				2
2. Basioccipital participating on	ly slig	htly in	the	formation	of the	occipital
condyle					C. ch	amaeleon
- Basioccipital composing	more	than	a	third of	f the	occipital
condyle				1	L. stellio,	Anguidae
- Basioccipital composin	ng a	a tl	hird	of	the	occipital
condyle			G	ekkota, La	certidae,	Scincidae

Sphenoid

2. Parasphenoid rostrum thick
- Parasphenoid rostrum thin or absent
3. Supravenous processes absentL. stellie
- Supravenous processes present4
4. Supravenous processes horizontal; groove of the lateral head vein
narrow5 (Gekkota)
- Supravenous processes vertical; groove of the lateral head vein wide
5. Groove of the lateral head vein enclosed in a canal
- Groove of the lateral head vein laterally open6
6. Sunken area on the ventral surface deep; presence of small cristae
ventrolateralesT. mauritanica
- Sunken area on the ventral surface shallow; absence of cristae ventrolaterales7
7. Cristae trabeculares low but visible
- Cristae trabeculares not distinguishable
8. Trabeculae cranii projecting beyond the anterior margin; posterolateral openings
of the vidian canals located on prootics
- Trabeculae cranii not projecting beyond the anterior margin; posterolateral
openings of the vidian canals located on the sphenoid, sometimes near the contact
with the prootics
9. Supravenous processes narrow
- Supravenous processes largerP. apodus
10. Parasphenoid rostrum present11 (Lacertidae)
- Parasphenoid rostrum absent
11. Basipterygoid processes narrowing proximally
O. elegans, juveniles of other lacertids
- Basipterygoid processes enlarged for their entire lengthAdults of other lacertide
12. Dorsum sellae well developed
- Dorsum sellae short or not developed14
13. Trabeculae cranii very poorly developed <i>T. aurata</i> 204

- Trabeculae cranii more developed	ocellatus
14. Cristae ventrolaterales absent; supravenous processes very narrowA.	kitaibelii
- Cristae ventrolaterales short; supravenous processes less narrow	15
15. Trabeculae cranii not in contact	16
- Trabeculae cranii contacting each other	17
17. Ventral surface displaying a shallow sunken area	chalcides
- Ventral surface flat	C. striatus
18. Trabeculae cranii very poorly developed; distinct cristae trabecul	lares not
presentO. puncte	atissimus
- Trabeculae cranii more developed; cristae trabeculares lo	ow but
distinctC. b	pedriagai

Element-X

1. Element-X present as distinct subovoid bonesB. cinereus, B. maria	e, B. strauchi
- Distinct element-X not present	."Lacertilia"

Supraoccipital

1. Processus ascendens absent	2 (Gekkota)
- Processus ascendens present	5
2. Absence of structures on the dorsal surface	E. europaea
- Presence of structures on the dorsal surface	3
3. Presence of a W-shaped ridge	T. mauritanica
- Presence of a pointed tubercle	4
4. Dorsal surface of the tubercle flat	H. turcicus
- Dorsal surface of the tubercle not flat	M. kotschyi
5. Processus ascendens originating a tall median crest dorsally	C. chamaeleon
- Processus ascendens not originating a median crest	6
6. Presence of a notch of the sphenoccipital foramen	L. stellio
- Notch of the sphenoccipital foramen not present	7
7. Anterior margin without ridges	8

- Presence of ridges on the anterior margin	12
8. Processus ascendens not compressed	9
- Processus ascendens more dorsoventrally compressed	10
9. Processus ascendens short and slender; supraoccipital crest absent.	C. chalcides
- Processus ascendens stocky and moderately ossified; supraocci	pital crest well
developed	C. ocellatus
10. Supraoccipital crest well developed in adults	B. cinereus,
B. mariae, B. strauchi	
- Supraoccipital crest always absent	11
11. Processus ascendens very short; marginal processes absent	A. kitaibelii
- Processus ascendens longer; marginal processes present	. punctatissimus
12. Supraoccipital crest present	13
- Supraoccipital crest absent	15
13. Processus ascendens not compressed	.14 (Lacertidae)
- Processus ascendens more dorsoventrally compressed	Anguidae
14. Anterolateral margins roughly parallel	A. erythrurus
- Anterolateral margins convergent	Other lacertids
15. Processus ascendens not compressed	C. striatus
- Processus ascendens more dorsoventrally compressed	T. aurata

Prootic

1. Anterior infe	erior process	reduced	and	widely	occupied	by	the	fenestra
ovalis				B. cin	ereus, B. n	ıaria	e, B.	strauchi
- Anterior inferi	or process not	reduced	and r	not wide	ly occupie	d by	the	fenestra
ovalis								2
2. Alar process a	bsent							3
- Alar process pr	esent							4
3. Crista prootica	a very well dev	eloped, at	least	in adults	; notch of	the s	phen	occipital
foramen present.							•••••	L. stellio

- Crista prootica very poorly developed; notch of the sphenoccipital foramen
absentC. chamaeleon
4. Crista alaris mediolaterally expanded; incisura prootica usually closed
dorsally5 (Gekkota)
- Crista alaris not mediolaterally expanded; incisura prootica not closed dorsally8
5. Alar process triangular in lateral view
- Alar process subtrapezoidal in lateral view7
6. Distal end of the alar process pointed
- Distal end of the alar process roundedT. mauritanica
7. Recessus vena jugularis ending ventrally to the facial foramen; entocarotid fossa
very distinctE. europaea
- Recessus vena jugularis reaching facial foramen; entocarotid fossa not
distinguishableM. kotschyi
8. Posterior opening of the vidian canal located on the anterior inferior
process
- Posterior opening of the vidian canal not located on the prootic10
9. Crista prootica lowAnguis gr. A. fragilis
- Crista prootica moderately developedP. apodus
10. Recessus vena jugularis shallow and very wide11 (Scincidae)
- Recessus vena jugularis not distinguishable15 (Lacertidae)
11. Margins of the facial foramen not raised; crista prootica low developed or
absent12
- Margins of the facial foramen raised; crista prootica well developed13
12. Alar process very short; crista prootica continuing posteriorlyA. kitaibelii
- Alar process long; crista prootica ending by the facial foramenO. punctatissimus
13. Crista prootica continuing posteriorly
- Crista prootica ending by or near to the facial foramen14
14. Alar process moderately short; crista prootica ending by the facial
foramenC. bedriagai, C. chalcides, C. striatus

- Alar process long; crista prootica extending slightly beyond the facial
foramenC. ocellatus
15. Paroccipital projection short in adults16
- Paroccipital projection long in adults19
16. Alar process moderately short in adults17
- Alar process longer in adults
17. Posterior portion of the crista prootica absentA. fitzingeri, A. marchi
- Posterior portion of the crista prootica presentA. moreoticus,
I. horvathi, O. elegans
18. Posterior portion of the crista prootica absentP. filfolensis,
P. muralis, P. tiliguerta
- Posterior portion of the crista prootica presentA. bedriagae,
I. cyreni, I. monticola cantabrica, P. bocagei, P. carbonelli, Po. hispanicus, P.
lilfordi, P. melisellensis, P. milensis, P. tauricus, Ps. hispanicus, Z. vivipara
19. Alar process moderately short in adults20
- Alar process longer in adults
20. Posterior portion of the crista prootica absentA. erythrurus
- Posterior portion of the crista prootica presentD. mosorensis
21. Posterior portion of the crista prootica absentA. nigropunctatus,
L. agilis, P. siculus, P. waglerianus
- Posterior portion of the crista prootica presentD. oxycephala,
E. arguta, H. graeca, I. bonnali, I. monticola monticola, L. bilineata, L. schreiberi,
L. trilineata, L. viridis, P. algirus, T. lepidus

Otooccipital

1. Paroccipital process very poorly developed, ridge-like	.B. cinereus,
B. mariae, B. strauchi	
- Paroccipital process more developed, not ridge-like	2
2. Otooccipital composing more or less than a third of the occipital condy	vle3

- Otooccipital composing a third of the occipital condyle
3. Otooccipital composing almost a half of the occipital condyle; presence of a
foramen representing the remains of the reduced lateral opening of the recessus
scalae tympaniC. chamaeleon
- Otooccipital composing less than a third of the occipital condyle; lateral opening
of the recessus scalae tympani not reduced to a foramen4
4. Paroccipital process very long; very well-developed ridge present on the proximal
half of the ventral surface of the paroccipital processL. stellio
- Paroccipital process shorter; ridge on the ventral surface of the paroccipital process
not present
5. Paroccipital process moderately shortAnguis gr. A. fragilis
- Paroccipital process longP. apodus
6. Distal end of paroccipital process not enlarged
- Distal end of paroccipital process more or less enlarged10
7. Paroccipital process short
- Paroccipital process long
8. Absence of ridges on the dorsal half of the anterior surface of the paroccipital
process
- Presence of a ridge on the dorsal half of the anterior surface of the paroccipital
process
9. Lateral half of the cavum capsularis undividedM. kotschyi
- Lateral half of the cavum capsularis divided by a ridgeT. mauritanica
10. Paroccipital process very shortA. kitaibelii, O. punctatissimus
- Paroccipital process short
A. marchi, A. moreoticus, I. cyreni, I. monticola cantabrica, O. elegans, P. bocagei,
P. carbonelli, P. filfolensis, Po. hispanicus, P. melisellensis, P. muralis, P. tauricus,
P. tiliguerta, P. waglerianus, Ps. hispanicus, Z. vivipara, juveniles of other lacertids,
C. chalcides, C. striatus, T. aurata
- Paroccipital process longAdults of other lacertids, C. ocellatus

Stapes

1. Footplate very large; shaft very shortB. cinered	us, B. mariae, B. strauchi
- Footplate smaller; shaft longer	2
2. Stapedial foramen present	Gekkota
- Stapedial foramen absent	3
3. Distal end of the shaft pointed	C. chamaeleon
- Distal end of the shaft not pointedL. stellio, Lacertic	dae, Scincidae, Anguidae

Dentary

1. Meckelian fossa entirely or almost entirely closed2
- Meckelian fossa open (if present, closure reduced to a small portion of it)5
2. Ventral projection of the superior posterior process not recognisable; rounded
expansion sometimes present on the dorsal margin of the inferior posterior
process
- Ventral projection of the superior posterior process present; rounded expansion
never present on the dorsal margin of the inferior posterior process3 (Gekkota)
3. Absence of groove by the anterior end; posterior notch of the Meckelian fossa U-
shapedT. mauritanica
- Presence of a groove by the anterior end; posterior notch V-shaped4
4. Posterior notch of the Meckelian fossa extending on the posterior third of the
alveolar shelfE. europaea
- Posterior notch of the Meckelian fossa extending on the posterior fourth of the
alveolar shelf
- Posterior notch of the Meckelian fossa extending on the posterior sixth of the
alveolar shelfM. kotschyi
5. Presence of a smooth subdental shelf devoid of subdental ridge; splenial spine
present
- Subdental ridge present; splenial spine absent7
6. Splenial spine moderately long and located by the beginning of the posterior fourth of the tooth row; posterior portion of the intramandibular septum free; opening of the alveolar canal located near the last tooth position; coronoid and surangular processes similar in size; surangular process devoid of the opening of the anterior - Splenial spine short and located by the beginning of the posterior third of the tooth row; posterior portion of the intramandibular septum fuse to the wall of the bone; opening of the alveolar canal located more anteriorly; coronoid process shorter than the surangular one; opening of the anterior surangular foramen present on the 7. Subdental ridge high; presence of a posterior recess between the posterior - Subdental ridge narrower; posterior recess not present between posterior processes; 8. Anterior half of the Meckelian fossa opening medially; posterior recess very narrow.....L. stellio - Anterior half of the Meckelian fossa opening ventrally; posterior recess 10. Meckelian fossa represented by a very narrow groove; subdental ridge moderately high; intramandibular septum originating a posterior portion fused to the wall of the bone......B. cinereus, B. mariae, B. strauchi - Meckelian fossa widening in the posterior half; subdental ridge narrower; intramandibular septum not extending posteriorly......11 11. Two posterior processes present on the posterior end; superior posterior process

- Three posterior processes present on the posterior end; superior posterior process posterodorsally and directed not composed by separated projections.....O. punctatissimus 12. Posterior processes similar in length......A. erythrurus, E. arguta, L. viridis, T. lepidus, adults of I. bonnali, L. agilis, L. bilineata, L. schreiberi, L. trilineata, P. bocagei, P. carbonelli, Po. hispanicus, P. muralis, P. algirus A. bedriagae, D. oxycephala, D. mosorensis, H. graeca, I. cyreni, I. horvathi, I. monticola, O. elegans, P. filfolensis, P. melisellensis, P. milensis, P. pityusensis, P. siculus, P. tauricus, P. tiliguerta, P. waglerianus, Ps. hispanicus, Z. vivipara, juveniles of I. bonnali, L. agilis, L. bilineata, L. schreiberi, P. bocagei, P. carbonelli, Po. hispanicus, P. muralis, P. algirus

Splenial

1. Splenial absent	L. stellio, C. chamaeleon
- Splenial present	2
2. Splenial small and thin	
- Splenial larger	7
3. Splenial pierced by a single foramen in the posterior hal	fB. cinereus,
B. mariae, B. strauchi	
- Splenial pierced in its anterior portion by two foramina,	sometimes represented by
a notch	4
4. Both foramina always represented by notches	A. kitaibelii
- Only the anterior mylohyoid foramen someti	mes represented by a
notch	5 (Gekkota)
5. Posterior corner not bending laterally	M. kotschyi
- Posterior corner bending laterally	6
6. Presence of a long posterior process	E. europaea, H. turcicus
- Absence of a long posterior process	T. mauritanica

7. Splenial clearly divided into an slender anterior half and a wide posterior half;
posterior end irregular, provided with three processesAnguidae
- Splenial not composed by two different-shaped halves; posterior end pointed8
8. Foramina shifted anteriorly; anterior inferior foramen not closed anteriorly; crests
on the lateral surface shifted ventrally; ventral margin straight9
- Foramina located roughly in the middle of the bone; anterior inferior foramen
completely closed; crests on the lateral surface more dorsally located; ventral margin
convex10 (Lacertidae)
9. Posterior portion of the dorsal margin wavyChalcides
- Posterior portion of the dorsal margin straightO. punctatissimus
- Posterior portion of the dorsal margin convex
10. Splenial ventrally expanded
- Splenial not ventrally expandedOther lacertids

Coronoid

1. Labial process absent or strongly reduced2
- Labial process present, not reduced
2. Presence of a notch for the mandibular central foramen on the anteromedial
process; on the lateral surface of the coronoid process, wide articular surface for the
superior posterior process of the dentary distinctly visible and bordered by a well-
developed ridgeB. cinereus, B. mariae, B. strauchi
- Notch for the mandibular central foramen not present; on the lateral surface of the
coronoid process, articular surface for the superior posterior process of the dentary
not distinguishable
3. Coronoid crescent-shaped in dorsal view; posterior process very small or absent;
posteromedial process lappet-likeO. punctatissimus
- Coronoid straight in dorsal view; posterior process more developed; posteromedial
process not lappet-like

4. Posterior process moderately short; posteromedial process long, straight and - Posterior process well developed; posteromedial process shorter, triangular and - Distal end of the posteromedial process rounded......*T. mauritanica* - Coronoid moderately medially concave in dorsal view......10 9. Coronoid process moderately thin; anterior projection of the anteromedial process - Coronoid process distinctly robust; anterior projection of the anteromedial process 11. Dorsal end of the coronoid process slightly posteriorly directed.....A. erythrurus, A. fitzingeri, A. marchi, O. elegans, juveniles of other lacertids Dorsal end of the coronoid dorsally _ process more

directed.....Adults of other lacertids 12. Low ridge connecting posterior the surface of the coronoid process and the dorsal portion of the posteromedial process present......*C. ocellatus* - Low ridge connecting posterior the surface of the coronoid process and the dorsal portion of the posteromedial process absent......Other scincids

Angular, surangular, prearticular and articular

Angular

1. Free angular absent	Gekkota
- Free angular present	2
2. Angular dorsoventrally enlarged	Lacertidae
- Angular slender	
3. On the medial surface, angular ridge present	4
- On the medial surface, angular ridge absent	
4. Presence of a clear constriction at mid-length.	Anguidae
- Angular not constricted at mid-length	Scincidae
5. Angular thin and laminar	B. cinereus, B. mariae, B. strauchi
- Angular thicker and dorsally or dorsolaterally co	oncaveL. stellio, C. chamaeleon
Compound bone	

5. Absence of a longitudinal lateral crest on the retroarticular process....E. europaea 6. Posterior surangular foramen located in the middle of the lateral surface; absence - Posterior surangular foramen shifted dorsally; presence of a ridge on the dorsal 7. Compound bone moderately short; tubercle on the articular condyle not present.....B. cinereus, B. mariae, B. strauchi - Compound bone long; presence of a tubercle by the anteromedial corner of the 8. Retroarticular process distinctly bending in ventral direction; ridge-like ventral - Retroarticular process posteriorly directed; ridge-like ventral expansion present 9. Retroarticular process more anteroposteriorly elongated......10 10. Retroarticular lobe-shaped; tympanic ridge process well developed......C. chalcides, C. striatus - Retroarticular process subrectangular; tympanic ridge less developed...A. kitaibelii 12. Retroarticular process lobe-shaped; tympanic ridge well developed.....T. aurata Retroarticular process subrectangular; tympanic ridge less developed......O. punctatissimus 13. Retroarticular process subtriangular; adductor fossa very wide.....14 (Lacertidae) - Retroarticular process quadrangular; adductor fossa reduced......15 (Anguidae) 14. Ventral expansion of the retroarticular process well developed (ventral margin

- Ventral expansion of the retroarticular process less dev	veloped (ventral margin
straight in lateral view)	Other lacertids
15. Anterior surangular foramen not shifted anteriorly	Anguis gr. A. fragilis
- Anterior surangular foramen shifted anteriorly into the a	rticular surface with the
dentary	P. apodus

Dentition

1. Acrodont teeth present
- Acrodont teeth absent
2. Premaxillary teeth and anteriormost maxillary and dentary teeth subpleurodont;
acrodont teeth usually closely spaced and extending onto the medial surface of the
alveolar shelfL. stellio
- All teeth acrodont; teeth carried on the edge of the tooth-bearing bones and usually
well-spacedC. chamaeleon
3. Bicuspid teeth with labial and lingual cusps
- Teeth monocuspid or with cusps longitudinally aligned7
4. Crown not curved and without striaeGekkota
- Crown slightly curved posteriorly and provided with a light striation on the lingual
surface
5. Teeth slenderA. kitaibelii, C. bedriagai, C. chalcides, C. striatus, T. aurata
- Teeth robust
6. Teeth very robust; crown blunt and enlargedC. ocellatus
- Teeth less robust; crown not blunt and not enlargedO. punctatissimus
7. Teeth pleurodont; presence of mono-, bi- or even tricuspid teethLacertidae
- Teeth subpleurodont; all teeth monocuspid
8. In the premaxilla, middle tooth larger than the other teeth; in the maxilla, tooth
size distinctly decreasing posteriorly; number of maxillary teeth up to 5; number of
dentary teeth 7, 8 or 9B. cinereus, B. mariae, B. strauchi

2.4. The recognisability of extant European non-snake squamates: an update

In a recent paper, Villa and colleagues (2017) presented an estimate of the recognisability of extant European lizards and worm lizards based on morphology only, discussing also the relationship between the identifiable taxa and their actual findings in the European fossil record. Here, an update on such issue is given, following the collection of more data on the comparative osteology of these squamates, in particular as far as lacertids and scincids are concerned. As in Villa et al.'s (2017) paper, the recognisability is in terms of Operational Taxonomic Units (OTUs), regardless of whether they represent family, genus or species level. This is because recognisable taxa are not always represented by species, but often by different kinds of higher taxonomic ranks.

After the addition of the new data, the estimated recognisability of the extant European non-snake squamates has significantly increased, moving from a 31% (24 OTUs out of 78 taxa; Villa et al. 2017) to a 54% (42 OTUs out of 78 taxa; Tab. 1). Scincidae are the group that benefits most from the new data from the recognisability point of view, since almost all European species appear now to be recognisable, in contrast with the worse scenario of just 3 recognisable OTUs reported by Villa et al (2017), with only *C. ocellatus* identifiable at the species level. Here, only *C. bedriagai* is still not recognisable at the species level, being identifiable only as

Chalcides sp., but this could be due to the poor sampling of this species in the herein conducted comparative analysis (a single specimen, whose articulated skull is largely covered by osteoderms). It is possible that, in the future, a deeper study of this scincid species would shed light on potential diagnostic characters of its skull osteology.

The recognisability of lacertids has also increased, even if a number of species can be recognised only based on few skeletal elements (e.g., *I. martinezricai* is recognisable based only on the squamosal, *P. pityusensis* based only on the parietal and *P. algirus* based only on the jugal). Moreover, it is here confirmed that there are no clear osteological features allowing a precise identification of the genus *Podarcis*. Again, the impossibility to better recognize at least some of the species now identifiable only at the family level might be linked to them being missing from the taxon sampling (see chapter 2.1 for a list of the species for which no specimen has been directly observed for the analysis). Except for *L. agilis, Lacerta* species are recognisable only at the genus level based on the osteology alone. Nevertheless, a specimen-level phylogenetic analysis has demonstrated that every single species can be identified using such methodology (Villa et al. 2017).

As for the other families, the degree of recognisability is the same as reported by Villa et al. (2017). The single change is observed in the amphisbaenians: the development of the ridge present on the inner side of the quadrate seems to be a useful feature to distinguish between the 3 European *Blanus* species. On the other hand, other skull elements still bear no clear diagnostic features allowing to discriminate between the different species, and only the premaxilla can be used to recognise the Western Group from the *B. strauchi* complex (Villa et al. in press - Atti XI Congresso SHI).

In parallel with the increase in the number of recognisable OTUs, there is a rather low but significant increase in the OTUs actually recognized in the fossil record too (Tab. 1): 33% of the 78 extant species contra 26% reported by Villa et al. (2017). However, if we compare the recognised OTUs with the recognisable one, a

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descreasing trend is evident: Villa et al. (2017) reported the identification in the fossil record of 83% of the recognisable OTUs, whereas here this percentage is 62%.

The herein conducted comparative analysis corroborates the hypothesis that diagnostic osteological features might indeed be present in the bones of extant European non-snake squamates and that deeper osteological studies are strongly needed to increase our ability to recognise their skeletal elements, and consequently fossil remains. Nevertheless, it has to be taken into account that the above-mentioned percentages are calculated on the implied premise of an equal probability of fossilization for all taxa, which is most probably not the case. Environments that are adverse to fossilization, scarce robustness of the bones and diagnostic features located on skeletal elements that are poorly represented in the fossil record (as e.g., the squamosal in the case of *I. martinezricai*) suggest that the taphonomic bias still has a major influence on our possibility to understand the past evolutionary history of small vertebrates such as lizards. However, the opening of promising scenaria is still feasible given the encouraging results derived from deepened comparative osteological studies (this work) and modern methodologies such as specimen-level phylogenetic analysis (Villa et al. 2017) and geometric morphometry (Dollion et al. 2015; Gray et al. 2017; Paluh et al. 2018).

Table 2	2.1) Recognisability	of European	lizards and	ł worm	lizards	and the	eir presence	in	the	fossil
record.										
-	Extant species]	Recognisable	OTU		Fossil r	record			

Extant species	Recognisable OTU	Fossil record	
Laudakia stellio	Agamidae indet.	Yes	
Chamaeleo chamaeleon	Chamaeleonidae indet.	Yes	
Euleptes europaea	E. europaea	Yes	
Hemidactylus turcicus	H. turcicus	Yes	
Mediodactylus kotschyi	M. kotschyi	No	
Tarentola mauritanica	T. mauritanica	Yes	
Acanthodactylus erythrurus	A. erythrurus	Yes	
Algyroides fitzingeri	Lacertidae indet.	Yes	

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Algyroides moreoticus Algyroides nigropunctatus Anatololacerta anatolica Anatololacerta pelasgiana Archaeolacerta bedriagae Dalmatolacerta oxycephala Darevskia armeniaca Darevskia lindholmi Darevskia praticola Darevskia saxicola Dinarolacerta montenegrina Iberolacerta aranica Iberolacerta aurelioi Iberolacerta cyreni Iberolacerta galani Iberolacerta monticola Podarcis bocagei Podarcis carbonelli Podarcis cretensis Podarcis erhardii Podarcis gaigeae Podarcis hispanicus Podarcis levendis Podarcis lilfordi Podarcis liolepis Podarcis milensis Podarcis muralis Podarcis peloponnesiacus Podarcis raffonei Podarcis tauricus

Podarcis vaucheri

Podarcis waglerianus

Algyroides marchi	A. marchi	No
Dinarolacerta mosorensis	D. mosorensis	No
Hellenolacerta graeca	H. graeca	No
Eremias arguta	E. arguta	No
Iberolacerta bonnali	I. bonnali	No
Iberolacerta horvathi	I. horvathi	No
Iberolacerta martinezricai	I. martinezricai	No
Lacerta agilis	L. agilis	Yes
Lacerta bilineata	L. bilineata	Yes
Lacerta viridis	L. viridis	Yes
Lacerta schreiberi	L. schreiberi	No
Lacerta trilineata	L. trilineata	Yes
Ophisops elegans	O. elegans	Yes
Podarcis filfolensis	P. filfolensis	No
Podarcis melisellensis	P. melisellensis	No
Podarcis pityusensis	P. pityusensis	Yes
Podarcis siculus	P. siculus	Yes
Podarcis tiliguerta	P. tiliguerta	Yes
Psammodromus algirus	P. algirus	Yes
Psammodromus hispanicus	P. hispanicus	No
Timon lepidus	T. lepidus	Yes
Zootoca vivipara	Z. vivipara	Yes
Ablepharus kitaibelii	A. kitaibelii	Yes
Chalcides bedriagai	Chalcides sp.	Yes
Chalcides chalcides	C. chalcides	Yes
Chalcides striatus	C. striatus	Yes
Chalcides ocellatus	C. ocellatus	Yes
Ophiomorus punctatissimus	O. punctatissimus	No
Trachylepis aurata	T. aurata	No
Anguis cephallonica	Anguis gr. A. fragilis	Yes
Anguis colchica		

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Anguis fragilis		
Anguis graeca		
Anguis veronensis		
Pseudopus apodus	P. apodus	Yes
Blanus cinereus	B. cinereus	Yes
Blanus mariae	B. mariae	No
Blanus strauchi	B. strauchi	No
78	42 (54%)	26 (33%)

3. Fossil record of Neogene and Quaternary lizards in Europe

A large number of fossils attributed to lizards and worm lizards are reported from Neogene and Quaternary localities from all over Europe. In this chapter, new material is described and identified, together with re-studied old material, in the light of the new information obtained in the comparative study conducted for this project. The fossil record of these reptiles is then summarized and discussed, in order to present a picture of the current knowledge of their evolutionary history in the continent during the last 23 millions of years.

3.1. Material & Methods

3.1.1. The new identifications

The herein studied material comes from 75 localities of 5 different European countries. The complete list of localities for each single country is given below, in chapter 3.2. For each locality, the age is reported, as well as the repository institution and a brief list of references with detailed chronological and geological informations. The identification is based both on criteria found in the existing literature and on the results of the herein carried out comparative analysis. The terminology used for skull bones is the same as in chapter 2 (mainly Evans 2008, but also Barahona 1996, Bell et al. 2003, Daza et al. 2008, Gans & Montero 2008 and Klembara et al. 2010, 2014), whereas it follows Tschopp (2016) for the vertebrae and Russell & Bauer (2009) for the appendicular skeleton. Pictures of selected specimens have been taken with the following sets:

- Leica M205 microscope equipped with the Leica application suite V 3.3.0 at the University of Torino;

- Leica M205 microscope equipped with the Leica application suite V 4.10 at the University of Torino;

- Leica MZ16 stereomicroscope equipped with a camera Leica IC 3D and the software Leica Application Suite version 2.8.1 at the Institut Català de Paleontologia Miquel Crusafont;

- Samsung WB252F Digital Camera;

- Scanning Electron Microscope Jeol JSM-IT300LV at the University of Torino;

- Environmental Scanning Electron Microscope Quanta 200 FEI, XTE 325/D8395 at the Universitat de Barcelona.

The anguid specimen IPS30710 was scanned at the American Museum of Natural History, New York. Some of the Spanish specimens required new repository numbers that were still not available at the moment when this thesis was written. They were therefore labelled with provisional numbers, under the acronyms CBTemp (remains coming from the Castell de Barberà locality), IndTemp (remains coming from other localities and stored in the Institut Català de Paleontologia Miquel Crusafont) and SemTemp (remains coming from different localities stored in the Museu Geòlogic del Seminari de Barcelona). Numbers with the acronym IPS followed by a question mark are also provisional. Repository numbers are also lacking for the fossil remains of most of the Greek localities and some of the Italian ones (namely, Caverna dei Parmorari, Caverna dell'Aurera, Ciabòt Cagna, Oderzo and Valdemino Cave)

Institutional abbreviations: BSPG - Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; **IPS** - Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; **MGB** - Museu Geòlogic del Seminari de Barcelona, Spain; **MGPT-PU** - Museo di Geologia e Paleontologia, Università degli Studi di Torino, Italy; **MSF** - Museo Civico di Scienze Naturali, Faenza, Italy; **MT** - Monte Tuttavista, Orosei - **RGM** - Naturalis Biodiversity Center, Leiden, The Netherlands; **RV-H** - Rivoli Veronese, herpetological fossil material; **UU** - University of Utrecht, The Netherlands.

3.1.2. The catalogue of European fossil lizards and worm lizards

In order to have a clear and rapidly accessible database of the Neogene and Quaternary fossil occurrences of lizards and amphisbaenians in Europe, a catalogue gathering all records mentioned in the consulted literature has been created (see Appendix 5). The structure of this catalogue is based on the Italian palaeoherpetological database created by Delfino (1997, 2002). Entries are represented by taxon/locality data (also known as SPLOC data: SPecies Locality OCcurences), that is each entry is defined by a taxon and the locality where such taxon has been found. Other information, such as the previous identifications of the taxon, the chronological data of the locality and the referred bibliography, have been added, but, since the catalogue is conceived as a synthetic tool, additional information has been kept to the essential points. The bibliographic references include all mentions of the related entry, being those in published papers, conference abstracts or online databases. Both published material and simple mentions have been considered, since the exclusion of the latter might have resulted in the loss of useful information related to less studied areas as well as important taxonomical comments. Bachelor or Master degree theses have not been considered. The catalogue is composed by three parts, respectively devoted to "Lacertilia", Amphisbaenia and to remains that have been previously attributed to lizards, but are now considered not to belong to such group. It has to be noted that the data included in the catalogue should not be considered separately from the related references, since only by consulting those references it is possible to completely understand the real nature of the identifications and the possible affinities of the fossil material.

3.2. Studied material

3.2.1. Germany

Five different German localities (Fig. 3.1) dated back to the Miocene are considered in this work. Two of them, Gisseltshausen and Stubersheim, include different fossil sites. Most of the anguid fossil remains coming from these localities were under study by Jozef Klembara when the hosting institution was visited and they are therefore not included here.

Localities

Gisseltshausen (Gisseltshausen 1a, Gisseltshausen 1b) (Fig. 3.1a)

Age: middle Miocene (Langhian, MN 5).

Repository: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

References: Abdul Aziz et al. 2008.

Griesbeckerzell 1a (Fig. 3.1b)

Age: middle Miocene (Langhian, MN 6).

Repository: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

References: Ivanov & Böhme 2011.

Kleineisenbach (Fig. 3.1c)

Age: middle Miocene (Serravallian, MN 8).

Repository: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

References: Prieto 2007, 2012.

Stubersheim (Stubersheim 2, Stubersheim 3) (Fig. 3.1d)

Age: early Miocene (Burdigalian, MN 3).

Repository: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

References: Ziegler 2006; Klietmann et al. 2015.

Walda 2 (Fig. 3.1e)

Age: early Miocene (Burdigalian, MN 5).

Repository: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

References: Klembara et al. 2010.

Systematic palaeontology

Gisseltshausen

"Lacertilia" Owen, 1842

Chamaeleonidae Gray, 1825

Chamaeleonidae indet. (Fig. A4.1A)

Material:

- Gisseltshausen 1a: 1 *Ib (a), Griesbe* fragment of tooth- *2 and 3 (d) and* bearing bone (BSPG 1982 X 7184).

Figure 3.1) Map of Germany, showing the position of the herein-considered German localities: Gisseltshausen 1a and 1b (a), Griesbeckerzell 1a (b), Kleineisenbach (c), Stubersheim 2 and 3 (d) and Walda 2 (e).

Description

BSPG 1982 X 7184 is a very small fragment of an indeterminate tooth-bearing bones, carrying two acrodont teeth. One of the teeth is partially broken, but the other one is better preserved. The latter is roughly triangular in medial view and displays small accessory cusps both anteriorly and posteriorly. Both teeth are located on the edge of the tooth-bearing bone, without expanding ventrally. A wide space is present between them. BSPG 1982 X 7184 is 1.9 mm-long.

Identification



In spite of it being represented only by a very poorly preserved fragment, BSPG 1982 X 7184 can be attributed to an indeterminate chamaeleonid because of the well-spaced and apically located acrodont teeth (Delfino et al. 2008; this work). It has to be noted, however, that Rage and Bailon (2011) stated that a certain degree of variability might be present in the main features used to distinguish tooth-bearing bones of chamaeleonids and agamids.

Gekkota Cuvier, 1817

Gekkota indet. (Fig. A4.1B-C) Material:

> - Gisseltshausen 1a: 1 dentary (BSPG 1982 X 7185); 1 fragment of toothbearing bone (BSPG 1982 X 7195).

Description

BSPG 1982 X 7185 is represented by a very small (roughly 2.3 mm in total length) dentary (Fig. A4.1B), missing the anterior end and most of the posterior one. Part of the lateral surface is also broken, exposing laterally the alveolar canal. The preserved portion of the lateral surface is smooth. On the medial side of the bone, the Meckelian fossa is enclosed in a tubular structure formed by both the subdental ridge and the ventral margin, which expand ventrally and dorsally respectively and fuse together at their meeting point. A remain of the suture line is still visible toward the posterior end. The posterior end of the tubular structure displays a deep and V-shaped notch in medial view. Dorsally, the tooth row bears closely-spaced tooth positions. Teeth are never well preserved, but their implantation is pleurodont. Only the inferior posterior process is present: it is short and posteriorly pointed.

The fragment of tooth-bearing bone (which is most probably a maxilla fragment; Fig. A4.1C) is very small, being roughly 1 mm in total length. The preserved portion of tooth row displays 6 tooth positions, with 4 well-preserved pleurodont, cylindrical,

slender and closely-spaced teeth. Tooth crowns are pointed, straight and unstriated. They are transversely bicuspid.

Identification

The attribution of these specimen to the gekkotan is based on the tubular structure enclosing the Meckelian fossa in the case of BSPG 1982 X 7185 and on the pleurodont, cylindrical, slender, unstriated and transversely bicuspid teeth provided with a not-curved and pointed crown in the case of BSPG 1982 X 7195 (Sumida & Murphy 1987; Evans 2008; this work).

Lacertidae Batsch, 1788 Janosikia Čerňanský et al., 2016b

Janosikia ulmensis (Gerhardt, 1903) (Fig. A4.1P-V) Material:

Gisseltshausen 1b: 5 frontals (BSPG 1982 X 7243/7244); 1 parietal (BSPG 1982 X 7245); 4 maxillae (BSPG 1982 X 7247/7249, 7251); 2 dentaries (BSPG 1982 X 7250, 7253); 2 fragments of tooth-bearing bones (BSPG 1982 X 7252, 7254).

Description

BSPG 1982 X 7243 (Fig. A4.1P-Q) is a very large right frontal, missing only the part of the anterior end corresponding to the articulation with the nasal and the anterior process. The length of the preserved portion of the bone is 15.8 mm. In dorsal view, the frontal is L-shaped, with an enlarged posterior end because of the presence of a moderately short posterolateral process. At mid-length, the lateral and the medial margins run parallel. The dorsal surface is completely covered by a very-welldeveloped dermal ornamentation. The groove separating the frontal and the frontoparietal shields is located roughly at 3/5 of the length of the specimen from the anterior end. Anteriorly a large prefrontal shield covers completely the anterior end. The articular surface with the maxilla is moderately reduced. In lateral view, both the articulation surfaces with the postfrontal and the prefrontal are visible, posteriorly and anteriorly respectively. The two surfaces are distinctly far from each other. Ventrally, the low posterior portion of a wide and robust crista cranii is present. The anterior part of the crista, and the anterior process, are broken off. The posterior margin of the bone is strongly interdigitated. A triangular articular surface with the parietal tab is present on the ventral surface of the posterolateral process. The other frontals are more poorly preserved, but both their size and morphology are fully comparable with BSPG 1982 X 7243.

The parietal (Fig. A4.1R-S) is very fragmentary, preserving only the left part of the posterior half of the parietal shelf. In spite of this fragmentary nature, the specimen is large (total length = 5.3 mm; total width = 6.3 mm). The dorsal surface is completely covered by a well-developed dermal ornamentation, which reaches the posterior margin of the bone. The occipital shield, the posterior half of the left lateral one and a small part of the interparietal are visible. The occipital shield is large and rather long. A large and roughly triangular parietal fossa is present on the ventral surface. Posteriorly to it, there is no parietal notch. A portion of the left posterolateral ventral crest is visible near the base of the broken left posterolateral process. Even though the left anterolateral ventral crest is not preserved, the left posterolateral ventral crest appears to end distinctly far from it.

The maxillae are fragmentary, but large. The largest fragment, BSPG 1982 X 7247 (Fig. A4.1T), is 10 mm long, even though it preserves only the posterior process. The other maxillae are more poorly preserved, but their size is comparable. Most of them are represented by portions of the middle part of the tooth row, but BSPG 1982 X 7251 preserves only the anterior end. All specimens but BSPG 1982 X 7251 carry large, very robust and pleurodont teeth, which are closely spaced and cylindrical in medial view. The crown is eroded in most of the preserved teeth, but when preserved it displays a blunt and rounded tip covered by a dense and strong striation on both the labial and the lingual sides (Fig. A4.1U). Low but distinct mesiodistal cutting

edges are also visible. Teeth of BSPG 1982 X 7251 are more similar to those of the fragmentary tooth-bearing bones (see below). The best-preserved specimen bears 8 tooth positions. A large and deep superior dental foramen is preserved in both BSPG 1982 X 7247 and 7248; it is followed by a shallow groove in the former specimen. The preserved portion of lateral surface is smooth, with 3 (BSPG 1982 X 7247) or 4 (BSPG 1982 X 7248) ventrolateral foramina. A very little portion of a ornamented cover is visible dorsally in BSPG 1982 X 7247.

The dentaries preserve only the anterior end, but the symphysial region is broken in BSPG 1982 X 7250 (Fig. A4.1V). The specimens are robust and have a high and well-developed subdental ridge on the medial side. Four tooth positions are visible in BSPG 1982 X 7250, whereas at least 7 are preserved in the other specimen. Only a single tooth is sufficiently preserved in the former. The tooth is morphologically similar to the maxillary teeth, even if it has a more slender aspect. The crown is mostly broken, but distinct striae are still visible both lingually and labially. The 2 preserved teeth of BSPG 1982 X 7253 are also similar to the maxillary teeth, but they are distinctly more slender and they totally miss the crown. The lateral surface appears rough. The roughness is strongly more evident in BSPG 1982 X 7250, but this could be due to taphonomical processes. The Meckelian fossa, preserved only in BSPG 1982 X 7253, is narrow, but it seems to widen posteriorly. The specimens are 5.6 mm-long (BSPG 1982 X 7250) and 6.5 mm-long (BSPG 1982 X 7253).

The fragments of tooth-bearing bone bear stocky and pleurodont teeth, which are closely-spaced and display a distinct striation on the lingual side. The labial side appears to be smooth. When preserved, the crown has a pointed tip and, in certain cases, a very small accessory cusp. In medial view, the teeth appear rather slender, but their shaft is strongly labiolingually expanded.

Identification

The morphology of the above-described specimens recalls the only species currently included in the genus *Janosikia*, a lacertid genus recently established by Čerňanský and colleagues (2016b) to reallocate fossil remains previously assigned to an anguid.

Among other features, *J. ulmensis* is diagnosed by its large size, strong dermal ornamentation, a large occipital shield on the parietal and an amblyodont dentition (Čerňanský et al. 2016b). All these features are found on the fossil remains here attributed to this species. The dentition, in particular, is very similar to that of *J. ulmensis*. The frontal is assigned to this species because of its large size, its strong dermal ornamentation and overall resemblance to that of *J. ulmensis* (Čerňanský et al. 2016b: fig. 5D-E). The tooth morphology of the maxilla BSPG 1982 X 7251 and of the fragments of tooth-bearing bones recalls that of the anterior portion of tooth-bearing bones of *J. ulmensis* in the pointed and more slender aspect and the swollen base (Čerňanský et al. 2016b). Bicuspid teeth can be present in this species, at least in juveniles (Čerňanský et al. 2016b).

Miolacerta Roček, 1984

cf. *Miolacerta* sp. (Fig. A4.1D) Material:

Gisseltshausen 1a: 2 fragments of tooth-bearing bone (BSPG 1982 X 7198, 7207).

Description

These very small fragments of indeterminate tooth-bearing bone preserve only 2 (BSPG 1982 X 7198; Fig. A4.1D) and 4 (BSPG 1982 X 7207) pleurodont, cylindrical, moderately robust, closely-spaced and distinctly tricuspid teeth. In medial view, the tricuspid crown has a symmetrical appearance.

Identification

The teeth of these tooth-bearing bones share with *Miolacerta* the very distinct tricuspid morphology (Roček 1984). Nevertheless, strong tricuspidity is also found in other lacertids, such as *Takydromus* and *Gallotia* (Kosma 2004), and therefore the identification as *Miolacerta* can just be tentative.

Lacertidae indet. (Fig. A4.1E-F, W-AA) Material:

- Gisseltshausen 1a: 1 maxilla (BSPG 1982 X 7201); 3 dentaries (BSPG 1982 X 7205, 7212); 8 fragments of tooth-bearing bone (BSPG 1982 X 7206, 7211).
- Gisseltshausen 1b: 1 postfrontal (BSPG 1982 X 7241); 1 pterygoid (BSPG 1982 X 7242); 3 dentaries (BSPG 1982 X 7230/7231, 7235); 13 fragments of tooth-bearing bone (BSPG 1982 X 7229, 7236); 1 tooth (BSPG 1982 X 7237).

Description

BSPG 1982 X 7201 (Fig. A4.1E-F) is a poorly preserved fragment of a maxilla carrying 8 tooth positions. Some of the best preserved teeth hosted in these tooth positions clearly show a bicuspid condition. In spite of the fragmentation, the specimen is almost 6 mm in length, representing therefore a rather large taxon.

The small postfrontal (Fig. A4.1W-X) preserves only the anterior end, displaying a slightly concave anterior margin in dorsal view. Both the anteromedial and the anterolateral processes are present. The latter is rather short. The former is expanded, but its tip is broken. A well-developed dermal ornamentation covers the dorsal surface of the bone, whereas the ventral one is smooth. In ventral view, a slender, moderately long and triangular articular surface for the anteromedial process of the postorbital is visible.

The pterygoid (Fig. A4.1Y-Z) is very large-sized, measuring roughly 11 mm in total length. The specimen misses the anterior tips of both the palatine process and the pterygoid flange, as well as most of the quadrate process. The palatine process is straight and moderately wide, without a strengthening in the middle. A single row of robust pterygoid teeth is present on its ventral surface. Both the dorsal and the ventral ridges on the pterygoid flange are well developed. The preserved portion of the

quadrate process displays a deep and subcircular fossa columellae dorsally. In spite of the poor preservational status, the basipterygoid fossa is clearly not marked by a lappet ventrally.

The dentary BSPG 1982 X 7230 (Fig. A4.1AA) is rather large, being roughly 9 mmlong even though it misses the posterior portion. Teeth are eroded, but similar to those of the maxilla. A bicuspid condition is still recognisable at least in some of them. The number of the preserved tooth positions is 14. The subdental ridge is high and the mandibular symphysis is narrow and horizontal. Most of the Meckelian fossa is missing. The remaining part of the lateral surface is smooth. Four mental foramina are still visible.

All other tooth-bearing bones are fragmentary and smaller in size, but they carry teeth similar to those of BSPG 1982 X 7201 and 7230. Sometimes, a rather asymetrically tricuspid morphology can also be recognised. The dentaries display a narrow subdental ridge on the medial surface.

Identification

All these specimens display a lacertid morphology (this work), but they cannot be attributed confidently either to *J. ulmensis* or to cf. *Miolacerta* sp. and are therefore here identified only as indeterminate members of the family. Nevertheless, tooth morphology of the tooth-bearing bones seems to be different from both the previously mentioned taxa, suggesting that a third lacertid might be also present in Gisseltshausen.

?Lacertidae indet. (Fig. A4.1G-H) Material:

- Gisseltshausen 1a: 2 maxillae (BSPG 1982 X 7202/7203).

Description

These two fragmentary maxillae bear cylindrical, pleurodont and closely-spaced teeth, the crown of which is rather eroded. Both preserve part of the facial process,

displaying a well-developed crust of dermal ornamentation on the lateral surface. In the largest and best preserved specimen, BSPG 1982 X 7202 (Fig. A4.1G-H), the ornamentation present the grooves separating the areas covered by internasal and prefrontal scales. The ventrolateral foramina are visible ventrally to the dermal ornamentation. BSPG 1982 X 7203 preserves part of the anterior premaxillary process, which shows a deeply concave area housing the vomeronasal foramen by the base of the facial process and a moderately long anterolateral process. The anteromedial process is broken, and it is therefore not possible to clearly evaluate the presence of a lappet on it. A well-developed, sharp and slightly arched ridge is visible on the medial surface of the ventral portion of the facial process in BSPG 1982 X 7202. This specimen is very large, measuring 6 mm despite the fragmentation, and its facial process bends distinctly in medial direction towards the dorsal end. Identification

These two specimens display the general morphology of the maxillae of some lacertids (e.g., strong dermal ornamentation on the lateral surface, anterior concavity housing the vomeronasal foramen, pleurodont, cylindrical and closely-spaced teeth; this work), but their fragmentary nature hinders the confirmation of their attribution to this family, in particular because of the poorly preserved tooth crowns.

Scincidae Gray, 1825 *Eumeces* Wiegmann, 1834

aff. *Eumeces* sp. (Fig. A4.1I) Material:

- Gisseltshausen 1a: 1 isolated tooth (BSPG 1982 X 7217).

Description

BSPG 1982 X 7217 is a rather robust tooth. It has a moderately blunt crown, which shows a light striation on the lingual side but not on the labial one. The tip of the

crown bends slightly in posteromedial direction, and it is composed by a labial and a lingual cusps, running in parallel by the sides of a shallow and longitudinal groove. Identification

This isolated tooth shows the features of the family Scincidae reported by Kosma (2004), that is slightly posteriorly bending crown, two parallel cusps running longitudinally and a light striation visible only on the lingual side. Its general morphology recalls that of the robust teeth of *Eumeces schneideri* (Kosma 2004).

Scincidae indet. (Fig. A4.1AB-AC) Material:

- Gisseltshausen 1b: 1 dentary (BSPG 1982 X 7255).

Description

This small and fragmentary dentary (Fig. A4.1AB) preserves 6 closely-spaced tooth positions. A single pleurodont, slender and cylindrical tooth is preserved (Fig. A4.1AC). The latter has a bicuspid crown, displaying a labial and a lingual cusps running longitudinally. The tip of the crown bends very slightly in posteromedial direction. Apparently, there are no striae visible, neither on the labial nor on the lingual surfaces. Ventrally to the tooth row, a slender subdental ridge is present, marking dorsally a medially-open Meckelian fossa. The ventral margin of the bone is broken.

Identification

Slender and pleurodont teeth with two longitudinal cusps on a slightly posteromedially-bending crown are found in most members of the family Scincidae (Townsend et al. 1999; Caputo 2004; Kosma 2004; this work). Skinks usually have a light striation on the lingual side of the tooth crown, a feature that is apparently not visible in the dentary from Gisseltshausen 1b. Even if a taphonomical explanation for this absence cannot be totally excluded, the possibility to assign the dentary to a gecko, whose dentition is similar to the scincid one but lacking striae (Sumida &

Murphy 1987; this work), should be taken into account. However, the bending of the tip and the open Meckelian fossa are in contrast to this attribution (Evans 2008; this work).

Scincomorpha indet.

Material:

- Gisseltshausen 1a: 8 dentaries (BSPG 1982 X 7200, 7208).
- Gisseltshausen 1b: 6 dentaries (BSPG 1982 X 7226).

Description

These fragmentary and small dentaries carry pleurodont, cylindrical, slender and monocuspid teeth. Ventrally to the latter, a moderately slender subdental ridge is visible.

Identification

The pleurodont dentition and the presence of a subdental ridge allow to assign these poorly-preserved dentaries to indeterminate scincomorphans (Evans 2008). Scincomorpha has been recently considered paraphyletic in phylogenetic analyses either based only on or including also molecular data (e.g., Reeder et al. 2015), but here we maintain it following its definition as reported by Gauthier et al. (2012), including Lacertoidea and Scincoidea.

Anguidae Gray, 1825 Anguinae Gray, 1825 *Ophisaurus* Daudin, 1803

Ophisaurus sp. (Fig. A4.1J-N) Material:

- Gisseltshausen 1a: 1 dentary (BSPG 1982 X 7186); 5 trunk vertebrae (BSPG 1982 X 7189/7190).
- Gisseltshausen 1b: 2 trunk vertebrae (BSPG 1982 X 7228).

Description

The small dentary BSPG 1982 X 7186 (Fig. A4.1J) is 4 mm in length and misses both the anterior and posterior ends. It carries 8 tooth positions, among which 4 still preserve almost complete teeth. The latter are closely-spaced, subpleurodont, roughly conical, with a pointed and distinctly posteromedially bending tip. A light striation is visible on the lingual surface of the teeth. Ventrally to the teeth, a welldeveloped subdental shelf is present, covering medially a narrow Meckelian fossa. The ventral margin of the bone is straight. The lateral surface is smooth, with 4 mental foramina.

Trunk vertebrae (Fig. A4.1K-N) are rather lightly-built and small-sized. The vertebral centrum of the largest one is 4.4 mm-long. The centrum is procoelous, dorso-ventrally compressed, ventrally flat and has concave and posteriorly-converging lateral margins in ventral view. There is no precondylar constriction. Synapophyses are dorso-ventrally elongated. The dorsal surface of the neural arch bears a well-developed neural spine. Zygapophyses are subcircular and dorsally tilted at 45°.

Identification

An indeterminate species of *Ophisaurus* is represented in Gisseltshausen by the dentary provided with subpleurodont, conical, lingually striated and posteromedially bending teeth and by trunk vertebrae with a dorso-ventrally compressed centrum with concave lateral margins converging posteriorly (Klembara 1981; Klembara et al. 2014).

Pseudopus Merrem, 1820 *Pseudopus laurillardi* (Lartet, 1851)

cf. Pseudopus laurillardi (Fig. A4.1O)

Material:

- Gisseltshausen 1a: 1 dentary (BSPG 1982 X 7219).

Description

BSPG 1982 X 7219 is a moderately large-sized dentary, preserving only part of the anterior end of the bone. The specimen is roughly 5.5 mm-long and displays at least 6 closely-spaced tooth positions. A single tooth is preserved: it is cylindrical, moderately slender, subpleurodont, unstriated and dorsally rounded. A well-developed subdental shelf is present on the medial side of the bone. A very low ridge is visible on the dorsal half of the shelf, but it does not mark a clear groove. The lateral surface is smooth, even though poorly preserved. Three mental foramina are present.

Identification

BSPG 1982 X 7219 can be attributed to *Pseudopus* based on the subpleurodont, cylindrical and dorsally rounded teeth (Klembara et al. 2014; this work). Among all species of this genus, the presence of a ridge on the subdental shelf is a diagnostic feature of *P. laurillardi* (Klembara et al. 2010). The possible presence of such a structure in this dentary, even though not distinctly developed, allow to tentatively assign it to this species.

Pseudopus sp. (Fig. A4.1AD-AE)

Material:

- Gisseltshausen 1a: 3 trunk vertebrae (BSPG 1982 X 7192/7194).
- Gisseltshausen 1b: 1 maxilla (BSPG 1982 X 7258); 3 dentaries (BSPG 1982 X 7256/7257).

Description

The 6.7 mm-long maxilla is represented only by a fragment the middle portion of the tooth row (Fig. A4.1AD). A moderately narrow superior dental foramen is present on the dorsal surface of the palatal shelf. The lateral surface is smooth, carrying 3 ventrolateral foramina. The alveolar border presents at least 4 tooth positions, two of which carry well-preserved teeth. Teeth are subpleurodont, cylindrical, very robust and stout. The crown is blunt, rounded, rather flat and unstriated.

The dentaries are poorly preserved and very fragmentary. They carry teeth that are very similar in morphology to the maxillary ones. Only in BSPG 1982 X 7256 (Fig. A4.1AE), the single preserved tooth is much more slender and slightly anteroposteriorly inclined. In the same specimen, part of a subdental shelf devoid of any ridge is visible ventrally to the tooth.

The procoelous trunk vertebrae are robust and have a dorso-ventrally compressed centrum devoid of precondylar constriction. The ventral surface of the centrum is flat, and its lateral margins are straight and converge posteriorly in ventral view. Only BSPG 1982 X 7192, the smallest specimen, has slightly concave margins. The synapophyses are elongated. The neural arch bears a neural spine, which is always broken, and subcircular and dorsally-tilted zygapophyses. In BSPG 1982 X 7193, the vertebral centrum reaches 4.5 mm in length, but BSPG 1982 X 7194, in which the centrum is partially broken, is strongly larger.

Identification

The trunk vertebrae share anguine features, such as the dorso-ventrally compressed centrum devoid of precondylar constriction (Estes 1983), and can be assigned to *Pseudopus* because of the posteriorly-convergent and straight lateral margins (Klembara 1981). The dentition of the tooth-bearing bones from Gisseltshausen 1b allows their attribution to the same anguid genus (Klembara et al. 2014; this work), but the absence of ridges in the single dentary preserving the shelf suggests that the species present in Gisseltshausen 1b was not *P. laurillardi* (Klembara et al. 2010), in contrast with that recovered at Gisseltshausen 1a (see above).

non-Anguis Anguinae indet.

Material:

- Gisseltshausen 1a: numerous osteoderms (BSPG 1982 X 7182/7183, 7213)
- Gisseltshausen 1b: numerous osteoderms (BSPG 1982 X 7220, 7227).

Description

Osteoderms are small-, medium- or large-sized. The best-preserved one has a subrectangular shape. Their external surface presents a smooth anterior gliding surface followed by an area covered by a vermicular ornamentation. A longitudinal keel can be present on the same surface.

Identification

In contrast with those of *Anguis*, other anguines present osteoderms that are keeled and have a subrectangular shape (Holman 1998; Delfino et al. 2011).

Anguidae indet.

Material:

- Gisseltshausen 1a: 1 premaxilla (BSPG 1982 X 7188); 1 cervical vertebra (BSPG 1982 X 7191); 5 caudal vertebrae (BSPG 1982 X 7187, 7214).
- Gisseltshausen 1b: 2 caudal vertebrae (BSPG 1982 X 7224).

Description

The premaxilla is small. The ascending nasal process is broken off, preserving only the narrow base. Compared to the narrow nasal process, the alveolar portion is moderately wide, with a maximum width of 3.1 mm. Six tooth positions are present, and one of them preserves a subpleurodont, roughly cylindrical, pointed and unstriated tooth. A second, more poorly preserved tooth is also present.

Cervical and caudal vertebrae are small-sized, procoelous and have a dorso-ventrally compressed vertebral centrum. When the posterior portion of the centrum is preserved, a pair of fused hemapophyses is visible on the ventral surface of the caudal vertebrae. The autotomy plane is present in all specimens of the latter. Identification

The premaxilla is attributed to an indeterminate anguid because of the subpleurodont and cylindrical dentition and the wide alveolar portion (this work), whereas the vertebrae are assigned to the same taxon because of the dorso-ventrally compressed centrum devoid of precondylar constriction and of the fused hemapophyses.

Anguimorpha indet.

Material:

- Gisseltshausen 1a: 2 dentaries (BSPG 1982 X 7216, 7218).

Description

These fragmentary dentaries have subpleurodont, but poorly preserved teeth. A moderately developed subdental shelf is visible on the medial side of the bone. Identification

The dentary of anguimorphans can be distinguished from that of scincomorphans because of the subdental shelf replacing the subdental ridge (Evans 2008). Poor preservations hinders a more precise identification of these two dentaries.

"Lacertilia" indet.

Material:

- Gisseltshausen 1a: 1 premaxilla (BSPG 1982 X 7215); 2 maxillae (BSPG 1982 X 7210, 7262); 2 dentaries (BSPG 1982 X 7196, 7199); 10 fragments of tooth-bearing bone (BSPG 1982 X 7197, 7204, 7209); 1 pelvic girdle (BSPG 1982 X 7263).
- Gisseltshausen 1b: 1 premaxilla (BSPG 1982 X 7233); 3 maxillae (BSPG 1982 X 7238, 7240, 7246); 1 jugal (BSPG 1982 X 7223); 1 dentary (BSPG

1982 X 7239); 6 fragments of tooth-bearing bone (BSPG 1982 X 7222, 7225); 3 teeth (BSPG 1982 X 7260/7261); 8 trunk vertebrae (BSPG 1982 X 7221); 1 fragment of vertebra (BSPG 1982 X 7259).

Identification

A number of specimens have been identified only as indeterminate lizards because of their fragmentary nature or the lack of significant diagnostic features.

Among others, isolated teeth are particularly interesting. They are rather large, canine-like and strongly posteromedially bending. They have a swollen proximal half, but a more labiolingually compressed distal part. Two well-developed and apparently unserrated keel runs dorsoventrally along the anterior and posterior margins of the teeth. There are no striae, except for a low number on the labial side of BSPG 1982 X 7261. However, these striae are present on a small part of the distal half of the labial surface only, and therefore they can just be the result of some taphonomical process. There is no spongy tissue by the base. These teeth seems to vaguely recall those of some anguimorphan, such as *Ophisaurus* (Klembara et al. 2014), in their general aspect, but they clearly differ from those of BSPG 1982 X 7186, the single tooth-bearing bone from Gisseltshausen attributed to *Ophisaurus*. The compressed distal part, the canine-like shape and the keels are somehow similar to the teeth of some varanoids, but the absence of striae and spongy tissue is an evidence of the lack of plicidentine, whose presence is considered a synapomorphy of this clade (Estes et al. 1988; Kearney & Rieppel 2006).

Amphisbaenia Gray, 1844

Amphisbaenia indet. (Fig. A4.1AF-AI) Material:

- Gisseltshausen 1b: 7 trunk vertebrae (BSPG 1982 X 7232, 7234).

Description

Trunk vertebrae are small and procoelous. The centrum reaches a maximum length of 3.3 mm in the largest specimen, BSPG 1982 X 7232 (Fig. A4.1AF-AI), and it is dorso-ventrally compressed, rather flat ventrally and provided with rather concave lateral margins. In ventral view, it displays a subrectangular shape and no precondylar constriction. Massive and rounded synapophyses are present on the lateral sides of the neural arch. The arch has a smooth dorsal surface, devoid of neural spine. The zygapophyses are suboval and slightly dorsally tilted. Short and rounded prezygapophyseal processes can be preserved ventrally to the prezygapophyses. There is no zygosphene.

Identification

The attribution of these vertebrae to indeterminate amphisbaenians is based on the dorso-ventrally compressed, ventrally-flat and subrectangular centrum, the massive and rounded synapophyses, the absence of a neural spine and a zygosphene and the short and rounde prezygapophyseal processes (Estes 1983; Delfino 2003).

<u>Griesbeckerzell 1a</u> "Lacertilia" Owen, 1842 Lacertidae Batsch, 1788 *Edlartetia* Augé & Rage, 2000 vel *Miolacerta* Roček, 1984

Edlartetia sp. vel Miolacerta sp. (Fig. A4.2A-B)

Material: 1 dentary (BSPG 1997 XIII 673).

Description

This dentary is long and very slender. It misses part of the ventral margin and the posterior end, but the preserved portion of the tooth row is roughly 11 mm in length. The preserved ventral margin is convex in medial view. A moderately slender and posteriorly narrowing subdental ridge marks dorsally the wide and medially-open Meckelian fossa. Even though partly broken, the mandibular symphysis is narrow

and subhorizontal. At least 21 tooth positions are present. They carry pleurodont, closely-spaced, cylindrical and slender teeth, whose crowns are eroded or missing in all of the cases. The lateral surface of the specimen is smooth, except for 6 anteroposteriorly aligned mental foramina.

Identification

This dentary pertains to a moderately large lacertid because of the widely-open Meckelian fossa and the convex ventral margin (Delfino et al. 2011; this work). Among Miocene lacertids, the slender general aspect and the narrow subdental ridge recalls the genera *Edlartetia* and *Miolacerta* (Roček 1984; Augé & Rage 2000). However, the main feature distinguishing these two genera is in the morphology of the tooth crowns, and the absence of these structures in BSPG 1997 XIII 673 hinders an attribution to either one or the other.

Janosikia Čerňanský et al., 2016b

Janosikia ulmensis (Gerhardt, 1903) (Fig. A4.2C-F)

Material: 1 pair of fused frontals (BSPG 1997 XIII 674); 1 dentary (BSPG 1997 XIII 675).

Description

BSPG 1997 XIII 674 is represented by two completely fused frontals (Fig. A4.2C-D), missing their anterior end. The specimen is large-sized, with a total length almost reaching 12 mm. In dorsal view, the lateral margins of the specimen are roughly parallel and the posterolateral process is moderately short. The dorsal surface is completely covered by a strong dermal ornamentation, made up mostly by pits and anastomosing ridges. A straight groove separating frontal and frontoparietal shields is located roughly at mid-length of the preserved portion of the specimen. In lateral view, the posterior end of the articulation surface with the prefrontal almost reaches the groove between frontal and frontoparietal shields. The articular surface housing the postfrontal is distinctly smaller. On the ventral surface, a hint of the suture line
seems to be recognisable towards the anterior end of the specimen. Two very massive cristae cranii are present along the lateral margins, but the anterior processes are broken off. The posterior margin is partly eroded, but moderate interdigitations are visible. By the posterolateral process, a long and triangular articulation surface with the parietal tabs is visible ventrally.

BSPG 1997 XIII 675 is a large-sized dentary (Fig. A4.2E-F), missing most of the posterior portion and the symphysial region. The length of the preserved portion of the specimen is 10.5 mm. A high and robust subdental ridge is visible on the medial side of the bone. On the ventral margin of the ridge, there is a long and distinct facet for the articulation with the splenial, which ends anteriorly in proximity of the symphysial region. The Meckelian fossa is wide and medially open. At least 13 tooth positions are preserved, with 6 rather well-preserved teeth. Teeth are pleurodont and closely spaced. Anteriorly, they are rather slender, but a strong posterior increase in robustness is visible, with the posteriormost preserved tooth that is far more stout and amblyodont. A moderate degree of erosion is recognisable on the tooth crowns, but striae are distinctly visible both labially and lingually at least on some of the teeth. The tip of the third and fourth posteriormost teeth seems to also show mesiodistal cutting edges. The lateral surface is smooth, with 6 mental foramina. Identification

Both these specimens have been previously tentatively attributed to cordylid lizards (Ivanov & Böhme 2011), but they are here referred to the lacertid *J. ulmensis*. Particularly significant for this identification are the general morphology of the dentary and the dentition, which are fully comparable with the fossil remains of *J. ulmensis* described by Čerňanský et al. (2016b) in the large size, the high subdental shelf and the robust, amblyodont and striated teeth with mesiodistal cutting edges. The fused frontals display a number of features that clearly identify it as pertaining to an adult lacertid (this work): suture line visible in ventral view, posterolateral processes and articular surfaces with the postfrontal present, cristae cranii not laminar, absence of a ventral lappet of the posterolateral process and posterior margin

interdigitated. Frontals of cordylids have a different ornamentation made up by more individualized ridges and grooves and usually show a narrow smooth area along the posterior margin (personal observation based on specimens stored in the BSPG), which is not present in BSPG 1997 XIII 674. The pair of fused frontal from Griesbeckerzell 1a is almost identical in both size and morphology to the one figured in the paper of Čerňanský and colleagues (Čerňanský et al. 2016b: fig. 5D-E), at least as far as the preserved part of the bone is concerned, and it is therefore here referred to *J. ulmensis* together with the dentary. It is worth noting that BSPG 1997 XIII 674 (and therefore the fused frontals of *Janosikia* too) is very similar to the fused frontals from Dolnice described by Čerňanský (2010), and therein attributed to *Lacerta* gr. *L. viridis*.

Lacertidae indet. (Fig. A4.2G-I)

Material: 1 maxilla (BSPG 1997 XIII 676); 1 dentary (BSPG 1997 XIII 677).

Description

The maxilla (Fig. A4.2G-I) is very poorly preserved, being represented only by a 5.5 mm-long fragment of the posterior process. The dorsal margin of the fragment is broken and so it is not possible to recognise the presence or absence of a step. In dorsal view, the posterior end of the process seems to slightly curve in lateral direction. The specimen preserves 6 tooth positions, carrying closely spaced, pleurodont and cylindrical teeth. Preserved teeth are very robust and tricuspid, despite the wearing.

The dentary misses the posterior end. Its preserved portion is 7.9 mm in length. The medial margin is distinctly convex in medial view. The Meckelian fossa is wide and medially open. Dorsally to the fossa, a rather high subdental ridge is present. The mandibular symphysis is broken, but the preserved part is narrow and subhorizontal. At least 17 tooth positions are preserved. Preserved teeth are pleurodont, closely spaced, slender anteriorly but more robust posteriorly. The crowns are rather eroded

in all the preserved teeth, but a bicuspid condition seems to be present in at least some of them. The lateral surface is smooth, except for 5 mental foramina. Identification

These specimens can both be confidently attributed to lacertids because of their tooth morphology (Bailon 1991; this work). Their size suggests the presence of a medium-sized taxon, but the preservational status hinders any further taxonomical comment. Nevertheless, these remains cannot be assigned to *E. sansaniensis* because of the absence of any constriction on the tooth shaft (Augé & Rage 2000). The tooth morphology seems to exclude an attribution to either *J. ulmensis* and *Miolacerta* too.

Scincomorpha indet. (Fig. A4.2J-K)

Material: 1 dentary (BSPG 1997 XIII 678).

Description

The dentary is roughly 5.5 mm in length, but it misses the posterior half. The anterior end displays a narrow and subhorizontal mandibular symphysis. A high subdental ridge is present medially. The Meckelian fossa is rather narrow in the preserved portion of the specimen; towards the anterior end, it tends to bend ventrally. The preserved portion of the ventral margin is slightly convex. The 13 preserved tooth positions carry-closely spaced, pleurodont and cylindrical teeth, which are rather slender anteriorly but become more robust posteriorly. Tooth crowns appear to be strongly eroded, but they seem to be unstriated. Except for the mental foramina, the lateral surface is smooth.

Identification

BSPG 1997 XIII 678 pertains to a scincomorphan lizard because of the presence of a subdental ridge, an open Meckelian fossa and pleurodont teeth (Evans 2008).

Anguidae Gray, 1825 Anguinae Gray, 1825 *Anguis* Linnaeus, 1758

Anguis sp. (Fig. A4.2L-O)

Material: 8 trunk vertebrae (BSPG 1997 XIII 679/680).

Description

These trunk vertebrae are rather lightly-built and moderately large-sized, with the vertebral centrum reaching up to 5 mm in the largest specimens. They are anteroposteriorly elongated and have a dorso-ventrally compressed vertebral centrum, devoid of precondylar constriction. In ventral view, the lateral margins of the centrum run parallel, at least in the posterior portion. The ventral surface of the centrum is flat. The neural arch is vaulted in anterior view. Zygapophyses are dorsally tilted at 30/45°. The dorsal surface of the neural arch displays a distinctly developed neural spine.

Identification

These trunk vertebrae can be assigned to an indeterminate species of the anguine genus *Anguis* because of the dorso-ventrally compressed vertebral centrum, devoid of precondylar constriction and provided with parallel lateral margins (Klembara 1981; Estes 1983; Holman 1998).

Ophisaurus Daudin, 1803

Ophisaurus sp. (Fig. A4.2P-S)

Material: 4 trunk vertebrae (BSPG 1997 XIII 681/682).

Description

These trunk vertebrae are rather lightly-built and moderately large-sized. The largest and most preserved one has a 5 mm-long vertebral centrum, but the other ones are slightly smaller. The vertebral centrum has a flat ventral surface and posteriorlyconvergent lateral margins, which appears concave in ventral view. There is no precondylar constriction. The neural canal is vaulted in anterior view and the zygapophyses are dorsally tilted at about 45°. The neural arch is not depressed and bears a well-developed neural spine on the dorsal surface.

Identification

According to Klembara (1981), the concave and posteriorly-convergent lateral margins of the centrum are a distinctive feature of the genus *Ophisaurus*. Because of this, these trunk vertebrae are here attributed to such genus. The only *Ophisaurus* species so far reported from Griesbeckerzell 1a is *Ophisaurus fejfari* (Klembara & Rummel 2016), but its identification can be based only on parietals.

Pseudopus Merrem, 1820

Pseudopus laurillardi (Lartet, 1851) (Fig. A4.2T-V)

Material: 1 pterygoid (BSPG 1997 XIII 683); 1 dentary (BSPG 1997 XIII 684). Description

Only the anterior part of the pterygoid is preserved (Fig. A4.2T-U), with the quadrate process almost completely missing. The tips of both the palatine process and the pterygoid flange are broken off. The palatine process is rather slender and seems to narrow toward its anterior end. It carries a wide patch of stocky and rounded pterygoid teeth on the ventral surface. The pterygoid flange is also slender. It bears a well-developed dorsal ridge and a less developed ventral ridge. A wide and deep pterygoid recess separates the two palatine process from the pterygoid flange. On the dorsal surface of the bone, a moderately deep articulation surface for the ectopterygoid is visible.

The dentary (Fig. A4.2V) is very fragmented, preserving part of the anterior end only. Despite its fragmentary status, it is very large-sized, having a total length of 12 mm. The preserved portion of mandibular symphysis is narrow and subhorizontal in medial view. A well-developed subdental shelf is present ventrally to the tooth row, covering medially the narrow Meckelian fossa. The latter opens therefore ventrally. A shallow groove marked by a low ridge is visible on the dorsal half of the subdental shelf. Dorsally to the shelf, the tooth row is strongly eroded and so it is not possible to clearly distinguish the different tooth position. Nevertheless, at least five of them were probably present in origin on the preserved part of the tooth row. A single tooth is well preserved. It has a cylindrical shape, a subpleurodont attachment and a robust aspect. The crown is blunt and unstriaded. The lateral surface of the specimen is smooth.

Identification

Dentaries of *Pseudopus* differ from those of others anguines because of the presence of robust and blunt teeth (Klembara et al. 2014; this work). Among extinct and extant *Pseudopus* species, only *P. laurillardi* displays a groove and a ridge on the subdental shelf (Klembara et al. 2010). This species was already reported from Griesbeckerzell 1a (Klembara et al. 2010). The pterygoid is assigned to the same species because of its strong similarity with other pterygoids of *P. laurillardi* described by Klembara et al. (2010).

Pseudopus sp. (Fig. A4.2W-Y)

Material: 1 cervical vertebra (BSPG 1997 XIII 685); 5 trunk vertebrae (BSPG 1997 XIII 686/687); 1 cloacal vertebra (BSPG 1997 XIII 688).

Description

The trunk vertebrae (Fig. A4.2W-Y) are large-sized and very robust. They are rather fragmentary, but the best-preserved one has a centrum length of roughly 7 mm. In ventral view, the dorso-ventrally-compressed centrum has a flat ventral surface and straight and posteriorly-convergent lateral margins. The precondylar constriction is lacking. The neural arch is strongly depressed. A well-developed, but broken in all cases, neural spine is present. In anterior view, the neural canal is vaulted. The facets of the zygapophyses are dorsally tilted at roughly 30°.

Both the cervical and the cloacal vertebrae are fully comparable in both morphology and size with the trunk vertebrae.

Identification

Large and robust vertebrae with straight lateral margins that converge posteriorly are typical of *Pseudopus* (Klembara 1981). It is possible that these vertebrae belong to *P. laurillardi*, as the above-described cranial bones, but since anguine vertebrae are not diagnostic at a species level, they are here identified only at genus level.

non-Anguis Anguinae indet.

Material: 189 osteoderms (BSPG 1997 XIII 689/691).

Description

Osteoderms are large-sized, robust and subrectangular. They have a smooth inner surface, and an ornamented external surface. The ornamentation is vermicular, composed by small tubercles and ridges, and is lacking from the anterior gliding surface. In most of the specimens, a low and longitudinal keel is present on the external surface.

Identification

The identification of these osteoderms as pertaining to non-*Anguis* anguines is based on their subrectangular shape and on their external keel (Holman 1998).

Anguidae indet.

Material: 1 trunk vertebra (BSPG 1997 XIII 692); 10 caudals (BSPG 1997 XIII 693/694).

Description

The small trunk vertebra has a dorso-ventrally compressed centrum, but due to its preservational status, it is not possible to state if the lateral margins of the latter were convergent or parallel in origin.

Caudal vertebrae are antero-posteriorly elongated and have a dorso-ventrally compressed vertebral centrum, provided with the bases of fused hemapophyses in the posterior portion of the ventral surface. There is no precondylar constriction. The autotomy plane can either be present or absent. These vertebrae can reach a large size.

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Identification

Caudal vertebrae with fused hemapophyses and a dorso-ventrally compressed centrum are attributed only to indeterminate anguids, but they do not present diagnostic features at generic level.

Amphisbaenia Gray, 1844

Amphisbaenia indet. (Fig. A4.2Z-AD)

Material: 1 trunk vertebra (BSPG 1997 XIII 695).

Description

This trunk vertebra is rather small. The vertebral centrum is partially broken, but its preserved portion is 2 mm in length. The centrum misses probably only it posterior end, and so it should not have been far longer in origin. In ventral view, the ventral surface of the centrum is flat and its lateral margins are roughly parallel, with only a light concavity visible. Two subcentral foramina are visible near the anterior end of the centrum. The poorly preserved synapophyses appear massive and rounded. A very short and distally rounded prezygapophyseal process is visible on the right side of the vertebra. The neural canal is vaulted in anterior view. The zigapophyses are tilted dorsally at about 45° in anterior view. There is no zygosphene and no neural spine on the dorsal surface of the neural arch. In spite of a partial breakage of the right postero-lateral corner of the neural arch, the vertebra has a distinct X-shape in dorsal view.

Identification

BSPG 1997 XIII 695 shares the diagnostic features of amphisbaenians trunk vertebrae, such as dorso-ventrally compressed centrum with a flat ventral surface and roughly straight lateral margins, massive and rounded synapopheses, and absence of neural spine (Estes 1983).

<u>Kleineisenbach</u> "Lacertilia" Owen, 1842 Gekkota Cuvier, 1817

Gekkota indet. (Fig. A4.3A-B)

Material: 1 dentary (BSPG 1972 XVI 2207); 2 fragment of tooth-bearing bones (BSPG 1972 XVI 2208/2209).

Description

The dentary (Fig. A4.3A) is small and fragmentary, with a total length of 1.5 mm. It preserves only part of the middle portion of the bone. It bears pleurodont, cylindrical, slender and closely-spaced teeth, but the crown is never preserved. The Meckelian fossa is closed in a tubular structure. The lateral surface is smooth.

The two fragments of tooth-bearing bones (Fig. A4.3B) are very poorly preserved. They are very small: the largest one does not exceed 2 mm in total length. They bear cylindrical, pleurodont, closely spaced and slender teeth. The tooth crown is pointed, not curved postero-medially, unstriated and provided with a labial and a lingual cusps that run longitudinally.

Identification

Despite the fragmentary nature of all the above-described specimens, some of their features are typical of geckos. These features are the tubular structure enclosing the Meckelian fossa for the dentary and the pointed and unstriated crown provided with parallel longitudinal cusps for the tooth-bearing bones (Sumida & Murphy 1987; Evans 2008; this work).

Lacertidae Batsch, 1788 Edlartetia Augé & Rage, 2000 Edlartetia sansaniensis (Lartet, 1851)

Edlartetia cf. *E. sansaniensis* (Fig. A4.3C) 255

Material: 1 maxilla (BSPG 1972 XVI 2210); 1 fragment of tooth-bearing bone (BSPG 1972 XVI 2211).

Description

The poorly-preserved tooth bearing bones carry pleurodont, cylindrical, closelyspaced and bicuspid teeth, with a large main cusp and a small accessory cusp located anteriorly. The tooth shaft displays a distinct constriction above the level of the alveolar margin of the bone. BSPG 1972 XVI 2210 displays a wide superior dental foramen and therefore it represents a portion of a maxilla (Fig. A4.3C).

Identification

Pleurodont teeth with the bicuspid condition showed by these two specimens are an evidence of them belonging to a lacertid (Bailon 1991; this work). Among the members of this lizard family, the constricted shaft is a unique feature of *E. sansaniensis*, unknown in other species (Augé & Rage 2000). Due to the poorly preserved status, however, the specimens are here only tentatively attributed to such species.

Miolacerta Roček, 1984

cf. *Miolacerta* sp. (Fig. A4.3D-E)

Material: 2 dentaries (BSPG 1972 XVI 2214/2215); 10 fragments of tooth-bearing bones (BSPG 1972 XVI 2212/2213).

Description

The dentaries (Fig. A4.3D) are slender and small-sized, reaching up to 2.7 mm in total length. They are poorly preserved, with both the anterior and posterior end missing in both cases. The subdental ridge is very narrow in medial view. The Meckelian fossa opens widely in medial direction. The ventral margin is broken. Teeth are pleurodont, cylindrical, slender and closely spaced. There is no constriction on the shaft. When preserved, tooth crowns are distinctly tricuspid. The lateral surface is smooth, except for the mental foramina.

The fragments of tooth-bearing bones (Fig. A4.3E) carry pleurodont, cylindrical, closely spaced and moderately robust teeth. The teeth show a very distinct tricuspid crown morphology, sometimes originating a roughly symmetrical aspect in medial view. The tooth shaft in not constricted.

Identification

Tricuspid teeth, in combination with mono- and bicuspid ones, are generally used to identify lacertids in European fossil-bearing localities. Given that, these specimens can be attributed to a lacertid lizard characterized by a distinct degree of tricuspidity such as *Miolacerta* (Roček 1984), well spread in the Miocene localities of Central Europe (Böhme & Ilg 2003). It has to be noted, however, that strongly tricuspid teeth are known also in other lacertids, such as *Takydromus* (see Kosma 2004). Because of this, the attribution of these fossils to *Miolacerta* is only tentative here, even if the slender general morphology and the thin subdental ridge seems to sustain it, at least as far as the dentaries are concerned (Roček 1984).

Lacertidae indet. (Fig. A43.F)

Material: 1 frontal (BSPG 1972 XVI 2216); 2 maxillae (BSPG 1972 XVI 2217/2218); 5 dentaries (BSPG 1972 XVI 2219/2220); 53 fragments of toothbearing bones (BSPG 1972 XVI 2221/2222).

Description

The frontal preserves only its posterior portion. It has a moderately long posterolateral process and a posterior margin provided with shallow interdigitations. The dorsal ornamentation is well-developed and the dorsal surface of the bone is almost completely covered by the frontoparietal shield. Nevertheless, a small portion of the frontal shield is also visible anteriorly. The ventral surface displays the low posterior portion of the crista cranii and a triangular articular surface for the parietal tab. The specimen is roughly 4 mm-long.

All the tooth-bearing bones, maxilla and dentaries included, are small and poorly preserved (Fig. A43.F). They carry cylindrical, pleurodont, mono-, bi- and tricuspid

teeth. In tricuspid teeth, the tricuspidity is less marked than it is in the specimens previously attributed to cf. *Miolacerta* sp. The tooth shaft does not display a constriction. A high subdental ridge is present on the medial side of the dentaries, the ventral margin of which is slightly convex.

Identification

The preservational conditions of these specimens do not allow a precise identification at generic or specific level, but they can be assigned to lacertids because of the interdigitated posterior margin of the frontal and the tooth morphology (Bailon 1991; this work). Because of the low degree of tricuspidity and the absence of constriction on the shaft, the tooth-bearing bones suggest the presence of a third lacertid taxon, different from both cf. *Miolacerta* sp. and *Edlartetia* cf. *E. sansaniensis*, in Kleineisenbach.

Scincomorpha indet.

Material: 19 dentaries (BSPG 1972 XVI 2223/2226).

Description

These fragmentary dentaries are poorly preserved. They bear cylindrical, slender, pleurodont and closely-spaced teeth, whose crown is damaged in all cases. A moderately high subdental ridge is present on the medial side of the bone.

Identification

Poorly preserved dentaries provided with a subdental ridge can be identified only as indeterminate scincomorphans (Evans 2008).

Anguidae Gray, 1825 Anguinae Gray, 1825 *Ophisaurus* Daudin, 1803

Ophisaurus sp. (Fig. A4.3G-J)

Material: 3 dentaries (BSPG 1972 XVI 2228/2230); 1 fragment of tooth-bearing bone (BSPG 1972 XVI 2231); 1 trunk vertebra (BSPG 1972 XVI 2227).

Description

The 3 dentaries (Fig. A4.3G-H) are very fragmentary and small-sized. The most preserved one, BSPG 1972 XVI 2230, is 5 mm-long and misses the anterior end, the posterior end and the ventral margin. The other specimens are represented by smaller fragments, but BSPG 1972 XVI 2228 preserves a narrow and subhorizontal mandibular symphysis. The dentaries display a moderately developed subdental shelf medially. Dorsally to the shelf, subpleurodont, closely-spaced and subconical teeth are present. Tooth crowns are unstriated in BSPG 1972 XVI 2228 and 2229, but they show light striae on the lingual side in BSPG 1972 XVI 2230; at least in the preserved teeth of the latter specimen, sharp carinae are also visible both anteriorly and posteriorly. The tip of the teeth appears to be rather labiolingually compressed and distinctly bending postero-medially. At least 8 tooth positions are recognisable in BSPG 1972 XVI 2230. In the same specimen, the intramandibular septum is preserved and is fused to the wall of the dentary. Posteriorly to its posterior end, a small surangular spine is visible. The lateral surface of the dentary is smooth, except for the mental foramina and, in BSPG 1972 XVI 2230, a small part of the articular surface with the surangular.

The tooth-bearing bone (Fig. A4.3I) is very poorly preserved and small. It carries a single preserved tooth, which is morphologically comparable to the teeth of BSPG 1972 XVI 2230. In this specimen, however, the striae on the lingual side are more marked.

The trunk vertebra (Fig. A4.3J) is moderately large, with a centrum length exceeding 5 mm. The procoelous centrum is dorso-ventrally compressed, ventrally flat and has posteriorly-convergent and concave lateral margins. There is no precondylar constriction. The neural arch is highly damaged, but the base of a well-developed neural spine is preserved. Only the right prezygapophyses is preserved: it is wide, roughly suboval in dorsal view and dorsally tilted of about 45° in anterior view.

Identification

Conical and posteromedially curved teeth, the presence of a surangular spine and the convergent and laterally concave lateral margins of the vertebral centrum are features distinguishing *Ophisaurus* from other anguines (Klembara 1981; Klembara et al. 2014). In this genus, the intramandibular septum is usually free in its posteroventral portion, but exceptions with a fused septum are present (see Klembara et al. 2014). The presence of both unstriated and striated teeth in different specimens might suggest the co-occurrence of different species at Kleineisenbach, but this cannot stated with certainty, since individual variation might not be completely excluded.

Pseudopus Merrem. 1820

Pseudopus sp. (Fig. A4.3K-L)

Material: 2 fragments of tooth-bearing bones (BSPG 1972 XVI 2232/2233); 1 trunk vertebra (BSPG 1972 XVI 2234); 1 vertebral centrum (BSPG 1972 XVI 2236); 1 cloacal vertebra (BSPG 1972 XVI 2235).

Description

The fragments of tooth-bearing bones (Fig. A4.3K) are small and poorly preserved. Both carry subpleurodont, stocky and dorsally rounded teeth. No striae are visible on the crowns.

The trunk vertebra (Fig. A4.3L) is procoelous and has a centrum length of 3.4 mm, being therefore moderately small. The centrum is ventrally flat and dorso-ventrally compressed. Its lateral margins are straight in ventral view. A precondylar constriction is not present. Synapophyses are dorso-ventrally elongated. Prezygapophyses are suboval in dorsal view and dorsally tilted at roughly 45°. Postzygapophyses are missing, since the posterior end of the neural arch is broken off. The base of a broken neural spine is visible on the dorsal surface of the arch.

The vertebral centrum is poorly preserved, missing the posterior condyle. It is 5 mmlong, dorsoventrally compressed and has a flat ventral surface and straight and posteriorly convergent lateral margins.

The cloacal vertebra is similar to the trunk one both in terms of morphology and of size (centrum length = 3.6 mm).

Identification

This specimens clearly display features of the anguine genus *Pseudopus*, such as subpleurodont, stocky and dorsally rounded teeth and vertebral centra with straight and posteriorly convergent lateral margins (Klembara 1981; Klembara et al. 2014; this work).

non-Anguis Anguinae indet.

Material: 1 trunk vertebra (BSPG 1972 XVI 2237); numerous osteoderms (BSPG 1972 XVI 2238/2241).

Description

The trunk vertebra has a dorso-ventrally compressed and procoelous vertebral centrum with posteriorly converging lateral margins. However, since the posterior half of the centrum is broken off, it is not possible to state whether the margins are straight or concave.

Osteoderms are either lightly built or moderately robust. They are subrectancular and a vermicular ornamentation is present on their external surface, except for the smooth anterior gliding surface. A longitudinal keel is present externally in most specimens. BSPG 1972 XVI 2241 is represented by two osteoderms fused together.

Identification

In contrast with other anguines, osteoderms of *Anguis* are usually rounded and devoid of any keel on the external surface (Holman 1998; Delfino et al. 2011). Given that, the above-described specimens cannot be attributed to such genus. Similarly, the fragmentary trunk vertebra differs from those of *Anguis* in having posteriorly-convergent margins (Klembara 1981).

Anguidae indet.

Material: 1 caudal vertebra (BSPG 1972 XVI 2242).

This specimen is a moderately large caudal vertebra, provided with a dorso-ventrally compressed vertebral centrum. The posterior condyle is broken. The bases of fused hemapophyses are visible near the posterior end of the centrum, on the ventral surface. There is no autotomy plane.

Identification

BSPG 1972 XVI 2242 can be assigned to an indeterminate anguid because of the dorso-ventrally compressed centrum with fused hemapophyses.

Varanidae Gray, 1827 (sensu Estes et al., 1988)

Varanidae indet. (Fig. A4.3M-N)

Material: 1 tooth (BSPG 1972 XVI 2243).

Description

This specimen is an isolated and small tooth. It is conical and medio-laterally compressed. A sharp keel is present both on the anterior and the posterior margins. The tooth base is partly broken, but it has a spongy aspect. Very light striae are visible by the basal portion of the tooth, both on the labial and the lingual sides. These striae reach up to the middle of the height of the specimen.

Identification

The spongy aspect of the tooth base and the basal striation suggest the presence of plicidentine in BSPG 1972 XVI 2243, a feature which is considered typical of varanoid teeth (Estes 1983; Bailon 1991; Pianka et al. 2004; Kearney & Rieppel 2006). Following Kearney and Rieppel (2006), this tooth pertains to a varanid because of the high development towards the tip of the striae, which are usually shorter in other varanoids.

"Lacertilia" indet.

Material: 1 premaxilla (BSPG 1972 XVI 2246); 1 maxilla (BSPG 1972 XVI 2249); 1 pterygoid (BSPG 1972 XVI 2245); 1 dentary (BSPG 1972 XVI 2244); 10 fragments of tooth-bearing bones (BSPG 1972 XVI 2248, 2251/2253); 4 teeth (BSPG 1972 XVI 2250); 1 trunk vertebra (BSPG 1972 XVI 2247); 1 cloacal vertebra (BSPG 1972 XVI 2254).

Identification

These specimens can be assigned only to indeterminate lizards.

Amphisbaenia Gray, 1844 Blanidae Kearney, 2003 *Blanus* Wagler, 1830

cf. *Blanus* sp. (Fig. A4.3O-P) Material: 1 dentary (BSPG 1972 XVI 2255).

Description

The dentary is small-sized and misses the anterior end, its ventral margin and most of its posterior end. The specimen is 2.3 mm in total length. In medial view, it displays a moderately high subdental ridge, marking dorsally a groove-like Meckelian fossa. Dorsally to the ridge, 5 teeth are preserved. The latter are subpleurodont, conical, pointed, closely-spaced and very slightly posteromedially bending by their tip. There are no striae on the crown, neither on the labial nor on the lingual surface. The alveolar canal opens posteriorly to the last tooth position, with a wide cavity. A long posterior extension of the posteroventral margin of the intramandibular septum gives a V-shaped appearance to the opening of the canal in medial view. The same margin of the septum is fused to the wall of the dentary. The lateral surface is smooth, with only a single mental foramen visible. Identification Despite its preservational status, the morphology of this dentary recalls that of the genus *Blanus* (this work). Because of this, it is here tentatively attributed to such genus.

<u>Stubersheim</u> "Lacertilia" Owen, 1842 Lacertidae Batsch, 1788 *Edlartetia* Augé & Rage, 2000

cf. *Edlartetia* sp. (Fig. A4.3Q) Material:

- Stubersheim 3: 1 fragment of tooth-bearing bone (BSPG 1982 X 7179).

Description

BSPG 1982 X 7179 is a poorly preserved fragment of tooth-bearing bone, measuring 3 mm in total length. The specimen carries 4 rather slender, pleurodont and closely-spaced teeth. The dorsal half of the tooth shaft is completely missing in all teeth but one. In the latter case, the crown recalls a tricuspid morphology, in spite of the erosion, and a distinct constriction is visible.

Identification

The constriction visible on the tooth shaft, associated with the tricuspid morphology of the tooth crown, approaches BSPG 1982 X 7179 to the lacertid genus *Edlartetia* (Augé & Rage 2000). However, given the very fragmentary nature of the specimen, this identification can only be tentative.

Mediolacerta Augé, 2005

Mediolacerta sp. (Fig. A4.3R-S) Material - Stubersheim 3: 1 dentary (BSPG 1982 X 7178).

Description

The dentary BSPG 1982 X 7178 is almost complete: it misses only the posterior end. The total length of the specimen is 11.5 mm. The posterior half of the ventral margin is broken, but the preserved portion is convex in medial view and does not bend in medial direction. A moderately high subdental ridge is visible on the medial side of the bone, ending anteriorly with a narrow and subhorizontal mandibular symphysis. The Meckelian fossa is moderately wide and medially open. The specimen carries 17 tooth positions, but teeth are preserved only in the posterior half of the tooth row. The latter are pleurodont, cylindrical, closely spaced and moderately amblyodont (sensu Hoffstetter 1944). They protrude over the dorsal margin of the alveolar border for roughly one third of their height. Most of the crowns are eroded, but the best preserved ones show light striae both lingually and labially. The posterior opening of the alveolar canal is located ventrally to the 15th tooth position. The lateral surface is smooth and carries 9 anteroposteriorly aligned mental foramina.

Identification

Because of the convex ventral margin and the wide and medially-open Meckelian fossa, BSPG 1982 X 7178 represents the dentary of a rather large larcertid (Bailon 1991; Delfino et al. 2011; this work). The tooth morphology clearly indicates that this lacertid was a moderately amblyodont form, such as *Amblyolacerta* Roček, 1984, *Escampcerta* Augé, 2005, *Mediolacerta* Augé, 2005 or *Quercycerta* Augé, 2005. Compared to *Quercycerta*, BSPG 1982 X 7178 has a lower number of teeth and does not display the medially-bending ventral margin that characterizes the genus (Augé 2005). Both *Amblyolacerta* and *Escampcerta* have smooth tooth crowns, whereas striae are present on the dentition of *Mediolacerta* (Roček 1984; Augé 2005). Given that, BSPG 1982 X 7178 can be assigned to this latter genus, but the absence of the anterior teeth hinders the recognition of the other main feature of the only known species of *Mediolacerta*, *Mediolacerta* roceki Augé, 2005: namely,

the presence of bi- or even tricuspid teeth on the anterior half of the tooth row (Augé 2005).

Lacertidae indet. (Fig. A4.3T)

Material:

Stubersheim 3: 5 dentaries (BSPG 1982 X 7140/7141, 7174); 4 fragments of tooth-bearing bones (BSPG 1982 X 7142).

Description

These dentaries (Fig. A4.3T) are very fragmentary and poorly preserved. They have a rather slender general morphology. They have a medially-open Meckelian fossa and a moderately high subdental ridge. The alveolar border carries closely-spaced, slender, cylindrical and pleurodont teeth. whose crown, when preserved, is bicuspid (with a small accessory cusp anteriorly). The teeth do not display a constriction near the crown. The lateral surface of the bone is smooth, except for the mental foramina. The tooth-bearing bones are also very fragmentary and very poorly preserved. They carry teeth that are morphologically similar to those of the dentaries.

Identification

These specimens clearly display lacertid features, particularly in their tooth morphology and in the presence of a wide and open Meckelian fossa (Bailon 1991; this work). Moreover, they are clearly different from either *Edlartetia* (no constricted shaft) and *Mediolacerta* (no amblyodont teeth), pointing out the presence of a third lacertid in Stubersheim 3.

?Lacertidae indet. Material:

- Stubersheim 2: 1 dentary (BSPG 1982 X 7114).

Description

The dentary is very poorly preserved and represented only by a small fragment. It displays a moderately high, but slightly narrowing posteriorly subdental ridge and a medially-open Meckelian fossa. At least 6 tooth positions are preserved, but only two teeth are still present. Teeth are closely spaced, pleurodont, cylindrical and slender. The crown is strongly eroded in both of them, but a bicuspid condition seems to be still recognisable at least in the anteriormost one.

Identification

BSPG 1982 X 7114 seems to share lacertid features such as the possible bicuspid crown and the medially-open Meckelian fossa (Bailon 1991; Delfino et al. 2011; this work), but this attribution is complicated by the very poor preservational conditions.

Scincidae Gray, 1825 *Eumeces* Wiegmann, 1834

aff. *Eumeces* sp. (Fig. A4.3U-V) Material:

- Stubersheim 2: 1 isolated tooth (BSPG 1982 X 7181).

Description

BSPG 1982 X 7181 is a very stout isolated tooth. It has a blunt crown provided with a labial and a lingual cusps, separated by a shallow groove. The labial surface of the crown is smooth, whereas the lingual one displays a large number of rather light but distinct striae. The cusps are not strongly bent in posteromedial direction.

Identification

According to Kosma (2004), slightly posteriorly-bending tooth crowns provided with parallel and longitudinal cusps and a light striation on the lingual side are found in the family Scincidae. BSPG 1982 X 7181 appears very similar to the anterior and larger teeth of the extant African skink *Eumeces schneideri* (Kosma 2004).

Scincomorpha indet.

Material:

- Stubersheim 3: 1 dentary (BSPG 1982 X 7168).

Description

This dentary is very small and very fragmentary. It carries a single pleurodont and slender tooth, not preserving the crown. A slender subdental ridge is present medially.

Identification

This poorly-preserved dentary is assigned to an indeterminate scincomorphan because of the presence of a pleurodont dentition and a subdental ridge (Evans 2008).

Anguidae Gray, 1825 Anguinae Gray, 1825 *Ophisaurus* Daudin, 1803

Ophisaurus holeci Klembara, 2015 (Fig. A4.3W-X) Material:

- Stubersheim 3: 1 parietal (BSPG 1982 X 7143).

Description

This parietal is moderately large. The parietal shelf is longer than it is large and has a maximum width of 7 mm and a maximum length of 8.2 mm. In dorsal view, the shelf slightly expands laterally towards the anterior end. A well-developed dermal ornamentation made up by short anastomosing ridges and a large number of distinct pits covers most of the dorsal surface, except for a smooth area levis in the posterior portion. The length of the area levis equals the length of the occipital shield. Four dermal shields are recognisable: the two lateral ones, the interparietal one and the occipital one. The lateral shields are wide and have roughly straight lateral margins. The interparietal shield is moderately narrow anteriorly, and the anterior end of the grooves that separate it from the two lateral shields is located distinctly medially compared to the anterolateral corner of the ornamented surface. The occipital shield is moderately small and has an arched posterior margin. The elliptical parietal foramen is located in the middle of the ornamented surface. The posterior end of the parietal is very poorly preserved, missing the postparietal processes and featuring a high degree of erosion. In spite of being almost completely broken off, the bases of the postparietal process indicate a low degree of divergence between them. The carina arcuata is strongly eroded, but it seems to have an arched shape. The ventral surface of the parietal shelf shows two moderately developed anterolateral ventral crests, which are distinctly concave in lateral direction in their anterior portion and located near the lateral margins. A wide facies muscularis (sensu Klembara et al. 2010) is therefore not present. The posterior portion of the anterolateral ventral crest is very low, almost not distinguishable. Only the proximal part of the posterolateral ventral crests is preserved. They meet the anterolateral ones roughly at the same height of the posteromedial margin of the floor of the parietal fossa, which is wide and deep.

Identification

BSPG 1982 X 7143 is attributed to *Ophisaurus* because of the absence of the facies muscularis along the lateral margins (in contrast with *Pseudopus*; Klembara 2015; Klembara & Rummel 2016) and the equally-long area levis and occipital shield (in contrast with *Anguis*; Klembara & Rummel 2016). Among Miocene *Ophisaurus* species based on parietals, BSPG 1982 X 7143 differs from *Ophisaurus fejfari* in the low divergence of the postparietal processes and in the laterally-concave anterior ventral crests, from *Ophisaurus spinari* in the arched posterior margin of the occipital shield and from *Ophisaurus robustus* in the straight lateral margins of the lateral shields (Klembara & Rummel 2016). On the other hand, it can be assigned to *O. holeci* on the basis of the ornamentation made up by short anastomosing ridges and distinct pits, the medially-located grooves separating lateral and interparietal

shields compared to the anterolateral corners of the ornamented cover, the concave anterior portion of the anterolateral ventral crest, the very low posterior portion of the anterolateral ventral crest and the contact between anterolateral and posterolateral ventral crests located at the same height of the posteromedial margin of the floor of the parietal fossa (Klembara 2015; Klembara & Rummel 2016).

Ophisaurus sp. (Fig. A4.3Y-AB) Material:

- Stubersheim 2: 1 fragment of tooth-bearing bone (BSPG 1982 X 7123); 1
 cervical vertebra (BSPG 1982 X 7121); 19 trunk vertebrae (BSPG 1982 X 7115, 7117, 7119/7120, 7122, 7125, 7127).
- Stubersheim 3: 2 maxillae (BSPG 1982 X 7149, 7152); 7 dentaries (BSPG 1982 X 7150, 7153, 7171, 7175/7176); 4 fragments of tooth-bearing bone (BSPG 1982 X 7144, 7151, 7170); 13 trunk vertebrae (BSPG 1982 X 7154, 7166, 7169).

Description

Maxillae are represented by small fragments (the largest one is 5 mm-long) preserving only part of the tooth row and of the anterior premaxillary process. They carry subpleurodont, rather cylindrical, closely-spaced and unstriated teeth, whose tip bends slightly in postero-medial direction.

The dentaries are small (the total length reaches a maximum of 4 mm in the bestpreserved specimens) and preserve only the middle or the posterior parts (Fig. A4.3Y-AB). They display a narrow subdental shelf and a medially open Meckelian fossa. The ventral margin and the inferior posterior process are broken off. The superior posterior process is preserved in BSPG 1982 X 7153 and partially in BSPG 1982 X 7176, and it is composed by short and pointed coronoid and surangular processes, separated by a moderately deep coronoid incisure. Ventrally to the superior posterior process, a short surangular spine is visible in medial view on the same specimens. Except for BSPG 1982 X 7176 (which displays a postero-ventrally free septum), the intramandibular septum seems to be fused to the wall of the dentary in its posteroventral portion. In BSPG 1982 X 7153, the posterior end of the septum (and therefore the opening of the alveolar foramen) is located between the third and the fourth posteriormost tooth positions, whereas in BSPG 1982 X 7176, it is placed ventrally to the second posteriormost one. Preserved teeth are subpleurodont, conical and pointed, without striae and with a slightly postero-medially curving tip. The lateral surface of the bone is smooth, except for the mental foramina. Posteriorly, there are the moderately shallow articular surfaces with the labial process of the coronoid and with the surangular.

The fragmentary tooth-bearing bones carry teeth that are morphologically similar to the ones of the dentary.

Both cervical and trunk vertebrae are procoelous and can reach a moderately large size (centrum length reaches up to 6 mm). The vertebrae have a dorso-ventrally compressed vertebral centrum, with a flat ventral surface, no precondylar constriction and posteriorly-convergent and concave lateral margins. Synapophyses are dorso-ventrally elongated. A neural spine is present dorsally, even though it is broken in almost all specimens. Zygapophyses are suboval and they are dorsally tilted at 45°.

Identification

In all the above-described tooth-bearing bones, the subpleurodont, cylindrical or subconical and slightly posteriorly-bending dentition recalls the genus *Ophisaurus* (Klembara et al. 2014). Similarly related to *Ophisaurus* (but also present in *Pseudopus ahnikoviensis*; Klembara 2012) is the surangular spine of the dentary (Klembara et al. 2014). The presence of an either fused or unfused intramandibular septum might be an evidence of the occurrence of at least two different, though indeterminate, species. The trunk vertebrae can also be assigned to *Ophisaurus* based on the dorso-ventrally compressed centrum with concave lateral margins (Klembara 1981).

Pseudopus Merrem. 1820

Pseudopus sp. (Fig. A4.3AC-AF) Material:

- Stubersheim 3: 2 fragments of tooth-bearing bone (BSPG 1982 X 7167, 7177); 1 trunk vertebra (BSPG 1982 X 7145).

Description

The tooth-bearing bones (Fig. A4.3AC) are very poorly preserved. They carry subpleurodont, stout, closely spaced and dorsally-rounded teeth. There are no distinct striae on the crown.

The trunk vertebra (Fig. A4.3AD-AF) is robust and large-sized, with a centrum length of 6.4 mm. The vertebral centrum has a flat ventral surface and no precondylar constriction. In ventral view, its lateral margins are straight and converge posteriorly. The neural arch is provided with a well-developed, though broken, neural spine. The zygapophyses are subelliptical and strongly tilted in dorsal direction (roughly 45°). Identification

Tooth-bearing bones and trunk vertebrae of *Pseudopus* are identified by the robust and stout teeth and by the straight and posteriorly-convergent lateral margins of the centrum respectively (Klembara 1981; Klembara et al. 2014; this work).

non-Anguis Anguinae indet.

Material:

- Stubersheim 2: 35 osteoderms (BSPG 1982 X 7116, 7118, 7126, 7128).
- Stubersheim 3: numerous osteoderms (BSPG 1982 X 7146/7147).

Description

The osteoderms are small-sized and very fragmentary. On the external surface, they have a vermicular ornamentation and most of them display a longitudinal keel too. The most-preserved ones can have either a subrectangular or a more rounded shape. Identification

Subrectangular osteoderms with an external keel are typical of non-*Anguis* anguines, such as *Ophisaurus* and *Pseudopus* (Holman 1998; Delfino et al. 2011).

Anguidae indet.

Material:

- Stubersheim 2: 1 premaxilla (BSPG 1982 X 7124); 20 caudal vertebrae (BSPG 1982 X 7129/7130).
- Stubersheim 3: 19 caudal vertebrae (BSPG 1982 X 7155, 7163).

Description

The premaxilla has a wide alveolar plate, which is 3.5 mm in total width. The palatal processes are broken, and the dorsal half of the ascending nasal process is also missing. The latter process displays a distinct narrowing by its base, and a distinct septonasal crest posteriorly. The anterior surface of the process is smooth. Eight tooth positions are present, with 2 moderately preserved teeth. Teeth are subpleurodont, cylindrical, rather slender and closely spaced. Their crowns are rather rounded, but this could be due to erosion.

Caudal vertebrae can either be small- or medium-sized and have a dorso-ventrally compressed centrum, with the bases of fused hemapophyses on the ventral surface and no precondylar constriction. The autotomy plane can either be present or absent. Identification

The premaxilla BSPG 1982 X 7124 is here attributed to an indeterminate anguid because of the wide alveolar plate and the subpleurodont teeth (this work). Caudal vertebrae can be assigned to the same taxon because of the dorso-ventrally compressed centrum with no precondylar constriction and fused hemapophyses.

Shinisauria Conrad, 2008

Merkurosaurus Klembara, 2008

Merkurosaurus sp. (Fig. A4.3AG-AH)

Material:

- Stubersheim 3: 1 maxilla (BSPG 1982 X 7180).

Description

BSPG 1982 X 7180 is a moderately well-preserved maxilla, missing most of the facial and the posterior processes. The anterior premaxillary process is strongly elongated and slightly anteromedially bending. Anterolateral and anteromedial processes are very little developed, and only a very small and shallow notch is visible in dorsal view by the anterior end of the anterior premaxillary process. A low lappet runs on the dorsal surface of the anteromedial process. The vomeronasal foramen opens in anteromedial direction. The palatal shelf is robust and swollen in its posterior portion. A very wide superior dental foramen is visible posteriorly. A welldeveloped and robust arched ridge is visible on the medial surface of the preserved portion of the facial process, marking anterodorsally a wide, deep and anteroposteriorly-elongated recess. The preserved portion of the tooth row carries at least 10 closely-spaced tooth positions. A single well-preserved tooth is present: it is subpleurodont, conical, pointed, slender and rather straight (the posteromedial bending of the tip is very low). The tooth bases of the well-preserved tooth and of three other more poorly preserved teeth do not show neither striation nor spongy tissue at the connection with the alveolar portion of the maxilla. The lateral surface of BSPG 1982 X 7180 presents 6 anteroposteriorly aligned ventrolateral foramina, the posteriormost of which is very large. Dorsally to these foramina, a rather light ornamentation made up by low tubercles and small pits is visible. The total length of the specimen is 10 mm.

Identification

The morphology of BSPG 1982 X 7180 is fully comparable with that of the maxillae figured and described by Klembara (2008) as part of the referred material of *Merkurosaurus ornatus*. In particular, BSPG 1982 X 7180 recalls those specimen in the elongated anterior premaxillary process, the anteromedially-directed vomeronasal foramen, the deep and anteroposteriorly-elongated recess on the medial surface, the tooth morphology and the dermal ornamentation (see Klembara 2008). Because of these similarities, this maxilla is here attributed to *Merkurosaurus*. Even though *M. ornatus* is the only species currently included in the genus, a cautious approach is here followed in the specific attribution of BSPG 1982 X 7180, pending the possible finding of other, more diagnostic bones of this lizard in Stubersheim.

Anguimorpha indet.

Material:

- Stubersheim 3: 1 dentary (BSPG 1982 X 7148).

Description

This dentary is poorly preserved, but clearly displays a subdental shelf on the medial surface. Only two teeth are still preserved: they are subpleurodont, closely spaced and cylindrical, but their crown is strongly eroded.

Identification

The subdental shelf is a typical feature of anguimorphan dentaries (Evans 2008). The poor preservational status of BSPG 1982 X 7148 hinders its attribution to any of the anguimorphan taxa recognized in Stubersheim.

"Lacertilia" indet.

Material:

- Stubersheim 2: 1 coronoid (BSPG 1982 X 7136); 6 trunk vertebrae (BSPG 1982 X 7132/7133, 7135); 3 cloacal vertebrae (BSPG 1982 X 7131); 1 caudal vertebra (BSPG 1982 X 7134).
- Stubersheim 3: 3 maxillae (BSPG 1982 X 7162); 6 fragments of toothbearing bone (BSPG 1982 X 7156, 7164, 7173); 1 cervical vertebra (BSPG 1982 X 7157); 7 trunk vertebrae (BSPG 1982 X 7159); 1 caudal vertebra (BSPG 1982 X 7158); 1 fragment of vertebra (BSPG 1982 X 7161).

Identification

Poorly-preserved or undiagnostic skeletal elements are attributed only to indeterminate lizards.

Amphisbaenia Gray, 1844

Amphisbaenia indet. (Fig. A4.3AI-AL) Material:

- Stubersheim 2: 3 trunk vertebrae (BSPG 1982 X 7137/7139).
- Stubersheim 3: 5 trunk vertebrae (BSPG 1982 X 7160, 7172); 1 caudal vertebra (BSPG 1982 X 7165).

Description

Trunk vertebrae (Fig. A4.3AI-AL) are procoelous and small-sized, with the largest of the most preserved ones that reaches 2.5 mm in centrum length. They have a dorsoventrally compressed and ventrally flat vertebral centrum, with almost parallel lateral margins. Synapophyses are rounded and rather massive. Very short prezygapophyseal processes are located ventrally to the prezygapophyses. In dorsal view, the vertebrae have a distinct X-shaped morphology.

The caudal vertebra has a roughly 1 mm-long procoelous centrum, which is not distinctly dorsoventrally compressed. The ventral surface bears the bases of two

fused hemapophyses. There is no autotomy plane. Cylindrical and antero-laterally directed transverse processes are present near the anterior end of the vertebra. The dorsal surface of the neural arch is smooth, without neural spine. The zygapophyses are small and suboval. They are tilted dorsally at 45°.

Identification

Vertebrae showing amphisbaenian features such as dorsoventrally compressed centrum with a flattened ventral surface and subparallel lateral margins, massive and rounded synapophyses and absence of both zygosphene and neural spine (Estes 1983; Delfino 2003) are found in both Stubersheim 2 and 3. Böhme (1999b) reported both *Palaeoblanus tobieni* and *Blanus antiquus* from Stubersheim 3, but these taxa can be recognised only on the basis of cranial remains, which are not present in the herein studied material.

Walda 2

"Lacertilia" Owen, 1842 Anguidae Gray, 1825 Anguinae Gray, 1825 *Pseudopus* Merrem, 1820

Pseudopus sp. (Fig. A4.3AM-AN)

Material: 2 dentaries (BSPG 1987 V 5/83, 9/82); 1 fragment of tooth-bearing bone (BSPG 1987 V 6/89).

Description

Both dentaries are very fragmentary, preserving either the anterior end (BSPG 1987 V 5/83; Fig. A4.3AM) or part of the posterior portion (BSPG 1987 V 9/82; Fig. A4.3AN). Teeth are subpleurodont, cylindrical and blunt. They are very stout in the posterior portion, but slender in the anterior one. There are no clear striae in the teeth preserving the crown. The well-developed subdental shelf is partly preserved only in the specimen preserving the anterior portion. There is no groove on the dorsal half

of the preserved shelf. The mandibular symphysis is narrow and subhorizontal. The Meckelian fossa is narrow in the anterior portion, but widens posteriorly. In the anterior portion, it opens ventrally because of the development of the shelf, which covers it medially. The alveolar foramen opens by the third posteriormost tooth position. It is marked by a fused intramandibular septum. Part of the short coronoid and surangular processes are preserved in the posterior portion. They are separated by a wide coronoid incisure. The lateral surface is smooth, except for the mental foramina. In the posterior portion, a deep articulation surface for the labial process of the coronoid is also visible by the posterior end. BSPG 1987 V 5/83 is 6 mm in length, whereas BSPG 1987 V 9/82 is 11 mm-long.

The fragment of tooth-bearing bone preserves only a single tooth, whose morphology is fully comparable with the one of the dentary teeth.

Identification

The cylindrical and stout tooth morphology identifies the genus *Pseudopus* among anguines (Klembara et al. 2014; this work). Klembara et al. (2010) report remains of *P. laurillardi* from Walda 2. The above described dentaries, however, apparently differ from those of the latter species in lacking a groove and a ridge on the subdental shelf. Nevertheless, since this absence might be simply a result of the fragmentary nature of the specimens, the presence of a second species of *Pseudopus* in Walda 2 cannot be stated with certainty.

3.2.2. Greece

Lizard remains coming from 31 Greek localities previously studied by Delfino (2004a) have been reviewed. Some of the localities have been the subject of deepened studies, including also other components of the herpetofauna (Georgalis et al. 2016a, b, 2017a, b). Some of the localities (namely, Ano Metochi, Liko, Spilia and Tomea Eksi) group different, but coeval fossil sites. Tourkobounia consists of five different localities, with an age spanning from the late Pliocene to the Middle Pleistocene.



Figure 3.2) Map of Greece, showing the position of the herein considered Greek localities: Aliveri (a), Anabussos (b), Ano Metochi (c), Apolakkia 2 (d), Arnissa (e), Biodrak (f), Kaiafa (g), Karpathos (h), Karydia 2 (i), Kastoria (j), Komanos 1 (k), Lefkon 1 (l), Liko (m), Limni 6 (n), Maramena (o), Maritsa A (p), Milatos 3 (q), Monasteri (r), Notio 1 (s), Pili B (t), Plakias (u), Rema Marmara 2 (v), Spilia (w), Tomea Eksi (x), Tourkobounia (y) and Vevi (z). Colors of the circles indicates a Miocene (red), Pliocene (orange) or Pleistocene (green) age.

Localities

Agia Loucas (Not mapped)

Age: Pleistocene (?).

Repository: University of Utrecht, The Netherlands.

References: Delfino 2004a.

Aliveri (Fig. 3.2a)
Age: early Miocene (Burdigalian, MN 4).
Repository: University of Utrecht, The Netherlands.
References: de Bruijn et al. 1980; Koufos 2006; Hoek Ostende et al. 2015; Koufos 2016.

Anabussos (Fig. 3.2b) Age: Pleistocene (?). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Ano Metochi (Ano Metochi-2 = AM-2, Ano Metochi-3 = AM-3) (Fig. 3.2c)
Age: late Miocene (Messinian, MN 13).
Repository: University of Utrecht, The Netherlands.
References: de Bruin 1989; Koufos 2006; Koufos 2016.

Apolakkia 2 (Fig. 3.2d)Age: Pliocene.Repository: University of Utrecht, The Netherlands.References: Weerd et al. 1982; Koufos 2016.

Arnissa (Fig. 3.2e)Age: late Pleistocene.Repository: University of Utrecht, The Netherlands.References: Mayhew 1978.

Biodrak (Fig. 3.2f) Age: late Miocene (MN 10). Repository: University of Utrecht, The Netherlands. 280 References: Koufos 2016.

Kaiafa (Fig. 3.2g)Age: Pleistocene.Repository: University of Utrecht, The Netherlands.References: Delfino 2004a.

Karpathos (Fig. 3.2h) Age: Pleistocene. Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Karydia 2 (Fig. 3.2i) Age: middle Miocene (MN 4). Repository: University of Utrecht, The Netherlands. References: Doukas 2003; Koufos 2006.

Kastoria (Fig. 3.2j) Age: Pliocene. Repository: University of Utrecht, The Netherlands. References: Koufos 2016.

Komanos 1 (Komanos 1 High A) (Fig. 3.2k) Age: early Pliocene (MN 14). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a; Koufos 2016.

Lefkon 1 (Fig. 3.21) Age: late Miocene (MN 10). Repository: University of Utrecht, The Netherlands. References: Koufos 2016.

Liko (Liko A, Liko BA, Liko C) (Fig. 3.2m) Age: Upper Pleistocene. Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Limni 6 (Fig. 3.2n) Age: Pliocene. Repository: University of Utrecht, The Netherlands. References: Koufos 2016.

Maramena (Maramena 1, 2, 3) (Fig. 3.20) Age: late Miocene (MN 13/14). Repository: University of Utrecht, The Netherlands. References: Koufos 2016.

Maritsa A (Fig. 3.2p) Age: early Pliocene (MN 14). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Milatos 3 (Fig. 3.2q) Age: Pleistocene (?). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Monasteri (Fig. 3.2r)
Age: late Miocene (Messinian, MN 13). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a; Koufos 2016.

Notio 1 (Fig. 3.2s) Age: early Pliocene (MN 15). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

*Pili B (Fig. 3.2t)*Age: Upper Pleistocene.Repository: University of Utrecht, The Netherlands.References: Delfino 2004a.

*Plakias (Fig. 3.2u)*Age: earliest late Miocene (MN 9).Repository: University of Utrecht, The Netherlands.References: de Bruijn et al. 2012; Koufos 2016.

Rema Aslan 1 (not mapped) Age: Miocene/Pliocene. Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Rema Marmara 2 (Fig. 3.2v) Age: late Miocene. Repository: University of Utrecht, The Netherlands. References: Koufos 2016. Spilia (Spilia 3, Spilia 4) (Fig. 3.2w)Age: late Pliocene.Repository: University of Utrecht, The Netherlands.References: Delfino 2004a.

Tomea Eksi (Tomea Eksi 1, Tomea Eksi 2) (Fig. 3.2x) Age: late Miocene (Messinian, MN 13). Repository: University of Utrecht, The Netherlands. References: Koufos 2016.

Tourkobounia (Tourkobounia 1, Tourkobounia 2, Tourkobounia 3, Tourkobounia 4, Tourkobounia 5) (Fig. 3.2y)

Age: late Pliocene (Tourkobounia 1); earliest early Pleistocene (Tourkobounia 2); latest early/earliest Middle Pleistocene (Tourkobounia 3, 4, 5).

Repository: University of Utrecht, The Netherlands.

References: Sindowski 1951; Bruijn & van der Meulen 1975; Symeonidis & Vos 1976.

Trilofon (not mapped)

Age: Miocene/Pliocene. Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Vevi (Fig. 3.2z) Age: early Pliocene (MN 15). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Xeros (not mapped)

Age: Pleistocene (?). Repository: University of Utrecht, The Netherlands. References: Delfino 2004a.

Systematic palaeontology

<u>Aliveri</u> "Lacertilia" Owen, 1842 Chamaeleonidae Gray, 1825 *Chamaeleo* Laurenti, 1768 *Chamaeleo andrusovi* Čerňanský, 2010b

Chamaeleo cf. C. andrusovi (Fig. A4.4A-D)

Material: 1 fragment of skull roofing bone (UU AL 3501).

Description

UU AL 3501 is a skull roofing bone fragment about 3×3 mm in diameter. A comparison with extant chamaeleonid material, stored in the collections of the University of Torino and the Muséum national d'Histoire naturelle, Paris, suggests that the fragment can be part of the circumorbital region (i.e., either a prefrontal or a postorbital), but its fragmentary status prevents a more precise determination. The fragment is flattened and its external surface is covered by an ornamentation made by various small tubercles grouped in four, well-separated and rounded clusters. Two of the four clusters are aligned along one of the margins of the fragment, which is a natural border and not the result of breakage (as the other margins). If the interpretation of the fragment as part of a circumorbital bone is correct, this would be the orbital margin. The inner surface of the specimen is smooth.

Identification

Because of the complex ornamentation and the well-spaced and complex clusters of tubercles (= pustular protuberances of Čerňanský 2010b), the skull bone fragment from Aliveri can be referred to *Chamaeleo* cf. *C. andrusovi*.

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Chamaeleonidae indet. (Fig. A4.4E-H)

Material: 2 fragments of tooth-bearing bone (UU AL 3502/3503).

Description

UU AL 3502 and 3503 are very fragmentary tooth-bearing bones. However, they clearly bear acrodont, large and triangular teeth, which are well-spaced and located on the edge of the bones. Two of them are preserved in UU AL 3502 and 3 of them are visible in UU AL 3503, even if in the latter specimen only one is well preserved. Small accessory cusps are recognizable anteriorly and posteriorly to the main one in one tooth of UU AL 3502 and in two teeth of UU AL 3503. Ventrally directed interdental grooves are present on the lateral surface. Due to the fragmentary nature of both specimens, it is currently impossible to determine whether these two tooth-bearing elements originate from the dentary or the maxilla.

Identification

The two tooth-bearing elements from Aliveri can be attributed to the family Chamaeleonidae on the basis of the well-spaced and apically located acrodont teeth (Delfino et al. 2008; this work). A more precise identification is hampered by the poor preservational conditions and the attribution of these specimens to the same taxon as the skull roofing bone cannot be ascertained.

Lacertidae Batsch, 1788

Lacertidae indet. (Fig. A4.4I-K) Material: 1 dentary (UU AL 3589); 7 fragments of tooth-bearing bone (UU AL 3520, 3542, 3557/3561).

Description

The dentary preserves only part of the middle portion of the bone. It is 4 mm in length. The Meckelian fossa is wide and opens medially. Teeth were pleurodont, cylindrical and slender, but no one is completely preserved. A moderately slender

subdental ridge is present. The ventral margin is distinctly convex in medial view. The lateral surface is smooth, even if a light roughness seem to be visible (but it could be caused by taphonomical agents). Two mental foramina are present. The fragments of indeterminate tooth-bearing bones (Fig. A4.4I-K) bear pleurodont,

cylindrical, mono-, bi- and tricuspid teeth, which generally show a certain degree of wearing. Teeth of the largest specimens (UU AL 3557 and 3559) are hypertrophied. Identification

The heterodont dentition of the indeterminate tooth-bearing bones is indicative of their belonging to an indeterminate lacertid (Bailon 1991; this work), which cannot be more precisely defined due to the poor preservational status of the fossil material. In spite of the absence of well-preserved teeth, the dentary is assigned to the same taxon because of the convex ventral margin, which is also found in lacertids (this work).

Scincomorpha indet. (Fig. A4.4L-M)

Material: 4 dentaries (UU AL 3519, 3521, 3524, 3549).

Description

These specimens are represented by poorly preserved fragments of dentary, whose total length is 3.5 mm (UU AL 3519; Fig. A4.4L-M), slightly less than 5 mm (UU AL 3521), roughly 2.5 mm (UU AL 3524) and roughly 3 mm (UU AL 3549). In medial view, the dentaries display a slender (UU AL 3519) or moderately high (other specimens) subdental ridge and a medially open Meckelian fossa. The ventral margin of the bone is missing in all specimens but UU AL 3549, in which it appears rather straight. At least 4 (UU AL 3519), 7 (UU AL 3524) and 10 (UU AL 3521) tooth positions are recognisable, but teeth are preserved only in UU AL 3519 (all four of them) and 3524 (a single one). They are slender, cylindrical and pleurodont. Those of UU AL 3519 are strongly eroded by the tip, but the preserved one of UU AL 3524 is monocuspid. UU AL 3549 preserves the anterior end, displaying a narrow and subhorizontal mandibular symphysis. The lateral surface is smooth, carrying some

mental foramina, in all specimen but UU AL 3519, in which it is slightly rugged (Fig. A4.4L).

Identification

The presence of a subdental ridge on the medial side discriminates dentaries of scincomorphan lizards from those of anguimorphan ones, but it is also present in iguanians and gekkotans (Evans 2008). Nevertheless, the combination of open Meckelian fossa and the pleurodont dentition allow to exclude the belonging of these dentaries to the latter two groups, rather favouring a scincomorphan (sensu Gauthier et al. 2012) assignment. The preservational conditions of the specimens hinders a taxonomic attribution even at the family level, but the presence of more than one taxon might be suggested by the difference in the smoothness of the lateral surface.

Anguidae Gray, 1825 Anguinae Gray, 1825

non-Anguis Anguinae indet. (Fig. A4.4N)

Material: 96 osteoderms (UU AL 3506/3518, 3543/3548, 3562/3575).

Description

Osteoderms are small, but rather thick and robust. They show a vermicular ornamentation and a well-developed longitudinal keel on the external surface. The most preserved ones are subrectangular in shape.

Identification

The presence of anguids in Aliveri is testified by a large number of osteoderms showing the typical vermicular ornamentation on the external surface. The thickness, the presence of a keel and the subrectangular shape are found in non-*Anguis* anguine taxa (i.e., either *Pseudopus* or *Ophisaurus*), contra smaller, rounded and unkeeled osteoderms in *Anguis* (Delfino et al. 2011).

"Lacertilia" indet.

Material: 1 pterygoid (UU AL 3588); 4 fragments of tooth-bearing bone (UU AL 3522/3523, 3525/3526); 1 caudal vertebra (UU AL 3527); 1 fragment of vertebra (UU AL 3528); 1 humerus (UU AL 3589).

Identification

These specimens are either too poorly preserved or they lack significant diagnostic features. Because of this, they are attributed only to indeterminate squamates.

<u>Ano Metochi</u> "Lacertilia" Owen, 1842 Lacertidae Batsch, 1788

Lacertidae indet. (Fig. A4.4O-X)

Material:

- AM-2: 1 maxilla (UU AM2 501); 3 dentaries (UU AM2 502/504); 2 fragments of tooth-bearing bone (UU AM2 505).
- AM-3: 1 premaxilla (UU AM3 501); 1 maxilla (UU AM3 502); 1 dentary (UU AM3 503).

Description

The premaxilla (UU AM3 501; Fig. A4.4O-P) is almost complete, lacking only the dorsal tip of the ascending nasal process. It is small-sized, with an alveolar plate that is 2.1 mm wide. It bears 7 pleurodont, cylindrical and slender teeth, whose crown is not preserved. The posterolateral tips of the palatal process are broken, but they are clearly separated by a wide and V-shaped notch. The incisive process is poorly developed. The ascending nasal process tends to slightly widen dorsally, but it does not show a leaf-shaped or an arrow-shaped morphology; its lateral margins are roughly subparallel in anterior view. A distinct septonasal crest is visible on the posterior surface of the process, whereas the anterior one is smooth.

The maxillae (UU AM2 501 and UU AM3 502; Fig. A4.4Q-R) are represented by small fragments (UU AM2 501 is roughly 4.5 mm in length, whereas UU AM3 502 is 3 mm in length) bearing pleurodont, cylindrical and slender teeth. Ten tooth positions are recognizable in UU AM3 502, but only 4 teeth are preserved; all of them are bicuspid. UU AM2 501, on the other hand, bears 3 teeth and 3 empty tooth positions. In the latter specimen, tooth crowns are rather eroded, but one of the teeth seems to show two small accessory cusps by the sides of the main one. On the dorsal surface of the palatal shelf of both maxillae there is a very large superior dental foramen, followed by a wide and deep groove. The lateral surface of the fragments is smooth, with 2 ventrolateral foramina in both of them. Moreover, it is distinctly concave in UU AM2 501.

UU AM2 502, 503 and 504 and UU AM3 503 (Fig. A4.4S-X) are partially preserved dentaries, missing the anteriormost and posteriormost parts. The length of the preserved portion of the specimens is 6.3 mm (UU AM2 502), 3 mm (UU AM2 503), 6.7 mm (UU AM2 504) and 3.3 mm (UU AM3 503). The dentaries are characterized by an heterodont dentition formed by pleurodont and cylindrical teeth. Eight tooth positions are visible in UU AM3 503, 10 in UU AM2 502, 9 in UU AM2 503 and 16 in UU AM2 504. The preserved teeth can be mono-, bi- or tricuspid. All teeth protrude well above the labial wall of the jaw. Also, teeth increase in basal diameter along the row, with the anteriormost having a narrower diameter than the posteriormost ones. The Meckelian fossa is moderately wide and opens medio-ventrally on the medial side of the bone. The lateral surface is smooth, with only 3 (UU AM2 503 and UU AM3 503) or 6 (UU AM2 504) labial foramina (not preserved in UU AM2 503), of which one is rather enlarged in UU AM3 503.

The fragments of tooth-bearing bones are small-sized and poorly preserved. They bear pleurodont, cylindrical, slender and bicuspid teeth.

Identification

The morphology of the teeth allows assignment of UU AM3 501, 502 and 503 to Lacertidae (Bailon 1991; this work). The width of the alveolar plate of UU AM3 501

fits within the ranges defined by Barahona and Barbadillo (1997) for *I. bonnali*, *P.* bocagei, Po. hispanicus and P. muralis (1.6 mm-2 mm) and for A. erythrurus, I. cyreni, I. monticola and P. algirus (2.3-2.4 mm). Moreover, according to the latter authors, 7 tooth positions are a characteristic feature of the premaxillae of A. erythrurus, I. bonnali, P. bocagei, Po. hispanicus and P. muralis, whereas the parallel lateral margins are typical of those of A. marchi, I. bonnali, P. bocagei, Po. hispanicus, P. muralis, P. algirus and Ps. hispanicus (Barahona & Barbadillo 1997). Accordingly so, UU AM3 501 seems to show affinities with the genus *Podarcis* and with *I. bonnali*. However, it has to be noted that the work of Barahona and Barbadillo (1997) is based only on Iberian lacertids and the above-mentioned features appear to be present in other small lacertids also (see Chapter 2). Following a cautious approach, UU AM3 501 can therefore be attributed to a small-sized indeterminate lacertid, even if the possibility that it belongs to a juvenile of some other, larger species cannot be totally ruled out. As for UU AM3 502 and 503 and all the remains from AM-2, their fragmentary nature precludes any taxonomic assignment with certainty, but their size is consistent with a small-sized taxon. It is thus not possible exclude neither the possibility that the material coming from the two localities pertains to the same taxon, nor that they represent two distinct lacertids from Ano Metochi.

Scincoidea Oppel, 1811 Cordylidae Fitzinger, 1826

Cordylidae indet. (Fig. A4.4Y-AD)

- AM-2: 1 maxilla (UU AM2 507); 2 dentaries (UU AM2 508/509); 1 one fragment of tooth-bearing bone (UU AM2 510).
- AM-3: 2 maxillae (UU AM3 505/506), 1 maxilla (UU AM3 507).

Description

The four maxillae (UU AM2 507, UU AM3 505, 506 and 507; UU AM3 506 is broken into two portions; Fig. A4.4Y-AA) are incomplete, but are moderately large (lengths are 7 mm for UU AM3 505, 5 mm for UU AM3 507, 8 mm for UU AM3 506, and 3.5 mm for UU AM2 507). They bear moderately robust, pleurodont and cylindrical teeth, whose crowns are blunt and show lingual and labial longitudinal cusps separated by a groove (similar to the morphotype F of Kosma 2004; Fig. A4.4AD). Moreover, the crowns are slightly curved in posteromedial direction and present striae on the lingual side. The preserved tooth positions are 10 for UU AM3 507, 13 for UU AM3 505, 20 for UU AM3 506, 6 for UU AM2 507. All teeth are closely spaced. UU AM3 506, the most complete specimen, shows a low arched ridge on the medial surface of the anterior half of the facial process and a deep and moderately large superior dental foramen followed by a shallow groove. A similar superior dental foramen is visible also in UU AM3 507. In UU AM2 507, the arched ridge is well developed. The lateral surface of all specimens is smooth, with only a number of ventrolateral foramina (3 in UU AM2 507, 5 in UU AM3 507 and 7 in UU AM3 505 and 506).

Tooth morphology of the two incomplete dentaries (UU AM2 507 and 509; Fig. A4.4AB-AC) is similar to the above described maxillae, even if teeth are slightly more slender. Both specimens still preserve 9 tooth positions only. UU AM2 508 is 3.8 mm-long, whereas UU AM2 509 is 3.4 mm in length. Both specimens are fragmentary and miss the posterior half, but UU AM2 509 preserves a narrow and horizontal mandibular symphysis. The Meckelian fossa is open medially. The lateral surface is smooth, with 2 (UU AM2 509) or 4 (UU AM2 508) mental foramina.

UU AM2 510 is a small fragment of tooth-bearing bone, bearing 2 teeth that are morphologically similar to the ones of UU AM2 507. It cannot be determined with certainty whether this material pertains to a dentary or a maxilla.

Identification

Pleurodont implantation, cylindrical shape and bicuspid crown provided with lingual and labial longitudinal cusps and with striae on the lingual side are typical of the teeth of Scincoidea (sensu Estes et al. 1988 and Gauthier et al. 2012), including Cordyliformes (Cordylidae and Gerrhosauridae) and Scincidae *sensu lato* (Kosma 2004). In gerrhosaurids, the striation is usually absent or poorly developed (Kosma 2004). A large number of cordylids and scincids, on the other hand, show this feature (Kosma 2004), but the distinction between the two families is often difficult (Čerňanský 2012). However, the remains from Ano Metochi, despite being incomplete have more robust teeth than those usually present in scincids and the striation is usually less distinct in the latter clade (Kosma 2004; this work). Moreover, the above-described tooth morphology is similar to those shown by a left dentary from the early Miocene of Switzerland, figured by Jost et al. (2015) and attributed to *Bavaricordylus* sp., as also by a right dentary from the early Miocene of Czech Republic, assigned to aff. *Palaeocordylus bohemicus* by Čerňanský (2012). Accordingly so, the above described specimens from Ano Metochi are attributed to indeterminate cordylids. Moreover, the cordylids from Ano Metochi are very similar to those found in Maramena (see below).

Anguidae Gray, 1825 Anguinae Gray, 1825 *Ophisaurus* Daudin, 1803

Ophisaurus sp. (Fig. A4.4AE-AN) Material:

- AM-2: 1 maxilla (UU AM2 512).
- AM-3: 4 dentaries (UU AM3 509/512), 51 presacral vertebrae (UU AM3 513).

Description

UU AM2 512 (Fig. A4.4AE) is a rather small fragment of maxilla, carrying 2 subpleurodont teeth. A third, empty tooth position is visible. The preserved teeth are

slender and slightly enlarged in their base. One of them preserves the tip, which is pointed and slightly bending in posteromedial direction. There are no clear striae, but two sharp carinae are present both in the anterior and the posterior sides of the tip. The lateral surface of the fragment is slightly concave and bears two ventrolateral foramina.

The dentaries (UU AM3 509, 510, 511 and 512) are small-sized and incomplete (Fig. A4.4AF-AI). UU AM3 512 represents the anterior end, UU AM3 510 is represented only by the posterior portion, UU AM3 511 preserves only the dorsal part of the posterior portion and UU AM3 509 misses both the anterior and the posterior ends. All specimens are 4 mm in length, except for UU AM3 511 which is smaller (2.8 mm-long). They bear subpleurodont, canine-like teeth, which are slightly posteromedially curved by their tip and slightly enlarged by their base. Teeth of UU AM3 512 are slightly more cylindrical and less enlarged. No striae can be seen on the lingual side of the teeth. Number of preserved tooth positions is 5 in UU AM3 511, 6 in UU AM3 510, 8 in UU AM3 509 and 9 in UU AM3 512. The Meckelian fossa (not preserved in UU AM3 511) is moderately narrow and opens ventromedially in UU AM3 509 and 510, but only ventrally in UU AM3 512, since a ventral expansion of the subdental shelf covers it laterally. The lateral surface is smooth, except for the presence of the mental foramina (1 in UU AM3 510 and 511, 3 in UU AM3 512 and 4 in UU AM3 509) and of a deep articulation surface for the angular. The mandibular symphysis (preserved only in UU AM3 512) is narrow and almost horizontal; its posterior end develops medially forming a short triangular expansion. The end of the intramandibular septum is visible in UU AM3 510 and 511: it is located by the second posteriormost tooth position in the former and by the third posteriormost one in the latter. The posterior end of the same specimens presents a well-developed coronoid process (although broken by the tip in the latter) and a less developed surangular process, separated by a moderately shallow coronoid incisure. The angular process (preserved only in UU AM3 510) seems not to develop beyond the posterior margin of the articulation surface with the angular, even though its tip could be broken. The surangular spine seems to be present but its posterior end is always broken and the splenial spine, when preserved, is poorly developed.

Presacral vertebrae (UU AM3 513; Fig. A4.4AJ-AN) are small (centrum length 1.9-4 mm) and have a dorso-ventrally compressed centrum with distinctly convergent lateral margins. The neural canal is subtriangular in anterior view and the pre- and postzygapophyses are rounded and strongly tilted dorsally (about 45°). A welldeveloped neural spine is present on the dorsal surface of the neural arch.

Identification

The dorsoventrally compressed vertebral centrum with convergent lateral margins clearly hint for the presence of a non-Anguis anguine taxon in Ano Metochi (Estes 1983). Furthermore, in a comparative study of the lower jaw of extant anguine genera, Klembara et al. (2014) stated that the presence of a surangular spine and of cylindrical and conical (canine-like) teeth slightly bending posteriorly by their tip distinguish dentaries of Ophisaurus from those of Anguis and Pseudopus (note that the latter authors considered Dopasia as a junior synonym of Ophisaurus; this taxonomic opinion is also followed here). The dentaries from Ano Metochi clearly do not belong to any of the extant species of the genus because of the absence of striae on the lingual side of the teeth and the poorly developed angular process (Klembara et al. 2014). Moreover, they can be differentiated from the extant species *Ophisaurus koellikeri* on the basis of their pointed end of the surangular process, from Ophisaurus ventralis on the basis of their coronoid process being longer than the surangular process, and from Ophisaurus attenuatus, Ophisaurus compressus, Ophisaurus mimicus and O. ventralis by the fact that the latter species have all their teeth slender (Klembara et al. 2014). Among fossil taxa, three species of *Ophisaurus* (including *Dopasia*) and related forms have been established on the basis of dentaries from the Oligocene of the Phosphorites du Quercy, France: *Ophisaurus coderetensis*, Ophisaurus frayssensis and Ophisaurus roqueprunensis (Augé 1992, 2005), with the former two having been recently reallocated to their own genus, Ophisauromimus (Čerňanský et al. 2016a). The dentaries from AM-3 differ from Ophisauromimus *coderetensis* in having a less marked coronoid incisure, from *Ophisauromimus frayssensis* in having a smaller size and less enlarged teeth, and from *Ophisaurus roqueprunensis* in having a surangular process shorter than the coronoid one and less enlarged teeth (Augé 1992, 2005). Eastern and Central European species of *Ophisaurus* have been erected based on parietals and therefore it is not possible to state if dentaries from AM-3 could belong to them or not. However, they differ from the ones attributed by Roček (1984) to *Ophisaurus* cf. *O. spinari* from Dolnice (early Miocene, MN 4), Czech Republic, because of shorter angular and surangular processes. The overall morphology of the herein described dentaries is similar to the one of those attributed to the 'Anguinae morphotype 2' from Merkur North (early Miocene, MN 3), Czech Republic (Klembara 2015) and to *Ophisaurus* sp. from Polgárdi (late Miocene, MN 13), Hungary (Venczel 2006). The latter locality has also yielded vertebrae and osteoderms that are similar in size and morphology to the ones from Ano Metochi (Venczel 2006).

Anguidae indet.

Material:

- AM-2: 1 fragment of osteoderm (UU AM2 513).
- AM-3: 25 caudal vertebrae (UU AM3 514); 41 osteoderms (UU AM3 515/520).

Description

Caudal vertebrae are small-sized (centrum length of the largest one is 3.9 mm). Their centrum is dorso-ventrally compressed and bears the proximal portions of fused haemapophyses. The autotomy plane is present.

Osteoderms are small, but moderately thick. They are subrectangular in shape and they show a low keel in the middle of their ornamented external surface. In UU AM2 513, the keel is distinct and sharp.

Identification

The subrectangular and thick osteoderms provided with a keel on the external surface indicates that they belong to a non-*Anguis* anguine. Furthermore, although it appears most probable that both osteoderms and caudal vertebrae belong to the same taxon described above (*Ophisaurus* sp.), this cannot be shown with certainty. The remains are therefore identified only at family level.

Maramena

"Lacertilia" Owen, 1842 Agamidae Spix, 1825 Agaminae Spix, 1825

Agaminae indet. (Fig. A4.5A-G) Material:

- Maramena 1: 1 premaxilla (UU MAA 7076); 3 maxillae (UU MAA 7043-7045); 5 dentaries (UU MAA 7041-7042, 7075, 7276, 7305); 15 fragments of tooth-bearing bone (UU MAA 7063, 7065-7074, 7264, 7303-7304, 7394); 5 caudal vertebrae (UU MAA 7062, 7064, 7302).
- Maramena 2: 1 frontal (UU MAA 7191).
- Maramena 3: 1 premaxilla (UU MAA 7341); 1 maxilla (UU MAA 7208); 1 dentary (UU MAA 7207).

Description

UU MAA 7191 is a fragment of an unpaired and robust frontal (Fig. A4.5A-B), preserving part of the anterior end of the bone. The anteriormost part (namely, the medial and lateral processes) are missing. The dorsal surface displays a distinctly sunken area in the middle towards the posterior end of the preserved portion and a faint ornamentation made by low irregularities. Anteriorly, two poorly distinct and U-shaped surfaces may represent the articulation surfaces with the nasals. Their outline is marked by very low ridges that laterally separate each of them from the

wide articulation surfaces with maxillae and prefrontals. The latter covers entirely the lateral surface of the preserved portion of the specimen, being marked both dorsally and ventrally by distinct ridges. Ventrally, the anterior end of the cristae cranii is visible. The cristae are wide and robust posteriorly, but they narrow towards the anterior end of the bone. There are no anterior processes and therefore the cristae remain low. The ventral surface between the cristae is smooth.

The small premaxillae have a 1.8 mm- (UU MAA 7341) or 2 mm-wide (UU MAA 7076) alveolar plate. They preserve only the alveolar portion of the bone, lacking the entire ascending nasal process and the palatal lamina. Two sub-pleurodont and stocky teeth are present. They have a distinctly swollen and bulbous base, but shrink towards the tip, displaying a sub-conical shape. The anterior surface is smooth, displaying only a small foramen near the right side of the base of the ascending nasal process.

The small maxillae are very fragmentary: only part of the middle portion of the tooth row is preserved in UU MAA 7044, 7045 and 7208, whereas UU MAA 7043 (Fig. A4.5C-D) preserves part of the anterior end. The latter carries 2 sub-pleurodont and canine-like teeth, slightly curved in posterior direction by their tip, followed by 2 small, acrodont and closely spaced teeth. The other specimens, on the other hand, carry 5 (UU MAA 7044), 6 (UU MAA 7045) or 7 (UU MAA 7208) acrodont and closely spaced teeth, whose tooth base is slightly developed towards the medial surface of the alveolar border. In all specimens, the acrodont teeth are triangular and can be provided with small accessory cusps anteriorly and posteriorly to the main one. The lateral process is partly preserved in UU MAA 7043, showing a hint of dorsal development towards the anterior end. Two ventrolateral foramina are visible on the otherwise smooth lateral surface in all specimens but UU MAA 7044.

UU MAA 7042 and 7305 (Fig. A4.5G) represent the anterior portion of the dentary. They preserve the symphysial region and 4 (UU MAA 7305) or 8 (UU MAA 7042) tooth positions. The mandibular symphysis is sub-horizontal in medial view. A high and robust subdental ridge is visible on the medial surface of the bone, posteriorly to it. Ventrally, a narrow and ventrally open Meckelian fossa runs anteroposteriorly. The lateral surface of the bone is smooth, bearing 4 mental foramina. As in the maxillae, two morphologically different kind of teeth are present: anteriorly, there are 2 sub-pleurodont teeth, followed posteriorly by acrodont ones. Among the large sub-pleurodont teeth, only the second one of UU MAA 7305 preserves more than the tooth base: it is conical, with a slightly posteriorly curved tip. The acrodont teeth are very small, closely spaced and poorly preserved in UU MAA 7305, but larger, more spaced, slightly developed towards the medial margin of the alveolar crest and triangular in the other specimen. Accessory cusps are present in the teeth of the latter specimen, together with deep and ventrally directed interdental grooves between them on the lateral surface. UU MAA 7041 (Fig. A4.5E-F) and 7207, on the other hand, preserve the middle portion of the dentary. In medial view, a very narrow Meckelian fossa is visible, opening medially. The fossa is partly covered dorsally by a high and ventrally expanded subdental ridge. The straight ventral margin of the dentary bends in medial direction, originating a ventral floor for the fossa. UU MAA 7041, 7075, 7207 and 7276 bear 3 to 10 acrodont, triangular and closely spaced teeth, provided with a main cusp and two small accessory cusps located anteriorly and posteriorly. The teeth develop slightly in ventral direction on the medial surface of the alveolar shelf. Moreover, they distinctly increase in size posteriorly. The lateral surface is smooth, except for the presence of deep and ventrally directed interdental grooves. UU MAA 7041, 7075 and 7276 display also few mental foramina.

The small fragments of tooth-bearing bones carry acrodont and triangular teeth, with a pointed tip. Accessory cusps can be either present or absent. The tooth base is slightly expanded in ventro-medial direction, towards the medial surface of the tooth-bearing bone. Teeth are usually closely spaced, even if those of UU MAA 7063, 7264 and 7304 are more spaced. Moderately wide and deep interdental grooves separate them in lateral view.

The caudal vertebrae are procoelous and very anteroposteriorly elongated. They have a sub-circular vertebral centrum, a sub-elliptical neural canal and a dorsally smooth neural arch. The zygapophyses are small, elliptical and tilted dorsally at 45°. There are no autotomy plane and no hemapophyses.

Identification

Maxillae and dentaries carrying both pleurodont and acrodont teeth can be confidently assigned to the family Agamidae (Delfino et al. 2008; Blain et al. 2014b; this work). Closely spaced acrodont teeth extending onto the lingual side of the alveolar border are usually used as an argument to support such assignment, in contrast with more spaced and apically located teeth in Chamaeleonidae (Evans et al. 2002; Delfino et al. 2008), but Rage and Bailon (2011) recently doubted this statement based on existing variation within the two families. A certain degree of variation in the spacing between teeth seems to be present in the material from Maramena also, but the general similarity in both teeth and tooth-bearing bones morphology supports the allocation of all the acrodont-tooth-bearing remains to the same taxon. Moreover, Maul et al. (2011) state that the presence of two subpleurodont teeth in both maxillae and dentaries distinguishes the subfamily Agaminae (sensu Macey et al. 2000; Group VI of Moody 1980) from the other agamids. The other remains (i.e., frontal, premaxillae and caudal vertebrae) are congruent in terms of morphology with the agamid specimens studied for this work and therefore are here attributed to the same taxon as the tooth-bearing bones.

Lacertidae Batsch, 1788

Lacertidae indet. (Fig. A4.5H-O) Material:

Maramena 1: 3 maxillae (UU MAA 7031-7032, 7438); 1 quadrate (UU MAA 7096); 3 pterygoids (UU MAA 7097-7099); 16 dentaries (UU MAA 7048-7061, 7095, 7424); 9 fragments of tooth-bearing bone (UU MAA 7087-7092, 7094, 7391); 1 isolated tooth (UU MAA 7392).

- Maramena 3: 1 dentary (UU MAA 7220).

Description

The maxillae are small-sized and very fragmentary. Except for UU MAA 7438, which is represented by the anterior premaxillary process, they preserve only part of the posterior half of the bone and they are 2.3 (UU MAA 7438), 3.5 (UU MAA 7032; Fig. A4.5H) or 4.5 mm (UU MAA 7031) in length. UU MAA 7438 has moderately developed lateral and medial processes, defining a wide, deep and U-shaped anterior concavity. Because of preservational reasons, it is not clear if the medial process either has or misses a lappet. A large vomeronasal foramen is present. The wide superior dental foramen is visible on the dorsal surface of the palatal shelf of UU MAA 7031 and 7032. The specimens bear 3 to 8 tooth positions. The preserved teeth are pleurodont, closely spaced, slender and cylindrical; the most preserved ones have a bicuspid crown. The lateral surface of the bone is smooth, with 1 or 2 ventrolateral foramina; when the second foramen is present, it is distinctly enlarged.

The quadrate (Fig. A4.5I-K) is small-sized, with a length of 3.6 mm. It is straight in anterior view and has a rounded anterior outline in medial view. A deep conch originated by a well-developed lateral lamina is present; the anterior surface of the lamina has a flat anterodorsal platform, bordered medially by a low ridge. A well-developed medial lamina is also present, showing a distinct pterygoid flange by its ventral end. The cephalic condyle is expanded in both posterior and mediolateral directions. The mandibular one is wide in posterior view and is composed by two similar sized portions. A wide and deep squamosal notch is present laterally to the cephalic condyle. Dorsally to the mandibular condyle, the quadrate is pierced by the quadrate foramen.

Pterygoids are very fragmentary and small-sized. The best preserved one, UU MAA 7099 (Fig. A4.5N-O), is 6.7 mm-long, but the other ones are similar in size. Both the palatine process and the pterygoid flange are never completely preserved: only their bases are visible, at different degrees of preservation, in the three specimens. The

most preserved flange is that of UU MAA 7097 (Fig. A4.5L-M), which displays the proximal portions of moderately developed dorsal and ventral ridges. Similar ridges are recognisable on UU MAA 7098 too, but in both specimens the real degree of development of the ridges cannot be defined because of the preservational status. The palatine process, which is more preserved in UU MAA 7097 and 7098 than in UU MAA 7099, has a wide patch with numerous pterygoid teeth on its ventral surface. The quadrate process is almost complete in UU MAA 7099, partly preserved in UU MAA 7097 and missing in UU MAA 7098. It is straight in dorsal view and displays a wide and circular fossa columellae, from which a well-developed pterygoid ridge starts. The basipterygoid fossa is wide and flat. UU MAA 7097 presents a probably pathological tubercle-like osseous proliferation ventrally to the fossa and a ridge-like osseous expansion dorsally to it, running anteriorly towards the dorsal surface of the palatine process.

UU MAA 7049, 7051, 7052, 7053, 7054, 7055, 7056, 7057, 7095, 7220 and 7424 are fragmentary dentaries missing both the anterior and posterior ends. UU MAA 7048, 7050, 7058, 7059, 7060 and 7061 are similar-sized fragmentary dentaries preserving also the symphysial region. The total length of the specimens goes from a minimum of 3.5 mm (UU MAA 7055) to a maximum of 7.4 mm (UU MAA 7048). A moderately high subdental ridge is present medially. UU MAA 7050, 7055, 7056, 7057 and 7220 preserve a wide and medially open Meckelian fossa also. When preserved, the mandibular symphysis is narrow and sub-horizontal. The bones preserve 8 to 17 closely spaced tooth positions. Well-preserved teeth are pleurodont, cylindrical and slender, with mono-, bi- or (only in UU MAA 7049) tricuspid crowns. The lateral surface is smooth, except for some mental foramina. UU MAA 7050, 7055, 7056, 7057, 7056, 7057 and 7220 display a convex ventral margin.

The small and very poorly preserved fragments of tooth-bearing bone preserve closely spaced, pleurodont, slender, cylindrical and bicuspid teeth. The same morphology characterize the isolated tooth, UU MAA 7392.

Identification

Lacertids are easily recognisable because of the presence of an heterodont dentition composed by mono-, bi- and tricuspid teeth (Bailon 1991; this work). Despite the fragmentary nature of most of the specimens, the size seems to indicate the presence of a small species. According to Barahona and Barbadillo (1997), the total length of the most preserved remain, the quadrate UU MAA 7096, fits within the maximum value for A. marchi, Ps. hispanicus and Z. vivipara (3.4 mm) and the minimum one for I. bonnali, I. cyreni, I. monticola, Po. hispanicus, P. bocagei and P. muralis (3.9 mm). This agrees with the clues given by the most preserved pterygoid, UU MAA 7099, whose length is comparable with the range of the latter group of species (6.4 mm - 8.6 mm; Barahona & Barbadillo 1997). These species, however, do not have pterygoid teeth (Barahona & Barbadillo 1997), which are present on larger species instead. It might be possible that the pterygoids from Maramena belong to juveniles of a larger species, but this seems unlikely because of the large number of pterygoid teeth, which are usually scarce or even absent in young individuals (Barahona & Barbadillo 1997, 1998). The fossils from Maramena represent, therefore, an indeterminate small-sized lacertid provided with pterygoid teeth.

Scincidae Gray, 1825

?Scincidae indet. (Fig. A4.5P-Q) Material:

- Maramena 1: 2 dentaries (UU MAA 7027, 7107).

Description

UU MAA 7027 (Fig. A4.5P) is a very small and poorly preserved dentary, roughly 3.5 mm in length. It misses both the anterior and posterior ends. In medial view, a moderately high subdental ridge and a narrow and ventrally open Meckelian fossa are visible. Nine tooth positions are preserved, housing 5 well-preserved teeth plus some more damaged ones. The teeth are closely spaced, pleurodont, slender and

cylindrical. They have a bicuspid crown, with a labial and a lingual cusps, and a pointed tip that is very slightly, not distinctly curved in medial direction. Both the labial and the lingual surfaces of the teeth are smooth, lacking evident striation. The ventral margin is straight in medial view. The lateral surface is smooth, bearing 4 mental foramina. UU MAA 7107 (Fig. A4.5Q) is a very small (total length = 2.5 mm) fragment of dentary. It bears 4 pleurodont teeth that are very similar to those of UU MAA 7027, even if they show light striae on the labial surface of the crown, plus 2 empty tooth positions. In this specimen, the wide alveolar foramen is visible in ventral view. The lateral surface is smooth, with a single mental foramen.

Identification

The tooth morphology of UU MAA 7027 and 7107, with the two parallel cusps, recalls the morphotype F of Kosma (2004). According to the latter author, this morphotype is typical of the Scincoidea (sensu Estes et al. 1988 and Gauthier et al. 2012), that is Cordyliformes (Cordylidae and Gerrhosauridae) and Scincidae sensu lato. Morphotype F teeth are also present in gekkotans (Sumida & Murphy 1987), but their teeth lack striae and are not curved by the tip. Moreover, dentaries of geckos have a closed Meckelian fossa (Evans 2008; this work). Compared to those of the herein described dentaries, cordyliforms have more robust and blunter teeth (Kosma 2004), whereas the more slender, pointed and slightly postero-medially curved morphology of the crown of small-sized scincids (Townsend et al. 1999; Caputo 2004; this work) seems to fit better with the Maramena specimens. Unfortunately, the few remains recovered and their poor preservational status prevents to be more confident with this identification.

Cordylidae Fitzinger, 1826 Palaeocordylus Roček, 1984

aff. *Palaeocordylus* sp. (Fig. A4.5R-W) Material:

- Maramena 1: 25 maxillae (UU MAA 7046-7047, 7077-7086, 7273, 7358, 7362-7365, 7370-7372, 7395-7396, 7437); 57 dentaries (UU MAA 7001-7025, 7034-7036, 7039-7040, 7104, 7108, 7266-7267, 7270, 7279, 7359, 7366-7369, 7397-7401, 7425-7426); 6 fragments of tooth-bearing bone (UU MAA 7037-7038).
- Maramena 3: 1 maxilla (UU MAA 7340); 8 dentaries (UU MAA 7199-7205, 7209); 1 fragment of tooth-bearing bone (UU MAA 7210).

Description

The maxillae are fragmentary and small-sized. UU MAA 7047 (Fig. A4.5R), 7371 and 7372 preserve the anterior end, UU MAA 7046, 7079, 7080, 7362 and 7437 the middle portion of the bone, UU MAA 7077 (Fig. A4.5S) and 7370 the complete posterior end, whereas the other specimens represent only poorly preserved and small portion of the posterior process. The number of preserved tooth positions varies from 4 to 14. The preserved teeth are pleurodont, moderately slender, cylindrical and closely spaced. They have a blunt and strongly postero-medially bending crown, provided with a labial and a lingual longitudinal cusps. The lingual surface of the crown displays a dense and distinct striation, which is on the other hand absent on the labial side. The tooth row reaches the posterior end of the bone, when the latter is preserved. UU MAA 7047 and 7372 preserve the anterior premaxillary process, which is provided with a deep anteriorly directed concavity defined by the short lateral and medial processes. A short lateral process is preserved also in UU MAA 7371. The vomeronasal foramen opens by the base of the anterior premaxillary process, in a shallow concave area, which is bordered medially by a low ridge. A low arched ridge is present on the medial surface of the preserved remnant of the facial process in UU MAA 7046, 7371 and 7372. In UU MAA 7077 and 7370, the posterior process appears moderately short and high in lateral view and has a forked posterior end, because of the presence of a wide and well-developed posterior projection of its dorsal margin; the projection is separated by the ventral

portion of the process by a deep U-shaped notch. The lateral surface is smooth, but UU MAA 7046, 7047, 7077, 7078, 7395 and 7396 display some ventrolateral foramina. Other smaller foramina are scattered on the lateral surface of the facial process in UU MAA 7046 and 7371, whereas UU MAA 7047 displays some grooves. Nevertheless, the latter can be due to taphonomic reasons.

The dentaries (Fig. A4.5T-W) are fragmentary and small-sized. A high subdental ridge is visible in medial view, covering the narrow Meckelian fossa in the anterior half of the bone. In those specimens in which the posterior portion is preserved, the ridge appears to narrow towards its posterior end and the fossa widens. A distinct facet for the articulation with the splenial is visible ventrally to the ridge when the posterior portion is preserved, but its anterior extension cannot be defined because of the fragmentary nature of the fossil material. A narrow and slightly dorsally inclined mandibular symphysis is preserved in UU MAA 7004, 7005, 7006, 7020, 7021, 7022, 7023, 7024, 7025, 7108, 7205, 7266, 7267, 7366, 7367 and 7368. Tooth morphology is the same as in the maxillae. The number of preserved tooth positions goes from 5 to 18. In UU MAA 7001, 7002, 7003, 7017, 7018, 7019, 7036, 7040, 7104, 7204, 7209, 7270, 7279, 7401 and 7426, the wide alveolar foramen is visible in ventral view. The lateral surface of the specimens is smooth, bearing a variable number of mental foramina. The single preserved one of UU MAA 7209 and those of UU MAA 7270 are very large; at least in the latter case, however, this could result from taphonomic processes. When preserved, the ventral margin is straight in medial view.

UU MAA 7037, 7038, 7210 and 7344 are small fragments of indeterminate toothbearing bones. They bear pleurodont teeth, which are similar to the ones described above for maxillae and dentaries in morphology.

Identification

As for the two dentaries assigned to possible scincids (see above), the tooth morphology of these remains resembles Kosma's (2004) morphotype F. In this case, however, the crown is blunt and distinctly bending postero-medially, in contrast with

UU MAA 7027 and 7107 and more similarly to the cordyliform condition. Among cordylids and gerrhosaurids, the dense and strong striation on the lingual surface is a common feature of the former, whereas striae are usually absent or poorly developed in the latter (Kosma 2004). Neogene cordylids from Europe are represented by two different genera: *Bavaricordylus* Kosma, 2004 and Palaeocordylus Roček, 1984. Bavaricordylus was erected in an unpublished work (namely, Kosma's PhD dissertation) and should therefore be considered as unavailable. In any case, the two species assigned to this genus, Bavaricordylus ornatus Kosma, 2004 and Bavaricordylus molassicus Böhme, 2010, clearly differ from the cordylid from Maramena in having a rough lateral surface of the dentary and striae on the labial surface of the teeth. The type species of *Palaeocordylus*, Palaeocordylus bohemicus Roček, 1984 from the early Miocene of Dolnice in Czech Republic, is more similar to the herein described specimens in terms of general morphology of the dentary. However, differences are present in the dentition (see Roček 1984): teeth of *P. bohemicus* are, in fact, more swollen lingually than those of the specimens from Maramena and, at least as far as the posterior teeth are concerned, more distinctly robust. Moreover, teeth of P. bohemicus can rarely be tricuspid and lightly striated on the labial surface according to Roček (1984). Given that, it appears clear that the cordylid from Maramena shares more affinities with Palaeocordylus than with Bavaricordylus, even if some difference is present. It has also to be noted that the herein described specimens from Maramena are very similar in terms of both tooth and general morphology to the right dentary from Merkur-North (early Miocene, Czech Republic) attributed to aff. Palaeocordylus bohemicus by Čerňanský (2012), to the fossils from Ano Metochi assigned to possible cordylids in this work (see also Georgalis et al. 2017a) and to the indeterminate scincoid described by Richter (1995) from the same Maramena.

Scincomorpha indet.

Material:

- Maramena 1: 29 dentaries (UU MAA 7026, 7106, 7357, 7361, 7379, 7402-7404, 7435-7436).
- Maramena 3: 1 dentary (UU MAA 7206).

Description

These dentaries are poorly preserved and very fragmentary. All specimens are smallsized and represented by only part of the tooth row. They display a well-developed and high subdental ridge. The tooth positions are occupied by pleurodont, slender, cylindrical and closely spaced teeth. The latter are either absent or they underwent a strong wearing, preventing us to clearly recognise the main features of the crowns. Identification

A precise identification of these remains is impossible because of their very poor preservational status. Anyway, the combination of pleurodont dentition, open Meckelian fossa and presence of the subdental ridge suggest that they cannot be assigned to Iguania, Gekkota or Anguimorpha and rather belonged to scincomorphan lizards (Evans 2008).

Anguidae Gray, 1825 Anguinae Gray, 1825 *Anguis* Linnaeus, 1758

Anguis sp. (Fig. A4.5X-Z) Material:

- Maramena 1: 36 trunk vertebrae (UU MAA 7181, 7263, 7274, 7280, 7332-7334, 7411, 7418); 1 cloacal vertebra (UU MAA 7269).
- Maramena 3: 2 trunk vertebrae (UU MAA 7217-7218).

Description

Trunk vertebrae are lightly built and small-sized. Centrum length varies from 2.4 mm to 3.7 mm. The vertebral centrum is procoelous and dorso-ventrally compressed.

There is no precondylar constriction. In ventral view, the lateral margins are straight and roughly parallel in the posterior portion of the centrum, slightly diverging anteriorly. The ventral surface is flat. The subcentral foramina goes from small to moderately large. The sinapophyses are dorso-ventrally elongated. The neural canal is subtriangular or subpentagonal. The neural arch bears a well-developed and laminar neural crest, originating a well-developed neural spine posteriorly. The zygapophyses are dorsally tilted at about 45° and subelliptical.

The cloacal vertebra is similar to the trunk vertebrae in both morphology and size. In ventral view, the vertebral centrum has straight and roughly parallel lateral margins in its posterior half.

Identification

These vertebrae can be allocated to *Anguis* because of the dorso-ventrally compressed centrum provided with straight and parallel lateral margins and flat ventral surface and devoid of precondylar constriction (Klembara 1981; Estes 1983). A species-level identification is not possible, because all *Anguis* species described from the Neogene of Europe are based on cranial material (Klembara & Rummel 2016).

Ophisaurus Daudin, 1803

Ophisaurus sp. (morphotype 1) (Fig. A4.5AA-AC) Material:

- Maramena 1: 1 maxilla (UU MAA 7324); 2 dentaries (UU MAA 7176-7177).

Description

The maxilla (Fig. A4.5AA) is small-sized and fragmentary. The total length is 3 mm. It preserves only part of the tooth row, missing part of the anterior end, most of the facial process and the posterior process. On the medial surface of the preserved portion of the facial process, there is the anteroventral part of a low but distinct

arched ridge. The lateral surface is smooth, except for 4 ventrolateral foramina. Teeth are subpleurodont and closely spaced. Five tooth positions are preserved, with 3 rather well preserved teeth. The best preserved tooth is distinctly conical, with a pointed and posteriorly curved tip. Low carinae might be present on the anterior and posterior sides of the crown, but this cannot be confirmed because of its preservational status. There are no striae on the crown.

All the dentaries are fragmentary. UU MAA 7177 (Fig. A4.5AC) is represented only by the middle portion of the bone, whereas UU MAA 7176 (Fig. A4.5AB) misses the anterior end and part of the posterior one (namely, the angular process and the coronoid process). Both specimen are small-sized, roughly 4 mm (UU MAA 7177) and 6 mm (UU MAA 7176) in length. Medially, the subdental shelf covers completely the narrow and ventrally opened Meckelian fossa in UU MAA 7177, whereas it is almost completely broken in UU MAA 7176. The opening of the alveolar foramen, visible only in UU MAA 7176, is located by the posterior-most tooth position. The intramandibular septum does not develop a clear posterior projection and its posteroventral margin is fused to the wall of the Meckelian fossa. Posteriorly to the opening of the alveolar canal, there is a small surangular spine. The surangular process is short and wide. UU MAA 7176 displays 7 tooth positions, whereas only 5 are preserved in UU MAA 7177. Teeth are subpleurodont and closely spaced, with a non-swollen tooth base. Only the posteriormost two are well preserved in UU MAA 7176, whereas a single rather well preserved tooth is present in UU MAA 7177: they are moderately slender and conical, displaying a light but distinct posterior curvature by their tip. Except for the single well preserved tooth of UU MAA 7177 (which displays a very light striation on the lingual side), there are no striae on the crown. The last tooth of UU MAA 7176 presents two very poorly recognisable carinae on the anterior and posterior sides. The crown of the other preserved teeth is too eroded to clearly state the presence or absence of such features. The lateral surface is smooth and displays 3 (UU MAA 7177) or 4 (UU MAA 7176) mental foramina. In UU MAA 7176, part of the articulation surface with the

surangular is visible in lateral view, ventrally to the surangular process. The ventral margin is rather straight.

Identification

According to Klembara et al. (2014), conical and slightly posteriorly curved teeth and a surangular spine on the dentary are diagnostic features of *Ophisaurus* among anguines, whereas an intramandibular septum ending by or near the last tooth position (that is, the alveolar foramen opens there) is typical of Anguis. This might cause a certain degree of uncertainty about the possible identification of the abovedescribed specimens, taking also into account the fact that both Anguis and *Ophisaurus* seem to be present in Maramena based on vertebral morphology. However, the fusion of the intramandibular septum with the wall of the Meckelian fossa is never present in Anguis, whereas it occurs in at least two extant species of Ophisaurus (Klembara et al. 2014): Ophisaurus gracilis and Ophisaurus koellikeri. Because of this, the assignment of UU MAA 7324, 7176 and 7177 to Ophisaurus is here favoured. Ophisauromimus from the Oligocene of France and Germany also has conical and slightly posteriorly curved teeth (Čerňanský et al. 2016a), but this genus is clearly different from the herein considered specimens because of the presence of a broad and plate-like intramandibular septum that is posteriorly free and develops a large posterior projection. The fragmentary nature of the specimens and the fact that most Neogene species of European Ophisaurus are based on parietals preclude a more precise identification.

Ophisaurus sp. (morphotype 2) (Fig. A4.5AD-AG) Material:

Maramena 1: 3 maxillae (UU MAA 7180, 7336-7337); 3 dentaries (UU MAA 7100, 7186, 7439); 1 fragment of tooth-bearing bone (UU MAA 7440).

Description

The maxillae are small and fragmentary, preserving only part of the tooth row. In all specimens, the posterior end is not preserved, whereas only in UU MAA 7180 part of the anterior one is still present (Fig. A4.5AD). Most of the facial process is lacking too. The total length of the specimen goes from 2.5 mm to 3.8 mm. A small vomeronasal foramen located in a shallow concavity is visible anteriorly in UU MAA 7180, whereas UU MAA 7336 preserves the wide superior dental foramen. UU MAA 7180 displays also part of a sharp and low arched ridge on the medial surface of the facial process. Preserved teeth are subpleurodont, closely spaced, slender and conical. They have a pointed and slightly posteriorly curved tip. There are no striae on the crown, but low carinae are present on the anterior and posterior sides at least in UU MAA 7336 and 7337. The lingual side of the tooth base is slightly swollen. UU MAA 7180 carries 7 tooth positions with 2 well-preserved teeth, whereas tooth positions and preserved teeth are respectively 5 and 2 in UU MAA 7336 and 3 and 3 in UU MAA 7337. The lateral surface is smooth in all specimens. Preserved ventrolateral foramina are 5 in UU MAA 7180 and 2 in UU MAA 7336. The dentaries preserve the anterior half (UU MAA 7186; Fig. A4.5AF-AG), the posterior half (UU MAA 7100; Fig. A4.5AE) or only a portion of the middle part of the bone (UU MAA 7439). They are small-sized, roughly 2.4 mm (UU MAA 7439) or 4 mm (other specimens) in total length. In medial view, the narrow and ventrally open Meckelian fossa of UU MAA 7186 and 7439 is completely covered by a welldeveloped subdental shelf. A narrow and sub-horizontal mandibular symphysis is present by the anterior end of the former specimen. On the other hand, the shelf is broken in UU MAA 7100. Four moderately preserved subpleurodont teeth are present in UU MAA 7186, together with 3 empty tooth positions, whereas UU MAA 7100 carries 5 empty tooth positions and a single well-preserved tooth and UU MAA 7439 bears 3 empty tooth positions and 1 well-preserved tooth. Teeth are closely spaced, slender and roughly conical. In UU MAA 7186 and 7439, their tip is missing because of their preservational status, but the crown appears to slightly curve posteriorly, as shown also by the preserved and pointed tip of the tooth of UU MAA

7100. There are no striae, whereas the anterior and posterior carinae are present only in UU MAA 7100 and 7439; however, their absence in the other specimen can also be due to a poor preservation. The tooth base is not distinctly swollen lingually. The alveolar foramen is visible in UU MAA 7100, located between the last and the second to last tooth positions. The intramandibular septum appears to be fused to the wall of the bone. Because of preservational reasons, it is not possible to state either if a surangular spine was present or not. The lateral surface is smooth, but carries 2 (UU MAA 7100 and 7439) or 3 (UU MAA 7186) mental foramina. The ventral margin is straight.

UU MAA 7440 is a small fragment of tooth-bearing bone, carrying 4 subpleurodont, slender, closely spaced and roughly conical teeth. Their tooth base is slightly swollen. There are no striae on the crown, but low carinae are visible both anteriorly and posteriorly at least in the best-preserved teeth.

Identification

The identification of these specimens as belonging to *Ophisaurus* is based on the same criteria used for those assigned to morphotype 1. The two morphotypes are indeed very similar, in particular as far as the position of the alveolar foramen is concerned, but they are kept separated here because of some difference in the tooth morphology (i.e., the less conical and more swollen teeth of the second morphotype). It is possible, however, that these slightly different morphologies are only due to some kind of individual variation and that morphotypes 1 and 2 might represent the same form.

Ophisaurus sp. (morphotype 3) (Fig. A4.5AH) Material:

- Maramena 1: 1 dentary (UU MAA 7313).

Description

UU MAA 7313 is a fragmentary left dentary, preserving part of the posterior portion of the bone, but missing the ventral margin and the posterior processes. It has a wide and laterally open Meckelian fossa, separated from the alveolar shelf by a narrow subdental shelf. The alveolar shelf preserves six tooth positions, with a single wellpreserved tooth and only part of a second one. Another very poorly preserved tooth is present both anteriorly and posteriorly to the five tooth positions. The preserved tooth is subpleurodont, cylindrical and slender; it displays a very slightly enlarged tooth base. The crown is blunt and does not show striae. The alveolar foramen is visible inside the Meckelian fossa ventrally to the preserved teeth, being located at least four teeth before the posterior end of the tooth-row. The intramandibular septum is fused to the wall of the bone, but a very small and shallow groove visible in ventral view can be a suture line. A longitudinal ridge starts by the end of the intramandibular septum and runs in posterior direction along the wall of the bone; this ridge might represent the base of the surangular spine, but because of a breakage by its posterior end, it is not possible to state if it is indeed the case. The lateral surface of the specimen is smooth, except for a mental foramen located anteriorly and a small portion of the articulation surface with the surangular. The total length of the specimen is 4.5 mm.

Identification

The subpleurodont, slender and cylindrical teeth and the possible presence of a surangular spine suggest that UU MAA 7313 can also be referred to *Ophisaurus* (Klembara et al. 2014). The different tooth morphology and the more anteriorly located alveolar foramen, however, clearly distinguish this specimen from the previously described ones.

Ophisaurus sp. (morphotype 4) (Fig. A4.5AI-AJ) Material:

- Maramena 1: 1 dentary (UU MAA 7175).

Description

UU MAA 7175 is a fragment of a dentary, missing the anterior portion, most of the posterior end and the ventral margin. It is small-sized: total length is roughly 6 mm. The subdental shelf is ventrally developed anteriorly, but very narrow posteriorly. A very small splenial spine is present by the end of the expanded part of the shelf, though its tip is broken. The alveolar foramen is located between the 4th and the 5th tooth positions, starting from the posterior end of the tooth row. The intramandibular septum projects posteriorly with a small and pointed projection, which is not fused with the wall of the bone. Nine tooth positions are preserved in the tooth row, carrying 4 rather well preserved teeth. Teeth are subpleurodont, cylindrical and rather slender, with a blunt and apically flat crown and a not-distinctly enlarged base. The crown displays no striae and is not curved posteriorly. The lateral surface is smooth and bears 3 mental foramina.

Identification

UU MAA 7175 is similar to UU MAA 7313 in tooth morphology and therefore it is here assigned to *Ophisaurus* too. A possibly significant difference between these two specimens, however, is found in the unfused intramandibular septum of the former. It has to be noted that Klembara (2015) seems to treat this difference as individual variation in the description of its Anguine morphotype 1 from Merkur-North. The presence of a suture line in UU MAA 7313 can support this view, suggesting that the two specimens might be attributed to the same morphotype.

Ophisaurus sp. (morphotype 5) (Fig. A4.5AK) Material:

- Maramena 1: 1 maxilla (UU MAA 7178).

Description

UU MAA 7178 is a small fragment of maxilla, measuring 2.7 mm in total length. It preserves only a part of the middle portion of the tooth row and of the facial process,

carrying 3 well-preserved teeth. The latter are subpleurodont, closely spaced and cylindrical, with a roughly pointed, labio-lingually compressed and slightly posteromedially bending crown. The tooth crown displays very light striae on the lingual side, whereas the labial one is smooth. A sharp carina is present on both the anterior and the posterior sides of the teeth. In medial view, the teeth appear moderately slender, but slightly thicker than the other morphotypes. Their base is not enlarged. On the medial surface of the preserved portion of the facial process, a very robust and well-developed arched ridge is present, defining ventrally a strongly medially concave area. By the posterior end of the preserved portion of the palatal shelf, the outline of the superior dental foramen is recognisable in dorsal view. The lateral surface of the bone carries 3 large ventrolateral foramina. Dorsally to them, a hint of dermal ornamentation is also visible.

Identification

As for the other morphotypes, tooth morphology suggests that UU MAA 7178 can be attributed to *Ophisaurus* too. However, the clear differences of its dentition lead to its assignment to a fifth morphotype.

Ophisaurus sp. (Fig. A4.5AL) Material:

- Maramena 1: 3 dentaries (UU MAA 7179, 7312, 7343); 41 trunk vertebrae (UU MAA 7173-7174, 7183, 7335, 7412, 7416).
- Maramena 3: 2 trunk vertebrae (UU MAA 7215-7216).

Description

UU MAA 7179 and 7312 are represented by the anterior end of small-sized dentaries. Their total length is roughly 3.6 mm in UU MAA 7179 and roughly 2.5 mm in UU MAA 7312. Both have a narrow and sub-horizontal mandibular symphysis and a very well ventrally developed subdental shelf, which covers completely the narrow Meckelian fossa in medial view. In both specimens, the tooth row preserves 5 tooth positions, with a single well preserved (UU MAA 7179) or poorly preserved (UU MAA 7312) tooth and two other preserved tooth bases. Teeth are subpleurodont and closely spaced. The well-preserved one of UU MAA 7179 is slender, cylindrical and narrows towards the tip, showing an enlarged base. The other preserved bases and the best preserved one of UU MAA 7312 (which misses the crown), however, do not show a clear enlargement. The crown of the well preserved tooth is rather blunt, smooth and not posteriorly curved. The lateral surface is smooth, with 1 (UU MAA 7179) or 2 (UU MAA 7312) mental foramina. The mental foramen of UU MAA 7179 is very large. UU MAA 7343, on the other hand, is a small fragment of a very poorly preserved dentary. It displays a well-developed subdental shelf and 4 subpleurodont and closely spaced teeth. The teeth are very poorly preserved also, but one of them seems to display a rather conical and slender morphology, even if the crown is lacking. The lateral surface is smooth, with 2 mental foramina.

Trunk vertebrae (Fig. A4.5AL) are procoelous, moderately robust and small- to medium-sized. The length of their vertebral centrum goes from 2.3 mm to 4.9 mm. The centrum is dorso-ventrally compressed and has a flat ventral surface, provided with small subcentral foramina. In ventral view, the centrum has a subtriangular shape, with posteriorly converging and laterally concave lateral margins. There is no precondylar constriction. The sinapophyses are dorsoventrally elongated. The neural canal is roughly subtriangular or subpentagonal in anterior view. The neural arch displays a high and laminar neural crest, originating a well-developed (but often broken) neural spine by its posterior end. Zygapophyses are tilted dorsally at about 45° and are subelliptical.

Identification

The trunk vertebrae clearly belong to *Ophisaurus* because of the dorsoventrally compressed and subtriangular vertebral centrum with concave lateral margins, a flat ventral surface and no precondylar constriction (Klembara 1981; Estes 1983). The dentaries are allocated to the same genus because of the presence of subpleurodont, slender and cylindrical or conical teeth (Klembara et al. 2014). The poor

preservational conditions of UU MAA 7343 prevents us to assign it to one of the 5 recognised morphotypes. Teeth of UU MAA 7179 and 7312, on the other hand, are similar to those of both morphotypes 3 and 4, but, since the posterior end is not preserved in these dentaries and the degree of fusion of the intramandibular septum is therefore not definable, they cannot be confidently attributed to either the third or the fourth morphotypes.

Pseudopus Merrem, 1820

Pseudopus sp. (Fig. A4.5AM-AS) Material:

- Maramena 1: 1 maxilla (UU MAA 7171); 1 dentary (UU MAA 7407); 1 fragment of tooth-bearing bone (UU MAA 7307); 2 trunk vertebrae (UU MAA 7172, 7328); 1 cloacal vertebra (UU MAA 7329).
- Maramena 3: 3 trunk vertebrae (UU MAA 7212-7214).

Description

UU MAA 7171 (Fig. A4.5AM-AN) is a fragment of a small maxilla (total length = 4.9 mm) preserving only part of the posterior process. The posterior tip of the process is missing. The lateral surface is smooth and carries 2 ventrolateral foramina, with the posterior-most that is distinctly larger than the other one. A wide superior dental foramen followed by a shallow longitudinal groove is present on the dorsal surface of the palatal shelf. The alveolar border of UU MAA 7171 carries 3 large, very robust and subpleurodont teeth, which decrease in size posteriorly. Their crown is blunt and does not displays distinct cusps. However, this latter feature could be due to weathering. A dense striation surrounds the tip of the teeth.

UU MAA 7407 is a very poorly preserved and fragmentary dentary, with a total length of 3 mm. In medial view, the subdental shelf can be recognised despite the poor preservational status. The specimen carries 5 cylindrical, subpleurodont and
very robust teeth, provided with a flat and blunt crown. Even if all teeth are distinctly eroded, a single and small cusp is still recognisable in the middle of the apical surface of some of them. A light and dense striation surrounds the cusp. The lateral surface of the specimen is smooth.

UU MAA 7307 (Fig. A4.5AO-AP) is a small fragment of tooth-bearing bone, carrying two very robust, cylindrical and subpleurodont teeth. Their tip is rounded, with a single and small cusp in the middle surrounded by a dense striation covering both the labial and the lingual side of the tooth crown.

Trunk vertebrae are robust and small- to medium-sized. The smallest one, UU MAA 7213, has a centrum length of 2 mm, whereas the largest one, UU MAA 7172 (Fig. A4.5AQ-AR), is 4.4 mm in length. The vertebral centrum is procoelous and dorso-ventrally compressed. In ventral view, it is distinctly triangular and devoid of precondylar constriction. The lateral margins are straight in UU MAA 7328 (Fig. A4.5AS), but slightly concave in the other specimens. The ventral surface of the centrum displays a low and wide convexity. The sinapophyses are dorsoventrally elongated. The neural canal is subtriangular or subpentagonal in anterior view. A well-developed neural crest is present on the dorsal surface of the neural arch; it forms a neural spine posteriorly, but the latter is always broken off. The zygapophyses are subelliptical and strongly tilted dorsally (45°).

The cloacal vertebra is very similar to the above described trunk vertebrae in robustness and morphology. Its centrum length is 4.5 mm.

Identification

Robust, cylindrical and striated subpleurodont teeth are one of the main features of the tooth-bearing bones of *Pseudopus* according to Klembara et al. (2014). Trunk vertebrae provided with a dorsoventrally compressed and triangular vertebral centrum, with straight (or concave in small specimens) lateral margins, a convex ventral surface and no precondylar constriction can be attributed to the same genus (Klembara 1981; Estes 1983). A species-level identification is prevented by the poor preservation of the few cranial remains, but the tooth-bearing bones from Maramena

differ clearly at least from those of *Pseudopus ahnikoviensis* from Merkur-North because of the striated teeth (Klembara 2012; Klembara & Rummel 2016).

non-Anguis Anguinae indet.

Material:

- Maramena 1: 188 osteoderms (UU MAA 7160-7170, 7262, 7265, 7268, 7271, 7275, 7306, 7314-7318).
- Maramena 2: 8 osteoderms (UU MAA 7187-7188, 7298).

Description

Osteoderms are usually small-sized and sub-rectangular in shape. The only exception are UU MAA 7160, 7161, 7162, 7163, 7164, 7165, 7166, 7169, 7314, 7315 and 7316, which are strongly larger and more robust than the other ones. The external surface displays a vermicular ornamentation, absent only anteriorly where the smooth gliding surface is located. A low longitudinal keel (sharper in UU MAA 7317 and 7318) runs in the middle of the same surface in many specimens. The inner surface, on the other hand, is smooth.

Identification

Sub-rectangular and keeled osteoderms are found in non-*Anguis* anguines, whereas those of *Anguis* are more rounded and devoid of any keel (Delfino et al. 2011). Because of the absence of clear diagnostic features, it is not possible to assign these osteoderms to either *Ophisaurus* or *Pseudopus*.

Anguidae indet.

Material:

Maramena 1: 1 quadrate (UU MAA 7408); 13 trunk vertebrae (UU MAA 7323, 7410, 7417); 77 caudal vertebrae (UU MAA 7182, 7184-7185, 7272,

7320-7321, 7325-7327, 7330-7331, 7409, 7423); 4 fused caudal vertebrae (UU MAA 7413).

- Maramena 2: 1 caudal vertebra (UU MAA 7301).
- Maramena 3: 4 caudal vertebrae (UU MAA 7211, 7219, 7338).

Description

The quadrate is 4 mm in length. In anterior view, it is straight and narrow. The lateral lamina is short and does not develop a deep and wide conch. A medial lamina is also present, but its margin is broken and so it is not possible to define its total development, as well as the presence or absence of a pterygoid flange. The mandibular condyle is wide and roughly flat, with two similar-sized portions. A quadrate foramen is visible dorsally to it on the anterior surface of the specimen. The cephalic condyle is strongly anteroposteriorly expanded; in medial view, its dorsal surface is flat and slightly convex. The anterior outline of the quadrate is distinctly angular, with an angle of about 90° composed by the cephalic condyle and the straight anterior margin of the bone. A deep squamosal notch is visible in dorsal view.

The small trunk vertebrae are fragmentary and poorly preserved, but they clearly display a dorsoventrally compressed and procoelous vertebral centrum, strongly dorsally tilted (roughly 45°) and subelliptical prezygapophyses and a sub-triangular neural canal. The synapophyses are dorsoventrally elongated.

The caudal vertebrae are medium- or small-sized and procoelous. They have a dorsoventrally compressed centrum and a sub-triangular neural canal. When the posterior portion of the centrum is preserved, the bases of the fused and thin hemaphophyses are present on its ventral surface. The zygapophyses are tilted dorsally at an angle of 45° and are sub-elliptical. A long and sub-cylindrical, though often broken, neural spine is present by the posterior end of the neural arch, when preserved. The transverse processes are usually broken off. The autotomy plane is

usually present, but sometimes it can be secondarily fused (e.g., UU MAA 7321, 7326 and 7327).

UU MAA 7413 is represented by the poorly preserved and fused vertebral centra of 4 small caudal vertebrae. The centra are dorsoventrally compressed and display the bases of fused hemapophyses on the ventral surface.

Identification

The vertebral remains clearly display anguid features, such as the dorsoventrally compressed centrum and, in the caudal vertebrae, the fused hemapophyses and the autotomy plane. The morphology of the quadrate is also congruent with that of anguid quadrates (this work). These specimens are most probably attributable to one of the above mentioned anguine taxa, but they are regarded as indeterminate anguids because of the absence of clear diagnostic characters useful to better allocate them.

Varanidae Gray, 1827 (sensu Estes et al., 1988) Varanus Merrem, 1820

Varanus sp. (Fig. A4.5AT-AX) Material:

- Maramena 1: 6 teeth (UU MAA 7029-7030, 7148-7151); 10 caudal vertebrae (UU MAA 7028, 7278, 7388-7389, 7429-7434).
- Maramena 3: 1 caudal vertebra (UU MAA 7198).

Description

The isolated teeth are labiolingually compressed, conical and slightly posteriorly curved by the pointed tip. The curve is more pronounced in UU MAA 7029. A sharp carina runs along the entire posterior margin; this carina is serrated in all specimens but UU MAA 7029 and 7148. Another, non-serrated carina is present also along the distal portion of the anterior margin, but it becomes less distinct towards the tooth base. This latter carina is more developed and serrated in UU MAA 7029, 7030 and

7151. The tooth base is almost always broken off, but well distinct striae are present on both the labial and the lingual side near the proximal end of the preserved portion of the specimens. The striation is very dense in UU MAA 7030 (Fig. A4.5AT-AU). Except for the latter specimen, the striae correspond interiorly to dentine lamellae projecting inside the pulp cavity. Part of the tooth base is preserved only in UU MAA 7029 and 7148: it shows a spongy structure, formed by a strong development of the lamellae.

The caudal vertebrae are procoelous and medium-sized. Their centrum is dorsoventrally compressed; the best-preserved and largest ones, those of UU MAA 7198 (Fig. A4.5AV-AX) and 7278, are roughly 7 mm and 8 mm in length respectively. In lateral view, the ventral margin of the anterior cotyle is located posteriorly compared to the dorsal one. A distinct precondylar constriction is visible in ventral view. Two robust pedestals for the chevron bone are present on the ventral surface. Only a hint of the base of the pedestrals is recognisable in UU MAA 7028. The neural canal is subtriangular in anterior view. The neural arch is mostly missing (completely absent in UU MAA 7388, but well preserved in UU MAA 7429), but its anterior end is dorsally flattened. Zygapophyses are subelliptical and tilted dorsally at an angle of 45° in anterior view. There is no sign of autotomy plane.

Identification

Varanoid features showed by the isolated teeth include a trenchant and keeled morphology, the presence of plicidentine (i.e., the infolding of dentine lamellae in the pulp cavity), basal striae and spongy tissue by the tooth base (Estes 1983; Bailon 1991; Pianka et al. 2004; Kearney & Rieppel 2006). Among varanoids, the basal striae are more developed towards the tip in varanids than in helodermatids and lanthanotids (Kearney & Rieppel 2006): in this, the specimens from Maramena appear to be more congruent with the former than with the latter. Moreover, the precondylar constriction in the vertebrae is mentioned as a synapomorphy of the family Varanidae by Bailon (1991). Two varanid genera are reported from Europe: *Saniwa* and *Varanus*. One of the main features distinguishing them is the presence

of a pseudozygosphene in the presacral vertebrae of the former (Hoffstetter 1943; Estes 1983). The pseudozygosphene, however, is not present in the caudal vertebrae (Estes 1983) and therefore this feature cannot be used to discriminate between *Saniwa* and *Varanus* when these bones are considered. Anyway, *Varanus* is the only valid varanoid genus currently known from the European Neogene (Delfino et al. 2013) and this view is here followed in assigning the fossils from Maramena to this genus.

Anguimorpha indet.

Material:

- Maramena 1: 1 dentary (UU MAA 7353).

Description

UU MAA 7353 is a small and very poorly preserved fragment of dentary. Teeth are subpleurodont, but not preserved. A well-developed subdental shelf is visible medially.

Identification

The presence of a subdental shelf devoid of subdental ridge is a distinctive feature of anguimorphan lizards (Evans 2008). A more precise identification of this dentary is impossible because of its poor preservational status.

"Lacertilia" indet. (Fig. A4.5AY-AZ)

Material:

Maramena 1: 1 premaxilla (UU MAA 7093); 8 maxillae (UU MAA 7342, 7355-7356, 7360, 7428); 6 dentaries (UU MAA 7103, 7105, 7427); 14 fragments of tooth-bearing bone (UU MAA 7033, 7102, 7311, 7354, 7393, 7405-7406); 3 axes (UU MAA 7346, 7378); 2 cervical vertebrae (UU MAA 7322, 7348); 13 trunk vertebrae (UU MAA 7110, 7345, 7382-7384, 7421); 2

cloacal vertebrae (UU MAA 7380-7381); 9 caudal vertebrae (UU MAA 7310, 7347, 7385-7387, 7390); 3 groups of regenerated caudal vertebrae (UU MAA 7414-7415, 7422); 11 ribs (UU MAA 7111, 7419); 7 humeri (UU MAA 7309, 7352); 2 pelvic girdles (UU MAA 7349, 7376); 14 femurs (UU MAA 7109, 7308, 7351, 7377, 7420); 1 tibia (UU MAA 7350).

- Maramena 2: 1 fragment of presacral vertebra (UU MAA 7299); 1 caudal vertebra (UU MAA 7300).
- Maramena 3: 1 fragment of tooth-bearing bone (UU MAA 7339); 1 caudal vertebra (UU MAA 7221).

Identification

All these remains are either very fragmentary specimens or specimens representing bones lacking significant diagnostic features. They can be therefore identified only as indeterminate lizards.

Among others, UU MAA 7033 (Fig. A4.5AY-AZ) is a very interesting specimen and might deserve a little more attention. It is a small fragment of an indeterminate toothbearing bone, with a total length of 3.4 mm. It preserves only a small part of the tooth row, with 5 tooth positions. Two rather-well-preserved teeth are present: they are pleurodont, slender, cylindrical and closely spaced. Though slightly eroded, their crown shows a tricuspid condition, with a large central cusp and two slightly smaller and similar-sized accessory cusps, located anteriorly and posteriorly to the main one. The accessory cusps are separated from the main one by evident grooves lingually, but this cannot be clearly stated labially because of the wearing. Because of the presence of the two accessory cusps, the crown appears slightly antero-posteriorly enlarged and roughly symmetrical in medial view.

Pleurodont and tricuspid teeth are present in a number of different lizard groups, such as iguanids and many scincomorphans (Montanucci 1968; Kosma 2004; Smith 2006; Augé & Pouit 2012). According to Smith (2006), tricuspid teeth of iguanids differ from those of the other lizards by having developed grooves separating the cusps on the labial surface of the crown. Lacertids usually display a difference in the size of the accessory cusps, with the anterior one that is larger than the posterior one, rather than a symmetrical condition. However, this difference might sometimes be less recognisable or even absent (e.g., in some species of *Gallotia* and *Takydromus*; Kosma 2004). Tricuspid teeth of teiids usually have a mesiodistally enlarged crown and considerable basal cementum (Smith 2006). Because of the fragmentary nature of the specimen and its wearing, UU MAA 7033 is not allocated to one of the different clades of tricuspid-teeth-bearing lizards, waiting for the discovery of other, more preserved remains bearing unambiguous diagnostic features (as e.g., dentaries). It has to be noted, however, that teeth of this specimen are distinctly different from those of the only other specimen bearing pleurodont and tricuspid teeth from Maramena, that is the indeterminate lacertid UU MAA 7049.

<u>Plakias</u>

Amphisbaenia Gray, 1844

Amphisbaenia indet. (Fig. A4.5BA-BD)

Material: 1 trunk vertebra (UU PL 733).

Description

UU PL 733 is a rather small, procoelous vertebra with a centrum length of only 1.2 mm. A slight degree of deformation is recognizable in anterior view. The centrum is dorsoventrally compressed and has a flattened ventral surface and subparallel lateral margins. A massive and rounded synapophysis is visible on the right side of the vertebra. In dorsal view, the neural arch is constricted in the middle. Its dorsal surface is flattened and the neural spine is lacking, as well as the zygosphene. Only the right prezygapophysis is preserved: it is roughly sub-elliptical and tilted dorsally about 30°. The prezygapophyseal process is rather short. Neither the posterior end of the neural arch nor the postzygapophyses are preserved.

Identification

The specimen can be attributed to Amphisbaenia on the basis of the combination of the following characters: small size, dorsoventrally compressed centrum with a flattened ventral surface and roughly parallel lateral margins, short and robust prezygapophyses, massive and rounded synapophyses, absence of zygosphene, and a dorsally flattened neural arch lacking a neural spine (Estes 1983; Delfino 2003). Isolated vertebrae of Amphisbaenia, however, do not show significant diagnostic features that would allow for a more precise identification (Estes 1983).

<u>Tourkobounia</u>

"Lacertilia" Owen, 1842 Agamidae Spix, 1825

Agamidae indet. (Fig. A4.6A) Material:

- Tourkobounia 1: 3 fragments of tooth-bearing bones.

Description

The tooth-bearing bones bear large, stocky and acrodont teeth, which are triangular in shape. Teeth are tricuspid, with a larger central cusp and much smaller anterior and posterior cusps, and close to each other. In medial view, they develop ventrally on the medial side of the alveolar border.

Identification

Even though Rage and Bailon (2011) have recently reported a certain degree of superimposition in the features distinguishing the acrodont dentition of chamaeleonids and agamids, closely-spaced and medioventrally developing acrodont teeth are usually attributed to the latter family (Evans et al. 2002; Delfino et al. 2008). This view is followed here, even if some variation has been detected in the comparative osteological analysis carried out in this thesis also (see Chapter 2).

Gekkota Cuvier, 1817

cf. Gekkota indet. (Fig. A4.6B) Material:

- Tourkobounia 1: 1 dentary.

Description

This small-sized fragment of dentary is about 4 mm in length. Teeth are pleurodont, cylindrical and slender, but crown morphology is not recognizable. The Meckelian fossa is entirely closed in a narrow tubular structure that shrinks anteriorly, originated by the fusion of a ventral expansion of the subdental ridge with the ventral margin. The lateral surface is smooth. A single mental foramen is clearly visible. Identification

Among Neogene and Quaternary European lizards, the complete closure of the Meckelian fossa is found in geckos and in the extant scincid genus *Ablepharus* (Evans 2008; this work). The dentary from Tourkobounia, however, is distinctly larger than the ones of the European representatives of *Ablepharus*, taking also into account that it does not represent a complete bone. Because of this, the tentative attribution of this specimen to an indeterminate gekkotan is herein favoured.

Lacertidae Batsch, 1788 Lacerta Linnaeus, 1758

cf. *Lacerta* sp. (Fig. A4.6C-G) Material:

- Tourkobounia 2: 1 quadrate.
- Tourkobounia 5: 1 maxilla; 1 pterygoid.

Description

The maxilla is represented by a moderately large fragment, whose preserved shelf is 3.8 mm in length. It bears three pleurodont, cylindrical and slender teeth, but three other tooth positions are recognizable. Two of the preserved teeth are bicuspid, whereas the crown of the third one is broken. A moderately developed, arched ridge runs posterodorsally on the median surface of the dorsal process, starting from the medial border of the shelf. A dermal ornamentation is present on the dorsal part of the lateral surface of the preserved portion of the facial process.

The quadrate (Fig. A4.6C-E) is very large-sized, having a total length of at least 7.5 mm (but the cephalic condyle is eroded). The conch is moderately deep, with a robust tympanic crest. The medial lamina present; it was probably rather well developed, but now it is broken. The two portions of the mandibular condyle are roughly similar in size. Anteriorly, the anterior platform is partly lacking, but it seems to be flat. A low but robust ridge borders the platform medially. Given that the dorsal part of the bone is partially broken, it is difficult to recognize its outline, but it seems to be rounded in medial view.

The pterygoid (Fig. A4.6F-G) includes part of the anterior portion and part of the quadrate process. It is 5.8 mm in length. The preserved portion of the quadrate process is straight and bears a large and circular fossa columellae and a wide and flat basipterygoid fossa not marked by flanges. The pterygoid ridge appears well developed. Pterygoid teeth are present in a patch on the ventral surface of the preserved part of the anterior portion (at least 9 teeth, whose size varies from small to large). On the dorsal surface of the preserved portion of the pterygoid flange, the starting of a robust ridge is recognisable.

Identification

The size of these specimens is comparable with that of a large sized lacertid. Because of their preservational status, the most informative element is the quadrate, whose attribution to a lacertid is confirmed by the lateral lamina not projecting anteriorly and originating a well-developed conch, the subrectangular and not medio-laterally expanded shape, the presence of the medial lamina and the not laterally-expanded cephalic condyle (this work). The length of the quadrate exceeds that of most extant European lacertids, reaching the one of the largest representatives of *Lacerta*, but not that of adults of *Timon* (this work). Its belonging to *Timon* can further be excluded because of the flat anterior platform (Barahona & Barbadillo 1997; this work). The size of the other specimens, whose attribution to a lacertid taxon is based on the dentition (as far as the maxilla is concerned) and on a set of features including straight quadrate process, unreduced and anterolaterally directed pterygoid flange, no flanges surrounding the basypterigoid fossa and no strengthening in the middle of the palatine process (for the pterygoid), is also consistent with a tentative identification as *Lacerta* (Bailon 1991; this work). The apparently well-developed pterygoid ridge and the presence of pterygoid teeth might further support this attribution (this work), at least in the case of the pterygoid.

Lacertidae indet. (Fig. A4.6H-L)

Material:

- Tourkobounia 1: 1 frontal; 1 dentary; 1 compound bone.
- Tourkobounia 2: 3 dentaries; 3 fragments of tooth-bearing bone; 3 splenials;
 2 compound bones.
- Tourkobounia 3: 1 frontal; 13 maxillae; 40 dentaries; 2 dentaries articulated with the splenial.
- Tourkobounia 4: 1 dentary.
- Tourkobounia 5: 3 premaxillae; 3 quadrates; 5 pterygoids; 6 dentaries; 2 compound bones.

Description

The maximum length of the frontal from Tourkobounia 1 (Fig. A4.6H-I) is 8 mm, even though it lacks the anterior end and probably also part of the posterior one. The bone is paired, anteroposteriorly elongated and roughly L-shaped, and a distinct middle constriction is visible in dorsal view. A well-developed dermal

ornamentation is present on the dorsal surface, being subdivided into frontal and frontoparietal shields by a transverse groove. On the lateral margin, the articular surfaces with the prefrontal and postfrontal are visible, but they are significantly distant from one another and do not touch each other. The crista cranii is low developed in the posterior portion, but anteriorly forms a well-developed anterior process, whose anteroventral end is missing. The frontal from Tourkobounia 3 is also small and it is represented only by the posterior portion of the bone (total length = 3.5 mm). Its morphology is fully comparable with the other specimen, but the preserved posterior margin displays little interdigitations.

Premaxillae are small-sized; in the largest one, the alveolar shelf is 2 mm-wide. Teeth are pleurodont, cylindrical, slender and monocuspid. Palatal processes are not preserved, but the presence of the incisive process near the base of the nasal process suggests that they were distinctly separated. The ascending nasal process always lacks the dorsal portion; it has parallel lateral margins and a smooth anterior surface. The septonasal crest is distinctly developed and runs along the entire preserved portion of the process. Number of teeth ranges from 5 to 7.

Maxillae are small: the best preserved specimen is 6.9 mm in length. They all bear pleurodont, cylindrical, slender, bi- and tricuspid teeth. In almost all of them, a large superior dental foramen is visible, continuing posteriorly in a deep posterior groove. Three of the best preserved ones show a very low ridge running postero-dorsally from the medial margin of the shelf to the middle of the medial surface of the dorsal process. When the ventral portion of the dorsal process is preserved, it shows a dermal ornamentation on the lateral surface. Two specimens preserve the posterior process: the smallest one shows no step (Fig. A4.6J-K), whereas a moderately steep one seems to be present in the largest bone (Fig. A4.6L).

The small quadrates have a moderately deep conch. The two portions of the mandibular condyle are roughly similar in size. The cephalic condyle is moderately expanded postero-ventrally. A moderately developed medial lamina is present. The

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anterior platform is flattened, and the anterior outline is rounded in medial view. The longest specimen is 3 mm in maximum length.

Pterygoids include the anterior half of the quadrate process and part of the anterior portion. All of them are small, with the maximum length of the longest one that is 3.5 mm. Only the longest one shows few (3) pterygoid teeth. The pterygoid flange is preserved in two specimens: it is small and pointed, with low-developed ridges. The pterygoid crest is rather well developed. The basipterygoid fossa is not marked by flanges.

The poorly preserved fragment of dentary from Tourkobounia 1 is 4 mm-long. It bears pleurodont, cylindrical, slender, bi- and tricuspid teeth. Other dentaries are better preserved, but similarly small-sized (the best-preserved one, in Tourkobounia 3, measures 7 mm). They bear similar teeth, even if monocuspid ones can be also present. A slender subdental ridge is present medially, covering dorsally a rather wide and medially open Meckelian fossa. Some specimens preserve a narrow and subhorizontal mandibular symphysis. When preserved, the ventral margin is convex. Indeterminate tooth-bearing bones bear teeth that are similar to the dentary ones.

Splenials are small, elongated and blade-like, even if the anterior end is always missing. The medial surface bears a well-developed medial crest ventrally and a similarly developed dorsal crest dorsally. The anterior inferior foramen is very much larger than the very small anterior mylohyoid foramen. Both foramina are located in the middle of the bone. These bones are not expanded ventrally.

Only part of the posterior end of the compound bones is preserved. They are small and display a triangular retroarticular process in medial view, provided with a rounded posterior end. There is neither an angular process nor a lateral crest. In medial view, the ventral margin of the bone is straight, not ventrally expanded. Identification

These specimens can be attributed to the family Lacertidae mainly because of the following features (Bailon 1991; Barahona & Barbadillo 1997; this work): frontals paired and elongated, provided with a visible articulation with the postfrontal, a well-

developed anterior process and an interdigitated posterior margin; premaxillae unpaired, unreduced, provided with well-separated palatal process and wide alveolar portion; dentaries provided with medially-open Meckelian fossa, slender subdental ridge and convex ventral margin; splenials with foramina located in the middle of the bone; compound bones without angular process and with a subtriangular and posteriorly-directed retroarticular process; pleurodont and heterodont dentition, with mono-, bi- and tricuspid teeth. Diagnostic features of the quadrates and pterygoids are the same as for the same bones above-identified as cf. *Lacerta* sp., but they cannot confidently assigned to the same taxon because of the distinctly smaller size. The size of the above-described specimens recalls the one of a medium-sized lacertid, but, given the absence of clear adult features, it is not possible to completely exclude that they pertain to juvenile individuals of the larger taxon identified in Tourkobounia. Nevertheless, the presence of both a stepped and an unstepped posterior process in the maxillae might suggest the occurrence of at least two different taxa.

Scincomorpha indet.

Material:

- Tourkobounia 1: 1 dentary.
- Tourkobounia 2: 1 dentary.

Description

These dentaries are small-sized and very poorly preserved. They have a slender subdental ridge, which apparently does not develop ventrally to close the (missing) Meckelian fossa. Only a single, monocuspid tooth is preserved in the specimen from Tourkobounia 1, but tooth positions are reminiscent of a pleurodont, cylindrical and slender dentition.

Identification

These dentaries can be assigned to indeterminate scincomorphans, because of the combination of pleurodont dentition, open Meckelian fossa and presence of the subdental ridge (Evans 2008).

Pseudopus sp. (Fig. A4.6M-N) Material:

- Tourkobounia 1: 1 dentary.

Description

The fragmentary dentary bears two stocky and cylindrical teeth. The latter are subpleurodont, with a rounded apex that apparently does not show striae. The base of a third tooth is visible anteriorly to the other ones. The teeth are close to each other. The rest of the dentary is rather poorly preserved.

Identification

Despite the generally poor preservational status, this dentary is here attributed to *Pseudopus* because of the stocky and cylindrical teeth (Klembara et al. 2014; this work). Tooth crowns are usually striated in *Pseudopus*, but smooth forms are also known (e.g., *Pseudopus ahnikoviensis*; Klembara 2012).

Anguidae indet.

Material:

- Tourkobounia 3: 1 caudal vertebra.

Description

This caudal vertebra is moderately large. Its centrum length is 4.3 mm. There is no autotomy plane and no precondylar constriction. The vertebral centrum is dorso-ventrally compressed and has slightly concave lateral margins. The ventral surface of the centrum is flattened and the bases of the fused hemapophyses are visible. On the dorsal surface of the neural arch, the neural spine is present.

Identification

This vertebra can be assigned to an indeterminate anguid because of the dorsoventrally compressed centrum, the absence of a precondylar constriction and the fused hemapophyses (Estes 1983).

Varanidae Gray, 1827 (sensu Estes et al., 1988) Varanus Merrem, 1820

Varanus sp. (Fig. A4.6O-U) Material:

Tourkobounia 5: 1 maxilla (UU TB5 1001); 1 dentary (UU TB5 1002); 1 tooth (UU TB5 1003).

Description

The maxilla (UU TB5 1001; Fig. A4.6O-Q) is fragmentary, lacking its anterior region (probably the region corresponding to the first three tooth positions) and the posterior tip. The preserved part is moderately robust and 17 mm long. The facial process is not fully preserved, but its anterior, ascending edge develops a medial lamina that shows a distinct ventromedial fold. On the dorsal surface of this fold, there is a wide and slightly anteroposteriorly elongated vomeronasal foramen. The foramen is flanked laterally by a ridge-like structure (a lappet), which marks the dorsal edge of the medial lamina. Because it is broken, the degree of development of this lappet cannot be determined. Because of its presence, however, the vomeronasal foramen opens at the base of the medial side of the anterior premaxillary process. A very low ridge is also visible on the dorsal surface of the lateral margin of the same process. The palatal shelf is broken, but a large superior dental foramen is visible by the posterior end of the fragment. The contact between the ventromedial fold and the palatal shelf forms a large, posteriorly open cavity. Five complete tooth positions are preserved (a sixth position may have been present posteriorly). Two of them house

well-preserved teeth. The most posterior position is occupied by the base of a third tooth. The most anterior, incomplete position bears a small basal portion of another tooth. The teeth are subpleurodont, elongated, conical, and pointed. Their tips are slightly posteromedially recurved and slightly labiolingually compressed, and their bases are slightly swollen lingually. Unserrated carinae are present on their anterior and posterior margins. Striations indicating infolding of dentine are present on the bases both lingually and labially. A spongy tissue connects the teeth to the alveolar portion of the maxilla. The longest tooth is roughly 4 mm in length. The lateral surface of the maxilla is smooth, with a row of six anteroposteriorly aligned ventrolateral foramina near the alveolar margin. Most foramina are small, but the posterior-most one is much larger than the others. Near the anterior end of the maxilla, a rather large foramen opens posterolaterally above the line of ventrolateral foramina.

The fragmentary dentary (UU TB5 1002; Fig. A4.6R-S), lacking the anterior portion and the posterior processes, is 15.7 mm long. The Meckelian fossa is wide and entirely open medially. The subdental shelf is broken, and it is not possible to determine to what extent it originally covered the fossa. Four complete tooth positions and a partial anterior fifth are preserved. The bases of two teeth are preserved. They are connected to the bone by a spongy tissue and show striae on both the lingual and the labial surfaces. The posterior opening of the alveolar canal is located by the last tooth position, and the intramandibular septum continues posteriorly as a ridge fused to the wall of the Meckelian fossa. Although it is partially broken, the superior posterior process appears to bend distinctly dorsally. The lateral surface is smooth, with two large mental foramina. The ventral margin of the dentary is straight in medial view.

The isolated tooth (UU TB5 1003; Fig. A4.6T-U) is subpleurodont, elongated, and conical, with a length of 3.9 mm. It has an enlarged base, a pointed tip, and sharp, unserrated carinae on both the anterior and posterior sides. The distal half of the tooth is labiolingually compressed, whereas the base is slightly swollen lingually. The

latter portion shows distinct striae on both the labial and the lingual surfaces. The contact surface with the tooth-bearing bone is elliptical and oblique, showing a spongy structure.

Identification

Trenchant and keeled or globular teeth, provided with spongy tissue for the connection with their tooth-bearing bone, and striation of the surface of the teeth near their base (indicating the presence of plicidentine, i.e., the infolding of the dentine and enamel at the basal portion of the tooth) are typical features of the clade Varanoidea (e.g., Estes 1983; Bailon 1991; Kearney & Rieppel 2006; Pianka et al. 2004; Luan et al. 2009). Moreover, certain features of the new Greek material exclude its referral to the non-varanid varanoids (helodermatids, necrosaurids, and lanthanotids). In Heloderma, striae due to the development of plicidentine are less extended towards the tip of the teeth in comparison with Varanus (Kearney & Rieppel 2006). In addition, the spongy tissue at the tooth base of helodermatids does not fully close the pulp cavity, as it does in Varanus and in the isolated tooth described herein (Kearney & Rieppel 2006). In Lanthanotus, striae are less developed towards the tip, whereas the shapes of the teeth, maxilla, and the dentary are very different to those of the new fossil material (McDowell & Bogert 1954; Kearney & Rieppel 2006). In necrosaurids, the presence of plicidentine is highly probable, but the anatomy of the maxilla and the dentary, and dental shape, is distinct (Augé 2005; Augé & Smith 2009). Moreover, in terms of the European fossil record, lanthanotids are totally absent, whereas helodermatids and necrosaurids are confined strictly to the Paleogene (Rage 2013). Within varanids, European fossils have only been attributed to the genera Saniwa and Varanus. The differentiation between the two is mostly based on stratigraphic rationale and osteological features of bones other than maxillae or dentaries, but a longer posterior process of the maxilla is generally present in Saniwa (Estes 1983). In any case, members of Saniwa are completely absent from Europe after the Eocene (Augé 2005), and Varanus is the only valid varanoid genus that has been reported from European Neogene localities

to date (Delfino et al. 2013). Varanus is also the sole recognized genus of Ouaternary and extant varanids (Pianka et al. 2004). Furthermore, the morphology of the Tourkobounia 5 specimens is consistent with the morphology of *Varanus*, so the material can be confidently referred to this genus. The morphology of the maxilla is different from that of the two extant species that could have potentially extended their range to Greece in the Middle Pleistocene: Varanus niloticus (Linnaeus, 1766) and Varanus griseus (Daudin, 1803). The former is characterized, along with all the other African taxa (Varanus ornatus (Daudin, 1803), Varanus exanthematicus Bosc, 1792, and Varanus albigularis Daudin, 1802), by posterior globular teeth in adult individuals (D'Amore 2015), whereas V. griseus, among others, is characterized by the absence of the medial lamina that is clearly developed in UU TB5 1001 on the sloping anterior edge of the facial process. The presence of this lamina in UU TB5 1001 is congruent with that of the extinct Varanus marathonensis Weithofer, 1888, from the late Miocene of Pikermi (also near Athens), as well as that of several extant Asian taxa, but the preservational status and the poor knowledge of the osteology of extant species precludes any specific identification.

"Lacertilia" indet.

Material:

- Tourkobounia 1: 1 pterygoid; 1 cervical vertebra; 8 caudal vertebrae; 5 humeri; 13 femurs; 1 tibia.
- Tourkobounia 2: 1 prefrontal; 1 pterygoid; 2 fragments of tooth-bearing bones; 3 coronoids; 1 compound bone; 1 axis; 5 trunk vertebrae; 3 cloacal vertebrae; 6 caudal vertebrae; 3 scapulocoracoids; 32 humeri; 6 ulnae; 16 pelvic girdles; 41 femurs; 14 tibiae.
- Tourkobounia 3: 1 quadrate; 3 trunk vertebrae; 7 caudal vertebrae; 2 humeri;
 1 pelvic girdle; 5 femurs; 1 tibia.

Tourkobounia 5: 1 maxilla; 7 quadrates; 3 pterygoids; 2 ectopterygoids; 1 dentary; 9 coronoids; 4 trunk vertebrae; 1 cloacal vertebra; 12 caudal vertebrae; 20 humeri; 1 ulna; 1 ilium; 2 pelvic girdles; 32 femurs; 13 tibiae.

Identification

A large number of specimens are identified only as pertaining to indeterminate lizards. It is possible, though, that at least the large-sized elements might be attributable to the large-sized lacertid from Tourkobounia.

Other Greek localities "Lacertilia" Owen, 1842 Agamidae Spix, 1825

Agamidae indet. (Fig. A4.6V-X) Material:

- Kastoria: 3 fragments of tooth-bearing bones.
- Maritsa A: 2 fragments of tooth-bearing bones.
- Pili B: 1 trunk vertebra; 1 caudal vertebra.
- Rema Aslan 1: 1 maxilla; 2 fragments of tooth-bearing bones; 1 caudal vertebra.
- Vevi: 1 fragment of tooth-bearing bone.

Description

The maxilla (Fig. A4.6V-W) is represented only by a small fragment of the anterior end, carrying a subpleurodont, large and canine-like tooth.

The tooth-bearing bones bear large, acrodont and triangular teeth, which are very close to each other. Small accessory cusps are present by the sides of the main one on the crown, but they are very poorly recognizable. The tooth base extends ventrally on the medial surface of the alveolar border. Only one of the specimens from Rema

Aslan carries a large, canine-like, slightly posteriorly curved and subpleurodont tooth, together with a small acrodont one (Fig. A4.6X).

The trunk vertebra is large. It has a procoelous centrum, which is slightly dorsoventrally compressed and 5.5 mm-long. The anterior cotyle is inclined ventrally. There are no keels or other structures on the ventral surface, which is ventrally convex. In ventral view, the anterior portion of the centrum is strongly expanded laterally. The synapophyses are small and circular. Pre- and postzygapophyses are large, subquadrangular and inclined at about 45° in dorsal direction. There is no constriction in the middle of the arch, but strong and well developed postzygoprezygapophyseal laminae are present. The dorsal surface of the arch is flattened. The neural crest is present and well developed, forming a neural spine posteriorly. Neither a zygosphene nor a zygantrum are present.

The caudal vertebra from Pili B is very narrow and elongated. The procoelous centrum is slightly dorso-ventrally compressed. There is no autotomy plane. A very low neural crest is present on the flat dorsal surface of the neural arch, but it does not originate a neural spine. The caudal vertebra from Rema Aslan 1 is represented only by the anterior end, but it is fully comparable in morphological terms with the other specimen.

Identification

Tooth-bearing bones of agamids are identifiable based on the presence of both subpleurodont and acrodont teeth (Evans et al. 2002; Delfino et al. 2008; this work). The latter are usually closely-spaced and extend on the medial surface of the bone (but see Rage & Bailon, 2011, for a criticism on the validity of these features). The general morphology of both trunk and caudal vertebrae is very similar to those of the respective bones described by Delfino et al. (2008) from Italy and by Blain et al. (2014b) from Spain, in both cases attributed to agamids.

Gekkota Cuvier, 1817 Gekkonidae Gray, 1825

Hemidactylus Oken, 1817

Hemidactylus turcicus (Linnaeus, 1758) (Fig. A4.6Y-Z) Material:

- Liko BA: 1 frontal.

Description

This frontal is unpaired, T-shaped and displays fused cristae cranii arranged in a tubular structure. The anterolateral processes are present by the anterior end, although poorly preserved. On the other hand, there is no anteromedial process. The anterolateral processes are covered dorsally by the articular surface with the nasals. A light ornamentation made up of grooves is visible on the dorsal surface of the bone. There are no lateral grooves on the posterior portion of the dorsal surface. The posterolateral processes are long and slender. The posterior margin of the bone is straight. Laterally, the articular surface with the maxilla and the prefrontal is moderately large, whereas the one with the postorbitofrontal is small. They are very far from each other. A single anterior process is preserved ventrally: it is very short and drop-like-shaped in anterior view. The length of the bone is 7 mm.

Identification

An unpaired and T-shaped frontal with cristae cranii forming a tubular structure reveals the occurrence of a gecko in Liko BA (Evans 2008; this work). Among European gekkotans, the faint ornamentation on the dorsal surface is a diagnostic feature of *H. turcicus* (this work). The frontal from Liko is therefore attributed to this species.

Gekkota indet. (Fig. A4.6AA) Material:

- Maritsa A: 4 dentaries; 1 fragment of tooth-bearing bone.

Description

All these small tooth-bearing bones, dentaries included, bear slender, cylindrical, pleurodont and bicuspid teeth provided with two parallel and longitudinal cusps. The crown is dorsally pointed and unstriated. In the highly fragmentary dentaries, the Meckelian canal is closed in a tubular structure that shrinks anteriorly.

Identification

Both the tooth morphology and the closed Meckelian fossa allow the attribution of these specimens to indeterminate gekkotans (Sumida & Murphy 1987; Evans 2008; this work), but a more precise identification is impossible due to their preservational conditions.

Lacertidae Batsch, 1788

Lacertidae indet. (large-sized taxon) (Fig. A4.6AB-AJ) Material:

- Arnissa: 1 jugal; 1 postfrontal; 1 pterygoid; 1 ectopterygoid; 3 dentaries; 2 fragments of tooth-bearing bones; 1 trunk vertebra.
- Liko A: 3 dentaries.
- Liko BA: 1 premaxilla.
- Liko C: 1 dentary.
- Spilia 3: 1 premaxilla.

Description

Both premaxillae are large-sized: the width of the dental shelf is 3.9 mm in the specimen from Liko BA (Fig. A4.6AB-AC) and at least 2.5 mm in the one from Spilia 3 (which is broken, though; Fig. A4.6AD-AE). In the premaxilla from Liko BA, the rather long ascending nasal process has roughly parallel lateral margins, even if a light lateral expansion seems to be present at mid-height. The premaxilla from Spilia 3, on the other hand, has a rather short and leaf-shaped ascending nasal

process. On the external surface, a strong dermal ornamentation covers the distal half of the process. On the internal surface, the septonasal crest is rather sharp; it reaches the dorsal end of the process only in the specimen from Spilia 3. The alveolar portion bears 9 (Liko BA) or at least 5 (Spilia 3) pleurodont, cylindrical and slender teeth, none of which is well preserved. The palatal process are well separated by a middle V-shaped notch, in which the incisive process is lodged.

The moderately large-sized and L-shaped jugal (Fig. A4.6AF-AH) displays a welldeveloped dermal ornamentation on the lateral surface. The articulation surface covers almost entirely the anterior part of the anterior process. Although broken at the end, the quadratojugal process is well developed. On the medial side of the bone, the palatal process is well-developed, and presents a moderately distinct medial process. Most of the rather slender posterodorsal process is missing.

The fragment of postfrontal preserves only the anteromedial corner. It is rather large and displays a well-developed dermal ornamentation on the dorsal surface. The anteromedial process is rather long and medio-laterally expanded.

The pterygoid (Fig. A4.6AI-AJ) is large, having a maximum length of the preserved portion reaching up to 7 mm. Pterygoid teeth arranged in a line are present, but in a moderately low number. The pterygoid recess is deep. The palatine process is flattened, with a rather robust medial margin. Ridges on the pterygoid flange are very well developed, particularly the ventral one. The quadrate process is almost entirely broken off, only its base is preserved. The fossa columellae is very large, very deep and circular in dorsal view The basipterygoid fossa is large and flattened.

The ectopterygoid is large and roughly L-shaped. Both anterolateral and posteromedial processes miss their tips, but the latter seems to be longer than the former. The posterolateral process is short. The ventral surface of the anterolateral process is completely covered by the articulation surface with the maxilla.

Most of the dentaries are represented by large-sized fragments bearing pleurodont, cylindrical, slender, bi- or tricuspid teeth. The Meckelian fossa is large and mediallyopened. The best preserved fragment is 6.7 mm-long. One of the specimens from Liko A and the dentary from Liko C are better preserved, missing only the posterior end. Their tooth row reaches 14.7 mm and 11 mm in total length, respectively. A distinct posterior increase in the robustness of the teeth is visible, at least in the specimens from Liko A.

The large-sized fragment of indeterminate tooth-bearing bone bear pleurodont, cylindrical, slender and bicuspid or tricuspid teeth.

The trunk vertebra is rather large (centrum length = 3.5 mm). It is slightly anteroposteriorly elongated and has a subcircular centrum, with a large, low, but distinctly developed keel on the ventral surface. A well-developed neural crest and a well-developed neural spine are present on the dorsal surface of the neural arch. Identification

Based on their morphology, the above described specimen can be assigned to a lacertid whose size is comparable with that of a large taxon such as Lacerta (Barahona & Barbadillo 1997; this work). Timon usually reaches a distinctly larger size, and, at least as far as the pterygoid is concerned, it has a shallow pterygoid recess (Barahona & Barbadillo 1997; this work). Even though the leaf-shaped ascending nasal process of the premaxilla from Spilia 3 and the expanded anterolateral process of the postfrontal from Arnissa are distinctive features of Lacerta (but they are found in Timon too; Barahona & Barbadillo 1997; this work), a completely confident attribution of all these specimens to this genus is hindered by other features. The ascending nasal process of the premaxilla from Liko BA has parallel lateral margins: this might be considered as a juvenile/subadult feature in a bone of Lacerta (or Timon), but this seems to be unlikely, since the large size of the specimen and the presence of a well-developed dermal ornamentation suggest that this might be an adult. Moreover, among extant European lacertids, a distinct medial process is usually present only in jugals of *Psammodromus*, with other genera that sometimes display a little-developed one (Barahona & Barbadillo 1997; this work). The medial process of the jugal from Arnissa seems to be rather intermediate between these two morphologies, and therefore the identification of the bone is

difficult. Given that, the taxonomic assignment of these Greek remains appears to be complicated, and therefore they are here attributed only to indeterminate large-sized lacertids. The observed morphological feature might also suggest that more than one taxon is represented.

Lacertidae indet. (Fig. A4.6AK-AR) Material:

- Anabussos: 1 maxilla; 8 dentaries.
- Arnissa: 3 premaxillae; 5 maxillae; 6 dentaries; 1 dentary articulated with the splenial; 2 fragments of tooth-bearing bones.
- Kaiafa: 10 maxillae; 1 quadrate; 16 dentaries; 25 fragments of tooth-bearing bones; 1 fragment of lower jaw.
- Karpathos: 1 fragment of tooth-bearing bone.
- Lefkon 1: 3 maxillae; 8 dentaries; 1 fragment of tooth-bearing bone.
- Milatos 3: 1 dentary.
- Notio 1: 1 dentary.
- Rema Marmara 2: 2 dentaries.
- Spilia 4: 1 fragment of tooth-bearing bone.
- Tomea Eksi 1: 1 premaxilla.
- Tomea Eksi 2: 1 fragment of tooth-bearing bone.
- Trilofon: 1 dentary.
- Xeros: 1 dentary.

Description

The premaxillae are small. In all of them, the palatal processes are well separated by a moderately wide incisive process. Teeth are pleurodont, cylindrical, slender and monocuspid. The septonasal crest is distinctly developed and runs along the entire length of the nasal process. In the specimens from Arnissa, the morphology of the ascending nasal process varies: in the first specimen, it is narrow and pointed, with parallel lateral margins (number of tooth positions = 7; width of the shelf = 1.6 mm; Fig. A4.6AK-AL); in the second one, it is similar, but slightly larger by its base (number of tooth positions = 7; width of the shelf = 1.7 mm; Fig. A4.6AM-AN); in the third one, it also has parallel lateral margins, but the process is larger than in the former specimen, and lacks the dorsal end (number of tooth positions = 7; width of the shelf = 1.9 mm; Fig. A4.6AO-AP). The ascending nasal process of the premaxilla from Tomea Eksi 1 has roughly parallel lateral margins (Fig. A4.6AQ-AR). The external surface of the process is smooth, except for the specimen from Tomea Eksi 1, which is ornamented, and maybe for the largest one from Arnissa, which seems to show a very poorly developed dermal ornamentation (however, this could be an artifact due to taphonomic processes).

The maxillae are small, fragmentary and bear pleurodont, cylindrical, slender and bicuspid teeth. When preserved, the vomeronasal foramen is housed in a shallow anteriorly-directed concavity, whereas anterolateral and anteromedial processes are little developed. In one specimen from Kaiafa, a lappet is visible on the anteromedial process. Except for 3 specimens from Kaiafa, no specimen bears ornamentation on the external surface of the facial process. A large infraorbital foramen is present on the dorsal surface of the shelf, followed by a large groove. An arched ridge can be visible on the medial surface of the facial process, when the related part of the bone is preserved.

The quadrate is small-sized, reaching up to 3.2 mm in length. It has a deep conch laterally, and a low medial lamina medially. The pterygoid flange is almost indistinct. In anterior view, the quadrate is subrectangular. The cephalic condyle develops posteroventrally. The anterior outline of the bone is rounded in medial view and the anterior platform is flat.

Dentaries are medium- to small-sized. Teeth are pleurodont, cylindrical, slender, mono-, bi- and tricuspid. The Meckelian fossa is medially opened and wide. When preserved, the mandibular symphysis is narrow and subhorizontal. A narrow subdental ridge is present medially. The ventral margin is convex in medial view.

The dentary articulated with the splenial from Arnissa is similar to the other ones described above. The highly-fragmentary splenial was anteroposteriorly elongated and blade-like. Part of a large anterior inferior foramen is still recognisable. The whole specimen is about 5 mm in length.

The small fragments of tooth-bearing bone bear pleurodont, cylindrical, slender and bicuspid teeth. Some of them seem to show a slight degree of hypertrophy.

The fragmentary lower jaw from Kaiafa includes the posterior portion of the dentary (except for the ventral posterior projection), part of the splenial, the anterior part of the coronoid and a very small portion of the compound bone. The dentary bears pleurodont, cylindrical, slender, bi- and tricuspid teeth and has a large and medially opened Meckelian fossa. The splenial is large. The anterior inferior foramen is very large and is placed dorsally to the much smaller anterior mylohyoid foramen. The complete length of the fragment is 6.5 mm, whereas the length of the preserved portion of dental shelf is 3.5 mm.

Identification

These specimens can also be attributed to lacertid lizards, like the large ones described above, but they are distinctly smaller in size, therefore possibly representing either medium- or small-sized taxa or juveniles of the large ones. A specific or even generic identification is not possible, but the presence of morphological differences (as e.g., in the premaxillae) might suggest the presence of different taxa.

Scincidae Gray, 1825 *Ophiomorus* Duméril & Bibron, 1839

aff. *Ophiomorus* sp. (Fig. A4.6AS-AT) Material:

- Kaiafa: 1 dentary.

Description

The dentary has a straight ventral margin in lateral view and is small-sized. The length of the dental shelf is 5 mm. The Meckelian fossa is opened all along the bone, but in its anterior part it is represented only by a ventrally directed groove, not clearly visible in medial view. A moderately high subdental ridge is present. The mandibular symphysis is very narrow and almost horizontal. Although broken, the posterior portion of the bone (posteriorly to the dental shelf) bends distinctly in dorsal direction. The teeth are pleurodont, cylindrical, and moderately slender; their crown is always rather eroded. The number of tooth position is 15. The lateral surface of the bone is smooth, carrying 5 mental foramina.

Identification

The following combination of characters identifies this specimen as a scincid dentary (this work): open and posteriorly-wider Meckelian fossa, presence of a moderately high subdental ridge, pleurodont and cylindrical dentition and straight ventral margin. Among extant European scincids, a dorsal bending of the superior posterior process is diagnostic for *O. punctatissimus* (this work). Nevertheless, the dentary from Kaiafa differs from *O. punctatissimus* in having less robust teeth and a larger size (this work). Given that, it is only tentatively assigned to aff. *Ophiomorus* sp.

Scincidae indet. (Fig A4.6AU-AV) Material:

- Notio 1: 1 dentary.

Description

This dentary misses both the anterior and posterior ends. It is small-sized, and the preserved portion is 4.3 mm-long. The Meckelian fossa is medially-opened in the posterior part of the fragment, but anteriorly it is enclosed in a very narrow tubular structure. This structure origins from a ventral expansion of the slender subdental ridge. The fossa is narrow, although the ventral margin of the wall is broken. Teeth

are pleurodont, cylindrical and slender; when preserved, their crown is dorsally rounded and displays a labial and a lingual longitudinal cusps (Fig A4.6AV). Light striae seem to be visible on the lingual side of the crown. The lateral surface is smooth, except for a single mental foramen.

Identification

The tooth morphology of the poorly preserved dentary from Notio 1 recalls the common scincid dentition, characterized by bicuspid crowns provided with longitudinal cusps and a light lingual striation (Townsend et al. 1999; Kosma 2004; this work). The partial closing of the Meckelian fossa due to a ventral expansion of the subdental ridge is also a feature that is sometimes present in scincid dentaries (Caputo 2004; this work). Due to the incomplete preservational status, a precise identification at either species or genus level is not possible, but the partial opening of the Meckelian fossa differs this specimen from *A. kitaibelii* and the slender teeth distinguish it from both *C. ocellatus* and *O. punctatissimus* (this work).

Scincomorpha indet.

Material:

- Anabussos: 3 dentaries.
- Arnissa: 5 dentaries.
- Kaiafa: 16 dentaries.
- Maritsa A: 1 dentary.
- Notio 1: 2 dentaries.
- Xeros: 1 dentary.

Description

These dentaries are small and very fragmentary. They carry pleurodont, cylindrical and slender teeth, whose crown is too much eroded to recognize the morphology. A narrow subdental ridge is present on the medial side of the bone.

Identification

Despite their fragmentary and poorly preserved nature, it is possible to state that these dentaries pertain to scincomorphan lizards due to the presence of a subdental ridge (Evans 2008).

Anguidae Gray, 1825 Anguinae Gray, 1825 *Anguis* Linnaeus, 1758

Anguis sp. (Fig. A4.6AW-AY) Material:

- Arnissa: 4 trunk vertebrae; 2 osteoderms.
- Notio 1: 2 trunk vertebrae.

Description

The trunk vertebrae are moderately small, with the centrum length of the biggest one that is 4.7 mm. The centrum is strongly dorso-ventrally compressed and has a flat ventral surface. In ventral view, the lateral margins of the posterior half of the centrum are subparallel. The vertebrae are procoelous and elongated and their neural arch is slightly constricted in the middle. Well-developed neural crest and neural spine are present.

Osteoderms are small, thin and suboval. The external surface shows a vermicular ornamentation, but no keel.

Identification

The identification of *Anguis* remains in Arnissa and Notio 1 is based on the dorsoventrally compressed vertebral centrum with parallel lateral margins and the small, rounded and unkeeled osteoderms (Klembara 1981; Holman 1998).

Pseudopus Merrem, 1820

Pseudopus sp. (Fig. A4.6AZ-BA) Material:

- Kaiafa: 1 fragment of tooth-bearing bone; 1 trunk vertebra; 5 osteoderms.
- Kastoria: 2 trunk vertebrae.

Description

The fragment of tooth-bearing (Fig. A4.6AZ) bone is very small, preserving only 2 tooth-positions. It is roughly 2 mm in length. A single subpleurodont, cylindrical and stocky tooth is preserved; its crown is striated, dorsally rounded and has a single point in the middle. The base of a second tooth is also present.

The trunk vertebrae (Fig. A4.6BA) are robustly-built and very large-sized. The one from Kaiafa has a total centrum length of 11.6 mm, whereas those from Kastoria are smaller. The centrum is dorsoventrally compressed and has a flat ventral surface and strongly posteriorly-convergent lateral margins. In ventral view, the lateral margins are straight, except for the smaller vertebra from Kastoria, in which these margins are laterally concave. There is no precondylar constriction.

Osteoderms are very large and thick, with a vermicular ornamentation on the external surface (except for the smooth gliding surface). Four of them show a low longitudinal ridge running in the middle of the same surface.

Identification

All these specimens can be clearly referred to *Pseudopus*. Important features on which the identification is based are the cylindrical, stocky and striated dentition, the robust and large vertebrae with a dorsoventrally compressed centrum provided with straight and posteriorly-convergent lateral margins and the large, thick and keeled osteoderms (Klembara 1981; Holman 1998; Klembara et al. 2014; this work). The laterally concave margins of the smaller vertebra from Kastoria suggest that such specimen pertained to a juvenile individual (Klembara 1981).

cf. Pseudopus sp. (Fig. A4.6BB-BD)

Material:

- Pili B: 1 caudal vertebra; 1 osteoderm.

Description

The caudal vertebra (Fig. A4.6BB-BD) is procoelous, very large (centrum length is roughly 7 mm, but the posterior condyle is missing) and robustly built. The proximal portions of fused hemapophyses are present on the ventral surface of the posterior half of the centrum. In anterior view, the neural canal is distinctly narrower than the cotyle. The dorsal surface of the neural arch lacks a neural crest, but a well-developed neural spine is present. Zygapophyses are large and tilted dorsally at an angle of roughly 45°. There is no autotomy plane.

The osteoderm is large and thick, with an external surface covered by a vermicular ornamentation, except for the smooth gliding surface anteriorly.

Identification

These specimens are tentatively assigned to the anguid genus *Pseudopus* because of the large size and the robust aspect. This attribution might be supported by the absence of autotomy plane in caudal vertebrae of *P. apodus* reported by Etheridge (1967), even if this statement seems to be sometimes not valid (e.g., the plane is present in the two specimens stored in the Department of Earth Sciences of the University of Torino, MDHC 214 and 215).

non-Anguis Anguinae indet.

Material:

- Karydia 2: 7 osteoderms (UU KR2 5006/5013).
- Komanos 1 High A: 1 osteoderm.
- Lefkon 1: 9 osteoderms.
- Spilia 4: 2 osteoderms.

Description

Osteoderms are large, thick and robust. Only those from Karydia 2 are smaller, but still robustly-built. The external surface shows a smooth gliding portion and a vermicular ornamentation on the rest of the surface. A well evident longitudinal keel crossing the external surface in the middle is present in some specimens.

Identification

Among anguines, osteoderms of Anguis are recognisable because of their thinness, small size and the absence of keel (Holman 1998). Given that, these specimens are here attributed to indeterminate non-*Anguis* members of the subfamily.

Anguidae indet.

Material:

- Kaiafa: 1 caudal vertebra.
- Notio 1: 2 caudal vertebrae.

Description

The caudal vertebra from Kaiafa is represented only by the anterior portion. It has a dorsoventrally compressed centrum. The other specimens are small-sized (centrum length varies from 2.9 mm to 4 mm) and provided with a dorsoventrally compressed centrum, which shows the bases of the hemapophyses on the ventral surface. There is no precondylar constriction. The neural arch has a developed neural crest.

Identification

These caudal vertebrae are assigned to indeterminate anguids because of the dorsoventrally compressed centrum, the absence of precondylar constriction and the presence of fused hemapophyses.

Varanidae Gray, 1827 (sensu Estes et al., 1988)

cf. Varanidae indet. (Fig. A4.6BE) Material: - Spilia 4: 1 tooth.

Description

This isolated tooth misses its proximal part. The preserved portion is 3.1 mm in length. The tooth is strongly labiolingually compressed, slightly curved posteriorly, canine-like and pointed. It is smooth, without longitudinal grooves. Two slightly serrated carinae are present on the anterior and posterior margins, the posterior one being more serrated than the other one.

Identification

The single and partial tooth from Spilia 4 is tentatively attributed to an indeterminate monitor lizard because of the overall similarity between it and the general morphology of varanid teeth (labio-lingual compression, presence of serrated carinae, posterior bending). Nevertheless, the attribution cannot be confidently confirmed because of the missing tooth base, whose absence hinders the recognition of the main apomorphy of varanoid teeth (namely, the presence of plicidentine; Estes et al. 1988; Kearney & Rieppel 2006).

"Lacertilia" indet.

Material:

- Agia Loucas: 2 fragments of tooth bearing bone; 1 caudal vertebra.
- Anabussos: 1 maxilla; 5 fragments of tooth-bearing bones; 1 femur.
- Apolakkia 2: 1 femur.
- Arnissa: 3 maxillae; 1 quadrate; 8 fragments of tooth-bearing bones; 1 axis;
 12 trunk vertebrae; 10 caudal vertebrae; 2 humeri; 1 fragment of pelvic girdle; 1 femur; 2 tibiae; 1 phalanx.
- Biodrak: 1 premaxilla.
- Kaiafa: 1 maxilla; 1 dentary; 6 fragments of tooth-bearing bones; 1 caudal vertebra; 1 vertebral centrum; 1 humerus; 1 femur.
- Karpathos: 1 fragment of tooth-bearing bone.
- Kastoria: 2 vertebrae.
- Lefkon 1: 1 premaxilla; 1 caudal vertebra; 1 humerus; 1 pelvic girdle.
- Liko A: 2 trunk vertebrae.
- Liko BA: 2 trunk vertebrae.
- Limni 6: 1 caudal vertebra.
- Maritsa A: 1 maxilla; 1 dentary; 1 fragment of tooth-bearing bone.
- Monasteri: 1 dentary.
- Notio 1: 1 trunk vertebra; 1 cloacal vertebra; 1 fragment of vertebra.
- Pili B: 1 humerus; 1 femur.
- Rema Aslan 1: 1 fragment of tooth-bearing bone.
- Spilia 4: 1 coronoid; 1 caudal vertebra; 5 ribs; 2 femurs.
- Tomea Eksi 1: 4 caudal vertebrae.
- Tomea Eksi 2: 1 fragment of tooth-bearing bone; 1 trunk vertebra; 1 caudal vertebra; 1 femur.
- Trilofon: 1 fragment of tooth-bearing bone.

Identification

Fossil remains lacking clear diagnostic features or displaying a poor preservational status are attributed to indeterminate lizards.

Amphisbaenia Gray, 1844

Amphisbaenia indet. (Fig. A4.6BF-BH)

Material:

- Spilia 4: 1 trunk vertebra (UU SPA 501).

Description

The vertebra is small (centrum length = 2.4 mm). It has a procoelous and dorsoventrally compressed centrum, which has a flattened ventral surface and

subparallel lateral margins. The dorsal surface of the neural arch is flattened, without neural spine. In dorsal view, the arch is constricted in the middle. There is no zygosphene and the prezygapophyseal processes are present, but very short. Identification

The following combination of characters allows the assignment of the vertebra from Spilia 4 to un indeterminate amphisbaenian (Estes 1983; Delfino 2003): small size, dorso-ventrally compressed centrum with a flattened ventral surface and roughly parallel lateral margins, short and robust prezygapophyses, massive and rounded synapophyses, absence of zygosphene, and a dorsally flattened neural arch lacking a neural spine. Currently, no significant diagnostic feature is known on isolated trunk vertebrae of this group of squamates (Estes 1983).

3.2.3. Italy

Thirteen Italian fossil sites have yielded the herein studied lizard fossils. Fossils from the locality of Cava Monticino have been retrieved from a large number of palaeokarstic fissures (Rook et al. 2015). When listing the studied material coming from this locality, the fissure of provenance is reported with the acronym BRS followed by a number. Remains from Monte Tuttavista and from the Gargano area also come from a number of fissure fillings (Delfino 2002; Abbazzi et al. 2004). Nevertheless, as far as Monte Tuttavista is concerned, only specimens previously attributed either to indeterminate geckos or to a large *Lacerta* species have been considered here. Similarly, only gekkotan remains from Gargano have been studied. Fossil remains from Tenuta Zuccarello have been found in two roughly contemporaneous infills of a roman pit (Bon et al. 2010).

Localities

Area del Gargano - Gargano "terre rosse" (Fig. 3.3a)
Age: late Miocene (Messinian)/early Pliocene.
Repository: Dipartimento di Scienze della Terra, Università di Firenze, Italy.
References: Freudenthal 1971; De Giuli & Torre 1984; Abbazzi et al. 1996.



Figure 3.3) Map of Italy, showing the position of the herein-considered Italian localities: Gargano "terre rosse" (a), Cava Monticino (b), Caverna dei Parmorari (c), Caverna dell'Aurera (d), Ciabòt Cagna (e), Fosso della Fittaia (f), Moncucco Torinese (g), Monte Tuttavista (h), Oderzo (i), Riparo dell'Aquila (j), Rivoli Veronese (k), Tenuta Zuccarello (l) and Valdemino Cave (m). Colors of the circles indicates a Miocene (red) or Quaternary (green) age.

Cava Monticino, Brisighella (Fig. 3.3b)

Age: late Miocene (latest Messinian, MN 13).

Repository: Museo Civico di Scienze Naturali, Faenza, Italy. References: Rook et al. 2015.

Caverna dei Parmorari (Fig. 3.3c)

Age: Upper Pleistocene/Holocene. Repository: Museo Archeologico del Finale, Finale Ligure, Italy. References: Richard 1932; Richard 1938; Richard 1939.

Caverna dell'Aurera (Fig. 3.3d) Age: ?Upper Pleistocene/Holocene Repository: Museo Archeologico del Finale, Finale Ligure, Italy. References: Giuggiola 1958.

Ciabòt Cagna (Fig. 3.3e) Age: late Miocene (late Messinian). Repository: Museo Civico "F. Eusebio", Alba, Italy. References: Cavallo et al. 1993.

Fosso della Fittaia (Fig. 3.3f) Age: late Miocene (MN 11). Repository: Museo di Storia Naturale, Università di Firenze, Italy. References: Cirilli et al. 2016.

Moncucco Torinese (Fig. 3.3g)

Age: latest Miocene (latest Messinian)

Repository: Museo di Geologia e Paleontologia, Università degli Studi di Torino, Italy.

References: Colombero et al. 2017.

Monte Tuttavista, Orosei (Cava IV Macaca, Cava VII Blocco Strada, Cava IX Prolagus) (Fig. 3.3h) Age: early/late Pleistocene. Repository: Soprintendenza dei Beni Archeologici, Nuoro, Italy. References: Abbazzi et al. 2004.

Oderzo (Fig. 3.3i) Age: Holocene (I/II cent. A.D.). Repository: Museo di Storia Naturale, Venezia, Italy. References: Delfino et al. 2008.

Riparo dell'Aquila (Fig. 3.3j) Age: Upper Pleistocene (Upper Paleolithic). Repository: Museo Archeologico del Finale, Finale Ligure, Italy. References: Arobba et al. 1987.

Rivoli Veronese (Fig. 3.3k) Age: early Pleistocene (MN 17). Repository: Dipartimento di Biologia ed Evoluzione, Università di Ferrara, Italy. References: Sala et al. 1994; Sala 1996.

Tenuta Zuccarello (Fig. 3.31) Age: Holocene (2000 ±40 BP). Repository: Museo di Storia Naturale, Venezia, Italy. References: Bon et al. 2010.

Valdemino Cave (Fig. 3.3m) Age: Middle Pleistocene. Repository: Museo Archeologico del Finale, Finale Ligure, Italy. References: Delfino 2004b.

Systematic palaeontology

Area del Gargano - Gargano "terre rosse" "Lacertilia" Owen, 1842 Gekkota Cuvier, 1817

Gekkota n.gen. n.sp. (Fig. A4.7A-L) Material:

- Chirò 80/1 NL: 3 dentaries (DSTF-GH 40/42).
- F1: 3 maxillae (DSTF-GH 26/28); 5 dentaries (DSTF-GH 29/31, 46).
- F1 SA 1: 2 maxillae (DSTF-GH 35/36); 2 dentaries (DSTF-GH 37/38).
- F8: 1 maxilla (DSTF-GH 45).
- F9: 1 dentary (DSTF-GH 43).
- F32 GA: 1 dentary (DSTF-GH 33).
- F32/1: 2 dentaries (DSTF-GH 32).
- F32/10: 1 dentary (DSTF-GH 39).
- Pirro 80/1: 1 maxilla (DSTF-GH 25); 1 dentary (DSTF-GH 44).
- San Giovannino F2 parte bassa: 1 maxilla (DSTF-GH 34).

Description

All specimens are very small-sized, lightly-built and rather fragmentary.

Maxillae (Fig. A4.7A-F) are usually represented only by parts of the middle portion of the bone, with both the anterior and posterior ends missing. The two ends are rarely preserved (e.g, the anterior one in DSTF-GH 26, Fig. A4.7A-C; the posterior one in DSTF-GH 36, Fig. A4.7F; part of both ones in DSTF-GH 25 and 34, Fig. A4.7D-E). The facial process is also always missing. When preserved, the anterior end displays a rather squared anterior premaxillary process, with a very shallow anterior concavity originated by very short and anteriorly rounded anterolateral and

anteromedial processes. The vomeronasal foramen is located by the base of the anterior end of the facial process, but it is not housed in a concavity. The thin palatal shelf is always broken. In DSTF-GH 36, on the dorsal surface of the preserved part of the shelf, a wide superior dental foramen is visible (Fig. A4.7F). The posterior process is rather short and narrows posteriorly, ending with a rather rounded posterior end. Dorsally, there is no groove for the lacrimal foramen. A small portion of the anterior margin of the facial process is preserved in DSTF-GH 25 and 34 (Fig. A4.7D-E): it does not show a distinct notch, but it is not possible to clearly state whether the margin was straight or slightly concave in origin. The alveolar border carries closely spaced tooth positions, housing slender, pleurodont and cylindrical teeth. The crown is almost always missing, but when preserved it is devoid of striae, pointed and displays two parallel and longitudinal cusps. The tooth row reaches the end of the posterior process. The lateral surface of the preserved portions of facial process is smooth, with some ventrolateral foramina (up to 6). The best-preserved specimens, DSTF-GH 25 and 34, bears 18 and 21 tooth positions and have a total length of roughly 2.5 mm and 3.9 mm respectively.

Dentaries (Fig. A4.7G-L) display a tubular structure composed of expansions of the subdental ridge and the ventral margin enclosing the Meckelian fossa. The fossa is very narrow and shrinks towards the anterior end of the bone. The anterior end is almost always missing. When preserved, it shows a very narrow mandibular symphysis, which is slightly dorsally inclined (Fig. A4.7G-H). The posterior end is also missing in almost all specimens, but when at least a part of it is preserved, a shallow articular surface for the anterior end of the splenial is visible on the medial surface of the tubular structure. A few specimens preserve a short and posteriorly pointed superior posterior process dorsally (Fig. A4.7I-J), and ventrally a much longer, medially concave and very wide inferior one, whose posterior end seems to be truncated (but this could be due to a breakage in the best preserved process; Fig. A4.7K-L). Either a U- or a V-shaped and rather short notch is visible in medial view by the end of the tubular structure. The ventral margin of the dentary is distinctly

straight in medial view, except for the inferior posterior process which slightly bends ventrally. The alveolar portion bears slender, pleurodont and closely-spaced teeth. Tooth crowns are usually missing or eroded, but the preserved ones show a pointed tip displaying two parallel cusps, a labial one and a lingual one. No striae are visible on the crowns. The best-preserved (almost complete) specimen, DSTF-GH 29, bears 27 tooth positions and is 4.9 mm in length. The lateral surface is smooth, carrying only some mental foramina. The number of mental foramina in DSTF-GH 29 is 4. Identification

The vomeronasal foramen not located in a concave area, the tubular structure enclosing the Meckelian fossa and the tooth morphology clearly identify this specimens as pertaining to a small gekkotan species (Sumida & Murphy 1987; Evans 2008; this work). They cannot, however, be assigned to any of the extant European species. As a matter of fact, maxillae from Gargano differ from H. turcicus in lacking the sigmoid ridge on the medial surface and the groove for the lacrimal foramen, from T. mauritanica in the absence of a deep notch on the anterior margin of the facial process and from all species but E. europaea in the rounded posterior end of the posterior process. Moreover, they differ from all extant European species in the very little development that characterize both anteromedial and anterolateral processes and in the short posterior process. Given the breakage of the facial process in all specimens, it is not possible to clearly state whether either a light ornamentation was present on the external surface (as in *H. turcicus*, but the preserved portion is always smooth) or the dorsal end of the process was devoid of any projection (as in E. europaea). The dentaries, on the other hand, are very different from those of all the extant species in having a pointed, and not forked, superior posterior process and a very wide and possibly truncated inferior posterior process. A comparison with almost all fossil gekkotan species known from the Cenozoic of Europe is also possible. Only Rhodanogekko vireti cannot be compared with the fossil material from Gargano, since it has been erected based only on an isolated frontal (Hoffstetter 1946; Augé 2005; Daza et al. 2014). Nevertheless, R. vireti represents a much larger

species than the Gargano gecko would have been (Daza et al. 2014). Even when fossil species are considered, maxillae from Gargano are unique in the short posterior process, a feature unknown in any other fossil European gecko whose maxillae are preserved (namely, Cadurcogekko piveteaui, Cadurcogekko verus, Gerandogekko arambourgi, Gerandogekko gaillardi, Euleptes gallica, Laonogekko lefevrei and Palaeogekko risgoviensis; Hoffstetter 1946; Schleich 1987; Müller 2001; Augé 2003, 2005; Čerňanský & Bauer 2010; Daza et al. 2014; Bolet et al. 2015). Dentaries are less common in the fossil record of these species, and in most cases the referred specimens miss the posterior processes, hindering a clear comparison of these structures with the one of the Gargano specimens. Well enough preserved dentaries are known only for C. piveteaui, G. gaillardi and P. risgoviensis. Both in G. gaillardi and in *P. risgoviensis*, the general morphology of the posterior processes recalls the one of the extant European gekkotans, with a short and forked superior posterior process and a long and rather slender inferior one (Hoffstetter 1946; Schleich 1987; Daza et al. 2014). In dentaries of C. piveteaui, on the other hand, the posterior end seems to be more similar to the condition seen in dentaries from Gargano (see fig. 58 in Augé 2005 and fig. 5E in Daza et al. 2014). Nevertheless, this could also be an artifact due to preservational reasons, and therefore it must be checked with a revision of all the fossil material attributed to this species. In any case, gekkotan remains from Gargano differ from both C. piveteaui and C. verus in the absence on the maxilla of rugosities on the lateral surface, of a groove starting from the last ventrolateral foramen and of a postnarial depression, and from C. piveteaui alone in the smaller size and the general absence of an elongated coronoid impression on the dentary (Hoffstetter 1946; Augé 2005; Bolet et al. 2015). Moreover, the herein described specimens differ from both E. gallica and P. risgoviensis in the smaller size, and from L. lefevrei in the steeper posterior margin of the maxilla (Schleich 1987; Müller 2001; Augé 2003, 2005; Čerňanský & Bauer 2010). Given all these differences, it appears not possible to assign the gekkotan fossils coming from the Neogene of Gargano to any of the known species of European geckos, either extant

or fossil. They might therefore belong to a new species, and maybe even a new genus, of small gecko. Nevertheless, a certain relation with *C. piveteaui* might be suggested by the possible similarity in the posterior processes of the dentary.

<u>Cava Monticino, Brisighella</u> "Lacertilia" Owen, 1842 Agamidae Spix, 1825 Agaminae Spix, 1825

Agaminae indet. (Fig. A4.7M-O) Material:

- BRS 25: 2 fragments of maxillae (BRS25/H/4, 5); 1 dentary (MSF 67).

Description

The fragmentary maxillae are robust and very poorly preserved. Both specimens carry acrodont teeth, whose number is 2 in BRS25/H/4 and 5 in BRS25/H/5 (Fig. A4.7M-N). The teeth are triangular and closely spaced. Despite the wearing, a very small cusp is visible in some of them, both anteriorly and posteriorly to the main tip. The tooth base is expanded towards the medial surface of the alveolar border, rather than being located on its edge. The size of the teeth increases towards one of the end of both bones, which is probably the posterior one. In lateral view, there are no interdental grooves.

The dentary (Fig. A4.7O) is almost complete, but still plunged in a block of sediment. Only the smooth lateral surface is visible, showing 4 mental foramina. The tooth row is roughly 17 mm-long and carries 19 teeth. The two anteriormost ones are subpleurodont, conical and pointed, whereas all other teeth are acrodont, closely spaced and subtriangular. Distinct interdental grooves are recognisable. The ventral margin of the bone is straight. The posterior end is broken off. Identification In spite of the possible presence of variability in the main characters used to separate the two families (see Rage & Bailon 2011), fragmentary tooth-bearing bones of Agamidae are usually distinguished from those of Chamaeleonidae because of the closely spaced acrodont teeth extending onto the lingual side of the alveolar border (Evans et al. 2002; Delfino et al. 2008; this work). The presence of an agamid in the late Miocene of Cava Monticino is further supported by the isolated dentary MSF 67, which carries both pleurodont and acrodont teeth (Delfino et al. 2008; Blain et al. 2014b; this work). The number of subpleurodont teeth suggests that MSF 67 might belong to a member of the subfamily Agaminae (Maul et al. 2011).

Lacertidae Batsch, 1788 Eremiadini Shcherbak, 1975

Eremiadini indet. (Fig. A4.7P-Q) Material:

- BRS 4: 1 pair of fused frontals (BRS4/H/23).
- BRS 5bis: 1 pair of fused frontals (BRS5bis/H/11).
- BRS 5 tg. 2: 1 pair of fused frontals (BRS5tg2/H/2).
- BRS 6: 1 pair of fused frontals (BRS6/H/3).
- BRS 24: 1 pair of fused frontals (BRS24/H/22).
- BRS 25; 1 fragment of a couple of fused frontals (BRS25/H/87).
- BRS No Number: 1 pair of fused frontals (BRSNoNumber/H/14).
- BRS ?: 1 pair of fused frontals (BRS?/H/14).

Description

Each specimen represents a pair of fused frontals. The anterior end is always missing, whereas the posterior one is preserved partially in BRS4/H/23 (which misses the posterior margin and the posterolateral processes), BRS5bis/H/11 and BRS6/H/3 (which both lack the right posterolateral process and the tip of the left one). In ventral

view, no suture line is visible in the middle. Two low and moderately robust cristae cranii run along the lateral margins. The cristae are more sharpened and slightly more developed in the anterior portion of BRS5bis/H/11, BRS5tg2/H/2, BRS6/H/3, BRS24/H/22 and BRS?/H/14, which preserve a larger part of the anterior half of the bone. In spite of the anterior portion being always absent, a middle constriction seems to be recognizable in dorsal view. The dorsal surface is covered by a dermal ornamentation made up of a crust covered by small pits and low ridges. Three grooves are visible on it, separating the frontal shield from the frontoparietal ones and the latter from one another. In BRS6/H/3, however, a small and triangular area (the vertex is directed posteriorly) is visible in the middle of the posterior end of the bone, between the frontoparietal shields. Moreover, the ornamentation is slightly less developed in this same specimen. The ornamentation is more developed on the frontoparietal shields, whereas it is poorly defined on the frontal one. The grooves separating frontal and frontoparietal shields are located posteriorly to the middle constriction. By the posterior margins of the preserved portion of the specimens, the anterior end of the articulation surfaces with the postfrontals are visible. A portion of those with the prefrontals is visible by the anterior end of the preserved portion of BRS5bis/H/11, BRS6/H/3, BRS24/H/22 and BRS?/H/14. The two articulation surfaces are far from each other. The length of the specimens is 2 mm in BRS5tg27h/2 (which, however, is only a very small fragment), 3 mm in BRS24/H/22, 4 mm in BRS6/H/3 and BRS?/H/14, 5.3 mm in BRSNoNumber/H/14, 5.5 mm in BRS4/H/23 and reaches 6 mm in BRS5bis/H/11.

BRS25/H/87 is represented only by a fragment of the anterior portion, but its morphology and its size are similar to those of the other specimens.

Identification

Among lacertids, fused frontals not showing a longitudinal suture line in ventral view (meaning that they fuse in an early stage of the ontogeny) are found only in some members of the tribe Eremiadini (Arnold 1989; Arnold et al. 2007; this work). The poor preservation of the specimens from Cava Monticino, the absence of other taxonomically significant elements clearly referable to this tribe of lacertids and the fact that no other Eremiadini-like frontals to which the herein considered remains could be compared are known from Miocene localities in Europe prevent a more precise identification.

Lacertidae indet. (Fig. A4.7R-U) Material:

- BRS 4: 1 dentary (BRS4/H/21); 2 fragments of dentaries (BRS4/H/20); 5 fragments of tooth-bearing bones (BRS4/H/19).
- BRS 4 (?): 1 fragment of maxilla (BRS4?/H/5); 1 fragment of tooth-bearing bone (BRS4?/H/6).
- BRS 5bis: 2 fragments of tooth-bearing bones (BRS5bis/H/10).
- BRS 5 tg. 2: 3 fragments of dentaries (BRS5tg2/H/16); 1 fragment of dentary articulated with the splenial (BRS5tg2/H/18); 6 fragments of tooth-bearing bones (BRS5tg2/H/17); 1 tooth (BRS5tg2/H/1).
- BRS 8: 3 fragments of dentaries (BRS8/H/1); 5 fragment of tooth-bearing bones (BRS8/H/2).
- BRS 15: 1 fragment of tooth-bearing bone (BRS15/H/6).
- BRS 16: 1 fragment of tooth-bearing bone (BRS16/H/4).
- BRS 18: 1 fragment of dentary (BRS18/H/6); 1 fragment of tooth-bearing bone (BRS18/H/5).
- BRS 19: 1 fragment of dentary (BRS19/H/11); 4 fragments of tooth-bearing bones (BRS19/H/10, 12).
- BRS 24: 2 fragments of maxillae (BrS24/H/17); 4 fragments of dentaries (BRS24/H/18, 21); 24 fragments of tooth-bearing bones (BRS24/H/19).
- BRS 25: 1 jugal (BRS25/H/187); 5 fragments of dentaries (BRS25/H/184);
 3 fragments of dentaries articulated with the splenial (BRS25/H/11, 12, 148);

14 fragments of tooth-bearing bones (BRS25/H/10, 47, 84, 147, 183); 1 tooth (BRS25/H/48).

- BRS 27: 1 fragment of dentary (BRS27/H/12); 7 fragments of tooth-bearing bones (BRS27/H/13).
- BRS 28: 1 fragment of maxilla (BRS28/H/17); 1 fragment of dentary (BRS28/H/18).
- BRS ?: 1 dentary (BRS?/H/13).

Description

All specimens are very fragmentary, poorly preserved and small- or medium-sized. The medium-sized jugal, BRS25/H/187 (Fig. A4.7R-T), preserves only the middle portion, where the anterior and the posterodorsal process meet. Both processes seem to be moderately robust and the base of a well-developed quadratojugal process is present, though its tip is missing. The palatal process is also well developed and seems to originate a very short medial process (Fig. A4.7T). A large foramen opens on the posteromedial surface of the bone, under this latter process. The lateral surface is completely covered by a light but distinct vermicular ornamentation.

The tooth-bearing bones bear cylindrical, slender and pleurodont teeth, among which the best preserved ones show a mono-, bi- or tricuspid crown. The best preserved specimens, BRS4/H/21 (Fig. A4.7U) and BRS?/H/13, are dentaries whose preserved portions reach about 6.5 mm in length and carry 18 and 17 tooth positions respectively; the posterior portion, however, is missing in both of them. The lateral surface of maxillae and dentaries is smooth and the one of BRS28/H/17, a maxilla, is also distinctly concave. Moreover, on the dorsal surface of the palatal shelf of the maxillae, there is a wide and posteriorly directed superior dental foramen, continuing posteriorly in a wide groove. When preserved, the mandibular symphysis of the dentaries is narrow and subhorizontal, whereas the Meckelian fossa is wide and medially opened. In BRS24/H/21 and BRS?/H/13, a convex ventral margin is also recognizable. In BRS5tg2/H/18, BRS25/H/11, BRS25/H/12 and BRS25/H/148, the fragment of dentary is still articulated with a fragment of the splenial. Though poorly preserved, the splenial is wide and narrows towards the anterior end. In BRS25/H/148, a large anterior inferior foramen (dorsally) and a very small anterior mylohyoid foramen (ventrally) are visible in the middle of the bone in medial view. Identification

The tooth morphology of the above-described tooth-bearing bones, as well as the convex ventral margin of BRS24/H/21 and BRS?/H/13 (Delfino 2002; Delfino et al. 2011; this work), is a clear evidence of them being attributable to the family Lacertidae. The jugal, on the other hand, can be assigned to lacertids because of the vermicular ornamentation and of the overall morphology not as slender as in scincids and anguids (this work). It is not clear if these specimens can belong to the previously recognised indeterminate member of the tribe Eremiadini or they represent a second lacertid taxon. Nevertheless, it has to be noted that in all extant European Eremiadini the palatal process of the jugal is poorly developed (this work), in contrast with the condition seen in BRS25/H/187.

Scincidae Gray, 1825

Scincidae indet. (Fig. A4.7V) Material:

- BRS 25: 1 fragment of dentary (BRS25/H/142).

Description

The specimen is a poorly preserved fragment of a small dentary, carrying pleurodont, cylindrical and slender teeth. Only two teeth are preserved, but they are in good preservational conditions. The crowns are bicuspid, with parallel lingual and labial cusps, and appear pointed in medial view. The tip curves slightly in postero-medial direction and light striae are visible only on the lingual surface of the tooth crowns. Identification

BRS25/H/142 is referred to Scincidae because of the pleurodont, bicuspid teeth provided with parallel labial and lingual cusps, a slightly bending crown and striae on the lingual surface (Townsend et al. 1999; Caputo 2004; this work), but the very poor preservational status prevent a more precise attribution.

?Scincidae indet. (Fig A4.7W-X) Material:

- BRS 27: 1 fragment of tooth-bearing bone (BRS27/H/15).

Description

BRS27/H/15 is a small fragment of tooth-bearing bone carrying 4 pleurodont, cylindrical and slender teeth. Teeth are well preserved and show a bicuspid crown, with parallel lingual and labial cusps. The cusps are little distinguishable, but this could be due to erosion. The tip of the crown is strongly curved in posteromedial direction and distinct striae are clearly visible on both the labial and lingual surfaces. Identification

Tooth morphology of BRS27/H/15 recalls the one of scincids (see above), but the strongly curved crown and the striae on the labial surface distinguish this specimen from the one attributed to this latter family, BRS25/H/142. According to Kosma (2004), the parallel cusps and the distinct lingual striation are also present in the dentition of Cordylidae, but teeth of this family are usually robust and lack striae on the labial surface. BRS27/H/15 is here tentatively attributed to an indeterminate scincid (maybe different from BRS25/H/142), but the possibility that it belongs to a different taxon cannot be totally ruled out.

Anguidae Gray, 1825 Anguinae Gray, 1825 *Ophisaurus* Daudin, 1803 Ophisaurus sp. (Fig. A4.7Y-AE)

Material:

- BRS 4: 1 fragment of tooth-bearing bone (BRS4/H/22).
- BRS 4 (?): 1 fragment of tooth-bearing bone (BRS4?/H/4).
- BRS 5 tg. 2: 1 fragment of maxilla (BRS5tg2/H/7); 1 fragment of toothbearing bone (BRS5tg2/H/6); 9 teeth (BRS5tg2/H/4).
- BRS 24: 1 tooth (BRS24/H/10).
- BRS 25: 1 frontal (BRS25/H/160); 1 parietal (BRS25/H/119); 1 fragment of parietal (BRS25/H/121); 2 dentaries (BRS25/H/7, 135); 3 fragments of tooth-bearing bones (BRS25/H/6, 137); 1 tooth (BRS25/H/136).
- BRS 25 (?): 1 tooth (BRS25?/H/2).
- BRS 27: 1 fragment of tooth-bearing bone (BRS27/H/14).

Description

BRS25/H/160 (Fig. A4.7Y-AA) is a medium-sized and well-preserved frontal (length = 9 mm), missing only the tip of the medial process and the anterior part of the crista cranii. In dorsal view, the anterior end is roughly half as wide as the posterior one and there is no lateral process. The articular surface with the nasal is clearly distinguishable by the anterior end. Moreover, the frontal is not constricted in the middle and its lateral margin is straight. The posterolateral process is short, moderately wide and roughly pointed. The posterior margin is straight, but slightly irregular. In lateral view, both the articulation surfaces with the prefrontal and the postfrontal are visible. The former is very wide and surpasses the middle of the length of the bone, whereas the latter is smaller and covers only the posterior fifth of the lateral margin. The two surfaces are distinctly separated from one another. A wide crista cranii is visible on the ventral surface: it is low in its posterior half, but becomes more ventrally developed anteriorly. The ventral portion of its anterior half, however, is missing. A well-developed dermal ornamentation is present on the dorsal surface, but the orbital margin remains smooth. The frontal shield covers almost entirely the

bone, but the small areas covered by the frontoparietal (laterally) and the interfrontal (medially) shields are visible by its posterior end. The ornamentation is less developed on these latter shields and the grooves separating them from the frontal one are recognisable.

BRS25/H/119 (Fig. A4.7AB-AC) is a fragmentary parietal, preserving only the right part of the shelf. A short, rounded and slightly laterally developed anterolateral process is present by the anterolateral corner. There are not distinct interdigitations on the anterior margin. The dorsal surface is covered by a strong dermal ornamentation, which does not reach the lateral margin. The ornamentation is made up of very low ridges and pits. A smooth area levis is also present posteriorly. The right lateral, interparietal and occipital shields are recognizable, whereas the right frontoparietal one is absent since the lateral one reaches the anterior margin. The occipital shield is small, whereas the interparietal one is very large. Anteriorly, the latter occupies a wide portion of the anterior margin, without reaching the anterolateral corner though. The lateral margin of the lateral shield is straight. The parietal foramen is large and circular and it is located anteriorly to the middle of the shelf. The ventral surface is smooth, except for a robust and well-developed anterolateral ventral crest running along the lateral margin. There is no facies muscularis (sensu Klembara et al. 2010) laterally to the crest. The specimen is largesized, being 9.5 mm in length. BRS25/H/121 is a fragment of a robust and largesized parietal, representing only the left anterolateral corner of the shelf. A poorly developed anterolateral process is recognizable and very little developed interdigitations are present along the anterior margin. The ventral surface shows the anterior end of the left anterolateral ventral crest, whereas the dorsal one bears a strong dermal ornamentation. A portion of the interparietal and of the left lateral shields are recognisable, since they are separated by a distinct groove. The latter reaches the anterior margin and so the left frontoparietal shield is not visible.

BRS5tg2/H/7 (Fig. A4.7AD) is a very fragmentary maxilla, preserving only part of the tooth row. The posterior process is completely missing, whereas only the

anterolateral portion of the anterior premaxillary one is preserved. The anterolateral process is long, pointed in dorsal view and rather rounded in lateral view. The lateral surface is smooth ant the ventrolateral foramina are not recognizable because of the poor preservational status. The specimen is moderately robust and 12.5 mm in length. It carries at least 10 tooth positions. The teeth are large, subpleurodont, closely spaced and canine-like, provided with a slightly posteromedially bending tip. No distinct striae are visible neither on the lingual, nor on the labial surface of the teeth. Two distinct cutting edges run along both the anterior and posterior margins of the crown, with the anterior one being strongly more developed than the posterior one.

BRS25/H/135 (Fig. A4.7AE) preserves only the anterior half of a left dentary, still plunged in the sediment. Only the external surface of the bone and the dorsal portions of four teeth are visible. Five labial foramina are visible on the lateral surface and a 6th one is cut by the posterior breakage. The teeth are conical, slender and slightly posteromedially bending by their pointed tip. There are no striae on their exposed surface. The second dentary, BRS25/H/7, includes the posterior half, even if the angular process and the ventral margin are missing. Teeth are morphologically similar to those of BRS5tg2/H/7 and a total of 8 tooth positions is present. A small and pointed splenial spine is present by the 5th tooth position from the end of the tooth row. The opening of the alveolar canal is visible, in ventral view, under the 3rd posteriormost tooth position. Because of the absence of the ventral half of the posterior end, it is not possible to see if a free posterior projection of the intramandibular septum was present or not. The superior posterior process is made up by two projections: the dorsal one (the coronoid process) is pointed and distinctly longer than the more rounded ventral one (the surangular process). Because of this, the notch between the two projections, the coronoid incisure, is very shallow in lateral view. The lateral surface is smooth, showing only two mental foramina. BRS4?/H/4, composed by two separated portions, was part of a large-sized toothteeth are well preserved, whereas only the base remains of the other two. The wellpreserved teeth are morphologically similar to those of BRS5tg2/H/7. The lateral surface of the tooth-bearing bone appears rough and 4 foramina are visible on it, roughly antero-posteriorly aligned.

The isolated teeth and the ones carried by most of the other fragments of toothbearing bones are similar in morphology to those of BRS4?/H/4 and BRS5tg2/H/7, even if BRS25/H/136 differs from them in the absence of the cutting edges. BRS25/H/137, on the other hand, shows teeth similar to those of the dentary BRS25/H/135. In the BRS25/H/137, the cutting edges are present, whereas they are not clearly visible in BRS25/H/135 because of this specimen being plunged in the matrix.

Identification

The tooth morphology of the above described tooth-bearing bones recalls that of Ophisaurus (Klembara et al. 2014). Despite being very fragmentary, BRS25/H/119 is clearly not attributable to Pseudopus (the only other anguid identified in the remains from Cava Monticino; see below) because of the absence of facies muscularis (Klembara 1986). Moreover, parietals of both Anguis and Pseudopus usually display small frontoparietal ornamented shields by the anterolateral corners of the shelf preventing the lateral shields to reach the anterior margin of the bone (this work). This appears not to be true for at least some Ophisaurus species (see e.g., Ophisaurus holeci in Klembara 2015). It seems possible, though, to assign the herein described parietals to Ophisaurus. The frontal from BRS 25 is also not attributable to Pseudopus because of the completely smooth lateral margin (Klembara 2015; this work). This is also a feature present in Anguis frontals, but in the latter genus this bone displays a contact between the articular surfaces of postfrontal and postorbital and a not clearly distinguishable articular surface with the nasal (this work). Given that, the above mentioned frontal is also assigned to Ophisaurus. Most of the Ophisaurus species known from European Neogene localities are described based on parietals, but because the very fragmentary nature

of the parietals from Cava Monticino, it is here preferred to identify them (and all other *Ophisaurus* remains) only at the generic level. It has to be noted, however, that the anterior margin of the interparietal shield not reaching the anterolateral corner (i.e, the anterior end of the sulcus between it and the lateral shield is located far from the corner) is a feature of *O. holeci*, in contrast with an interparietal shield more laterally expanded or even contacting the anterolateral corner in the other species for which the parietal is known (Klembara 2015; Klembara & Rummel 2016): *Ophisaurus fejfari, Ophisaurus spinari* and *Ophisaurus robustus*.

Pseudopus Merrem, 1820

Pseudopus sp. (Fig. A4.7AF-AK) Material:

- BRS 25: 2 frontals (BRS25/H/117-118); 1 fragment of maxilla (BRS25/H/182); 1 fragment of tooth-bearing bone (BRS25/H/122).

Description

BRS25/H/117 (Fig. A4.7AF-AH) is a well-preserved left frontal, lacking only the anterior end. It is roughly 8.5 mm-long. In dorsal view, there is no constriction at mid-length and both the lateral and medial margins are straight and roughly parallel. In lateral view, the articulation surface with the prefrontal is moderately wide and long, reaching mid-length, whereas the one with the postfrontal is smaller and shorter. The surfaces are not in contact, but they are not far from one another. The posterolateral process is wide, pointed and moderately long. A poorly developed lappet is present on its ventral surface. A small and triangular articulation surface is visible ventrally, medially to the lappet. Though broken, the crista cranii is clearly robust and well developed. A strong dermal ornamentation covers almost completely the dorsal surface of the bone, except for the posterolateral process. The ornamentation reaches the lateral margin and is made up of low ridges and pits.

Because of the smooth surface of the posterolateral process, the frontoparietal shield cannot be recognized, but the oblique groove between it and the frontal shield is distinguishable. The margin of the frontal shield marked by this groove, the posterolateral margin, is distinctly longer than its posteromedial margin. Moreover, the frontal shield reaches the posterior margin, excluding therefore the interfrontal shield from the dermal cover of the frontal. The second frontal, BRS25/H/118, is more poorly preserved, being represented only by a moderately eroded posterior half. However, its morphology recalls that of BRS25/H/117, except for the presence of a moderately developed dermal cover on the posterolateral process also. BRS25/H/118 is roughly 5.3 mm in length.

BRS25/H/182 (Fig. A4.7AI) is a fragmentary and very poorly preserved maxilla, representing the anterior portion of the bone. The anterior premaxillary process is clearly composed by an anterolateral and an anteromedial process, of which the former is twice as robust as the latter. Both processes are strongly eroded and the anteromedial one also misses its anterior end. They are separated by a roughly U-shaped notch. The anterior concavity in which the vomeronasal foramen opens is bordered both laterally and medially by low ridges, but the foramen is not clearly distinguishable because it is covered by matrix. The medial ridge continues on the dorsal surface of the anteromedial process in a moderately low lappet. The lateral surface of the specimen is smooth, carrying only 4 ventrolateral foramina. Four tooth positions are visible and 3 teeth are still present, though eroded. The teeth are subpleurodont, cylindrical and distinctly robust; their crown is blunt and rounded. It seems that some striae are present on both the lingual and the labial surface of the teeth, but this cannot be ascertained because of the erosion. The size of the teeth increases posteriorly.

BRS25/H/122 (Fig. A4.7AJ-AK) is a very poorly preserved fragment of an indeterminate robust and large-sized tooth-bearing bone. The bone carries a single, well-preserved tooth, which is subpleurodont, robust, cylindrical and monocuspid.

Its crown is rather rounded and bears distinct striae on both the labial and lingual surfaces.

Identification

These specimens are clearly referable to Pseudopus because of the dermal ornamentation reaching the lateral margin of the frontals and the cylindrical and robust teeth with a blunt crown (Klembara et al. 2014; Klembara 2015; this work). The specific identification, on the other hand, is more complex, because of a number of features or combination of features that seems to distinguish the *Pseudopus* remains found in Cava Monticino from the other Neogene Pseudopus species. First, both the ornamentation reaching the lateral margin for the entire length and the very long posterolateral margin of the frontal shield compared to its posteromedial margin separate the frontals BRS25/H/117 and 118 from *P. ahnikoviensis* and *P. laurillardi*, in which the ornamented cover touches the lateral margin only near the anterior end and the posterolateral margin of the frontal shield is either as long as (in P. ahnikoviensis) or slightly longer (in P. laurillardi) than the posteromedial one (Klembara et al. 2010; Klembara 2012; Klembara & Rummel 2016). Pseudopus ahnikoviensis differs from the herein described remains also because it does not show striae on the dentition (Klembara 2012; Klembara & Rummel 2016). The interfrontal shield, absent in the two frontals from Cava Monticino, is on the other hand present and distinctly large in all Pseudopus species, but P. apodus and P. confertus, in which it can be either absent or narrow (Klembara et al. 2010; Klembara 2012; Klembara 2015; Klembara & Rummel 2016; this work). The frontal referred to P. *confertus* (= *P. rugosus*) by Klembara (2015) displays a dermal ornamentation which is distinctly different from the one of BRS25/H/117 and 118. Therefore, the *Pseudopus* from the late Miocene of Cava Monticino seems to be somehow different from all other species of the genus found in European Neogene localities. Nonetheless, given the scarce amount of remains and the absence of other taxonomically important skeletal elements (i.e., parietals), either a possible

identification as a new taxon or a tentative attribution to one of the known species are here avoided and the fossils are attributed only to *Pseudopus* sp.

non-Anguis Anguinae indet.

Material:

- BRS 1bis: 3 osteoderms (BRS1bis/H/1).
- BRS 3: 1 osteoderm (BRS3/H/1).
- BRS 4: 3 fragments of trunk vertebrae (BRS4/H/5); 3 caudal vertebrae (BRS4/H/6); 111 osteoderms (BRS4/H/1-4).
- BRS 5bis: 9 fragments of trunk vertebrae (BRS5bis/H/2); 7 fragments of caudal vertebrae (BRS5bis/H/3); 109 osteoderms (BRS5bis/H/1).
- BRS 5 tg. 2: 1 fragment of maxilla (BRS5tg2/H/8); 2 pterygoids (BRS5tg2/H/3, 22); 1 ectopterygoid (BRS5tg2/H/23); 4 fragments of tooth-bearing bones (BRS5tg2/H/5); 8 fragments of trunk vertebrae (BRS5tg2/H/20); 5 fragments of caudal vertebrae (BRS5tg2/H/21); 110 osteoderms (BRS5tg2/H/27).
- BRS 6: 1 fragment of tooth-bearing bone (BRS6/H/2); 3 osteoderms (BRS6/H/1).
- BRS 8: 2 osteoderms (BRS8/H/5).
- BRS 9: 1 fragment of trunk vertebra (BRS9/H/2); 43 osteoderms (BRS9/H/1).
- BRS 15: 1 fragment of trunk vertebra (BRS15/H/5); 6 osteoderms (BRS15/H/4).
- BRS 16: 2 fragments of trunk vertebrae (BRS16/H/2); 2 caudal vertebrae (BRS16/H/3); 15 osteoderms (BRS16/H/1).
- BRS 18: 59 osteoderms (BRS18/H/1).
- BRS 19: 1 fragment of trunk vertebra (BRS19/H/7); 2 caudal vertebrae (BRS19/H/8); 79 osteoderms (BRS19/H/6, 9).

- BRS 24: 1 fragment of maxilla (BRS24/H/13); 1 trunk vertebra (BRS24/H/9); 3 fragments of trunk vertebrae (BRS24/H/11); 2 caudal vertebrae (BRS24/H/12); 433 osteoderms (BRS24/H/8, 23-24).
- BRS 25: 1 fragment of tooth-bearing bone (BRS25/H/140); 1 trunk vertebra (BRS25/H/166); 35 fragments of trunk vertebrae (BRS25/H/1, 45, 111, 170-171); 30 caudal vertebra (BRS25/H/46, 112-114, 127, 139, 168, 172); 1331 osteoderms (BRS25/H/2, 19, 110, 120, 123-126, 167, 185-186).
- BRS 25 (?):1 caudal vertebra (BRS25?/H/1).
- BRS 27: 45 osteoderms (BRS27/H/1-3).
- BRS 28: 2 trunk vertebrae (BRS28/H/4, 15); 53 osteoderms (BRS28/H/1-2, 16).
- BRS No Number: 2 fragments of trunk vertebrae (BRSNoNumber/H/16); 2 caudal vertebrae (BRSNoNumber/H/15); 33 osteoderms (BRSNoNumber/H/17).
- BRS ?: 289 osteoderms (BRS?/H/8-12).

Description

Pterygoids are medium-sized and moderately robust. Both specimens are very fragmentary, preserving only the base of the quadrate process and part of the anterior half of the bone (part of the palatine process in BRS5tg2/H/3 and part of the pterygoid flange in BRS5tg2/H/22). The palatine process shows a large number of pterygoid teeth on the ventral surface, whereas a well-developed ridge runs along the lateral margin on the ventral surface of the pterygoid flange. The preserved portion of the quadrate process presents a wide and flattened basipterygoid fossa, which is marked ventrally by a distinctly developed and roughly thumb-like basisphenoid process (sensu Klembara et al. 2010). Part of a deep fossa columellae is visible dorsally in BRS5tg2/H/22.

BRS5tg2/H/23 is a fragmentary, but very robust and large-sized ectopterygoid, which lacks almost completely the anterior end and the posterior-most portions of

the posterior one. The bone has a medially concave shape and presents a dorsomedially expanded posterior portion, whose lateral surface bears a wide and deep articulation surface for the pterygoid flange of the pterygoid. The anterior half of the lateral surface, on the other hand, is covered by the very narrow articulation surface with the posterior process of the maxilla. The two articular surfaces contact each other. A small and anterolaterally directed flange marks ventrally the anterior articulation surface. The medial surface of the specimen is smooth.

The fragments of tooth-bearing bone, BRS5tg2/H/8 included, are very poorly preserved. Each of them carries subpleurodont, large-sized and moderately preserved tooth. The preserved teeth seem to narrow dorsally, suggesting a possible conical shape, but, since they lack the crown, it is not possible to say whether the tip was pointed or not. No striae are visible on the preserved portion of the teeth, but in BRS5tg2/H/8 and BRS24/H/13, they show the anterior and posterior cutting edges visible in the above described *Ophisaurus* sp. BRS5tg2/H/8 is particularly robust and is 8 mm in length.

BRS24/H/9, BRS28/H/4 and BRS28/H/15 have a medium size (centrum length goes from 4 mm to 6 mm) and a dorsoventrally compressed, procoelous centrum, provided with a smooth and flattened ventral surface and lacking a precondylar constriction. In ventral view, the centrum is subtriangular, since its lateral margins converge posteriorly. The neural arch is low. The neural spine was present, but it is broken in both specimens. When preserved, the zygapophyses are suboval in dorsal view and dorsally tilted at an angle of about 45°. Though the specimens are very poorly preserved, the preserved portions of the fragments of trunk vertebrae are morphologically similar to the two above described specimens. Some of the fragmentary vertebrae are very large-sized (e.g., the centrum of BRS25/H/171 is 1 cm long).

The caudal vertebrae present a dorsoventrally compressed centrum and the bases of broken hemapophyses on the ventral surface. Some of the best-preserved specimens are robust and very large (centrum length reaches 1.1 cm in BRS25/H/114 and 172),

whereas the other ones are smaller. When preserved, the neural arch and the zygapophyses are similar to those of the above described trunk vertebrae. The autotomy plane is clearly lacking, except for BRS25/H/113.

Osteoderms, whose preservational status varies from complete to very fragmentary, are mainly large- to very-large-sized and robust, even if there are also smaller specimens. They usually have a subrectangular shape, but some more subtrapezoidal or more suboval specimen is also present (e.g., BRS27/H/2). A vermicular ornamentation is always present on the external surface (except for the smooth anterior gliding surface), whereas the inner one is smooth. The rectangular osteoderms bear also a distinct longitudinal keel in the middle of the external surface. Identification

Numerous vertebrae and osteoderms are assigned to indeterminate non-Anguis Anguinae because of the large size, the dorsoventrally compressed centrum with posteriorly convergent lateral margins, the absence of precondylar constriction and, as far as the osteoderms are concerned, the rectangular shape and the external keel (Klembara 1981; Estes 1983; Holman 1998; Delfino et al. 2011). Both the pterygoids and the ectopterygoid display anguid features (e.g., osseous expansion marking ventrally the basipterygoid fossa, articular surface with the maxilla limited to the lateral surface of the anterior half of the ectopterygoid; this work). The large size suggests that they can be attributed to a non-Anguis taxon, like the other similarsized specimens from Cava Monticino, but since these skeletal elements are not clearly known for the Neogene anguid species, they are not assigned neither to *Pseudopus* nor to *Ophisaurus*. The dentition of the fragmentary tooth-bearing bones is also comparable with that of a non-Anguis anguine, but due to their poor preservation, it is not possible to confidently assign them to a particular taxon. The only exceptions might be BRS5tg2/H/8 and BRS24/H/13, whose teeth are more similar to those of the specimens attributed to *Ophisaurus*.

Varanidae Gray, 1827 (sensu Estes et al., 1988)

Varanus Merrem, 1820

Varanus sp. (Fig. A4.7AL-AP)

Material:

- BRS 5bis: 1 tooth (BRS5bis/H/13).
- BRS 6: 1 tooth (BRS6/H/7); 1 trunk vertebra (BRS6/H/4); 1 fragment of vertebra (BRS6/H/5).
- BRS 25: 1 trunk vertebra (BRS25/H/138); 3 fragments of trunk vertebrae (BRS25/H/85, 129, 181); 1 caudal vertebra (BRS25/H/130); 1 humerus (BRS25/H/128).
- BRS 27: 1 caudal vertebra (BRS27/H/4).
- BRS No Number: 3 fragment of vertebra (BRSNoNumber/H/1-2).

Description

Both teeth (Fig. A4.7AL-AO) are medium-sized and lack their tip. BRS6/H/7 is also slightly eroded. They are canine-like in shape and distinctly posteriorly curved. The implantation was subpleurodont and the tooth base shows a labially directed area made of spongy tissue. BRS5bis/H/13 is still connected to part of the original tooth-bearing bone. The teeth are mediolaterally compressed and present sharpened anterior and posterior margins, on which a light milling is still visible in spite of the erosion. Both the lingual and the labial surfaces of BRS5bis/H/13 show a number of dorsoventrally directed striae near the tooth base. In BRS6/H/7, such striae are not visible on the labial surface, but this could be due to the preservational status.

The trunk vertebrae are procoelous, robust and large-sized (the centrum length of the best preserved one, BRS25/H/138, is 1 cm). BRS25/H/138 is almost complete and roughly as long as it is large. It has a wide and dorsoventrally compressed centrum, provided with a smooth and flattened ventral surface, strongly posteriorly convergent lateral margins (giving it a triangular shape in ventral view) and a distinct precondylar constriction. The neural arch has a subtriangular section in anterior view

and carries a neural spine, which is, however, broken. Dorsally, there is no pseudozygosphene. Both the zygapophyses and the synapophyses are missing. In BRS6/H/4, only the anterior end of the centrum and part of its prezygapophyses are preserved. Size, robustness and general morphology of this specimen is similar to the other trunk vertebra. The prezygapophyses are slightly eroded, but they appear dorso-ventrally inclined at about 45° in anterior view.

The vertebral fragments are very poorly preserved, but they are very large and robust. The size and the robustness of the specimens is comparable with those of the other remains attributable to *Varanus*, but some of them are even larger (e.g, BRS25/H/85). BRS25/H/85, 129, 181 and BRSNoNumber/H/1 show a wide and dorsoventrally compressed posterior condyle, preceded by a strong precondylar constriction (Fig. A4.7AP).

BRS25/H/130 is the posterior portion of a moderately large-sized caudal vertebra, provided with a dorsoventrally compressed centrum and a wide posterior cotyle. A precondylar constriction is present and the bases of two unfused hemapophyses are visible on the ventral surface, near the cotyle. The postzygapophyses are suboval and dorsally tilted at 45°. A broken, but strongly dorsally projecting neural spine is present. The autotomy plane is recognizable anteriorly. BRS27/H/4 is less preserved, but has a comparable size and a similar morphology, in particular for what the bases of the hemapophyses are concerned. This specimen is also split into two portions, but it is not clear if the separation plane between them is a real autotomy plane or just the result of breakage.

BRS25/H/128 is the poorly preserved distal epiphysis of a very large-sized and very robust humerus.

Identification

Together, the precondylar constriction and the absence of the pseudozygosphene are distinctive features of the trunk vertebrae of *Varanus* (Hoffstetter 1943; Estes 1983; Bailon 1991). Caudal vertebrae and teeth also display varanid features, such as the precondylar constriction in the former and the presence of long basal striae and

spongy tissue (suggesting the presence of plicidentine) in the latter (Estes 1983; Bailon 1991; Pianka et al. 2004; Kearney & Rieppel 2006). Because of the comparable size and the fact that, among Varanidae, only *Varanus* has been reported from the European Neogene so far (Delfino et al. 2013), both caudal vertebrae and teeth can be confidently attributed to this taxon too. The humerus is assigned to *Varanus* because of its very large size, which is comparable only with *Varanus* among all limbed lizards identified in Cava Monticino.

"Lacertilia" indet.

Material:

- BRS 2: 1 fragment of vertebra (BRS2/H/3); 1 pelvic girdle (BRS2/H/1); 1 tibia (BRS2/H/2).
- BRS 4: 1 quadrate (BRS4/H/7); 1 pterygoid (BRS4/H/8); 2 fragments of dentaries (BRS4/H/9); 4 fragments of tooth-bearing bones (BRS4/H/10); 12 fragments of vertebrae (BRS4/H/11); 2 pectoral girdles (BRS4/H/12); 2 humeri (BRS4/H/13); 1 ulna (BRS4/H/14); 1 pelvic girdle (BRS4/H/15); 1 indeterminate element (BRS4/H/16).
- BRS 5bis: 1 fragment of tooth-bearing bone (BRS5bis/H/12); 2 fragments of trunk vertebrae (BRS5bis/H/4, 9); 1 humerus (BRS5bis/H/7); 1 ulna (BRS5bis/H/6); 2 pelvic girdles (BRS5bis/H/5); 1 tibia (BRS5bis/H/8).
- BRS 5 tg. 2: 1 premaxilla (BRS5tg2/H/19); 2 fragments of maxillae (BRS5tg2/H/14); 1 fragment of dentary (BRS5tg2/H/13); 12 fragments of tooth-bearing bones (BRS5tg2/H/15); 1 fragment of vertebra (BRS5tg2/H/12); 1 humerus (BRS5tg2/H/11); 1 ulna (BRS5tg2/H/10); 1 femur (BRS5tg2/H/9).
- BRS 8: 3 fragment of vertebrae (BRS8/H/3); 1 femur (BRS8/H/4).

- BRS 9: 2 fragments of tooth-bearing bones (BRS9/H/3); 2 fragments of trunk vertebrae (BRS9/H/4); 2 humeri (BRS9/H/5); 1 pelvic girdle (BRS9/H/6); 4 femurs (BRS9/H/7).
- BRS 15: 1 pterygoid (BRS15/H/7), 1 pelvic girdle (BRS15/H/8).
- BRS 16: 4 fragments of vertebrae (BRS16/H/5).
- BRS 18: 2 fragments of tooth-bearing bones (BRS18/H/4); 1 fragment of vertebra (BRS18/H/2); 1 femur (BRS18/H/3).
- BRS 19: 2 fragments of vertebrae (BRS19/H/13); 1 humerus (BRS19/H/14);
 1 femur (BRS19/H/15).
- BRS 24: 2 fragment of maxilla (BRS24/H/14); 1 fragment of pterygoid (BRS24/H/20); 1 fragment of dentary (BRS24/H/15); 13 fragments of tooth-bearing bones (BRS24/H/16); 2 fragment of vertebrae (BRS24/H/5); 2 humeri (BRS24/H/3); 3 ulnae (BRS24/H/6); 2 pelvic girdles (BRS24/H/4); 4 femurs (BRS24/H/7).
- BRS 25: 1 pterygoid (BRS25/H/116); 3 fragment of dentary (BRS25/H/41, 83); 13 fragments of tooth-bearing bones (BRS25/H/40, 82, 115, 149, 164);
 2 axes (BRS25/H/49, 100); 2 cervical vertebrae (BRS25/H/43, 61); 5 fragments of trunk vertebrae (BRS25/H/42, 106); 1 cloacal vertebra (BRS25/H/107); 1 caudal vertebra (BRS25/H/69); 31 fragments of vertebrae (BRS25/H/44, 162, 173); 3 ribs (BRS25/H/37); 8 humeri (BRS25/H/39, 70, 80, 108, 161); 4 ulnae (BRS25/H/36); 4 femurs (BRS25/H/38, 81, 109, 163); 1 tibia (BRS25/H/68).
- BRS 28: 1 femur (BRS28/H/14).
- BRS 28 (?): 2 fragments of caudal vertebrae (BRS28?/H/3).
- BRS ?: 1 dentary (BRS?/H/1); 2 fragments of tooth-bearing bones (BRS?/H/2, 15); 1 ulna (BRS?/H/16).
- BRS No Number: 1 humerus (BRSNoNumber/H/13).

Identification

All these specimens are either too fragmentary or considered not taxonomically significant and therefore can be identified only as belonging to indeterminate lizards.

Amphisbaenia Gray, 1844

Amphisbaenia indet. (Fig. A4.7AQ-AU) Material

- BRS 19: 2 trunk vertebrae (BR19/H/1, 2).
- BRS 25: 2 trunk vertebrae (BRS25/H/17, 86); 1 fragment of trunk vertebra (BRS25/H/18).

Description

The trunk vertebrae are very small, with the centrum length of the best preserved ones that is 2 mm in BR19/H/1 (Fig. A4.7AQ-AT), 2.2 mm in BRS25/H/86 and 2.4 mm in BR19/H/2. BR19/H/1 is almost complete, lacking only the posterior portion of the neural arch, whereas the other specimens are more fragmentary. The vertebral centrum is procoelous, dorsoventrally compressed and has a flattened ventral surface. Its lateral margin are very slightly concave and roughly parallel in ventral view. The synapophyses are bulbous and massive. The prezygapophyses are suboval in dorsal view and dorsally tilted at roughly 30° in anterior view. In BR19/H/1 and BRS25/H/17, the dorsal surface of the neural arch is smooth and there is no trace of a neural spine in its preserved portion. A very small and rounded prezygapophyseal process is visible in BRS25/H/18 (Fig. A4.7AU) and 86, but it is almost indistinct in other specimens preserving the prezygapophyses (i.e., BRS19/H/1 and 2).

Identification

Small trunk vertebrae without zygosphene and neural spine and provided with a dorsoventrally compressed centrum with a flattened ventral surface and subparallel lateral margins can be referred to indeterminate amphisbaenians (Estes 1983; Delfino 2003), but a more precise identification is not possible.

<u>Caverna dei Parmorari</u> "Lacertilia" Owen, 1842 Lacertidae Batsch, 1788 *Timon* Tschudi, 1836

Timon lepidus (Daudin, 1802) (Fig. A4.7AV-AW) Material: 1 parietal; 1 dentary; 1 compound bone Description

The very large parietal (Fig. A4.7AV-AW) has an elongated shelf, which is 15.5 mm-long and 12 mm-wide. The anterior margin is mostly broken, but moderately-developed interdigitations are present in the small preserved part. A well-developed dermal ornamentation is present dorsally, and the occipital shield is very large. There is no area levis and no parietal notch. Though missing the tips, the postparietal processes are distinctly widened proximally. Ventrally, the posterolateral ventral crests do not touch the anterolateral ones. The parietal fossa is wide and subtriangular.

The dentary is well preserved and very long, with a 21 mm-long tooth row. It has a narrow and subhorizontal mandibular symphysis and a narrow subdental ridge. The Meckelian fossa is wide and medially open. In medial view, the ventral margin is distinctly convex. The tooth row carries 28 tooth positions, most of which are still occupied by slender, cylindrical, pleurodont and closely-spaced teeth. All tooth crowns are more or less eroded, but both mono- and bicuspid teeth are visible. The alveolar canal is located roughly at mid-length, between the 17th and the 18th tooth positions. The posterior processes are equally long. The lateral surface of the specimen is smooth, with 8 mental foramina.

The compound bone is very large. It is 38 mm in length. In medial view, it has a straight ventral margin and a very wide adductor fossa. A moderately-developed tubercle is present on the articular condyle. The retroarticular process is

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subtriangular. The lateral surface of the bone is smooth, displaying the articular surface with the angular medioventrally and a distinct ridge dorsally to the latter. Identification

These specimens testify for the presence of a very large-sized lacertid, whose size is comparable with *T. lepidus* (this work). The large occipital shield of the parietal confirms this attribution (Barahona & Barbadillo 1997; this work).

"Lacertilia" indet.

Material: 1 sacral vertebra.

Identification

This medium-sized sacral vertebra (centrum length = 4 mm) might be also referred to *T. lepidus*, but since its size is comparable with a medium-sized taxon such as *Lacerta* too, it is here assigned only to an indeterminate lizard.

<u>Caverna dell'Aurera</u> "Lacertilia" Owen, 1842 Lacertidae Batsch, 1788

Lacertidae indet. (Fig. A4.7AX) Material: 1 splenial. Description

This splenial is very large and anteroposteriorly elongated. It has a forked anterior end and a pointed posterior one. On the lateral surface, a sharp medial crest runs longitudinally near the convex ventral margin, from the anterior end to the posterior one. A dorsal crest is also visible, running along the dorsal margin. The very large anterior inferior foramen and the strongly smaller anterior mylohyoid one pierce the bone roughly in the middle. The splenial does not display a ventral expansion. Identification Given its large size, the pointed posterior end, the foramina located in the middle and completely closed and the convex ventral margin, the splenial represents a large-sized lacertid (this work). The very large size might suggests that it belonged to an adult individual of *T. lepidus*, the largest lacertid currently living near the finding locality (Sillero et al. 2014).

<u>Ciabòt Cagna</u> "Lacertilia" Owen, 1842 Anguidae Gray, 1825 Anguinae Gray, 1825

non-Anguis Anguinae indet. (Fig. A4.7AY)

Material: 1 fragment of trunk vertebra, 1 caudal vertebra, 4 osteoderms.

Description

Remains are poorly preserved and small-sized. The fragment of trunk vertebra shows the anterior end of the centrum and the left prezygapophysis: the former is concave and slightly dorsoventrally compressed, whereas the latter is large, elliptical and dorsally tilted at about 45°. The caudal vertebra seems to have a slightly dorsoventrally compressed centrum. The autotomy plane is present and the specimen represents only the posterior portion of the vertebra. Osteoderms (Fig. A4.7AY) are thin, sub-rectangular, antero-posteriorly elongated and present a vermicular ornamentation on the external surface. A low and sharp keel crosses the same surface longitudinally.

Identification

These remains display morphological features that allow their identification as indeterminate non-Anguis Anguinae, such as the dorsoventrally compressed vertebral centrum, the subrectangular shape of the osteoderms and the keel on their external surface (Estes 1983; Holman 1998; Delfino et al. 2011).

"Lacertilia" indet. Material: 6 fragments of vertebra. Identification These vertebrae are too poorly preserved for a precise identification.

Amphisbaenia Gray, 1844 Blanidae Kearney, 2003 *Blanus* Wagler, 1830

Blanus sp. (Fig. A4.7AZ-BA)

Material: 1 dentary.

Description

The dentary is small-sized (length of the alveolar border is 2.4 mm) and misses only the mandibular symphysis and the tip of the superior posterior process. the Meckelian fossa is very narrow and the subdental ridge is moderately high. The alveolar canal opens posteriorly by the end of the bone, with a very large opening. This opening is marked ventrally by a long and pointed extension of the intramandibular septum, which is fused to the wall of the dentary. Two posterior processes are present by the posterior end: the superior one is almost entirely lacking, but it was developed in postero-dorsal direction; the inferior one is long, slender and pointed. There is no central process between them. The lateral surface of the bone is smooth, except for 3 large mental foramina. Eight teeth are preserved, even if the lacking of the symphysial portion does not allow to exclude the presence of another one by the anterior end. They are moderately large and subpleurodont. The most complete ones are roughly canine-like, with a pointed tip and a crown that does not curves distinctly in posterior direction. The largest teeth are located in the middle of the tooth row.

Identification
Despite some minor differences (i.e., the absence of a central superior process), the morphology of the dentary from Ciabòt Cagna recalls the one of the dentary of *Blanus* (this work). Dentaries of extant *Blanus* species display a strongly homogeneous morphology (Villa et al. in press - Atti XI Congresso SHI; this work), and therefore a specific identification is here avoided.

Fosso della Fittaia

"Lacertilia" Owen, 1842 Anguidae Gray, 1825 Anguinae Gray, 1825 *Anguis* Linnaeus, 1758

Anguis sp. (Fig. A4.7BB-BF) Material: 1 trunk vertebra (IGF102243).

Description

IGF102243 is a well-preserved vertebra of small size. The neural arch is relatively depressed and characterized by a low neural crest that terminates in a spine that does not project beyond the posterior edge of the postzygapophyseal facets. The anterior edge of the neural arch is moderately convex in dorsal view, but markedly tectiform in anterior view. The neural canal is moderately broad. The pre- and postzygapophyses are tilted in dorsolateral direction; their facets are rather oval in shape. There is no hint of prezygapophyseal processes. Dia- and parapohyses are moderately developed and not distinctly separated from each other. The centrum, and therefore the cotyle and condyle, are markedly depressed dorsoventrally. The ventral surface of the centrum is flat, devoid of any trace of keel or hypapophysis, and laterally delimited by parallel edges that only anteriorly tend to modestly diverge. There is no hint of precondylar constriction.

Identification

IGF102243 clearly shows the adult morphology (among others, the neural canal is not as broad as in juvenile squamates) of a small-sized anguine lizard. The referral to anguine lizards, and to *Anguis* in particular, is based on the general morphology of the vertebra, and the flatness of the centrum that shows parallel edges in particular (Klembara 1981; Estes 1983). The relative anteroposterior shortness of the centrum and the slightly diverging edges in the anterior region of the centrum could indicate that the vertebra comes from the most anterior trunk sector. In absence of diagnostic osteological characters, the recent split of the extant species *Anguis fragilis* Linnaeus, 1758 into several different species (see a summary in Gvoždík et al. 2013) hinders the specific identification of fossil material.

non-Anguis Anguinae indet. (Fig. A4.7BG-BL)

Material: 2 trunk vertebrae (IGF102244/102245); 1 fragmentary caudal vertebra (IGF102246); 40 osteoderms or osteoderm fragments (IGF102247/102249).

Description

The incomplete trunk vertebra IGF102244 is relatively large (preserved centrum length of 5.4 mm; Fig. A4.7BG-BK). It shares several characters with the above described vertebra referred to *Anguis*, but differs in having strongly diverging lateral sides of the centrum. IGF102245 is the posterior region of the centrum of a large-sized trunk vertebra showing a flat ventral surface and the absence of precondylar constriction. The tail vertebra IGF102246 preserves only the portion posterior to the autotomic plane. The neural arch is devoid of a crest, but the neural spine is proportionally long and tall, and it is directed posterodorsally. The preserved portion of the centrum is 3.2 mm long and bears the traces of fused haemapophyses. All the available osteoderms are characterized by being approximately rectangular or squared and relatively large (up to 4.4 x 4.3 mm). The external surface has an anterior, or anterior and lateral smooth surface. The rest of the surface is vermiculated by grooves/furrows and pustules/pits (Fig. A4.7BL). Some of the osteoderms bear a longitudinal keel that divides the vermiculated surface.

Identification

The morphology and size of the vertebrae and the osteoderms described above clearly differs from that of *Anguis* and is broadly congruent to that of non-*Anguis* anguine taxa (Klembara 1981). These are easily identifiable on the basis of tooth bearing elements (Klembara et al. 2014), but the identification of isolated vertebrae and osteoderms is still problematic because of the absence of comparative studies. Nevertheless, IGF102244 is similar to the vertebrae of *Pseudopus* in both robustness and morphology of the vertebral centrum (Klembara 1981).

"Lacertilia" indet.

Material: 1 highly fragmentary tooth-bearing bone, 1 fragment of frontal and 5 vertebral fragments (IGF102250).

Identification

None of these highly fragmentary skeletal elements can be confidently identified because of preservational reasons.

<u>Moncucco Torinese</u> "Lacertilia" Owen, 1842 Agamidae Spix, 1825

Agamidae indet. (Fig. A4.7BM)

Material: 11 fragments of tooth-bearing bone (MGPT-PU 132435/132439).

Description

The tooth-bearing bones carry acrodont, triangular and closely-spaced teeth, which extend slightly onto the medial surface of the alveolar portion of the bone. Teeth are usually worn. The most preserved specimen, MGPT-PU 132438, is 6 mm-long. Identification

Acrodont and closely-spaced teeth extending onto the medial surface lead to the identification of these fragmentary remains as indeterminate agamids (Evans et al.

2002; Delfino et al. 2008; this work). The attribution of these remains to the family Chamaeleonidae can be ruled out by the marked teeth proximity, even if some variation may sometimes be present in this feature (Rage & Bailon 2011).

Gekkota Cuvier, 1817 Sphaerodactylidae Underwood, 1954 *Euleptes* Fitzinger, 1843

cf. *Euleptes* sp. (Fig. A4.7BN-BO)

Material: 1 maxilla (MGPT-PU 132432); 1 trunk vertebra (MGPT-PU 132589); 1 caudal vertebra (MGPT-PU 132590).

Description

MGPT-PU 132432 (Fig. A4.7BN-BO) is a very small fragment of maxilla (about 1.3 mm in length), carrying a single pleurodont, cylindrical, slender tooth, provided with an unstriated bicuspid crown composed by parallel lingual and labial cusps. The rest of the fragment is very poorly preserved, but a distinct concavity is visible on the preserved anterior margin of the facial process.

The two vertebrae are small-sized and amphicoelous. The centrum length of the best preserved one, MGPT-PU 132589, is 1.2 mm.

Identification

The morphology of the single preserved tooth clearly identifies the fragmentary maxilla as belonging to a gekkotan (Sumida & Murphy 1987; this work). The specimen recalls *E. europaea* in the very small size and in the distinct anterior concavity on the facial process (this work), but a precise identification is hampered by the very poor preservational status. The small-sized vertebrae are tentatively attributed to the same taxon.

Lacertidae Batsch, 1788 Lacerta Linnaeus, 1758 cf. Lacerta sp. (Fig. A4.7BP-BS)

Material: 46 frontals (MGPT-PU 132464/132469, 132532/132533); 14 parietals (MGPT-PU 132476/132481, 132535); 26 premaxillae (MGPT-PU 132425. 132544/132547. 132549/132550); 12 maxillae (MGPT-PU 132515. 132555/132560); 16 jugals (MGPT-PU 132470/132475, 132534); 2 postfrontals (MGPT-PU 132536/132537); 3 fused postorbitofrontals (MGPT-PU 132627/132628); 5 quadrates (MGPT-PU 132489/132490, 132542); 32 pterygoids (MGPT-PU 132483/132487, 132541); 1 supraoccipital (MGPT-PU 132495); 6 dentaries (MGPT-PU 132501, 132552/132554); 128 fragments of tooth-bearing bone (MGPT-PU 132411/132414, 132421/132423); 6 trunk vertebrae (MGPT-PU 132574, 132578/132579); 7 cloacal vertebrae (MGPT-PU 132564, 132568/132570, 132588); 175 caudal vertebrae (MGPT-PU 132566/132567, 132571/132572, 132575, 132582, 132584); 32 fragments of vertebrae (MGOT-PU 132561, 132586). Description

All specimens are moderately large. The best preserved or most significant ones are here described.

MGPT-PU 132532 (Fig. A4.7BP-BQ) is represented by a pair of fused frontals, still showing the suture line in ventral view. Part of both the anterior and the posterior ends are broken off. In dorsal view, the lateral margins are almost parallel, and therefore there is no clear constriction at mid-length. The dorsal surface of the bone is completely covered by a well-developed dermal ornamentation. The grooves separating frontal and frontoparietal shields are located roughly by the beginning of the posterior third of the bone. Strong interdigitations are recognisable on the preserved portion of the posterior margin. Posteriorly low, but anteriorly rising cristae cranii run along the lateral margins on the ventral surface. The anterior processes are well-developed and slender. The specimen is 9 mm-long.

MGPT-PU 132535 is a fragmentary parietal, missing the posterolateral corners of the shelf, postparietal processes included. The shelf is longer than it is large, with a

maximum length of 7 mm and a maximum width of 6 mm. The anterior margin displays distinct interdigitations. The anterolateral corners are damaged, but apparently the anterolateral processes are not laterally developed. A strong dermal ornamentation is present on the dorsal surface, reaching the posterior margin. The occipital shield is not much enlarged. The ventral surface shows well-developed anterolateral and medial ventral crests, but the posterolateral ones are not visible since they do not reach the anterolateral ones and the posterolateral corners of the bone are missing. The parietal fossa appears wide and subtriangular.

The premaxilla MGPT-PU 132547 misses only part of the alveolar portion. It preserves 7 tooth positions, 5 of which are still occupied by well-preserved teeth. Teeth are closely-spaced, slender, cylindrical, pleurodont and monocuspid. The ascending nasal process is roughly leaf-shaped and presents a well-developed dermal ornamentation on the dorsal half of its anterior surface. The total width of the preserved portion of the alveolar plate is 3 mm.

MGPT-PU 132556 is a fragmentary maxilla carrying 4 well-preserved teeth and 5 empty tooth positions. Teeth are pleurodont, cylindrical, closely-spaced and either mono- or bicuspid. Their size increases distinctly in posterior direction. The fragment is more than 5 mm in length. The anterior premaxillary process presents a well-developed and pointed anterolateral process. The anteromedial process is broken, but a lappet seems to be present on its dorsal surface. Most of the facial process is missing, as well as the posterior half of the bone.

MGPT-PU 132534 is a large-sized jugal. Only the tips of the anterior and posterodorsal processes are broken. A distinct quadratojugal process is present. The lateral surface of the bone is smooth. Judging from the preserved portion of the articular surface with the maxilla, it probably covered most of the anterior portion of the anterior process. The moderately developed palatal process does not develop a medial process.

MGPT-PU 132489 and 132542 are two large quadrates, measuring 6 mm and 5 mm respectively. Both are fragmentary, preserving only the medial half in the former and

the lateral half in the latter. MGPT-PU 132489 has a well-developed medial lamina, provided with a moderately developed pterygoid flange by the ventral end. MGPT-PU 132542, on the other hand, shows a well-developed lateral lamina originating a deep conch. In anterior view, this lamina presents a concave anterior platform in its dorsal portion. The anterior outline of MGPT-PU 132542 is rounded in lateral view. MGPT-PU 132541 is a moderately preserved pterygoid, missing the tip of the three branches composing it. The wide and straight palatine process presents a large patch of pterygoid teeth on the ventral surface. The pterygoid flange is poorly preserved. Nevertheless, a deep pterygoid recess is recognisable between the two anterior branches of the bone. The quadrate process is straight in ventral view. The total length of the pterygoid is 7 mm.

MGPT-PU 132501 (Fig. A4.7BR-BS) is an almost complete and large dentary, with a total length of 7.5 mm. In medial view, it displays a convex ventral margin and a wide and medially open Meckelian fossa, which narrows towards the anterior end. A slender subdental ridge is present. Anteriorly, the mandibular symphysis is narrow and roughly horizontal. Teeth are pleurodont, cylindrical, closely-spaced and mono-, bi- or tricuspid. There are 17 of them, in addition to 3 empty tooth positions. A posterior increase in the robustness of teeth is distinctly visible. The lateral surface is smooth, pierced by 6 mental foramina. The posterior processes are broken.

Identification

These specimens display the general morphology of a moderately large lacertid species, fully comparable with the size reached by the species of the genus *Lacerta* (Barahona 1996; Barahona & Barbadillo 1997; this work). The parallel lateral margins of the frontals support an affinity with the latter genus. The concave anterior platform of MGPT-PU 132542, however, is a feature that usually distinguishes the quadrates of *T. lepidus* from those of the other lacertids (Barahona & Barbadillo 1997; this work). Nevertheless, quadrates of *T. lepidus* usually reach a much larger size in adults (up to 11 mm in length; this work). The identification of the large-sized

lacertid from Moncucco appears, therefore, complicated, and the hypothesys of the presence of more than one taxon cannot be totally ruled out.

Lacertidae indet.

Material: 6 premaxillae (MGPT-PU 132426, 132430/132431); 82 maxillae (MGPT-PU 132509/132510, 132512, 132516); 192 dentaries (MGPT-PU 132496/132500, 132502/132508); 2 trunk vertebrae (MGPT-PU 132580/132581); 62 caudal vertebrae (MGPT-PU 132565, 132573, 132576/132577, 132585); 11 fragments of vertebra (MGPT-PU 132562, 132587).

Identification

All the above-listed specimens show the lacertid morphology, but they are either too fragmentary or too small to be confidently referred to the large-sized taxon. Therefore, they can either represent juveniles of the above-mentioned taxon or adults of other lacertids virtually present in the late Miocene of Moncucco Torinese.

Anguidae Gray, 1825 Anguinae Gray, 1825

non-Anguis Anguinae indet. (Fig. A4.7BT-BW)

Material: 3 premaxillae (MGPT-PU 132548, 132551); 8 maxillae (MGPT-PU 132443, 132446, 132449, 132543); 14 dentaries (MGPT-PU 132444/132445, 132447/132448, 132450, 132482); 4 fragments of tooth-bearing bones (MGPT-PU 132420, 132441); 83 trunk vertebrae (MGPT-PU 132599, 132601, 132603/132604, 132606, 132608, 132611/132612, 132617/132618, 132621); 1 cloacal vertebrae (MGPT-PU 132620); 169 caudal vertebrae (MGPT-PU 132595/132598, 132600, 132602, 132605, 132607, 132609/132610, 132613/132616, 132619, 132622/132624); 9267 osteoderms (MGPT-PU 132356/132368, 132518/132531). Description

These specimens are large-sized and robust. The following description are focused on the most preserved and most significant specimens.

MGPT-PU 132543 is a 2.5 mm-long fragment of maxilla carrying 4 subpleurodont, conical and slightly posteriorly curved teeth and two more empty tooth positions. Teeth have a robust aspect and do not show striae neither on the labial nor on the lingual surface. Another maxilla, MGPTPU 132443, carries similar, but more slender teeth.

The fragmentary dentary MGPT-PU 132482 (Fig. A4.7BT-BU) bears 4 subpleurodont, conical and slightly posteriorly bending teeth and 4 empty tooth positions. There are no striae on the tooth crowns. A moderately-developed subdental shelf is present ventrally to the teeth. The ventral margin of the bone is broken, as well as the anterior end and the inferior posterior process. The superior posterior process is composed by a coronoid and a surangular processes, separated by a moderately wide coronoid incisure. The lateral surface is smooth, except for the mental foramina. The fragment is 4 mm in length.

MGPT-PU 132612 (Fig. A4.7BU-BW) is a very large procoelous trunk vertebra, with a vertebral centrum that reaches 8 mm in total length. The centrum is dorsoventrally compressed and triangular in ventral view, with posteriorly converging lateral margins and no precondylar constriction. Both cotyle and condyle are distinctly ellipsoidal. In anterior view, the neural canal is vaulted and smaller than the cotyle. Synapophyses are dorsoventrally elongated. The dorsal surface of the neural arch displays a well-distinct, though broken, neural spine. There is no pseudozygosphene by the anterior margin of the arch. Zygapophyses are rounded and dorsally tilted at about 30°. Other trunk vertebrae are similar in morphology, but smaller; moreover, the lateral margins of their centrum can also appear vaguely parallel in the posterior portion.

MGPT-PU 132610, a small-sized caudal vertebra, has an elongated shape and bears the proximal part of fused hemapophyses on the ventral surface of the centrum. The centrum is dorsoventrally compressed and provided with ellipsoidal cotyle and condyle. The autotomy plane is present. Zygapophyses are rounded and dorsally tilted at roughly 30°.

MGPT-PU 132367 and 132530 are two robust and squared osteoderms. The former is very large (8 x 9 mm), whereas the latter is smaller, but still large (4 x 4 mm). Except for the smooth gliding surface, the external surface is covered by a vermicular ornamentation. MGPT-PU 132530 also shows a longitudinal and distinct keel in the middle. Other osteoderms share a similar morphology. Most of them are keeled. Identification

The size of the remains, together with the convergent (or vaguely parallel posteriorly) margins of the centrum of the trunk vertebrae, and the thickness, the squared shape and the keeled external surface of most of the osteoderms, suggest the presence of a large-sized, non-*Anguis* anguine taxon (Estes 1983; Holman 1998; Delfino et al. 2011). The slender and conical teeth, very slightly posteriorly curved by their tip, are comparable to the teeth of *Ophisaurus* according to Klembara et al. (2014), but the remains from Moncucco Torinese do not show striae on the lingual side. Nevertheless, teeth of MGPT-PU 132543 are similar, but more robust. The generic identification of these remains is therefore difficult, and they are here attributed only to indeterminate non-*Anguis* Anguinae.

"Lacertilia" indet.

Material: 4 premaxillae (MGPT-PU 132424, 132428/132429); 48 maxillae (MGPT-PU 132416/132417, 132511, 132513/132514, 132517); 1 squamosal (MGPT-PU 132494); 6 quadrates (MGPT-PU 132491/132492); 6 pterygoids (MGPT-PU 132488, 132538/132540); 6 ectopterygoids (MGPT-PU 132461/132463); 4 dentaries (MGPT-PU 132415, 132418); 9 fragments of tooth-bearing bone (MGPT-PU 132419, 132440); 11 coronoids (MGPT-PU 132453/132455); 13 compound bones (MGPT-PU 132451/132452); 21 fragmentary teeth (MGPT-PU 132433/132434); 1 cervical vertebra (MGPT-PU 132404/132410); 7 shoulder girdles (MGPT-PU 132583); 77 ribs (MGPT-PU 132404/132410); 7 shoulder girdles

(MGPT-PU 132402/132403, 132493); 85 humeri (MGPT-PU 132369/132373); 5 ulnae (MGPT-PU 132381/132383); 20 ilia (MGPT-PU 132384/132387); 10 ischia (MGPT-PU 132388/132391); 4 pubes (MGPT-PU 132392); 34 pelvic girdles (MGPT-PU 132393/132398); 62 femurs (MGPT-PU 132374/132380); 7 tibiae (MGPT-PU 132399/132401).

Identification

A large number of fragmentary or non-diagnostic remains are attributed only to indeterminate lizards.

Amphisbaenia Gray, 1844

Amphisbaenia indet. (Fig. A4.7BX-BZ)

Material: 1 dentary (MGPT-PU 132442); 7 trunk vertebrae (MGPT-PU 132591/132593); 1 caudal vertebra (MGPT-PU 132594).

Description

The dentary is fragmentary, small-sized and has a straight ventral margin. The preserved portion of the bone, missing both the anterior and posterior ends, is roughly 2.5 mm-long. In medial view, a very narrow Meckelian fossa is visible, located ventrally to a narrow subdental ridge. The preserved portion of the alveolar canal, which is closed by the intramandibular septum, strongly widens posteriorly. Three tooth positions are still preserved, 2 of which still carry well-preserved teeth. Teeth are subpleurodont, roughly conical and their tip bends slightly in posteromedial direction. No striae are visible on the crown. The lateral surface is smooth, showing a single mental foramen.

The trunk vertebrae (Fig. A4.7BX-BZ) share the following characters: small size (centrum length of about 2 mm), very small prezygapophyses, absence of neural crest, neural spine replaced by a flattened area, bulbous and massive synapophyses, dorso-ventrally flattened cotyle and condyle, ventral surface of the centrum flat and delimited by straight lateral margins. Very small prezygapophyseal processes are

present, whereas there is no zygosphene. In dorsal view, the most preserved vertebrae are distinctly X-shaped.

The general morphology of the caudal vertebra recalls that of the trunk vertebrae. The bases of fused hemapophyses are visible on the ventral surface of the centrum. There is no autotomy plane.

Identification

The above-described vertebrae clearly share amphisbaenian features, such as the absence of neural crest and neural spine, the shape of the synapophyses and the flattened centrum (Estes 1983). Nevertheless, isolated vertebrae of amphisbaenians cannot be identified even at the family level. The narrow Meckelian fossa allows to assign also the fragmentary dentary to an indeterminate amphisbaenian (this work).

<u>Monte Tuttavista, Orosei</u> "Lacertilia" Owen, 1842 Gekkota Cuvier, 1817 Sphaerodactylidae Underwood, 1954 *Euleptes* Fitzinger, 1843 *Euleptes europaea* (Gené, 1839)

Euleptes cf. *E. europaea* (Fig. A4.8A-S) Material:

- Cava VI 3: 6 maxillae (MT-VI-001/002); 1 dentary (MT-VI-004); 8 trunk vertebrae (MT-VI-005/006); 2 articulated trunk vertebrae (MT-VI-007).
- Cava VI Banco 6: 3 frontals (MT-VIb6-005/7); 2 maxillae (MT-VIb6-002/3);
 1 dentary (MT-VIb6-004); 1 compound bone (MT-VIb6-008); 4 trunk vertebrae (MT- VIb6-001).
- Cava VII Blocco Strada: 1 maxilla (MT-BS-002).
- Cava XI Canidae: 2 frontals (MT-XIc-004/005); 1 dentary (MT-XIc-003); 4 trunk vertebrae (MT-XIc-001/002).

- Cava XI rondone: 1 otooccipital region (MT-XIr-001).

Description

All specimens are small-sized and lightly-built.

Frontals (Fig. A4.8A-C) are unpaired and roughly hourglass-shaped in dorsal view. They have a distinct constriction at mid-length and the lobed anterior end is almost half as wide as the posterior end. The anterior margin is always broken, but the articulation surfaces with the nasals are visible running for the entire width of the margin at least in the most preserved specimen, MT-VIb6-005 (Fig. A4.8A-B). The posterolateral processes are rather long. Dorsally, two shallow grooves are visible, running along the anterolateral margin of the processes (Fig. A4.8B-C). The dorsal surface of the bone is smooth and flattened. The cristae cranii are ventrally developed and fuse to each other to form a tubular structure enclosing the olfactory lobes. Anteriorly, the anterior processes are very short. They have a teardrop shape and a ventrally-pointed aspect in anterior view. On the lateral surfaces, the articulation surfaces with maxillae and prefrontals are rather small. Those with the postorbitofrontal, on the other hand, are not visible. The longest frontals reach up to 3.9 mm in total length.

The best-preserved maxilla, MT-VI-001 (Fig. A4.8D-E), has a 3.7 mm long toothrow, but misses both the anterior and posterior tips. Larger, but less complete specimens are also present (e.g., MT-BS-002; Fig. A4.8F-G). The anterior premaxillary process is almost always broken off, either completely or partially. It is preserved in MT-BS-002 only, displaying a shallow anterior concavity flanked by short anterolateral and anteromedial processes. The posterior process is long and slender. Dorsally, it does not show neither a step nor a groove for the lacrimal foramen. The vomeronasal foramen is small and located on the dorsal surface of the anterior premaxillary process. The superior dental foramen is also rather small. Teeth are usually poorly preserved. They are slender, cylindrical, pleurodont and closelyspaced. Maxillary tooth crowns are usually too much eroded to clearly recognise their morphology, but MT-BS-002 shows 3 well-preserved teeth displaying a pointed tip composed by two longitudinal cusps running parallel on the labial and lingual sides of the crown. There are no striae. MT-VI-001 has up to 22 tooth positions. The facial process is largely missing in most specimens. When preserved, it subtrapezoidal in lateral view. The dorsal end of the process is rounded, without any projection. Both the lateral and the medial surfaces of the process are smooth. The facial process of MT-BS-002 clearly shows a rather steep and anteriorly-inclined anterior margin. Count of the ventrolateral foramina on the lateral surface reach 7 in the best preserved specimen.

The otooccipital region (Fig. A4.8H-J) is moderately preserved: it misses most of the basioccipital, part of the sphenoid (including both basipterygoid processes) and the anterodorsal portions of both prootics. The region is very slightly dorsoventrally compressed. The occipital condyle is completely missing. The lateral opening of the recessus scalae tympani is elliptical and rather large. The semicircular canals are narrow. The preserved portion of the basioccipital displays a smooth ventral surface and a very small right sphenooccipital tubercle. The preserved portion of sphenoid is represented mostly by the posterior half, posteriorly to the crista sellaris. The latter does not develop a dorsum sellae. The supraoccipital has no processus ascendens, displaying a completely smooth dorsal surface. The prootics have a very little-developed crista prootica. The U-shaped incisura prootica is not closed anterodorsally. The lateral surface of both otooccipitals is poorly preserved, hindering a clear description of its morphology. Moreover, both paroccipital processes are broken.

All dentaries but MT-XIc-003 are poorly preserved, missing the entire anterior half and most of the posterior end (Fig. A4.8M-N). In MT-XIc-003 (Fig. A4.8K-L), on the other hand, only the posterior processes are broken off. The tooth row of MT-XIc-003 is 5 mm in length. The Meckelian fossa is narrow and closed in a tubular structure. It shrinks anteriorly. A narrow and roughly V-shaped notch is visible in medial view by the posterior end of the tubular structure. In MT-XIc-003, the notch extends for the posterior fifth of the tooth row. Teeth are similar to those of the maxillae. Preserved crowns are eroded also in the dentaries, but a pointed tip is recognisable in medial view in those of MT-VI-004. Thirty-one tooth positions are present in the most preserved specimen (MT-XIc-003). The lateral surface is smooth, displaying some mental foramina.

The compound bone (Fig. A4.8O-P) misses most of the prearticular portion, but its posterior end shows that it was at least partially fused with the dorsal half of the bone. The remaining part of the specimen is well preserved. In medial view, the anterior end has a pointed aspect. The surangular portion is dorsally convex and displays a large and deeply concave surface on its medial side, marked posterodorsally by a ridge. The articular condyle is subcircular and bears no tubercles. The medially-concave retroarticular process is elongated and rather slender in medial view; its posterior margin is broken. There is no sign of a longitudinal crest on its lateral surface. The lateral surface of the compound bone is smooth. A wide posterior surangular foramen is visible near the articular condyle, in proximity of the dorsal margin of the bone.

Trunk vertebrae (Fig. A4.8Q-S) have a roughly cylindrical and amphicoelous centrum, whose length reaches up to 1.1 mm. In lateral view, a distinct ventral concavity is visible. Synapophyses are small and rounded. The neural arch is rather flattened dorsally and has a very low neural spine. There is no zygosphene/zygantrum complex. Zygapophyses are small and subelliptical. They are slightly tilted in dorsal direction.

Identification

All the above-described specimens can be attributed to a gekkotan because of the following features (Hoffstetter & Gasc 1969; Sumida & Murphy 1987; this work): unpaired and hourglass-shaped frontals with a tubular structure originated by the fusion of the cristae cranii; maxillae with a long posterior process, a subtrapezoidal facial process with no arched medial ridge, a vomeronasal foramen located on the dorsal side of the anterior premaxillary process; processus ascendens lacking on the

supraoccipital; Meckelian fossa closed in a tubular structure on the dentaries; compound bone provided with a slender, elongated and not rod-like retroarticular process and no articular surface for the angular laterally; morphotype F (sensu Kosma 2004) and unstriated dentition; amphicoelous vertebrae. The very small size, the smooth dorsal surface with lateral grooves of the frontals, the facial process of the maxilla provided with a rounded dorsal end and devoid of ornamentation and ridges on both the lateral and the medial surfaces, the completely smooth dorsal surface of the supraoccipital and the elongated retroarticular process lacking a lateral longitudinal crest are all distinctive features of E. europaea among European gekkotans (this work). It would appear therefore possible to assign the remains coming from the different fissures of Monte Tuttavista to this species. Nevertheless, they display some features that are unusual to find in bones belonging to this taxon, and to gekkotan in general in some cases. The otooccipital region, for example, is usually more compressed in *E. europaea*, and the posterior notch of the dentary usually extends along the posterior third of the tooth row in such species (this work), in contrast with the smaller extension along the posterior fifth seen in the best preserved dentary from Orosei (namely, MT-XIc-003). Moreover, the crista prootica is well developed in European geckos as a rule, and the incisura prootica is anterodorsally closed (this work), even though very rare exceptions to the latter features are reported (e.g., T. mauritanica MDHC 98; see chapter 2.2.1). Given that, it is here preferred to attribute the Sardinian remains only tentatively to *E. europaea*, or at least to a form that is morphologically very close to it.

Lacertidae Batsch, 1788 *Timon* Tschudi, 1836

Timon sp. (Fig. A4.8T-CQ, A4.9A-O) Material:

- Cava IV *Macaca*: 1 frontal (MT-IV-001); 1 parietal (MT-IV-002); 1 maxilla (MT-IV-003); 1 jugal (MT-IV-008); 2 dentaries (MT-IV-004/005); 6 cranial osteoderms (MT-IV-009); 10 presacral vertebrae (MT-IV-006); 9 caudal vertebrae (MT-IV-007).
- Cava VI antica (Cava VI 3): 4 frontals (MT-VIa-009/010); 9 parietals (MT-VIa-008); 8 premaxillae (MT-VIa-004); 32 maxillae (MT-VIa-005); 1 jugal (MT-VIa-012); 1 postorbitofrontal (MT-VIa-011); 1 pterygoid (MT-VIa-013); 3 otooccipital regions (MI-VIa-001/003); 46 dentaries (MT-VIa-006); 80 fragments of tooth-bearing bones (MT-VIa-007); 64 presacral vertebrae (MT-VIa-014).
- Cava VI Banco 6: 1 maxilla (MT-VIb6-009); 1 sacral vertebra (MT-VIb6-010); 4 caudal vertebrae (MT-VIb6-011/012).
- Cava VII Blocco Strada: 1 maxilla (MT-BS-001).
- Cava IX Prolagus: 1 nasal (MT-IX-048); 48 frontals (MT-IX-012, 021, 049, 078); 12 parietals (MT-IX-009/011, 022, 050, 070, 081); 15 premaxillae (MT-IX-001/003, 023, 72); 250 maxillae (MT-IX-006/008, 024/025, 035/036, 073); 19 jugals (MT-IX-015, 026, 077); 7 postorbitofrontals (MT-IX-052/53, 069, 079/080); 15 quadrates (MT-IX-054, 082); 16 pterygoids (MT-IX-013/014, 027, 075); 1 ectopterygoid (MT-IX-068); 469 dentaries (MT-IX-004/005, 028, 037, 055, 074); 1 dentary articulated with the splenial (MT-IX-056); 92 fragments of tooth-bearing bone (MT-IX-038, 076); 3 coronoids (MT-IX-057, 084); 3 compound bones (MT-IX-058, 085/086); 5 cranial osteoderms (MT-IX-0083); 2 axes (MT-IX-059, 071); 154 presacral vertebrae (MT-IX-020, 029/030, 087); 13 sacral vertebrae (MT-IX-060, 87 caudal vertebrae (MT-IX-019, 031, 061/062, 089); 1 (088):scapulocoracoid (MT-IX-063); 44 humeri (MT-IX-017, 032, 090); 1 ulna (MT-IX-064); 86 pelvic girdles (MT-IX-018, 033, 091); 10 ilia (MT-IX-092); 2 ischia (MT-IX-093); 30 femurs (MT-IX-016, 034, 039, 094); 18

tibiae (MT-IX-065, 095); 1 astragalocalcaneum (MT-IX-066); 4 metapodials (MT-IX-067, 096).

- Cava X G3: 1 fragment of tooth-bearing bone (MT-XG3-002); 4 presacral vertebrae (MT-XG3-001); 2 caudal vertebrae (MT-XG3-003).
- Cava X 3 uccelli: 1 parietal (MT-X3u-001); 4 fragments of tooth-bearing bones (MT-X3u-002).
- Cava XI Canidae: 2 caudal vertebrae (MT-XIc-006).
- Cava XI Dic. 2001: 1 maxilla (MT-XId-001); 1 dentary (MT-XId-002); 1 axis (MT-XId-003).
- Cava XI G3: 1 maxilla (MT-XIG3-001); 1 dentary (MT-XIG3-002); 1 fragment of tooth-bearing bone (MT-XIG3-003).
- Cava XI rondone: 1 presacral vertebra (MT-XIr-002).

Description

The nasal (Fig. A4.8T-U) is anteroposteriorly elongated and displays a long anteromedial process, whose tip is missing, and a rather short anterolateral process. The posterior end is convex. The ventral surface is smooth, whereas the dorsal one is covered by a very distinct dermal ornamentation. Roughly at midlength, the oblique sulcus between the prefrontal and the internasal shields is visible. The maximum anteroposterior length of the specimen is 7.1 mm.

Almost all frontals are large and unpaired, being composed by two fused symmetrical elements (Fig. A4.8V-Y). Only few specimens are represented by unfused paired elements. In fused specimens, the longitudinal suture line is not clearly recognisable on the ventral surface posteriorly, but a remnant of it is visible in the anterior portion of the most complete specimens. None of the specimens is complete, but the most complete ones miss only part of the anterior end. The interdigitations on the posterior margin are poorly preserved. The frontals are anteroposteriorly elongated, with the posterior end that is roughly twice as large as the anterior one. A very weak constriction is present at mid-length. Two small, fused

frontals have more concave lateral margins compared to the larger elements, which probably represent ontogenetic variations (Barahona & Barbadillo 1998). The anterolateral and anteromedial processes are always missing, but distinct and rounded articular surfaces with the nasals are visible in the most complete specimens. The dorsal surface is completely covered by a very well developed dermal ornamentation, composed by the large frontal shield anteriorly and the smaller frontoparietal shields posteriorly. As visible in the most complete specimens, the transverse sulcus separating the former from the latter is located roughly at the beginning of the posterior third of the bone. When the anterior end is preserved, an oblique sulcus separating the frontal shield from the smaller prefrontal shield located by the anterolateral corner is visible by each side of the frontal. In some specimens, the sulci delimiting the prefrontal shield posteromedially meet each other at the midline, whereas in the majority of specimens they remain separated throughout their length. On the lateral surface, both a very large articular surface with the prefrontal and a smaller articular surface with the postfrontal are present; they are very far from each other. Cristae cranii are low posteriorly, but develop long and moderately thin anterior processes by their anterior end. The longest and most complete frontal, MT-IX-012, is 15.4 mm-long.

Most of the large parietals are moderately well preserved. They have a longer than wide parietal shelf (Fig. A4.8Z-AC), which is completely covered by a well-developed dermal ornamentation (there is no area levis). The dorsal ornamentation shows six distinct, symmetrically-placed shields separated by grooves: two bilaterally symmetrical frontoparietal shields anteriorly, the interparietal shield in central position, two lateral shields posterolaterally, and the occipital shield posteromedially. There is a little variation in the posterior width of the moderately large occipital shield, which is slightly wider compared to the posterior margin of the ornamented surface in MT-IX-009 than in other specimens (Fig. A4.8Z-AA). Moreover, a small parietal (MT-IX-050; Fig. A4.8AD-AE) has a relatively much wider occipital shield than larger specimens, but this could also be due to ontogeny,

as occurs in *Gallotia* (Barahona & Barbadillo 1998). In general, the occipital shield is of approximately the same anteroposterior length as the interparietal shield (even though some variation may occur), and of similar to slightly larger transverse width. A subelliptical parietal foramen pierces the shelf in the middle of the interparietal shield. Some elements lack their anterior part, and in all but one parietal, the frontal lappets are broken off. The anterior margin is relatively straight, with a slight interdigitation, such as in MT-IX-010 (Fig. A4.8AB-AC), but this could be due to taphonomic reasons. The postparietal processes are often missing too, but when preserved they are robust and distinct widened proximally. Well-developed ventral crests are visible on the ventral surface; the proximal end of the posterolateral ones is very far from the anterolateral ones. The parietal fossa is deep and triangular. There is no parietal notch, nor projection along the posterior margin. MT-IX-009, the largest parietal, is 11.5 mm in length and 9.1 mm in maximum width.

The premaxillae (Fig. A4.8AF-AK) are variably complete. Many of them lack at least part of the nasal process, and some preserve only one half of the alveolar plate. These bones are large and provided with a leaf-shaped ascending nasal process. The nasal process projects straight posterodorsally, and is slightly dorsoventrally constricted at about mid-length. It forms an acute angle with the horizontal shelf in lateral view. The anterior surface of this process is covered by a well-developed dermal ornamentation, at least in its dorsal half, whereas a well-distinct septonasal crest runs longitudinally along the entire posterior surface. Anyway, a certain degree of individual variation in the development of the ornamentation is displayed. The dorsal half of the septonasal crest is flanked by two shallow but distinct articular facets for the nasals. The crest is only distinct in the dorsal part, and appears to fade gradually towards the tip in one element (MT-IX-002; Fig. A4.8AI-AK), whereas in the other elements, where the dorsal tip is preserved, the septonasal crest forms a distinct posterodorsal process below the tip of the dorsal shelf of the nasal process (as e.g., MT-IX-001; Fig. A4.8AF-AH). A pair of foramina for the longitudinal canals is visible by the base of the ascending nasal process. The contact between the nasal process and the alveolar plate is slender, with an ellipsoid to subtriangular, anteroposteriorly compressed cross section. The palatal processes are usually broken posteriorly, but in the most preserved specimens a wide and V-shaped notch seems to separate them. Except for the fragmentary specimens, the preserved portion of alveolar plate bears 8 or 9 pleurodont, cylindrical and moderately slender teeth, which are smaller than the maxillary teeth. In the elements without a complete alveolar plate, the estimated tooth count is always 8 or more. Tooth crowns are too worn to clearly state whether all teeth were unicuspid or bicuspid ones were also present. The maximum width of the alveolar plate reaches up to 4.8 mm.

The preservational status of the maxillae varies from very well preserved to fragmentary. They are large, robust and provided with a subtriangular facial process (Fig. A4.8AL-AO). The lateral surface of the same process is covered by a welldeveloped dermal ornamentation dorsally, which can display deep sulci marking the contact of the different scales. Ventrally to the ornamented area, the lateral surface bears 5 to 7 ventrolateral foramina. A low arched ridge is visible on the medial surface of the process. The dorsal projections are usually missing, but when preserved they are short and wide. The anterior premaxillary process bears welldeveloped anterolateral and anteromedial processes, defining a deep and U- to Vshaped anterior concavity. A distinct and robust lappet is present on the dorsal surface of the anteromedial process. The concave area housing the vomeronasal foramen is shallow; it is marked laterally by a very low ridge, whereas medially there is a more developed and robust ridge which merges with the lappet. The superior dental foramen is very wide and opens in posterior direction by the anterior end of a wide groove. The posterior process is wide and posteriorly pointed; in dorsal view, it tends to curve in lateral direction towards the posterior end. The dorsal margin of this latter process is not stepped. The teeth are very robust and clearly hypertrophied, but their size decreases towards the anterior and posterior ends of the tooth row. Nevertheless, some elements bear strongly enlarged teeth in the posterior, and sometimes also the anterior half of the tooth row. Teeth are pleurodont, cylindrical and subject to a high degree of wearing. In some specimens, however, it is possible to recognise a mono- and a bicuspid condition. The tooth row ends very close to the posterior end of the bone and carries 11 to 15 teeth in the best-preserved specimens. The largest specimens reach anteroposterior lengths greater than 15.5 mm.

The large and robust jugals (Fig. A4.8AP-AQ) are well preserved, even if the tips of the branches of the bone are usually broken off. A well-developed quadratojugal process is always present, as well as a moderately developed palatal process originating a small but clearly distinct medial process by its posterior end. When preserved, the pointed anterior end of the anterior process is largely covered laterally by the articular surface with the maxilla. The rest of the lateral surface of the anterior process is covered by a well-developed dermal ornamentation. The distal end of the posterodorsal process is often missing, but where it is preserved, it curves distinctly posteriorly towards its tip. A very distinct and large articular surface with the postorbital is visible medially, along its dorsal margin. In postero-medial view, a foramen opens by the meeting point of the three processes composing the bone, ventrally to the medial process. The largest jugal from Cava IX *Prolagus* measures 14.4 mm in a straight distance from the posterior-most point of the quadratojugal process to the anterior-most point of the anterior process.

The postfrontals and postorbitals are always fused, forming a postorbitofrontal (Fig. A4.8AR-AS). Only one of these bones is reasonably complete, but all of them miss variable portions of their posterior section. The tips of the anterior processes are often broken as well. The anteromedial process is longer than the anterolater process, and the two form an angle of approximately 70°. Between the two, a short, subtriangular process projects anteriorly. From a point straight ventral to this projection, a weak ridge extends towards the medial edge, almost perpendicular to the long axis of the bone, and crossing the anteromedial process ventrally. The frontal facet on the anterolateral one. The latter is also marked by a longitudinal, weak ridge, dividing the concavity into a dorsal and a ventral portion. The dorsal surface is nearly entirely covered by

ornamentation, which follows the same pattern showed by other ornamented skull bones (as e.g., frontals and parietals). Only the anteromedial portion and the anteromedial process lack such a cover. The entire dorsal surface is strongly convex transversely. The ventral surface is concave. This concavity is distinctly bordered anteriorly and anteromedially. The medial margin is always damaged anteriorly, so that it is impossible to tell whether it was expanded or not. The most complete postorbitofrontal has an anteroposterior length of 13.6 mm.

The quadrates from Monte Tuttavista are very stout elements (Fig. A4.8AT-AV). They are generally well preserved and complete, but a small number of elements miss parts of their medial lamina. The cephalic condyle has a subrectangular outline, being slightly longer than wide. A short medial lamina is present, provided with a rather well-developed pterygoid flange. The anterior surface has a complex morphology. It is generally concave transversely and convex dorsoventrally. Dorsally, it bears a very distinct, slightly concave anterior platform on the lateral half. The anterior platform forms a distinct, pointed ventral step, and is strongly offset from the rest of the anterior surface. The pointed ventral tip results in an angular anterior margin of the quadrate in medial and lateral view. The mandibular condyle is saddle-shaped, being concave transversely, and convex anteroposteriorly. The lateral portion is slightly larger than the medial one. In some specimens, the anterior surface is pierced by a small quadrate foramen, right above the mandibular condyle. The largest specimen has a dorsoventral length of 7.4 mm.

The large pterygoids (Fig. A4.8AW-AX) are moderately preserved. The anterior portion of the two anterior branches are always broken off, whereas the quadrate process is moderately preserved in MT-IX-014 and 027 and mostly missing in MT-IX-013. The palatine process is a large and laminar structure, provided with a low number of pterygoid teeth on the ventral surface. In most elements, the teeth are anteroposteriorly aligned to form a kind of tooth row, whereas in some pterygoids, they are aggregated, forming a small patch (e.g., MT-IX-014; Fig. A4.8AW). Such a change in the tooth arrangement can occur during ontogeny in some lizards (e.g.,

Gallotia; Barahona et al. 2000). In spite of the breakage, the pterygoid flange displays well-developed dorsal and ventral ridges. Because of the preservational status of the anterior end, it is not possible to clearly recognise the complete development of the concave pterygoid recess, but the angle originated by the palatine process and the pterygoid flange by the posterior margin of the recess seems to be larger than 90°. The quadrate process is straight in dorsal view, wide and flange-like in lateral view. It shows a deep and subelliptical fossa columellae and a strongly developed pterygoid ridge. On the medial surface, a shallow basipterygoid fossa continues posteriorly in a wide and strongly concave surface. One of the largest specimens, MT-IX-014, has a preserved anteroposterior length of 14.4 mm.

The only preserved ectopterygoid (Fig. A4.8AY-AZ) misses the tips of its three processes. It has a long, tapering anterolateral process. A posterolateral process was present, as indicated by broken bone surface, but it is impossible to tell if it was welldeveloped or not. The posteromedial process expands dorsoventrally towards its medial end, where it is bifurcated, and clasps the ectopterygoid process of the pterygoid dorsally, anteriorly, and ventrally. Due to the incomplete preservation, it is impossible to tell, which of the lappets is the longest. The preserved anteroposterior length of the lateral articular facet for the external skull is 5.6 mm. The otooccipital regions (Fig. A4.8BA-BE) are very large and robust. The different bones composing the region are completely fused in all three specimens. On the whole, the region is not dorsoventrally compressed. In posterior view, the foramen magnum is wide and circular. The largest element, MT-VIa-001, has a foramen magnum with a maximum diameter of 3.3 mm. On the lateral surface, the lateral opening of the recessus scalae tympani is very wide and anteroposteriorly elongate. The fenestra ovalis is also wide, even though smaller compared to the abovementioned opening. Inside the recessus scalae tympani, wide and subelliptical medial opening and perilymphatic foramen are present. The semicircular canals are poorly prominent. The occipital condyle is robust and shows no posterior notch in dorsal view. Given the complete fusion of the bones composing the braincase, it is not

possible to recognise the different (basioccipital and otooccipital) components of the condyle. The basic participate is mushroom-shaped and wider than it is long in ventral view, with the posterolateral sides being composed by ridge-like expansions. The sphenooccipital tubercles are well developed. Both the ventral and the dorsal surface of the bone are smooth. The sphenoid is completely or almost completely missing in all specimens. The most-preserved one is found in MT-VIa-002, in which it preserves part of the posterior half and seems to show a deeply sunken area on the ventral surface. The supraoccipital displays a very robust, cylindrical and welldeveloped processus ascendens, which is however broken in all cases. The processus continues posteriorly with a sharp and well-developed supraoccipital crest running in the middle of the dorsal surface of the bone. In dorsal view, the anterolateral margins of the bone are convergent. The prootics always miss most of both the alar and the anterior inferior processes. The posterior process has a long posterior projection and a well-developed (but generally broken) crista prootica continuing posteriorly on the projection. Ventrally to the crista, there is a moderately large facial foramen, whose anterior margin is marked by a high ridge that partially covers the foramen in lateral view. The foramen is not located in an entocarotid fossa. The prootic portion of the recessus vena jugularis, which is very shallow and clearly recognisable only in MT-VIa-002 because of the preservation of the posterior openings of the vidian canals, ends ventrally to the facial foramen. The otooccipitals bear a very long and robust paroccipital process, whose distal end is never preserved. The vagus foramen is moderately small compared to the hypoglossal foramina. A number of three of the latter are recognisable in the specimen in which this area is best preserved, MT-VIa-002.

As in the maxillae, the preservational status of the dentaries (Fig. A4.8BF-BI) ranges from fragmentary to moderately well preserved. The posterior processes are almost never completely preserved, except for very few specimens. The dentaries are generally large and robust, but smaller specimens are also present. They have a very wide and medially open Meckelian fossa, which narrows towards the anterior end. The subdental ridge is robust, slightly dorso-ventrally expanded anteriorly but narrowing posteriorly. The mandibular symphysis is narrow and slightly dorsally inclined in medial view. The ventral margin is strongly convex. Teeth are pleurodont and cylindrical, increasing in size in posterior direction. The largest teeth are located in the second half of the tooth row, but the last ones tend to be slightly smaller than the preceding ones. In some dentaries, the posterior teeth are much smaller than the central and anterior ones. Some specimens show a rather gradual decrease in tooth size posteriorly, whereas others show a distinct separation from large to small teeth. The number of small teeth is variable as well, reaching up to 7 teeth in some dentaries. Anterior teeth seem to be monocuspid, but it is usually difficult to recognise the crown morphology of the other teeth because of the wearing. Nevertheless, a distinct bicuspid or even tricuspid condition in the central teeth is clearly visible in some specimens. Thirteen to 17 teeth are present. When preserved, the inferior posterior process is posteriorly directed and pointed. The superior posterior process, on the other hand, is always damaged, and therefore its size and shape are never recognisable. The lateral surface shows a variable number of mental foramina and a distinct articular surface with the coronoid on the postero-dorsal corner. The rest of the surface can either be smooth (in most cases) or present a more or less developed cover of dermal ornamentation. Similar sized specimens can either present the ornamentation or not. The dentaries reach preserved lengths greater than 18.3 mm.

The fragments of tooth-bearing bones are very poorly preserved, but the morphology of their teeth is comparable with that of the above-described maxillae and dentaries. The elongate splenial (Fig. A4.8BH) has a rhomboid outline in medial view, with pointed anterior and posterior ends. The tallest dorsoventral height is located below the distal-most teeth. A large anterior inferior foramen pierces the splenial at around midlength, and a small anterior mylohyoid foramen occurs right ventral to the large one, separated from it by a very narrow, horizontal bony crest. The lateral surface of

the splenial is weakly concave dorsoventrally. The medial surface is not visible, since the splenial is still articulated with the dentary.

The three coronoids (Fig. A4.8BJ-BK) are all of different sizes, and miss part of their labial, anteromedial, and posteromedial processes. The angle between the anteromedial process and the posteromedial process is relatively narrow. The posterior process is very short. The coronoid process is robust, dorsally-directed and triangular in medial and lateral views. Its dorsal end is rather rounded. A robust coronoid ridge is present medially, as well as a second, moderately developed ridge connecting the coronoid process with the posterior one. The largest coronoid has a preserved height of 7.2 mm.

Few compound bones are preserved, and all miss most of the part composed of the surangular, and the anterior tips (Fig. A4.8BL). The lateral side is formed by a thin bony wall, which bears the facet for the angular laterally. This facet has a pointed posterior end, and a straight ventral margin, which extends anteroventrally from the posterior tip to participate in the ventral edge of the mandible. The retroarticular process is triangular in lateral view, with a truncated posterior end. The lateral surface is smooth, whereas the medial one is concave and presents a large foramen for the chorda tympani, and, ventrally, a sharp tympanic ridge. The ventral, ridge-like portion of the retroarticular process does not expand strongly in ventral direction, giving a straight appearance to the ventral margin of the bone. Nevertheless, a short ventral expansion is visible slightly anteriorly. The articular surface with the mandibular condyle of the quadrate is quadrangular. Its anterodorsal margin is damaged. Compound bones from Monte Tuttavista reach a preserved length of 13.7 mm.

None of the osteoderms is preserved completely. The largest reaches 11.4 mm, probably in anteroposterior length. As is typical for osteoderms, they have a smooth internal and a rugose external surface. They are variably convex externally.

The axes (Fig. A4.8BM-BQ) are all fused with the odontoid process, and have thus biconvex centra. The anterior articular surface is wider than tall. Due to the anteriorly

projecting odontoid process on the dorsal part of the facet, the entire surface is dorsoventrally concave. Two small fossae mark the dorsal surface of the odontoid process. The lateral surface of the centrum is anteroposteriorly concave, and dorsally bordered by a distinct posterior centrosynapophyseal lamina. Ventrally, the lateral surface curves gently into the ventral surface, which bears a weak, but distinct longitudinal keel along its midline. This keel connects the base of the second intercentrum anteriorly with the base of the third intercentrum (which is broken off) posteriorly. Where preserved, the intercentrum does not have an anterior projection, and extends posteroventrally. The lateral surface of the intercentrum is marked by a weak crest, which connects the ventral blade with the vertebral centrum, and which bears two small, subtriangular posterior projections to the left and to the right of the ventral blade. The synapophysis always lacks the tip, but it is clear that it forms a distinct process projecting posterolaterally. It is anteriorly supported by a short anterior centrosynapophyseal lamina. The dorsal surface of the centrum forms the floor of the neural canal. It bears a continuous, longitudinal ridge along its midline, separating two elongate concavities within the neural canal. The posterior condyle is slightly taller than wide, but otherwise nearly hemispherical. The pedicels of the neural arch have concave anterior and posterior margins, which are formed by thin centroprezygapophyseal and centropostzygapophyseal laminae, respectively. The centroprezygapophyseal laminae are oriented subvertically, and support the prezygapophyses from below. The prezygapophyses themselves are not preserved. The centropostzygapophyseal laminae support the postzygapophyses, which have transversely concave articular facets. Medial to the facets, there are distinct pseudozygosphenes. The postzygapophyses are connected with the synapophyses by a weak postzygosynapophyseal lamina, and with the prezygapophyses through a weak postzygoprezygapophyseal lamina. The neural spine is supported by the spinoprezygapophyseal lamina anteriorly and the spinopostzygapophyseal lamina posteriorly. It has a horizontal spine summit towards is posterior tip, and curves ventrally at its anterior end. It is transversely wider at its posterior end than anteriorly. A weak longitudinal groove extends along the midline on the ventral surface from the posterior to the anterior end of the neural spine, thereby marking also the roof of the neural canal.

Presacral vertebrae, including both cervical (Fig. A4.8BR-BV) and dorsal (Fig. A4.8BW-CA) ones, are large and robust. They are procoelous and more or less anteroposteriorly elongated. Cotyle and condyle are subcircular or slightly subelliptical. A distinct groove occurs around the base of the posterior condyle. The vertebral centrum shows a well-developed keel on the ventral surface. The neural canal is subpentagonal and slightly larger than the cotyle in anterior view. The synapophyses are small, rounded and slightly dorsoventrally elongated, especially in the cervical vertebrae. A distinct posterior centrosynapophyseal lamina is always present; it often bifurcates anteriorly, with a ventral branch connecting to the synapophysis, and a dorsal branch connecting to the prezygapophysis. The dorsal surface of the neural arch is wide and roughly flat, with a light interzygapophyseal constriction. It displays a moderately high neural crest, originating a very well developed neural spine posteriorly. A distinct pseudo-zygosphene is present on the anterior margin. Pre- and postzygapophyses are wide, suboval and tilted dorsally at an angle of about 30° . The postzygapophyses extend far more posteriorly than the neural canal pedicels, and also somewhat more than the centrum. The prespinal lamina is strongly concave in lateral view, and is more inclined than the posterior edge of the neural spine at its base, although they become nearly parallel towards the spine summit. Here, the prespinal lamina bears a short anterior projection in some elements. The prespinal lamina and the neural canal floor form an angle that is always greater than 40° . The lateral surface of the neural spine also bears a spinoprezygapophyseal lamina, which has only been recognized in the lacertid axis by Tschopp (2016).

None of the sacra is complete. Most of them lack parts of their pleurapophyses. The smaller sacral vertebrae are single, whereas the larger elements are fused (Fig. A4.8CB-CD). The centra are procoelous as the presacral vertebrae. The ventral

surfaces of the centra lack a distinct longitudinal keel. The pleurapophyses have distinct anterior centrosynapophyseal lamina and prezygosynapophyseal laminae and weakly developed posterior centrosynapophyseal lamina and postzygosynapophyseal lamina in the sacral vertebra 1, whereas the opposite is the case in sacral vertebra 2. The pleurapophyses of the two sacral vertebrae tend to fuse at their lateral ends in large individuals, and both are oriented obliquely towards each other, such that their point of fusion is in line with the boundary of the two centra in ventral view. The first element has very distinct, and widely spread prezygapophyses and a well-developed pseudozygosphene, whereas all the other zygapophyses in the sacrum are reduced, and no pseudozygosphene is present in the second vertebra. The neural spine is less elevated compared to the most complete presacral vertebrae. A distinct postspinal lamina marks the neural spine of the second sacral vertebra. The most complete sacrum has a total width across the pleurapophyses of 12.9 mm.

Caudal vertebrae (Fig. A4.8CE-CQ) have an overall good status of preservation, though the transverse processes and the neural spines often miss their distal ends. The anterior, non-autotomic caudal vertebrae (Fig. A4.8CE-CI) are large with long and laminar transverse processes. In all specimens, the cotyles and condyles have a rounded outline. There are no distinct hemapophyses on the ventral surface of the vertebral centra. The neural canal is slightly larger than the centrum. The neural canal is triangular, both in anterior and in posterior view. The pseudozygosphene is scarcely developed, laterally bordered by the two symmetrical prezygapophyseal facets, which are dorsoventrally slanted and anterolaterally directed. Posteriorly, the postzygapophyses are somewhat smaller and more medially directed than the prezygapophyses. Pre- and postzygapophyses are interconnected with a distinct postzygoprezygapophyseal lamina, especially in more posterior, non-autotomic caudal vertebrae. The neural spine is greatly elevated in the anteriormost elements. Autotomic caudal vertebrae (Fig. A4.8CJ-CQ) have subparallel transverse processes on both halves, with the posterior ones being shorter than the anterior ones (corresponding to "Pattern B" of Arnold, 1989). The centra are elongate and procoelous when articulated. There is a distinct posterior centrosynapophyseal lamina, but no postzygoprezygapophyseal lamina. In contrast to the non-autotomic vertebrae, autotomic elements also have a distinct interpostzygapophyseal lamina bordering a deep fossa below the neural spine summit. The neural spine is marked by a postspinal lamina.

The scapulocoracoid (Fig. A4.9A) misses the dorsal portion of the scapula, the ventral half of the coracoid, and the procoracoid. The bone is convex dorsoventrally in axial view. No suture is visible between the scapula and the coracoid. The scapular blade has subparallel anterior and posterior margins close to the glenoid surface, but appears to expand anteroposteriorly towards its dorsal end, which is broken off. A distinct, elevated, dorsoventrally elongate facet is located on the posterior margin, close to the glenoid. The cross-section of the scapular blade is oval, with a pointed anterior corner, and a transversely wider posterior portion. The glenoid is saddleshaped, being convex anteroposteriorly, and concave dorsoventrally. The scapular portion of the glenoid is wider than the contribution from the coracoid. The coracoid is marked by two distinct depressions, one between the procoracoid and the mesocoracoid, where also the supracoracoid foramen is located. The second concavity lies ventral to the mesocoracoid, but due to its incompleteness, it remains unclear if there could have been a distinct emargination as in teiids (Lécuru 1968; Estes et al. 1988). The coracoid foramen is located at about the centre of the glenoid facet. The preserved dorsoventral length of the scapulocoracoid is 10.8 mm.

Most humeri miss either the distal or the proximal end. Only MT-IX-017 (Fig. A4.9B-C) is completely preserved. These bones are large and have a long and slender shaft. The length of MT-IX-017 is 18 mm. The proximal epiphysis bears a moderately small humeral condyle, flanked by well-developed medial and lateral tuberosities. Two sharp ridges, the humeral and the deltopectoral crests respectively, run distally from the two tuberosities. In dorsal view, the margin connecting the humeral condyle and the lateral tuberosity is steeply inclined. A moderately deep bicipital fossa is present on the ventral surface of the proximal epiphysis. The

diaphysis is straight, and tends to be dorsoventrally flattened. It forms almost two fifths of the total length of the humerus. On the anterior surface of the distal epiphysis, the radial condyle is slightly narrower, slightly longer and distinctly more anteriorly developed than the ulnar one. The two condyles are separated by a shallow condylotrochlear gutter and a deep radioulnar fossa is located proximally to them. A robust entepicondyle is present on the ventral side of the epiphysis, whereas on the dorsal side there is a less developed ectepicondyle. The latter is marked proximally by a sharp ectepicondylar crest and is pierced by the ectepicondylar foramen. The entepicondylar foramen, on the other hand, is not present. When both ends are preserved, the epiphyses have a subequal width.

The completely-preserved ulna (Fig. A4.9D-E) is a slender bone, which curves ventrally and slightly laterally towards its distal end. The proximal end bears the olecranon process, with a proximodistally concave articular facet for the humerus. The facet is wide proximally and tapers to a point distally, forming a distinct process projecting medially. A weak ridge follows the curvature of the articular facet posterior to it. The posterior surface of the olecranon process is concave for the reception of the radius, whereas the anterior surface is flat to slightly convex. The shaft is transversely compressed, most strongly around midshaft. Transverse width continuously decreases from proximal to distal, and reaches its minimum length close to the distal articular surface. The distal surface is expanded in anterior view, medially more so than laterally. It bears a semispherical articular surface for the carpals. The specimen is 14.2 mm long and has a minimum transverse shaft width of 0.8 mm.

All pelvic girdles (Fig. A4.9F-G) are large and composed by completely fused ilium, ischium and pubis. They are often fragmentary and the pubis is almost completely missing in all specimens. The acetabulum is large and either subcircular or suboval, with no trace of suture line. The ilium is long, medio-laterally compressed and posteriorly narrowing, even if the posterior end is always broken off. Its dorsal margin can show a very low angle in lateral view. A well-developed and thumb-like

preacetabular process is present by its base, dorsally to the acetabulum. The process projects almost perpendicular to the long axis of the iliac blade. The ischium is always badly preserved and mostly broken, but in the most complete specimens it distinctly enlarges distally to form a wide laminar portion. This portion of the girdle is triangular, and forms a 90-95° angle with the ilium. As written above, the pubis is not preserved, but the wide obturator foramen (or at least its posterior margin) is still visible in some specimen. In the largest specimens, the maximum diameter of the acetabulum is 4.5 mm.

Most femurs are almost complete. Only MT-IX-039 misses the distal epiphysis. These bones are large and provided with a long and roughly straight shaft, forming more than two thirds of the length of the bone. MT-IX-016, the best-preserved one (Fig. A4.9H-I), is 24 mm in length. The proximal epiphysis bears a well-developed femoral condyle and a robust internal trochanter, separated by a deep intertrochanteric fossa in ventral view. The distal epiphysis is composed by a well-developed posterior condyle and by a smaller anterior condyle. The related small epicondyles are located proximally to each condyle. In ventral view, the intercondylar groove is very shallow, as well as the "popliteal" fossa. In dorsal view, a low and sharp ridge is visible on the anterior portion of the epiphysis. The linea aspera is not recognisable on the ventral surface of the shaft.

Most of the recovered tibiae (Fig. A4.9J-K) are preserved completely, but some lack their distal end. These bones are straight in dorsal view, and slightly curved in anterior view. The proximal epiphysis bears two subparallel condyles for the articulation with the femur. A distinct cnemial crest extends ventrally from the posterodorsal corner of the articular surface for about one fifth of the entire proximodistal length of the tibia. A ventral crest marks the anteroventral edge of the shaft approximately at the level, where the cnemial crest fades out. The dorsal surface of the shaft between the two crests is slightly concave anteroposteriorly. The ventral crest bears a small tubercle for the insertion of the M. femorotibial gastrocnemius (Russell & Bauer 2009). At midshaft, the diaphysis has a subtriangular cross-section,

with a flat dorsal and a pointed ventral surface. The distal portion of the shaft is marked by a distinct tubercle for the insertion of the distal tibiofibular ligament (Russell & Bauer 2009). This tubercle is located on the anterodorsal edge of the distal shaft. The distal articular surface is oval in distal view, being taller dorsoventrally in its posterior half. The anterior portion of the articular surface projects further distally than the posterior one. The longest specimen has a length of 19.3 mm.

The only preserved tarsal bone (MT-IX-066, an astragalocalcaneum; Fig. A4.9L-M) is complete, and has a maximal transverse width of 6.1 mm. MT-IX-066 has two distinct articular surfaces for the tibia and fibula. The facet for the tibia is transversely convex, and curves somewhat onto the medial surface of the bone. The fibular facet is dorsoventrally narrower than the tibial one, and transversely concave. The two facets are separated by a groove, and well offset from the rest of the bone. A dorsoventrally compressed bony shelf projects laterally, forming the lateral margin of the element. The medial margin is subparallel to the lateral one, but taller dorsoventrally, and bears a short longitudinal ridge on the anteroventral edge. The dorsal surface is transversely convex anterior to the tibial facet. The ventral surface is relatively uniform. The distal surface is irregularly sinuous, bearing the facets for the distal tarsals.

The four preserved metapodials (Fig. A4.9N-O) are nearly complete. The longest one has a proximodistal length of 12.6 mm, and a minimum shaft width at midshaft of 0.9 mm. The four bones are probably all from different positions in the manus or pes, but their exact identity could not be identified. They have an elongate shaft, with expanded proximal and distal ends. The proximal ends are expanded more widely than the distal ones, and bear concave articular facets, whereas the distal surface bears condyles for the articulation of the phalanges.

Identification

All the fossil material from Monte Tuttavista previously referred to *Lacerta* sp. is herein considered to belong to a single species of large-sized lacertid lizard. This attribution is supported by several lines of evidence. First, lacertid species of similar

size to the above-described fossil material (i.e., large species of *Gallotia* and *Timon*) do generally not have overlapping species ranges today (Barahona et al., 2000; Ahmadzadeh et al. 2016), indicating that mutual exclusion patterns occur at a certain size. There is only one case of a narrow contact zone between T. lepidus and Timon *nevadensis* in Spain, which probably resulted from a secondary contact (Miraldo et al. 2013; Ahmadzadeh et al. 2016). Second, the variable osteological features in the single elements discussed in the description can be explained by a combination of patterns. Some cases can be attributed to ontogenetic or size-related changes (as e.g., the variability in the concavity of the lateral margins of the frontals). In the majority of other cases, variability among the fossil material was also found to be variable within extant species, implying that they stem from individual variation. Finally, dentition and ornamentation are similar in all cranial bones. Therefore, it appears most plausible that only one large-sized lacertid occurs in the Pleistocene of Monte Tuttavista. The attribution of this species to the genus Lacerta, however, is hindered by some features (Barahona & Barbadillo 1997; Arnold et al. 2007; this work): namely, the weak constriction at midlength of the frontals, the rather large occipital shield of the parietal, the unstepped posterior process of the maxilla and the slightly concave anterior platform of the quadrate. Among extant European lacertids, the latter feature is found exclusively in adults of T. lepidus (Barahona & Barbadillo 1997; this work), but the Sardinian fossils cannot be assigned to this species due to a less enlarged occipital shield of the parietal and a well-developed pterygoid ridge. A distinct separation between large and very small teeth in the posterior portion of the dentary tooth-row, and a high number of small distal teeth has initially been proposed as a diagnostic feature of the extinct lacertid "Lacerta" siculimelitensis (Böhme & Zammit-Maempel 1982; see also Delfino 2001). However, this species has later generally been considered invalid, mostly because the variability in the dentition of *Timon* appears to include also such extreme cases as has been considered autapomorphic for "L." siculimelitensis (Mateo 1988). Given the peculiar combination of features shown by the fossil bones of the large lacertid from Monte Tuttavista, a phylogenetic analysis has been conducted to better understand its uncertain taxonomic identity. This analysis resulted in its assignment to a still indeterminate species of *Timon* (see chapter 4 for details).

Oderzo

"Lacertilia" Owen, 1842 Lacertidae Batsch, 1788

Lacertidae indet. (large size) (Fig. A4.9P-S)

Material: 1 dentary; 1 lower jaw.

Description

The isolated dentary (Fig. A4.9P-Q) is very large. It bears pleurodont, cylindrical, closely-spaced, mono-, bi- or tricuspid teeth. A strong increase in the thickness of the teeth is visible towards the posterior end. The tooth row is roughly 10 mm-long and hosts 22 tooth positions. The Meckelian fossa is large and medially open. Dorsally, it is marked by a slender subdental ridge. The mandibular symphysis is narrow and subhorizontal. The ventral margin is partially broken, but it appears convex in medial view. Six mental foramina are present on the otherwise smooth lateral surface. The posterior processes are broken off.

The articulated lower jaw (Fig. A4.9R-S) is large, with a total length of 18.9 mm from the anterior end of the dentary to the posterior tip of the retroarticular process. The dentary has a convex ventral margin, a wide and medially open Meckelian fossa and a rather slender subdental ridge in medial view. The mandibular symphysis is narrow and subhorizontal. The tooth row, which is 8.6 mm-long, carries pleurodont, cylindrical and mono-, bi- or tricuspid teeth. The robustness of the teeth increases toward the posterior end of the tooth row. The number of tooth positions is 24. The lateral surface is smooth, except for the presence of at least 7 mental foramina. Another foramen is present posteriorly to the seventh one, but due to its much larger size and its shifting compared to the line formed by the other ones might suggest that
it is due to taphonomical reasons rather than be a real mental foramen. The inferior posterior process appears distinctly longer than the superior one. The splenial is blade-like, not ventrally expanded and is pierced in the middle by a very large anterior inferior foramen. A very small anterior mylohyoid foramen is visible ventrally to the anterior inferior one. The ventral margin of the splenial follows that of the dentary in being convex. The coronoid has a tall and slender coronoid process, whose dorsal end does not bend distinctly in posterior direction. In dorsal view, the coronoid is slightly medially concave. The anterior portion of the bone is composed of a small labial process and a larger anteromedial process. Posteriorly, there are a large and roughly lappet-like posteromedial process and a distinct and pointed posterior process. The notch marking the anterior margin of the adductor fossa is therefore deep. On the medial surface of the bone, there is a sharp and welldeveloped coronoid ridge. The angular is elongated, wide and posteriorly forked. The compound bone has a straight ventral margin in medial view. The adductor fossa is very large. The articular condyle is subquadrangular and displays a distinct tubercle anterodorsally. The retroarticular process is subtriagular and posteriorly truncated. Where not covered by other bones, the lateral surface of the compound bone is smooth. A low longitudinal ridge is visible, running slightly dorsally to the articulation surface with the angular. The anterior surangular foramen is located ventrally to the coronoid, whereas the posterior one is visible near the condyle. Identification

The lower jaw pertains to a large-sized lacertid, as evidenced by a number of features such as tooth morphology, wide Meckelian fossa, convex ventral margin of dentary and splenial, shallow medial concavity of the coronoid, width of the angular, subtriangular retroarticular process and large adductor fossa (Barahona 1996; Delfino et al. 2011; this work). Among large-sized lacertids, the presence of an inferior posterior process which is longer than the superior one is found in *A. bedriagae*, *D. oxycephala*, *D. mosorensis*, *H. graeca* and some large species of *Podarcis* (e.g., *P. melisellensis* and *P. siculus*; this work). Although the presence of

A. bedriagae and H. graeca in the Holocene of Oderzo might be considered unlikely due to their current distribution (they live in Corsica and Sardinia and in continental Greece respectively; Sillero et al. 2014), the other species cannot be easily excluded based on geography. Nevertheless, among the considered species, only *P. siculus* is currently living in the area, whereas the other ones live in nearby countries (Sillero et al. 2014). *Podarcis siculus* might be therefore the most probable candidate to be represented in the fossil assemblage of Oderzo, but this cannot be ascertained. It has to be noted that the longer inferior process is present also in juveniles of other large lacertids, such as *Lacerta* and *Timon*, but the size and the not posteriorly directed coronoid process seems to suggest that the lower jaw from Oderzo could represent an adult (Barahona 1996; Barahona & Barbadillo 1997; this work).

The isolated dentary is slightly larger than the related skeletal element in the articulated lower jaw, but its size is comparable with a large specimen of *P. siculus* (this work). Nevertheless, since the posterior processes are missing in this specimen, it is not possible to confidently exclude that it belongs to another large-sized lacertid.

<u>Riparo dell'Aquila</u> "Lacertilia" Owen, 1842 Lacertidae Batsch, 1788

Lacertidae indet. (Fig. A4.9T-U)

Material: 1 dentary articulated with the splenial (MAF 4466).

Description

The ventral margin is convex in medial view. The symphysis is narrow and horizontal. The subdental ridge is narrow, whereas the Meckelian fossa is wide and medially open. The alveolar border is 11 mm in length and carries at least 22 tooth positions. Teeth are sub-pleurodont, cylindrical and slender, but the cusps are eroded. The posterior teeth are slightly more robust than the anterior ones, but a real hypertrophy is not present. The posterior end is broken off. The lateral surface is

smooth, but it carries 6 mental foramina. The anterior half of a large and long splenial is visible in medial view.

Identification

The convex ventral margin and the wide Meckelian fossa allow to attribute this large specimen to a lacertid (Bailon 1991; Delfino et al. 2011; this work). The absence of the posterior processes hinders any further attempt of identification, but the length of the alveolar border fits within the range of a number of moderately-large-sized lacertids (e.g., members of the genus *Lacerta*, subadults of *Timon*, but also large *Podarcis* species).

<u>Rivoli Veronese</u> "Lacertilia" Owen, 1842 Lacertidae Batsch, 1788 *Lacerta* Linnaeus, 1758 *Lacerta viridis* Laurenti, 1768

Lacerta gr. L. viridis (Fig. A4.9V-Z)

Material: 1 frontal (RV-H-143); 1 premaxilla (RV-H-154); 2 jugals (RV-H-015, 158); 4 quadrates (RV-H-016, 147/149); 3 pterygoids (RV-H-169/171); 1 ectopterygoid (RV-H-163); 1 dentary (RV-H-014); 1 splenial (RV-H-161); 1 angular (RV-H-162).

Description

RV-H-143 is a large and paired frontal (Fig. A4.9V-Z), distinctly anteroposteriorly elongated and roughly L-shaped in dorsal view. The posterior end is slightly larger (less than twice as large) than the anterior one. At mid-length, the lateral and medial margins are parallel. The anterior end is poorly preserved, but the posterior margin of the rounded articular surface with the nasal is distinguishable. The posterior margin is also eroded and therefore it is not possible to recognise the development

of the interdigitations. The dorsal surface is completely covered by a well-developed dermal ornamentation. The sulcus separating frontal and frontoparietal shields is scarcely visible roughly by the beginning of the posterior third of the total length of the bone. Another, very scarcely marked groove is present near the anterolateral corner of the bone, located between frontal and prefrontal shields. A large articular surface with the prefrontal reaching mid-length is present on the lateral margin, whereas a moderately small articular surface with the postfrontal is visible covering laterally the poorly developed posterolateral process. A distinctly developed and anteriorly rising crista cranii is present on the ventral surface, but the anterior process is broken. Posteriorly, the ventral surface of the posterolateral process displays a triangular articular surface for the parietal tab. The specimen is 10.5 mm in total length.

The premaxilla is moderately large, with an alveolar plate that is 2.3 mm-wide. Despite being partially broken by the distal end, the ascending nasal process is moderately short, stocky and roughly leaf-shaped in anterior view. Its posterior surface bears a well distinct septonasal ridge, ending before reaching the distal end. The anterior end, on the other hand, is smooth. The short palatal processes are separated medially by a narrow, deep and V-shaped notch. Teeth are pleurodont, cylindrical, slender and monocuspid. A single one seems to show a small accessory cusp, being therefore bicuspid. Nine tooth positions are visible.

The jugals are large and present a very well developed quadratojugal process. Both the anterior and the posterodorsal process are only partially preserved. A distinctly developed palatal process is present, but it does not originate a clear medial process posteriorly. The lateral surface of the bone is covered by a well-marked dermal ornamentation.

The best-preserved specimens among the large quadrates reach 5.5 mm in length. They have a dorsoventrally elongated shape in anterior view and a rounded anterior outline in medial view. The lateral lamina is well developed, originating a deep conch. A flat platform marked by low ridges is present on its anterior surface. The medial lamina is distinctly developed and shows a well-developed pterygoid flange. The cephalic condyle develops posteroventrally and is flanked laterally by a wide squamosal notch. The mandibular condyle is wide and composed by two similarsized portions.

All pterygoids are fragmentary and large-sized. Their total length varies from 5 mm to 7.5 mm, but since they all miss most of the palatine process and a large part of the quadrate process, they would have reached a much higher length in origin. Pterygoid teeth are visible on the ventral surface of the remaining portion of the palatine process. They are arranged in a row in RV-H-169, the largest specimen, but apparently have a more patch-like distribution in the other specimens. The pointed and anterolaterally-directed pterygoid flange is preserved only in RV-H-170. This structure displays a well-developed ridge on both the dorsal and the ventral surface. The quadrate process is straight in dorsal view. It bears a deep fossa columellae and a flat basipterygoid fossa, continuing posteriorly in a wide and medially concave surface. The preserved portion of the pterygoid ridge is well developed.

RV-H-163 is a large-sized and roughly L-shaped ectopterygoid. The long and pointed anterolateral process is largely covered by the articular surface with the maxilla ventrally. A short posterolateral process is present. The posteromedial process is composed by three lappets. Dorsally, the bone is smooth.

The dentary is large-sized, with a total length of 11.5 mm. It has a wide and medially open Meckelian fossa and a convex ventral margin. The posterior end is missing, as well as the entire posterior half of the tooth-row. A narrow subdental ridge is present, ending anteriorly with a narrow and subhorizontal mandibular symphysis. The preserved portion of the tooth-row bears 14 tooth positions. Teeth are pleurodont, slender and cylindrical, with a distinct trend towards a posterior strengthening. All preserved teeth are distinctly bicuspid, with a large main cusp located posteriorly to a smaller secondary cusp. The lateral surface is smooth, displaying 5 mental foramina.

The splenial is large-sized and blade-like. Both anterior and posterior ends are roughly pointed, but present a small notch that gives them a more forked appearance. The bone is pierced by two foramina in the middle: a very large anterior inferior foramen dorsally and a very small anterior mylohyoid foramen ventrally. The medial surface is smooth, whereas two well-developed ridges run longitudinally along the lateral one: the ventral crest is located in the middle of the bone, whereas the dorsal one runs just ventrally to the dorsal margin. The ventral margin of the bone is convex and not strongly expanded.

The angular is large, anteroposteriorly elongated and moderately wide in lateral view. It has a pointed anterior end and an irregular posterior end. The ventral margin is thickened and pierced dorsoventrally by the posterior alveolar foramen roughly at mid-length. The thick area is marked dorsally by the angular ridge.

Identification

All the above-described specimens clearly belong to a similarly large-sized lacertid, such as members of the genera *Lacerta* and *Timon* (Barahona & Barbadillo 1997; this work). The unconstricted frontal with parallel margins is a distinctive feature of *Lacerta* (Barahona & Barbadillo 1997; this work) and RV-H-143 recalls *L. bilineata*, *L. trilineata* and *L. viridis* in having a posterior end that is less than twice as large as the anterior one (this work). The premaxilla and the pterygoid are also consistent with an attribution to *Lacerta* because of the size range, the morphology of the ascending nasal process, the presence of a bicuspid teeth in RV-H-154, the well-developed pterygoid ridge and the presence of pterygoid teeth (Barahona & Barbadillo 1997; this work).

Zootoca Wagler, 1830 Zootoca vivipara (Jacquin, 1787)

cf. *Zootoca vivipara* (Fig. A4.9AA-AB) Material: 1 pair of fused frontals (RV-H-144).

Description

RV-H-144 is a small pair of fused frontals. Only the posterior portion of the bone is preserved, with the anterior end and the right posterolateral process missing. In ventral view, the suture line is still distinguishable longitudinally. Due to the absence of the entire anterior portion, it is not possible to clearly recognise the presence of a constriction at mid-length. The posterolateral process is long in dorsal view. It displays a very small articular surface for the postfrontal on its lateral margin. A rather well developed dermal ornamentation, clearly divided into frontal and frontoparietal shields, covers the specimen dorsally. Interdigitations on the posterior margin are poorly developed. Cristae cranii runs along the lateral margins ventrally, being mostly low but tending to rise towards the missing anterior end. The triangular articular surface for the left parietal tabs is poorly marked. The total length of the specimen is roughly 4 mm.

Identification

RV-H-144 is small-sized, but it is clearly an adult due to the fusion of the two paired frontals, which occurs late in ontogeny in most lacertids (Barahona 1996; Barahona & Barbadillo 1997; this work). A poorly interdigitated posterior margin is typical of *A. marchi, A. moreoticus, I. bonnali, I. horvathi, P. filfolensis, P. lilfordi* and *Z. vivipara* (this work), but, in terms of adult size, only *A. marchi, P. filfolensis* and *Z. vivipara* are comparable with RV-H-144, with other species usually reaching distinctly longer frontals (this work, but see also Barahona & Barbadillo 1997). *Algyroides marchi* currently lives only in a small area in southeastern Iberian Peninsula, whereas *P. filfolensis* is endemic of the Maltese Archipelago and the Pelagie Islands (Sillero et al. 2014; Speybroeck et al. 2016). Because of this, it appears possible to tentatively assign RV-H-144 to *Z. vivipara*.

Lacertidae indet. (Fig. A4.9AC-AF)

Material: 5 frontals (RV-H-145/146); 1 parietal (RV-H-165); 4 premaxillae (RV-H-155/157, 222); 15 maxillae (RV-H-174/177, 201, 224); 2 prefrontals (RV-H-160,

193); 6 jugals (RV-H-159, 185/186, 213); 4 quadrates (RV-H-150, 194); 1 pterygoid (RV-H-172); 1 ectopterygoid (RV-H-164); 60 dentaries (RV-H-178/179, 184, 206, 220); 9 fragments of tooth-bearing bones (RV-H-166, 204, 227); 1 splenial (RV-H-199); 3 coronoids (RV-H-152, 192); 1 compound bone (RV-H-153).

Description

Frontals are paired, L-shaped and antero-posteriorly elongated. Their size varies from very small to moderately large, with the maximum length reached by RV-H-145 (9 mm). They present a weak but distinct middle constriction. None of the specimens is complete, missing part of either the anterior or the posterior ends (usually both). The dorsal surface is covered by a dermal ornamentation, which is well developed in RV-H-145 and distinctly less developed in the other specimens. On the lateral margin of the ventral surface, the cristae cranii are posteriorly low, but develop an (always broken) anterior process anteriorly. When partially preserved, the latter process appears moderately narrow in lateral view. The only specimen preserving the posterior end, RV-H-145, shows distinctly developed interdigitations. RV-H-165 is a very small and very poorly preserved fragment of parietal (Fig. A4.9AC-AD), represented only by the area of the shelf surrounding the parietal fossa. The latter is wide and U-shaped. On the ventral surface, the wide medial ventral crest is visible anteriorly to it, contacting laterally the low and rounded anterior ventral crests. In the middle of the anterior margin of the preserved portion of the shelf, the posterior margin of the parietal foramen is visible. The dorsal surface is covered by a moderately developed dermal ornamentation. A small occipital shield is recognisable, together with parts of the lateral and the interparietal shields. An area levis seems not to be present.

RV-H-155 and 156 (Fig. A4.9AE-AF) are small premaxillae, bearing a slender and pointed ascending nasal process provided with roughly parallel lateral margins. The anterior surface of the process is smooth in the former, but presents a lightly developed dermal ornamentation by the tip in the latter. Posteriorly, the septonasal crest is sharp in RV-H-156 and less distinct in RV-H-155. In both cases, it reaches

the distal end of the preserved portion of the process. Palatal processes are broken in both specimens. Teeth are pleurodont, slender and cylindrical. They are well preserved only in RV-H-155, showing a monocuspid crown. The number of tooth position is 9 in RV-H-155. The tooth row of RV-H-156 is partially missing, but at least 5 tooth positions are still present. The alveolar border is 2 mm-wide in RV-H-155 and more than 1.5 mm-wide in RV-H-156. RV-H-157 is poorly preserved, but strongly larger than the two other specimens (the width of the preserved portion of the alveolar border is 2.5 mm). This specimen misses the ascending nasal process, but the general morphology, as well as the tooth one, is similar to the previously described premaxillae. At least 7 tooth positions are preserved. The small RV-H-222 is also poorly preserved and similar in morphology to the other premaxillae. It clearly bears both mono- and bicuspid teeth.

Most maxillae are very fragmentary, but two moderately preserved specimens (RV-H-174 and 75) are also present. The two best preserved specimens represent moderately large individuals (length of the tooth row reaches 9 mm and at least 7.8 mm respectively), but the other fragments include smaller ones also. The anteromedial process is never preserved, but a well-developed lappet is recognisable at least in RV-H-174. The facial process, which is never completely preserved, displays a low arched ridge on the medial surface and a dermal ornamentation on the lateral one. The ornamentation is always poorly developed. The posterior process is rather well preserved only in RV-H-174 and 175. Both specimens show a distinct step on its dorsal margin, near the posterior end. The step is not provided with a distinct spur. Teeth are pleurodont, cylindrical, slender, mono-, bi- and tricuspid. A light increase in the robustness of the teeth is visible posteriorly in some specimens. Among prefrontals, RV-H-160 is moderately large, whereas RV-H-193 is very small. The anterior anterodorsal process is covered dorsally by a dermal ornamentation, which is well developed in the former and less developed in the latter. The lateral margin of the posteroventral process is always broken and so the lacrimal notch is not visible. The dorsal process is moderately long and pointed. In lateral

view, it appears roughly as long as the anterodorsal process in RV-H-160 and shorter than it in RV-H-193. A moderately developed palpebral crest is present on its lateral surface.

The jugals are small and poorly preserved. Both the anterior and the posterodorsal process are broken. A well-developed quadratojugal process is present, as well as a moderately developed palatal process. The latter does not show a medial process. The dermal ornamentation on the lateral surface is not distinctly developed.

The small and fragmentary quadrates always miss the lateral lamina and are represented only by the pillar and by the moderately developed medial lamina. The latter develops a very low pterygoid flange by the ventral end. The cephalic condyle is slightly posteroventrally developed, whereas the mandibular one is composed by two similar-sized portions. The length of the quadrate reaches 3.5 mm.

The pterygoid is small-sized and poorly preserved. It does not have pterygoid teeth. The anterior portion of the bone is almost completely missing. The quadrate process is straight in dorsal view and bears a well-developed pterygoid ridge.

RV-H-164 is a poorly preserved and small ectopterygoid. It is represented only by a posteromedial process composed by three lappets and by a small part of the anterolateral process. The remaining part of the ventral surface of the latter is covered by the articular surface with the maxilla.

The preservational status of the dentaries is very variable, with both very fragmentary and almost complete specimens represented. The posterior processes, however, are never preserved. Different sizes are recognisable: specimens can be either very small or moderately large. The largest one, RV-H-178, reaches up to 9 mm in length. In medial view, the dentaries have a more or less convex ventral margin, a narrow subdental ridge and a narrow and subhorizontal mandibular symphysis. The lateral surface is smooth, displaying only the mental foramina. Teeth are pleurodont, cylindrical, mono-, be- or tricuspid. They are generally slender, but a trend towards a more robust morphology is recognisable posteriorly in many specimens. The fragments of tooth-bearing bones are poorly preserved, but bear pleurodont, cylindrical and bi- or tricuspid teeth. Some specimens are larger and carry more robust teeth than others.

RV-H-199 is a fragment of a small and blade-like splenial. The bone is pierced in the middle by a wide anterior inferior foramen and a very small anterior mylohyoid foramen.

The coronoids are small and thin. In dorsal view, they are slightly medially concave. Anteriorly, a moderately developed labial process and a partially broken anteromedial process are present. The coronoid process is low, thin, dorsally rounded and posteriorly directed in RV-H-152, more dorsally directed in the other specimens. The posterior end is broken, but it appears wide in lateral view. A laminar coronoid ridge runs from the posterior margin of the coronoid process on the medial surface of the posterior end.

Only the posterior end of the small compound bone is preserved. It has a quadrangular articular cotyle provided with a small tubercle on the antero-medial corner. The retroarticular process is subtriangular and roughly posteriorly truncated in lateral view. Its lateral surface is smooth, whereas a sharp tympanic ridge is present medially. Ventrally to this ridge, the bone is not strongly expanded. Identification

These specimens present clearly a lacertid morphology (this work), but in most cases it is difficult to state if they represent adults of small-sized taxa or juveniles/subadults of larger ones. At least for the largest specimens, small lacertids can be excluded, but the size they reach is consistent either with an adult of medium-sized species (as e.g., large *Podarcis*) or with subadults of *Lacerta* gr. *L. viridis*, the only large lacertid confidently identified in Rivoli Veronese. Nevertheless, some example of certified adult is indeed present, as for example the small coronoids with a dorsally-directed coronoid process. The most significant adult specimens are the parietal RV-H-165 and the premaxilla RV-H-156. The small-sized RV-H-165 is undoubtedly an adult because of the distinctly developed ornamentation reaching the posterior margin of

the shelf (Barahona & Barbadillo 1997; Barahona & Barbadillo 1998; this work). The absence of the smooth posterior area levis rules out the assignment of this specimen to *Z. vivipara* (Barahona & Barbadillo 1997; this work), and therefore suggests the presence of a second small-sized lacertid in the early Pleistocene of Rivoli Veronese. The presence of this other lacertid species is testified also by RV-H-156, which can be considered an adult because of the dermal ornamentation it carries. As for the parietal, RV-H-156 belongs to a small-sized taxon, but *Z. vivipara* is excluded by the morphology of the ascending nasal process, which is not leaf-shaped (Barahona & Barbadillo 1997; this work).

Scincomorpha indet.

Material: 8 dentaries (RV-H-167, 180/181, 229).

Description

These specimens are poorly preserved fragments of dentary. Teeth are pleurodont, cylindrical and slender, but they are never preserved. Ventrally to them, a narrow subdental ridge is present.

Identification

Despite being poorly preserved, these specimens can be attributed to indeterminate scincomorphans because of the pleurodont dentition and the narrow subdental ridge (Evans 2008). Even if clear diagnostic features are absent because of the preservational status of the remains, they most probably belong to the only scincomorphans recognized in Rivoli Veronese: i.e., lacertids.

Anguidae Gray, 1825 Anguinae Gray, 1825 Anguis Linnaeus, 1758 Anguis fragilis Linnaeus, 1758

Anguis gr. A. fragilis (Fig. A4.9AG-AJ)

Material: 1 frontal (RV-H-236); 1 jugal (RV-H-237); 1 pterygoid (RV-H-173); 2 dentaries (RV-H-034/035); 1 coronoid (RV-H-191); 1 cervical vertebra (RV-H-038); 67 trunk vertebrae (RV-H-036/037, 215); 4 cloacal vertebrae (RV-H-041); 45 caudal vertebrae (RV-H-039, 40, 065, 168, 214, 238); 21 osteoderms (RV-H-029, 219). Description

The frontal is small, paired and antero-posteriorly elongated, with parallel lateral and medial margins. The preserved portion of the specimen, which misses the anterior end, is 3.3 mm-long. On the dorsal surface, a well-developed dermal ornamentation is visible, but it does not contact the lateral margin of the bone. Most of the ornamentation is represented by the large frontal shield, but posteriorly small interfrontal (medially) and frontoparietal (laterally) shields are present. The degree of development of the latter shield is lower than in the frontal one. A short posterolateral process is present, developing a short and posteriorly directed lappet on its ventral surface. The crista cranii is very well developed and laminar. It seems not to develop an anterior process. Laterally, a moderately large articular surface with the prefrontal is visible along half of the preserved portion of the specimen. This surface almost reaches the articular surfaces with the postfrontal, which covers the lateral surface of the posterolateral process, but the two surfaces are not in direct contact.

The jugal is small and slender. It has a distinct, though not strongly developed, quadratojugal process and a very poorly developed palatal process devoid of medial process. The anterior process displays a ventrally shifted articular surface with the maxilla anteriorly and a smooth lateral surface. A single foramen pierces the lateral surface, generating a canal that opens on the medial surface also. The posterodorsal process is mostly missing.

The pterygoid is moderately small-sized (total length is 4.1 mm) and misses a large part of both the anterior end and of the quadrate process. The preserved portion of palatine process appears slender, straight and devoid of pterygoid teeth. Moderately developed ridges are visible on the pterygoid flange, both dorsally and ventrally. In dorsal view, the quadrate process is straight. A moderately developed pterygoid ridge is present posteriorly to the deep and anteroposteriorly elongated fossa columellae. The basipterygoid fossa is marked both dorsally and ventrally by flanges. The ventral flange is moderately developed and rounded.

Dentaries are small: the tooth row of the most preserved one (RV-H-034; Fig. A4.9AG) is 6 mm-long, even if, based on tooth size, the other one could have been larger in origin. Both specimens have a ventrally developed subdental shelf, which covers the narrow Meckelian fossa medially. Anteriorly, a narrow and subhorizontal mandibular symphysis is present. In dorsal view, the posterior end of the symphysis develops a small medial expansion. The posterior end, partially preserved in RV-H-034, bends in dorsal direction. Preserved teeth are subpleurodont, well-spaced and canine-like, provided with a pointed tip distinctly bending posteriorly. Eight tooth positions are recognisable in RV-H-034, whereas 4 are preserved in RV-H-035. The posterior end of the intramandibular septum is free; in RV-H-034, it is located slightly anteriorly to the last tooth position. The lateral surface is smooth, with up to 5 mental foramina. The ventral margin of the bone is straight.

The coronoid is moderately small-sized. A short labial process is present, whereas the anteromedial one is broken. The coronoid process is moderately robust and dorsally rounded in medial view. Posteriorly, it is linked to the posteromedial process by a well-developed and thin osseous lamina. The posteromedial process is moderately wide, long and posteriorly lobe-shaped. It does not bend distinctly in ventral direction. In dorsal view, the coronoid is rather straight.

Presacral vertebrae are small-sized and antero-posteriorly elongated (Fig. A4.9AH-AJ). Their vertebral centrum is procoelous and dorso-ventrally compressed, with a length reaching up to 4.8 mm. In ventral view, the lateral margins of the centrum are parallel in the posterior half. Synapophyses are dorsoventrally elongated. A distinct neural spine is present on the dorsal surface. Zygapophyses are subelliptical and dorsally tilted.

Cloacal vertebrae are morphologically and dimensionally similar to the presacral vertebrae, but present wide transverse processes by the sides.

Caudal vertebrae are procoelous, small-sized and provided with a dorso-ventrally compressed centrum. The bases of fused hemapophyses are clearly present on the ventral surface. The autotomy plane is also visible in almost all of the vertebrae. Osteoderms are thin and rounded. Their external surface is composed by a smooth gliding surface and by an area covered by a vermicular ornamentation.

Identification

These specimens belong to a small-sized anguid, which can be identified as a member of the *Anguis fragilis* species complex because of the dermal ornamentation not reaching the lateral margin of the frontal, unornamented jugal without medial process and with a distinct quadratojugal process, ventral flange of the basipterygoid fossa rounded, absence of pterygoid teeth, intramandibular septum free posteriorly and ending near the last tooth position, thin lamina on the coronoid, canine-like, well-spaced and unstriated teeth, small-sized vertebrae with parallel lateral margins in the posterior portion of the centrum and thin and rounded osteoderms (Klembara 1981; Holman 1998; Klembara et al. 2014; this work).

?Anguis sp. (Fig. A4.9AK-AL)

Material: 1 dentary (RV-H-235).

Description

RV-H-235 is a small dentary, missing the anterior end. The preserved portion of the tooth row is 3.9 mm in length. A well-developed subdental shelf is present medially. The shelf develops a small, but broken, splenial spine in its posterior portion. Only the superior posterior process is preserved posteriorly. It is distinctly bent in dorsal direction and composed by two small projections separated by a shallow coronoid incisure. Six tooth positions are visible, carrying two well-preserved teeth by the posterior end of the tooth row. Teeth are sub-pleurodont, well-spaced, unstriated, canine-like and distinctly postero-medially bending by their tip. The posterior end of

the intramandibular septum is located slightly posteriorly to the second posteriormost tooth position and the splenial spine. Its ventral margin is fused to the wall of the bone. The lateral surface of the specimen is smooth and displays 3 mental foramina.

Identification

The general morphology of RV-H-235 is very similar to that of the dentaries previously attributed to *Anguis* gr. *A. fragilis*. In *Anguis*, however, the posterior portion of the intramandibular septum is free (Klembara et al. 2014; this work), casting some doubts on the correct attribution of this specimen.

Pseudopus Merrem, 1820

cf. Pseudopus sp. (Fig. A4.9AM-AP)

Material: 1 dentary (RV-H-033); 1 caudal vertebra (RV-H-030); 3 osteoderms (RV-H-007/008, 028).

Description

RV-H-033 (Fig. A4.9AM) is a small fragment of dentary, measuring 4.5 mm in length. It has a narrow subdental shelf, which covers a narrow and ventrally open Meckelian fossa. At least 4 tooth positions are recognisable, but only a single tooth is well preserved. The latter is subpleurodont, moderately robust and subcylindrical. The crown displays a pointed tip and no striae, neither on the lingual nor on the labial surface.

The caudal vertebra (Fig. A4.9AN-AP) is large and poorly preserved. Its general aspect is blurred, maybe suggesting some kind of chemical erosion. The vertebral centrum is procoelous and dorsoventrally compressed. In spite of the wearing, a hint of the base of the right hemapophysis is recognisable on the ventral surface. There is no autotomy plane.

Though fragmentary, the osteoderms are large and robust. They display a distinct ornamentation composed by tubercles and grooves on the external surface, except for the smooth gliding surface.

Identification

The robustness of both the caudal vertebra and the osteoderms prevent the assignment of these remains to *Anguis*, rather indicating the presence in Rivoli Veronese of a second, large-sized anguid. The tooth preserved in RV-H-033 recalls the tooth morphology of *Pseudopus* in being cylindrical and moderately robust (Klembara et al. 2014; this work), and, according to Etheridge (1967), caudal vertebrae devoid of autotomy plane compose the tail of *P. apodus*. It is therefore possible to tentatively assign these specimens to this genus. It has to be noted, however, that caudal vertebrae of two of the specimens of *P. apodus* used as comparative material (MDHC 214 and 215) present the autotomy plane.

"Lacertilia" indet.

Material: 3 quadrates (RV-H-202); 1 pterygoid (RV-H-196); 1 dentary (RV-H-209); 1 compound bone (RV-H-198); 1 atlas (RV-H-197); 9 cervical vertebrae (RV-H-217, 239, 242); 28 trunk vertebrae (RV-H-218, 221, 241, 243); 3 cloacal vertebrae (RV-H-244, 248); 27 caudal vertebrae (RV-H-210, 223, 240, 245, 246); 8 ribs (RV-H-031/032, 066, 195, 249); 3 scapulocoracoids (RV-H-251); 52 humeri (RV-H-017, 207, 253); 6 ulnae (RV-H-114, 208, 247); 19 pelvic girdles (RV-H-252); 63 femurs (RV-H-205, 254); 23 tibiae (RV-H-203, 250).

Identification

These specimens are either strongly damaged or missing diagnostic features and are therefore attributed only to indeterminate lizards. Nevertheless, it is possible that at least the largest specimens might belong to *Lacerta* gr. *L. viridis*.

Tenuta Zuccarello

"Lacertilia" Owen, 1842

Lacertidae Batsch, 1788 Lacerta Linnaeus, 1758 *Lacerta viridis* Laurenti, 1768

Lacerta gr. *L. viridis* (Fig. A4.9AQ-AV) Material:

- I infill: 3 frontals (MSNVE-23366/6-7); 5 premaxillae (MSNVE-23366/12); 28 maxillae (MSNVE-23366/2-5); 3 jugals (MSNVE-23366/34); 1 postorbital (MSNVE-23366/15); 6 quadrates (MSNVE-23366/16-17); 5 (MSNVE-23366/8-9); 4 otooccipital regions pterygoids (MSNVE-23366/10); 1 sphenoid (MSNVE-23366/11); 26 dentaries (MSNVE-23366/1, 30-31); 1 splenial (MSNVE-23366/29); 1 coronoid (MSNVE-23366/36); 1 angular (MSNVE-23366/37); 3 articulars fused with surangulars (MSNVE-23366/20); 1 surangular (MSNVE-23366/35); 6 axes (MSNVE-23366/41); 228 presacral vertebrae (MSNVE-23366/40); 14 cloacal vertebrae (MSNVE-23366/45); 1 pair of fused cloacal vertebrae (MSNVE-23366/46); 69 caudal vertebrae (MSNVE-23366/42-43); 1 chevron (MSNVE-23366/44); 1 rib (MSNVE-23366/47); 5 clavicles (MSNVE-23366/32-33); 20 humeri (MSNVE-23366/25-26); 4 ilia (MSNVE-23366/23-24); 8 ischia (MSNVE-23366/18-19); 5 pubes (MSNVE-23366/27-28); 18 pelvic girdles (MSNVE-23366/38-39); 24 femurs (MSNVE-23366/21-22); 23 tibiae (MSNVE-23366/13-14).
- II infill: 2 caudal vertebrae (MSNVE-23378/1-2).

Description

Unfused frontals reach 13 mm in length. They are not constricted in the medial region and show a strongly interdigitated posterior margin. In dorsal view, the articulation surface with the dorsal process of the maxilla is very small. Premaxillae have a leaf-shaped posterodorsal process and show 9 to 11 tooth positions. The maximum width of their shelf reaches 3.8 mm.

Maxillae are very large and present 16 to 20 tooth positions. Their maxillary shelf reaches a maximum length of 11.5 mm. The anterior projection of the dorsal process and the lappet on the anterior process are well developed (except for the lappet of MSNVE-23366/2 and 4, which is poorly developed). The posterior process shows a clear step near its end.

Jugals are large and are provided with a well-developed quadratojugal process. There is no medial process on the palatal process. In lateral view, the exposed portion of the anterior part is very small.

The postorbital is large and not fused with the postfrontal. The anteromedial process is present and well developed.

Pterygoids are very large, reaching 16 mm in length. They present a strong pterygoid recess and a large number of pterygoid teeth.

In medial view, quadrates have a rounded anterior outline. Their anterior platform is flat and they reach a maximum length of 6 mm.

Bones composing the otooccipital regions are very large. The sphenoid shows an undepressed ventral surface and strongly laterally expanded basipterygoid processes. Its cristae ventrolaterales form the anterior wall of the sphenooccipital tubercles. Prootics have a very well developed alar process and a very distinct posterior process. The paroccipital process of the otooccipital is very long. The anterolateral margins of the supraoccipital are distinctly convergent and the processus ascendens is largely ossified.

Dentaries (Fig. A4.9AQ-AR) have a large and medially opened Meckelian fossa. They are very large, with a tooth row reaching 14 mm in length. The posterior processes are almost equal in size. Number of tooth positions goes from 21 to 27. Articulars are large and straight in medial view. They are fused with surangulars. Teeth on maxillae and dentaries are pleurodont, cylindrical and mono-, bi- or tricuspid. In premaxillae, only mono- and bicuspid morphologies are present. Vertebrae are large and antero-posteriorly elongated. Their centrum is circular in posterior view, with a well-developed keel on the ventral surface (only in the cloacal ones the keel is less developed). The maximum centrum length of presacral vertebrae is 4.8 mm. Caudal vertebrae (Fig. A4.9AS-AV) do not present fused hemapophyses. Autotomy plane can be present (MSNVE-23366/42) or absent (MSNVE-23366/43 and 23378/1-2). MSNVE-23366/46 is a pair of fused cloacal vertebrae.

All other bones are large.

Identification

Maxillae and dentaries bearing pleurodont, cylindrical, mono-, bi- or tricuspid teeth are a feature of the family Lacertidae (Bailon 1991; Delfino 2002; Delfino et al. 2011; this work). Following Barahona and Barbadillo (1997), the largest remains can be assigned to *Lacerta* gr. *L. viridis*, a species complex comprising middle-sized European lacertids of the genus *Lacerta*. Assignment of the remains to *Timon lepidus*, the largest lacertid currently living in Europe, is prevented by frontals not constricted, stepped posterior process of the maxillae, flat anterior platform of the quadrates, strong pterygoid recess and sphenoids with an undepressed ventral surface (Barahona & Barbadillo 1997; this work).

Lacertidae indet. (Fig. A4.9AW-AX) Material:

I infill: 19 maxillae (MSNVE-23367/1-2); 2 postorbitals (MSNVE-23367/31); 1 quadrate (MSNVE-23367/32); 2 pterygoids (MSNVE-23367/21); 23 otooccipital regions (MSNVE-23367/27); 1 basioccipital (MSNVE-23367/28); 3 sphenoids (MSNVE-23367/29); 1 otooccipital (MSNVE-23367/30); 17 dentaries (MSNVE-23367/29); 1 otooccipital (MSNVE-23367/30); 17 dentaries (MSNVE-23367/ 3-6, 8); 12 axes (MSNVE-23367/7); 41 presacral vertebrae (MSNVE-23367/9, 11); 2 pairs of fused cloacal vertebrae (MSNVE-23367/14-15); 87 caudal vertebrae (MSNVE-23367/10, 12); 1 chevron (MSNVE-23367/13); 5 interclavicles

(MSNVE-23367/19); 7 humeri (MSNVE-23367/16, 22-23); 14 femurs (MSNVE-23367/17-18, 23-24); 2 tibiae (MSNVE-23367/26); 12 indeterminate elements (MSNVE-23367/20).

Description

Remains assigned to indeterminate lacertids are morphologically similar to those referred to *Lacerta* gr. *L. viridis*, but much smaller. The maximum length of the shelf of the maxillae is 6 mm and they bear 13 to 17 tooth positions. The maximum length of the quadrate is 3.4 mm. Pterygoids reach a maximum length of 9 mm and have no pterygoid teeth. As for the dentaries (Fig. A4.9AW-AX), the maximum length is 7 mm and the number of tooth positions goes from 16 to 23. The inferior posterior process is longer than the superior one. Otooccipital regions are not completely fused. Alar and posterior processes of the prootics, paroccipital processes of the otooccipitals and the processus ascendens of the supraoccipital are less developed than the same structures in remains referred to *Lacerta* gr. *L. viridis*. Maximum centrum length of presacral vertebrae is 2.3 mm. Autotomy plane is absent in MSNVE-23367/10 and present in MSNVE-23367/12. MSNVE-23367/14 and 15 comprehend two fused cloacal vertebrae. Interclavicles are small and cross-shaped. Identification

Smaller remains of lacertids have been attributed only to indeterminate members of the family. They could represent another smaller species, but also juveniles of *Lacerta* gr. *L. viridis*. The length of the posterior processes of MSNVE-23367/5 might support the second hypothesys (Barahona & Barbadillo 1997; this work).

Anguidae Gray, 1825 Anguinae Gray, 1825 Anguis Linnaeus, 1758 Anguis fragilis Linnaeus, 1758 *Anguis* gr. *A. fragilis* (Fig. A4.9AY-BE) Material:

- I infill: 1 frontal (MSNVE-23368/12); 3 parietals (MSNVE-23368/6-7, 14);
 1 premaxilla (MSNVE-23368/1); 13 maxillae (MSNVE-23368/2-3); 1
 quadrate (MSNVE-23368/26); 39 dentaries (MSNVE-23368/4-5); 1
 coronoid (MSNVE-23368/27); 6 compound bones (MSNVE-23368/28-29);
 3 axes (MSNVE-23368/25); 92 cervical vertebrae (MSNVE-23368/8); 1732
 trunk vertebrae (MSNVE-23368/16-17, 24); 63 cloacal vertebrae (MSNVE-23368/19-23); 4
 osteoderms (MSNVE-23368/11, 13).
- II infill: 1 maxilla (MSNVE-23379/4); 2 dentaries (MSNVE-23379/5-6); 1 cloacal vertebra (MSNVE-23379/3); 44 caudal vertebrae (MSNVE-23379/1-2).

Description

MSNVE-23368/12 is a small, paired frontal with a moderately ornamented dorsal surface and a well-developed crista cranii frontalis. In dorsal view, it is triangular and anteroposteriorly elongated. A well-developed posterolateral process is visible by the posterolateral corner of the bone. In lateral view, the articulation surface with the prefrontal covers two thirds of the length of the bone and no ventral process of the crista cranii is recognizable.

Small, unpaired parietals show a moderately developed ornamentation on the dorsal surface and a large parietal foramen in the middle of the parietal table (although partially obliterated in MSNVE-23368/6). A small and smooth area levis is present between the dorsal ornamentation and the posterior margin of the bone, whose center is marked by a deep parietal notch. A long and slender postparietal process runs posteroventrally from each posterolateral corner of the bone. In ventral view, one can see the very small parietal fossa, strongly smaller than the parietal notch.

The small, unpaired premaxilla has a large and arrow-shaped nasal process. It bears five conical, monocuspid teeth, provided with a slightly posteriorly curved and non-striated tip.

Maxillae are small and bear large, conical, monocuspid teeth, strongly curving posteriorly at the tip. Teeth are well spaced and do not show striae. Their number ranges from 4 to 7.

The quadrate and the coronoid are small-sized.

Dentaries (Fig. A4.9AY-AZ) are small and distinctly curved dorsally in the posterior portion. They bear teeth similar to those of the maxillae, whose number goes from 4 to 9. The intramandibular septum ends by the last tooth position or slightly anteriorly. No surangular spine can be seen on the posterior margin of the bone and the posterior end of the angular process is located strongly anteriorly to that of the coronoid process.

Compound bones are small and have a short and quadrangular retroarticular process. All vertebrae (Fig. A4.9BA-BE) are small-sized and slightly anteroposteriorly elongated. They have a dorsoventrally compressed centrum with parallel lateral margins in the posterior half. No keel is present on the ventral surface of the centrum of trunk and cloacal vertebrae, whereas the caudal ones show a well-developed hemal arch fused with the centrum. The autotomy plane can be either present (MSNVE-23368/20 and 23379/2) or absent (MSNVE-23368/19 and 23379/1). The left lateral apophysis of MSNVE-23368/10 presents a thick osseous swelling near its base, whereas the lateral one of MSNVE-23368/18 is lacking (probably it is not broken). A number of caudals show a pathological osseous proliferation posteriorly (MSNVE-23368/21 and 22: 13 vertebrae) or anteriorly (MSNVE-23368/23: 1 vertebra); some of them (MSNVE-23368/22: 11 vertebrae) are fused with a consecutive anomalously ossified vertebra.

Osteoderms are very small and very thin. They are suboval in shape and have no ridges on the external surface.

Identification

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The presence of a small-sized species of anguid is testified by the small vertebrae with a dorsoventrally compressed centrum (Estes 1983; Delfino et al. 2011). Anguid remains can be referred to *Anguis* gr. *A. fragilis* (including *A. cephallonica*, *A. colchica*, *A. fragilis*, *A. graeca* and *A. veronensis*; Gvoždík et al. 2013) because of: large, conical, monocuspid and strongly posteriorly curved teeth without striae on the tip; strongly reduced parietal fossa; end of the intramandibular septum located by or nearly to the last tooth position; posterior portion of dentaries dorsally curved; no surangular spine; short retroarticular process; elongation of vertebrae; parallel margins in the posterior half of the centrum; small size, thin and rounded shape of the osteoderms; absence of ridges on the latter (Holman 1998; Delfino 2002; Delfino et al. 2011; Klembara et al. 2014; this work).

Valdemino Cave

"Lacertilia" Owen, 1842 Gekkota Cuvier, 1817 Gekkonidae Gray, 1825 *Hemidactylus* Oken, 1817 *Hemidactylus turcicus* (Linnaeus, 1758)

Hemidactylus cf. H. turcicus (Fig. A4.9BF-BI)

Material: 1 frontal; 1 maxilla; 2 dentaries.

Description

The frontal (Fig. A4.9BF-BG) is unpaired and T-shaped, with concave lateral margins originating a distinct middle constriction. The anterior end is partly damaged, but the bases of two wide lateral processes are visible, separated by a wide notch. The articular surface with the nasal is recognisable dorsally to the processes. The posterior end displays two long posterolateral processes and a slightly concave posterior margin. The dorsal surface of the bone is smooth, lacking any trace of

ornamentation. Cristae cranii are well developed and fused into a tubular structure. Anteriorly, the structure present two moderately developed anterior processes.

The maxilla (Fig. A4.9BH-BI) is well preserved, missing only the dorsal tip of the facial process. Anteriorly, moderately short anterolateral and anteromedial processes are present. A long, slender, pointed and unstepped posterior process develops posteriorly. The tooth row covers the whole length of the bone, bearing closely-spaced, pleurodont, slender and cylindrical teeth. In lateral view, the facial process is subtrapezoidal and has a smooth lateral surface, pierced by 7 ventrolateral foramina. Its anterior margin presents a shallow concavity. On the medial surface, a distinct sigmoid ridge is present in the anterior portion of the bone. The total length of the maxilla is 6.7 mm and carries 31 tooth positions.

Dentaries are fragmentary. They carry a large number of teeth, whose morphology is similar to that of the maxillary teeth. A ventral development of the subdental ridge covers the Meckelian fossa.

Identification

These bones have already been described by Delfino (2004b) in his overview of the fossil herpetofauna from Valdemino Cave. Based on size, morphology of the anterior premaxillary process, width and robustness of the palatal shelf and medial inclination of the facial process, he assigned the remains to *Tarentola* cf. *T. mauritanica*. Nevertheless, the sigmoid ridge on the medial surface of the maxilla and the large lateral processes of the frontal are distinctive features of *H. turcicus* (this work). In contrast, *T. mauritanica* has a smooth maxillary medial surface and no lateral processes on the frontal. The size is also comparable with a large individual of *H. turcicus*. Yet, it has to be noted that this species usually displays a faint ornamentation on both the frontal and the maxilla (this work), and this is an important difference with the specimens from Valdemino. Because of this, the fossils are here identified as *Hemidactylus* cf. *H. turcicus*, but it is not possible to exclude that they belong to another, still unrecognised species of *Hemidactylus*.



Figure 3.4) Map of Spain, showing the position of the Vallès-Penedès Basin in Catalonia (red circle).

3.2.4. Spain

All the studied Spanish localities are located in the Vallès-Penedès Basin, in Catalonia (Fig. 3.4). Abocador de Can Mata does not represent a single fossiliferous locality, but rather a set of different sites located in the fossiliferous area of els Hostalets de Pierola (Alba et al. 2009). This is also the case of Autovia Orbital de Barcelona, Ecoparc de Can Mata and the Hostalets de Pierola localities. The localities Sant Quirze and Trinxera del Ferrocarril might represent the same fossiliferous site (David M. Alba, pers. comm.). Remains attributable to the same clade but coming from different localities are here lumped together for convenience, but it has to be noted that they might represent non-conspecific taxa.

Localities

Abocador de Can Mata (ACM/BCV1, ACM/C1-E, ACM/C1-E9, ACM/C2-B2, ACM/C2-B3, ACM/C3-A6, ACM/C3-A7, ACM/C3-B2, ACM/C3-B3, ACM/C4-A1,

ACM/C4-A2, ACM/C4-C2, ACM/C5-A, ACM/C5-D, ACM/C5-Dd, ACM/C5-D1, ACM/C6-A5, ACM/C6-C1, ACM/C6-C2, ACM/C6-C3, ACM/C6-C4, ACM/C8-A4, ACM/C8-C)

Age: middle Miocene (MN 6/MN 7+8).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Alba et al. 2009; Casanovas-Vilar et al. 2011a.

Autovia Orbital de Barcelona, section Olesa de Montserrat–Viladecavalls (B400V/S5C)

Age: late Miocene (MN 9).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Alba et al. 2010.

Ca n'Almirall

Age: middle Miocene (MN 6).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2011a.

Can Jofresa

Age: late Miocene (MN 10).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Can Llobateres

Age: late Miocene (MN 9).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Can Missert

Age: late Miocene (MN 9).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Robles et al. 2011; Casanovas-Vilar et al. 2016.

Can Perellada

Age: late Miocene (MN 10).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain.

Can Poncic

Age: late Miocene (MN 9). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Can Sant Feliu

Age: late Miocene (MN 9).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain.

Castell de Barberà

Age: late Miocene (MN 9). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Alba & Moyà-Solà 2012; Casanovas-Vilar et al. 2016.

Creu Conill 22

Age: late Miocene (MN 9). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Ecoparc de Can Mata (ECM/VCE-C) Age: late Miocene (MN 9). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Alba et al. 2012.

El Repetidor

Age: late Miocene (MN 9 or MN 10). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain.

Els Casots

Age: early Miocene (MN 4). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2011b.

Hostalets de Pierola (Hostalets de Pierola indeterminate, Hostalets de Pierola Inferior, Hostalets de Pierola P550) Age: middle/late Miocene (MN 7+8/MN 9). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

La Gornal 1

Age: middle Miocene (MN 6).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Rubí-Papiol

Age: early Miocene (MN 3 or MN 4). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2011b.

Sant Andreu de la Barca

Age: early Miocene (MN 3). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2011b.

Sant Mamet

Age: early Miocene (MN 4).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2011b.

Sant Miquell del Toudell

Age: late Miocene (MN 10).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; Museu Geologic del Seminari de Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Sant Quirze

Age: middle Miocene (MN 7+8).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; Museu Geòlogic del Seminari de Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Santiga

Age: late Miocene (MN 9).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Trinxera del Ferrocarril, Sant Quirze de Terrassa

Age: middle Miocene (MN 7+8).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain.

References: Casanovas-Vilar et al. 2016.

Trinxera Nord Autopista

Age: late Miocene (MN 10).

Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Viladecavalls

Age: late Miocene (MN 10). Repository: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain. References: Casanovas-Vilar et al. 2016.

Systematic palaeontology

"Lacertilia" Owen, 1842 Gekkota Cuvier, 1817

Gekkota indet. (Fig. A4.10A-C)

Material:

- ACM/BCV1: 1 maxilla (IPS82748).
- Can Jofresa: 1 dentary (IPS82718).
- ECM/VCE-C: 1 maxilla (IPS55559); 3 dentaries (IPS55554, 55563, 55564).

Description

The fragments of maxilla are very small and thin. They are both roughly 2 mm in length and bear 5 (IPS55559) or 13 (IPS82748) tooth positions. Teeth are pleurodont and closely spaced. Only one of them is preserved in both specimens, being cylindrical, slender and provided with parallel lingual and labial cusps. The crown does not bend postero-medially and displays no striae. The lateral surface of the fragments is smooth.

The tooth morphology of the dentaries is similar to that of the maxilla. The Meckelian fossa is closed in a very narrow tubular structure, composed by the expansion of both the subdental shelf and the ventral margin. The mandibular symphysis, preserved in IPS55563 only (Fig. A4.10A), is narrow and dorsally inclined at an angle of about 30°. The ventral margin of the bone is straight. The lateral surface is smooth, showing only the labial foramina. IPS82718, which is very fragmentary, is 2.8 mm-long and bears 8 tooth positions, with 2 preserved teeth. IPS55554, 55563 and 55564 (Fig. A4.10B), on the other hand, are more complete (but they still lack the posterior end and, with the exception of IPS55563, the anterior one also), and are 4.3 mm-long, 3.3 mm-long and 2.5 mm-long respectively. At least 4 teeth are visible in IPS55554, but it is not possible to count the exact number of preserved tooth positions since the bone is still partially covered by matrix. IPS55563 and 55564, on the other hand, carry at least 10 and 7 tooth positions, with 3 and 2 well-preserved teeth respectively (Fig. A4.10C).

Identification

The tooth morphology and the closed Meckelian fossa lead to the attribution of these specimens to small-sized gekkotans (Evans 2008; this work). The poor preservational status, however, hinders the possibility to have a more precise identification.

Lacertidae Batsch, 1788 Amblyolacerta Roček, 1984

cf. *Amblyolacerta* sp. (Fig. A4.10D) Material:

- Els Casots: 1 dentary articulated with the splenial (IPS82706).

Description

IPS82706 is a partial dentary lacking both the anterior and posterior ends and measuring 5.5 mm in maximum length. It has 8 pleurodont, homodont and columnarshaped teeth, provided with a blunt and rounded crown and projecting very slightly beyond the margin of the alveolar shelf. Two empty tooth-positions are also recognizable anteriorly. Resorption pits are present by the bases of several teeth, varying from small fissures to large cavities, and a newly formed tooth is also visible. There are no striae neither on the labial nor on the lingual surface. Ventrally to the teeth, there is a narrow subdental ridge. The Meckelian fossa is wide and opens medially. It is almost completely covered by a fragment of a blade-like splenial, whose lateral surface is smooth and slightly concave. The ventral margin of the dentary is slightly convex. Its lateral surface is smooth, showing only a single ventrolateral foramen.

Identification

Because of its widely open Meckelian fossa, the narrow subdental ridge and the convex ventral margin, IPS82706 can be attributed with confidence to the family Lacertidae (this work). The dentition, on the other hand, is remarkably peculiar in showing a low degree of amblyodonty (sensu Hoffstetter 1944), which is a feature that has been described in four extinct European lacertid genera up to now: Amblyolacerta Roček, 1984, Escampcerta Augé, 2005, Mediolacerta Augé, 2005 and Quercycerta Augé, 2005. Lacertids with a higher degree of amblyodonty are also known (e.g., Maioricalacerta Bailon et al., 2014), but the robustness of their teeth is clearly different from that of IPS82706. Quercycerta maxima from the Eocene of the Phosphorites du Quercy (France) is a very large species, that differs from IPS82706 in the size and in the morphology of the ventral margin of the bone, which bends slightly in medial direction in the French taxon. The absence of striae on the tooth crown approaches IPS82706 to Amblyolacerta and Escampcerta, but not to the striated Mediolacerta. The main difference between Amblyolacerta and *Escampcerta* is in the height of the teeth, which are less protruding beyond the alveolar shelf in the former than in the latter. According to this feature, IPS82706 resembles *Amblyolacerta* more than *Escampcerta*. This identification can only be tentative, however, because of the fragmentary nature of the specimen.

Lacertidae indet. (Fig. A4.10E-I)

Material:

- ACM/BCV1: 1 fragment of tooth-bearing bone (IPS133).
- ACM/C2-B2: 1 dentary (IndTemp038); 3 fragments of tooth-bearing bone (IPS?20).
- ACM/C2-B3: 2 dentaries (IPS?18, IndTemp043); 3 fragments of toothbearing bone (IndTemp042, 044, 045).
- ACM/C3-A7: 1 fragment of tooth-bearing bone (IndTemp039).
- ACM/C5-D1: 5 maxillae (IPS48500, 48501, 48502, 48503, 60487); 9 dentaries (IPS43765, 48471, 48493/48499); 46 fragments of tooth-bearing bones (IPS48472/48492, IndTemp015); 4 trunk vertebrae (IPS48424, 48572, 48598, 48599).
- ACM/C6-C1: 1 dentary (IPS57447); 2 fragments of tooth-bearing bone (IPS55108).
- ACM/C6-C2: 1 dentary (IPS55114); 1 fragment of tooth-bearing bone (IPS60500).
- ACM/C6-C4: 1 maxilla (IPS55130).
- ACM/C8-A4: 2 fragments of dentary (IPS?102, ?103); 2 fragments of toothbearing bone (IPS?104, ?106).
- B40OV/S5C: 1 fragment of frontal (IndTemp082).
- Can Llobateres: 10 fragment of dentary (IPS92186, ?142, ?143, IndTemp052); 1 fragment of dentary fused with the splenial (IPS?177); 1 fragment of compound bone (IPS22942c); 1 fragment of tooth-bearing bone (IPS?178); 1 trunk vertebra (IPS?176).

- Can Missert: 1 fragment of maxilla (IPS18903f); 1 fragment of dentary (IPS18903i); 7 fragments of tooth-bearing bone (IPS18900c, 18903d, 18903g, 82669).
- Can Perellada: 1 fragment of tooth-bearing bone (IPS9365).
- Can Poncic: 1 dentary (IPS9368); 2 fragments of tooth-bearing bone (IPS9363c, IndTemp083).
- Can Sant Feliu: 1 fragment of dentary (IPS?129).
- Castell de Barberà: 3 maxillae (IPS9397b, CBTemp377, 395); 1 jugal (CBTemp216); 1 pterygoid (CBTemp217); 1 ectopterygoid (CBTemp003); 8 dentaries (CBTemp001, 010, 028, 336, 338, 378, 380, 397); 1 fragment of compound bone (CBTemp004); 8 fragments of tooth-bearing bone (CBTemp026, 149, 193, 206, 341, 376, 379, 396).
- ECM/VCE-C: 1 premaxilla (IPS55561); 2 fragments of dentary (IPS55556, 55562); 2 fragments of tooth-bearing bone (IPS55560, 55566).
- El Repetidor: 1 dentary (IPS9612a).
- Els Casots: 8 dentaries (IndTemp053, 067); 7 fragments of tooth-bearing bone (IndTemp054, 068); 1 isolated tooth (IndTemp066).
- Hostalets de Pierola: 1 maxilla (IPS9488a).
- La Gornal 1: 1 dentary (IndTemp033).
- Sant Andreu de la Barca: 1 frontal (IPS?259).
- Sant Mamet: 1 fragment of tooth-bearing bone (IPS?265).
- Sant Miquell del Toudell: 1 fragment of tooth-bearing bone (SemTemp006).
- Sant Quirze: 1 premaxilla (IPS9639e).
- Trinxera Nord Autopista: 2 dentaries (IPS87393, IndTemp048).

Description

The best-preserved frontal, IPS?259, preserves only the posterior portion. It is paired and shows a moderately developed dermal ornamentation covering the dorsal surface and small interdigitations on the posterior margin. The posterolateral process is short, but its tip is missing. On its lateral surface, the small articulation surface with the postfrontal is visible. The ventral surface bears a low and wide crista cranii, but it is otherwise smooth. The fragments show a similar morphology and a similar ornamentation on the dorsal surface.

The tooth-bearing bones are usually fragmentary. They carry pleurodont, slender, cylindrical teeth, provided with one, two or three cusps. In the most complete premaxilla, IPS55561, 7 tooth positions are recognizable. The ascending nasal process and most of the palatal process are always lacking. However, despite the absence of most of the nasal process, its base appears to be narrow. The most complete maxilla, IPS55130 (Fig. A4.10E-F), is large-sized (maximum length = 12mm), but it preserves only part of the tooth row and lacks both ends and almost the entire facial process. It carries 17 tooth positions and at least 5 ventrolateral foramina. A well-developed dermal ornamentation is visible on the lateral surface. Such an ornamentation is visible also on IPS18903f, IPS48502, IPS48503, IPS9397b, CBTemp377 and CBTemp395, which are represented only by a fragment of the same bone. CBTemp377, moreover, shows a sharp arched ridge on the medial surface, running posterodorsally from the palatal shelf. The posterior process is preserved in IPS9397b, an 8.4 mm-long fragment: it is straight, posteriorly pointed and has no step on its dorsal margin (Fig. A4.10G). In the dentaries, the Meckelian fossa is wide and opens medially. When preserved, the mandibular symphysis is narrow and subhorizontal. The ventral margin of these bones is convex in medial view. The lateral surface is smooth and presents some labial foramina. Their size is variable, with the maximum length reaching up to 9.5 mm (but fragment of larger specimens are also present: e.g., CBTemp397). Teeth are slightly more robust in the posterior portion of the dentaries than in the anterior one. A different pattern, on the other hand, is recognizable in the maxilla IPS55130, which shows thicker teeth also in the anteriormost part (Fig. A4.10E-F).

The jugal (Fig. A4.10H-I) has a long anterior process, whose lateral surface is almost entirely covered by the articulation surface with the maxilla in its anterior half (even
if the anterior tip is broken). The rest of the lateral surface of the specimen is covered by a very light dermal ornamentation. The palatal process is moderately developed, but there is no medial process. There is, on the other hand, a well-developed and triangular quadratojugal process. The posterodorsal process is missing.

Only the quadrate process of the pterygoid is preserved. It is straight, posteriorly pointed and strongly laterally directed in dorsal view. In lateral view, it is moderately wide, with a roughly flange-like shape. The fossa columellae is wide and subcircular. The basipterygoid fossa is moderately concave. A distinct pterygoid ridge runs posteriorly from the fossa columellae, on the lateral surface of the specimen.

The poorly preserved ectopterygoid is small and medially concave. Most of the laminar anterolateral process is lacking, as well as the posterolateral one. The posteromedial process has a V-shaped concavity for the articulation with the pterygoid flange of the pterygoid. The concavity is defined by a ventral and a dorsal pointed lappet, of which the ventral one is the longest. An anteromedial lappet was also present in origin, but it is broken.

The fragments of compound bone are represented by the area surrounding the articular condyle. IPS22942c preserves the retroarticular process, whereas CBTemp004 preserves part of the adductor fossa. The condyle is squared in dorsal view and slightly concave. The best preserved one, that of CBTemp004, shows a moderately developed tubercle by its dorsomedial corner. The retroarticular process is sub-triangular in medial view, with a slightly truncated posterior end. A well-developed tympanic ridge runs anteroposteriorly on the medial surface of the process, near its ventral margin. A large foramen for the chorda tympani is visible by the anterior end of this ridge. Ventrally to the ridge, there is a ridge-like expansion of the retroarticular process is smooth and very slightly concave. The adductor fossa appears to be wide.

The trunk vertebrae are procoelous and anteroposteriorly elongated. The vertebral centrum is sub-cylindrical and has a maximum length that reaches 4.7 mm (in

IPS48572 and IPS48599). A low and wide keel is visible on the ventral surface. The neural canal is arched in anterior view. The zygapophyses are sub-elliptical and slightly dorsally inclined. A well-developed neural spine is present on the dorsal surface of the neural arch.

Identification

All the above described remains display the typical lacertid morphology (Barahona 1996; this work), but the preservational status or the lack of significant diagnostic features prevent to identify them in a more precise way. The tooth morphology resembles the standard lacertid condition and so the tooth-bearing bones represent lacertids different than the amblyodont *Amblyolacerta*. Large-sized specimens such as the maxilla IPS55130 account for the presence of at least one large taxon.

Scincidae Oppel, 1811

Scincidae indet. (Fig. A4.10J) Material:

- Can Missert: 1 fragment of dentary (IPS18900b).
- Castell de Barberà: 1 fragment of maxilla (IPS82716).
- Els Casots: 1 fragment of maxilla (IPS82688).

Description

IPS82716 (Fig. A4.10J) is a roughly 4 mm-long fragment of maxilla, preserving only part of the posterior half of the bone. The posterior end is lacking. There are 10 tooth positions. Teeth are closely spaced, pleurodont, cylindrical and slender. Their crown is blunt and slightly bending in medial direction. Two low cusps are visible, located lingually and labially and separated by a shallow groove. Very light striae are present on the lingual side of the crown, but not on the labial one. The lateral surface of the bone is smooth and very slightly concave. A single ventrolateral foramen is visible. Though the posterior end is missing, the posterior process appears to be rather short.

Its dorsal margin does not show steps. IPS82688 is less preserved, representing part of the anterior premaxillary process. It is less than 2 mm in length. It bears 3 teeth, whose morphology is comparable with the one of IPS82716. An anteriorly directed concavity housing a small vomeronasal foramen is visible by the anterior end of the fragment. Medially, the concavity is marked by a low ridge, whereas no distinct ridge is visible by its lateral side. The lateral surface of the fragment is smooth, with a single ventrolateral foramen.

The fragment of dentary is very poorly preserved. It is 2 mm in length and bears 5 tooth positions. Teeth are closely spaced, pleurodont, cylindrical and slender. Only a single one is preserved, even though its crown is slightly eroded. Despite the erosion, the crown is medially bending and shows very light striae on the medial surface. A bicuspid morphology, similar to the one of the above described maxillae, seems also recognizable. The lateral surface is smooth, with 2 mental foramina. Identification

The dentition and the size clearly identify these specimens as small members of the family Scincidae (this work). The preservational status, however, is poor bad to confidently hypothesize their specific or even generic attribution.

Anguidae Gray, 1825 Anguinae Gray, 1825 *Anguis* Linnaeus, 1758

?*Anguis* sp. (Fig. A4.10K-N) Material:

- ACM/C5-D1: 1 trunk vertebra (IPS48678).
- Castell de Barberà: 2 trunk vertebrae (CBTemp049, 187).
- Trinxera Nord Autopista: 1 trunk vertebra (IPS87396b).

Description

The trunk vertebrae are relatively large (centrum length reaches 6.6 mm). They are procoelous and antero-posteriorly elongated. The centrum is dorso-ventrally compressed, provided with a flat and smooth ventral surface and parallel lateral margins. Synapophyses are neither massive nor rounded, but more slender and elongated instead. There are no prezygapophyseal processes. In IPS48678, the neural arch lacks the posterior portion and its dorsal surface is covered by matrix, and so it is not possible to clearly state if a neural spine is present or not. However, the latter is clearly present and well developed in the other specimens. The zygosphene is not present. Zygapophyses are suboval and dorsally tilted at an angle of about 30°. Identification

The dorsoventrally compressed centrum devoid of precondylar constriction and provided with parallel lateral margins indicate the presence in at least some of the localities of the Vallès-Penedès Basin of an anguine that can be attributed the genus *Anguis* (Klembara 1981; Estes 1983; Holman 1998). It has to be noted, however, that *Anguis* vertebrae are usually distinctly smaller in size and the herein described specimens might be the largest ones possibly attributed to the genus. It is also possible that they pertain to the indeterminate, possibly new anguid represented by MGB-V60, whose vertebral morphology is not known thus far.

Pseudopus Merrem, 1820

Pseudopus sp. (Fig. A4.10O-X) Material:

- ACM/C4-A1 : 1 parietal (IPS33113).
- ACM/C5-D: 1 dentary (IPS60498).
- ACM/C5-D1: 1 dentary (IndTemp019); 1 fragment of tooth-bearing bone (IPS48468).
- ACM/C6-A5: 1 dentary (IPS57445).

- ACM/C6-C1: 1 fragment of tooth-bearing bone (IPS57448).
- ACM/C6-C3: 2 dentaries (IPS50294, 50963).
- ACM/C8-C: 1 dentary articulated with the splenial (IPS57443).
- Can Llobateres: 1 maxilla (IPS?141); 2 dentaries (IndTemp008, 009).
- Can Missert: 1 fragment of dentary (IPS18903h).
- Can Poncic: 1 parietal (IndTemp084); 3 fragments of tooth-bearing bone (IPS9369d, IndTemp035, 036).
- Castell de Barberà: 1 frontal (CBTemp153); 2 parietals (CBTemp223, 311);
 8 maxillae (IPS9398a, CBTemp169, 174, 180, 391, 392, 393, 394); 1 palatine (CBTemp283); 3 pterygoids (CBTemp209, 266, 309); 23 dentaries (CBTemp014/016, 020/022, 137, 152, 156, 172, 176, 178, 197, 204, 213, 227, 381/388); 1 dentary articulated with the splenial (IPS9397a); 14 fragments of tooth-bearing bone (CBTemp210/212, 229, 233, 242/243, 310, 314, 323, 326, 334, 389/390).
- Hostalets de Pierola Inferior: 3 dentaries (IPS9490a, 82642, 82643).
- Sant Miquel del Toudell: 3 dentaries (IPS57438b, SemTemp011/012), 1 fragment of tooth-bearing bone (IPS57438a).
- Sant Quirze: 1 maxilla (IPS9635a); 2 dentaries (IndTemp026/027).
- Santiga: 1 dentary (IPS9642).
- Trinxera Nord Autopista: 1 maxilla (IPS9653e); 1 dentary (IPS82772); 1 fragment of tooth-bearing bone (IPS82773).

Description

CBTemp153 is a 5 mm-long fragment of a left frontal, representing the posterior portion of the bone. The posterior margin is roughly straight, showing some irregularities but no distinct interdigitations. A well-developed dermal ornamentation made up by low ridges and pits covers entirely the dorsal surface of the specimen, lateral margin included. The ornamentation is represented almost completely by the frontal shield, but a very small frontoparietal shield is visible by

the posterolateral corner. The interfrontal shield appears to be absent, since the contact between the frontal and the interparietal scales correspond to the frontoparietal suture. The posterolateral process is short and rounded. The small articulation surface with the postfrontal is visible along the lateral margin. Due to the preservational status of the specimen, it is not possible to understand if it touched the one with the prefrontal in origin or not. On the ventral surface of the specimen, the low posterior portion of the crista cranii is visible, and a triangular articulation surface for the ventral lappet of the parietal is present medially to it.

The best preserved parietal, CBTemp223 (Fig. A4.10O-P), is almost complete, lacking only the postparietal processes and the left antero-lateral corner of the parietal shelf. The specimen is moderately large: the maximum length of the shelf is roughly 12 mm, whereas its maximum width is more than 9.5 mm (the exact value cannot be established because of the missing corner). The shelf is, therefore, rectangular and longer than it is large. The anterior margin is straight and very slightly irregular, lacking distinct interdigitations. The right anterolateral process is poorly developed and does not extend strongly in lateral direction. A small articular surface for the posterolateral process of the frontal is visible on its ventral surface, and a small and triangular ventral lappet is present medially to it. Except for a small area levis by the posterior margin, the dorsal surface of the shelf is entirely covered by a well-developed dermal ornamentation, which is squared and made up by pits and low tubercles in the central portion and by low ridges and grooves towards the periphery. The interparietal, the two lateral and the occipital shields are recognizable. The anterior end of the large interparietal shield is wide, but it does not extend much towards the anterolateral corners of the bone. The occipital shield is moderately wide and roughly as long as one third of the ornamented surface. The anterolateral ventral crests are well developed and sharp. Nevertheless, they have a lower (but still moderately high) posterior portion, extending posteriorly to the opening of the parietal fossa. The preserved portion of the posterolateral ventral crests is low and rounded; they are located in the middle of the postparietal process and touch the

anterolateral crests. The medial ventral crest is wide and touches the anterolateral ones. The deep and wide parietal fossa is visible in ventral view, since the medial crest does not cover it. A well-developed carina arcuata is present dorsally, hiding the parietal notch in dorsal view. Wide but low epipterygoid processes are present by the contact between each anterolateral and posterolateral ventral crest. Laterally to each anterolateral ventral crest, there is a wide muscular surface, which is half as wide as the surface comprised between the two crests. The parietal foramen is elliptical and is located anteriorly compared to the mid-length of the parietal shelf. The other parietals, IPS33113, CBTemp311 and IndTemp084, are more poorly preserved: IPS33113 is a fragmentary shelf, lacking most of the anterior half as well as the postparietal processes and the parietal fossa; CBTemp311 is a poorly preserved fragment, representing only the left posterolateral corner of the shelf and the proximal part of the left postparietal process; IndTemp084 preserves part of the posterior half of the shelf. Their morphology is comparable with the related parts of CBTemp223, even though in IndTemp084 the ornamentation is less developed.

All tooth-bearing bones carry closely spaced, subpleurodont, large and robust teeth, with a blunt and rounded crown. The tip of the crown is usually smooth, without cusps or evident striae. This is not the case, however, of IPS9653e (a maxilla), IPS9490a and 82772 (two dentaries), IPS57438a (a very large indeterminate and fragmentary tooth-bearing bone), IPS82642, 82773, 9369d, SemTemp011 and 012 (smaller fragments of tooth-bearing bone), whose teeth show a distinct and dense striation on both the labial and the lingual sides. Teeth of IPS57438a, moreover, are very stocky. Very light striae are visible on the lingual side of the teeth preserved by IPS82643 (Fig. A4.10X) and IndTemp036 too. The specimens can reach a very large size, even if they are often fragmentary. All maxillae but IPS9653e lack the anterior premaxillary process. It is very poorly preserved in the latter specimen also, but a well-developed lappet is clearly present on the anteromedial process. When preserved, the posterior process is long, moderately large in lateral view and posteriorly pointed; it does not show a step on in its dorsal margin. Only in IPS9635a

(Fig. A4.10O-R), the posterior process appears to be forked, but this is due to a breakage. The wide superior dental foramen continues posteriorly with a wide groove that runs on the dorsal surface of the posterior process. A second groove is visible laterally to the former in IPS9653e. IPS9635a, CBTemp169 and 174 present a very light ornamentation made up of rugosities on the lateral surface of the preserved portion of the facial process. Such an ornamentation could have been present in other specimens also, but the facial process is always broken and so it is probably not visible. Given that, most maxillae show only the anteroposteriorly aligned ventrolateral foramina near the ventral margin. The largest maxillary teeth are located in the middle of the tooth-row. The best-preserved specimens, IPS9398a, 9635a, 9653e and CBTemp392, show 7 (IPS9635a and 9653e; Fig. A4.10S-T) or 9 (other specimens) tooth positions. In the dentaries (Fig. A4.10U-W), the size of the teeth increases towards the posterior end of the tooth-row, even though posteriormost teeth are smaller than the preceding ones. A well-developed subdental shelf is present, dorsomedially covering the open Meckelian fossa; the shelf is less developed in the posterior third of the bone. The Meckelian fossa is moderately narrow anteriorly, but grows larger in the posterior part. The ventral margin of the bone is straight in medial view. When preserved, the mandibular symphysis is narrow and almost horizontal. The splenial spine is never recognizable, maybe because of taphonomical reasons and posterior breakage rather than of a real absence. The lateral surface is smooth and pierced by the labial foramina. The posterior part of the dentary, which is partially preserved in IPS9490a, 9642, 50294, 50963, 57443, 82642, 82772, CBTemp137, 152, 385, 386 and IndTemp026, bends slightly in dorsal direction. In IPS50963 and CBTemp385, the location of the posterior opening of the alveolar canal is recognizable: it is placed between the 3rd and the 4th posteriormost tooth position in the former and between the 4th and the 5th ones in the latter. The posterior portion of the intramandibular septum is fused to the medial wall of the bone. There is no surangular spine. The superior posterior process is preserved in IPS50963, CBTemp386 and partially in CBTemp137, 152 and IndTemp026: it is

split into two pointed portions separated by a wide, deep and roughly V-shaped (U-shaped in IndTemp026) coronoid incisure. The dorsal portion, the coronoid process, is distinctly shorter than the ventral one, the surangular process, which is roughly twice as long as the former. In CBTemp386, a shallow concavity on the ventral margin of the surangular process can be a trace of the anterior surangular foramen (Fig. A4.10V-W). Two anterior teeth of IPS50294 are stuck in another indeterminate bone fragment.

The fragmentary palatine is very poorly preserved and includes only a portion of the pterygoid process. The ventral surface is covered by a large number of small and rounded teeth, whereas the sulcus dorsalis crosses anteroposteriorly the dorsal one. Almost all of the pterygoids miss most of the three branches, preserving only their meeting point. The only exception is CBTemp209, which is represented by a portion of the palatine process. In all specimens, a large number of rounded teeth is present on the ventral surface of the latter process. The size of these teeth varies from small to rather large. The fossa columellae is sub-circular. The basipterygoid fossa is marked both dorsally and ventrally by well-developed flanges (preserved only in CBTemp309). The dorsal flange is rounded, whereas the ventral one has a thumb-like shape.

A fragment of the splenial is visible in IPS9397a and 57443, but it is poorly preserved in both cases.

Identification

The above described specimens display typical features of anguids and, in particular, of *Pseudopus*. Among them, some of the most important are the dermal ornamentation reaching the lateral margin on the frontal, the presence of a muscular surface on the parietal and the large and robust teeth provided with a blunt and rounded crown (Klembara 1986; Klembara et al. 2014; Klembara 2015; this work). It has to be noted that also the indeterminate, possibly new taxon from the Vallès-Penedès (see below) has frontals with ornamentation reaching the lateral margin, but CBTemp153 is here attributed to *Pseudopus* because it displays the same dermal

ornamentation present on the parietal CBTemp223, which is clearly different from the parietal of MGB-V60. The well-preserved parietal from Castell de Barberà is different from the parietals of all the species of *Pseudopus* currently known from the European Neogene. It differs from *Pseudopus ahnikoviensis* Klembara, 2012 in the posterolateral ventral crest located in the middle of the postparietal process and in the morphology of the dermal ornamentation, from Pseudopus confertus Klembara & Rummel, 2016 in the location of the parietal foramen and in the morphology of the dermal ornamentation (Klembara 2015), from Pseudopus laurillardi (Lartet, 1851) in the anterolateral processes not laterally extended and in the dermal ornamentation (Klembara et al. 2010) and from Pseudopus pannonicus (Kormos, 1911) in the squared ornamented surface and in the occipital shield as long as one third of the ornamentation (Klembara et al. 2010). Moreover, CBTemp223 contrasts with *P. apodus* in having a moderately high posterior portion of the anterolateral ventral crest (Klembara et al. 2010). Nevertheless, it recalls P. pannonicus in having a wide facies muscularis and both *P. pannonicus* and *P. apodus* in the morphology of the dermal ornamentation (Klembara et al. 2010). All the above listed differences seems to suggest that a new species of *Pseudopus* might have been present in the Miocene of the Vallès-Penedès, at least in Castell de Barberà. A possible new species of this genus has been already considered by Bolet et al. (2014a) based on IPS9653e (Fig. A4.10S-T), the maxilla coming from Trinxera Nord Autopista.

Anguidae new taxon? (Fig. A4.11, A4.12A-L) Material:

- ACM/C5-D1: 1 dentary (IPS48526).
- Can Sant Feliu: 1 fragment of dentary (IPS?130).
- Castell de Barberà: 1 fragment of tooth-bearing bone (CBTemp300).
- Els Casots: 1 fragment of tooth-bearing bone (IndTemp023).

- Hostalets de Pierola Inferior: 1 partial skull and 1 associated portion of tail (IPS30710).
- Sant Miquel del Toudell: 1 articulated skull (MGB-V60).

Description

MGB-V60 (Fig. A4.11A-D) is an articulated skull, partially plunged in the matrix. It is strongly deformed and the bones are strongly damaged. The specimen is roughly 53 mm in maximum length and roughly 20 mm in maximum width, but these measures are influenced by the deformation. Only the right nasal is preserved enough to be described (Fig. A4.11E). It is antero-posteriorly elongated and widens posteriorly. The anterior end is poorly preserved, but the anteromedial process seems more developed than the anterolateral one. A light dermal ornamentation is recognizable on the dorsal surface, at least in the posterior portion of the bone. The frontals (Fig. A4.11F) are roughly 14 mm in length. Their posterior end is twice as large as the anterior one. The latter is covered by the matrix. The posterolateral process is short and pointed. The posterior margin is straight and there is no middle constriction (i.e., lateral margins of the frontals are parallel). The dorsal surface is covered by a low-developed dermal ornamentation made up by a crust pierced by scattered small pits. The ornamentation reaches the lateral margin. There is no frontoparietal shield. The parietal (Fig. A4.11G) has a sub-trapezoidal shelf, which is slightly longer than it is large (maximum width: 14 mm; maximum length: 15 mm). The anterolateral processes do not project anteriorly, but they are distinctly developed laterally. This originates a strong constriction at mid-length in the parietal. Postparietal processes are long and wide; the distal end is lacking in both of them. A low-developed dermal ornamentation similar to the one of the frontals is present on the dorsal surface. The interparietal, lateral and occipital shields are recognizable, whereas it is not clear if the two frontoparietal ones are present by the anterolateral corners of the bone. The interparietal shield is large, occupying almost half of the anterior margin. The occipital shield is also large and it seems to be less than one third of the shelf in length. A large and smooth area levis is present on the posterior fourth of the parietal shelf. The morphology of the parietal notch and of the parietal foramen are not recognizable because of the preservational status of the specimen. The maxillae are 23 mm (the right one) and 21 mm (the left one, but it lacks the posterior tip) in length. The anterior premaxillary process of the maxillae is not clearly visible, whereas the posterior one is long and wide, without steps on its dorsal margin. In lateral view, the facial process is sub-trapezoidal and has a slightly convex dorsal margin and concave anterior and posterior margins. The process is as long as half the length of the bone. The lateral surface is smooth. Teeth are not preserved or still plunged in the matrix and therefore their shape cannot be recognized. The left prefrontal has a long and slender dorsal process, but the rest of its morphology is not clearly visible. The right jugal (Fig. A4.11H) is rather slender. In lateral view, the anterior and the posterodorsal processes have a similar thickness. In both processes, the tip is not recognizable, either because it is missing (posterodorsal one) or it is plunged in the matrix (anterior one). Because of this, the length ratio between the two processes cannot be stated. A distinct quadratojugal process is present, even if it lacks the tip. The lateral surface of the bone is smooth. In the dentaries, the length of the tooth-row is not clearly measurable since they are fragmentary and exposed in ventro-lateral view. However, in the left one, it is at least 24 mm-long. The lateral surface of the dentaries is smooth, with only some labial foramina. The ventral margin is rather convex, despite the poor preservational status, whereas the posterior portion bends distinctly in dorsal direction. The teeth of the right dentary are not visible because of the matrix covering them, but some of those of the left one are partially exposed. They are sub-pleurodont, closely-spaced, rather slender and provided with a pointed tip, which bends very slightly in postero-medial direction (Fig. 3.5). The best preserved one shows a very low carina both on the anterior and the posterior sides. There are no striae, neither on the labial nor on the lingual surfaces. Only the slender and pointed anterior part of the splenials is visible, covering the Meckelian fossa ventrally. A dorsally rounded and posteriorly directed coronoid process is the only exposed portion of the right coronoid. The left one, on the other hand, is not visible. Angulars are very poorly preserved. Surangular, articular and prearticular are completely fused to form a compound bone. The retroarticular process is poorly preserved both in the right and in the left bones, but it is short, wide and subquadrangular-shaped in lateral view. Moreover, it is dorsoventrally expanded, giving a ventrally concave aspect to the bone. The articular condyles are not clearly visible. The anterior surangular foramen is located ventrally to the coronoid process of the coronoid and is not covered by the superior posterior process of the dentary. The posterior surangular foramen cannot be identified with certainty.

The articulated skull of IPS30710 (Fig. A4.12A-J) preserves the rostral portion, including the nasals, the anterior portion of the frontals, the premaxilla, the maxillae, at least part of the prefrontals, the lacrimals, the vomers, the septomaxillae, the palatines, part of the dentaries and the anterior portion of the splenials. Both nasals

and frontals are poorly preserved, but a ornamentation is dermal clearly recognisable on their dorsal surface. In anterior view, the premaxilla has a wide and low alveolar plate, carrying 7 pleurodont and cylindrical teeth. The crown is preserved only in a single tooth, which is partially plunged in the matrix: it appears to be pointed and slightly posteriorly bending. The ascending nasal process is narrow, slightly widening towards the dorsal end. Maxillae have a smooth lateral surface, with only 4 ventrolateral foramina near the ventral margin, and a



Figure 3.5) Anguidae new taxon? from the Vallés-Penedés: close-up of a dentary tooth of MGB-V60. Scale bar = 1 mm.

subtrapezoidal facial process. The left maxilla preserves a well-developed and pointed anterolateral process. The posterior process is slender and does not show a step on the dorsal margin. Maxillary teeth are conical and have a very slightly posteriorly bending crown. The left maxilla carries at least 10 teeth, whereas at least 7 are present on the right one. Apparently, there are no striae on the labial surface. The most preserved maxilla is 13 mm-long. Both prefrontals miss the dorsal process. In posterior view, they present a short and subtriangular orbitonasal flange projection and a posteroventral process, which is longer and more slender. The dorsal surface of the bone is smooth. The lacrimals are laminar, anteroposteriorly elongated and widening anteriorly. Vomers are narrow and anteroposteriorly elongated. They are strongly dorsally concave. There are no vomerine teeth. Septomaxillae are shifted from their original position. These bones have a roughly subtriangular shape in dorsal view because of an undeveloped anterolateral process. The posteromedial and the posterolateral processes are more developed. The latter bends in dorsal direction, as a distinct and rounded flange. The palatines have a well-developed maxillary process, which is pierced by a very large infraorbital foramen. The pterygoid process is only partly preserved in both the left and the right palatines, but the left one clearly shows a slender morphology and at least one palatine tooth on the ventral surface. Both dentaries lack the posterior end. The smooth lateral surface carries some labial foramina (at least 5 in the left one and at least 6 in the lateral one). The ventral margin is straight in lateral view. Both in the left and in the right one, the preserved portion is 12 mm in length. Dentary teeth are morphologically similar to the ones of the maxillae. Nine and 8 teeth are preserved on the left and on the right dentaries respectively. A smooth subdental shelf is present ventrally to them, on the medial side of the bone. The shelf covers medially the narrow Meckelian fossa. The preserved portion of the splenial is very slender and pointed. The tail portion (Fig. A4.12K-L) is covered by a dense layer of osteoderms. They are moderately small, thin and roughly sub-quadrangular. Their external surface is covered by a vermicular ornamentation and a low but distinct keel runs anteroposteriorly on it. Two vertebrae and a small portion of a third one are preserved inside the tail portion. They have a dorsoventrally compressed centrum and fused hemapophyses on the ventral surface. The other specimens have subpleurodont, closely spaced, moderately slender and canine-like teeth. Their tip bends slightly in postero-medial direction. There are no striae on the crown, neither on the labial nor on the lingual side. A sharp carina, on the other hand, is present on both the anterior and the posterior margin. The tooth base is slightly swollen, except for IPS?130. IPS48526 is a fragment of dentary missing the anterior half and most of the posterior end. Ventrally to the teeth, there is the subdental shelf. Roughly at mid-length of the preserved shelf, there is a very small splenial spine, followed by a distinct concavity. The posterior end of the fragment bends slightly in dorsal direction, but the posterior processes are broken. Identification

MGB-V60 is a large-sized anguid, whose morphology shows a peculiar combination of characters distinguishing it from the other anguid genera most commonly found in Neogene and Quaternary European localities: namely, Anguis, Ophisaurus (= Dopasia) and Pseudopus. MGB-V60 shares with Pseudopus the dermal ornamentation reaching the lateral margin on the frontals (Klembara 2015; this work). This feature is not present neither in Anguis nor in Ophisaurus, whose frontal displays a smooth lateral margin. In contrast with Pseudopus, on the other hand, MGB-V60 has a distinct quadratojugal process on the jugal and an anterior surangular foramen that is not covered by the surangular process of the dentary (Klembara et al. 2014; this work). Moreover, it lacks the cylindrical and stout teeth that are typical of the genus (Klembara et al. 2014; this work). The parietal is particularly significant because it resembles an isolated parietal found in the Austrian locality of Gratkorn (Böhme & Vasilyan 2014: fig. 3f) in having a dermal ornamentation widening anteriorly and a parietal shelf that is strongly laterally developed in its anterior portion. The authors assign this specimen to Ophisaurus spinari, but Klembara and Rummel (2016) state that in the latter species the parietal ornamentation is rectangular, not widening. Moreover, according to these latter authors, the anterior widening of the parietal shelf is unknown in all species of *Anguis*, *Ophisaurus* and *Pseudopus*. This further confirms that MGB-V60 cannot be attributed to these three genera. In addition to being different from *Pseudopus*, tooth morphology deviates also from the one of *Anguis*, whose teeth are more posteriorly curved and well-spaced (Klembara et al. 2014; this work). Teeth of *Ophisaurus* are more similar to the ones of MGB-V60, but they usually show striae on the lingual side (Klembara et al. 2014). The dentition of MGB-V60 appears very similar to those of *Ophisauromimus* from the late Oligocene of France and Germany (Čerňanský et al. 2016a) and maybe also *Ragesaurus* from the early Pleistocene of Spain (Bailon & Augé 2012). Remains attributed to these genera are represented only by dentaries, and their main diagnostic features are located on the medial side of these bones. Because of this, it is currently not possible to clearly state whether MGB-V60 might be assigned to them or not. Further analyses, including high-resolution computed tomography, are required to solve this issue. The other specimens are assigned to the same taxon as MGB-V60 because of strong similarities in tooth morphology.

non-Anguis Anguinae indet.

Material:

- ACM/C1-E: 1 trunk vertebra (IndTemp059); 12 osteoderms (IPS33109); 3 blocks of sediment with osteoderms (IndTemp060).
- ACM/C1-E9: 1 block of sediment with numerous osteoderms (IPS50118).
- ACM/C2-B2: 2 trunk vertebrae (IPS45773, IPS?10a); 3 osteoderms (IPS?10b).
- ACM/C2-B3: 47 osteoderms (IPS82647, 82650).
- ACM/C3-A6: 11 osteoderms (IndTemp025).
- ACM/C3-A7: 10 osteoderms (IPS82653, IPS?6).
- ACM/C3-B2: 1 osteoderm (IPS82654).
- ACM/C3-B3: 1 caudal vertebra (IPS45774); 1 osteoderm (IPS82646).

- ACM/C4-A1: 3 trunk vertebrae (IPS48044, IPS48047, IPS48058); 1 caudal vertebra (IPS48091).
- ACM/C4-A2: 1 trunk vertebra (IPS48062).
- ACM/C4-C2: 1 partial articulated skeleton (IPS43712).
- ACM/C5-A: 1 trunk vertebra (IPS45785).
- ACM/C5-Dd: 1 osteoderm (IPS45389).
- ACM/C5-D1: 47 trunk vertebrae (IPS43775, 43780, 43901, 44172, 44287, 45239, 48399/48400, 48605, 48609/48610, 48618, 48620, 48624, 48630/48631, 48634, 48639/48644, 48650/48655, 48659, 48661/48662, 48664, 48667, 48669/48670, 48673, 48676, 48682/48683, 48688, 48690, 48694/48695, 49413, 50116, IndTemp011); 3 cloacal vertebrae (IPS43769, 48614, 48638); 68 caudal vertebrae (IPS43766/43767, 43773, 43776, 44258, 45359, 45435, 45440, 48398, 48527, 48601/48604, 48606/48608, 48611/48612, 48615/48617, 48619, 48621/48623, 48625/48629, 48632, 48635, 48636/48637, 48645/48649, 48656/48658, 48663, 48665/48666, 48668/48669, 48671, 48674/48675, 48677, 48679, 48684/48687, 48689, 48691, 48693, 48696, 48697, 49412, 49415, 50115, 60502); 126 osteoderms (IPS44197, 48534).
- ACM/C6-C1: 1 trunk vertebra (IPS57446); 1 caudal vertebra (IPS55125).
- ACM/C6-C2: 1 trunk vertebra (IPS55116).
- ACM/C6-C3: 2 caudal vertebrae (IPS50293, 50960).
- ACM/C8-A4: 2 trunk vertebrae (IPS?98, IndTemp005).
- B40OV/S5C: 1 caudal vertebra (IPS55755); 1268 osteoderms (IPS57464).
- Ca n'Almirall: 11 osteoderms (IPS9194).
- Can Llobateres: 1 cervical vertebra (IPS28977d); 4 trunk vertebrae (IPS11607b, 28977c, IPS?163, 172); 4 caudal vertebrae (IPS?162, 171, 173, 186); 5 osteoderms (IPS9218a, IPS?182).
- Can Missert: 3 trunk vertebrae (IPS18903c, 82709); 2 caudal vertebrae (IndTemp049/050); 17 osteoderms (IPS18900e, 18903e).

- Can Poncic: 1 caudal vertebra (IPS37619); 147 osteoderms (IPS9369a).
- Castell de Barberà: 2 fragments of frontal (CBTemp226, 232); 1 axis (CBTemp236); 3 cervical vertebrae (CBTemp117, 235, 373), 40 trunk vertebrae (CBTemp018, 023, 033, 039, 073, 078, 085/086, 102, 122, 150, 192, 198, 202/203, 222, 224, 229, 231, 234, 254, 259, 270, 281, 298, 325); 2 cloacal vertebrae (IPS91934, CBTemp154); 49 caudal vertebrae (CBTemp006, 012, 025, 029, 042, 080, 082, 096, 113, 123/124, 126, 129, 131, 135, 138, 147, 155, 170, 173, 175, 177, 179, 181/186, 207/208, 264, 279, 296, 301/302, 307, 313, 327, 335, 339), 69 osteoderms (IPS9398a, CBTemp002, 027, 043, 081, 118, 143, 215, 221, 225, 253, 265278, 297, 322, 374).
- Creu Conill 22: 5 osteoderms (IPS11537).
- El Repetidor: 3 osteoderms (IPS9612b).
- Els Casots: 5 trunk vertebrae (IndTemp022, 077/078); 6 caudal vertebrae (IPS9452b, IndTemp024, 061, 079/080); 38 osteoderms (IPS9449, 9455b, IPS?280, 290, 293).
- Hostalets de Pierola: 8 trunk vertebrae (IPS9489).
- Hostalets de Pierola Inferior: 3 trunk vertebrae (IPS17051, 30660b, 30660c);
 2 caudal vertebrae (IPS9490b, 30660f).
- Hostalets de Pierola P550: 1 caudal vertebra (IPS41999).
- La Gornal 1: 1 cervical vertebra (IndTemp031); 1 trunk vertebra (IndTemp034); 3 caudal vertebrae (IndTemp029/030, 032); 16 osteoderms (IPS?270).
- Rubí-Papiol: 1 trunk vertebra (IPS?217).
- Sant Andreu de la Barca: 2 fragments of vertebra (IPS?258); 8 osteoderms (IPS9620, IPS?257, IndTemp057).
- Sant Mamet: 1 trunk vertebra (IPS?222); 1 osteoderm (IPS?264).

- Sant Miquel del Toudell: 5 trunk vertebrae (IPS57439a-d, SemTemp003); 8 caudal vertebrae (IPS57439e-k, SemTemp004); 4 osteoderms (SemTemp005).
- Sant Quirze: 3 trunk vertebrae (SemTemp001); 1 caudal vertebra (MGSB31638e); 137 osteoderms (SemTemp002).
- Trinxera del Ferrocarril, Sant Quirze de Terrassa: 2 trunk vertebrae (IPS9639b).
- Trinxera Nord Autopista: 2 caudal vertebrae (IPS87396a); 17 osteoderms (IPS9653d).
- Viladecavalls: 2 blocks of sediment with vertebrae and osteoderms (IPS?39, IndTemp014).

Description

The best-preserved fragment of frontal, CBTemp226, preserves only the posterior end. A well-developed dermal ornamentation covers the dorsal surface, but it seems not to reach the lateral margin. The posterior portion of the frontal shield, the frontoparietal shield and the interfrontal shield are present. The posterolateral process is short and distally rounded. Ventrally, it is provided with a posteriorly developed lappet. Medially to the lappet, there is the articulation surface for the ventral lappet of the parietal. The wide and low posterior portion of the crista cranii is present on the lateral margin of the ventral surface. The small articulation surface with the postfrontal covers the lateral margin of the specimen. The other fragment, CBTemp231, includes only the posterolateral process, which has the same morphology as the former specimen and is covered dorsally by the frontoparietal shield.

Cervical, trunk and cloacal vertebrae are procelous. The vertebral centrum is dorsoventrally compressed and has a triangular shape in ventral view and a flat ventral surface. There is no precondylar constriction. The neural canal is arched in anterior view. The dorsal surface of the neural arch presents a distinct neural spine. The zygapophyses are subcircular and dorsally tilted at an angle of about 45°. The cervical vertebra bears a distinct keel on the ventral surface of the centrum, whereas the cloacal ones have two wide, though always broken, transverse processes.

Caudal vertebrae are procoelous and have a dorsoventrally compressed vertebral centrum. The ventral surface of the centrum is flat and the bases of the hemapophyses are present, though the latter are always broken. The neural canal is small and sub-triangular in anterior view. Transverse process are usually broken. A neural spine is present. The zygapophyses are suboval and twisted dorsally at an angle of about 45°. The autotomy plane can be either present or absent; when present, it can be partially fused.

Osteoderms can be very robust and reach a very large size, but smaller and thinner ones are also present. They are usually subrectangular (but there are also rounded ones) and show a smooth internal surface and a vermicular ornamentation on most of the external one. The ornamentation lacks only on the anterior portion of the bone, the so-called gliding surface. Moreover, in most specimens, a distinct keel runs anteroposteriorly on the ornamented area.

IPS43712 is represented by a block of sediment containing a partial articulated skeleton and by three smaller blocks containing groups of osteoderms. The skeleton included in the main block is exposed in ventral view. Its anterior portion is still covered by osteoderms, which are small and roughly subquadrangular. A vermicular ornamentation is present on their external surface, except for the anterior gliding surface. Some of the osteoderms, apparently those located towards the lateral sides of the animal, show a low but distinct longitudinal keel. In the posterior part of the specimen, a series of 7 connected trunk vertebrae is exposed. Only the ventral surface of the centrum is visible: it is flat, smooth and has a subtriangular shape in ventral view. The maximum length reached by the centra is 3.8 mm.

IPS?39 and IndTemp014 are blocks of sediment with large-sized vertebrae and osteoderms. IPS?39 includes three poorly preserved caudal vertebrae, whereas IndTemp014 includes two better-preserved trunk vertebrae. The only vertebra whose

centrum is exposed, a trunk one from IndTem014, has a centrum length of 7 mm. The morphology of both vertebrae and osteoderms recalls the above described ones. The best-preserved caudal vertebra of IPS?39 shows the autotomy plane.

Identification

Vertebrae can be attributed to an indeterminate anguine taxon because of the dorsoventrally compressed centrum devoid of precondylar constriction (Estes 1983). The subtriangular shape of the vertebral centrum in ventral view, as well as the squared and keeled morphology of the osteoderms, exclude the possibility that they belong to the genus *Anguis* (Klembara 1981; Holman 1998). Most probably, these remains can be linked to the ones above-identified as *Pseudopus* sp., but since the vertebral morphology of the taxon represented by MGB-V60 is still unknown, a more cautious identification is here favoured. The possible unornamented lateral margin of the frontal CBTemp226 might suggest that this specimen is nor referable neither to *Pseudopus* nor to the other unidentified anguid (see above). Nevertheless, the ornamentation reaching the lateral margin is a feature that varies ontogenetically (this work), and the possibility that CBTemp226 is a juvenile or a subadult cannot be excluded a priori.

Varanidae Gray, 1827 (sensu Estes et al., 1988)

Varanidae indet. (Fig. A4.10Y-Z) Material:

- Els Casots: 1 caudal vertebra (IndTemp081).

Description

IndTemp081 is a fragment of a moderately small-sized caudal vertebra, preserving only the posterior part of the vertebral centrum. The total length of the fragment is 5 mm. The centrum is dorsoventrally compressed and has a posterior condyle (procoelous vertebra), even if the latter is partially eroded. Despite the erosion, a moderate precondylar constriction is visible on the right side of the specimen. On the ventral surface, there are the bases of two distinctly robust pedestals for the chevron bone.

Identification

The precondylar constriction permits to assign IndTemp081 to the family Varanidae (Bailon 1991). Its poor preservational status, on the other hand, prevents any further identification.

"Lacertilia" indet.

Material:

- ACM/BCV1: 2 fragment of tooth-bearing bone (IPS?132/133).
- ACM/C2-B2: 2 dentaries (IndTemp037).
- ACM/C2-B3: 2 dentaries (IndTemp047); 2 fragments of tooth-bearing bone (IPS?19, IndTemp046).
- ACM/C3-A7: 1 fragment of parietal (IPS?21); 1 maxilla (IndTemp041); 1 fragment of tooth-bearing bone (IndTemp040); 1 humerus (IPS?22).
- ACM/C5-D1: 3 maxillae (IndTemp016, 021); 6 dentaries (IPS44503, 48470, IndTemp018); 8 fragments of tooth-bearing bone (IndTemp012/013, 017, 020); 1 humerus (IPS?15).
- ACM/C6-C3: 1 fragment of vertebra (IPS5518).
- ACM/C8-A4: 1 fragment of pterygoid (IPS?105).
- Can Llobateres: 1 fragment of dentary (IPS?181); 1 vertebral centrum (IPS22942c); 1 ilium (IPS22942c); 1 fragment of femur (IPS911607c).
- Can Missert: 3 fragments of dentary (IPS18900d); 1 fragment of toothbearing bone (IndTemp063); 2 fragment of vertebra (IPS82707).
- Can Sant Feliu: 1 fragment of tooth-bearing bone (IPS?131).

- Castell de Barberà: 1 frontal (CBTemp125); 1 maxilla (CBTemp111); 2 quadrates (CBTemp096, 103); 1 dentary (CBTemp097); 1 vertebra (CBTemp119); 1 humerus (CBTemp277).
- ECM/VCE-C: 2 fragments of dentary (IPS55553, 55558); 3 fragments of tooth-bearing bones (IPS55555, 55557, CBTemp340).
- Els Casots: 1 premaxilla (IPS87394); 1 fragment of tooth-bearing bone (IndTemp065); 1 trunk vertebra (IndTemp076); 1 fragment of trunk vertebra (IndTemp069); 3 ribs (IndTemp070/072); 1 ulna (IndTemp075); 2 femurs (IndTemp073/074).
- La Gornal 1: 7 fragments of vertebra (IndTemp028).
- Sant Mamet: 3 fragments of dentaries (IPS?265); 1 humerus (IPS?266); 1 pelvic girdle (IPS?266).
- Sant Miquell del Toudell: 8 fragments of vertebra (SemTemp008); 1 rib (SemTemp007); 2 indeterminate elements (SemTemp009/010).

Identification

Skeletal elements either too fragmented or lacking diagnostic features are attributed only to indeterminate lizards.

Amphisbaenia Gray, 1844 Blanidae Kearney, 2003 *Blanus* Wagler, 1830

Blanus sp. (Fig. A4.12M-T) Material:

- ACM/C3-A6: 1 dentary (IPS87808).
- Can Missert: 1 maxilla (IndTemp064); 3 dentaries (IPS9363a, 82667, 82668).

- Els Casots: 2 premaxillae (IPS82691, IndTemp062); 1 maxilla (IPS82705);
 1 dentary (IPS82704); 1 isolated tooth (IndTemp056).
- Sant Mamet: 1 dentary (IPS?267).

Description

The premaxillae are small-sized. IPS82691 (Fig. A4.12M-O) lacks most of the ascending nasal process and the palatal processes, whereas the former is almost completely preserved in IndTemp062 (except for the tip). The preserved portion of the nasal process is wide in anterior view and carries a well-developed septonasal crest on the posterior surface, which is very enlarged in its ventral part. It has convergent lateral margins. Two pairs of large foramina for the longitudinal canals are visible by the sides of the base of the process and another pair of large foramina is visible on the posterior surface, flanking the septonasal crest. IPS82691 bears 7 pleurodont, cylindrical and monocuspid teeth. The middle tooth is distinctly larger than the other ones. In IndTemp062, the alveolar portion is almost completely missing, but the middle tooth is still present. In lateral view, the anterior surface of the premaxilla is flat.

IPS82705 (Fig. A4.12P) and IndTemp064 (Fig. A4.12Q) are poorly preserved fragments of maxilla, measuring 2.3 mm and 2.1 mm respectively in total length and lacking almost completely the anterior premaxillary, the posterior and the facial processes. The specimens have a well-developed, though broken, palatal shelf, which carries 3 (IPS82705) and 4 (IndTemp064) subpleurodont, short, pointed (at least in IPS82705, since in the other specimen the crown is always broken) and moderately robust teeth, whose tip bends very slightly in posterior direction. The size of the teeth decreases significantly posteriorly. A moderately small superior dental foramen is visible on the medial surface, near the posterior breakage of the specimen, whereas the preserved part of the lateral surface is smooth, except for two ventrolateral foramina.

The dentaries have a medially open Meckelian fossa, which is narrow and groovelike. The mandibular symphysis is dorsally inclined at an angle of about 45° . The subdental ridge is moderately wide. Teeth are subpleurodont, short, moderately slender in the anterior part of the bone, but slightly more robust in the posterior one. They have a pointed and very slightly posteromedially bending tip. In IPS82668 (Fig. A4.12R) and 87808, the crown of the anteriormost teeth is rather blunt, but a more pointed morphology seems to be recognizable posteriorly. The blunt crown may be also an effect of erosion. Six (IPS87808), 7 (IPS82704) and 8 (IPS9363a) teeth are present on the preserved portion of the best-preserved specimens. The ventral margin of the dentary is straight in medial view. The lateral surface is smooth, except for the labial foramina. All specimens but IPS9363a (Fig. A4.12S-T) and 82667 lack the posterior part and so the complete length of their tooth-row cannot be ascertained; anyway, they are all small-sized and the tooth-row of the most complete ones, IPS9363a and 82704, is 3 mm in length. It should be noted, however, that IPS82667 and 82668, which are represented only by the posterior (the former) and anterior (the latter) halves of the dentary, reach respectively 2.6 mm and 2.9 mm in total length, suggesting the presence of even larger individuals. Two processes are present by the posterior end of IPS9363a, which is apparently devoid of a central posterior process. Both posterior processes are broken and miss their tip, but the superior one is wider than the inferior one. Moreover, the superior posterior process is posterodorsally directed, whereas the inferior one projects posteriorly. IPS82667, on the other hand, preserves only the pointed and posterodorsally directed superior posterior process. In IPS9363a, the posterior opening of the alveolar canal is also visible: the canal opens with a very wide cavity located posteriorly to the last tooth position; the ventral margin of this cavity is marked by the intramandibular septum, which continues posteriorly with a laminar portion fused to the wall of the dentary.

The morphology of the isolated tooth is comparable to that of the teeth of the above described maxillae and dentaries.

Identification

The morphology of the above described specimens is fully comparable with amphisbaenians of the genus Blanus (this work). Members of this genus show a rather homogeneous morphology in the skull bones (Villa et al. in press - Atti XI Congresso SHI; this work) and so it is very difficult to assign isolated and poorly preserved skeletal elements to a particular species. Nevertheless, at least the premaxillae from Els Casots display a distinctive feature of the Western clade (including the extant species Blanus cinereus, Blanus mariae, Blanus mettetali and Blanus tingitanus; Sampaio et al. 2015), that is the flat anterior surface in lateral view (Villa et al. in press - Atti XI Congresso SHI; this work). An extinct Blanus species, Blanus mendezi Bolet et al., 2014b, has been recently described based on a complete skull from Abocador de Can Mata. It is possible that at least some of the isolated specimens might pertain to this species, but the presence of a second, still unknown species cannot be discounted. The blunt tooth crowns of IPS82668 and 87808 might recall the tooth morphology of the genus Palaeoblanus Schleich, 1988, but the preservational status of the two specimens suggests to be cautious with this attribution because a taphonomical origin of this morphology cannot be excluded. Moreover, the validity of *Palaeoblanus* have been recently questioned by Čerňanský et al. (2016a).

Amphisbaenia indet.

Material:

- ACM/C5-D1: 15 trunk vertebrae (IPS43772, 48561/48571, 48600, 48613, 48692).
- ACM/C8-A4: 10 trunk vertebrae (IPS63994, 82766/82767, IndTemp001/004).
- Can Missert: 19 trunk vertebrae (IPS18901, 18903b, 18903d, 82708, 87392, IndTemp006/007); 1 caudal vertebra (IndTemp051).
- Can Poncic: 7 trunk vertebrae (IPS87403).

- Els Casots: 17 trunk vertebrae (IPS9455a, IPS?276, IndTemp055, 058).
- Sant Miquell del Toudell: 1 trunk vertebra (MGSB31640a).
- Trinxera Nord Autopista: 2 trunk vertebrae (IPS82672).

Description

Trunk vertebrae are small, procoelous and anteroposteriorly elongated. The centrum is dorsoventrally compressed and has a flat and smooth ventral surface; its lateral margins are subparallel, but very slightly concave. The synapophyses are massive and rounded. The zygapophyses are subelliptical and slightly dorsally tilted (about 30°). Very short prezygapophyseal process are present under the prezygapophyses. The dorsal surface of the neural arch is flat and smooth, without neural spine. There is no zygosphene/zygantrum complex. In dorsal view, a strong constriction at midlength is visible.

The morphology of the caudal vertebra recalls that of the trunk vertebrae. The bases of unfused hemapophyses are visible on the ventral surface and there is no autotomy plane.

Identification

Amphisbaenian trunk vertebrae are recognisable because of the small size, the absence of zygosphene and neural spine and the presence of a dorsoventrally compressed centrum with a flattened ventral surface and roughly parallel lateral margins and of massive and rounded synapophyses (Estes 1983; Delfino 2003). However, they do not bear diagnostic features allowing a more precise identification.

?Amphisbaenia indet.

Material:

- Castell de Barberà: 1 trunk vertebra (CBTemp268).

Description

CBTemp268 is a very small and procoelous vertebral centrum, with a maximum length of 2.3 mm. The entire neural arch is missing. The centrum is dorsoventrally compressed and has subparallel lateral margins, showing a very slight concavity if seen in ventral view.

Identification

This specimen has a morphology that recalls trunk vertebrae of amphisbaenians, but an attribution to this group of squamates is only tentative and cannot be ascertained, since the entire neural arch is lacking and there are no other, better preserved remains supporting it.

3.2.5. The Netherlands

Fossil remains from a single Dutch locality have been considered in this work.

Localities

Russel-Tiglia-Egypte pit, Tegelen (Fig. 3.6)
Age: early Pleistocene (Gelasian, Biozone MNR 1).
Repository: Naturalis Biodiversity Center, Leiden, The Netherlands.
References: Kortenbout van der Sluys & Zagwijn 1962; Zagwijn 1963; Hoek
Ostende & Vos 2006.

Systematic palaeontology

"Lacertilia" Owen, 1842 Lacertidae Batsch, 1788 *Lacerta* Linnaeus, 1758

Lacerta sp. (Fig. A4.13A-C) Material: 1 dentary (RGM 816720). Description



Figure 3.6) Map of The Netherlands, showing the position of the village of Tegelen (green circle).

RGM 816720 includes two portions of a broken large-sized left dentary, provided with a distinctly convex ventral margin. The alveolar shelf is 11.5 mm-long and bears 17 pleurodont, cylindrical, mono-, bi- and tricuspid teeth. Five empty tooth positions are also visible, resulting in a total number of 22 tooth positions. The Meckelian fossa is wide for the entire length of the specimen and it is not closed by folds of the bone. The lateral surface is smooth, with 5 mental foramina. The posteroventral end of the bone is broken.

Identification

RGM 816720 can be referred to a lacertid because of the presence of cylindrical, pleurodont, mono-, bi- and tricuspid teeth, the medially-opened, wide Meckelian fossa and the convex ventral margin (Delfino 2002; Delfino et al. 2011; this work). The length of the alveolar shelf falls within the range of the largest species of the genus *Lacerta* and of *T. lepidus* (see also Barahona & Barbadillo 1997). *Timon*, however, reaches much higher dimensions compared to *Lacerta*: up to 60 cm in total length, with documented specimens measuring 80/90 cm in length (Delfino 2002 and reference therein). It is then possible to assign RGM 816720 to a large *Lacerta* species.

Lacertidae indet. (Fig. A4.13D-L)

Material: 1 parietal (RGM 816758); 1 maxilla (RGM 816759); 1 pterygoid (RGM 816743); 3 dentaries (RGM 816760/816762); 2 cervical vertebrae (RGM 817012/817013); 14 trunk vertebrae (RGM 816739/816741, 816745/816748, 816755/816756); 4 cloacal vertebrae (RGM 816753/816754, 817340, 817765); 11 caudal vertebrae (RGM 816738, 816742, 816744, 816749/816752, 816757).

Description

RGM 816758 (Fig. A4.13D-E) is a fragment of parietal preserving only the posterior portion of the parietal shelf. The bone is very thin and is about 4.2 mm in maximum width. The dorsal surface is covered by the small occipital shield and by the posterior portion of the lateral and interparietal ones. The shields are composed by a welldeveloped vermicular ornamentation, which does not reach the posterior margin of the shelf. A very narrow area levis is therefore present. In the middle of the anterior margin of the preserved portion of the specimen there is the posterior margin of the parietal foramen, which therefore opens near the posterior end of the interparietal shield. Both postparietal processes are broken. On the ventral surface, the anterolateral ventral crests touch medially the wide medial ventral crest. A contact seems to be present also between the posterolateral and the anterolateral ventral crests. In ventral view, the parietal fossa is wide and U-shaped. In dorsal view, a small and shallow parietal notch is visible posteriorly to the fossa. The postparietal processes are broken, but their bases are narrow.

The pterygoid, RGM 816743 (Fig. A4.13F-G), is well preserved and has a maximum length of 3.6 mm. Anteriorly, the pterygoid recess is well marked. There are no pterygoid teeth on the ventral surface. The palatine process is straight and moderately narrow. The pterygoid flange displays a well-developed ridge on the dorsal surface and a low developed one on the ventral surface. The quadrate process is straight in dorsal view. It misses its posterior tip. A wide and deep fossa columellae is visible dorsally, followed by a moderately developed pterygoid ridge.

The tooth-bearing bones are small and fragmentary. They bear pleurodont, cylindrical and bi- or tricuspid teeth.

Presacral vertebrae (Fig. A4.13H-L) are procoelous and small-sized. The cervical ones are slightly wider than they are long, whereas the trunk ones are anteroposteriorly elongated. The centrum length goes from 1.4 mm to 1.7 mm in the cervical vertebrae and from 1.5 mm to 2.5 mm in the trunk vertebrae. In ventral view, the centrum is subtriangular and bears a distinct hemal keel in the middle. The anterior cotyle is subcircular or subelliptical, whereas the posterior condyle is subcircular. The neural canal is subcircular in anterior view. Synapophyses are narrow and elongated in the cervical vertebrae, small and suboval in the trunk ones. The zygapophyses are suboval or subelliptical and tilted dorsally at an angle of 20/45°. The tilt seems to be lower in the trunk vertebrae. Pseudozygosphenial and pseudozygantric facets are visible medially to the pre- and postzygapophyses respectively. A neural crest generating a neural spine posteriorly is present on the dorsal surface of the neural arch.

Cloacal vertebrae are similar to the presacral ones in both general morphology and size (centrum length goes from 1.5 mm to 1.7 mm). They are roughly as long as they are large and bear laterally-developed transverse process, which are not pointed distally.

Caudal vertebrae are procoelous, elongated and provided with circular cotyle and condyle. The centrum length varies between 1.5 mm and 2 mm. The centrum is triangular in ventral view and presents a poorly defined hemal keel. There are no fused hemapophyses. Transverse processes are almost always broken, but when preserved they narrow distally to form a pointed end. They are strongly dorsoventrally compressed and distinctly ventrolaterally directed. In anterior view, the neural canal has a vaulted section. Zygapophyses are subcircular or subelliptical and dorsally inclined at an angle of 30°. Pseudozygosphenial and pseudozygantric facets are present. A very low neural crest runs along the dorsal surface of the neural arch, originating a tubular neural spine.

Identification

All the above described specimens are small-sized, suggesting the presence of a small lacertid taxon in the fossil material coming from Tegelen. However, it has to be noted that the only skeletal elements that can possibly have a diagnostic significance (namely, the parietal and the pterygoid, since the tooth-bearing bones are too fragmentary) do not show clear adult features, and therefore they can simply represent juveniles of a larger taxon. Because of this, this fossils are here attributed only to indeterminate lacertids.

Anguidae Gray, 1825 Anguinae Gray, 1825 Anguis Linnaeus, 1758 Anguis fragilis Linnaeus, 1758

Anguis gr. A. fragilis (Fig. A4.13M-V)

Material: 1 partial parietal (RGM 816693); 1 maxilla (RGM 816701); 56 trunk vertebrae (RGM 816661, 816663/816664, 816668, 816676/816677, 816681, 816684/816685, 816688/816689, 816695/816696, 816698, 816703, 816705, 816709, 816712); 2 cloacal vertebrae (RGM 816704, 816707); 34 caudal vertebrae

(RGM 816662, 816665, 816667, 816669, 816678/816679, 816682, 816694, 816697, 816706, 816708, 816710/816711, 816713/816715, 816763/816777); 143 osteoderms (RGM 816660, 816666, 816670/816674, 816683, 816686/816687, 816690/816691, 816699/816700, 876702).

Description

The preserved fragment of parietal, RGM 816693 (Fig. A4.13M-N), includes only the anterior portion of the right supratemporal process and the portion of the shelf located anteriorly to it. The specimen is thin and 4 mm in total length. The anterior part of the preserved shelf is covered dorsally by the remaining part of the right lateral shield, apparently not touching the lateral margin of the bone. By the anteromedial corner of the specimen, the margin of the parietal foramen is visible, flanked laterally by the groove separating the interparietal and the right lateral shields. A wide area levis is visible posteriorly. The preserved portion of supratemporal process is wide. Medially, on the dorsal surface, there is the poorly developed carina arcuata. The ventral surface of the specimen does not develop a facies muscularis parietalis (sensu Klembara et al. 2010) and so the lateral margin of the bone is marked by the anterolateral ventral crest. Posteriorly, the latter touches the posterior margin of the bone. The right margin of a deep parietal notch is preserved, as well as a small remnant of the parietal fossa. The posterolateral ventral crest is well developed and marks the lateral margin of the supratemporal process, due to the absence of the facies ventrolateralis (sensu Klembara et al. 2010).

RGM 816701 (Fig. A4.13O-P) is a left maxilla preserving the anterior portion only. The fragment is about 3.2 mm-long. A moderately long and distally truncated anterolateral process is preserved, but the anteromedial one is missing. The facial process is mostly missing, but its lateral surface is smooth, with 4 large ventrolateral foramina. The medial surface of the process displays a distinct arched ridge. Dorsally to this ridge, the anterior portion of the medial surface presents distinct rugosities. Two subpleurodont teeth are visible, separated by an empty tooth position. They are large, canine-like and posterolingually bending. They do not show striae. Trunk vertebrae (Fig. A4.13Q-U) are procoelous and elongated. The most preserved ones have a centrum length going from 1.2 mm to 3.8 mm. The vertebral centrum is strongly dorsoventrally compressed and subrectangular in ventral view, with parallel lateral margins in the posterior portion. The ventral surface is smooth, with two variably developed subcentral foramina. When preserved, synapohyses are robust and subelliptical. The neural canal is subtriangular. A well-developed neural crest is present on the dorsal surface of the neural arch, forming a triangular neural spine posteriorly. Zygapophyses are wide, circular and dorsally tilted at an angle of about 30/45°.

Cloacal vertebrae are morphologically similar to the trunk ones, but a pair of transverse processes are present in place of the synapophyses. The processes are always broken, but their base is wide. The length of the vertebral centrum of the two specimens is 2.5 mm and 2.9 mm.

Caudal vertebrae are procoelous and distinctly anteroposteriorly elongated. The centrum reaches up to 4 mm in length. It is strongly dorsoventrally compressed and presents the bases of fused hemapophyses on the posterior portion of its ventral surface. The autotomy plane is present in most of the vertebrae.

Osteoderms (Fig. A4.13V) are small, thin and rounded. Three different morphologies are recognisable: subcircular, subovoidal and subtrapezoidal. The external surface presents a smooth gliding surface followed by a larger area covered by a vermicular ornamentation. The inner surface is smooth and provided with some small foramina in the middle and a variable number of shallow grooves directed posteriorly from the perforated area.

Identification

The dorsoventrally compressed centrum of presacral vertebrae devoid of precondylar constriction is a feature of the subfamily Anguinae according to Estes (1983) and the size of the above described ones suggest their attribution to a small-sized taxon. Because of the parallel margins in the posterior portion of the centrum, they can be assigned to *Anguis* (Klembara 1981; Holman 1998). Maxilla and parietal can be

attributed to the same genus because of the presence of large, canine-like, unstriated and curved teeth on the former (Klembara et al. 2014; this work) and the deep parietal notch on the latter (Delfino et al. 2011; this work). The identification of the osteoderms is based on the small size, the rounded shape, the thin morphology and the absence of keels on the external surface (Holman 1998; Delfino et al. 2011). Since a comparative osteological study of the different *Anguis* species is still missing, the material have been identified only at the level of species complex.

Pseudopus Merrem, 1820

cf. *Pseudopus* sp. (Fig. A4.13W-X)

Material: 1 osteoderm (RGM 816716).

Description

RGM 816716 represents a fragment of osteoderm, which is much bigger and much more robust than the ones assigned to *Anguis* gr. *A. fragilis*. The fragment is about 4.3 mm-long. Its thickness decreases posteriorly. The external surface shows an ornamentation made by foramina and stocky but little developed tubercles. A low and straight ridge crosses longitudinally the external surface, running medially in anteroposterior direction. This ridge is flanked by a shallow groove in the posterior half of its length. The internal surface is smooth, with some foramina on the thickest portion of the bone. A shallow groove can be seen in the thinnest part, in correspondence to the ridge present on the external surface.

Identification

The size of RGM 816716 suggests the presence of a large-sized anguid. Size, thickness and the ridge on the external surface preclude the attribution of this osteoderm to *Anguis* (Holman 1998; Delfino et al. 2011). In the European Pleistocene, findings confidently attributable to *Ophisaurus* are reported only from Southern Spain (Barranco León and Fuente Nueva 3; Bailon & Blain 2007; Blain 2009), whereas *Pseudopus* is the only non-*Anguis* anguid known from northern

countries. Moreover, the Spanish remains represents much smaller animals than the osteoderm found at Tegelen. Thus, RGM 816716 can be tentatively attributed to cf. *Pseudopus* sp., the only large-sized anguid genus so far certainly identified from European Pleistocene localities so far.

"Lacertilia" indet.

Material: 2 dentaries (RGM 816722, 816726); 1 trunk vertebra (RGM 816721); 1 caudal vertebra (RGM 816737); 1 fragment of vertebra (RGM 817011); 4 ribs (RGM 816675, 816680, 816692, 816734); 1 scapulocoracoid (RGM 816729); 5 humeri (RGM 816728, 816730/816731, 816735/816736); 1 ulna (RGM 816733); 3 ilia (RGM 816725, 816732); 4 femurs (RGM 816723/816724, 816727).

Identification

A number of poorly-preserved or non-diagnostic skeletal elements have been identified only as indeterminate lizards.

3.3. A summary of the fossil lizards from the European Neogene and Quaternary

Remains of Neogene and Quaternary lizards and amphisbaenians are rather common across Europe, with more than 3200 SPLOC data distributed in more than 800 localities spanning from the early Miocene to the Holocene (Fig. 3.7; see also Appendix 5). A large number of these data pertains to occurrences dated back to the Miocene, followed by the Pleistocene ones in terms of abundance. Pliocene and in particular Holocene data are significantly less represented. A deeper attention to these two periods is needed in order to enhance our knowledge of the evolutionary dynamics of these reptiles in the continent, given also that potentially interesting localities are indeed present (e.g., Tenuta Zuccarello; Villa et al. 2015; this work) even though their palaeoherpetofaunas might remain unstudied for a long time. Moreover, it must be taken also into account that there is still a lot of material that,


Figure 3.7) Distribution of Neogene and Quaternary occurrences of European fossil lizards. despite being mentioned in online databases or in publications not directly focused on it, remains either completely unpublished or in need of being thoroughly described and identified following the currently available criteria and information. Because of that, in spite of the large quantity of fossil occurrences reported, a lot of work still need to be done by palaeoherpetologists in order to have a clearer understanding of the palaeontological history of lizards and worm lizards in Europe during the last 23 millions of years.

In the following pages, the currently available information on the fossil record of each family of lizards that lived in Europe during Neogene and Quaternary are briefly summarized.

3.3.1. Agamidae

Fossil agamids are reported in Europe since the early Miocene up to the Upper Pleistocene, even though they are distinctly not as common as other groups of lizards living in the continent. In the past, the trend was to assign all agamid findings to the genus *Agama* in a wide sense (including also *Laudakia*), which leaded to numerous

mentions of the genus in both the Neogene and Ouaternary of the continent. Even if some tentative attributions to Laudakia are also known (e.g., in Almenara Casablanca and Vallirana in Spain; Blain 2005, but later mentioned as Agamidae indet., as in e.g., Blain, 2009, and Blain et al., 2016a), Delfino et al. (2008) demonstrated that the few characters used to discriminate Agama sensu stricto and Laudakia most probably originated from the study of limited comparative material and need to be checked on larger comparative samples before being considered valid. The wide sense with which the name Agama has been used and the apparent absence of clearly recognised diagnostic features might suggest that identification of most of the European Neogene and Quaternary remains as indeterminate members of the family Agamidae (or maybe sometimes even of the subfamily Agaminae) could be of equivalent use. It has to be noted, however, that excluding attribution to some extant genera is sometimes possible, as is the case for example of the agamids from Monte Tuttavista, which are clearly different from *Phrynocephalus* and *Trapelus* according to Delfino et al. (2008). The absence of deepened comparative studies of extant and fossil forms, as well as the preservational status of most of the remains, might have also contributed to the absence of extinct species described from the Neogene and Quaternary of Europe.

The geographical and temporal distribution of agamids in Europe has been briefly summarized in a recent paper by Blain and colleagues (2016a). As shown by the authors, a trend towards a southward shifting of their distribution probably linked with climate changes is evident from the Miocene onwards, starting from an Eocene distribution that reached Belgium in the North. During the Pliocene and even more during the Pleistocene, agamids appear to be confined in Mediterranean countries, such as Spain, Mediterranean France, Italy and Greece. The Italian post-Miocene record is particularly scarce, with a single occurrence in continental Italy (early Pleistocene, MN 17, of Montagnola Senese; Delfino, pers. obs in Delfino et al. 2008; note that this locality is incorrectly included in the Pliocene range in Blain et al., 2016a) and a rather high number of remains from Monte Tuttavista in Sardinia (early

to possibly Middle Pleistocene; Delfino et al. 2008). Agamids then disappeared from Western Europe by the end of the early Pleistocene, with a single dentary from Sardinia possibly representing the only evidence of a Middle Pleistocene European agamid. However, Delfino and colleagues (2008) do not exclude that this isolated remain could be an allochtonous intruder coming from older fissure fillings of Monte Tuttavista. In spite of a gap in the record between the end of the Pliocene and the present days, poorly filled by a couple of isolated and poorly diagnostic vertebrae from the Upper Pleistocene of Pili B in the island of Kos (this work), Greece is the only European country still hosting agamids (namely, *L. stellio*) in its extant herpetofauna. The absence of significant fossils younger than Pliocene in age from the country, however, hinders the tracking of the origins of the extant Greek populations, even though it might also suggest a rather recent invasion from the east (as already stated by Delfino et al. 2008). If future findings would allow to clearly attribute the remains of Pili B to *Laudakia*, its possible arrival in the country would have taken place at least before the end of the Pleistocene.

A few remains previously assigned to agamids are now not considered to pertain to the family anymore. Two fragments coming from the late Miocene of Ano Metochi 3 in Greece (Delfino 2004a) and from the Upper Pleistocene of Tokod in Hungary (Meszoely & Gasparik 2002) have been subsequently reassigned to cyprinid fish by Georgalis et al. (2017a) and Gaudant (pers. comm. in Rage 2013). Młynarski (1956) tentatively identified a possible agamid fragment of mandible from Węże I (Pliocene of Poland), but later he retracted this identification (Młynarski 1962). Judging from the figure reported in his original paper (Młynarski 1956: fig. 3), the specimen is indeed different from a standard agamid dentary in both tooth and overall morphology, and can be therefore considered as an indeterminate squamate.

3.3.2. Chamaeleonidae

European fossil chamaeleons are rather important in the context of the poor fossil record of this family, since this area is one of the richest worldwide in term of

remains attributable to these lizards (Böhme & Ilg 2003; Bolet & Evans 2013; Georgalis et al. 2016a). Central Europe, in particular, has yielded an unexpectedly high number of Neogene chamaeleon fossils, if compared with the very scanty palaeontological record of the family in the rest of the world. This scant nature of the record holds true for the rest of Europe also, where just very few occurrences are reported (one from Greece, one from Serbia and two from Spain).

All but one occurrences come from early to middle Miocene localities, spanning from MN 3 to MN 7. The single post-Miocene occurrence is represented by remains coming from the Holocene site of Cueva de la Victoria, near Málaga in Southern Spain (Talavera & Sanchiz 1983), and attributed to the extant species *C. chamaeleon*, still living in the area. Because of the scarce information given by the fossil record, it is not clear when and why the Neogene species disappeared from the continent and when the single autochthonous extant European species (namely, *C. chamaeleon*) firstly spread into the country.

Six extinct European species have been described, all of them belonging to the genus *Chamaeleo: C. andrusovi* Čerňanský, 2010b, *Chamaeleo bavaricus* Schleich, 1983, *Chamaeleo caroliquarti* Moody & Roček, 1980, *Chamaeleo pfeili* Schleich, 1984, *Chamaeleo simplex* Schleich, 1994 and *Chamaeleo sulcodentatus* Schleich, 1994. Nevertheless, Čerňanský (2010b, 2011) considered both *C. caroliquarti* and *C. pfeili* as *nomina dubia*, because of them being based only on fragmentary tooth-bearing bones lacking clear apomorphic features allowing the identification of new species. A similar argument may hold true for *C. simplex* and *C. sulcodentatus* too, which in turn have been described based on fragmentary remains, but a revision of the type material would be needed to clarify this.

Because of the poor fossil record of European chamaeleons on the whole, the known geographic range of most of the described extinct species is scarcely understood. Most species are known only from one or few, very close localities: so far, *C. simplex* has been found only in the type locality, the German site of Randecker Maar, whereas the occurrences of *C. bavaricus*, *C. pfeili* and *C. sulcodentatus* are limited to

Southern Germany (with the single exception of a mention of the latter species from Switzerland; Böhme 2003; Böhme & Ilg 2003). *Chamaeleo caroliquarti* seems to have a wider record, but still it is mainly centred in Southern Germany, even though the type locality is in Czech Republic (Moody & Roček 1980). If confirmed, a possible occurrence of this species in the Burdigalian of Southern Spain (Agramón, province of Albacete; Böhme & Ilg 2003) would be very interesting, but it is still unpublished and therefore must be taken with caution. The distribution of *C. andrusovi* is rather interesting too, even though it is currently known from very few localities: this species has been originally described from Dolnice, in Czech Republic (Čerňanský 2010b), but later few remains coming from other two localities have been attributed to *Chamaeleo* aff. *C. andrusovi*. Interestingly, these two new localities, Hambach 6C in Northwestern Germany (Čerňanský et al. 2016c) and Aliveri in Greece (Georgalis et al. 2016a), are located at the opposite sides of Europe, largely extending the known range of the species.

In terms of temporal distribution, *C. caroliquarti* is also the extinct species that spans for the longest time interval (MN 3a to MN 6), overlapping the stratigraphical range of other species too. The range of other species is obviously restricted by their fewer occurrences, with *C. andrusovi* reported from MN 4 to MN 5, *C. bavaricus* from MN 5 to MN 6, *C. pfeili* only from MN 4b, *C. simplex* only from MN 5 and *C. sulcodentatus* from MN 5 to MN 6. However, it has to be noted that, following Čerňanský in considering at least some of these species as *nomina dubia*, possible synonymy between at least some of them might result in the extension of their range in the future, both geographically and stratigraphically.

3.3.3. Gekkota

Fossil remains of gekkotans are known throughout the entire Neogene and Quaternary of Europe. Today these reptiles are confined to Mediterranean countries, with *M. kotschyi* alone present also along the coasts of the Black Sea (Sillero et al. 2014), but as for other lizards groups their distributional range was far more

widespread during the Miocene, reaching up to Southern Germany and Northwestern Czech Republic in the North at least. A constriction towards a circum-Mediterranean distribution appears to be recognisable already in the Pliocene, and no occurrence is known outside this range subsequently. This is similar to the trend shown by agamid fossils in the continent (Blain et al. 2016a; see also chapter 3.3.1) and could be equally due to a progressive cooling of the climate in Europe.

Traditionally, geckos were subdivided into two families, Gekkonidae and Pygopodidae (Evans 2008; Vitt & Caldwell 2009), but recent phylogenetic analyses have recognised a wider diversity at the family level, leading to the creation of seven different families (see e.g., Gamble et al. 2012, 2015). In the same way as most of the agamid fossils were attributed to Agama (see above), most European remains of indeterminate geckos have been attributed to Gekkonidae (i.e., non-pygopodid gekkotans) in the past, as a result of the traditional classification. Again, most of these attributions would be more probably compatible with an identification as indeterminate gekkotans now, even though the possible presence of diagnostic features allowing their identification as members of other gekkotan families must not be discounted without a revision of each single occurrence. Nevertheless, remains of undisputed gekkonids are indeed present in Europe: they all pertain to the genus Hemidactylus and come from the Middle Pleistocene to Holocene of France (Middle Pleistocene/Holocene of Lazaret Cave; Bailon 1991), Greece (Upper Pleistocene of Liko BA; this work) and Italy (Middle Pleistocene of Valdemino Cave and Holocene of Grotta Curbeddu; Delfino 2004b, 2006; this work). Even if the attribution to the extant species H. turcicus of the remains from Liko BA seems to be well-sustained, the absence of the faint ornamentation characterizing some skull bones of such a species in the remains from Valdemino suggests that either a different species of the genus or a variant of H. turcicus was present in Liguria during the Middle Pleistocene. In this context, it is interesting to note that Bailon (1991) described a smooth lateral surface also for the maxillae from Lazaret Cave, which is located in Southeastern France not so far from Valdemino Cave. However, the maxillae are not figured in Bailon's thesis and they have never been properly published, so it is not possible to check if the ornamentation is indeed lacking or it just went unnoticed. If the absence of this feature in the French maxillae is confirmed, it would become clear that a peculiar population of *Hemidactylus* (or *H. turcicus*) was present along the coast of the Ligurian Sea during the Middle Pleistocene. Böhme & Ilg (2003) report another gekkonid, namely *Gekko* sp., from a few French sites dated back to the early Miocene (MN 2): Chavroches P1, Chavroches P1C2, Le Gondailly and Montaigule-Blin. However, Böhme (2003) mentions the same occurrences as pertaining only to indeterminate Gekkonidae. Given that no other fossil occurrence of this Southeast Asian genus is currently known in Europe (except for another, unpublished mention from the Chattian of Gannat, still in France, included by Böhme and Ilg in their online database) or nearby countries, the identification of the French remains is rather dubious and they should likely be considered indeterminate gekkotans pending a thorough study.

Two other gekkotan families are recorded with fossil representatives in the Neogene and Quaternary of Europe: Phyllodactylidae and Sphaerodactylidae. This means that all three families that are currently present in the continent are also reported in the fossil record, even though only sphaerodactyls are undisputedly present before the late Pliocene (phylogenetic relationships of Paleogene species are still unclear; see Daza et al. 2014 and Bolet et al. 2015). The oldest European phyllodactylids are known from Spain, where *Tarentola* has been reported from the Gelasian of Almenara Casablanca 1 (Blain 2005, 2009) and *T. mauritanica* from the Calabrian of Cueva Victoria (Blain 2005, 2009, 2012-2014) and Quibas (Montoya et al. 2001; Agustí et al. 2009), as well as from the early Pleistocene (early Biharian) of Cementerio de Orce (Bailon 1991). An even older possible occurrence of a form morphologically similar to *Tarentola* might be represented by some few dentaries found in Cova Bonica (MN 16 of Northeastern Spain), but this identification is mainly based on the size of the remains and should therefore been taken with caution (Blain 2009). Very few other localities from the Iberian Peninsula, France and Italy

have yielded younger remains of *Tarentola*. Finding the oldest representatives of *T. mauritanica* (or closely morphologically related taxa) in Spain agrees with the hypothesys of an Iberian origin of the extant European populations of this gecko inferred from molecular analyses (Rato et al. 2010). However, given that fossil occurrences are also found in Pleistocene sites of other European countries, fossil evidence are in contrast with the idea of a recent, rapid and maybe human mediated colonization, again suggested by molecular data (Harris et al. 2004; Rato et al. 2010). A similar colonization pattern has been suggested for *H. turcicus* too (Carranza & Arnold 2006; Rato et al. 2011), but again the presence of European Pleistocene fossils might reject this hypothesys. Of course, a recent recolonization of areas previously occupied by older populations of *H. turcicus* and/or *T. mauritanica* might also be the case.

Sphaerodactyls are present in Europe since at least the early Miocene. Earliest representatives of this clade in the continent already include members of the extant genus *Euleptes*, among which the extinct species *E. gallica* from the early Miocene of France (Müller 2001) and Czech Republic (Čerňanský & Bauer 2010), as well as indeterminate Euleptes from the early Miocene of Germany (Müller & Mödden 2001) and the middle Miocene of Slovakia (Estes 1969; Daza et al. 2014). A second genus, Gerandogekko, was also present during the Miocene in France, including two species that are known from the Aquitanian (G. arambourgi, from Saint-Gérand-le-Puy; Hoffstetter 1946) and the upper Miocene (G. gaillardi, from La Grive-Saint-Alban; Hoffstetter 1946). However, arguments used by Hoffstetter (1946) and later Estes (1983) to separate the two species are considered rather weak by Daza et al. (2014), even though the latter authors do not directly suggest a synonymy due to the scarce material available. A long gap in the record then covers the whole Pliocene, with sphaerodactyls that are later recovered only in the Pleistocene of Sardinia (this work). This latter occurrence, spanning for almost the whole Pleistocene, represents the only known fossil record of a form closely related to the extant *E. europaea*.

Two other fossil taxa with uncertain phylogenetic relationships are reported from the Neogene of Europe. The first one is the German species *Palaeogekko risgoviensis* (middle Miocene; Schleich 1987; Böhme 2003), whose systematic affinities are rather dubious but almost certainly not related to either eublepharids or pygopodoids (Schleich 1987; Daza et al. 2014). Given that the latter taxon include Pygopodidae, Carphodactylidae and Diplodactylidae, P. risgoviensis should belong to either one of the three gekkotan families already recognised in Europe or to another, still unrecognised family. It has to be noted that Daza and colleagues (2014) do not discount the possibility that the material assigned to *P. risgoviensis* belong instead to more than one species. The second uncertainly related taxon is the new gecko described in this work based on fossils from the Gargano "Terre Rosse" area (see chapter 3.2 for a detailed discussion about the identification of these remains). A deeper study of these remains, including specimens stored in the Naturalis Biodiversity Center in Leiden that were not considered in this work and a phylogenetic analysis, is needed in order to clarify its possible affinities with other taxa.

In the end, Augé & Rage (2000) stated that *Lacerta? ambigua*, a species described by Lartet (1851) from Sansan, might be in fact a gecko. Unfortunately, the type material is now lost and there are no figures in Lartet's work. Because of that, this hypothesis cannot be either confirmed or rejected. Moreover, a fragment attributed to a possible gecko by Młynarski (1956) from the Pliocene of Węże I is not a gecko. Similarly to the possible agamid he mentioned from the same site, he later corrected this identification, referring the fossil to an indeterminate squamate (Młynarski 1962).

3.3.4. Lacertidae

During the Neogene and Quaternary, Lacertidae is by far the most represented lizard family in the European fossil record. Lacertids are reported almost continuously from the beginning of the Miocene up to the Holocene, and the geographic distribution of their fossil occurrences is also equally wide for this entire period of time. This might of course be due to a taphonomic-based underrepresentation of other families in the record, but it could also represent a real dominance of this family in the continent since the Miocene at least, as it is the case in its modern lizard fauna.

Both extinct and extant taxa are known as fossils. Extinct ones are mainly confined to the Miocene, even though a few exceptions from the Pliocene and the Pleistocene exist. It has to be noted, however, that a number of extinct species erected in the past are now considered either not valid or problematic. This is the case, for example, of most of the lacertid species named by Lartet (1851) from the middle Miocene of Sansan, in France. Of the five species he mentioned, only *Lacerta sansaniensis* (now Edlartetia sansaniensis; see below) is currently considered as a valid species, following the description of new material by Augé & Rage (2000). The descriptions of the other four species, Lacerta ponsortiana, Lacerta bifidentata, Lacerta philippiana and Lacerta? ambigua, given by Lartet (1851) in his work are very brief and, given that the remains are not figured and the original material is currently lost, inadequate for sustaining their validity. Because of this, all of them have been subsequently considered nomina dubia (Estes 1983; Augé & Rage 2000). Both Estes (1983) and Augé & Rage (2000) noted that at least some of these species might not even be attributable to lacertids, as e.g., Lacerta? ambigua, which might instead represent a gekkotan.

Two Pliocene species have also been questioned: *Lacerta crassidens* and *Lacerta ruscinensis*. The former was briefly described by Gervais (1859) based on few remains coming from Issoire (France), but Estes (1983) considered these remains too fragmentary and undiagnostic and the species as a *nomen dubium*. Remains of *L. ruscinensis*, a dentary and a vertebra found in the Pliocene sediments of the French locality of Roussillon and described as a new species by Depéret (1890), appear to be very similar in size and morphology to the ocellated lizard, from which it differs only based on few (and probably devoid of real diagnostic significance) characters: that is, slightly more delicate tooth morphology and a lower number mental foramina

(see also Estes 1983). Based on the current knowledge, it seems not possible to clearly separate these remains from those belonging to extant large lacertid species and therefore a possible attribution to one of the latter should not be excluded, as already suggested by Estes (1983). Also because of that, the occurrence of L. *ruscinensis* in Csarnóta 2 (early Pliocene of Hungary) mentioned (but neither described nor figured) by Jánossy (1986) appears doubtful.

In the Pleistocene, problematic taxa come from Austria, France, Italy and Malta. Rauscher (1992) described two new species from Bad Deutsch-Altenburg, in Austria: Lacerta altenburgensis and Podarcis praemuralis. Lacerta altenburgensis is based on a single specimen, a maxilla, which is considered aberrant by the author. However, this supposed aberrant morphology is due to the fragmentary nature of the specimen, and no significant diagnostic feature can be observed in its preserved portions (E. Tschopp, pers. comm.). Podarcis praemuralis, on the other hand, is based on more material. Nevertheless, the main features that are reported to differentiate this species from the very similar P. muralis (such as a wider and more rounded ascending nasal process of the premaxilla, a slightly less wavy crista dentalis of the maxilla and a less developed carina zygomatica) might alternatively fall into the normal individual variation of the latter species. Because of that, both these Austrian species are here considered nomina dubia. Lacerta fossilis, reported by Pomel (1853) from Upper Pleistocene localities in France and attributed to an indeterminate species of Lacerta by Böhme & Ilg (2003), is a nomen dubium, as already stated by Estes (1983) and Holman (1998). Indeed, the original description of the species is too vague to sustain its validity and no figure is given by the author. As is the case for other problematic lacertid species, the original material studied by Pomel is currently lost. Lacerta castellanensis, a possible endemic Sicilian species based on a single specimen found in Castellana (De Gregorio 1925), is most probably not a *Lacerta* according to Kotsakis (1977). This hypothesys has been generally followed by later authors (e.g., Estes 1983; Caloi et al. 1986; Holman 1998) and a revision of the type material would be needed in order to clarify the taxonomic

assignment of this taxon. The problematic taxon from Malta is *Lacerta melitensis*, which is a *nomen nudum* (Böhme & Zammit-Maempel 1982; Bailon 2004). As a matter of fact, the first mention of the species is found in a review of the fossil animals from the island presented by Gulia (1913) at the IX International Congress of Zoology. In that circumstance, he listed the new specific name in brackets referring to a large-sized lizard he already mentioned one year before (Gulia 1912), but without giving neither any explanation for the mention of the new name nor any description or figure. Later, Savona Ventura (1984) stated that the remains assigned to *L. melitensis* by Gulia were in fact those of a lizard reported from Ta' Gandja and Benghisa Gap and attributed simply to *Lacerta* sp. by Adams (1866). Nevertheless, this material is lost (Böhme & Zammit-Maempel 1982) and therefore it is not possible to check whether *L. melitensis* could be considered a valid species or it must be considered conspecific with the other large lacertid known from the Pleistocene of Malta, that is "*Lacerta*" siculimelitensis.

Among the valid species, particularly interesting are the amblyodont forms. Amblyodonty (sensu Hoffstetter 1944) was not uncommon among lacertids during the Paleogene (for a review of Paleogene amblyodont taxa, see Augé et al., 2003, Augé, 2005, and Bailon et al., 2014), and the success of this peculiar feature seems to have lasted into the Neogene at least until the middle Miocene. The most widespread genus is the moderately amblyodont *Amblyolacerta* (type and only know species: *Amblyolacerta dolnicensis*), which is known from the early to middle Miocene spanning from Czech Republic to Germany and France, and maybe also to Switzerland and Spain. The degree of amblyodonty is higher in both *Ligerosaurus pouiti* and *J. ulmensis*, two species currently found only in the middle Miocene of Northwestern France (Augé 1993; Augé et al. 2003) and in the early to middle Miocene of Southern Germany (Čerňanský et al. 2016b; this work) respectively. Southern Germany has yielded also the youngest representative of *Mediolacerta*, a genus with a moderate degree of amblyodonty previously found only in the Oligocene of both France (Augé 2005) and Germany (Čerňanský et al. 2016a). It

appears, therefore, that amblyodont (either at a moderate or an higher degrees) lacertids and the feeding habits linked with their tooth morphology still had a role in Miocene ecosystems, at least previous to the late Miocene. Then, this morphology disappeared in European lacertids, remaining limited to some other lizard group (that is, anguids of the genus *Pseudopus*, whose increasing distribution is considered a possible cause for the disappearance of amblyodont lacertids by Augé and colleagues, 2003). Only a single lacertid species showed again an amblyodont dentition by the beginning of the Pliocene: *Maioricalacerta rafelinensis*. However, the range of this species is limited to the island of Mallorca, and its high degree of amblyodonty was probably evolved independently under the particular insular conditions from an ancestral form provided with a more generalized dentition (Bailon et al. 2014).

The European Miocene hosts other lacertid taxa with a peculiar, even though nonamblyodont, dentition, such as *Edlartetia*. The type species, *E. sansaniensis*, was originally described as Lacerta sansaniensis by Lartet (1851), but later moved on its own genus by Augé & Rage (2000) because of its unique dentition provided with a constriction below the crown, a feature never found in any other lacertid lizard neither fossil nor extant. The type locality of the species is Sansan (middle Miocene, MN 6, of France), but it has been later reported from the Burdigalian (MN 5) and maybe Serravallian (MN 8) of Germany (Böhme 2010; this work) and from the Tortonian (MN 11) of Austria (Tempfer 2005) too. Other remains attributed, or tentatively attributed, to the genus are known also from other German and Austrian early to middle Miocene localities (Böhme & Ilg 2003; Böhme & Vasilyan 2014; this work). A possible, though still unpublished occurrence is also mentioned by Böhme and Ilg (2003) from the middle Miocene of Toril 2, in Spain. The dentition of *Miolacerta*, a genus known from a number of localities in Central and Eastern Europe spanning from the early to the late Miocene, was also considered distinctive in having a strongly tricuspid crown in the posterior teeth (Roček 1984). Given that a similarly high degree of tricuspidity is not unknown among other lacertids (being present in *Takydromus* and *Gallotia* among extant genera, for example; see Kosma 2004), it is not unlikely that at least some fragmentary remains previously tentatively identified as pertaining to *Miolacerta* (e.g., fossils from Sandelzhausen and Gisseltshausen; Böhme 2010; this work) could belong to other lacertids instead. Nevertheless, rather confident occurrences of *Miolacerta tenuis*, the only species currently included in the genus, are reported from Czech Republic (early Miocene of Dolnice; Roček 1984) and Austria (late middle Miocene of Gratkorn and upper Miocene of Kohfidisch; Tempfer 2005; Böhme & Vasilyan 2014).

Another extinct Miocene species, *Lacerta poncenatensis*, is known from few early Miocene localities. This species was firstly described from Poncenat, in France, by Müller (1996), and it was later recovered in Germany at Wiesbaden-Amöneburg (Čerňanský et al. 2015) and possibly in Austria at Oberdorf (Čerňanský 2016). In spite of the few known occurrences, therefore, L. poncenatensis could have had a moderately wide distribution during the early Miocene. Čerňanský and colleagues (2015) observed that certain features present in the specimens they assign to this species, such as the presence of slightly tricuspid teeth, reduce the differences between L. poncenatensis and another species reported from Poncenat: namely, Lacerta filholi. Nevertheless, they still considered the two species as distinct, given the maintenance of other differences, even though hinting at a possible future synonymy due to the desirable finding of new specimens. In any case, the record of L. filholi at Poncenat (Augé & Smith 2009) is one of its latest occurrences, together with Montaigu-le-Blin (Augé et al. 2003). This species is largely known from the Oligocene of France and Belgium (Böhme & Ilg 2003), but then it apparently had a drop by the Oligocene/Miocene boundary, a period that has already been considered critical for squamates reptiles (see Rage & Szyndlar, 2005, and Rage, 2013). The two French occurrences are the only mentions of the species in the Neogene, likely indicating that it quickly went extinct after the boundary for some reason.

The youngest extinct species known from Europe is "Lacerta" siculimelitensis, a large-sized lacertid described from the Upper Pleistocene of Malta by Böhme &

Zammit-Maempel (1982) and associated by the same authors with other fossils coming from the Middle Pleistocene of Sicily previously mentioned as a large Lacerta species by Kotsakis (1977). Other Middle/Upper Pleistocene Sicilian remains were subsequently attributed to the species by following authors (Caloi et al. 1986; Bonfiglio & Insacco 1992; Bonfiglio et al. 2002), and Delfino & Bailon (2000) recognised a shared dental morphology also in remains attributed to Lacerta from the early Pleistocene of Pirro Nord in Apulia. The validity of "Lacerta" siculimelitensis, however, has been questioned by authors such as Mateo (1988) and Barahona & Barbadillo (1997), based on the fact that the main diagnostic features seem to fall into the range of variation of other lacertids such as T. lepidus. The taxonomic status of this species is therefore in need of a revision, which is currently underway. A preliminary report (Tschopp et al. 2016) seems to confirm the validity of the species, even though including it in Timon. According to the same report, remains from Monte Tuttavista herein reported as Timon sp. (see chapters 3.2.3 and 4) could belong to this species, whereas Apulian fossils would belong to T. lepidus. The presence in Europe of taxa that were closely related to extant species is attested since the beginning of the Neogene, with the oldest representatives of lacertids of the green lizards group reported from the early Miocene (MN 4b) of Dolnice in Czech Republic (Čerňanský 2010a; Rage 2013). Except for two other occurrences of the same species complex in the upper Miocene (Kohfidisch in Austria and Polgárdi 4 in Hungary; Tempfer 2005; Venczel 2006), all other reports of extant species or related forms are younger than the Miocene/Pliocene boundary. This could mean that, even though some taxa might have started to evolve earlier, the settling of most of the modern lizard fauna of the continent has to be traced back to the second part of the Neogene. It has to be taken into account, however, that a lot of remains attributed only to indeterminate lacertids (sometimes assigned to the former basket taxon *Lacerta* sp. in a broad sense) have been indeed yielded by a very high number of Neogene localities, and some modern taxon might have passed unnoticed in older sites given the overall difficulty in identify isolated lacertid bones (see chapter 2.4).

Another issue that has to be considered is that identifications of extant taxa from the fossil sites might also sometimes be questionable. One of the main reasons that originate this issue is the trend to assign fossils from (usually) young localities to extant taxa based on a biogeographical criterion, assuming that the species that are currently present in the proximity of the site could also have been present there in not-so-older times. This, flanked with misidentifications due to poor osteological knowledge, might cause erroneous palaeobiogeographical reconstructions, such as in the case of the purported stability throughout the Pleistocene and Holocene of North American herpetofauna (Bell et al. 2010). An example of such issue could be the identification of *L. agilis* and *Z. vivipara* in Steinheim an der Murr (Upper Pleistocene of Germany; Bloos et al. 1991). A quick review of this material, stored in the context of the herein reported comparative study, it might be more confident to assign most of the remains to indeterminate lacertids, even though at least two different species might indeed be present (pers. obs.).

After having specified that, the current fossil record of extant lacertids indicates that green lizards are widely reported throughout Europe from the Zanclean onwards (adding to the three Miocene occurrences, of course). A similar stratigraphic distribution is observable for *Podarcis*, even though most of the specific identifications might be based mainly on biogeography (e.g., occurrences of *P. lilfordi* in the Balearic Islands, *P. pityusensis* in Ibiza and *P. tiliguerta* in Corsica). *Acanthodactylus erythrurs* (or related forms) is known in the Iberian Peninsula since the early Pleistocene, but Böhme & Ilg (2003) reported a single dentary of *Acanthodactylus* sp. from the Zanclean of La Gloria 4. This latter occurrence, still unpublished, needs to be confirmed. *Psammodromus* has a similar early Pleistocene to Holocene Iberian record, with most of the occurrences pertaining to *P. algirus* and a single mention of cf. *Psammodromus hispanicus* from the Middle Pleistocene of Áridos-1 (Blain et al. 2014c, 2015). Early Pleistocene to Holocene records are known also for *T. lepidus* and *Z. vivipara*, even if their geographical range is higher than the

previously mentioned Iberian species (in particular as far as *Z. vivipara* is concerned). Remains of *A. bedriagae* are mentioned from a number of Middle Pleistocene to Holocene localities in Corsica, and from a single late Pliocene/early Pleistocene site in Sardinia. The single fossil occurrences of *D. oxycephala* and *O. elegans* are in the Plio-Pleistocene site of Bad Deutsch-Altenburg (Rauscher 1992), whereas *Eremias* sp. is mentioned from Ozyornoye-1 in Ukraine (Middle Pleistocene; Böhme & Ilg 2003).

In the end, it is worth mentioning the finding of indeterminate Eremiadini in the karstic network of Cava Monticino, in Italy (this work). This late Miocene (MN 13) occurrence is the only known mention of this lacertid tribe in Italy, both if considering the fossil record and the extant herpetofauna.

3.3.5. Scincidae

Considering only Neogene and Quaternary, skinks are reported in Europe from the beginning of the Miocene up to the Holocene, even if they are not as common in the fossil record as other groups such as lacertids or anguids. Similarly to other families, their geographic range was wider during the Miocene, compared to following epochs. From the Pliocene onwards, as a matter of fact, they are found only in Mediterranean countries, with the sole exception of a single occurrence in Bulgaria during the Gelasian (Varshets; Böhme & Ilg 2003). However, even if this is rather consistent with their current distribution in Europe, it must not be excluded that it results from a biased record hindering the recognition of a wider past range, taken also into account that Pliocene occurrences are particularly scarce.

Two extinct species are known, both from the Miocene of Southern Germany. *Bavariascincus mabuyaformis* was tentatively attributed to Scincidae by its author, Kosma (2004). The type material comes from Petersbuch 2 and Rembach, both MN 4 in age. However, the original description of the species is found in Kosma's PhD thesis, and it has never been published elsewhere. Because of this, both the genus *Bavariascincus* and the species *B. mabuyaformis* should be considered unavailable

names. In any case, the dentition of the material from both Petersbuch and Rembach indeed recalls scincid tooth morphology. A revision is needed in order to attest their assignment to their own genus and species. A third occurrence of *B. mabuyaformis* is reported by Böhme & Ilg (2003) from Forsthart, still MN 4 of Southern Germany. The second species, *Tropidophorus bavaricus*, has been described by Böhme (2010) based on material coming from the MN 5 of Sandelzhausen, with additional material reported from the similarly-aged locality of Oggenhausen 2 (Böhme & Ilg 2003). This species is rather interesting because it is the only known fossil record of *Tropidophorus*, a genus currently living in Southeastern Asia. Moreover, the presence in the early Miocene of Europe of a skink with Asian affinities might agree with the supposed Asian origins reported for other European Miocene lizards, such as varanids (Georgalis et al. 2017b).

Among extant taxa, *Chalcides* is the most represented genus in the European skink fossil record. It is already reported from the middle/late Miocene of the Felsötárkány Basin in Hungary, where a species close to *C. ocellatus* could have been present (Venczel & Hír 2013). The oldest specific mentions of extant species date back to the early Pleistocene (*C. bedriagai*; Blain et al. 2008, Blain 2012-2014), Middle Pleistocene (*C. chalcides* and *C. striatus*; Delfino 2002, 2013; Blain et al. 2012) and Upper Pleistocene (*C. ocellatus*; Delfino 2002; Delfino & Rook 2008). Nevertheless, it must be taken into account that, at least in some cases, these mentions could be based on a biogeographical criterion.

Few fossil occurrences are known for other extant European taxa: *A. kitaibelii* is reported in Greece from Vraona Cave, Pleistocene/Holocene in age (Rauscher 1995), a dentary that shares affinities with *Ophiomorus* has been found in the Pleistocene site of Kaiafa, still in Greece (this work), and *Trachylepis* cf. *T. aurata* is mentioned by Böhme & Ilg (2003) from Varshets, in the Gelasian of Bulgaria. All these records are remarkable in being the only known fossil occurrences of their own taxa. Fossils from a number of localities spanning from the early Miocene to the early Pleistocene have been assigned, or tentatively assigned, to the genus *Mabuya*. Currently, species

of *Mabuya* s.s. live in the Neotropics (Karin et al. 2016), but a number of other genera were also included into it in the past. The Eurasiatic T. aurata (Heremites auratus according to Karin et al., 2016) is one of the species previously included in *Mabuya*. It is therefore likely that European fossil records of Mabuya sp., cf. Mabuya sp. and aff. Mabuya sp. might be better identifiable as pertaining to Mabuya s.l. Affinities with either Trachylepis/Heremites or one of the other African/Asiatic genera defined by Karin et al. (2016) is not possible without a thorough revision of all the material. Southern Germany has also yielded other findings of possible skinks with extra-European affinities: namely, possible remains of *Eumeces* coming from few early to middle Miocene sites (Böhme & Ilg 2003; this work). Even though these remains are still unpublished, the direct analysis of at least some of them (see chapter 3.2.1) supports their possible attribution to this scincid genus, which is currently found in North Africa and the Middle East (Uetz et al. 2017). If the identification is confirmed by further studies, these would be the first mentions of the genus in Europe. Nevertheless, Eumeces was not apparently a long-lasting inhabitant of the continent, even though future findings could eventually change this view.

3.3.6. Cordylidae

Few fossil occurrences of cordylids are known in the Miocene of Europe, whereas there is no record of this lizard family from the Pliocene onwards. The earliest Neogene European cordylids date to the early Miocene (MN 3), whereas the youngest ones come from late Messinian deposits (MN 13/14). Therefore, a survival of the family in the continent throughout the entire Miocene is likely, even though a shifting of their distributional range towards Southeastern Europe (maybe also Southwestern Europe, if the identification of a possible indeterminate cordylid from the Tortonian of Los Aguanaces, in Spain, is confirmed; Böhme & Ilg 2003) seems evident. Nevertheless, as far as our current knowledge can tell, they went locally extinct by the Miocene/Pliocene boundary.

Adding to a limited number of still indeterminate forms, the Miocene of Europe hosted two different cordylid genus. The first one, *Bavaricordylus*, is known only in the Burdigalian of Southern Germany, with two different species, and in the early middle Miocene of Switzerland, with remains unassigned to species. The type species of the genus, *B. ornatus* from Petersbuch 2, was described by Kosma (2004) in his PhD thesis. Similarly to his *Bavariascincus mabuyaformis* (see above), this description should not be considered valid according to the rules of the International Code of Zoological Nomenclature, given also the absence of successive paper sustaining it, and both *Bavaricordylus* and *B. ornatus* should be considered unavailable names. This put an issue on the generic attribution of the second species, *B. molassicus* from Puttenhausen 2 and Sandelzhausen (Böhme 2010), too. A revision of the type material of both species of *Bavaricordylus* to assess their taxonomical identity is in progress.

The second genus is *Palaeocordylus*, including a single species, *P. bohemicus*, originally described by Roček (1984) from the MN 4 of Dolnice in Czech Republic and later tentatively reported also from the slightly younger Czech locality of Merkur North by Čerňanský (2012). Remains attributed to this genus are reported also from Lautern 2 in Germany (Aquitanian, though still unpublished; Böhme & Ilg 2003) and tentatively from Maramena in Greece (late Miocene; this work). Böhme & Ilg (2003) mention a second species of Palaeocordylus, Palaeocordylus ulmensis, from a few Southern German localities dated back to the late Oligocene and early Miocene. This is clearly a reallocation to the cordylid genus of Ophisaurus ulmensis Gerhardt, 1903, but no explanation supporting it is given. Recently, remains of O. ulmensis coming from its type locality Ulm Westtangente have been recognised as pertaining to a lacertid lizard for which a new genus, Janosikia, has been erected (Čerňanský et al. 2016b). Other remains attributed to P. ulmensis by Böhme and Ilg come from localities that are very close to Ulm Westtangente both in geographical and stratigraphical terms, and it is therefore possible that they also belong to *Janosikia*. However, a direct check of the fossils is necessary in order to confirm this.

3.3.7. Anguidae

After lacertids, anguids are the second most represented lizard group in the Neogene and Quaternary fossil record of Europe. They are widely recorded from the beginning of the Neogene onwards, with a rather high diversity during the Miocene that later shows a decreasing trend going from the Pliocene to the Holocene. Their distributional range has always been wide as a family, but in recent times most of their occurrences outside Southern European countries are represented almost solely by the genus *Anguis*.

Known fossil remains of the latter genus are mostly assigned to the extant A. fragilis (or better to say, to the A. fragilis species complex), which is recorded in Europe since at least the late Miocene (e.g., a tentative record from the Felsötárkány Basin; Venczel & Hír 2013). In any case, pre-Pleistocene occurrences of A. fragilis are scarce. Two, or maybe more, extinct species are also known, even if their fossil record is very poor. Anguis rarus has been recently described based on a single parietal coming from the early Miocene (MN 3) of Petersbuch 62, in Southern Germany (Klembara & Rummel 2016). Anguis stammeri also comes from Germany, namely from Fuchsloch (Brunner 1954), but it is distinctly younger, being Upper Pleistocene in age. Both Estes (1983) and Klembara & Rummel (2016) consider A. stammeri as a possible valid species, although suggesting a revision, but it has to be noted that Młynarski (1962) pointed out *Ophisaurus* affinities for the type material. Due to some apparent morphological similarities, it is also possible that specimens attributed to A. fragilis or closely related forms, such as Anguis cf. A. fragilis reported by Młynarski (1962), might instead belong to this species (Estes 1983; Klembara & Rummel 2016). A possible third extinct species of Anguis is ?Anguis polgardiensis, originally described by Bolkay (1913) from Polgárdi 2 (MN 13 of Hungary) and later reported also from the older (MN 10) locality of Vösendorf, in Austria, by Papp et al. (1954). According to Estes (1983), this species is a junior synonym of *Pseudopus* pannonicus, but more recently Klembara (2015) and Klembara & Rummel (2016)

stated that it is not possible to clearly allocate this material at generic level (mostly because the type parietal is lost and Bolkay did not provide figures of its ventral surface). Nevertheless, Klembara (2015) noted similarities between the dorsal ornamented surface of the parietals of *?Anguis polgardiensis* and *O. spinari. Anguis? acutidentatus* and *Anguis? bibronianus* were erected by Lartet (1851), but similarly to most of the species named by this author from Sansan, their description is too vague to support their validity and there are no figures of them. Młynarski (1962) considered them as synonym of *P. moguntinus* (that is, *P. laurillardi* in a modern view; see below), but since the type material is lost in both cases it is better to considered them as *nomina dubia* following Estes (1983) and Augé & Rage (2000). In any case, the presence in Europe of unidentified species of *Anguis* is known since the very beginning of the Miocene, and older remains are also known in the Paleogene (see e.g., Augé 2005).

Pseudopus, the other anguid genus that still has extant representatives in Europe, is also present in the continent since the early Miocene, with few possible occurrences in the Oligocene too (Böhme & Ilg 2003). The oldest known species of the genus are P. ahnikoviensis and P. confertus. The latter (originally named Pseudopus rugosus, but later changed to *P. confertus* due to a possible risk of synonymy; Klembara 2015; Klembara & Rummel 2016) is known only from its type locality, Merkur North in Czech Republic (MN 3). *Pseudopus ahnikoviensis*, on the other hand, has a slightly longer stratigraphical distribution, spanning from the MN 3 to the MN 4 (maybe even MN 2 to MN 5). It has been found in Czech Republic and maybe Germany (Pseudopus cf. P. ahnikoviensis from Wiesbaden-Amöneburg and Hambach 6C; Cerňanský et al. 2015, 2016c). At least by the beginning of the MN 4, another species appears in the fossil record: P. laurillardi. Originally described by Lartet (1851) as Anguis? laurillardi from Sansan, it includes also *Pseudopus fraasi* (alternatively assigned also to Ophisaurus or to Propseudopus) and Pseudopus moguntinus (sometimes attributed to *Ophisaurus*) according to Klembara et al. (2010). It has to be noted that the type material of P. moguntinus was reported from the Upper

Oligocene of Germany (Boettger 1875; Estes 1983; Klembara et al. 2010), thus leading to the supposed presence of an older occurrence of P. laurillardi. Nevertheless, Klembara et al. (2010) stated that *P. moguntinus*, as originally defined, should be considered a *numen nudum*, due to the fact that it is based on an unspecified number of poorly described and unfigured osteoderms, which are currently lost. Moreover, they add that the localities from which Boettger (1875, 1876/1877) reported his species are now considered to be dated between the middle Oligocene and the early Miocene. Because of all of this, they considered a Paleogene occurrence of *P. moguntinus* (and therefore of *P. laurillardi*) doubtful. Based on the current knowledge, the stratigraphical distribution of *P. laurillardi* spans from the MN 4 to the MN 9 and its geographical range includes Central and Western Europe. By the MN 9, P. laurillardi seems to be replaced by P. pannonicus, a species that is almost constantly found up to the Middle Pleistocene. Pseudopus pannonicus has a rather wide and stable distribution for most of its evolutionary history, being recorded from Western, Central and Eastern Europe in the Miocene, Pliocene and early Pleistocene. Nevertheless, its youngest and only Middle Pleistocene-aged occurrence, Cengelle (the age of Canal Negre 1 in Spain is uncertain and could be older; Blain et al. 2016a), is located in northeastern Italy (Delfino 2002). This might suggest a shrinking towards the southern margin of the continent during the Quaternary, as is the case for other lizards, but this is only a conjecture due to the poor Middle Pleistocene record. As for P. laurillardi, other species have been synonymized with P. pannonicus. Part of the type material of Varanus deserticolus Bolkay, 1913 from Beremend 1 in Hungary is actually referable to a large anguid, probably P. pannonicus (Estes 1983; Georgalis et al. 2017b). Pseudopus novorossicus, from the late Miocene of Ukraine (locality of Zhoften, also known as Petroviérovak; Alexejew 1912), is also considered a synonym of *P. pannonicus* (Estes 1983), as well as Ophisaurus intermedius, erected by Bolkay (1913) from Pliocene/Pleistocene Hungarian localities and later mentioned by Jánossy (1986) also. The few fossil remains of the extant P. apodus are known since the late Pliocene. They are confined

to Eastern Europe, suggesting that this species might have never expanded towards the Western part of the continent. Nevertheless, remains found in Hungary, Poland and Slovakia hint for a distinctly larger range of the species during the late Pliocene and the Pleistocene. In the end, a possible new species of *Pseudopus* is present in the Vallès-Penedès Basin (middle to late Miocene, Northeastern Iberian Peninsula; Bolet et al. 2014a; this work). Taxonomical affinities of this new species are still under study.

The genus Ophisaurus (as intended by Klembara et al. 2014, that is including the American Ophisaurus, the Asiatic Dopasia and the African Hyalosaurus), which is currently absent from Europe, was also present in the continent during the Neogene and the early Pleistocene. The few Middle and Upper Pleistocene occurrences of the genus are questionable, as all of their mentions dates back to a period in which Pseudopus was also included in Ophisaurus and therefore they might represent occurrences of the former genus instead. The same taxonomic issue might also hold true for other indeterminate Ophisaurus occurrences from the continent. In any case, clear European Ophisaurus remains have been found from the Aquitanian (Ophisaurus cf. O. fejfari, MN 1/MN 2 of Oschiri in Sardinia, Italy; Venczel & Sanchiz 2006) to the late early Pleistocene (Ophisaurus sp., Barranco Léon and Fuente Nueva 3 in Southern Spain; Blain & Bailon 2010). Once again, the distribution of this genus shows a southward shrinking, starting from a wide range during the Miocene and narrowing towards Southern European countries in the Pliocene and the early Pleistocene. In terms of taxonomical diversity, all Pleistocene occurrences and almost all the Pliocene ones are identified only at the genus level, but during the Miocene five different species are known. Most of these species but Ophisaurus acuminatus are based on parietals, resulting in difficult comparisons between the latter species and the other ones. Nevertheless, O. acuminatus, which is represented only by a partial skull found in Tortonian sediments of Höwenegg in Germany (Jörg 1965), indeed displays some differences from other Miocene Ophisaurus species, such as in the morphology of the dermal ornamentation of skullroofing bones (Klembara & Rummel 2016), and can be therefore maintained as a distinct species. *Ophisaurus feifari* is known from Czech Republic and Germany, from MN 3 to MN 8, but tentatively-attributed material comes from older ages also (namely, MN 1/MN 2). It is interesting to note that this earlier occurrence comes from Sardinia (Oschiri; Venczel & Sanchiz 2006), fairly extending the possible geographical distribution of the species. Tentative identifications of O. fejfari are known from the MN 5 of the Austrian Korneuburg Basin too (Böhme 2002; Tempfer 2003). The stratigraphical and geographical distributions of the remains attributed to O. holeci and O. robustus (formerly Anguis robustus; Klembara 1979) are similar to those of O. feifari, for they are known from a few Czech, Southern German and, as far as O. robustus is concerned, Hungarian localities spanning a range of time included between MN 3 and MN 6/MN 7 (the former) and MN 3 and MN 7+8 (the latter). Ophisaurus spinari, on the other hand, has a longer evolutionary history, since it has its oldest occurrence in the Aquitanian (MN 2 of Wiesbaden-Amöneburg; Čerňanský et al. 2015) and the younger one in the Piacenzian (Capo Mannu D1 Local Fauna; Delfino et al. 2011; Klembara et al. 2016). Given that, O. spinari is the only European species of Ophisaurus that crossed the Miocene/Pliocene boundary, even if no other Pliocene occurrence is currently known. Geographically speaking, O. spinari is reported from Czech Republic, Germany, Slovakia and tentatively Austria during the Miocene and, as already mentioned above, from the Italian island of Sardinia during the Pliocene. Venczel & Hír (2013) reported Ophisaurus cf. O. spinari also from Hungary, in different MN 7+8 to MN 9 sites of the Felsötárkány Basin. However, at least one of the remains they describe, the parietal MMP 2009.532, is assigned to O. robustus by Klembara & Rummel (2016). Given that, it is possible that at least some, if not all, of the other remains attributed to Ophisaurus cf. O. spinari belongs to the other species as well, and the possible occurrence of O. spinari in Hungary is here considered in need of a complete revision.

During the early Pleistocene, another anguid lived on Meda Grande, one of the Medas Islands along the coast of Northeastern Spain. This anguid, named *Ragesaurus medasensis* by Bailon & Augé (2012), is currently known only from its type locality. The taxonomic affinities of this taxon have not been thoroughly assessed yet, due also to the fact that it is represented only by an isolated dentary, but Čerňanský et al. (2016a) noted similarities between Ragesaurus and Ophisauromimus from the Oligocene of France and Germany. If this affinity is confirmed by further studies, *Ragesaurus* might represent the last, relict occurrence of a ghost lineage of anguids present in Europe since at least the late Paleogene. It is interesting to note that the supposed new Miocene taxon herein described from different localities in the Vallès-Penedès Basin seems to share a similar tooth morphology with both *Ophisauromimus* and *Ragesaurus*, possibly representing an intermediate occurrence of this ghost lineage. However, the taxonomic affinities of the new Vallès-Penedès anguid still have to be clearly understood, and so this hypothesis should be considered a mere conjecture pending a deepened analysis. To this it could be possibly added an isolated parietal from Gratkorn (late middle Miocene of Austria), attributed by Böhme & Vasilyan (2014) to O. spinari but clearly displaying a very different morphology (Klembara & Rummel 2016). This parietal morphology seems to recall the one of the new Vallès-Penedès anguid, suggesting a link between the Iberian and the Austrian remains. A possible new anguid species, not linked to the above mentioned ones, is also reported from Sandelzhausen (MN 5) by Böhme (2010). Due to the very fragmentary nature of the specimens representing it, this species has been left unnamed, even if similarities with Ophisaurus have been highlighted.

All the previously mentioned anguid genera are members of the subfamily Anguinae, which clearly represents the great majority of anguid occurrences in Europe from the Neogene onwards. However, Anguinae might not be the only anguid subfamily to have been represented in the continent during the Miocene. Indeed, Böhme & Ilg (2003) mention members of the anguid subfamily Glyptosaurinae from Dolnice in Czech Republic (MN 4), Sandelzhausen in Germany (MN 5) and, with doubt, Mühlrüti Pt. 806 in Switzerland (MN 6). Glyptosaurs from Sandelzhausen have been

previously mentioned as indeterminate Glyptosaurini by Böhme (1999a), whereas those from Dolnice are attributed to Melanosaurini by Böhme and Ilg themselves. In his paper on the fossil lizards coming from the Czech locality, Roček (1984) mentioned cf. Xestops sp. This attribution was based on a comparison with the material of Xestops weigelti (now Placosauriops weigelti; Augé & Sullivan 2006) from the middle Eocene of Geiseltal. Placosauriops is a member of the tribe Melanosaurini and therefore the fossil material described by Roček might correspond to the indeterminate member of the tribe mentioned by Böhme and Ilg. Rather interesting, but at the same time rather doubtful, is the possible occurrence of an indeterminate member of the subfamily Gerrhonotinae from Vračević in Serbia (MN 7+8; Jovanović et al. 2002). Gerrhonotine lizards, both fossils and extant species, are currently known only from North and Central America (Estes 1983; Böhme & Ilg 2003; Vitt & Caldwell 2009) and, given the general absence of other fossils of this subfamily from either Europe or other nearby countries, the Serbian occurrence is highly unlikely. However, given that the material mentioned by Jovanović and colleagues is neither described nor figured, this cannot be ascertained from their paper alone.

3.3.8. Shinisauria

Klembara (2008) described a new anguimorph based on cranial material and osteoderms coming from the early Miocene (MN 3) of Merkur North, naming it *Merkurosaurus ornatus*. In his work, he mentioned affinities with the Asian taxon *Shinisaurus crocodilurus*, and later Conrad et al. (2010) include *Merkurosaurus* in the clade Shinisauria, defined as "all taxa sharing a more recent common ancestor with *Shinisaurus crocodilurus* than with *Anguis fragilis*, *Heloderma suspectum*, and *Varanus varius*" by Conrad (2008: p. 119). Subsequently, *Merkurosaurus* remains have been reported also from MN 2 and MN 3 of Germany (Čerňanský et al. 2015; this work). In particular, fossils from the MN 2 locality of Wiesbaden-Amöneburg have been assigned to the type and only known species (Čerňanský et al. 2015).

Given the clear similarities that *Merkurosaurus* shares with *Shinisaurus*, it has to be taken into account that also two occurrences of aff. *Shinisaurus* sp. from Weißenburg 6 (Oligocene/Miocene boundary, MN 1, Germany) and Wintershof West (MN 3, Germany) reported by Böhme & Ilg (2003) might instead represent the European taxon. This could be supported by the fact that other former occurrences mentioned by Böhme & Ilg (2003) of either cf. or aff. *Shinisaurus* sp. were later reallocated to *Merkurosaurus* (namely, those from Wiesbaden-Amöneburg and Stubersheim 3; Čerňanský et al. 2015; this work), but in any case this has to be confirmed after a direct study of the involved specimens.

Even though there are very few of them, the occurrences of a shinisaur in the early Miocene of Europe raise interesting questions on when this clade firstly enter the continent and why it apparently survived there only for such a short time and in such a restricted area (that is, Central Europe). The recent description of an isolated tail of an indeterminate crocodile-tailed lizard (clade *Pan-Shinisaurus* Smith & Gauthier, 2013, which is equivalent to Shinisauria Conrad, 2008) from the Middle Eocene of Messel, Germany (Smith 2017), possibly hints for a distinctly older settlement of the clade in Europe. Nevertheless, due to the presence of a large stratigraphical gap between the Eocene and the Miocene occurrences and lacking a clear assessment of the phylogenetical relationships between the Messel specimen and *Merkurosaurus*, the alternative hypothesys of two distinct wave of colonization of the European territory by shinisaurs cannot be excluded a priori.

3.3.9. Varanidae

Monitor lizards are well known from the Miocene of Europe, showing then a very strong reduction in terms of abundance of remains during the Pliocene and the Pleistocene, when they ultimately disappeared from the continent. This reduction is linked to a narrowing of their former wide geographical distribution, since this anguimorph lizards show the same shrinking towards Southern European countries displayed by other squamates.

Only one genus is currently reported from European Neogene and Quaternary localities: *Varanus*, whose stratigraphical distribution spans from the early Miocene to the Middle Pleistocene. A second, extinct genus, *Iberovaranus* (type species: *Iberovaranus catalaunicus* Hoffstetter, 1969) was reported in the past from early to middle Miocene localities of the Iberian Peninsula and tentatively Germany. However, as demonstrated by Delfino et al. (2013), the general morphology of the holotype of *I. catalaunicus*, an isolated trunk vertebra coming from Can Mas near El Papiol (Vallès-Penedès Basin, NE Iberian Peninsula; Hoffstetter 1969), fits well with that of *Varanus* vertebrae and *Iberovaranus* has therefore to be considered a synonym of *Varanus*. Based on the very few varanid remains found in Can Mas (that is, just Hoffstetter's holotype vertebra and a second, cervical vertebra), it is currently not possible to either confirm the validity of *"Iberovaranus" catalaunicus* as a species of *Varanus* or synonymize it with another, already known species (Delfino et al. 2013). For the moment, the species is regarded as a *nomen dubium* and all past occurrences of *Iberovaranus* are assigned only to *Varanus* sp.

Besides the numerous occurrences unassigned to species, a few extinct species of *Varanus* have been named based on Miocene remains. In the early Miocene, two species are known. The recently described *Varanus mokrensis* is known only from its type locality in Czech Republic (Mokrá-Western Quarry, MN 4; Ivanov et al. 2017), whereas *Varanus hofmanni* has a wider distribution both in stratigraphical and possibly geographical terms. As a matter of fact, it is reported in Germany from the early to the middle Miocene (Burdigalian to Langhian; Roger 1898; Estes 1983; Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017), but tentative attributions are known also from Austria, France, Hungary, Moldova and Spain (Hoffstetter 1969; Estes 1983; Böhme 2003; Böhme & Ilg 2003; Rage & Bailon 2005; Venczel 2006; Ivanov et al. 2017), reaching up to the late Messinian (MN 13). The validity of *V. hofmanni*, however, has been questioned, since its original description is based only on vertebral material found in Stätzling (middle Miocene of Germany; Roger 1898). Given that diagnostic significance at species level is uncertain for *Varanus* vertebrae

compared to the more informative skull elements (Holmes et al. 2010; Delfino et al. 2013), *V. hofmanni* is considered a *nomen dubium* by some authors (Ivanov et al. 2017). The same argument holds true for three other species named from late Miocene vertebral remains: *Varanus lungui* (MN 9 of Moldova; Zerova & Chkhikvadze 1986), *Varanus tyrasiensis* (MN 9 of Moldova as well; Lungu et al. 1983) and *Varanus semjonovi* (MN 13 of Ukraine; Zerova & Chkhikvadze 1986). All these three species are reported only from their type localities. The late Miocene *Varanus amnhophilis*, on the other hand is based on cranial material (Conrad et al. 2012). This latter species is also known only from its type locality: namely, Q1 locality in the Mytilinii Formation (Samos, Greece).

The last named species is Varanus marathonensis, originally described by Weithofer (1888) and known from the late Miocene of Greece and possibly Spain (Weithofer 1888; Ivanov et al. 2017). Due to the rules of priority, Varanus atticus is a synonym of this species, because this name was created by Nopcsa (1908) to name a single vertebra coming from the type locality of V. marathonensis and firstly reported by Gaudry (1862) as possibly pertaining to Varanus, but later associated to the latter species by Weithofer (1888) himself. Varanus marathonensis is then reported from the Pliocene of Hungary. Part of the Hungarian material was originally attributed to the new species Varanus (= Monitor) deserticolus by Bolkay (1913), together with anguid remains. The varanid part of the type material of V. deserticolus was later linked to V. marathonensis (Estes 1983; Georgalis et al. 2017b). In spite of this, Jánossy (1986) still mentioned V. deserticolus from the Pliocene and even the lower Pleistocene of Hungary, without figuring or describing the findings. Given that, even though the Pliocene record could indeed represent V. marathonensis (the locality mentioned by Jánossy, Csarnóta, indeed yielded the latter taxon according to other authors; Estes 1983; Ivanov et al. 2017), its Pleistocene report is here considered dubious pending a revision of the material. The Middle Pleistocene occurrence of V. marathonensis from Petralona Cave in Greece (Sickenberg 1971; the specific name is uncorrectly spelled in the paper) is also questionable, since figures and description

of the specimens are lacking again and the material is currently lost (Georgalis et al. 2017b). It is interesting to note that this finding was attributed to Varanus *intermedius*, possibly referable to *Ophisaurus intermedius* (now *P. pannonicus*), by Kretzoi & Poulianos (1981). The alternative possibility that the fossil material from Petralona Cave indeed pertained to a large anguid should therefore not be discounted. Adding to the two above mentioned uncertain occurrences of V. deserticolus and Varanus aff. V. marathonensis, there are two other Pleistocene mentions of Varanus. The oldest and less certain one is from the Gelasian of Ukraine (Kotlovina; Böhme & Ilg 2003), whereas the youngest one is from the latest early/earliest Middle Pleistocene Greek site of Tourkobounia 5 (Georgalis et al. 2017b; this work). An even younger occurrence would have been the Varanus lower jaw reported by Morelli (1891) from Upper Pleistocene layers of the Arene Candide Cave, in Northern Italy. The specimen is currently lost, but Delfino (2002) discarded the possibility that it represented a varanid based on Morelli's drawing. Lizards whose size is comparable with Morelli's specimen are still present not so far from the Arene Candide Cave (namely, the lacertid T. lepidus), but some differences between the lower jaw and the standard lacertid morphology seem to be present. Because of this, a non-lacertilian nature of the specimen cannot be excluded, even though Delfino (2002) cautiously considered it as an indeterminate lizard pending a possible review following its rediscovery. Given that, the above-mentioned Tourkobounia findings mark the last known occurrence of the family in Europe, before its disappearance from the continent.

3.3.10. Other lizards

A large number of remains coming from numerous Neogene and Quaternary localities in Europe are assigned to indeterminate acrodontans, scincomorphs, anguimorphs or generically lizards. In most cases, these fossils represent skeletal elements that are either too fragmentary or considered undiagnostic, but might possibly be associated with other lizard occurrences coming from the same localities. Nevertheless, more complex situations are also present. The case of the Arene Candide varanid is reported above, in chapter 3.3.9, but a similar problematic occurrence is the presumed *Uromastyx* tibia mentioned by Mangili (1980) from the late Pleistocene of Simonelli Cave, in Crete. This occurrence, referred to as *Uromastyx spinipes* (= *Uromastyx aegyptia*), cannot be confirmed, since the whereabouts of the fossil studied by Mangili are unknown and there are no figures in his paper. Caloi et al. (1986) referred it to ?*Agama* sp., but provided no justification for their assignment. Taking also into account the presence of large-sized lacertids in the Pleistocene of Mediterranean islands, Delfino et al. (2008) proposed to consider the tibia from Crete only as an indeterminate lizard waiting for a formal revision.

A fragmentary dentary of the amblyodont scincomorph *Hugueneysaurus globidens* has been found at Moissac 1 (Aquitanian, MN 1, of France; Augé 2005). *Hugueneysaurus*, known also from two other French localities late Oligocene in age (Coderet and La Colombière; Augé 2005), has a dentary morphology that is lacertid-like on the whole, but seems to also display a supposed synapomorphy of Scincoidea (that is, a labial cover of the coronoid by the dentary; Augé 2005). This complicates its assignment to either one of the two scincomorph clades: Lacertoidea and Scincoidea. Subpleurodont posterior teeth and a strongly narrow anterior portion of the Meckelian fossa might also support scincoid affinities (Augé 2005). In any case, *H. globidens* represent another amblyodont taxon inhabiting Europe between the Palaeogene and the beginning of the Neogene, adding to the amblyodont lacertids reported in chapter 3.3.4. Among these amblyodont forms, *H. globidens* is rather interesting in being only the second one crossing the Oligocene/Miocene boundary, together with *Mediolacerta*.

The genus *Sauromorus* was erected by Pomel (1853), who included two species in it: *Sauromorus ambiguus* and *Sauromorus lacertinus*. According to the author, both these species come from lower Miocene sites in France: from Langy and Marcouin (or Marcoin) the former and from Langy only (not Marcoin as reported by Estes,

1983) the latter. There is a certain degree of uncertainty on the family in which this genus has to be included, with all Scincidae, Anguidae and Lacertidae that have been taken into account in the past (Zittel 1889; Nopcsa 1908; Hoffstetter 1944; Estes 1983). Nevertheless, the type material is lost since at least the first half of the XX century (Hoffstetter 1944) and this issue cannot be checked, given also that Pomel (1853) gave no figure of his specimens. Therefore, both species of *Sauromorus* should be referred to as *nomina dubia*, as already pointed out by Estes (1983).

3.3.11. Amphisbaenia

The evolutionary history of worm lizards in Europe dates back at least to the early Paleocene (Augé 2012; Folie et al. 2013) and these squamates are rather well known from Neogene and Quaternary deposits in the continent. Their Miocene record spans most of Europe, whereas they are already confined to Mediterranean countries during the Pliocene. Except for a few Italian localities, the Pleistocene/Holocene occurrences come only from the Iberian Peninsula, where most of the extant European amphisbaenians live today.

The most common remains of this group of squamates found in the continent are vertebrae, which are not considered significant from a diagnostic point of view even at the family level (Estes 1983). Because of that, it is possible that most indeterminate members of the family Amphisbaenidae mentioned in the past from European deposits are better identifiable as indeterminate amphisbaenian, representing the past trend to attribute all amphisbaenian remains to the only worm lizard family known to live in Europe back then (prior to the split of Blanidae by Kearney, 2003). Currently, fossil worm lizard remains yielded by Neogene and Quaternary localities in Europe that have been confidently identified below family level are assigned to Blanidae.

Possible occurrences of the problematic species *Omoiotyphlops edwardsi* are reported from three Miocene localities in France: Sansan, La-Grive-Saint-Alban and Saint-Gérand-le-Puy. These occurrences are originally mentioned by Hoffstetter

(1942), but they are later reprised by Estes (1983) and Schleich (1985). *Omoiotyphlops edwardsi* is as a synonym of *Omoiotyphlops priscus*, a species of presumed scolecophidian snake named by De Rochebrune (1884) from the Phosphorites du Quercy. The name *O. edwardsi* (reported by Estes, 1983) most probably originates from the mislabeling of the *O. priscus* figures, which were labelled as *"Typhlops edwardsi"* by De Rochebrune himself (see Hoffstetter 1942). Later, Hoffstetter (1942) demonstrated that the type vertebrae of *O. priscus* belong in fact to an amphisbaenian, moving De Rochebrune's species to this group though briefly questioning the validity of the genus. The same author then mentioned remains similar to the Quercy species from the three above mentioned French localities, providing no descriptions. However, being based on non-diagnostic remains (i.e., vertebrae), *O. priscus* is currently considered a *nomen dubium* (Estes 1983; Augé 2012). Given that, possible Neogene French occurrences of this species are most probably better referred to as indeterminate amphisbaenians.

The best represented amphisbaenian genus in the Neogene and Quaternary fossil record of Europe is *Blanus*, but a second genus, *Palaeoblanus*, is present in the Miocene of the continent. The type and only known species of the genus, *Palaeoblanus tobieni*, was described by Schleich (1988) based on fossils coming from the Aquitanian of Weisenau near Mainz, in Germany. The same author also described remains found in the similarly-aged locality Budenheim, still located near Mainz. The species was later reported from Stubersheim 3 (Böhme 1999b) and tentatively from Unterempfenbach 1b (Böhme 2003; Böhme & Ilg 2003), extending its German record up to the early Burdigalian and maybe the Langhian. *Palaeoblanus tobieni* therefore has a rather restricted distribution during the Neogene, both geographically and stratigraphically. The genus, on the other hand, also occurs in France during the Aquitanian and the Langhian/Serravallian, in Spain from the Burdigalian to the Langhian (maybe Serravallian, if the attribution to aff. *Palaeoblanus* sp. of remains from Las Planas 5L is confirmed; Böhme & Ilg 2003) and in Italy in the late Miocene/possibly early Pliocene. Moreover, Böhme (2010)

assigned a premaxilla and a fragmentary dentary from Sandelzhausen (late Burdigalian of Germany) to a possible second species of *Palaeoblanus*, however without naming it. Nevertheless, it has to be noted that Čerňanský et al. (2016a) recently questioned the validity of the genus, stating that its diagnostic features are plesiomorphic for amphisbaenians.

Blanus is reported since the beginning of the Miocene. Four extinct species are known, all Miocene in age. The oldest ones are Blanus gracilis and Blanus thomaskelleri. Blanus gracilis was originally described as Omoiotyphlops gracilis by Roček (1984), its type material coming from the MN 4 of Dolnice in Czech Republic. As reported above, *Omoiotyphlops* is not a valid genus and so this species cannot be included in it. Both Venczel & Sanchiz (2006) and Venczel & Stiucă (2008) referred it to Blanus, while reporting B. gracilis from the MN 1/MN 2 of Oschiri, in Sardinia, and Blanus cf. B. gracilis from the MN 8 of Taut, in Romania, respectively. Recently, Bolet et al. (2014b) placed B. gracilis well nested inside Blanus, as part of the eastern clade of the genus together with B. strauchi. Blanus thomaskelleri has been found in Wiesbaden-Amöneburg (Aquitanian, MN 2/MN 3, of Germany; Čerňanský et al. 2015), but an isolated dentary coming from the Burdigalian (MN 3) of Merkur North, in Czech Republic (previously reported as Blanus sp.; Čerňanský & Venczel 2011), has been also assigned to it (Čerňanský et al. 2015). Another species, *Blanus antiquus*, is known only from the late early to middle Miocene of Austria and Germany. Blanus antiquus has sometimes been considered a synonym of B. gracilis (e.g., Böhme 1999b; Augé & Rage 2000), but Bolet et al. (2014b) support the separation of the two species, placing *B. antiquus* as a basal taxon sister to all other *Blanus* in their figured evolutionary tree of the genus. In the end, a well-preserved skull from the middle Miocene of Abocador de Can Mata, one of the localities of the Vallès-Penedès Basin in Catalunya (Northeastern Iberian Peninsula), has been attributed to the new species *B. mendezi*, which is considered as the most basal taxon of the western *Blanus* clade (Bolet et al. 2014b). This finding, together with the inclusion of *B. gracilis* in the eastern clade, suggests an early Miocene or even pre-Miocene dating of the separation between the two main clades of *Blanus* currently recognised on molecular bases (see Sindaco et al., 2014, and Sampaio et al., 2015, for the molecular data supporting these two clades).

Possible representatives of an extant Blanus species are firstly reported in the Pliocene. As a matter of fact, B. cinereus or morphologically related forms have been found in the middle to late Pliocene of both France and Spain. Later, during the Pleistocene and Holocene, this species is found only in the Iberian Peninsula. Since it appears almost impossible to distinguish bones of B. cinereus from those of B. *mariae* (see chapter 2), it is also possible that at least part of these remains pertains to the latter species. Amphisbaenians are currently absent from Italy, showing a disjunct range in Northern Mediterranean countries today. However, they were indeed present in the Appennine Peninsula and in Italian islands until the Pleistocene. They have been found in the early Pleistocene of Apulia (Cava dell'Erba at Pirro Nord), in the early and Upper Pleistocene of Sardinia (Cava VI 3 and Cava VI Banco 6 at Monte Tuttavista) and in the Middle/Upper Pleistocene of Sicily (K 22, near San Vito lo Capo). The Apulian remains are assigned to an indeterminate species of Blanus (Delfino & Bailon 2000; incorrectly reported as Blanus cf. B. strauchi by Holman, 1998), whereas only isolated worm lizard vertebrae are known from the other Italian Pleistocene localities (Delfino 2003; Rook et al. 2003; Abbazzi et al. 2004).
4. Phylogenetic analysis of the large lacertid remains from Monte Tuttavista

As reported in the previous chapter, fossil remains of a large lacertid lizard previously assigned to *Lacerta* sp. have been found in the Pleistocene locality of Monte Tuttavista, in Sardinia (Abbazzi et al. 2004). The revision of these remains, however, has pointed out that they cannot pertain to *Lacerta*, because of the absence of some important osteological features of the genus. On the other hand, the large lacertid from Monte Tuttavista seems to share some features with both *T. lepidus* and the extinct "*L*." *siculimelitensis*. In order to clarify its identification, a phylogenetic analysis has been conducted. Results of this analysis are reported in this chapter.

4.1. Material & Methods

The phylogenetic analysis is based on an updated version of the matrix used for the *Lacerta* case study in Villa et al. (2017). Some characters were added based on literature (Hoffstetter & Gasc 1969; Lécuru 1968, 1969; Estes et al. 1988; Al-Hassawi 2004; Arnold et al. 2007; Bailon et al. 2014; Čerňanský et al. 2016b) and on personal observations of additional specimens studied in the meantime. A complete character list is given in Appendix 6.

Taxon sampling has been adapted such that specimen-level operational taxonomic units (OTUs) in Villa et al. (2017) were collapsed to represent single species (see Appendix 7 for the list of specimens studied per species, and for additional sources from the literature). Because the material was initially referred to *Lacerta* sp. (Abbazzi et al. 2004), we included all species of *Lacerta*, except for *Lacerta pamphylica* from Turkey, of which no skeletal specimen could be found in any museum collection. In addition, all three species-complexes of *Timon*, all lacertid species currently existing on Sardinia, and additional representative species of all genera currently living in the surrounding countries (Algeria, France, Italy, Spain,

Tunisia) are included. Two species of *Gallotia* and the fossil lacertid *Maioricalacerta rafelinensis* from the Pliocene of Mallorca (Spain; Bailon et al. 2014) are also added, given that they are or were large-sized lacertids living on islands, as well as two fossil representatives of Gallotiinae from France and Germany, *Pseudeumeces cadurcensis* and *Janosikia ulmensis* (Augé & Hervet 2009; Čerňanský et al. 2016b). The outgroup consists of a teiid (*Salvator merianae*), a scincoid (*Chalcides ocellatus*), and *Varanus exanthematicus*, representing successively more distantly related clades to Lacertidae (Gauthier et al. 2012; Pyron et al. 2013; Reeder et al. 2015). The complete matrix (see Appendix 8) was constructed in Mesquite (v. 3.2, build 801; Maddison & Maddison 2017), and consists of 223 character statements (156 cranial and 67 postcranial ones) and 36 species-level operational taxonomic units.

In order to include some information concerning intraspecific variability, majority scoring is used for polymorphic characters, or polymorphic scores in cases where an equal number of specimens was scored for conflicting character states (sensu Wiens 1995, 1998, 2000).

The fossil material from Orosei has been scored as a single, combined OTU assuming that there was only one large-sized lacertid (see chapter 3). The fossils were not scored for quantitative characters that code for ratios between different bones or average ratios of a series of vertebrae, because a correct scoring of these characters depends on a consistent use of vertebrae from similar serial positions throughout the presacral column, and requires that the bones to be compared are from the same individual. Given that this could not be guaranteed due to the disarticulated and incomplete state of the fossil material, scoring of these quantitative characters is here avoided.

The phylogenetic analysis was performed with TNT v. 1.1 (Goloboff et al. 2008), under equal weighting. Meristic and quantitative multistate characters, as well as discrete ones that code for an obvious morphocline were treated as ordered, following Brazeau (2011). The New Technology Searches is used, using all available

algorithms with their default settings, and stabilizing the consensus tree five times with a factor of 75. After a first iteration of tree searches, the resulting shortest trees were taken as a starting point for a second round of tree bisection and reconnection, in order to find all possible shortest trees.

4.2. Results

A first, unconstrained analysis yielded four most parsimonious trees of a length of 1000 steps. However, the strict consensus tree did not retrieve the monophyly of several clades that have repeatedly been found as such by the latest phylogenetic analyses based on molecular studies. These include Lacertinae and Lacertini (Arnold et al. 2007; Kapli et al. 2011), and the genera Algyroides (Mendes et al. 2016), Iberolacerta (Carranza et al. 2004; Mendes et al. 2016), Lacerta (Carranza et al. 2004; Sagonas et al. 2014; Marzahn et al. 2016; Mendes et al. 2016), and Podarcis (Carranza et al. 2004; Carretero 2008; Mendes et al. 2016), which were all recovered as paraphyletic in the unconstrained search herein. Therefore, a second analysis was run with seven a priori constraints, in order to find the generally accepted basic structure of the phylogenetic tree, but treating the extinct species P. cadurcensis, J. ulmensis, M. rafelinensis and the OTU representing the material from Sardinia described herein as wild-card taxa, meaning that they can be recovered anywhere in the tree by the analysis. The monophyly constraints implemented in this second iteration of the analysis were defined for Gallotiinae (Gallotia and Psammodromus), Lacertinae (Eremiadini and Lacertini), Lacertini (Algyroides, Archaeolacerta, Iberolacerta, Lacerta, Podarcis, Timon, and Zootoca), as well as the genera Algyroides, Iberolacerta, Lacerta, and Podarcis. Other than for these constraints, the methodological details for this second iteration remained the same as in the first one. The second iteration found 19 constrained trees with a minimum length of 1040 steps, 40 steps more than the unconstrained searches (corresponding to an increase in tree length of 4%). As in the study of Čerňanský et al. (2016b), P. cadurcensis and J. ulmensis are recovered within the clade Gallotiinae, as is M. rafelinensis. The material from Orosei is recovered as the sister-taxon to the three species complexes of *Timon* (Fig. 4.1).

The following synapomorphies recovered for Lacertidae also occur in the fossil material from Monte Tuttavista: 1) frontals with an anterior transverse width that is greater than 1.2 times the minimum transverse width (at least in the majority of the preserved frontals); 2) a subrectangular dorsal, ornamented surface of the parietal; and 3) a weakly developed pterygoid recess.

Potential synapomorphic features supported in some but not all topologies found, and shared by most lacertid species and the taxon from Monte Tuttavista include a well-developed dermal ornamentation on the parietal, with distinct, symmetrical grooves delimiting the shields. Other features mentioned as possibly diagnostic characters for Lacertidae in the literature (e.g., Hoffstetter 1944; Augé et al. 2003; Bailon et al. 2014), which are present in the Sardinian material are 1) generally arched dentaries with a continuously widening Meckelian fossa extending from the symphysis backwards; 2) a well-developed splenial facet on the subdental ridge of the dentary, which reaches close to the symphysis; 3) the presence of a distinct coronoid facet on the posterodorsal portion of the labial surface of the dentary; 4) a well-developed carina maxillaris on the medial surface of the facial process of the maxilla; 5) pleurodont, cylindrical teeth with replacement teeth situated at their base. An attribution to Lacertinae is supported by the absence of pedicels for the chevrons on the caudal vertebrae. Potential synapomorphies of Lacertinae found in some topologies are the absence of an anterior or anterodorsal projection on the anterior margin of the facial process of the maxilla; and the presence of a short, longitudinal ridge on the dorsomedial portion of the central pillar of the quadrate.

The dorsoventral constriction in the ascending nasal process of the premaxilla was found as a synapomorphy for Lacertini. Additional, potentially synapomorphic features for this clade include the maximum number of cusps in any tooth being three; and a large maxillary facet on the lateral surface of the jugal. The fossil material considered herein shares the following synapomorphies of the clade uniting Timon and *Lacerta*: 1) the presence of pterygoid teeth; 2) the splenial reaches far anteriorly. Synapomorphies of this clade found in some but not all topologies, which also occur in the material from Monte Tuttavista are: 3) a transversely expanded ascending nasal process on the premaxilla; and 4) welldeveloped parietal tabs that underlie the frontals.

Nine synapomorphies unite the material from Monte Tuttavista with the extant species of *Timon*. None of them is exclusive to this clade, and all of them also occur in individuals of some species of *Lacerta*.





However, the combination

of these traits does not appear like this in any of the studied specimens of extant lacertids. The features are the following: 1) the maxillary tooth row curves laterally towards its posterior end (this feature also occurs in *Lacerta media* and some

specimens of L. trilineata); 2) postfrontal and postorbital are fused (also present in L. schreiberi); 3) a concave anterior platform on the quadrate; 4) the fossa triangularis and the parietal fossa on the ventral surface of the parietal are connected by a narrow bony ridge (also present in large-sized species of *Lacerta*); 5) long paroccipital processes (also present in large-sized species of *Lacerta*); 6) a mushroom-shaped basioccipital (variable within Lacerta); 7) a flat to weakly concave anterior portion of the lateral surface of the splenial (shared with L. bilineata and L. strigata); 8) the teeth overtop the dental crest of the dentary by less than half the height of their crown (variable within *Lacerta*); and 9) short posterior projections lateral to the ventral keel on the axial intercentrum (occurs as well in L. trilineata, L. viridis, and some L. schreiberi). Two additional potential synapomorphies were found by some but not all topologies: 1) a weak pterygoid recess; and 2) a distinct symphyseal facet on the dentary. Whereas the latter character seems relatively constant, the weak pterygoid recess is also found as synapomorphic for Lacertidae, shows a reversal in a basal node within Lacertini, close to the split with Eremiadini, and remains variable within *Timon* and *Lacerta*, so that it is not clear if it is really possible to consider this feature as taxonomically useful within Lacertini.

The Monte Tuttavista lacertid can be excluded from *Lacerta* because individuals of the latter genus generally have 1) a reduced or no maxillary facet on the frontal for the anterior prefrontal process of the maxilla; 2) no dorsoventral constriction of the ascending nasal process of the premaxilla (except for *L. trilineata* and some specimens of *L. viridis*); and 3) straight articular facets of the postzygapophyses (with the exception of *L. trilineata* and some specimens of *L. viridis*). Although these traits are variable within *Lacerta*, no variability could be observed in the fossil material. An additional feature usually cited as diagnostic for the genus *Lacerta* is a step-like morphology of the dorsal margin of the posterior process of the maxilla. Such a step is lacking in all maxillae from Monte Tuttavista studied herein, further arguing against a referral of this material to the genus *Lacerta*.

It is interesting to note that although phylogenetic analysis finds the lacertid from Monte Tuttavista outside *Lacerta*, several traits are shared with one *Lacerta* species in particular: the large-sized *L. trilineata*. Nonetheless, the two species can also be distinguished based on numerous features: 1) the position of the sulcus delimiting the frontoparietal shield on the dorsal surface of the frontal is situated more anteriorly in L. trilineata than in the fossil material; 2) the septonasal crest on the ascending nasal process of the premaxilla is more strongly developed in the fossil material compared to L. trilineata and forms a posterior projection instead of fading out posterodorsally; 3) the maxillary facet on the premaxilla is larger in the material from Monte Tuttavista than in any species of *Lacerta*; 4) *L. trilineata* has significantly more maxillary teeth than the fossil material; 5) there is no step on the posterior process of the maxilla in the Monte Tuttavista lacertid; 6) the articular facet for the palatine on the palatal shelf of the maxilla is more distinct in the fossil material than in L. trilineata; 7) the fossil frontals are mostly fused; 8) L. trilineata does not bear a subtriangular anterior projection on the postfrontal; 9) the lateral shield covers more of the postfrontal in the fossil material compared to L. trilineata and most other species of Lacerta; 10) L. trilineata lacks a medial process on the medial ridge of the jugal; 11) differences in tooth size along the dentary tooth row are much more distinct in the fossil material than in *L. trilineata*, and the tooth row curves dorsally towards its distal end in the former taxon; 12) the coronoid facet is less distinct in L. *trilineata* than in the fossil dentaries and the coronoid process reaches less dorsally, where this feature is preserved; 13) the splenial from Monte Tuttavista has a single posterior end instead of being bifurcated; 14) L. trilineata bears a longitudinal ridge in the neural canal floor of the axis, which is interrupted at midlength, whereas it remains distinct throughout its length in the fossil material.

4.3. Discussion: taxonomic assignment

Following the phylogenetic analysis, the Monte Tuttavista lacertid is here referred to *Timon* sp. (in contrast to Abbazzi et al., 2004, who referred it to *Lacerta* sp.), even

though it would be equally parsimonious to attribute the material to a new genus, given the more basal position of the Monte Tuttavista lacertid compared to the extant species complexes of *Timon*. However, the split between the currently living eastern and western species complexes of *Timon* has been dated to well-before the Pleistocene (Ahmadzadeh et al. 2016), so that the Monte Tuttavista sites fall within the purported life span of the genus. A referral of the Monte Tuttavista lacertid to *Timon* therefore seems the most reasonable systematic approach to date. Nonetheless, both the geographical distance from current species ranges, and several morphological traits indicate that the Sardinian material cannot be confidently attributed to any of the extant species or species complexes of *Timon*.

The most significant differences are found in the maxillary dentition and the dentary, indicating that the Sardinian form had to adapt to a different food source. The ornamentation on the lateral surface and the distinct dorsal curvature of the distal tooth row in some dentaries from Monte Tuttavista could not be observed among individuals of the studied extant species of Timon, which also lack the well-defined articular facet for the labial process of the coronoid. Furthermore, in the extant species, the largest maxillary teeth are the caniniform teeth located in the mesial half of the tooth row (Estes & Williams 1984; Mateo & Lopez-Jurado 1997), whereas the fossil maxillae often bear greatly enlarged teeth on the distal half of the tooth row. However, these enlarged teeth do not reach the distalmost tooth positions, but are distally followed by a number of distinctively smaller teeth. A similar pattern as in the maxilla also occurs in most fossil dentaries from Monte Tuttavista, which furthermore also have a reduced number of dentary teeth (15-21), especially compared to adult individuals of extant *Timon* species, which reach up to 31 teeth (T. lepidus MRAC 3390). Although the number of dentary teeth increases during ontogeny in L. viridis (Roček 1980a) and T. lepidus, which can have as few as 15 teeth in small juveniles (Mateo & Lopez-Jurado 1997), the difference between the sample from Monte Tuttavista (15-21 dentary teeth) and extant *Timon* (up to 31 dentary teeth) cannot be explained by ontogeny alone, given that many of the largest fossil specimens still bear less than 20 tooth positions. The most similar dentition to the one found here, occurs in fossil specimens from the Pleistocene of Malta, Sicily, and Apulia referred to "*Lacerta*" siculimelitensis (Kotsakis 1977; Böhme & Zammit-Maempel 1982; Delfino 2001). Because of this similarity, and the uncertain taxonomic status of this extinct species (see Mateo 1988; Barahona & Barbadillo 1997; Holman 1998; Delfino & Bailon 2000), the establishment of a new taxon for the Monte Tuttavista lacertid in not suggested here, awaiting a detailed reassessment of "*Lacerta*" siculimelitensis (currently in progress). Caution is furthermore warranted concerning the species identification of the Monte Tuttavista material because "*L*." siculimelitensis has been found in equally old strata on the neighbouring island Sicily, and because some authors proposed that this species might be referable to *Timon* (Mateo 2009; Ahmadzadeh et al. 2016).

5. Contributions of non-snake squamates to palaeoenvironmental and palaeobiogeographical studies

Because of the strong relationship between their distribution and the environmental conditions (in particular as far as temperature and pluviometry are concerned; among others, Antúnez et al. 1988; Currie 1991; Rage & Roček 2003; Vitt & Caldwell 2009), fossil amphibians and reptiles have been largely used as indicators of palaeoclimate (e.g., Böhme 2003; Böhme et al. 2006; Bailon & Blain 2007; Agustí et al. 2009; Blain et al. 2013, 2014a; López-García et al. 2014). Pleistocene fossils are particularly useful in this sense because they are often attributed to extant taxa (Blain et al. 2009). This chapter presents the results of two palaeoenvironmental studies based on the fossil herpetofaunas coming from two different early Pleistocene localities, whose lizard components have been studied as part of this thesis.

In addition to that, a tentative palaeobiogeographic analysis of the late Miocene Italian herpetofaunas is also reported. This analysis is focused on understanding the affinities of the different faunas using a rarely-used (at least in palaeontological studies) method: the network analysis of the faunal complexes.

5.1. Material & Methods

5.1.1. Palaeoclimatic reconstruction

The palaeoclimate reconstruction has been done in collaboration with Dr. Hugues-Alexandre Blain using a quantitative climate reconstruction method, the Mutual Ecogeographic Range (MER; Blain et al. 2009, 2016b). Analysis of the MER is based on the distribution atlas of the European herpetofauna (Sillero et al. 2014), with 50 \times 50 km resolution maps in the Universal transverse Mercator (UTM) georeferenced system. Climatic parameters have been estimated for each 50 \times 50 km UTM square, using climatic database from Climate-Data.org. The complete herpetofauna from the early Pleistocene of Tegelen, lizards included, is composed by at least 18 taxa (Villa et al. 2016; Villa et al. in review - Quaternary Science Reviews): *Triturus* gr. *T. cristatus, Lissotriton* sp., *Palaeobatrachus eurydices, Pelobates fuscus, Bufo bufo, Bombina* sp., *Pelophylax* sp., *Rana* sp., *Hyla* gr. *H. arborea, Pelodytes* sp., *Mauremys* sp., *Lacerta* sp., Lacertidae indet., *Anguis* gr. *A. fragilis,* cf. *Pseudopus* sp., Colubrinae indet., *Natrix natrix* and *Vipera* sp. Fossil amphibians and reptiles from the early Pleistocene of Rivoli Veronese, on the other hand, include 16 taxa (Delfino & Sala 2007; Villa et al. in press - Palaeogeography, Palaeoclimatology, Palaeoecology): *Albanerpeton pannonicum, Speleomantes* sp., *Ichthyosaura alpestris, Bombina* sp., *B. bufo, Hyla* gr. *H. arborea, Rana* sp., *Lacerta* gr. *L. viridis,* cf. *Pseudopus* sp, *Coronella* sp., *Zamenis longissimus, Natrix* sp. and *Vipera* gr. *V. aspis.*

5.1.2. Palaeobiogeographical analysis

In the network theory, a network is a structure composed by nodes, representing defined items, which are connected by edges, representing the relations between such items (Newman 2003). Networks are used in biological analyses to reconstruct trophic chains (e.g., Niquil et al. 1999), biogeographical connections (e.g., Moalic et al. 2012) or even phylogenies (e.g., Morrison 2005, 2016), but they have been rarely applied to palaeontological issues. Recent exceptions in this sense are the analysis by Sidor and colleagues (2013) of the effect the end-Permian extinction had on African tetrapod communities, the model developed by Baucon & Felletti (2013) to study ichnoassociations (see also Baucon et al. 2014) and the reconstruction of dinosaur macrobiogeographical patterns by Dunhill and colleagues (2016).

Here, a network including the 6 best-known Italian palaeoherpetofaunas dated back to the late Miocene is considered. The studied palaeoherpetological assemblages are those recovered from Cava Monticino (Delfino 2002; Rook et al. 2015; Villa et al. 2016; this work), Ciabòt Cagna (Cavallo et al. 1993; this work), Fosso della Fittaia

(Cirilli et al. 2016; this work), Area del Gargano - Gargano "terre rosse" (Delfino 2002; this Torinese work). Moncucco (Colombero et al. 2017; this work) and Verduno (Colombero et al. 2014). A map showing the position of the localities is given in Fig. 5.1, whereas the complete list of the taxa found is reported in Fig. 5.2.

Representatives of *Pelophylax* (*Pelophylax* gr. *P. ridibundus* at Cava Monticino and Gargano, *Pelophylax* sp. at Moncucco Torinese), crocodylians (Crocodylia indet. at Cava Monticino



Figure 5.1) Map of the Italian late Miocene localities included in the network considered in the palaeobiogeographical analysis. Abbreviations: CaM, Cava Monticino; CC, Ciabòt Cagna; FdF, Fosso della Fittaia; Gar, Area del Gargano - Gargano "terre rosse"; MCC, Moncucco Torinese; Ver, Verduno.

and Moncucco Torinese, *Crocodylus* sp. at Gargano) and *Eryx* (*Eryx* cf. *E. jaculus* at Cava Monticino, *Eryx* sp. at Ciabòt Cagna and Moncucco Torinese) are herein treated as single items (*Pelophylax*, Crocodylia and *Eryx*, respectively) given that there are no evidences of the remains pertaining to different species and different identifications in different localities might just represent different uses of the open nomenclature by the authors. The anguid from Moncucco Torinese is treated as *Ophisaurus* to show the possible affinities with this genus displayed by its toothbearing bones. The presumed palaeobatrachid occurrence from Ciabòt Cagna is based on a single fossil, a partially preserved synsacrum, whose identification is rather doubtful (vertebral centrum is subcylindrical and not dorsoventrally compressed as in palaeobatrachids; AV, pers. obs.); because of this, palaeobatrachids are not included here in the faunal list of Ciabòt Cagna.

	CaM	CC	FdF	Gar	MCC	Ver		CaM	CC	FdF	Gar	MCC	Ver
Albanerpeton	-	-	-	-		-	cf. Euleptes	-	-	-	-		
Chelotriton			-	-		-	Gekkota (small size)	-	-	-		-	
Lissotriton	-	-	-	-		-	Eremiadini		-	-		-	-
Bufo bufo		323	-			-	Lacerta	-	-	-			-
Bufo gr. B. viridis		-	-				Lacertidae (small size)	-	-	-		-	
Latonia cf. L. gigantea	1.000		-		-	200	Scincidae		-	-	-	-	-
Latonia	•	-	-			-	Varanus		-	-	-	-	
Discoglossinae (small size)	-	84		-	14	1	Blanus	-		-	-	-	-
Hyla gr. H. arborea		-	-			-	Palaeoblanus			-		_	-
Pelobates		-	-	-			Amphishaania						
Pelophylax		1.0	-				Saala conhidio				-		
Rana s.l.	-	-	-	-			Scolecophidia	-					
Crocodylia			-			-	Eryx			-	-		-
Mauremys	-	-	-	-			cf. Erycinae	-	-		-	-	-
Testudo		-		-			Coluber planicarinatus		-	-		-	10
Testudininei (medium size)	-	-	-			-	Elaphe	-	- 220	-		-	3 4
Agamidae		-	-	-			Telescopus	-	-	-		-	-
Ophisaurus			-	-		-	Colubrinae (n.sp.)	-	-	-		-	-
Pseudopus		-	-			-	Colubrinae		-				
Anguis	-	-		-	-	1.20	Natrix		-	-	-	-	
non-Anguis Anguinae	-			-	-		Vipera		-	-			-

Figure 5.2) List of the taxa considered in the palaeobiogeographical analysis of the late Miocene Italian herpetofaunas. Abbreviations are the same as Fig. 5.1.

Following the methodology of Sidor et al. (2013), the network composed by the late Miocene Italian herpetofaunas is a bipartite network, in which the nodes represent both localities and taxa and edges stand for the occurrence of a certain taxon in a certain locality. However, Sidor and colleagues' analysis is conducted at the species level, with a dataset that is generally consistent with this hierarchical level. Commonly, this is not the case when one considers Neogene herpetofaunas, in which remains are often identified at the generic or suprageneric level and precision of the identification may strongly vary within different localities. In order to have better comparisons between such faunas, a new kind of edge, called semiconnection, is here added (Fig. 5.3): the semiconnection links two taxon nodes and represents the systematical relation occurring between them (namely, one of the two taxa represented by the nodes is included in the other). Therefore, this new edge favours the recognition of less strong, but still possible, connections between localities with taxa identified at different hierarchical levels, avoiding the loss of biogeographical information.



Figure 5.3) Example of semiconnection (red edge) compared to the standard connections of a single taxon (Taxon 1) shared by two localities.

Still according to Sidor et al. (2013), the herein-conducted network analysis consists of two parts. First, the network is visualized using the Gephi software (version 0.9.1: https://gephi.org/), with the same parameters settings as in Sidor et al. (2013) except for scaling set as 250.0 instead of 10.0. After this graphical part, a numerical quantification of the biogeographic connectedness (BC; see Sidor et al., 2013, for details) has been calculated.

When a semiconnection is present, the node representing the lower taxon is excluded from the number of taxa considered in the BC equation, and a single edge with a value of 0.5 (instead of 1) connecting the higher taxon to the locality with the lower one is counted in the number of links.

Judging from both the low number of identified taxa and the low number of collected remains, palaeoherpetological assemblages of Ciabòt Cagna, Fosso della Fittaia and, to a lesser extent, Verduno appear to be subject to some kind of bias, being it either a taphonomical or a collection one. This biased nature strongly conditions the analysis, both in the graphical and the numerical parts. Because of that, the palaeobiogeographical study has been separated into two different portions. First, a complete analysis of the network composed by Cava Monticino, Gargano and Moncucco Torinese, the most comparable localities in terms of number of taxa and remains (that is, most probably the less biased ones), has been carried out. Subsequently, all three other localities have been added in the graphical analysis and

each of them has been individually compared to each one of the former three, in order to quantify their BC keeping a stable bias effect.

Another correction, linked with a particular case, has been applied in the BC quantification. In Cava Monticino, both *Ophisaurus* and *Pseudopus* are reported, representing all non-*Anguis* anguine taxa currently known from the Neogene. Given that, in the cases of a semiconnection between Cava Monticino and the localities in which only undetermined non-*Anguis* Anguinae have been reported (namely, Ciabòt Cagna, Fosso della Fittaia and Verduno), *Ophisaurus* and *Pseudopus* are considered together and the semiconnection is considered as a normal connection between Cava Monticino and the non-*Anguis* Anguinae indet.

5.2. Results and discussion

5.2.1. Palaeoclimate and palaeoenvironment of Tegelen

The whole fossil assemblage from Tegelen has no modern analogue, because its extant taxa do not co-occur in the present-day fauna. Nevertheless, overlap of the ranges of most of the taxa is possible if we exclude from the analysis the extinct P. *euridyces* and the extant genus *Pelodytes* that currently has a disjoined distribution in southern Europe that seems not to be climate-related (Pearman et al. 2010). In addition we should take into account that the modern distribution of P. fuscus in the Balkan area is probably influenced by the competition with *Pelobates syriacus* (Tarkhnishvili et al. 2009; Iosif et al. 2014). To resolve the last point, an overlap with the modern fauna has been obtained by merging the present distribution of both P. fuscus and P. syriacus. As a result, an analogue of the fauna can be found in three UTM squares (Fig. 5.4A). These 50 x 50 km UTM squares occur in a relatively similar climatic environment in southern Bulgaria at the border with Greece and Turkey (cities of Burgas, Svilengrad and Sandanski). Such an overlap corresponds to a mean value of 13.4 ± 0.3 °C of mean annual temperature and 542 ± 50 mm of mean annual precipitation (Tab. 5.1). The climate can be characterized as temperate, with a very high atmospheric temperature range. The summer is warm and the winter



Figure 5.4) Monthly palaeoclimatic reconstructions for Tegelen based on its fossil herpetofaunal assemblage. A: overlaps of the current distribution done in 50×50 km UTM squares; B: quantitative reconstruction according to the Mutual Ecogeographic Range method compared with current data. is cold. Rainfall is low, but its distribution is fairly regular, with the highest amount during winter and to a lesser extent spring. Three months during summer and early autumn (from July to September) are considered to be dry, according to the Gaussen

Index (Fig. 5.4B). According to the Köppen-Geiger classification of climates, such an overlap corresponds to the humid subtropical climate (Cfa). The Lautensach-Mayer and De Martonne Indices suggest a semi-humid continental Mediterranean climate with three dry months in summer (Fig. 5.4B; Tab. 5.2). By contrast, the Dantin-Revenga Aridity Index classifies the climate as semi-arid (Tab. 5.2).

In comparison to the current climatic data from Tegelen area (Oceanic climate, Cfb) the MER-estimated MAT is much higher (+3.4°C) than at present (Tab. 5.1). Such warmer climatic conditions during the early Pleistocene are mainly linked with a greater increase in temperature in summer (between +5.1°C and +6.0°C) than in winter (+0.4°C and +1.7°C). The total amount of rainfall is somewhat lower (-227 mm) than at present in the Tegelen area leading to three months of aridity, whereas today the Oceanic climate from Tegelen shows no dry month (Fig. 5.4B). This is corroborated by the value of the Aridity Indices, suggesting that, at the time of deposition, conditions in Tegelen were much drier than today, especially during summer.

Table 5.1) Climatic parameters calculated with the Mutual Ecogeographic Range method for the early Pleistocene of Tegelen and current climatic values from the Tegelen area. MAT: mean annual temperature; MAP: mean annual precipitation; SD: standard deviation; Δ : difference between Early Pleistocene estimated and current values.

					٦	Tempe	rature	(in ⁰C)				
	MAT	J	F	М	А	М	J	J	А	S	0	Ν	D
MEAN	13.4	2.6	4.4	7.5	12.5	17.3	21.3	23.7	23.1	19.8	14.9	9.2	4.5
SD	0.3	0.1	0.4	0.7	0.6	0.6	0.5	0.6	0.7	0.6	0.8	0.6	0.6
Today	10.0	2.2	2.7	5.8	9.1	13.2	16.2	17.7	17.6	15.2	10.9	6.2	3.4
Δ	+3.4	+0.4	+1.7	+1.7	+3.4	+4.1	+5.1	+6.0	+5.5	+4.6	+4.0	+3.0	+1.1
					F	Precipit	tation ((in mm)				
	MAP	J	F	М	А	М	J	J	А	S	0	Ν	D
MEAN	542	46	44	41	45	51	46	34	28	37	45	67	59
SD	50	9	6	7	5	1	3	4	4	11	7	6	9

Today	769	63	49	58	51	65	76	75	72	63	62	66	69
Δ	-227	-17	-5	-17	-6	-14	-30	-41	-44	-26	-17	1	-10

Table 5.2) Climatic interpretation of the modern and Early Pleistocene climatograms of Tegelen. MTC: mean temperature of the coldest month.

		Today	1	Early Pleistocene			
	Mean annual temperature	10.0°C	temperate	13.4°C	temperate		
	Atmospheric temperature range	15.5°C	medium	21.1°C	very high		
	Summer temperature	0 months>22°C	temperate	2 months>22 C	。 warm		
Temperature	Winter temperature	MTC = 2.2°C	cold	MTC = 2.6°C	cold		
	Mean annual precipitation	769 mm	low	542 mm	low		
	Distribution of rainfall	no month<30 mm	regular	1 month<30 mm	fairly regular		
Rainfall	Type of precipitation	rain		ra	ain		
	Gaussen Index	0	Oceanic	3	Mediterranean		
	Lautensach-Mayer Index	0	humid	3	semi-humid		
	Dantin-Revenga Index	1.3	humid	2.5	semi-arid		
Aridity	De Martonne Index	38.5	humid	23.2	semi-humid		

The climate of Tegelen and the survival of palaeobatrachids in Western Europe In The Netherlands, the Pleistocene is characterized by a marked palaeoclimatic cyclic nature, involving alternating glacial and interglacial phases (Drees 2005 and references therein). After a first glacial period, the Pretiglian, interglacial conditions set up during the Tiglian stage, even though cool oscillations were still present (Reid & Reid 1915; Vlerk & Florschütz 1953; Zagwijn 1963; Drees 2005). Based on

palynological analyses, the Tiglian stage was separated by Zagwijn (1963) into three different substages (TA, TB and TC), the latter of which is further composed by six sections (TC1 to TC6). According to the palaeoclimatic quantitative reconstructions of the Dutch pollen sequence (Zagwijn 1963, 1989; Kasse 1988, 1993; Kasse & Bohncke 2001), the TC5 section of the Tiglian is separated in three phases: warmcold-warm. The deciduous vegetation of the warm periods (TC5a and c) indicates that the mean summer temperature was around 18°C (mean temperature of the warmest month = 18 to 20°C according to Pross & Klotz 2002), the mean winter temperature above $-1^{\circ}C$ (mean temperature of the coldest month = -2 to $0^{\circ}C$ according to Pross & Klotz 2002) and the mean annual temperature circa 10°C (i.e., similar to current value). The German pollen record from Lieth (zone E5; Pross & Klotz 2002) provides for the TC5 a mean January temperature estimate of -1°C and mean July temperatures between 14 and 21.5 °C consistent with the estimation by Zagwijn (1963, 1989) for Tegelen. The palaeoclimatic reconstruction based on the amphibian and reptile assemblage from Tegelen thus suggests that some of these early Pleistocene interglacial periods in northern Europe would have been somewhat warmer than previously reconstructed with mean temperature of the warmest month reaching up to $23.7 \pm 0.6^{\circ}$ C and mean temperature of the coldest month $2.6 \pm 0.1^{\circ}$ C. The light degree of dryness based on herpetological evidence is apparently in contradiction with the palaeoenvironmental information given by some components of the fauna. For one, the best represented group in the fauna are the beavers (Schreuder 1929), to the point that the Tegelen Clay was sometimes referred to as the Trogontherium Clay, because of the numerous finds of this extinct beaver. However, the herpetofauna stems from a stream gully cutting into the palustrine sequence, which could be seen as confirmation that we are indeed dealing with a dryer period. Nevertheless, the micromammal fauna, which was retrieved together with the herpetofauna, refutes overly dry conditions. Desmans are numerous (Rümke 1985) and the diverse shrew fauna indicates a humid environment. Among the voles, typical steppe elements of the era, such as Borsodia, are conspicuously absent and the presumably semi-aquatic *Mimomys pliocaenicus* is numerous. In addition, the assemblage show a high proportion of various forest and shrub dwellers, such as *Apodemus*, *Clethrionomys* and the glirids, *Muscardinus* and *Glirulus*.

Part of the apparent inconsistency in the palaeoenvironmental reconstructions based on different groups can be explained by the absence of recent analogues of the conditions in the Villafranchian. As noted above, there is no strict present-day analogue of the herpetofauna, which is not surprising as the same holds true for the flora and the mammal fauna. The former still contains a number of Tertiary elements, whereas the dormouse *Glirulus* is now restricted to Japan. In finding a modern analogue, we had discarded the only extinct member of the herpetofauna, P. euridyces. As a palaeobatrachid, P. euridyces is considered to have been extremely adapted to a water-dwelling life (Villa et al. 2016), therefore needing permanent water bodies to survive. The combination of increasing drought and periglacial areas with low temperatures during winter leading to a freezing of the water bodies is thought to have caused the definitive extinction of palaeobatrachid anurans during the Middle Pleistocene, and the aridization is usually singled out for their previous disappearance from Western Europe (Wuttke et al. 2012). The presence at Tegelen of a member of this group is an evidence of the persistence of suitable water bodies during the whole year, without a significant period of freezing during winter (as confirmed by our palaeoclimatic results) and despite the relatively arid months during summer. The fairly regular pluviometric regime might have contributed to maintain the availability of wet environments and, in addition, the vicinity to the Rhine river would also have ensured the presence of permanent water bodies. A similarly moist landscape might have been present in another, slightly older locality not so far from Tegelen, in which rare palaeobatrachid remains have been found: Hambach 11 (late Pliocene, MN 16) in northwestern Germany (Mörs 2002). Hambach 11 shows a lower diversity in the amphibians and reptiles assemblage compared to Tegelen (Mörs 2002; Čerňanský et al. 2016c), but also a striking difference in the composition of the fauna, which includes cryptobranchids, proteids,

discoglossids and chelydrids. The presence of an anguid related with *Pseudopus pannonicus*, which is considered to be linked with sub-humid/humid climates (Čerňanský et al. 2016c), might be an evidence of moist condition in Hambach during the late Pliocene. This seems to be further confirmed by the fish remains (Mörs 2002). It can be therefore supposed that a rather humid climate might have somehow persisted in this part of Western Europe, favouring the survival of palaeobatrachids. Nevertheless, given our current knowledge of Dutch climate and herpetofaunas at the early/Middle Pleistocene transition, it is not possible to state whether the following disappearance of these anurans from this region could be linked with decreasing temperature, increasing aridization, a combination of both or even with other, still unrecognised reasons.

5.2.2. Palaeoclimate and palaeoenvironment of Rivoli Veronese

As a whole, the palaeoherpetofauna from Rivoli Veronese also has no modern analogue. Nevertheless, overlap of the ranges of most of the taxa is possible, although excluding from the analysis the extinct *Albanerpeton* and *Speleomantes* because of its very restricted modern range. Such an overlap gives a unique 50 x 50 km UTM square, located at the boundary between Slovenia and Croatia, mainly centered on the southwestern Slovenian city of Ilirska Bistrica (red square in Fig. 5.5A). Such an area (comprised between 400 and 600 meters above sea level) corresponds to a mean annual temperature (MAT) that varies between 12.4 and 9.8°C and very high mean annual precipitation (MAP) comprised between 1320 and 1340 mm.

If we closely compare Ilirska Bistrica and Rivoli Veronese modern values (1982-2002; Tab. 5.3), the early Pleistocene climate deduced for Rivoli Veronese would have been characterized as cold and with a very high atmospheric temperature range, temperate summer and cold winter (Figure 5.5B; Tab. 5.4). Rainfall was very abundant, with a regular distribution over the year and with the highest amount occurring during winter and to a lesser extent spring. No dry month is evidenced thus



Figure 5.5) Monthly palaeoclimatic reconstructions for Rivoli Veronese based on its fossil herpetofaunal assemblage. A: overlaps of the current distribution done in 50×50 km UTM squares without Speleomantes (red square) and without Speleomantes and Pseudopus (black and red squares). B: climatograms from Ilirska Bistrica (southwestern Slovakia; red square) that would represent the early Pleistocene paleoclimate occurring at Rivoli Veronese according to the MER method compared with current data of Rivoli Veronese.

characterizing the climate as mountainous humid to very humid, according to the Aridity Indexes (Tab. 5.4). In comparison with the current climatic data from Rivoli

Veronese area, the MER-estimated MAT would have been somewhat colder (-0.8°C) than at present (Tab. 5.3). Such colder climatic conditions during the early Pleistocene are linked with a decrease in temperature during the spring and summer months (between -1.1°C and -1.9°C), but not during the winter, which is warmer (+0.2°C and +2.0°C). The total amount of rainfall would have been much higher (+488 mm) than at present in the Rivoli Veronese area. The frequency of precipitation would also have been much higher than the modern-day climate, especially during the fall and winter months (from September to January). Such higher humidity is confirmed by the De Martonne Index (Tab. 5.4).

To confirm these results, a second overlap is undertaken, excluding from the analysis the genus *Pseudopus*, a large anguid lizard currently absent from Italy, as it was the taxon that strongly constrained the previous one-UTM square overlap. According to the MER method, when a taxon is removed from the analysis, the resulting overlap is supposed to be still valid even if less precise. When removing *Pseudopus* from the assemblage, the obtained overlap is much larger, comprising a total of 90 UTM squares (black and red squares on Fig. 5.5A). These UTM 50 x 50 km squares mainly correspond to mountainous areas and are distributed from the western borders of Romania and Bulgaria, the eastern border of Hungary in the East, and up to the western-central part of France in the West. It also encompasses the south of Austria and Switzerland, northernmost Italy and a large area of central-eastern France.

	Temperature (in °C)												
	MAT	J	F	Μ	А	Μ	J	J	А	S	0	Ν	D
Ilirska Bistrica	11.6	2.8	3.3	6.3	10.3	14.7	18.3	21.1	20.7	17.3	12.6	7.5	4.7
Rivoli Veronese	12.4	1.4	3.9	8.0	12.2	16.5	20.2	22.6	21.8	18.6	13.0	7.3	2.7
Difference	-0.8	+1.4	-0.6	-1.7	-1.9	-1.8	-1.9	-1.5	-1.1	-1.3	-0.4	+0.2	+2.0
	Precipitation (in mm)												
	MAP	J	F	Μ	А	Μ	J	J	А	S	0	Ν	D
Ilirska Bistrica	1322	96	88	90	101	101	110	90	101	131	141	146	127

Table 5.3) Comparison between modern climatic parameters of Ilirska Bistrica and Rivoli Veronese.

Rivoli Veronese	834	46	46	53	70	81	87	65	85	72	87	85	57
Difference	+488	+50	+42	+37	+31	+20	+23	+25	+16	+59	+54	+61	+70

Table 5.4) Climatic interpretation of Rivoli Veronese and Ilirska Bistrica. MTC: mean temperature of the coldest month.

		Rivoli Verone 2002	ese (1982- 2)	Ilirska Bistrica	(1982-2002)
Φ	Mean annual temperature	12.4°C	cold- temperate	11.6°C	cold
nperatur	Atmospheric temperature range	21.2°C	very high	18.3°C	very high
Ter	Summer temperature	0 months>22°C	temperate	0 months>22°C	temperate
	Winter temperature	MTC = 1.4°C	cold	MTC = 2.8°C	cold
nfall	Mean annual precipitation	834 mm	abundant	1322 mm	very abundant
Rai	Distribution of rainfall	mm	regular	mm	regular
	Type of precipitation	rair	า	rair	ı
	Gaussen Index	0	Mountain	0	Mountain
dity	Lautensach-Mayer Index	0	humid	0	humid
Ari	Dantin-Revenga Index	1.5	humid	0.9	humid
	De Martonne Index	37.2	humid	61.2	very humid

Such an overlap corresponds to a mean annual temperature of $10.6 \pm 1.7^{\circ}$ C and a mean annual precipitation of 839 ± 233 mm. This further verifies a cold (-1.8°C compared to present conditions in Rivoli Veronese) and humid (similar to present values in that case) pattern for the palaeoclimatic reconstruction of the Early Pleistocene site.

Rivoli Veronese: a humid and forested refugium for the last allocaudates?

Within the biochronological range given by the rodent assemblage from Rivoli Veronese (Kotsakis et al. 2003; Sala & Masini 2007) that suggest a late Villanyan (MN17) age, which has also been constrained by palaeomagnetism studies (Bellucci et al., 2014) that is between 2.13 and 2.0 Ma, our palaeoherpetofaunal based climate reconstruction suggests that fossil remains found at Rivoli Veronese may have been deposited during a cold phase (i.e. MIS 78, 76 or 74) of the late Gelasian. Similar to

the conditions evidenced by the pollen record in the Appennine side of the Po Plain (Fauquette & Bertini 2003; Bertini 2010), the climate in Rivoli Veronese during this cold phase was characterized by a rather strong degree of humidity (Tab. 5.4). This confirms the climatic peculiarity of Northern Italy during the Gelasian when compared with the drier glacial phases of the rest of the peninsula. The presence of either temporary or permanent water bodies is further evidenced by the high number of water-linked taxa recognised in the herpetofauna, particularly Natrix and all amphibians. Given the absence of both palynological and palaeobotanical data from the locality, an estimate of the probable vegetation must be indirectly inferred from the usual environmental preferences of the identified taxa. On the whole, the amphibians and reptiles assemblage includes taxa that are indicative of a forested environment (see Speybroeck et al., 2016, for a brief summary of their ecological requirements). Extant I. alpestris and plethodontids of the genus Speleomantes, for example, frequent respectively water bodies and intersticies, crevices and caves that are surrounded by forests respectively. Zamenis longissimus is also considered a forest-dweller (even though alternating with more open basking areas). Hyla gr. H. arborea, cf. Zootoca vivipara and Coronella might support the presence of open environments near the edge of the forest (Speybroeck et al. 2016), but the few remains confidently attributed to these taxa might suggest that open areas were not the dominant environment in the vicinity of the karst fissures of Rivoli Veronese. In any case, these open meadows might have been also used by Lacerta gr. L. viridis for basking. Generalist taxa such as B. bufo and Rana were also present, neither confirming nor contradicting the palaeoenvironmental indications as given by the rest of the herpetofauna. A humid and forested environment is also consistent with the mammal remains, due to the finding of hygrophilous insectivores and flying squirrels (Sala et al. 1994; Fanfani & Masini 1997).

As noted by Delfino and Sala (2007), such a humid environment contrasts with the past common view of Neogene and Quaternary allocaudates being dry-adapted taxa, and is more consistent with Gardner and Böhme's (2008) hypothesis of a group with

wider habitat tolerances, but with a preference for moist and forested karstic areas. Given these ecological preferences, questions might be raised as to why they went extinct after the early Pleistocene. Such humid and forested conditions were still present in the Southern Alps during the Calabrian, despite some possible and brief drier period with more open vegetation (Ravazzi & Rossignol Strick 1995). It can be argued that whilst these periods may have had a negative impact on the survival of allocaudates in Northern Italy, an even stronger change in environmental conditions from a forested to a grassland/steppe environment had had virtually no effects on A. pannonicum in its type locality, Csarnóta 2 (Venczel & Gardner 2005). The burrowing lifestyle of allocaudates has been suggested as the likely reason behind the low impact of the environmental changes at Csarnóta 2, and so this hypothesis might also hold true for those living in Northern Italy. Yet these organisms still went extinct. It is interesting to note that another interstitial amphibian found in Rivoli Veronese, Speleomantes, also disappeared from the area after the Gelasian. Therefore it seems likely that the cause of their disappearance could still overcome the resilience provided by their interstitial habits.

It is commonly thought that glacial phases during the first part of the early Pleistocene were of a rather low amplitude, with the first major glaciation occurring during the Marine Isotope Stage (MIS) 22 (0.87 Ma; Muttoni et al. 2003, 2007). According to Muttoni and colleagues (2007), the magnitude of this glacial event was comparable to that of the Last Glacial Maximum, and it is possible that during this period, the ice cap covering the Alps were also similarly expanded towards the southern margin of the mountain range. Reconstructions of the Last Glacial Maximum place the ice cap margin very close to, if not covering, the area of Rivoli Veronese (see fig. 1 in Muttoni et al., 2003, and fig. 1a in Muttoni et al., 2007). It is therefore possible that the proximity of the ice cap might have made the karstic fissures unsuitable for both *Albanerpeton* and *Speleomantes*, which were not able to either migrate further south or recolonize the area during the following interglacial. Following the reconstructions reported in Muttoni et al. (2003, 2007), Rivoli

Veronese was encircled by two different extensions of the ice cap during the Last Glacial Maximum, both from the Lake Garda and the Adige River sides. If a similar pattern is also valid for the MIS 22 glaciation, the Rivoli Veronese amphibians and reptiles may have found themselves trapped, with low possibilities of moving away from the glacier margin. In any case, if this part of Northern Italy acted as an early Pleistocene refugium for allocaudates (as it seems suggested by the absence of other coeval or younger findings), it appears that the loss of suitable conditions resulted in, or at the very least pushed them towards, their extinction.

Herpetofaunal extinction or extirpation events during the Pleistocene are also well known also in the two other European peninsulae facing the Mediterranean (namely, the Iberian and the Balkan Peninsulae). In both cases, the disappearance of taxa followed a southward trend, with their distributional ranges showing a contraction towards the southern portions of the two peninsulae over time (see e.g., varanids in Greece, Georgalis et al., 2017b, and agamids in Spain, Delfino et al., 2008; Blain et al., 2016a). It is interesting to note how the disappearance of "exotic" amphibians and reptiles in Iberia seems to be geographically linked with particular moments in time (Blain et al. 2016a): i.e., the Olduvai palaeomagnetic event in the northern part of the country and the Jaramillo event in the southern part. However, it must be stressed that these extirpations concern mainly thermophilous reptiles (with the only exception of the green toad, Bufotes viridis s.l.), whose disappearance is usually linked with the cooling associated with glaciation events (even if competitive exclusion caused by other taxa could have also played a role). Given that, it is most likely that their local disappearance and that of the cold-tolerant Albanerpeton and Speleomantes in the northern side of the Po Plain might not be linked to the same causes.



Figure 5.6) Bipartite network representing the palaeoherpetological assemblages of Cava Monticino (CaM), Area del Gargano - Gargano "terre rosse" (Gar) and Moncucco Torinese (MCC). Black circles represent the localities, grey circles are taxa occurring in a single locality, yellow circles are taxa occurring in two localities, green circles are taxa occurring in all three localities. Semiconnections are shown in red.

5.2.3. Palaeobiogeographic affinities of the Italian herpetofaunas during

the late Miocene

The network including Cava Monticino, Gargano and Moncucco Torinese is shown in Figure 5.6, whereas Figure 5.7 displays the complete network of the late Miocene Italian herpetofaunas. Table 5.5 shows the BC, both for the network composed by the three most comparable localities and for the comparison between them and each one of the other three localities.

On the whole, the reduced network displays a moderately low degree of faunal homogeneity, as depicted in the graph by the high number of taxa recovered from a

single locality and quantitatively by the BC value, which is closer to 0 than to 1. Nevertheless, the complex does not show a complete absence of connectedness, since at least six taxa are shared by all three localities. When the localities are compared in pairs, a stronger connection between Cava Monticino and Moncucco Torinese is highlighted, whereas each one of these latter localities shows a lower BC value with Gargano. It has to be noted that the BC between Cava Monticino and Moncucco Torinese still represents a condition of intermediate homogeneity, due to the rather high number of taxa that are present in one of the sites but not in the other (5 in the former, 9 in the latter). The Gargano area, on the other hand, seems to be more linked with Cava Monticino than with Moncucco. As far as Ciabòt Cagna, Fosso della Fittaia and Verduno are concerned, a lower connection with Gargano than with the other two localities is also shown, both in graphical and numerical terms. Overall, BC values are lower for Ciabòt Cagna and Fosso della Fittaia, but this is most probably due to the higher bias effect they are subject to compared to Verduno.

	Total	CaM - MCC	CaM - Gar	Gar - MCC
BC	0.31	0.46	0.31	0.24
BC	CaM		Gar	МСС
CC	0.21		0.03	0.10
FdF	0.16		0.07	0.10
Ver	0.39		0.17	0.37

Table 5.5) Biogeographic connectedness. Abbreviations are the same as in Fig. 5.1.

Herpetofaunal complexes in Italy during the late Miocene

Among late Miocene Italian faunal associations, those recovered from the karstic fissure fillings exposed in the Gargano quarries are distinguished by a strong degree of endemism developed in an insular context (Masini et al. 2010; Savorelli & Masini 2016; Savorelli et al. 2016). This is mainly due to the high number of truly endemic genera and species of mammals that have been described throughout the years based



Figure 5.7) Bipartite network representing all the late Miocene Italian herpetofaunas herein considered. Abbreviations are the same as in Figure 5.1. Color of the circles are the same as in Figure 5.6, plus blue circles representing taxa occurring in four or more localities. Semiconnections are shown in red.

on remains coming from those fissures, pertaining to both small (e.g., *Mikrotia*, *Mystemys*, *Apatodemus*; Freudenthal 1976; Savorelli & Masini 2016; Savorelli et al.

2016) and large (e.g., *Deinogalerix*, *Hoplitomeryx*; Freudenthal 1972; Leinders 1984) mammals.

The low BC showed in the herein considered network by the Gargano palaeoherpetofauna might lead to presume that a similar degree of endemism is also found among amphibians and reptiles. However, this is not the case, at least based only on the currently available data: the low BC is indeed due to a number of taxa that have not been recovered in the other Italian localities, but most of them represent taxa that are well know from other European sites. Only the two possible new species of geckos (see chapter 3.2.3) and colubrines (Delfino 2002) might represent true endemites, even if the presence of unrecognised endemic species of taxa currently identified only at supraspecific level cannot be completely excluded.

Nevertheless, being them either endemic taxa or not, a clear difference in the herpetofaunal composition between the Gargano "terre rosse" and the other Italian localities is indeed present. As shown in Tab. 5.5 and in Fig. 5.7, such a difference is less strong when these other localities are compared. This suggests that all Italian late Miocene herpetofaunas but Gargano might be grouped together, whereas the latter represents its own palaeoherpetofaunal complex. A possible exception, however, might be represented by Fosso della Fittaia, whose very poorly-known herpetofauna seems to display some peculiar component, such as the possible non-*Latonia* discoglossine, *Anguis* and the possible but strange erycine snake (Cirilli et al. 2016). Given that Fosso della Fittaia has also yielded a number of endemic mammals probably evolved on an archipelago (Cirilli et al. 2016), it is possible that new amphibians and reptiles remains collected in future excavations might reduce the connectedness between Fosso della Fittaia and the other localities, pointing to the recognition of a third palaeoherpetofaunal complex.

The intermediate degree of BC displayed by Cava Monticino and Moncucco Torinese is also rather interesting. This might suggest the possibility of separating even these herpetofaunas into two different complexes (or maybe subcomplexes), but a local or taphonomic origins of at least some of these faunal differences must also be taken into account. As far as caudates are considered, for example, Moncucco Torinese has yielded fossils of at least two different taxa (namely, *Chelotriton* and *Lissotriton*), whereas no genus or species belonging to this group of amphibians have been clearly identified in Cava Monticino. Nevertheless, very few caudate remains have been found in the latter site too (Rook et al. 2015; Villa et al. 2016), even if they are not diagnostic and cannot be identified more precisely than at order level. The presence of similar caudate taxa in both Moncucco Torinese and Cava Monticino might therefore be possible. Moreover, the finding of *Varanus* in Verduno supports the presence of this lizard genus in the late Miocene of Piedmont, suggesting that its absence in Moncucco Torinese might be due to some kind of local effect. On the other hand, of course, other missing taxa might have been truly absent in the original biocoenosis.

Network analysis as a tool to study palaeoherpetofaunal communities

It appears clear that using network analysis to quantitatively study the late Miocene Italian herpetofaunas indeed leads to some obstacles due to the mixed taxonomical nature of their identified components. It is often very difficult, if not impossible in some cases, to precisely identify amphibians and reptiles remains coming from fossil sites (see e.g., Villa et al. 2017 and chapter 2.4 in this work for a brief review of the problems in recognising lizard bones), and this results in faunal lists that very rarely are represented only by species or even genera. This, however, does not mean that such faunas must not be compared, and that palaeobiogeographical inferences based on amphibians and reptiles are totally impossible. Just like as other fossil organisms, on the contrary, even rare and poorly preserved remains can prove themselves interesting from this point of view (see, for example, the contribution to the evolutionary history of anguines in the Eastern Mediterranean Basin given by fossils from Turkey recently reported by Čerňanský and colleagues, 2017). In this context, in spite of the possible obstacles and approximations, network analysis still figures as a promising tool to understanding connections and relationships between different

palaeoherpetofaunas, adding both graphical and numerical information to the simple inferences that can be gained by a standard comparison between faunal lists.

6. Conclusions

Same as in modern times, lizards have been an important component of the European herpetofauna during the whole Cenozoic. The time interval considered in this thesis, the last 23 millions of years, makes no exception. Nevertheless, old studies dealing with lizard fossils from the continent were strongly biased by a scarce knowledge of the comparative osteology of these animals, as suggested for example by the largely common practice of identifying all lacertid and agamid remains simply as undetermined members of *Lacerta* s.l. and *Agama* s.l. respectively.

This fact highlights the need of an improvement in the knowledge we have of their comparative anatomy, in order to better understand differences and similarities that could have taxonomic and diagnostic significance. The first part of the work presented herein fits in this need, trying to give a detailed view on the cranial anatomy of most European lizard and worm lizard species. In this context, the main result obtained is the diagnostic key presented in chapter 2.3, which aims to be a very useful tool for researchers working on fossil lizards assemblages in the future (as well as for other scholars such as neoherpetologists willing to identify remains found in bird pellets, for example). It has to be noted, however, that since this comparative analysis is focused on extant European species, it obviously does not take into account extra-European taxa. This has to be considered when dealing with time periods when lizard groups that are currently locally extinct were still present in Europe (as e.g., cordylids during the Miocene or varanids up to the Pleistocene), as well as when studying extra-European fossil assemblages of course.

The comparative analysis also evidenced that, in an ideal scenario of all bones and species having equal probabilities of being preserved, roughly half of the extant diversity of lizards could be recognised as fossil, providing a more optimistic estimate than the one presented in a recent paper by Villa et al. (2017). It is likely that more deepened studies, including also taxa that are missing in the herein reported

analysis, could increase this recognisability. Further improvements could be gained by extending the analysis to the postcranium, as well as by applying promising methods such as specimen-level phylogenetic analysis and geometric morphometrics. It remains clear, of course, that a complete knowledge of the past lizard diversity would still be impossible to get in spite of an improving understanding of their comparative osteology, because of the persistence of other biases such as taphonomic and collection ones.

The comparative osteological analysis has already proved itself useful in the identification of the about 24400 remains coming from 75 localities of five different European countries reported in chapter 3. The study of these fossils has highlighted the interesting data that may lie hidden even in fragmentary remains of lizards that are often overlooked in fossil assemblages. Significant examples of this might be:

- the dentary of *Mediolacerta* found in Stubersheim, which might be important in order to shed light on the different effect the Oligocene/Miocene transition had on different lizards;

- the greek remains of chamaeleons from Aliveri, representing the single record of the family from the early Miocene of Southeastern Europe and therefore an important tile in understanding the evolutionary history of the group in the continent;

- the undetermined Eremiadini identified in Cava Monticino, whose remains testify for a past presence of this lacertid tribe in Italy, where they are completely absent now and from other fossil sites.

Therefore, it appears once again clear that a better identification of isolated fossil remains of lizards is crucial in order to better comprehend the evolutionary history of this group of reptiles first, but also of the European herpetofauna in general, given the importance that lizards have in terms of diversity and ecological role among amphibians and reptiles in the continent.

A review of the known fossil record of lizards in the Neogene and Quaternary of Europe highlights that the palaeodiversity of these reptiles were rather high during the Miocene, but then underwent an impoverishment in the Quaternary. A number

of mainly termophilic groups that were once spread in the northern part of Europe display a clear withdrawal towards Mediterranean countries, where their last representatives in the continent are found (being them still present there, such as non-Anguis anguines and agamids, or not, such as varanids). This agrees with what previously reported by authors such as e.g., Rage (2013) and Blain et al. (2016a). Even though the Miocene lizard fauna still appears to be different from the Paleogene one, with the appearance and spread of new groups such as chamaeleons and anguids of the genus Pseudopus, some recent finds might support the idea that some Oligocene forms might have survived at least up to the beginning of the Neogene. Amblyodont lacertids, for example, were thought to have been mainly a Paleogene component of the lizard fauna of Europe, but remains of *Mediolacerta* (this work) and of Janosikia (Čerňanský et al. 2016b; this work) coming from the early to middle Miocene of Germany show that they were still present in the Neogene with both Oligocene and Miocene forms. The transition from the highly diverse Neogene fauna to the extant one was then likely driven by the deterioration of the climate, culminated with the Pleistocene glaciations.

As already stated above, help in improving our ability to identify lizard fossils might came from the application of methodologies other than classical morphological comparison. Here, this is exemplified by the application of a phylogenetic approach to the identification of the large lizard remains coming from Monte Tuttavista, whose taxonomical assignment was otherwise puzzling. The phylogenetic analysis has pointed out the affinities between the Sardinian material and the genus *Timon*, even though excluding its belonging to any of the extant species. Moreover, similarities in the dentition might link these remains to the extinct "Lacerta" siculimelitensis (sometimes referred to Timon as well), but this species needs to be revised after having been questioned by some authors and therefore a clear association with the Sardinian *Timon* must await for a new formal study of the Sicilian/Maltese species. Also, a better comprehension of the lizard palaeodiversity has obvious implications studies in which the palaeoherpetofauna is for used to reconstruct
palaeoenvironments and palaeogeographical patterns. Here, the new identifications of lizards remains coming from two localities, namely Tegelen in The Netherlands and Rivoli Veronese in Italy, helped to reconstruct the palaeoclimate of the two sites during the early Pleistocene, adding to the rest of the herpetofauna. The application of the Mutual Ecogeographic Range Method to both cases has resulted in a humid subtropical climate with low but fairly regular rainfalls for the Dutch site and in a cold and humid climate with regular and abundant rainfalls for the Italian one.

In the end, Italian late Miocene palaeoherpetofaunas, including newly identified lizard remains, have been analysed using a new network-based approach in order to understand whether this kind of method could be applied to palaeoherpetological data from Neogene and Quaternary localities. Biogeographically speaking, the whole set of faunas displays a moderately low degree of faunal homogeneity, but two possible complexes seem indeed to be recognisable, separating the Gargano palaeoherpetofauna from all other ones. A third complex might be represented by Fosso della Fittaia, which is considered to represent a palaeoarchipelago, but this cannot be confirmed since the few amphibians and reptiles remains currently available do not allow a clear separation from the other non-Apulian localities. Further remains collected in future excavations might give new clues on this issue. In conclusion, a network analysis of Neogene and Quaternary palaeoherpetofaunas might be complicated by some problems linked with poorly known faunas or taxa identified at different taxonomical ranks in different sites, but nevertheless it might represent a useful source of both graphical and quantitative information about palaeogeographical patterns.

7. Acknowledgements

It is really not easy to sum up all the people that helped during the three-years-long work that resulted in this thesis. A high number of person gave their contribution, both directly and indirectly. Their help, guidance, support or simple company has been greatly appreciated.

A first thank is due to all those people that made available specimens of extant European lizards under their care or helped with the scanning of some of those specimens: Aaron M. Bauer (Villanova University, Villanova); Alberto Venchi (Queensland Museum, Brisbane); Claudio Tuniz ('Abdus Salam' International Centre for Theoretical Physics, Trieste); Annelise Folie and Wim Van Neer (Royal Belgian Institute of Natural Sciences, Brussels); Federico Bernardini (Centro Fermi, Museo Storico della Fisica e Centro di Studi e Ricerche "Enrico Fermi", Roma and 'Abdus Salam' International Centre for Theoretical Physics, Trieste); Josep Fortuny (Institut Català de Paleontologia Miquel Crusafont, Barcelona); Juan D. Daza (Sam Houston State University, Huntsville); Marta Calvo Revuelta (Museo Nacional de Ciencias Naturales, Madrid); Martin Kirchner and Johannes Müller (Museum für Naturkunde, Berlin); Ralf Kosma (Staatliche Naturhistorische Museum, Braunschweig); Roberto Sindaco (Museo Civico di Storia Naturale, Carmagnola). It would not have been possible to obtain such a large survey of the comparative osteology of these animals without the help of all these people.

Visits to the collections of the Muséum national d'Histoire naturelle (Paris) and the Naturhistorisches Museum Wien (Vienna) have been possible thanks to the support of two Synthesys grants: SYNTHESYS FR-TAF-5007 and AT-TAF-4591, respectively. Staff members of the two institutions are thanked for their hospitality and their help during my stay: Salvador Bailon, Corentin Bochaton, Virginie Bouetel, Annemarie Ohler and Laure Pierre (Paris); Heinz Grillitsch and Georg Gassner (Vienna). I am also indebted to Alexander Kupfer and Erin Maxwell for their helpfulness during my brief visit at the Staatliches Museum für Naturkunde in Stuttgart.

The numerous fossils studied in this thesis have been accessed thanks to: David M. Alba and Àngel H. Luján (Institut Català de Paleontologia Miquel Crusafont, Barcelona); Daniele Arobba and Andrea De Pascale (Museo Archeologico del Finale, Finale Ligure); Mauro Bon (Museo di Storia Naturale di Venezia); Lars W. van den Hoek Ostende (Naturalis Biodiversity Center, Leiden); Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie, Munich); Lorenzo Rook (University of Florence); Benedetto Sala (University of Ferrara); Marco Sami (Museo Civico di Scienze Naturali "Malmerendi", Faenza); Caterinella Tuveri (Soprintendenza Archeologia, Belle Arti e Paesaggio per le prov. di Sassari e Nuoro, Nuoro); Wilma Wessels and Hans de Bruijn (University of Utrecht). Fossils of lizards and amphisbaenians from Greece are studied together with Georgios L. Georgalis (University of Fribourg), as part of a larger project dealing with fossil amphibans and reptiles from the country. The help of Hugues-Alexandre Blain (Institut Català de Paleoecologia Humana i Evolució Social, Tarragona) was fundamental for the two palaeoclimatic analyses reported in chapter 5.

I acknowledge the European Association of Vertebrate Palaeontologists for supporting my first visit at the Bayerische Staatssammlung für Paläontologie und Geologie (Munich) with an EAVP Research Grant. Oliver Rauhut and all the other people I met there (Diego, Femke, Jeff, Lukardis, Mario, Melanie and Tom) are deeply thanked for all the help, discussions and time spent together.

I am deeply indebted to Marco Pavia for all the support and technical assistance with the Leica microscope, and to Simona Cavagna for the help with the Scanning Electron Microscope at the University of Torino. Claudio Sormani is thanked for the technical and computer assistance he friendly gave me since when we first met years ago: I'm still writing these words using one of his creations.

Nikos Poulakakis (University of Crete), Davit Vasilyan (JURASSICA Museum, Porrentruy) and Andrea Savorelli (University of Florence) provided relevant literature. I would also like to acknowledge the Google Books team for having digitalized some classic palaeontological books, difficult to be accessed otherwise. The original maps used for the figures in chapter 3 are freely available online at d-maps.com (http://www.d-maps.com/index.php?lang=it). Josep Fortuny prepared the original picture for Figure 2.20A.

This thesis was improved by the comments of Aaron M. Bauer and Davit Vasilyan, who kindly spent their time to review and evaluate it.

A huge "gràcies" for everything goes to all those people I met during my Erasmus Traineeship at the Institut Català de Paleontologia Miquel Crusafont: David M. Alba, Isaac Casanovas Vilar, Krystallia Chitoglou, Daniel DeMiguel, Joan Femenias-Gual, Josep Fortuny, Jordi Galindo, Sílvia Jovells Vaqué, Àngel H. Luján, Raef Minwer-Barakat, Salvador Moyà Solà, Guillem Orlandi Oliveras, Rosa Maria Pérez, Marta Pina and of course my old tentmate Alessandro Urciuoli. Thanks are also due to Leonardo, Giulia, Antonella and Eva: two months in Carrer de Provença with you have been definitely an experience, but please turn off the lights when you leave the room!

Also, I want to say thank you to all the team of the Anthropo-archaeological and geopalaeontological mission in the Dancalian Depression (Eritrea), for all the amazing weeks spent together in the desert. We won the Buya game, in the end...

I owe the same gratitude to all the people that I met during the last three years at the University of Torino, being them PhD students, undergraduate students, researchers or others staff members of the University. Definitely, these three years would have been significantly less enjoyable without all the time spent together.

In the end, this work would not have been possible without the important help and support of Massimo Delfino, Emanuel Tschopp and Arnau Bolet. I would like to say thanks to Arnau for the useful discussions we had in Barcelona and for his correction and suggestions to an earlier version of this thesis. The help of Emanuel has been really important for the development of this work, in particular for the phylogenetic analysis and the translations of papers written in German. Last but certainly not least, Massimo has been the first promoter of this project. Many thanks are really due to him for having believed in me and in my work since the beginning, and for having supported me with all his suggestions, corrections and expertise in the field of amphibians and reptiles palaeontology and comparative anatomy.

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Appendix 1

List of studied specimens included in the comparative analysis. Abbreviations: HUJ.OST -Osteological collection of the Hebrew University of Jerusalem, Israel; ICP - Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; IRSNB - Royal Belgian Institute of Natural Sciences, Brussels, Belgium; JDD - Juan D. Daza Herpetological Collection; MCCI - Museo Civico di storia naturale di Carmagnola, Italy; MCZ - Museum of Comparative Zoology, Harvard University, Cambridge (MA), U.S.A.; MDHC - Massimo Delfino Herpetological Collection, Departement of Earth Sciences, University of Torino, Italy; MNCN - Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN - Muséum national d'Histoire naturelle, Paris, France; MRAC - Royal Museum for Central Africa, Tervuren, Belgium; NHMW - Naturhistorisches Museum Wien, Austria; PIMUZ - Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SMNS - Staatliches Museum für Naturkunde Stuttgart; SRK - Ralf Kosma's personal collection; UAM.R - Universidad Autonoma de Madrid (Reptiles), Spain; ZMS - Zoologische Staatssammlung München, Germany.

Agamidae

Laudakia stellio (6 specimens): HUJ.OST-Z-5, 423, 424; MDHC 245; NHMW 570, 587.

Chamaeleonidae

Chamaeleo chamaeleon (9 specimens): HUJ.OST-Z-380, 425; MNHN 241, 1942-103, 2002-24, 1887-875; NHMW 611, 717, 721.

Sphaerodactylidae

Euleptes europaea (3 specimens): MDHC 384, 388, 389.

Gekkonidae

Hemidactylus turcicus (3 specimens): JDD 326–327; MDHC 26, 238. *Mediodactylus kotschyi* (4 specimens): MDHC 201, 285, 418, 419.

Phyllodactylidae

Tarentola mauritanica (7 specimens): MDHC 97, 98, 119, 194, 302; NHMW 2484, 31945.

Lacertidae

Acanthodactylus erythrurus (2 specimens): UAM.R.ACVII; EBD 1266 (specimen from the collection of Salvador Bailon).

- Algyroides fitzingeri (1 specimen): MDHC 351.
- Algyroides marchi (1 specimen): SRK 00.038.
- Algyroides moreoticus (1 specimen): MDHC 174.
- Algyroides nigropunctatus (3 specimens): MDHC 171, 242, 243.
- Archaeolacerta bedriagae (3 specimens): MDHC 167; SRK 00.120; unnumbered specimen
 - from the collection of Salvador Bailon.
- Dalmatolacerta oxycephala (4 specimens): NHMW 629, 651, 695-1, 695-2.
- Dinarolacerta mosorensis (2 specimens): NHMW 660, 684.
- Eremias arguta (1 specimen): MNHN 1944-168.
- Hellenolacerta graeca (4 specimens): MDHC 422, 423, 424; NHMW 693.
- Iberolacerta bonnali (1 specimen): UAM.R.Lm28A.
- Iberolacerta cyreni (1 specimen): UAM.R.Lm4.
- Iberolacerta horvathi (1 specimen): NHMW 687.
- Iberolacerta monticola (2 specimens): UAM.R.Lm77, Lm92.
- Lacerta agilis (10 specimens): MDHC 176, 177, 178, 230, 231; SMNS 06810, 10503, 10699, 10700, 11055.
- *Lacerta bilineata* (10 specimens): MDHC 15, 48, 73, 77, 84, 381, 420; SMNS 06829, 11242; UAM.R.Q21.
- Lacerta schreiberi (1 specimen): UAM.R.S-6.
- Lacerta trilineata (4 specimens): MDHC 240, 241, 295, 356.
- Lacerta viridis (3 specimens): MRAC 91-077-R-76; NHMW 662, 663.
- *Ophisops elegans* (3 specimens): MDHC 281, 282; unnumbered specimen from the collection of Salvador Bailon.
- Podarcis bocagei (1 specimen): UAM.R.PB48.
- Podarcis filfolensis (1 specimen): MDHC 385.
- *Podarcis hispanicus* (3 specimens): UAM.R.H30; two unnumbered specimens from the collection of Salvador Bailon.
- *Podarcis lilfordi* (2 specimens): two unnumbered specimens from the collection of Salvador Bailon.
- *Podarcis melisellensis* (10 specimens): MDHC 217, 218; NHMW 628, 650, 692, 683-1, 683-2, 683-3, 696-1, 696-2.
- Podarcis milensis (1 specimen): MDHC 425.

- *Podarcis muralis* (10 specimens): MDHC 6, 66, 72, 81, 222, 311, 312, 313, 395; MNHN 1992.192.
- *Podarcis pityusensis* (3 specimens): MNCN 16503;): two unnumbered specimens from the collection of Salvador Bailon.
- Podarcis siculus (4 specimens): MDHC 25, 91, 125, 229.
- Podarcis tauricus (2 specimens): MDHC 244, 426.
- Podarcis tiliguerta (2 specimens): MDHC 153, 154.
- Podarcis waglerianus (3 specimens): MDHC 390; MNHN 1992.189, 1992.190.
- Psammodromus algirus (2 specimens): MNHN 1992.41; UAM.R.Ps9.
- *Timon lepidus* (12 specimens): IRSNB Reg 3390; MDHC 216; MNHN 1988.6629, 1991.4010, 1991.4242; MRAC 91-077-R-75, 92-048-R-17, 92-050-R-1; NHMW 625, 681, 16413; unnumbered specimen stored in the ICP.
- Zootoca vivipara (8 specimens): MDHC 179; NHMW 631, 652, 653, 654; SMNS 06795, 10704; UAM.R.Lv24.

Scincidae

- Ablepharus kitaibelii (4 specimens): MDHC 239; MRAC A1-079-R-05; NHMW 751a, 751b.
- *Chalcides bedriagai* (1 specimen): unnumbered specimen from the collection of Salvador Bailon.
- Chalcides chalcides (4 specimens): MDHC 94, 329, 398, 408.
- *Chalcides ocellatus* (4 specimens): MDHC 193, 250; MNHN 1992.193; specimen number 28 from the collection of Salvador Bailon.
- *Chalcides striatus* (3 specimens): MDHC 404; MNCN 16508; unnumbered specimen from the collection of Salvador Bailon.

Ophiomorus punctatissimus (2 specimens): MCZ 38517; MDHC 427.

Trachylepis aurata (2 specimens): MDHC 280; MNHN 1887-863.

Anguidae

Anguis gr. A. fragilis (5 specimens): MDHC 49, 67, 102, 213, 221.

Pseudopus apodus (5 specimens): MDHC 214, 215; MNHN 1918.95, 1992.199; PIMUZ A/III0975.

Blanidae

Blanus cinereus (9 specimens): MDHC 156; ZSM 175-1993-1, 175-1993-2, 227-1975, 548-2003, 652-0-1, 652-0-2, 653-0-1, 653-0-2.

Blanus mariae (2 specimens): ZSM 27-1988-1, 27-1988-2.

Blanus strauchi (6 specimens): MCCI R-1635, 1668; MDHC 93, 286, 287, 288.

Appendix 2

List of the published works dealing with the osteology of extant European lizards and worm lizards consulted in this work.

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Appendix 3

Figure A3.1) Nasals - A-B: L. stellio (HUJ.OST-Z-424), right nasal in dorsal (A) and ventral (B) views. C: L. stellio (MDHC 245), left nasal in ventral view. D-E: C. chamaeleon (NHMW 611), right nasal in dorsal (D) and ventral (E) views. F-G: E. europaea (MDHC 389), left nasal in dorsal (F) and ventral (G) views. H-I: *H. turcicus* (MDHC 238), left nasal in dorsal (H) and ventral (I) views. J-K: M. kotschyi (MDHC 285), right nasal in dorsal (J) and ventral (K) views. L-M: T. mauritanica (MDHC 302), left nasal in dorsal (L) and ventral (M) views. N-O: A. erythrurus (UAM.R.ACVII), left nasal in dorsal (N) and ventral (O) views. P-Q: A. nigropunctatus (MDHC 242), articulated nasals in dorsal (P) and ventral (Q) views. R-S: L. bilineata (MDHC 381), left nasal in dorsal (R) and ventral (S) views. T-U: O. elegans (MDHC 281), right nasal in dorsal (T) and ventral (U) views. V-W: C. chalcides (MDHC 398), right nasal in dorsal (V) and ventral (W) views. Y: C. ocellatus (MDHC 250), left nasal in ventral view. Y-Z: T. aurata (MDHC 280), left nasal in dorsal (Y) and ventral (Z) views. AA-AB: Anguis gr. A. fragilis (MDHC 221), left nasal in dorsal (AA) and ventral (AB) views. AC-AD: P. apodus (MDHC 214), right nasal in dorsal (AC) and ventral (AD) views. Abbreviations: alp, anterolateral process; amp, anteromedial process; asf, articulation surface with the frontal; asm, articulation surface with the maxilla; asp, articulation surface with the premaxilla; le, lateral expansion; pp, posterior process; r, ridge; ve, ventral expansion. Scale bars = 1 mm.



Figure A3.1

Figure A3.2) Frontals - A-B: L. stellio (MDHC 245), frontal in dorsal (A) and ventral (B) views. C-D: L. stellio (HUJ.OST-Z-423), frontal in dorsal (C) and ventral (D) views (the medial process is broken). E-F: C. chamaeleon (NHMW 611), frontal in dorsal (E) and ventral (F) views. G-H: E. europaea (MDHC 389), frontal in dorsal (G) and ventral (H) views. I-J: H. turcicus (MDHC 238), frontal in dorsal (I) and ventral (J) views. K-L: M. kotschvi (MDHC 285), frontal in dorsal (K) and ventral (L) views. M-N: T. mauritanica (MDHC 97), frontal in dorsal (M) and ventral (N) views. O-P: A. erythrurus (UAM.R.ACVII), frontal in dorsal (O) and ventral (P) views. Q-R: L. viridis (MRAC 91-077-R-76), left frontal in dorsal (Q) and ventral (R) views. S-T: P. muralis (MDHC 311), right frontal in dorsal (S) and ventral (T) views. U-V: T. lepidus (MDHC 216), left frontal in dorsal (U) and ventral (V) views. W: T. lepidus (MNHN 1991.4242), articulated frontals in dorsal view. X-Y: Z. vivipara (UAM.R.Lv24), left frontal in dorsal (X) and ventral (Y) views. Z-AA: A. kitaibelii (MDHC 239), frontal in dorsal (Z) and ventral (AA) views. AB-AC: C. ocellatus (MDHC 250), right frontal in dorsal (AB) and ventral (AC) views. AD-AE: C. striatus (MDHC 404), left frontal in dorsal (AD) and ventral (AE) views. AF-AG: O. punctatissimus (MDHC 427), right frontal in dorsal (AF) and ventral (AG) views. Abbreviations: asm, articulation surface with the maxilla; asn, articulation surface with the nasal; aspt, articulation surface with the parietal tabs; cc, crista cranii; lblp, lateral branch of the lateral process; lp, lateral process; mblp, medial branch of the lateral process; mp, medial process; pf, parietal foramen; plp, posterolateral process; sffs, sulcus separating frontal and frontoparietal shields. Scale bars = 1 mm.





Figure A3.3) Frontals (continues) - A-B: *T. aurata* (MDHC 280), frontal in dorsal (A) and ventral (B) views. C-D: *Anguis* gr. *A. fragilis* (MDHC 102), left frontal in dorsal (C) and ventral (D) views. E-F: *P. apodus* (MDHC 214), left frontal in dorsal (E) and ventral (F) views. G: *L. stellio* (MDHC 245), frontal in right lateral view. H: *E. europaea* (MDHC 389), frontal in right lateral view. I: *H. turcicus* (MDHC 238), frontal in right lateral view. J: *M. kotschyi* (MDHC 285), frontal in right lateral view. K: *T. mauritanica* (MDHC 97), frontal in left lateral view. L: *L. viridis* (MRAC 91-077-R-76), left frontal in lateral view. M: *A. kitaibelii* (MDHC 239), frontal in right lateral view. N: *C. striatus* (MDHC 404), left frontal in lateral view. O: *C. ocellatus* (MDHC 250), right frontal in lateral view. P: *O. punctatissimus* (MDHC 427), right frontal in lateral view. Q: *Anguis* gr. *A. fragilis* (MDHC 102), left frontal in lateral view. R: *P. apodus* MDHC 214), left frontal in lateral view. Abbreviations: ap, anterior process; aslp, articulation surface with the lappet of the parietal; asmp, articulation surface with the maxilla and the prefrontal; asp, articulation surface with the postfrontal/postorbitofrontal; cc, crista cranii; fs, frontal shield; fps, frontoparietal shield; ifs, interfrontal shield; 1, lappet; r, ridge. Scale bars = 1 mm.

Figure A3.3



Figure A3.4) Parietals - A-B: L. stellio (MDHC 245), parietal in dorsal (A) and ventral (B) views. C-D: C. chamaeleon (NHMW 611), parietal in dorsal (C) and ventral (D) views. E-F: E. europaea (MDHC 384), left parietal in dorsal (E) and ventral (F) views. G-H: H. turcicus (JDD 326-327), right parietal in dorsal (G) and ventral (H) views. I-J: M. kotschvi (MDHC 285), right parietal in dorsal (I) and ventral (J) views (the anteromedial corner is broken). K-L: T. mauritanica (MDHC 97), right parietal in dorsal (K) and ventral (L) views. M-N: A. erythrurus (UAM.R.ACVII), parietal in dorsal (M) and ventral (N) views. O-P: L. schreiberi (UAM.R.S-6), parietal in dorsal (O) and ventral (P) views. Q-R: O. elegans (MDHC 281), parietal in dorsal (Q) and ventral (R) views. S-T: T. lepidus (MDHC 216), parietal in dorsal (S) and ventral (T) views. U-V: Z. vivipara (UAM.R.Lv24), parietal in dorsal (U) and ventral (V) views. W-X: A. kitaibelii (MDHC 239), parietal in dorsal (W) and ventral (X) views. Y-Z: C. chalcides (MDHC 398), parietal in dorsal (Y) and ventral (Z) views. AA-AB: C. ocellatus (MDHC 250), parietal in dorsal (AA) and ventral (AB) views. AC-AD: O. punctatissimus (MDHC 427), parietal in dorsal (AC) and ventral (AD) views. AE-AF: T. aurata (MDHC 280), parietal in dorsal (AE) and ventral (AF) views. AG-AH: Anguis gr. A. fragilis (MDHC 102), parietal in dorsal (AG) and ventral (AH) views. Abbreviations: al, area levis; alp, anterolateral process; as, anterior section of the anterolateral ventral crest; aspa, articulation surface with the processus ascendens of the supraoccipital; avc, anterolateral ventral crest; fps, frontoparietal shield; ips, interparietal shield: II, lateral lamina: Is, lateral shield: myc, medial ventral crest; os, occipital shield; pc, parietal crest; pfr, parietal foramen; pfs, parietal fossa; pn, parietal notch; pot, posterior tab; pp, posterior process; ppp, postparietal process; ps, posterior section of the posterolateral ventral crest; pt, parietal tab; pvc, posterolateral ventral crest; r, ridge; s, parietal shelf; sl, suture line; tp, triangular process. Scale bars = 1 mm.



Figure A3.4

Figure A3.5) Parietals (continues) - A-B: *P. apodus* (MDHC 214), parietal in dorsal (A) and ventral (B) views (postparietal processes are broken). C: *P. apodus* (PIMUZ A/III0975), parietal in dorsal view. D: *L. stellio* (MDHC 245) in right lateral view. E: *C. chamaeleon* (NHMW 611), parietal in right lateral view. F: *E. europaea* (MDHC 384), left parietal in lateral view. G: *H. turcicus* (JDD 326–327), right parietal in lateral view. H: *M. kotschyi* (MDHC 285), right parietal in lateral views. I: *T. mauritanica* (MDHC 97), right parietal in lateral view. J: *L. bilineata* (MDHC 381), parietal in left lateral view. K: *C. ocellatus* (MDHC 250), parietal in left lateral view. L: *O. punctatissimus* (MDHC 427), parietal in left lateral view. M: *T. aurata* (MDHC 280), parietal in left lateral view. N: *Anguis* gr. *A. fragilis* (MDHC 102), parietal in left lateral view. O: *P. apodus* (MDHC 214), parietal in right lateral view (postparietal processes are broken). Abbreviations: al, area levis; as, anterior section of the anterolateral ventral crest; aslf, articulation surface with the lappet of the frontal; ca, carina arcuata; ep, epipterygoid process; fps, frontoparietal shield; 1, lappet; 11, lateral lamina; mc, median crest; pc, parietal crest; pfs, parietal fossa; ps, posterior section of the posterolateral ventral crest. Scale bars = 1 mm.

Figure A3.5



Figure A3.6) Premaxillae - A-C: L. stellio (HUJ.OST-Z-424), premaxilla in anterior (A), left lateral (B) and posterior (C) views. D: C. chamaeleon (NHMW 721), articulated premaxilla in anterior view. E-I: E. europaea (MDHC 388), premaxilla in anterior (E), posterior (F), dorsal (G), ventral (H) and left lateral (I) views. J-N: H. turcicus (JDD 326-327), premaxilla in anterior (J), posterior (K), right lateral (L), dorsal (M) and ventral (N) views. O-S: M. kotschyi (MDHC 285), premaxilla in anterior (O), posterior (P), dorsal (Q), ventral (R) and right lateral (S) views. T-X: T. mauritanica (MDHC 194), premaxilla in anterior (T), posterior (U), dorsal (V), ventral (W) and left lateral (X) views. Y-AB: A. erythrurus (UAM.R.ACVII), premaxilla in anterior (Y), posterior (Z), left lateral (AA) and ventral (AB) views. AC-AF: I. monticola monticola (UAM.R.Lm77), premaxilla in anterior (AC), posterior (AD), right lateral (AE) and dorsal (AF) views. AG-AJ: L. bilineata (MDHC 15), premaxilla in anterior (AG), posterior (AH), left lateral (AI) and dorsal (AJ) views. AK-AN: P. waglerianus (MDHC 390), premaxilla in anterior (AK), posterior (AL), right lateral (AM) and dorsal (AN) views. AO: Z. vivipara (UAM.R.Lv24), premaxilla in posterior view. AP-AS: C. chalcides (MDHC 94), left premaxilla in anterior (AP), posterior (AQ), lateral (AR) and dorsal (AS) views. Abbreviations: am, alveolar margin; anp, ascending nasal process; ap, alveolar plate; flc, foramen of the longitudinal canal; ip, incisive process; pp, palatal process; sc, septonasal crest. Scale bars = 1 mm.





Figure A3.7) Premaxillae (continues) - A-D: *C. ocellatus* (MDHC 250), right premaxilla in anterior (A), posterior (B), dorsal (C) and lateral (D) views. E-H: *Anguis* gr. *A. fragilis* (MDHC 102), premaxilla in anterior (E), posterior (F), left lateral (G) and ventral (H) views. I-J: *P. apodus* (MDHC 215), premaxilla in anterior (I) and posterior (J) views (the right side of the alveolar plate is broken). Abbreviations: ip, incisive process; mp, maxillary process; n, notch; pp, palatal process; sc, septonasal crest; vp, vomerine process. Scale bars = 1 mm.



Figure A3.7

Figura A3.8) Maxillae - A-B: L. stellio (HUJ.OST-Z-423), left maxilla in lateral (A) and medial (B) views (the maxilla is broken and lacks part of the tooth row). C: L. stellio (HUJ.OST-Z-5), articulated right maxilla in lateral view. D-E: C. chamaeleon (NHMW 611), right maxilla in lateral (D) and medial (E) views. F-G: E. europaea (MDHC 389), right maxilla in lateral (F) and medial (G) views. H-I: H. turcicus (JDD 326-327), left maxilla in lateral (H) and medial (I) views. J: M. kotschvi (MDHC 285), left maxilla in lateral view. K: M. kotschvi (MDHC 201), left maxilla in medial view. L-M: T. mauritanica (MDHC 302), right maxilla in lateral (L) and medial (M) views. N-O: A. erythrurus (UAM.R.ACVII), left maxilla in lateral (N) and medial (O) views. P-O: L. bilineata (MDHC 15), right maxilla in lateral (P) and medial (Q) views. R: L. bilineata (MDHC 381), right maxilla in lateral view. S-T: P. melisellensis (NHMW 628), left maxilla in lateral (S) and medial (T) views. U-V: P. algirus (UAM.R.Ps9), left maxilla in lateral (U) and medial (V) views. W: T. lepidus (NHMW 625), right maxilla of a juvenile individual in medial view. X: T. lepidus (NHMW 681), detail of the hyperthrophied dentition (not to scale). Abbreviations: ab, alveolar border; adp, anterior dorsal process; alp, anterolateral process; amp, anteromedial process; ap, alveolar portion; app, anterior premaxillary process; ar, arched ridge; fp, facial process; l, lappet; pp, posterior process; ppj, posterodorsal projection; ps, palatal shelf; r, ridge; sp, spur; vlf, ventrolateral foramen. Scale bars = 1 mm.




Figure A3.9) Maxillae (continues) - A-B: Z. vivipara (UAM.R.Lv24), left maxilla in lateral (A) and medial (B) views, C-D: A. kitaibelii (MDHC 239), left maxilla in lateral (C) and medial (D) views. E-F: C. chalcides (MDHC 398), right maxilla in lateral (E) and medial (F) views. G-H: C. ocellatus (MDHC 250), right maxilla in lateral (G) and medial (H) views. I-J: O. punctatissimus (MDHC 427), left maxilla in lateral (I) and medial (J) views. K-L: T. aurata (MDHC 280), right maxilla in lateral (K) and medial (L) views. M-N: Anguis gr. A. fragilis (MDHC 102), right maxilla in lateral (M) and medial (N) views. O-P: P. apodus (MDHC 215), left maxilla in lateral (O) and medial (P) views (the anterior tip of the anteromedial process is broken and there is a pathologically-growth tooth). O: E. europaea (MDHC 389), right maxilla in dorsal view. R: H. turcicus (JDD 326-327), left maxilla in dorsal view. S: M. kotschvi (MDHC 201), left maxilla in dorsal view. T: T. mauritanica (MDHC 302), right maxilla in dorsal view. U: A. erythrurus (UAM.R.ACVII), left maxilla in dorsal view. V: L. bilineata (MDHC 381), right maxilla in dorsal view. W: C. chalcides (MDHC 398), right maxilla in medial view. X: C. ocellatus (MDHC 250), right maxilla in dorsal view. Y: O. punctatissimus (MDHC 427), left maxilla in dorsal view. Z: Anguis gr. A. fragilis (MDHC 102), left maxilla in dorsal view. Abbreviations: alp, anterolateral process; amp, anteromedial process; app, anterior premaxillary process; ar, arched ridge; l, lappet; ps, palatal shelf; sdf, superior dental foramen; vnf, vomeronasal foramen. Scale bars = 1 mm.





Figure A3.10) Prefrontals - A-B: L. stellio (HUJ.OST-Z-5), right prefrontal in dorsal (A) and dorsolateral (B) views. C: C. chamaeleon (MNHN 2002-24), right prefrontal in posterior view. D-E: C. chamaeleon (NHMW 611), left prefrontal in dorsal (D) and medial (E) views. F-H: E. europaea (MDHC 388), left prefrontal in posterior (F), lateral (G) and dorsal (H) views. I-K: H. turcicus (MDHC 238), right prefrontal in dorsal (I), posterior (J) and lateral (K) views. L-N: *M. kotschvi* (MDHC 285), right prefrontal in dorsal (L), posterior (M) and lateral (N) views, O-Q: T. mauritanica (MDHC 97), right prefrontal in dorsal (O), posterior (P) and lateral (Q) views. R-T: L. bilineata (MDHC 381), left prefrontal in dorsal (R), lateral (S) and posterior (T) views. U-W: O. elegans (MDHC 281), right prefrontal in dorsal (U), posterior (V) and lateral (W) views. X-Z: T. lepidus (MDHC 216), left prefrontal in dorsal (X), posterior (Y) and lateral (Z) views. AA-AC: A. kitaibelii (MDHC 239), right prefrontal in dorsal (AA), posterior (AB) and lateral (AC) views. AD-AF: T. aurata (MDHC 280), left prefrontal in dorsal (AD), posterior (AE) and lateral (AF) views. AG-AI: Anguis gr. A. fragilis (MDHC 102), left prefrontal in dorsal (AG), posterior (AH) and lateral (AI) views. AJ-AL: P. apodus (MDHC 214), left prefrontal in dorsal (AJ), posterior (AK) and lateral (AL) views. Abbreviations: adp, anterodorsal process; dp, dorsal process; n, notch of the lacrimal foramen; ofp, orbitonasal flange projection; onf, orbitonasal flange; pc, palpebral crest; pj, projection; pvp, posteroventral process; t, tubercle. Scale bars = 1 mm.



Figure A3.10

Figure A3.11) Jugals - A-B: L. stellio (HUJ.OST-Z-424), left jugal in lateral (A) and medial (B) views. C-D: C. chamaeleon (NHMW 611), left jugal in lateral (C) and medial (D) views. E-F: E. europaea (MDHC 388), left jugal in dorsal (E) and ventral (F) views. G-H: H. turcicus (MDHC 238), right jugal in dorsal (G) and ventral (H) views. I-J: M. kotschyi (MDHC 285), left jugal in dorsal (I) and ventral (J) views. K: T. mauritanica (NHMW 31945), right jugal in dorsal view. L-M: A. erythrurus (UAM.R.ACVII), left jugal in lateral (L) and medial (M) views (the dorsal margin of the anterior process is damaged). N-O: O. elegans (MDHC 281), left jugal in lateral (N) and medial (O) views. P-Q: P. algirus (UAM.R.Ps9), right jugal in lateral (P) and medial (Q) views. R-S: T. lepidus (MDHC 216), right jugal in lateral (R) and medial (S) views. T-U: A. kitaibelii (MDHC 239), right jugal in lateral (T) and medial (U) views. V-W: C. chalcides (MDHC 398), left jugal in lateral (V) and medial (W) views. X-Y: O. punctatissimus (MDHC 427), left jugal in lateral (X) and medial (Y) views. Z-AA: Anguis gr. A. fragilis (MDHC 102), right jugal in lateral (Z) and medial (AA) views. AB-AC: P. apodus (MDHC 215), left jugal in lateral (AB) and medial (AC) views. Abbreviations: ap, anterior process; asm, articulation surface with the maxilla; aspo, articulation surface with the postorbital; mp, medial process; pdp, posterodorsal process; pp, palatal process; gip, quadratojugal process. Scale bars = 1 mm.



Figure A3.11

Figure A3.12) Postfrontals, postorbitals and postorbitofrontals - A-B: L. stellio (MDHC 245), right postorbital in dorsal (A) and ventral (B) views. C-D: C. chamaeleon (NHMW 611), left postorbital in lateral (C) and medial (D) views. E: C. chamaeleon (MNHN 2002-24), left postorbital in dorsal view, F-G: E. europaea (MDHC 388), left postorbitofrontal in dorsal (F) and ventral (G) views. H-I: H. turcicus (MDHC 238), left postorbitofrontal in dorsal (H) and ventral (I) views. J-K: M. kotschvi (MDHC 285), right postorbitofrontal in dorsal (J) and ventral views (K). L-M: T. mauritanica (MDHC 97), left postorbitofrontal in dorsal (L) and ventral (M) views. N-O: L. agilis (MDHC 176), right prefrontal in dorsal (N) and ventral (O) views. P-Q: L. bilineata (MDHC 381), right prefrontal in dorsal (P) and ventral (Q) views. R-S: O. elegans (MDHC 281), right prefrontal in dorsal (R) and ventral (S) views. T: I. bonnali (UAM.R.Lm28A), left postorbital in ventral view. U-V: P. bocagei (UAM.R.PB48), right postorbital in dorsal (U) and ventral (V) views. W-X: P. algirus (UAM.R.Ps9), right postorbitofrontal in dorsal (W) and ventral (X) views. Y-Z: A. kitaibelii (MDHC 239), right prefrontal in dorsal (Y) and ventral (Z) views. AA-AB: C. chalcides (MDHC 398), left postfrontal in dorsal (AA) and ventral (AB) views. AC-AD: C. ocellatus (MDHC 250), left postfrontal in dorsal (AC) and ventral (AD) views. AE-AF: O. punctatissimus (MDHC 427), right postfrontal in dorsal (AE) and ventral (AF) views. AG-AH: T. aurata (MDHC 280), right prefrontal in dorsal (AG) and ventral (AH) views. AI-AJ: C. chalcides (MDHC 398), left postorbital in dorsal (AI) and ventral (AJ) views. AK-AL: C. ocellatus (MDHC 250), left prefrontal in dorsal (AK) and ventral (AL) views. AM-AN: Anguis gr. A. fragilis (MDHC 102), right prefrontal in dorsal (AM) and ventral (AN) views. AO-AP: P. apodus (MDHC 214), left prefrontal in dorsal (AO) and ventral (AP) views. AQ: P. apodus (MDHC 215), right prefrontal in dorsal view. Abbreviations: alp, anterolateral process; amp, anteromedial process; ap, anterior process; apo, articulation surface with the postorbital; asf, articulation surface with the frontal; asj, articulation surface with the jugal; asp, articulation surface with the parietal; asq, articulation surface with the squamosal; ex, osseous expansion; lp, lateral process; pp, posterior process; vp, ventral process. Scale bars = 1 mm.



Figure A3.12

Figure A3.13) Squamosals - A-B: *L. stellio* (MDHC 245), left squamosal in lateral (A) and medial (B) views. C-D: *C. chamaeleon* (NHMW 611), right squamosal in lateral (C) and medial (D) views. E-F: *T. mauritanica* (MDHC 97), right squamosal in lateral (E) and medial (F) views. G-H: *P. muralis* (MDHC 312), left squamosal in lateral (G) and medial (H) views. I-J: *L. viridis* (MRAC 91-077-R-76), right squamosal in lateral (I) and medial (J) views. K-L: *C. chalcides* (MDHC 398), right squamosal in lateral (K) and medial (L) views. M-N: *Anguis* gr. *A. fragilis* (MDHC 102), left squamosal in lateral (M) and medial (N) views. O-P: *P. apodus* (MDHC 215), left squamosal in lateral (O) and medial (P) views. Abbreviations: ap, anterior process; asjp, articulation surface with jugal and postorbital; dpp, dorsal parietal process; pp, posterior process; qp, quadrate process; r, ridge. Scale bars = 1 mm.



Figure A3.14) Quadrates - A-B: L. stellio (MDHC 245), right quadrate in anterior (A) and posterior (B) views. C-D: C. chamaeleon (NHMW 611), left quadrate in anterior (C) and posterior (D) views. E-F: E. europaea (MDHC 388), right quadrate in anterior (E) and posterior (F) views. G-H: H. turcicus (JDD 326-327), right quadrate in anterior (G) and posterior (H) views. I-J: M. kotschyi (MDHC 285), right quadrate in anterior (I) and posterior (J) views. K-L: T. mauritanica (MDHC 97), left quadrate in anterior (K) and posterior (L) views. M-O: A. erythrurus (UAM.R.ACVII), right quadrate in anterior (M), posterior (N) and medial (O) views. P-R: P. bocagei (UAM.R.PB48), right quadrate in anterior (P), posterior (Q) and medial (R) views. S-U: T. lepidus (MDHC 216), right quadrate in anterior (S), posterior (T) and medial (U) views. V-X: C. chalcides (MDHC 398), right quadrate in anterior (V), posterior (W) and medial (X) views. Y-AA: C. ocellatus (MDHC 250), right quadrate in anterior (Y), posterior (Z) and medial (AA) views. AB-AD: O. punctatissimus (MDHC 427), left quadrate in anterior (AB), posterior (AC) and medial (AD) views. AE-AG: T. aurata (MDHC 280), right quadrate in anterior (AE), posterior (AF) and medial (AG) views. AH-AJ: Anguis gr. A. fragilis (MDHC 102), right quadrate in anterior (AH), posterior (AI) and medial (AJ) views. AK-AM: P. apodus (MDHC 214), left quadrate in anterior (AK), posterior (AL) and medial (AL) views. Abbreviations: ap, anterior platform; asq, articulation surface with the squamosal; c, conch; cc, cephalic condyle; lh, lateral head; ll, lateral lamina; mc, mandibular condyle; mh, medial head; ml, medial lamina; p, pillar; pf, pterygoid flange; qf, quadrate foramen; tc, tympanic crest. Scale bars = 1 mm.



Figure A3.15) Epipterygoids - A: *L. stellio* (NHMW 570; not to scale). B: *T. mauritanica* (MDHC 97). C: *L. bilineata* (MDHC 381). D: *C. chalcides* (MDHC 94). E: *O. punctatissimus* (MDHC 427; reversed for comparison). F: *Anguis* gr. *A. fragilis* (MDHC 102). Abbreviations: e, epipterygoid; p, prootic. Scale bars = 1 mm.



Figure A3.16) Vomers - A: L. stellio (HUJ.OST-Z-5), articulated vomers in ventral view. B: L. stellio (HUJ.OST-Z-424), right vomer in dorsal view. C-D: C. chamaeleon (NHMW 611), vomer in dorsal (C) and ventral (D) views, E: C. chamaeleon (NHMW 721), articulated vomers in ventral view. F-G: E. europaea (MDHC 384), right vomer in ventral (F) and dorsal (G) views. H-I: *H. turcicus* (JDD 326–327), right vomer in ventral (H) and dorsal (I) views. J-K: M. kotschvi (MDHC 285), left vomer in ventral (J) and dorsal (K) views. L-M: T. mauritanica (MDHC 302), right vomer in ventral (L) and dorsal (M) views. N-O: A. erythrurus (UAM.R.ACVII), right vomer in dorsal (N) and ventral (O) views. P-Q: L. bilineata (MDHC 381), right vomer in dorsal (P) and ventral (Q) views. R-S: A. kitaibelii (MDHC 239), fused vomers in dorsal (R) and ventral (S) views. T-U: C. ocellatus (MDHC 250), fused vomers in dorsal (T) and ventral (U) views. V-W: O. punctatissimus (MDHC 427), left vomer in dorsal (V) and ventral (W) views. X-Y: T. aurata (MDHC 280), left vomer in dorsal (X) and ventral (Y) views. Z-AA: Anguis gr. A. fragilis (MDHC 102), left vomer in dorsal (Z) and ventral (AA) views. AB: P. apodus (MDHC 215), left vomer in dorsal view (the specimen is broken roughly at midlength). Abbreviations: asp, articulation surface with the premaxilla; asy, articulation surface with the vomerine process of the palatine; lg, lacrimal groove; nr, nasal region; nvf, notch of the vomeronasal fenestra; pp, posterior process; vr, vomeronasal region. Scale bars = 1 mm.



Figure A3.17) Septomaxillae - A-D: E. europaea (MDHC 384), left septomaxilla in dorsal (A), ventral (B), lateral (C) and medial (D) views. E-H: *H. turcicus* (JDD 326–327), right septomaxilla in dorsal (E), ventral (F), lateral (G) and medial (H) views. I-K: M. kotschvi (MDHC 285), right septomaxilla in dorsal (I), ventral (J) and lateral (K) views. L: M. kotschvi (MDHC 285), left septomaxilla in medial view. M-P: T. mauritanica (MDHC 302), left septomaxilla in dorsal (M), ventral (N), lateral (O) and medial (P) views. R-S: I. bonnali (UAM.R.Lm28A), right septomaxilla in dorsal (R) and ventral (S) views. T-U: L. bilineata (MDHC 381), left septomaxilla in dorsal (T) and ventral (U) views. V-W: O. elegans (MDHC 281), right septomaxilla in dorsal (V) and ventral (W) views. X-Y: A. kitaibelii (MDHC 239), left septomaxilla in dorsal (X) and ventral (Y) views. Z-AA: C. ocellatus (MDHC 250), right septomaxilla in dorsal (Z) and ventral (AA) views. AB-AC: Anguis gr. A. fragilis (MDHC 102), left septomaxilla in dorsal (AB) and ventral (AC) views. AD-AE: P. apodus (MDHC 215), left septomaxilla in dorsal (AD) and ventral (AE) views. Abbreviations: aex, anteroventral expansion; alp, anterolateral process; ar, arched ridge; fr, forked ridge; g, groove; lp, lateral process; lr, lateral ridge; mp, medial process; mr, medial ridge; pex, posteroventral expansion; plp, posterolateral process; pmp, posteromedial process; tp, triangular process. Scale bars = 1 mm.



Figure A3.17

Figure A3.18) Palatines - A-B: L. stellio (HUJ.OST-Z-424), right palatine in dorsal (A) and ventral (B) views. C-D: C. chamaeleon (NHMW 611), left palatine in dorsal (C) and ventral (D) views, E-F: *E. europaea* (MDHC 384), right palatine in dorsal (E) and ventral (F) views. G-H: H. turcicus (JDD 326-327), left palatine in dorsal (G) and ventral (H) views. I-J: M. kotschvi (MDHC 285), left palatine in dorsal (I) and ventral (J) views. K-L: T. mauritanica (MDHC 97), right palatine in dorsal (K) and ventral (L) views, M-N: A. ervthrurus (UAM.R.ACVII), right palatine in dorsal (M) and ventral (N) views. O-P: I. monticola cantabrica (UAM.R.Lm92), left palatine in dorsal (O) and ventral (P) views. Q-R: A. kitaibelii (MDHC 239), left palatine in dorsal (Q) and ventral (R) views. S-T: C. chalcides (MDHC 398), left palatine in dorsal (S) and ventral (T) views. U-V: O. punctatissimus (MDHC 427), right palatine in dorsal (U) and ventral (V) views. W-X: T. aurata (MDHC 280), right palatine in dorsal (W) and ventral (X) views. Y-Z: Anguis gr. A. fragilis (MDHC 102), left palatine in dorsal (Y) and ventral (Z) views. AA-AB: P. apodus MDHC 215), left palatine in dorsal (AA) and ventral (AB) views (the anterior end is broken). Abbreviations: ap, anterior projection of the vomerine process; asm, articulation surface with the maxilla; asp, articulation surface with the pterygoid; cc, choanal duct; if, infraorbital foramen; l, lappet; mp, maxillary process; pp, pterygoid process; pr, palatine ridge; sd, sulcus dorsalis; vp, vomerine process. Scale bars = 1 mm.



Figure A3.18

Figure A3.19) Pterygoids - A-B: L. stellio (HUJ.OST-Z-423), right pterygoid in dorsal (A) and ventral (B) views. C-D: E. europaea (MDHC 384), left pterygoid in dorsal (C) and ventral (D) views. E-F: H. turcicus (JDD 326-327), left pterygoid in dorsal (E) and ventral (F) views. G-H: M. kotschvi (MDHC 285), right pterygoid in dorsal (G) and ventral (H) views. I-J: T. mauritanica (MDHC 97), right pterygoid in dorsal (I) and ventral (J) views. K-L: A. fitzingeri (MDHC 351), left pterygoid in dorsal (K) and ventral (L) views. M-N: T. lepidus (MDHC 216), left pterygoid in dorsal (M) and ventral (N) views. O-P: A. kitaibelii (MDHC 239), left pterygoid in dorsal (O) and ventral (P) views. Q-R: C. chalcides (MDHC 94), left pterygoid in dorsal (Q) and ventral (R) views (the tip of the pterygoid flange is broken). S-T: C. ocellatus (MDHC 250), right pterygoid in dorsal (S) and ventral (T) views. U-V: O. punctatissimus (MDHC 427), right ptervgoid in dorsal (U) and ventral (V) views. W-X: T. aurata (MDHC 280), left pterygoid in dorsal (W) and ventral (X) views. Y-Z: Anguis gr. A. fragilis (MDHC 102), right pterygoid in dorsal (Y) and ventral (Z) views. AA-AB: P. apodus (MDHC 215), left pterygoid in dorsal (AA) and ventral (AB) views (the anterior end of the palatine process is broken). AC-AD: L. stellio (HUJ.OST-Z-423), right pterygoid in lateral (AC) and medial (AD) views. AE-AF: C. chamaeleon (NHMW 611), right pterygoid in lateral (AE) and medial AF) views. Abbreviations: bf, basipterygoid fossa; bp, basisphenoid process; fc, fossa columellae; isp, insertion surface of the pterygoideus muscle; pf, pterygoid flange; pp, palatine process; pre, pterygoid recess; pri, pterygoid ridge; qp, quadrate process; rpm, ridge for the insertion of the pterigomandibular muscle; rsp, ridge for the insertion of the superficial pseudotemporal muscle; vf, ventral flange. Scale bars = 1mm.





Figure A3.20) Pterygoids (continues) - A-B: *A. fitzingeri* (MDHC 351), left pterygoid in lateral (A) and medial (B) views. C-D: *T. lepidus* (MDHC 216), left pterygoid in lateral (C) and medial (D) views. E-F: *A. kitaibelii* (MDHC 239), left pterygoid in lateral (E) and medial (F) views. G-H: *C. chalcides* (MDHC 94), left pterygoid in lateral (G) and medial (H) views (the tip of the pterygoid flange is broken). I-J: *C. ocellatus* (MDHC 250), right pterygoid in lateral (I) and medial (J) views. K-L: *O. punctatissimus* (MDHC 427), right pterygoid in lateral (K) and medial (L) views. M-N: *T. aurata* (MDHC 280), left pterygoid in lateral (M) and medial (N) views. O-P: *Anguis* gr. *A. fragilis* (MDHC 102), right pterygoid in lateral (O) and medial (P) views. Q-R: *P. apodus* (MDHC 215), left pterygoid in lateral (Q) and medial (R) views (the anterior end of the palatine process is broken). Abbreviations: bf, basipterygoid fossa; isp, insertion surface of the pterygoideus muscle; pri, pterygoid ridge. Scale bars = 1 mm.



Figure A3.21) Ectopterygoids - A-E: L. stellio (MDHC 245), left ectopterygoid in anterior (A), dorsal (B), ventral (C), medial (D) and lateral (E) views. F-J: C. chamaeleon (MNHN 2002-24), right ectopterygoid in anterior (F), dorsal (G), ventral (H), medial (I) and lateral (J) views. K-L: *E. europaea* (MDHC 388), right ectopterygoid in ventral (K) and dorsal (L) views. M-N: H. turcicus (JDD 326-327), left ectopterygoid in dorsal (M) and ventral (N) views. O-P: M. kotschvi (MDHC 285), right ectopterygoid in ventral (O) and dorsal (P) views. Q-R: T. mauritanica (MDHC 97), right ectopterygoid in ventral (Q) and dorsal (R) views. S-T: A. erythrurus (UAM.R.ACVII), right ectopterygoid in ventral (S) and dorsal (T) views. U-V: L. agilis (MDHC 176), left ectopterygoid in ventral (U) and dorsal (V) views. W-X: Z. vivipara (UAM.R.Lv24), right ectopterygoid in ventral (W) and dorsal (X) views. Y-Z: A. kitaibelii (MDHC 239), right ectopterygoid in ventral (Y) and dorsal (Z) views. AA-AB: C. ocellatus (MDHC 250), right ectopterygoid in ventral (AA) and dorsal (AB) views. AC-AD: O. punctatissimus (MDHC 427), right ectopterygoid in ventral (AC) and dorsal (AD) views. AE-AF: T. aurata (MDHC 280), right ectopterygoid in ventral (AE) and dorsal (AF) views. AG-AH: Anguis gr. A. fragilis (MDHC 102), right ectopterygoid in ventral (AG) and dorsal (AH) views. AI-AJ: P. apodus (MDHC 215), left ectopterygoid in ventral (AI) and dorsal (AJ) views. Abbreviations: al, anteromedial lappet of the posteromedial process; alp, anterolateral process; asm, articulation surface with the maxilla; asp, articulation surface with the pterygoid flange; dl, dorsal lappet of the posteromedial process; plp, posterolateral process; pmp, posteromedial process; vl, ventral lappet of the posteromedial process; vp, ventral process. Scale bars = 1 mm.



Figure A3.21

Figure A3.22) Otooccipital regions - A-E: *E. europaea* (MDHC 384), otooccipital region in anterior (A), left lateral (B), posterior (C), dorsal (D) and ventral (E) views. F-J: *H. turcicus* (MDHC 26), otooccipital region in anterior (F), left lateral (G), posterior (H), dorsal (I) and ventral (J) views. Abbreviations: asc, anterior semicircular canal; b, basioccipital; bp, basipterygoid process; cc, cochlear cavity; fma, foramen magnum; fo, fenestra ovalis; hsc, horizontal semicircular canal; o, otooccipital; oc, occipital condyle; p, prootic; pap, paroccipital process; pf, perilymphatic foramen; psc, posterior semicircular canal; sp, sphenoid; su, supraoccipital; svp, supravenous process; tc, trabecula cranii. Scale bars = 1 mm.



Figure A3.23) Otooccipital regions (continues) - A-E: *M. kotschyi* (MDHC 285), otooccipital region in anterior (A), left lateral (B), posterior (C), dorsal (D) and ventral (E) views. F-J: *T. mauritanica* (MDHC 97), otooccipital region in anterior (F), left lateral (G), posterior (H), dorsal (I) and ventral (J) views. Abbreviations: aovc, anterior opening of the vidian canal; ap, alar process; ca, crista alaris; ci, crista interfenestralis; cp, crista prootica; ctr, crista trabecularis; ctu, crista tuberalis; ff, facial foramen; glhv, groove of the lateral head vein; hf, hypophysial fossa; ip, incisura prootica; l, lamina; lrst, lateral opening of the recessus scalae tympani; povc, posterior opening of the vidian canal; pp, posterior process of the prootic; rst, recessus scalae tympani; rvj, recessus vena jugularis; st, sphenooccipital tubercle; vf, vagus foramen. Scale bars = 1 mm.



Figure A3.24) Otooccipital regions (continues) - A-E: *A. erythrurus* (UAM.R.ACVII), otooccipital region in anterior (A), right lateral (B), posterior (C), dorsal (D) and ventral (E) views. F-J: *L. bilineata* (MDHC 15), otooccipital region in anterior (F), right lateral (G), posterior (H), dorsal (I) and ventral (J) views. The parasphenoid rostrum is broken in both specimens. Abbreviations: glhv, groove of the lateral head vein. Scale bars = 1 mm.



Figure A3.25) Otooccipital regions (continues) - A-E: *P. bocagei* (UAM.R.PB48), otooccipital region in anterior (A), left lateral (B), posterior (C), dorsal (D) and ventral (E) views. F-J: *A. kitaibelii* (MDHC 239), otooccipital region in anterior (F), right lateral (G), posterior (H), dorsal (I) and ventral (J) views. Scale bars = 1 mm.





Figure A3.26) Otooccipital regions (continues) - A-E: C. chalcides (MDHC 398), otooccipital region in anterior (A), right lateral (B), posterior (C), dorsal (D) and ventral (E) views. F-J: C. ocellatus (MDHC 250), otooccipital region in anterior (F), right lateral (G), posterior (H), dorsal (I) and ventral (J) views. Abbreviations: sc, supraoccipital crest. Scale bars = 1 mm.



Figure A3.27) Otooccipital regions (continues) - A-E: *O. punctatissimus* (MDHC 427), otooccipital region in anterior (A), left lateral (B), posterior (C), dorsal (D) and ventral (E) views. Scale bars = 1 mm.





Figure A3.28) Otooccipital regions (continues) - A-E: *Anguis* gr. *A. fragilis* (MDHC 102), otooccipital region in anterior (A), left lateral (B), posterior (C), dorsal (D) and ventral (E) views (the parasphenoid rostrum is broken). F-J: *P. apodus* (MDHC 215), otooccipital region in anterior (F), right lateral (G), posterior (H), dorsal (I) and ventral (J) views (the anterior end of the sphenoid and the basipterygoid processes are broken). Scale bars = 1 mm.



Figure A3.29) Basioccipitals - A-B: *L. stellio* (MDHC 245), basioccipital in dorsal (A) and ventral (B) views. C-D: *C. chamaeleon* (HUJ.OST-Z-380), basioccipital in dorsal (C) and ventral (D) views. E: *T. mauritanica* (MDHC 302), basioccipital in dorsal view. F: *P. muralis* (MDHC 312), basioccipital in dorsal view. G: *T. aurata* (MDHC 280), basioccipital in dorsal view. H: *Anguis* gr. *A. fragilis* (MDHC 49), basioccipital in dorsal view. Abbreviations: cc, cranial depression; lw, lateral wing; oc, occipital condyle; rst, recessus scalae tympani; st, sphenooccipital tubercle. Scale bars = 1 mm.



Figure A3.29

Figure A3.30) Sphenoids - A-D: *L. stellio* (MDHC 245), sphenoid in dorsal (A), anterior (B), left lateral (C) and ventral (D) views. E-H: *C. chamaeleon* (MNHN 2002-24), sphenoid in dorsal (E), anterior (F), right lateral (G) and ventral (H) views. I-J: *T. mauritanica* (MDHC 302), sphenoid in dorsal (I) view. J-L: *A. nigropunctatus* (MDHC 242), articulated sphenoid in dorsal (J), ventral (K) and anterior (L) views. M-N: *L. agilis* (MDHC 231), sphenoid in dorsal (M) and anterior (N) views (the parasphenoid rostrum is broken). O-P: *A. kitaibelii* (MDHC 239), articulated sphenoid in dorsal (O) and anterior (P) views. Q-R: *C. ocellatus* (MDHC 193), articulated sphenoid in dorsal (Q) and anterior (R) views. S-T: *Anguis* gr. *A. fragilis* (MDHC 49), sphenoid in dorsal (S) and anterior (T) views (the parasphenoid rostrum is broken). Abbreviations: af, abducens foramen; aov, anterior opening of the vidian canal; ap, alar process; bp, basipterygoid process; cs, crista sellaris; ct, crista trabeculares; cvl, crista ventrolaterales; ds, dorsum sellae; icf, internal carotid foramen; pov, posterolateral opening of the vidian canal; pr, parasphenoid rostrum; rvj, recessus vena jugularis; st, sella turcica; svp, supravenous process; tc, trabecula cranii. Scale bars = 1 mm.



Figure A3.30

Figure A3.31) Supraoccipitals - A: *L. stellio* (MDHC 245), supraoccipital (broken) in dorsal view. B: *C. chamaeleon* (MNHN 2002-24), supraoccipital in left lateral view. C: *C. chamaeleon* (NHMW 611), supraoccipital in dorsal view. D: *T. mauritanica* (MDHC 302), supraoccipital in ventrolateral view. E: *P. muralis* (MDHC 312), supraoccipital in dorsal view. F: *T. aurata* (MDHC 280), supraoccipital in dorsal view. Abbreviations: asc, anterior semicircular canal; cac, cavum capsularis; cc, common crus; ef, endolymphatic foramen; lc, lateral crest; mc, median crest; mp, marginal process; pa, processus ascendens; psc, posterior semicircular canal. Scale bars = 1 mm.



Figure A3.32) Prootics - A-C: *L. stellio* (MDHC 245), right prootic in lateral (A), medial (B) and posterior (C) views. D-E: *C. chamaeleon* (NHMW 611), left prootic in lateral (D) and medial (E) views. F-G: *T. mauritanica* (MDHC 302), left prootic in medial (F) and posterior (G) views. H-I: *P. muralis* (MDHC 312), left prootic in medial (H) and posterior (I) views. J-K: *H. graeca* (MDHC 423), right prootic in medial (J) and posterior (K) views. L-M: *C. striatus* (MDHC 404), right prootic in medial (L) and posterior (M) views. N-O: *Anguis* gr. *A. fragilis* (MDHC 49), left prootic in medial (N) and posterior (O) views. Abbreviations: aaf, anterior acoustic foramen; aip, anterior inferior process; amr, ampullary recess; ap, alar process; ar, acoustic recess; asc, anterior semicircular canal; ca, crista alaris; cac, cavum capsularis; ccr, cochlear crest; coc, cochlear cavity; cp, crista prootica; ff, facial foramen; gpd, groove for the perilymphatic duct; hsc, horizontal semicircular canal; ip, incisura prootica; paf, posterior acoustic foramen; pp, posterior process; ppp, projection of the posterior process; sf, notch of the sphenoccipital foramen; stp, superior trabecular process. Scale bars = 1 mm.



Figure A3.33) Otooccipitals and stapes - A-D: L. stellio (MDHC 245), left otooccipital in anterior (A), medial (B), lateral (C) and posterior (D) views. E-G: C. chamaeleon (HUJ.OST-Z-425), right otooccipital in anterior (E), lateral (F) and posterior (G) vies (the distal portion of the paroccipital process is broken). H: C. chamaeleon (MNHN 2002-24), right otooccipital articulated with the basioccipital in posterior view. I-J: T. mauritanica (MDHC 302), right otooccipital in anterior (I) and medial (J) views. K-L: P. muralis (MDHC 312), right otooccipital in anterior (K) and medial (L) views. M-N: T. aurata (MDHC 280), right otooccipital in anterior (M) and medial (N) views. O-P: Anguis gr. A. fragilis (MDHC 49), left otooccipital in anterior (O) and medial (P) views. Q: C. chamaeleon (NHMW 611), stapes. R: T. mauritanica (MDHC 97), stapes. S: A. nigropunctatus (MDHC 242), stapes. T: C. chalcides (MDHC 398), stapes. U: Anguis gr. A. fragilis (MDHC 102), stapes. Abbreviations: amr, ampullary recess; cac, cavum capsularis; coc, cochlear cavity;f, footplate; hf, hypoglossal foramen; hsc, horizontal semicircular canal; lrst, lateral opening of the recessus scalae tympani; oc, occipital condyle; pop, paroccipital process; psc, posterior semicircular canal; s, shaft; sf, stapefial foramen; ur, utricular recess; vf, vagus foramen. Scale bars = 1 mm.

Figure A3.33



Figure A3.34) Dentaries - A-B: L. stellio (MDHC 245), right dentary in medial (A) and lateral (B) views. C-D: C. chamaeleon (NHMW 611), left dentary in medial (C) and lateral (D) views, E-F: *E. europaea* (MDHC 384), right dentary in medial (E) and lateral (C) views. G-H: H. turcicus (JDD 326–327), left dentary in medial (G) and lateral (H) views. I-J: M. kotschvi (MDHC 285), right dentary in medial (I) and lateral (J) views. K-L: T. mauritanica (MDHC 302), left dentary in medial (K) and lateral (L) views, M-N: L. bilineata (MDHC 84), left dentary in medial (M) and lateral (N) views. O-P: Z. vivipara (MDHC 179), right dentary in medial (O) and lateral (P) views. Q-R: A. kitaibelii (MDHC 239), left dentary in medial (Q) and lateral (R) views. S-T: C. ocellatus (MDHC 250), right dentary in medial (S) and lateral (T) views. U-V: O. punctatissimus (MDHC 427), left dentary in medial (U) and lateral (V) views. W-X: T. aurata (MDHC 280), right dentary in medial (W) and lateral (X) views. Y-Z: Anguis gr. A. fragilis (MDHC 102), right dentary in medial (Y) and lateral (Z) views. AA-AB: P. apodus (MDHC 214), right dentary in medial (AA) and lateral (AB) views. Abbreviations: ac, alveolar canal; as, alveolar shelf; asf, opening of the anterior surangular foramen; cp, central posterior process; ig, interdental groove; ip, inferior posterior process; is, intramandibular septum; mfr, mental foramen; mfs, Meckelian fossa; ms, mandibular symphysis; pr, posterior recess; sp, superior posterior process; sr, subdental ridge; ssh, subdental shelf; ssp, splenial spine. Scale bars = 1 mm.



Figure A3.34

Figure A3.35) Splenials - A-B: *E. europaea* (MDHC 384), left splenial in lateral (A) and medial (B) views. C-D: *H. turcicus* (MDHC 238), left splenial in lateral (C) and medial (D) views. E-F: *M. kotschyi* (MDHC 285), right splenial in lateral (E) and medial (F) views. G-H: *T. mauritanica* (MDHC 302), right splenial in lateral (G) and medial (H) views. I-J: *A. erythrurus* (UAM.R.ACVII), left splenial in lateral (I) and medial (J) views. K-L: *P. tauricus* (MDHC 153), left splenial in lateral (K) and medial (L) views. M-N: *T. lepidus* (MDHC 216), left splenial in lateral (M) and medial (N) views. O: *A. kitaibelii* (NHMW 751b), right splenial in medial view. Q-R: *C. chalcides* (MDHC 398), right splenial in lateral (Q) and medial (R) views. S-T: *O. punctatissimus* (MDHC 427), left splenial in lateral (S) and medial (T) views. U-V: *T. aurata* (MDHC 280), right splenial in lateral (U) and medial (V) views. Y-Z: *P. apodus* (MDHC 215), left splenial in lateral (Y) and medial (Z) views. Abbreviations: aif, anterior inferior foramer; amf, anterior mylohyoid foramer; dc, dorsal crest; mc, medial crest; s, splenial. Scale bars = 1 mm.



Figure A3.36) Coronoids - A-B: *L. stellio* (MDHC 245), right coronoid in lateral (A) and medial (B) views. C-D: *C. chamaeleon* (NHMW 611), right coronoid in lateral (C) and medial (D) views. E-F: *E. europaea* (MDHC 388), left coronoid in lateral (E) and medial (F) views. G-H: *H. turcicus* (MDHC 238), left coronoid in lateral (G) and medial (H) views. I-J: *M. kotschyi* (MDHC 285), right coronoid in lateral (I) and medial (J) views. K-L: *T. mauritanica* (MDHC 302), right coronoid in lateral (K) and medial (L) views. M-N: *A. erythrurus* (UAM.R.ACVII), right coronoid in lateral (M) and medial (N) views. O-P: *P. muralis* (MDHC 311), right coronoid in lateral (O) and medial (P) views. Q-R: *C. chalcides* (MDHC 398), right coronoid in lateral (Q) and medial (R) views. S-T: *C. ocellatus* (MDHC 250), right coronoid in lateral (V) views. U-V: *O. punctatissimus* (MDHC 427), left coronoid in lateral (U) and medial (V) views. W-X: *Anguis* gr. *A. fragilis* (MDHC 102), right coronoid in lateral (W) and medial (X) views. Y-Z: *P. apodus* (MDHC 214), right coronoid in lateral (Y) and medial (Z) views. Abbreviations: amp, anteromedial process; apj, anterior projection of the anteromedial process; pp, posterior process. Scale bars = 1 mm.



Figure A3.37) Angulars - A-B: *L. stellio* (HUJ.OST-Z-423), left angular in dorsal (A) and medial (B) views. C-D: *C. chamaeleon* (HUJ.OST-Z-425), right angular in dorsal (C) and medial (B) views. E: *P. algirus* (UAM.R.Ps9), left angular in lateral view. F-H: *T. lepidus* (MDHC 216), left angular in lateral (F), medial (G) and dorsal (H) views. I-J: *C. ocellatus* (MDHC 250), left angular in lateral (I) and medial (J) views. K-L: *Anguis* gr. *A. fragilis* (MDHC 102), right angular in lateral (K) and medial (L) views. M-N: *P. apodus* (MDHC 214), right angular in lateral (M) and medial (N) views. Abbreviations: ar, angular ridge; asd, articulation surface for the dentary; paf, posterior alveolar foramen. Scale bars = 1 mm.


Figure A3.38) Compound bones - A-B: L. stellio (MDHC 245), right surangular in medial (A) and lateral (B) views. C-D: L. stellio (HUJ.OST-Z-424), fused left prearticular and articular in medial (C) and lateral (D) views. E-F: C. chamaeleon (NHMW 611), right compound bone in medial (E) and lateral (F) views. G-H: E. europaea (MDHC 388), left compound bone in medial (G) and lateral (H) views. I-J: H. turcicus (JDD 326-327), left compound bone in medial (I) and lateral (J) views. K-L: M. kotschvi (MDHC 285), left compound bone in medial (K) and lateral (L) views. M-N: T. mauritanica (MDHC 302), right compound bone in medial (M) and lateral (N) views. O: A. erythrurus (UAM.R.ACVII), left compound bone in medial view. P-Q: L. agilis (MDHC 176), left compound bone in medial (P) and lateral (Q) views. R: L. viridis (MRAC 91-077-R-76), right compound bone in medial view. S-T: A. kitaibelii (MDHC 239), left compound bone in medial (S) and lateral (T) views. U-V: C. ocellatus (MDHC 250), right compound bone in medial (U) and lateral (V) views. W-X: O. punctatissimus (MDHC 427), right compound bone in medial (W) and lateral (X) views. Y-Z: T. aurata (MDHC 280), left compound bone in medial (Y) and lateral (Z) views. AA-AB: Anguis gr. A. fragilis (MDHC 102), right compound bone in medial (AA) and lateral (AB) views. AC-AD: P. apodus (MDHC 214), left compound bone in medial (AC) and lateral (AD) views. AE: L. stellio (MDHC 245), left compound bone in dorsal view. AF: E. europaea (MDHC 388), left compound bone in dorsal view. AG: H. turcicus (JDD 326-327), left compound bone in dorsal view. AH: M. kotschyi (MDHC 285), left compound bone in dorsal view. AI: T. mauritanica (MDHC 302), right compound bone in dorsal view. AJ: L. agilis (MDHC 176), left compound bone in dorsal view. AK: C. ocellatus (MDHC 250), right compound bone in dorsal view. AL: Anguis gr. A. fragilis (MDHC 102), right compound bone in dorsal view. AM: P. apodus (MDHC 214), left compound bone in dorsal view. Abbreviations: ac, articular condyle with the quadrate; af, adductor fossa; ap, angular process; ar, articular; asa, articulation surface with the angular; asd, articulation surface with the dentary; asf, anterior surangular foramen; fct, foramen for the chorda tympani; lc, lateral crest; pra, prearticular; psf, posterior surangular foramen; rap, retroarticular process; sa, surangular; t, tubercle; tr, tympanic ridge. Scale bars = 1 mm.

Figure A3.38



Figure A3.39) Skulls of *Blanus* - A-E: *B. cinereus* (ZSM 652-0-2), skull in dorsal (A), ventral (B), left lateral (C), right lateral (D) and anterior (E) views. F-K: *B. mariae* (ZSM 27-1988-1), skull in dorsal (F), ventral (G), left lateral (H), right lateral (I), anterior (J) and posterior (K) views. Abbreviations: a, angular; b, basioccipital; c, coronoid; cb, compound bone; d, dentary; ec, ectopterygoid; ep, epipterygoid; f, frontal; flc, foramen of the longitudinal canal; m. maxilla; n, nasal; o, otooccipital; p, parietal; pa, palatine; pf, prefrontal; pm, premaxilla; pr, prootic; pt, pterygoid; q, quadrate; s, squamosal; so, supraoccipital; sp, sphenoid; v, vomer. Not to scale.



Figure A3.39

Figure A3.40) Skull of *Blanus* (continues) - A-F: *B. strauchi* (MCCI R-1635), skull in dorsal (A), ventral (B), left lateral (C), right lateral (D), anterior (E) and posterior (F) views. Not to scale.





Figure A3.41) Isolated bones of Blanus - A-B: B. strauchi (MDHC 288), left nasal in dorsal (A) and ventral (B) views. C-E: B. strauchi (MDHC 286), left frontal in dorsal (C), ventral (D) and lateral (E) views, F-H: B. strauchi (MDHC 286), parietal in dorsal (F), ventral (G) and left lateral (H) views. I-K: B. strauchi (MDHC 287), premaxilla in anterior (I), posterior (J) and right lateral (K) views. L-N: B. strauchi (MDHC 287), left maxilla in dorsal (L), medial (M) and lateral (N) views. O-P: B. strauchi (MDHC 287), left prefrontal in lateral (O) and dorsal (P) views. O-T: B. cinereus (MDHC 156), left quadrate in anterior (O), posterior (R), medial (S) and lateral (T) views. U-X: B. strauchi (MDHC 287), left quadrate in anterior (U), posterior (V), medial (W) and lateral (X) views. Y-Z: B. strauchi (MDHC 288), left vomer in dorsal (Y) and lateral (Z) views. AA-AB: B. strauchi (MDHC 287), right septomaxilla in dorsal (AA) and ventral (AB) views. Abbreviations: adp, anterodorsal process; alp, anterolateral process; amp, anteromedial process; anp, ascending nasal process; ap, anterior process; apa, articulation surface with the parietal; apf, articulation surface with the prefrontal; app, anterior premaxillary process; asm, articulation surface with the maxilla: asp, articulation surface with the premaxilla; cc, crista cranii; cco, cephalic condyle; dp, dorsal process; f, foramen; fp, facial process; lp, lateral process; lw, lateral wing; mco, mandibular condyle; mp, medial process; njo, notch of the foramen for the Jacobson's organ; nvf, notch of the vomeronasal fenestra; of, orbitonasal flange; pap, palatal process; pf, parietal fossa; plp, posterolateral process; pmp, posteromedial process; pn, parietal notch; pp, posterior process; ppl, posterior plates; ps, palatal shelf; pvp, posteroventral process; sc, sagittal crest; sdf, superior dental foramen; vlf, ventrolateral foramen; vp, ventral process. Scale bars = 1 mm.



Figure A3.41

Figure A3.42) Isolated bones of Blanus (continues) - A-B: B. strauchi (MDHC 287), left palatine in dorsal (A) and ventral (B) views. C-D: B. strauchi (MDHC 287), right pterygoid in dorsal (C) and ventral (D) views. E-F: B. strauchi (MDHC 288), left ectopterygoid in medial (E) and lateral (F) views. G-H: B. cinereus (MDHC 156), tabulosphenoid in dorsal (G) and ventral (H) views (the left posterior process is broken). I-J: B. strauchi (MDHC 287), tabulosphenoid in dorsal (I) and ventral (J) views. K-O: B. strauchi (MDHC 287), otooccipital region in anterior (K), posterior (L), left lateral (M), dorsal (N) and ventral (O) views. P-Q: B. strauchi (MDHC 287), right dentary in medial (P) and lateral (Q) views. R-S: B. strauchi (MDHC 287), left coronoid in medial (R) and lateral (S) views. T-U: B. cinereus (MDHC 156), right compound bone in lateral (T) and medial (U) views. Abbreviations: ac, alveolar canal; aco, articular condyle; af, adductor fossa; alp, anterolateral process; amp, anteromedial process; ap, alar process; apd, articulation surface with the superior posterior process of the dentary; as, alveolar shelf; asa, articulation surface with the angular; asd, articulation surface with the posterodorsal process of the ectopterygoid; asf, anterior surangular foramen; asm, articulation surface with the maxilla; asp, articulation surface with the palatine; asr, articulation surface with the parasphenoid rostrum of the sphenoid; asy, articulation surface with the posteroventral process of the ectopterygoid; avc, anterior opening of the vidian canal; bf, basipterygoid fossa; bp, basipterygoid process; cd, choanal duct; cp, coronoid process; cpp, central posterior process; cr, coronoid ridge; dp, dentary process; fct, foramen for the chorda tympani; ff, facial foramen; fm, foramen magnum; fo, fenestra ovalis; ip, incisura prootica; ipp, inferior posterior process; is, intramandibular septum; jf, jugular foramen (concavity of the vagus foramen); mcf. notch of the mandibular central foramen; mf, Meckelian fossa; mfo, mental foramen; mp, maxillary process; ms, mandibular symphysis; mvc, medial opening of the vidian canal; oc, occipital condyle; pa, processus ascendens; pap, palatine process; pdp, posterodorsal process; pmp, posteromedial process; pop, paroccipital process; pr, palatine ridge; pro, parasphenoid rostrum; psf, posterior surangular foramen; ptf, pterygoid flange; ptp, pterygoid process; ptr, pterygoid recess; pvc, posterolateral opening of the vidian canal; pvp, posteroventral process; qp, quadrate process; rp, retroarticular process; rsp, ridge for the insertion of the superficial pseudotemporal muscle; sc, supraoccipital crest; spp, superior posterior process; sr, subdental ridge; vp, vomerine process. Scale bars = 1 mm.



Figure A3.42

Appendix 4

Figure A4.1) Lizards from Gisseltshausen 1a (A-O) and 1b (P-AI). Chamaeleonidae indet.: fragment of tooth-bearing bone (BSPG 1982 X 7184) in medial view (A). Gekkota indet.: right dentary (BSPG 1982 X 7185) in medial view (B); fragment of tooth-bearing bone (BSPG 1982 X 7195) in medial view (C). cf. *Miolacerta* sp.: fragment of tooth-bearing bone (BSPG 1982 X 7198) in medial view (D). Lacertidae indet.: left maxilla (BSPG 1982 X 7201) in medial (E) and lateral (F) views. ?Lacertidae indet.: left maxilla (BSPG 1982 X 7202) in medial (G) and lateral (H) views. aff. Eumeces sp.: isolated tooth (BSPG 1982 X 7217) in mesial or distal view (I). Ophisaurus sp.: left dentary (BSPG 1982 X 7186) in medial view (J); trunk vertebra (BSPG 1982 X 7190) in right lateral (K), anterior (L), dorsal (M) and ventral (N) views. cf. Pseudopus laurillardi: right dentary (BSPG 1982 X 7219) in medial view (O). Janosikia ulmensis: right frontal (BSPG 1982 X 7243) in dorsal (P) and ventral (Q) views; parietal (BSPG 1982 X 7245) in dorsal (R) and ventral (S) views; right maxilla (BSPG 1982 X 7247) in medial view (T); detail of the tooth crown of BSPG 1982 X 7247 in ventromedial view (U); right dentary (BSPG 1982 X 7250) in medial view (V). Lacertidae indet.: left postfrontal (BSPG 1982 X 7241) in dorsal (W) and ventral (X) views; right pterygoid (BSPG 1982 X 7242) in dorsal (Y) and ventral (Z) views; left dentary (BSPG 1982 X 7230) in medial view (AA). Scincidae indet.: right dentary (BSPG 1982 X 7255) in medial view (AB); detail of the tooth crown of BSPG 1982 X 7255 in lingual view (AC). Pseudopus sp.: right maxilla (BSPG 1982 X 7258) in medial view (AD); right dentary (BSPG 1982 X 7256) in medial view (AE). Amphisbaenia indet.: trunk vertebra (BSPG 1982 X 7232) in ventral (AF), dorsal (AG), left lateral (AH) and right lateral (AI) views. Scale bars are 1 mm, except for I, U and AC, in which it is 0.2 mm.

Figure A4.2) Lizards from Griesbeckerzell 1a. *Edlartetia* sp. vel *Miolacerta* sp.: right dentary (BSPG 1997 XIII 673) in lateral (A) and medial (B) views. *Janosikia ulmensis*: pair of fused frontals (BSPG 1997 XIII 674) in dorsal (C) and ventral (D) views; left dentary (BSPG 1997 XIII 675) in medial (E) and lateral (F) views. Lacertidae indet.: right maxilla (BSPG 1997 XIII 676) in medial (G), lateral (H) and dorsal (I) views. Scincomorpha indet.: right dentary (BSPG 1997 XIII 676) in medial (G), lateral (H) and lateral (K) views. *Anguis* sp.: trunk vertebra (BSPG 1997 XIII 678) in dorsal (L), ventral (M), anterior (N) and left lateral (O) views. *Ophisaurus* sp.: trunk vertebra (BSPG 1997 XIII 680) in dorsal (L), ventral (M), anterior (N) and left lateral (O) views. *Ophisaurus* sp.: trunk vertebra (BSPG 1997 XIII 682) in dorsal (P), ventral (Q), anterior (R) and left lateral (S) views. *Pseudopus laurillardi*: right pterygoid (BSPG 1997 XIII 683) in dorsal (T) and ventral (U) views; left dentary (BSPG 1997 XIII 684) in medial view (V). *Pseudopus* sp.: trunk vertebra (BSPG 1997 XIII 687) in anterior (W), ventral (X) and right lateral (Y) views. Amphisbaenia indet.: trunk vertebra (BSPG 1997 XIII 695) in ventral (Z), dorsal (AA), left lateral (AB), right lateral (AC) and anterior (AD). Scale bars = 1 mm.







Figure A4.2

Figure A4.3) Lizards from Kleineisenbach (A-P), Stubersheim (Q-AL) and Walda 2 (AM-AN). Gekkota indet.: left dentary (BSPG 1972 XVI 2207) in medial view (A); fragment of tooth-bearing bone (BSPG 1972 XVI 2209) in medial view (B). Edlartetia cf. E. sansaniensis: left maxilla (BSPG 1972 XVI 2210) in medial view (C). cf. Miolacerta sp.: left dentary (BSPG 1972 XVI 2214) in medial view (D); fragment of tooth-bearing bone (BSPG 1972 XVI 2212) in medial view (E). Lacertidae indet.: left maxilla (BSPG 1972 XVI 2217) in medial view (F). Ophisaurus sp.: left dentary (BSPG 1972 XVI 2229) in medial view (G); left dentary (BSPG 1972 XVI 2230) in medial view (H); fragment of tooth-bearing bone (BSPG 1972 XVI 2231) in medial view (I); trunk vertebra (BSPG 1972 XVI 2227) in ventral view (J). Pseudopus sp.: fragment of tooth-bearing bone (BSPG 1972 XVI 2232) in medial view (K); trunk vertebra (BSPG 1972 XVI 2234) in ventral view (L). Varanidae indet.: tooth (BSPG 1972 XVI 2243) in either anterior or posterior (M) and lingual (N) views. cf. Blanus sp.: left dentary (BSPG 1972 XVI 2255) in medial (O) and lateral (P) views. cf. Edlartetia sp.: fragment of tooth-bearing bone (BSPG 1982 X 7179) in medial view (Q). Mediolacerta sp.: right dentary (BSPG 1982 X 7178) in medial (R) and lateral (S) views. Lacertidae indet.: left dentary (BSPG 198 X 7140) in medial view (T). aff. Eumeces sp.: isolated tooth (BSPG 1982 X 7181) in labial view (U); detail of the crown of BSPG 1982 X 7181 in lingual view (V). Ophisaurus holeci: parietal (BSPG 1982 X 7143) in dorsal (W) and ventral (X) views. Ophisaurus sp.: right dentary (BSPG 1982 X 7150) in medial (Y) and lateral (Z) views; right dentary (BSPG 1982 X 7153) in medial (AA) and lateral (AB) views. Pseudopus sp.: fragment of tooth-bearing bone (BSPG 1982 X 7177) in medial view (AC); trunk vertebra (BSPG 1982 X 7145) in left lateral (AD), dorsal (AE) and ventral (AF) views. Merkurosaurus sp.: right maxilla (BSPG 1982 X 7180) in lateral (AG) and medial (AH) views. Amphisbaenia indet .: trunk vertebra (BSPG 1982 X 7139) in left lateral (AI), anterior (AJ), dorsal (AK) and ventral (AL) views. *Pseudopus* sp.: left dentary (BSPG 1987 V 5/83) in medial view (AM); right dentary (BSPG 1987 V 9/82) in medial view (AN). Scale bars are 1 mm, except for B, U and V, in which it is 0.2 mm.



Figure A4.4) Fossil lizards from Aliveri (A-N) and Ano Metochi (O-AN). Chamaeleo cf. C. andrusovi: skull roofing bone (UU AL 3501) in external (A) and internal (B) views; interpretative drawing of UU AL 3501 in external (C) and lateral (D) views. Chamaeleonidae indet.: fragment of tooth-bearing bone (UU AL 3502) in lateral (E) and medial (F) views; fragment of tooth-bearing bone (UU AL 3503) in lateral (G) and medial (H) views. Lacertidae indet.: fragment of tooth-bearing bone (UU AL 3542) in medial view (I); fragment of tooth-bearing bone (UU AL 3557) in medial view (J); fragment of tooth-bearing bone (UU AL 3559) in medial view (K). Scincomorpha indet.: left dentary (UU AL 3519) in lateral (L) and medial (M) views. non-Anguis Anguinae indet.: osteoderm (UU AL 3516) in external view (N). Lacertidae indet .: premaxilla (UU AM3 501) in anterior (O) and posterior (P) views; right maxilla (UU AM3 502) in lateral (O) and medial (R) views; right dentary (UU AM3 503) in medial (S) and lateral (T) views; right dentary (UU AM2 504) in lateral (U) and medial (V) views; right dentary (UU AM2 502) in medial (W) view; left dentary (UU AM2 503) in medial (X) view. Cordylidae indet.: right maxilla (UU AM3 506) in lateral (Y) and medial (Z) views; left maxilla (UU AM3 507) in ventral (AA) view; right dentary (UU AM2 508) in lateral (AB) and medial (AC) views; close-up of the teeth of UU AM3 506 in lingual view (AD). Ophisaurus sp.: left maxilla (UU AM2 512) in medial view (AE); left dentary (UU AM3 510) in medial (AF) and lateral (AG) views; right dentary (UU AM3 512) in medial (AH) and lateral (AI) views; presacral vertebra (UU AM3 513) in posterior (AJ), anterior (AK), ventral (AL), dorsal (AM) and left lateral (AN) views. Scale bars = 1 mm. The interpretative drawing of UU AL 3501 has been prepared by Gaetano Pitruzzella.



Figure A4.5) Fossil lizards from Maramena (A-AZ) and Plakias (BA-BD). Agaminae indet.: frontal (UU MAA 7191) in dorsal (A) and ventral (B) views; right maxilla (UU MAA 7043) in medial (C) and lateral (D) views: right dentary (UU MAA 7041) in medial (E) and lateral (F) views; right dentary (UU MAA 7305) in medial view (G). Lacertidae indet.: right maxilla (UU MAA 7032) in lateral view (H); right quadrate (UU MAA 7096) in anterior (I), posterior (J) and medial (K) views; right pterygoid (UU MAA 7097) in dorsal (L) and ventral (M) views; left pterygoid (UU MAA 7099) in dorsal (N) and ventral (O) views. ?Scincidae indet.: left dentary (UU MAA 7027) in medial view (P); right dentary (UU MAA 7107) in medial view (Q). aff. Palaeocordylus sp.: right maxilla (UU MAA 7047) in medial view (R); right maxilla (UU MAA 7077) in medial view (S); right dentary (UU MAA 7004) in lateral (T) and medial (U) views; left dentary (UU MAA 7199) in medial (V) and lateral (W) views. Anguis sp.: trunk vertebra (UU MAA 7181) in dorsal (X) and ventral (Y) views; trunk vertebra (UU MAA 7263) in ventral view (Z). Ophisaurus sp. (morphotype 1): right maxilla (UU MAA 7324) in medial view (AA); right dentary (UU MAA 7176) in medial view (AB); right dentary (UU MAA 7177) in medial view (AC). Ophisaurus sp. (morphotype 2): left maxilla (UU MAA 7180) in medial view (AD); left dentary (UU MAA 7100) in medial view (AE); left dentary (UU MAA 7186) in medial (AF) and lateral (AG) views. Ophisaurus sp. (morphotype 3): left dentary (UU MAA 7313) in medial view (AH). Ophisaurus sp. (morphotype 4): left dentary (UU MAA 7175) in medial (AI) and lateral (AJ) views. Ophisaurus sp. (morphotype 5): left maxilla (UU MAA 7178) in medial view (AK). Ophisaurus sp.: trunk vertebra (UU MAA 7215) in ventral view (AL). Pseudopus sp.: right maxilla (UU MAA 7171) in lateral (AM) and medial (AN) views; fragment of tooth-bearing bone (UU MAA 7307) in lateral (AO) and medial (AP) views; trunk vertebra (UU MAA 7172) in dorsal (AQ) and ventral (AR) views; trunk vertebra (UU MAA 7328) in ventral view (AS). Varanus sp.: tooth (UU MAA 7030) in lingual (AT) and anterior (AU) views; caudal vertebra (UU MAA 7198) in dorsal (AV), ventral (AW) and left lateral (AX) views. "Lacertilia" indet.: fragment of tooth-bearing bone (UU MAA 7033) in lateral (AY) and medial (AZ) views. Amphisbaenia indet.: trunk vertebra (UU PL 733) in dorsal (BA), ventral (BB), right lateral (BC) and anterior (BD) views. Scale bars = 1 mm.



Figure A4.5

Figure A4.6) Fossil lizards from Tourkobounia (A-U) and other Greek localities (V-BH). Agamidae indet.: fragment of tooth-bearing bone from Tourkobounia 1 in medial view (A). cf. Gekkota indet.: right dentary from Tourkobounia 1 in medial view (B). cf. Lacerta sp.: right quadrate from Tourkobounia 2 in anterior (C), posterior (D) and medial (E) views; left pterygoid from Tourkobounia 5 in dorsal (F) and ventral (G) views. Lacertidae indet.: left frontal from Tourkobounia 1 in dorsal (H) and ventral (I) views; unstepped left maxilla from Tourkobounia 3 in lateral (J) and medial (K) views; stepped right maxilla from Tourkobounia 3 in medial view (L). Pseudopus sp.: right dentary from Tourkobounia 1 in medial (M) and lateral (N) views. Varanus sp.: right maxilla (UU TB5 1001) in lateral (O), medial (P) and dorsal (Q) views; right dentary (UU TB5 1002) in medial (R) and lateral (S) views; isolated tooth (UU TB5 1003) in medial (T) and labial (U) views. Agamidae indet.: left maxilla from Rema Aslan 1 in dorsal (V) and medial (W) views; fragment of toothbearing bone frome Rema Aslan 1 in media view (X). Hemidactylus turcicus: frontal from Liko BA in dorsal (Y) and ventral (Z) views. Gekkota indet.: right dentary from Maritsa A in medial view (AA). Lacertidae indet. (large-sized taxon): premaxilla from Liko BA in anterior (AB) and posterior (AC) views; premaxilla from Spilia 3 in anterior (AD) and posterior (AE) views; left jugal from Arnissa in dorsal (AF), medial (AG) and lateral (AH) views; left pterygoid from Arnissa ind dorsal (AI) and ventral (AJ) views. Lacertidae indet .: first premaxilla from Arnissa in anterior (AK) and posterior (AL) views; second premaxilla from Arnissa in anterior (AM) and posterior (AN) views; third premaxilla from Arnissa in anterior (AO) and posterior (AP) views; premaxilla from Tomea Eksi 1 in anterior (AQ) and posterior (AR) views. aff. Ophiomorus sp.: left dentary from Kaiafa in medial (AS) and lateral (AT) views. Scincidae indet.: right dentary from Notio 1 in medial view (AU); closeup of the dentition in medial view (AV). Anguis sp.: trunk vertebra from Arnissa in left lateral (AW), dorsal (AX) and ventral (AY) views. Pseudopus sp.: fragment of tooth-bearing bone from Kaiafa in medial view (AZ); trunk vertebra from Kaiafa in ventral view (BA). cf. *Pseudopus* sp.: caudal vertebra from Pili B in dorsal (BB), ventral (BC) ad right lateral BD) views. cf. Varanidae indet.: isolated tooth from Spilia 4 in either labial or lingual view (BE). Amphisbaenia indet.: trunk vertebra from Spilia 4 (UU SPA 501) in dorsal (BF), left lateral (BG) and ventral (BH) views. White arrows in P and Q mark the cavity between the ventromedial fold and the palatal shelf in the maxilla of *Varanus* sp. Abbreviations: ml, medial lamina; vf, vomeronasal foramen; vmf, ventromedial fold. Scale bars are 1 mm, except for AV, in which it is 0.2 mm.



Figure A4.7) Fossil lizards from Gargano "terre rosse" (A-L), Cava Monticino (M-AU), Caverna dei Parmorari (AV-AW), Caverna dell'Aurera (AX), Ciabòt Cagna (AY-BL) and Moncucco Torinese (BM-BZ). Gekkota n.gen. n.sp.: right maxilla (DSTF-GH 26) in dorsal (A), lateral (B) and medial (C) views; left maxilla (DSTF-GH 34) in lateral (D) and medial (E) views; right maxilla (DSTF-GH 36) in dorsal view (F); left dentary (DSTF-GH 29) in lateral (G) and medial (H) views; left dentary (DSTF-GH 38) in medial view (I); left dentary (DSTF-GH 42) in medial view (J); right dentary (DSTF-GH 37) in lateral (K) and medial (L) views. Agaminae indet.: left maxilla (BRS25/H/5) in lateral (M) and medial (N) views; left dentary (MSF 67) in lateral view (O). Eremiadini indet.: pair of fused frontals (BRS4/H/23) in dorsal (P) and ventral (Q) views. Lacertidae indet.: right jugal (BRS25/H/187) in medial (R), lateral (S) and dorsal (T) views; left dentary (BRS4/H/21) in medial view (U). Scincidae indet.: right dentary (BRS25/H/142) in medial view (V). ?Scincidae indet.: fragment of tooth-bearing bone (BRS27/H/15) in medial (W) and lateral (X) views. Ophisaurus sp.: left frontal (BRS25/H/160) in lateral (Y), dorsal (Z) and ventral (AA) views; parietal (BRS25/H/119) in dorsal (AB) and ventral (AC) views; right maxilla (BRS5tg2/H/7) in medial view (AD); left dentary (BRS25/H/135) in lateral view (AE). Pseudopus sp.: left frontal (BRS25/H/117) in dorsal (AF), ventral (AG) and lateral (AH) views; right maxilla (BRS25/H/182) in medial view (AI); fragment of tooth-bearing bone (BRS25/H/122) in medial (AJ) and lateral (AK) views. Varanus sp.: isolated tooth (BRS5bis/H/13) in labial (AL) and lingual (AM) views; isolated tooth (BRS6/H/7) in labial (AN) and lingual (AO) views; fragment of trunk vertebra (BRS25/H/129) in ventral view (AP). Amphisbaenia indet.: trunk vertebra (BRS19/H/1) in dorsal (AQ), ventral (AR), right lateral (AS) and anterior (AT) views; fragment of trunk vertebra (BRS25/H/18) in right lateral view (AU). Timon lepidus: parietal in dorsal (AV) and ventral (AW) views. Lacertidae indet.: left splenial in medial view (AX). non-Anguis Anguinae indet.: osteoderm in external view (AY). Blanus sp.: right dentary in lateral (AZ) and medial (BA) views. Anguis sp.: trunk vertebra (IGF102243) in dorsal (BB), ventral (BC), left lateral (BD), anterior (BE) and posterior (BF) views. non-Anguis Anguinae indet.: trunk vertebra (IGF102244) in ventral (BG), dorsal (BH), posterior (BI), right lateral (BJ) and anterior (BK) views; osteoderm (IGF102247) in external view (BL). Agamidae indet.: fragment of tooth bearing bone (MGPT-PU 132438) in lateral view (BM). cf. Euleptes sp.: left maxilla (MGPT-PU 132432) in lateral (BN) and medial (BO) views. cf. Lacerta sp.: fused frontals (MGPT-PU 132532) in dorsal (BP) and ventral (BQ) views; right dentary (MGPT-PU 132501) in medial (BR) and lateral (BS) views. non-Anguis Anguinae indet.: right dentary (MGPT-PU 132482) in medial (BT) and lateral (BU) views; trunk vertebra (MGPT-PU 132612) in dorsal (BV) and ventral (BW) views. Amphisbaenia indet.: trunk vertebra (MGPT-PU 132593) in dorsal (BX), ventral (BY), and left lateral (BZ) views. Scale bars = 1 mm. The interpretative drawing of MSF 67 has been prepared by Massimo Delfino.



Figure A4.8) Fossil lizards from Monte Tuttavista. *Euleptes* cf. *E. europaea*: frontal (MT-VIb6-005) in ventral (A) and dorsal (B) views; frontal (MT-XIc-004) in dorsal view (C); right maxilla (MT-VI-001) in lateral (D) and medial (E) views; left maxilla (MT-BS-002) in lateral (F) and medial (G) views; otooccipital region (MT-XIr-001) in anterior (H), dorsal (I) and right lateral (J) views; left dentary (MT-XIc-003) in lateral (K) and medial (L) views; right dentary (MT-VIb6-004) in lateral (M) and medial (N) views; right compound bone (MT-VIb6-008) in lateral (O) and medial (P) views; trunk vertebra (MT-VI-005) in dorsal (Q), ventral (R) and right lateral (S) views. Timon sp.: left nasal (MT-IX-048) in dorsal (T) and ventral (U) views; fused frontals (MT-IX-012) in dorsal (V) and ventral (W) views; fused frontals (MT-IX-049) in dorsal (X) and ventral (Y) views; parietal (MT-IX-009) in dorsal (Z) and ventral (AA) views; parietal (MT-IX-010) in dorsal (AB) and ventral (AC) views; parietal (MT-IX-050) in dorsal (AD) and ventral (AE) views; premaxilla (MT-IX-001) in anterior (AF), posterior (AG) and left lateral (AH) views; premaxilla (MT-IX-002) in anterior (AI), posterior (AJ) and left lateral (AK) views; right maxilla (MT-IX-006) in lateral (AL), medial (AM), dorsal (AN) and ventral (AO) views; left jugal (MT-IX-015) in lateral (AP) and medial (AQ) views; left postorbitofrontal (MT-IX-069) in dorsal (AR) and ventral (AS) views; left quadrate (MT-IX-054) in anterior (AT), medial (AU) and posterior (AV) views; right pterygoid (MT-IX-014) in ventral (AW) and dorsal (AX) views; left ectopterygoid (MT-IX-068) in dorsal (AY) and ventral (AZ) views; otooccipital region (MT-VIa-001) in right lateral (BA), anterior (BB), posterior (BC), ventral (BD) and dorsal (BE) views; right dentary (MT-IX-055) in lateral (BF) and medial (BG) views; left dentary articulated with the splenial (MT-IX-056) in medial (BH) and lateral (BI) views; left coronoid (MT-IX-057) in medial (BJ) and lateral (BK) views; left compound bone (MT-IX-058) in lateral view (BL); axis (MT-IX-059) in right lateral (BM), anterior (BN), left lateral (BO), ventral (BP) and ventral (BQ) views; cervical vertebra (MT-IX-020) in dorsal (BR), ventral (BS), right lateral (BT), anterior (BU) and posterior (BV) views; dorsal vertebra (MT-IX-029) in dorsal (BW), ventral (BX), anterior (BY), posterior (BZ) and left lateral (CA) views; sacral vertebrae (MT-IX-060) in dorsal (CB), ventral (CC) and anterior (CD) views; non-autotomic caudal vertebra (MT-IX-019) in anterior (CE), posterior (CF), left lateral (CG), dorsal (CH) and ventral (CI) views; anterior portion of autotomic caudal vertebra (MT-IX-061) in dorsal (CJ), posterior (CK), right lateral (CL) and anterior (CM) views; posterior portion of autotomic caudal vertebra (MT-IX-062) in anterior (CN), dorsal (CO), ventral (CP) and left lateral (CQ) views. Scale bars = 1 mm.



Figure A4.9) Fossil lizards from Monte Tuttavista (A-O), Oderzo (P-S), Riparo dell'Aquila (T-U), Rivoli Veronese (V-AP), Tenuta Zuccarello (AO-BE) and Valdemino Cave (BF-BI). Timon sp.: left scapulocoracoid (MT-IX-063) in ventrolateral view (A); right humerus (MT-IX-017) in dorsal (B) and ventral (C) views; left ulna (MT-IX-064) in posterior (D) and anterior (E) views; right pelvic girdle (MT-IX-018) in medial (F) and lateral (G) views; right femur (MT-IX-016) in dorsal (H) and ventral (I) views; right tibia (MT-IX-065) in anterior (J) and ventral (K) views; left astragalocalcaneum (MT-IX-066) in proximal (L) and dorsal (M) views; metapodial (MT-IX-067) in uncertain views (N, O). Lacertidae indet. (large size): right dentary in lateral (P) and medial (O) views; left lower jaw in medial (R) and lateral (S) views. Lacertidae indet.: left dentary (MAF 4466) in lateral (T) and medial (U) views. Lacerta gr. L. viridis: right frontal (RV-H-143) in ventral (V) and dorsal (Z) views. cf. Zootoca vivipara: fused frontals (RV-H-144) in ventral (AA) and dorsal (AB) views. Lacertidae indet.: parietal (RV-H-165) in dorsal (AC) and ventral (AD) views; premaxilla (RV-H-156) in anterior (AE) and posterior (AF) views. Anguis gr. A. fragilis: left dentary (RV-H-034) in medial view (AG); trunk vertebra (RV-H-036) in left lateral (AH), dorsal (AI) and ventral (AJ) views. ?Anguis sp.: left dentary (RV-H-235) in medial (AK) and ventromedial (AL) views. cf. Pseudopus sp.: fragment of dentary (RV-H-033) in medial view (AM); caudal vertebra (RV-H-030) in dorsal (AN), ventral (AO) and right lateral (AP) views. Lacerta gr. L. viridis: left dentary (MSNVE-23366/1) in lateral (AQ) and medial (AR) views; caudal vertebra (MSNVE-23378/1) in dorsal (AS), anterior (AT), ventral (AU) and posterior (AV) views. Lacertidae indet.: left dentary (MSNVE-23367/3) in lateral (AW) and medial (AX) views. Anguis gr. A. fragilis: right dentary (MSNVE-23379/6) in lateral (AY) and medial (AZ) views; trunk vertebra (MSNVE-23368/16) in anterior (BA), dorsal (BB), right lateral (BC), posterior (BD) and ventral (BE) views. Hemidactylus cf. H. turcicus: frontal in dorsal (BF) and ventral (BG) views; left maxilla in medial (BH) and lateral (BI) views. The white arrow in AL marks the fused intramandibular septum. Scale bars = 1 mm. The interpretative drawings of the remains from Valdemino Cave have been prepared by Massimo Delfino.



Figure A4.10) Fossil lizards from the Vallès-Penedès Basin. Gekkota indet.: left dentary (IPS55563) in medial view (A); left dentary (IPS55564) in medial view (B); close-up of the teeth (IPS55564) in lingual view (C). cf. *Amblyolacerta* sp.: left dentary articulated with the splenial (IPS82706) in medial view (D). Lacertidae indet.: left maxilla (IPS55130) in lateral (E) and medial (F) views; right maxilla (IPS9397b) in lateral view (G); right jugal (CBTemp216) in lateral (H) and medial (I) views. Scincidae indet.: left maxilla (IPS82716) in medial view (J). *?Anguis* sp.: trunk vertebra (IPS87396b) in ventral (K), dorsal (L), right lateral (M) and anterior (N) views. *Pseudopus* sp.: parietal (CBTemp223) in dorsal (O) and ventral (P) views; right maxilla (IPS9635a) in medial (Q) and lateral (R) views; right maxilla (IPS9653e) in lateral (S) and medial (T) views; right dentary (IPS50294) in medial view (U); left dentary (CBTemp386) in medial (V) and lateral (W) views; close up of the teeth (IPS82643) in lingual view (X). Varanidae indet.: caudal vertebra (IndTemp081) in ventral (Y) and posterior (Z) views. The anterior teeth stuck in the undetermined bone fragment of IPS50294 are not figured. Abbreviations: ubf, undetermined bone fragment. The white arrow in X marks the striation on the tooth crown. Scale bars = 1 mm.

Figure A4.11) Anguidae new taxon? from the Vallès-Penedès Basin. Articulated skull (MGB-V60): left lateral (A), right lateral (B), dorsal (C) and ventral (D) views; right nasal in dorsal view (E); frontals in dorsal view (F); parietal in dorsal view (G); right jugal in lateral view (H). Abbreviations: cb, compound bone; d, dentary; f, frontal; j, jugal; m, maxilla; n, nasal; p, parietal. Scale bars = 1 cm (A-D); 1 mm (E-H).

Figure A4.12) Anguids and amphisbaenians from the Vallès-Penedès Basin. Anguidae new taxon?: articulated skull of IPS30710 in dorsal (A, E), ventral (B, F), anterior (C, G), left lateral (D, H), right lateral (I) and posterior (J) views; tail portion of IPS30710 in right lateral view (K); close-up of the caudal vertebrae of IPS30710 in postero-lateral view (L; not to scale). *Blanus* sp.: premaxilla (IPS82691) in anterior (M), posterior (N) and right lateral (O) views; right maxilla (IPS82705) in medial view (P); right maxilla (IndTemp064) in medial view (Q); left dentary (IPS82668) in medial view (R); right dentary (IPS9363a) in medial (S) and lateral (T) views. Abbreviations: d, dentary; 1, lacrimal; m, maxilla; n, nasal; pa, palatine; pf, prefrontal; pm, premaxilla; sm, septomaxilla; sp, splenial; v, vomer. Scale bars = 1 cm (A-K); 1 mm (M-T).

Figure A4.13) Lizards from the Russel-Tiglia-Egypte pit. *Lacerta* sp.: left dentary (RGM 816720) in dorsal (A), lateral (B) and medial (C) views. Lacertidae indet.: parietal (RGM 816758) in dorsal (D) and ventral (E) views; right pterygoid (RGM 816743) in ventral (F) and dorsal (G) views; trunk vertebra (RGM 816739) in anterior (H), posterior (I), right lateral (J), dorsal (K) and ventral (L) views. *Anguis* gr. *A. fragilis*: parietal (RGM 816693) in dorsal (M) and ventral (N) views; left maxilla (RGM 816701) in lateral (O) and medial (P) views; trunk vertebra (RGM 816676) in dorsal (Q), ventral (R), anterior (S), posterior (T) and left lateral (U) views; osteoderm (RGM 816699) in external view (V). cf. *Pseudopus* sp.: osteoderm (RGM 816716) in external (W) and internal (X) views. Scale bars = 1 mm.













Appendix 5

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Taxon	Family	Previous identifications	Locality	Country	Age	Bibliography
Agama sp.	Agamidae		Litke 2	Hungary	Miocene (Langhian, MN 6)	Böhme & Ilg 2003; Čerňanský et al. 2016c
Agama sp.	Agamidae		Rümikon	Switzerland	Middle Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Delfino et al. 2008b; Blain et al. 2016a
Agama sp.	Agamidae		Maramena	Greece	Late Miocene (MN 13/14)	Richter 1995; Georgalis et al. 2017a
Agama sp.	Agamidae	Agama s.l.; Agamidae indet.	Sète	France	Middle Pliocene (MN 15)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a
Agama sp.	Agamidae	Agama s.l.; Agamidae indet.	Mas Genegals	France	Late Pliocene (MN 15/16)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a
Agama sp.	Agamidae	<i>Agama</i> s.l.; Agamidae indet.; Chamaeleonidae indet.	Seynes	France	Late Pliocene (MN 16)	Estes 1983; Bailon 1987; Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a
Agama sp.	Agamidae		Sarrión 1	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a
Agama (s.l.) sp.	Agamidae		Cava VI 3, Monte Tuttavista	Italy	Pleistocene (Calabrian)	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a
Agama (s.l.) sp.	Agamidae		Cava VII blocco strada, Monte Tuttavista	Italy	Pleistocene (Calabrian)	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a
Agama (s.l.) sp.	Agamidae		Cava XI - Canidae, Monte Tuttavista	Italy	Middle Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a
aff. Stellio sp.	Agamidae		Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Delfino et al. 2008b; Blain et al. 2016a
Agaminae indet.	Agamidae	Agama sp.; Agama s.l.; Agamidae indet.	Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Delfino 2002; Böhme & Ilg 2003; Rook et al. 2005; Rook & Delfino 2007; Delfino et al. 2008b; Blain et al. 2014a; Rook et al. 2015; Blain et al. 2016a; Villa et al. 2016b; this work
Agaminae indet.	Agamidae	Agama s.l.; Agama sp.	Maramena 1	Greece	Late Miocene (MN 13/14)	Böhme & Ilg 2003; Delfino 2004b; Delfino et al. 2008b; Blain et al. 2016a; this work
Agaminae indet.	Agamidae		Maramena 2	Greece	Late Miocene (MN 13/14)	this work
Agaminae indet.	Agamidae	Agama s.l.; Agama sp.	Maramena 3	Greece	Late Miocene (MN 13/14)	Delfino 2004b; Blain et al. 2016a; this work

Agamidae indet. 1	Agamidae	Agamidae indet.	Burtenbach 1 b (b. Thannhausen)	Germany	Early Miocene (MN 5)	Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2010; Delfino et al. 2008b; Blain et al. 2016a
Agamidae indet. 2	Agamidae	Agamidae indet.	Burtenbach 1 b (b. Thannhausen)	Germany	Early Miocene (MN 5)	Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2010; Delfino et al. 2008b; Blain et al. 2016a
Agamidae indet.	Agamidae		Schnaitheim 1	Germany	Miocene (Burdigalian, MN 3a/4b)	Schleich 1985b
Agamidae indet.	Agamidae	Agamidae indet. 2	Unterempfenbach 1b	Germany	Early Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Delfino et al. 2008b; Blain et al. 2016a
Agamidae indet.	Agamidae		Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Delfino et al. 2008b: Blain et al. 2016a
Agamidae indet.	Agamidae		Tăşad	Romania	Middle Miocene (Serravallian, MN 8)	Böhme & Ilg 2003Delfino et al. 2008b; Blain et al. 2016a
Agamidae indet.	Agamidae	?Agamidae indet.	Furth 460 m	Germany	Middle Miocene	Böhme & Ilg 2003; Delfino et al. 2008b; Blain et al. 2016a
Agamidae indet.	Agamidae		Gritsev	Ukraine	Late Miocene (Serravallian/Tortonian, MN 9)	Böhme & Ilg 2003; Delfino et al. 2008b; Blain et al. 2016a
Agamidae indet.	Agamidae		Moncucco Torinese	Italy	Latest Miocene (Messinian, p- ev2)	Colombero et al. 2014b; Colombero et al. 2017; this work
Agamidae indet.	Agamidae		Verduno	Italy	Miocene (Messinian)	Böhme & Ilg 2003; Carnevale et al. 2014; Colombero et al. 2014a
Agamidae indet.	Agamidae		"Lyonnais"	France	Miocene	Delfino et al. 2008b; Blain et al. 2016a
Agamidae indet.	Agamidae	Agama s.l.; Agama sp.	Rema Aslan 1	Greece	Miocene/Pliocene	Böhme & Ilg 2003; Delfino 2004b; Delfino et al. 2008b; Blain et al. 2016a; this work
Agamidae indet.	Agamidae	Chamaeleo sp.	Canal Negre 1	Spain	Latest Miocene/Middle Pleistocene (earliest Pleistocene?)	Blain et al. 2016a
Agamidae indet.	Agamidae	Agama s.l.; Agama sp.	Maritsa A	Greece	Early Pliocene (MN 14)	Böhme & Ilg 2003; Delfino 2004b; Delfino et al. 2008b; Blain et al. 2016a; this work
Agamidae indet.	Agamidae	Agama s.l.; Agama sp.	Vevi	Greece	Early Pliocene (MN 15)	Böhme & Ilg 2003; Delfino 2004b; Delfino et al. 2008b; Blain et al. 2016a; this work
Agamidae indet.	Agamidae	Agama s.l.; cf. Agama sp.	Balaruc II	France	Middle/late Pliocene (MN 15/16)	Bailon 1989; Bailon 1991; Bailon 1995; Böhme & Ilg 2003; Bailon & Blain 2007
Agamidae indet.	Agamidae	Agama s.l.	Balaruc VI	France	Late Pliocene (MN 16)	Bailon 1991; Bailon & Blain 2007
Agamidae indet.	Agamidae	Agama s.l.; Agama sp.	Tourkobounia 1	Greece	Late Pliocene (MN 16)	Böhme & Ilg 2003; Delfino 2004b; Delfino et al. 2008b; Blain et al. 2016a; this work
Agamidae indet.	Agamidae		Cova Bonica	Spain	Late Pliocene/early Pleistocene (MN 16)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Delfino et al. 2008; Agustí et al. 2009; Blain 2009; Blain et al. 2016a
Agamidae indet.	Agamidae	Agama s.l.; Agama sp.	Kastoria	Greece	Pliocene	Böhme & Ilg 2003; Delfino 2004b; Delfino et al. 2008b; Blain et al. 2016a; this work
Agamidae indet.	Agamidae		Estepa 1	Spain	Earliest Pleistocene (Villafranchian)	Blain et al. 2016a

Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Burdigalian/Langhian, MN 5)	Germany	Aresing		Chamaeleonidae	Chamaeleo bavaricus
Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Burdigalian, MN 5)	Germany	Unterempfenbach 1a	Chamaeleo sp.	Chamaeleonidae	Chamaeleo bavaricus
Schleich 1983; Schleich 1984; Schleich 1985b; Böhme 1999a; Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Böhme 2010b; Bolet & Evans 2013b; Čerňanský et al. 2016c; Georgalis et al. 2016a	Miocene (Burdigalian, MN 5)	Germany	Sandelzhausen		Chamaeleonidae	Chamaeleo bavaricus
Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Burdigalian, MN 5)	Germany	Arth 1a		Chamaeleonidae	Chamaeleo bavaricus
Böhme & IIg 2003; Delfino 2004b; Georgalis et al. 2016a; this work	Early Miocene (MN 4)	Greece	Aliveri	Chamaeleo cf. C. caroliquarti ; Chamaeleonidae indet.	Chamaeleonidae	Chamaeleo cf. C. andrusovi
Mörs 2002; Böhme 2003; Bolet & Evans 2013b; Čerňanský et al. 2016c; Georgalis et al. 2016a	Early middle Miocene (Langhian, MN 5)	Germany	Hambach 6C	Chamaeleonidae indet.; <i>Chamaeleo</i> sp.	Chamaeleonidae	Chamaeleo aff. C. andrusovi
Böhme & Ilg 2003; Čerňanský 2010a; Bolet & Evans 2013b; Čerňanský 2016; Čerňanský et al. 2016c; Georgalis et al. 2016a	Early Miocene (Burdigalian, MN 4b)	Czech Republic	Dolnice		Chamaeleonidae	Chamaeleo andrusovi
this work	Upper Pleistocene	Greece	Pili B		Agamidae	Agamidae indet.
Böhme & Ilg 2003; Mancheño et al. 2009; Blain et al. 2014a; Blain et al. 2016a	Late early Pleistocene	Spain	Quibas		Agamidae	Agamidae indet.
Bailon 1991; Rage & Augé 1993; Böhnne & Ilg 2003; Bailon & Blain 2007; Delfino et al. 2008b; Agustí et al. 2009; Blain et al. 2016a	Early Pleistocene	Spain	Medas Islands	Agama s.l.	Agamidae	Agamidae indet.
Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Delfino et al. 2008b; Agustí et al. 2009; Blain 2009; Mancheño et al. 2009; Blain et al. 2014a; Blain et al. 2016a	Early Pleistocene (Gelasian)	Spain	Vallirana	cf. Laudakia sp.	Agamidae	Agamidae indet.
Böhme & Ilg 2003; Blain 2005; Delfino et al. 2008b; Agustí et al. 2009; Blain 2009; Blain et al. 2014a: Blain et al. 2016a	Early Pleistocene (Gelasian)	Spain	Almenara Casablanca 4	cf. Laudakia sp.	Agamidae	Agamidae indet.
Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Delfino et al. 2008b; Agustí et al. 2009; Blain 2009; Mancheño et al. 2009; Blain et al. 2014a; Blain et al. 2016a	Early Pleistocene (Gelasian)	Spain	Almenara Casablanca 1	cf. Laudakia sp.	Agamidae	Agamidae indet.
Böhme & Ilg 2003; Delfino et al. 2008b; Blain et al. 2014a; Blain et al. 2016a	Early Pleistocene (MN 17)	Italy	Montagnola Senese	Agama sp.	Agamidae	Agamidae indet.

Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Langhian)	Germany	Untereichen-Altenstadt 565m	Chamaeleo sp.	Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Langhian, MN 6)	Germany	Wannenwaldtobel 2		Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Langhian, MN 6)	Germany	Petersbuch 39	Chamaeleo cf. C. caroliquarti	Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Bolet & Evans 2013b; Georgalis et al. 2016a	Middle Miocene (Langhian, MN 6)	Germany	Laimering 3		Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (MN 6)	Germany	Laimering 2a		Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Ivanov & Böhme 2011; Bolet & Evans 2013b; Čerňanský et al. 2016c; Georgalis et al. 2016a	Miocene (Langhian, MN 5)	Germany	Griesbeckerzell 1b		Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Langhian, MN 5)	Germany	Gisseltshausen 1b	Chamaeleo cf. C. caroliquarti	Chamaeleonidae	Chamaeleo caroliquarti
Böhme & IIg 2003; Abdul Aziz et al. 2008; Georgalis et al. 2016a	Miocene (Burdigalian)	Germany	Puttenhausen E		Chamaeleonidae	Chamaeleo caroliquarti
Böhme & IIg 2003; Abdul Aziz et al. 2008; Georgalis et al. 2016a	Miocene (Burdigalian)	Germany	Puttenhausen A		Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Burdigalian, MN 4)	Germany	Petersbuch 36 II	Chamaeleo cf. C. caroliquarti	Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Burdigalian, MN 4)	Germany	Petersbuch 36	Chamaeleo cf. C. caroliquarti	Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (MN 4b)	Germany	Erkertshofen 1		Chamaeleonidae	Chamaeleo caroliquarti
Moody & Roček 1980; Estes 1983; Roček 1984; Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Čerňanský 2010a; Bolet & Evans 2013b; Čerňanský et al. 2016c; Georgalis et al. 2016a	Early Miocene (Burdigalian, MN 4b)	Czech Republic	Dolnice		Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (Burdigalian, MN 4a)	Germany	Petersbuch 28		Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Čerňanský 2010a; Čerňanský 2011a; Bolet & Evans 2013b; Rage 2013; Čerňanský et al. 2015b; Čerňanský et al. 2016c; Georgalis et al. 2016a	Lower Miocene (Burdigalian, MN 3a)	Czech Republic	Merkur North	Chamaeleonidae indet.	Chamaeleonidae	Chamaeleo caroliquarti
Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Bolet & Evans 2013b; Georgalis et al. 2016a	Miocene (MN 6)	Germany	Laimering 2a		Chamaeleonidae	Chamaeleo bavaricus
Chamaeleo caroliquarti	Chamaeleonidae		Unterzell 1a	Germany	Miocene (Langhian)	3öhme & Ilg 2003; Georgalis et al. 2016a
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Chamaeleo aff. C. caroliquarti	Chamaeleonidae		Agramon	Spain	Miocene (Burdigalian)	3öhme & Ilg 2003; Georgalis et al. 2016a
Chamaeleo cf. C. caroliquarti	Chamaeleonidae	Chamaeleo caroliquarti	Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Moody & Roček 1980; Estes 1983; Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Čerňanský 2011a; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo aff. C. caroliquarti	Chamaeleonidae	Chamaeleo caroliquarti	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	3öhme 1999a; Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Böhme 2010b; Bolet & Evans 2013b; Čerňanský et al. 2016c; Georgalis et al. 2016a
Chamaeleo chamaeleon	Chamaeleonidae		Cueva de la Victoria, near Rincón de la Victoria, Málaga	Spain	Holocene	Falavera & Sanchíz 1983; Masseti 2009; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo pfeili	Chamaeleonidae		Langenau 1	Germany	Miocene (Burdigalian, MN 4b)	3öhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo pfeili	Chamaeleonidae		Rauscheröd	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1984; Schleich 1985b; Böhme 2003; 3öhme & Ilg 2003; Čerňanský 2011a; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo simplex	Chamaeleonidae		Randecker Maar	Germany	Miocene (MN 5)	Schleich 1994; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sulcodentatus	Chamaeleonidae		Massendorf	Germany	Miocene (Burdigalian, MN 5)	schleich 1994; Böhme 2003; Böhme & Ilg 2003; 3olet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sulcodentatus	Chamaeleonidae	Chamaeleo cf. C. sulcodentatus	Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	3öhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sulcodentatus	Chamaeleonidae		Göttschlag 1b	Germany	Miocene (MN 6)	3öhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sulcodentatus	Chamaeleonidae	Chamaeleo cf. C. sulcodentatus	Rümikon	Switzerland	Middle Miocene (Langhian/Serravallian, MN 6)	3öhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo ?sulcodentatus/bavaricus	Chamaeleonidae	Chamaeleo bavaricus	Puttenhausen classic (=Puttenhausen 1)	Germany	Miocene (Burdigalian, MN 5)	3öhme 2003; Böhme & IIg 2003; Abdul Aziz et ıl. 2008; Abdul Aziz et al. 2010; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae	Chamaeleo sp. 1; Chamaeleo sp. 2	Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	3öhme 2003; Böhme & Ilg 2003; Kosma 2004; 3olet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae	Chamaeleo (vel Agama) sp.	Rembach, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Kosma 2004; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae	Chamaeleo (vel Agama) sp.	Puttenhausen E	Germany	Miocene (Burdigalian)	Schleich 1985b; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Georgalis et al. 2016a

Chamaalao en	Chamaalaonidaa		Hibodan	Switzerland	Miocene (Burdigalian, MN	Böhme 2003; Böhme & Ilg 2003; Bolet & Evans
Cimmeteo ap.	Chanacteonnac		TIDOUCI	DW ILZCI TAILO	4a/MN 4b)	2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae		Altenstadt	Germany	Miocene (MN 5)	Böhme 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae		Niederaichbach	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae		Niederaichbach (links)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003, Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae	Chamaeleo (vel Agama) sp.	Puttenhausen 2	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae		Schiessen	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae	?Chamaeleo sp.	Walda 2 (oben)	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae		Steinberg (Ries)	Germany	Middle Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae		Uzwil-Nutzenbuech	Switzerland	Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleo sp.	Chamaeleonidae		Ornberg	Switzerland	Miocene (Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Čerňanský 2011a; Bolet & Evans 2013b; Georgalis et al. 2016a
cf. Chamaeleo sp.	Chamaeleonidae		Langenau 1	Germany	Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Georgalis et al. 2016a
Chamaeleonidae sp. B	Chamaeleonidae		Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2010b; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleonidae indet.	Chamaeleonidae		Petersbuch 2	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme & Ilg 2003; Čerňanský 2011a; Čerňanský 2016, Georgalis et al. 2016a
Chamaeleonidae indet.	Chamaeleonidae		Langenau 1	Germany	Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Čerňanský 2011a; Bolet & Evans 2013b; Georgalis et al. 2016a
Chamaeleonidae indet.	Chamaeleonidae	Chamaeleo cf. C. caroliquarti	Aliveri	Greece	Early Miocene (MN 4)	Böhme & Ilg 2003; Delfino 2004b; Georgalis et al. 2016a; this work
Chamaeleonidae indet.	Chamaeleonidae		Sibnica	Serbia	Early Miocene (MN 4)	Jovanović et al. 2002; Đurić 2016
Chamaeleonidae indet.	Chamaeleonidae	'Agama sp.; ?Chamaeleo sp.; Agamidae vel Chamaeleonidae indet.	Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Chamaeleonidae indet.	Chamaeleonidae	Reptilia incertae sedis	Opole 2 (= Nowa Wies Królewska II)	Poland	Miocene (Serravallian, MN 7)	Młynarski et al. 1982; Böhme & Ilg 2003; Georgalis et al. 2016a
?Chamaeleonidae tooth morphotype 1	Chamaeleonidae		Hambach 6C	Germany	Early middle Miocene (Langhian, MN 5)	Čerňanský et al. 2016c

?Chamaeleonidae tooth mornhotyne 2	Chamaeleonidae		Hambach 6C	Germany	Early middle Miocene (I anghian, MN 5)	Čerňanský et al. 2016c
?Chamaeleonidae indet.	Chamaeleonidae		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
?Chamaeleonidae indet.	Chamaeleonidae		Wannenwaldtobel 2	Germany	Miocene (Langhian, MN 6)	Čerňanský 2011a; Georgalis et al. 2016a
Agamidae vel Chamaeleonidae indet.	Agamidae/Chamaeleonid ae		Günzburg 2/4 Umgehung tiefere Bereiche der Sande	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Agamidae vel Chamaeleonidae indet.	Agamidae/Chamaeleonid ae		Attenfeld	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Agamidae vel Chamaeleonidae indet.	Agamidae/Chamaeleonid ae		Eitensheim	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Agamidae vel Chamaeleonidae indet.	Agamidae/Chamaeleonid ae		Unterempfenbach 1b	Germany	Early Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Agamidae vel Chamaeleonidae indet.	Agamidae/Chamaeleonid ae		Aliveri	Greece	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Agamidae vel Chamaeleonidae indet.	Agamidae/Chamaeleonid ae		Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Agamidae vel Chamaeleonidae indet.	Agamidae/Chamaeleonid ae		Laimering 4a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Acrodonta indet.	Acrodonta indet.	Agama sp.; Agamidae indet.	La Grive-Saint-Alban	France	Miocene	Estes 1983; Bailon 1991; Delfino et al. 2008b; Blain et al. 2016a
Hemidactylus turcicus	Gekkonidae		Lazaret Cave	France	Middle Pleistocene/Holocene	Bailon 1991
Hemidactylus turcicus	Gekkonidae	Gekkonidae indet.	Liko BA	Greece	Upper Pleistocene	Delfino 2004b; this work
Hemidactylus turcicus	Gekkonidae		Grotta Corbeddu	Italy	Holocene	Delfino 2006
Hemidactylus cf. H. turcicus	Gekkonidae	Tarentola cf. T. mauritanica; Tarentola mauritanica	Valdemino Cave	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2004c; Delfino 2006; Villa 2015; Villa & Delfino 2015; this work
Gekkonidae indet. sp. 1	Gekkonidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Gekkonidae indet. sp. 2	Gekkonidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Gekkonidae indet. sp. A	Gekkonidae		Sète	France	Middle Pliocene (MN 15)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007
Gekkonidae indet.	Gekkonidae		Oschiri	Italy	Lower Miocene (Aquitanian, MN 1/MN 2b)	Böhme & Ilg 2003; Venczel & Sanchíz 2006; Zoboli & Pillola 2017
Gekkonidae indet.	Gekkonidae	<i>Gekko</i> sp.	Chavroches P1	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	<i>Gekko</i> sp.	Chavroches P1C2	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	<i>Gekko</i> sp.	Le Gondailly	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	<i>Gekko</i> sp.	Montaigu-le-Blin 87 a Sorex	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme 2003; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae		Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Schleich 1985b

Gekkonidae indet.	Gekkonidae	Béon 1 (= Montréal-du-Gers)	France	Lower Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Rage & Bailon 2005
Gekkonidae indet.	Gekkonidae	Rembach, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Kosma 2004
Gekkonidae indet.	Gekkonidae	Obergänserndorf, Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003; Tempfer 2005
Gekkonidae indet.	Gekkonidae	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b
Gekkonidae indet.	Gekkonidae	Unterempfenbach 1b	Germany	Early Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Walda	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b
Gekkonidae indet.	Gekkonidae	Artesilla	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Córcoles	Spain	Early Miocene (Burdigalian)	Bailon 1991; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	San Roque 5	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Vargas 1A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Schmiedrued-Pyffrüti level 642, Swiss Molasse Basin	Switzerland	Early Middle Miocene (Langhian)	Böhme & Ilg 2003; Jost et al. 2015
Gekkonidae indet.	Gekkonidae	Puttenhausen	Germany	Miocene (MN 5/6)	Schleich 1985b
Gekkonidae indet.	Gekkonidae	Goldberg 9	Germany	Miocene (Langhian, MN 6)	Schleich 1985a; Schleich 1985b
Gekkonidae indet.	Gekkonidae	Petersbuch 39	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Caseton 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Las Umbrias 11	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Las Umbrias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Regajo 2	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Valdemoros 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Valdemoros 3B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Valdemoros 3F	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Valdemoros 7B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Valdemoros 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Valdemoros 8C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003

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: Ilg 2003	: IIg 2003	: Ilg 2003	: Ilg 2003; Böhme & Vasilyan 2014	: Ilg 2003; Venczel & Știucă 2008	: Ilg 2003	: Ilg 2003	: Ilg 2003	: Ilg 2003	: Ilg 2003; Venczel & Hir 2013	: Ilg 2003; Venczel & Hir 2013	: Ilg 2003; Tempfer 2005	: Ilg 2003; Bover et al. 2014	002; Böhme & Ilg 2003; Delfino 2013	c Ilg 2003; Bailon et al. 2005; Bailon et Bover et al. 2014	t Ilg 2003; Bailon et al. 2005; Bailon et Bover et al. 2014	2001; Böhme & Ilg 2003	& Gardner 2005				
Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Böhme &	Delfino 2	Böhme & al. 2010;	Böhme & al. 2010;	Venczel 2	Venczel d				
Middle Miocene (Langhian)	Middle Miocene (Langhian)	Middle Miocene (Langhian)	Late middle Miocene	Late middle Miocene (Serravallian, MN 8)	Miocene (Serravallian)	Miocene (Serravallian)	Miocene (Serravallian/Tortonian)	Late Miocene (Serravallian/Tortonian, MN 9)	Miocene (Vallesian, MN9)	Miocene (Vallesian, MN9)	Upper Miocene (Tortonian, MN 11)	Miocene/Pliocene (Messian/Zanclean)	Upper Miocene (Messinian)/lower Pliocene	Between upper Miocene and Pleistocene	Between upper Miocene and Pleistocene	Pliocene (Zanclean, MN 14)	Pliocene (Zanclean, MN 15)				
Spain	Spain	Spain	Austria	Romania	Spain	Spain	Spain	Ukraine	Hungary	Hungary	Austria	Spain	Italy	Italy	Italy	Italy	Italy	Spain	Spain	Hungary	Hungary
Vargas 6	Vargas 7	Vargas 8B	Gratkorn	Tauț	Las Planas 5L	Las Umbrias 21	Escobosa de Calatañazor	Gritsev	Felsötárkány 1	Felsötárkány 2	Kohfidisch	Na Burguesa-1, Mallorca	Bosco, Gargano "Terre Rosse"	Cantatore, Gargano "Terre Rosse"	Chirò, Gargano "Terre Rosse"	Falcone, Gargano "Terre Rosse"	Rinascita, Gargano "Terre Rosse"	Punta Nati 3, Menorca	Punta Nati 12, Menorca	Osztramos 1	Csarnóta 2
			-												-						
Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae	Gekkonidae
Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.	Gekkonidae indet.

Gekkonidae indet.	Gekkonidae		Balaruc II	France	Middle/late Pliocene (MN 15/16)	Bailon 1989; Bailon 1991; Bailon 1995; Böhme & Ilg 2003; Bailon & Blain 2007
Gekkonidae indet.	Gekkonidae		Capo Mannu D1 Local Fauna (= Mandriola)	Italy	Late Pliocene (Piacenzian)	Kotsakis 1980; Estes 1983; Bailon 1991; Vigne et al. 1997; Böhme & Ilg 2003; Delfino et al. 2011
Gekkonidae indet.	Gekkonidae		Cueva Victoria	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae		Almenara Casablanca 1	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae	Gekkonidae indet. Type B	Medas Islands	Spain	Early Pleistocene	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Agustí et al. 2009; Blain et al. 2016a
Gekkonidae indet.	Gekkonidae		Ponton	Spain	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Gekkonidae indet.	Gekkonidae		Torralba den Salort, Menorca	Spain	Holocene (III/II century BC)	Sanders 1984
Gekkonidae indet.	Gekkonidae		Monte di Tuda T2	France	Holocene (Roman Age)	Böhme & Ilg 2003; Bailon 2004
Gekkonidae indet.	Gekkonidae		Monte di Tuda T3	France	Holocene (Iron Age/Present)	Vigne et al. 1997
Gekkonidae indet.	Gekkonidae		Monte di Tuda T1	France	Holocene (Middle Age/Present)	Vigne et al. 1997
Gekkonidae indet.	Gekkonidae		Unknown locality, Corsica	France	Holocene	Bailon & Rage 2012
aff. Gekkonidae indet.	Gekkonidae		San Roque 3	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Tarentola mauritanica	Phyllodactylidae	Tarentola sp.	Cueva Victoria	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008a; Agustí et al. 2009; Blain 2009; Blain 2012- 2014
Tarentola mauritanica	Phyllodactylidae		Quibas	Spain	Early Pleistocene (Calabrian)	Montoya et al. 1999; Montoya et al. 2001; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009
Tarentola mauritanica	Phyllodactylidae		Cementerio de Orce	Spain	Early Pleistocene	Bailon 1991; Blain 2005; Blain 2009
Tarentola mauritanica	Phyllodactylidae		Lazaret Cave	France	Middle Pleistocene/Holocene	Bailon 1991
Tarentola mauritanica	Phyllodactylidae		Higueral de Valleja Cave	Spain	Upper Pleistocene (late Paleolithic)	Böhme & Ilg 2003; Jennings et al. 2009
Tarentola mauritanica	Phyllodactylidae		Gorham's Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001; Böhme & Ilg 2003; Blain et al. 2013
Tarentola mauritanica	Phyllodactylidae		Vanguard Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001; Böhme & Ilg 2003
Tarentola mauritanica	Phyllodactylidae	Tarentola cf. T. mauritanica	K 22, San Vito lo Capo	Italy	Late Pleistocene (or Holocene)	Delfino 2002; Böhme & Ilg 2003; Delfino 2006; Villa 2015; Villa & Delfino 2015
Tarentola mauritanica	Phyllodactylidae		Unknown locality, Corsica	France	Holocene (middle/late Neolithic)	Bailon & Rage 2012
Tarentola mauritanica	Phyllodactylidae		Cova Colomera A sup., Sierra de Montsec	Spain	Holocene (Bronze Age)	Böhme & Ilg 2003; Blain et al. 2016b
?Tarentola mauritanica	Phyllodactylidae		A Teppa di U Lupinu Cave, Corsica	France	Latest Pleistocene/earliest Holocene	Salotti et al. 2008

Böhme & Ilg 2003	López-García et al. 2014	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009	Forgia et al. 2013	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009	Delfino 2002; Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; this work	this work	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; this work	this work	Delfino 2002; Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; this work	Müller 2001; Böhme & Ilg 2003; Čerňanský & Bauer 2010; Daza et al. 2014; Čerňanský et al. 2015b	Böhme & Ilg 2003; Čerňanský & Bauer 2010; Rage 2013; Daza et al. 2014; Čerňanský et al. 2015b; Čerňanský 2016	Müller 2001; Müller & Mödden 2001; Böhme & Ilg 2003; Daza et al. 2014; Čerňanský et al. 2015b	Estes 1969; Estes 1983; Bailon 1991; Müller 2001; Müller & Mödden 2001; Čerňanský 2011b; Daza et al. 2014	Villa 2015; Colombero et al. 2017; this work	Hoffstetter 1946; Estes 1969; Estes 1983; Schleich 1987; Bailon 1991; Müller & Mödden 2001: Daza et al. 2014; Čerňanský et al. 2015b
Upper Pleistocene	Upper Pleistocene	Early Pleistocene (Gelasian)	Holocene	Late Pliocene/early Pleistocene (MN 16)	Early Pleistocene (Gelasian)	Pleistocene (Calabrian)	Pleistocene (Calabrian)	Middle Pleistocene	Middle Pleistocene	Upper Pleistocene	Lower Miocene (Aquitanian, MN 2a)	Lower Miocene (Burdigalian, MN 3a)	Lower Miocene (Aquitanian, MN 2)	Middle Miocene	Latest Miocene (Messinian, p- ev2)	Miocene (Aquitanian)
Spain	Spain	Spain	Italy	Spain	Spain	Italy	Italy	Italy	Italy	Italy	France	Czech Republic	Germany	Slovakia	Italy	France
Cueva del Boquete de Zafarraya	Galls Carboners Cave	Almenara Casablanca 1	Vallone Inferno	Cova Bonica	Vallirana	Cava VI 3, Monte Tuttavista	Cava VII blocco strada, Monte Tuttavista	Cava XI - Canidae, Monte Tuttavista	Cava XI rondone, Monte Tuttavista	Cava VI Banco 6, Monte Tuttavista	Montaigu-le-Blin	Merkur North	Inflata beds, Oppenheim/Nierstein quarry	Devínska Nová Ves	Moncucco Torinese	Saint-Gérand-le-Puy
		Tarentola cf. T. mauritanica; Tarentola mauritanica		cf. Tarentola mauritanica	cf. Tarentola mauritanica; Tarentola mauritanica	Gekkonidae indet.		Gekkonidae indet.		Gekkonidae indet.				cf. Phyllodactylus sp.; Phyllodactylus sp.		
Phyllodactylidae	Phyllodactylidae	Phyllodactylidae	Phyllodactylidae	Phyllodactylidae	Phyllodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae	Sphaerodactylidae
Tarentola cf. T. mauritanica	cf. Tarentola mauritanica	Tarentola sp.	Tarentola sp.	cf. Tarentola sp.	cf. Tarentola sp.	Euleptes cf. E. europaea	Euleptes cf. E. europaea	Euleptes cf. E. europaea	Euleptes cf. E. europaea	Euleptes cf. E. europaea	Euleptes gallica	Euleptes gallica	Euleptes sp.	Euleptes sp.	cf. Euleptes sp.	Gerandogekko arambourgi

Gerandogekko gaillardi	Sphaerodactylidae		La Grive-Saint-Alban	France	Upper Miocene (Vindobonian)	Hoffstetter 1946; Estes 1969; Estes 1983; Schleich 1987; Bailon 1991; Müller & Mödden 2001; Daza et al. 2014
Palaeogekko risgoviensis	Gekkonoidea exclusive of Eublepharidae	Gekkonidae indet.	Goldberg 10	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Palaeogekko risgoviensis	Gekkonoidea exclusive of Eublepharidae	Gekkonidae indet.	Steinberg (Ries)	Germany	Middle Miocene (Langhian/Serravallian, MN 6)	Schleich 1985b; Schleich 1987; Bailon 1991; Böhme & Ilg 2003; Daza et al. 2014
Gekkota n.gen. n.sp.	Gekkota indet.	Euleptes sp.; Gekkonidae indet.	Cava Pirro, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2013; Villa 2015; Villa & Delfino 2015; this work
Gekkota n.gen. n.sp.	Gekkota indet.	Euleptes sp; Gekkonidae indet.	Chirò, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2013; Villa 2015; Villa & Delfino 2015; this work
Gekkota n.gen. n.sp.	Gekkota indet.	Euleptes sp.; Gekkonidae indet.	San Giovannino, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2013; Villa 2015; Villa & Delfino 2015; this work
Gekkota n.gen. n.sp.	Gekkota indet.	Euleptes sp.; Gekkonidae indet.	Gargano "Terre Rosse" (F - Coll. Firenze)	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2013; Villa 2015; Villa & Delfino 2015; this work
Gekkota indet.	Gekkota indet.		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b
Gekkota indet.	Gekkota indet.		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Gekkota indet.	Gekkota indet.		Sibnica	Serbia	Early Miocene (MN 4)	Đurić 2016
Gekkota indet.	Gekkota indet.	Gekkonidae indet.	Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Gekkota indet.	Gekkota indet.	Gekkonidae indet.	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Müller 2001; Böhme & Ilg 2003; Čerňanský & Bauer 2010; Daza et al. 2014
Gekkota indet.	Gekkota indet.	Gekkonidae indet.	Abocador de Can Mata, Vallès Penedès Basin	Spain	Middle Miocene (MN 6/MN 7+8)	Böhme & Ilg 2003; this work
Gekkota indet.	Gekkota indet.	Gekkonidae indet.	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Gekkota indet.	Gekkota indet.		Ecoparc de Can Mata, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	this work
Gekkota indet.	Gekkota indet.		Can Jofresa, Vallès Penedès Basin	Spain	Late Miocene (MN 10)	this work
Gekkota indet.	Gekkota indet.	Gekkonidae indet.	Maritsa A	Greece	Early Pliocene (MN 14)	Delfino 2004b; this work
Gekkota indet.	Gekkota indet.	Gekkonidae indet.	San Teodoro	Italy	Late Pleistocene	Bonfiglio et al. 2001; Delfino 2002; Böhme & Ilg 2003; Villa 2015; Villa & Delfino 2015
cf. Gekkota indet.	Gekkota indet.		Tourkobounia 1	Greece	Late Pliocene (MN 16)	this work
Acanthodactylus erythrurus	Lacertidae		Cueva Victoria	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2012-2014

3öhme & Ilg 2003; Jennings et al. 2009	Gleed-Owen 2001; Böhme & Ilg 2003; Blain 2012-2014; Blain et al. 2013	Gleed-Owen 2001; Böhme & Ilg 2003; Blain 2012-2014	Crespo 2001; Crespo 2002; Böhme & Ilg 2003	3arbadillo et al. 1997; Crespo 2001	3öhme & Ilg 2003; Blain 2005	3arbadillo 1989; Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009; Blain 2009; Blain 2012-2014	3öhme & Ilg 2003	Marquina et al. 2017	3öhme & Ilg 2003	Roček 1984; Augé & Rage 2000; Böhme 2003; Böhme & Ilg 2003; Augé et al. 2003; Čerňanský 2016	3öhme 1999a; Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008	3öhme 2003	3öhme 2003; Böhme & Ilg 2003	Augé & Rage 2000; Böhme & Ilg 2003	3öhme 2003; Böhme & Ilg 2003	3öhme 2003; Böhme & Ilg 2003	Müller 2001	his work	3öhme & Ilg 2003; Bailon 2004; Delfino 2006	salotti et al. 1997; Böhme & Ilg 2003; Bailon 2004; Bailon & Rage 2012
Upper Pleistocene (late	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene	Plio-Pleistocene	Early Pleistocene (Gelasian)	Middle Pleistocene (close to 600 ka)	Upper Pleistocene	Upper Pleistocene/Holocene (middle Palaeolithic, MIS 3)	Early Pliocene (Zanclean)	Early Miocene (Burdigalian, MN	Miocene (Burdigalian, MN 5)	Miocene (MN 4b)	Miocene (Burdigalian, MN 5)	Middle Miocene (Langhian/Serravallian; MN 6)	Middle Miocene (Langhian/Serravallian, MN 6)	Miocene (Serravallian, MN 8)	Lower Miocene (Aquitanian, I MN 2a)	Early Miocene (MN 4)	Late Pliocene/early Pleistocene	Middle Pleistocene
Spain	England	England	Portugal	Spain	Spain	Spain	Spain	Spain	Spain	Czech Republic	Germany	Germany	Germany	France	Switzerland	Switzerland	France	Spain	Italy	France
Higueral de Valleja Cave	Gorham's Cave, Gibraltar	Vanguard Cave, Gibraltar	Guia	Guadix-Baza	Almenara Casablanca 1	Cúllar de Baza 1	Cueva del Boquete de Zafarraya	El Salt	La Gloria 4	Dolnice	Sandelzhausen	Erkertshofen 1	Walda 2 (oben)	Sansan	Rümikon	Imenberg	Montaigu-le-Blin	Els Casots, Vallès Penedès Basin	Nuraghe Su Casteddu	Castiglione 3, Corsica
	cf. Acanthodactylus erythrurus	cf. Acanthodactylus erythrurus																	Archaeolacerta cf. A. bedriagae	
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Acanthodactylus erythrurus	Acanthodactylus erythrurus	Acanthodactylus erythrurus	Acanthodactylus erythrurus	Acanthodactylus cf. A. erythrurus	Acanthodactylus cf. A. erythrurus	Acanthodactylus cf. A. erythrurus	Acanthodactylus cf. A . erythrurus	cf. Acanthodactylus erythrurus	Acanthodactylus sp	Amblyolacerta dolnicensis	Amblyolacerta dolnicensis	Amblyolacerta sp.	Amblyolacerta sp.	Amblyolacerta sp.	?Amblyolacerta sp.	?Amblyolacerta sp.	cf. Amblyolacerta sp.	cf. Amblyolacerta sp.	Archaeolacerta bedriagae	Archaeolacerta bedriagae

Archaeolacerta bedriagae	Lacertidae		Gritulu GR1	France	Late Pleistocene (Tardiglacial)	Vigne et al. 2002; Böhme & Ilg 2003; Bailon 2004
Archaeolacerta bedriagae	Lacertidae		Castiglione 1, Corsica	France	Upper Pleistocene	Ferrandini et al. 1995; Vigne et al. 1997; Böhme & Ilg 2003; Bailon 2004
Archaeolacerta bedriagae	Lacertidae		A Teppa di U Lupinu Cave, Corsica	France	Latest Pleistocene/earliest Holocene	Salotti et al. 2008
Archaeolacerta bedriagae	Lacertidae		Monte di Tuda T3	France	Holocene (Iron Age/Present)	Vigne et al. 1997
Archaeolacerta bedriagae	Lacertidae		Monte di Tuda T1	France	Holocene (Middle Age/Present)	Vigne et al. 1997
cf. Archaeolacerta bedriagae	Lacertidae		Macinaggio	France	Upper Pleistocene/Holocene	Böhme & Ilg 2003; Bailon 2004
cf. Archaeolacerta bedriagae	Lacertidae	Archaeolacerta bedriagae	Monte Leone ML2	France	Holocene (early Neolithic)	Vigne et al. 1997; Böhme & Ilg 2003; Bailon 2004
cf. Archaeolacerta bedriagae	Lacertidae	Archaeolacerta bedriagae	Monte di Tuda T2	France	Holocene (Roman Age)	Böhme & Ilg 2003; Bailon 2004
Dalmatolacerta oxycephala	Lacertidae		Bad Deutsch-Altenburg 4B	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007
Edlartetia sansaniensis	Lacertidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003; Böhme 2010b
Edlartetia sansaniensis	Lacertidae	Lacerta sansaniensis	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Lartet 1851; Gervais 1859; Młynarski 1956; Młynarski 1962; Roček 1984; Augé & Rage 2000: Böhme & Ilg 2003; Rage & Bailon 2005; Tempfer 2005
Edlartetia sansaniensis	Lacertidae		Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Böhme & Ilg 2003; Tempfer 2005
Edlartetia cf. E. sansaniensis	Lacertidae		Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Edlartetia sp.	Lacertidae		Massendorf	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003
Edlartetia sp.	Lacertidae		Gratkorn	Austria	Late middle Miocene	Böhme & Ilg 2003; Böhme & Vasilyan 2014
?Edlartetia sp.	Lacertidae		Toril 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
cf. Edlartetia sp.	Lacertidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Villa & Delfino 2017; this work
Eremias sp.	Lacertidae		Ozyornoye-1, east bank of Jalpug Lake	Ukraine	Middle Pleistocene/Holocene	Böhme & Ilg 2003
Janosikia ulmensis	Lacertidae	Ophisaurus moguntinus; Ophisaurus ulmensis ; Palaeocordylus ulmensis	Ulm Westtangente	Germany	Early Miocene	Gerhardt 1903; Młynarski 1956; Böhme & Ilg 2003; Čerňanský et al. 2016b
Janosikia ulmensis	Lacertidae		Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Villa & Delfino 2017; this work

						Böhme & Ilg 2003: Ivanov & Böhme 2011:
Janosikia ulmensis	Lacertidae	?Cordylidae indet.	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Čerňanský et al. 2016c; Villa & Delfíno 2017;
						this work
Lacerta agilis	Lacertidae		Bad Deutsch-Altenburg 3	Austria	Plio-Pleistocene	Rauscher 1992
Lacerta agilis	Lacertidae		Bad Deutsch-Altenburg 12	Austria	Plio-Pleistocene	Rauscher 1992
Lacerta agilis	Lacertidae		Bad Deutsch-Altenburg 30A	Austria	Plio-Pleistocene	Rauscher 1992
Lacerta agilis	Lacertidae		Bad Deutsch-Altenburg 2C1	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007
Lacerta agilis	Lacertidae		Bad Deutsch-Altenburg 4B	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007
Lacerta agilis	Lacertidae	?Lacerta cf. L. agilis	Kielniki 3A	Poland	Lower Pleistocene	Młynarski 1977; Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae	Lacerta sp. (cf. agilis)	Zalesiaki A	Poland	Lower Pleistocene	Młynarski 1977; Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Potocka Zijalka	Croatia	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Hunas	Germany	Middle Pleistocene	Böhme 1997; Holman 1998; Böhme & Ilg 2003; Böhme 2011
Lacerta agilis	Lacertidae	Lacerta sp. (cf. ?agilis)	Kozi Grzbiet	Poland	Middle Pleistocene	Młynarski 1977; Szyndlar 1981; Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Chernyi Yar-Nizhnee Zaimishche, Volgograd	Russia	Middle Pleistocene	Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Koziy Ovrag	Russia	Middle Pleistocene	Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Kuznetsovka, left board of Podgornyi Buerak	Russia	Middle Pleistocene	Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Vol`naya Vershina-3	Russia	Middle Pleistocene	Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Šandalja near Pula	Croatia	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Betzenstein	Germany	Upper Pleistocene	Estes 1983
Lacerta agilis	Lacertidae		Gaiskirche	Germany	Upper Pleistocene	Estes 1983
Lacerta agilis	Lacertidae		Grundfelsen Cave	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Ranis Ilsenhöhle	Germany	Upper Pleistocene	Böhme 1997; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Steinheim an der Murr	Germany	Upper Pleistocene	Bloos et al. 1991; Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Weimar-Ehringsdorf Site Complex, Pariser Unit	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Pisede	Germany	Upper Pleistocene/Holocene	Holman 1998; Böhme & Ilg 2003
Lacerta agilis	Lacertidae		Smolucka Pećina Cave	Serbia	Upper Pleistocene/Holocene	Paunović & Dimitrijević 1990; Holman 1998; Böhme & Ilg 2003
cf. Lacerta agilis	Lacertidae	Lacerta agilis	Kärlich G	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003; Holman & van Kolfschoten 2011
Lacerta cf. L. agilis	Lacertidae		Ivanovce	Slovakia	Upper Pliocene (Zanclean, MN 15)	Böhme & Ilg 2003; Čerňanský 2011b
Lacerta cf. L. agilis	Lacertidae		Chismikioi	Moldova	Lower Pleistocene (Calabrian)	Redkozubov 2003
Lacerta cf. L. agilis	Lacertidae		Koziy Ovrag	Russia	Middle Pleistocene	Böhme & Ilg 2003

Böhme & Ilg 2003	Böhme & Ilg 2003	Blain et al. 2014c; Blain et al. 2014d	Ivanova et al. 2016	Holman 1998; Böhme & Ilg 2003	Virág et al. 2013	Ratnikov 1996	Jánossy 1986	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007	Lartet 1851; Gervais 1859; De Stefano 1903; Estes 1983; Roček 1984; Augé & Rage 2000	Bailon 1991; Hanquet et al. 2010; Bailon & Rage 2012	Bailon & Rage 2012	Moncel et al. 2010	Gervais 1859; Estes 1983; Roček 1984; Rage & Augé 1993	Augé & Smith 2009; Böhme & Ilg 2003; Čerňanský et al. 2015b	Augé et al. 2003	Müller 1996; Böhme 2002; Augé et al. 2003; Böhme & Ilg 2003; Čerňanský et al. 2015b	Böhme & Ilg 2003; Čerňanský et al. 2015b	Čerňanský 2016	Jánossy 1986	Depéret 1890; Młynarski 1956; Estes 1983; Roček 1984	Caloi et al. 1986; Bonfiglio & Insacco 1992; Bonfiglio et al. 1997; Delfino & Bailon 2000; Bailon 2004; Tschopp et al. 2016	Bonfiglio et al. 1997; Delfino & Bailon 2000; Bonfiglio et al. 2002; Bailon 2004; Tschopp et al. 2016
Middle Pleistocene	Middle Pleistocene	Middle/Upper Pleistocene (MIS 5/3)	Late Pleistocene	Upper Pleistocene	Upper Pleistocene	Holocene	Pliocene (Zanclean, MN 15)	Lower Pleistocene	Middle Miocene (Langhian/Serravallian; MN 6)	Middle Pleistocene (MIS 6)	Late Pleistocene (Isotopic Stage 5)	Upper Pleistocene	Pliocene	Lower Miocene (Aquitanian, MN2a)	Lower Miocene (Aquitanian, MN 2a)	Lower Miocene (Aquitanian, MN2a)	Miocene (Aquitanian, MN 2a)	Early Miocene (MN 4)	Pliocene (Zanclean, MN 15)	Pliocene	Middle Pleistocene	Middle/Late Pleistocene
Russia	Ukraine	Belgium	Bulgaria	Germany	Hungary	Belarus	Hungary	Austria	France	France	France	France	France	France	France	France	Germany	Austria	Hungary	France	Italy	Italy
Kuznetsovka, left board of Podgornyi Buerak	Nagornoye-1, east shore of Kagul Lake	Scladina	Magura Cave	Grabschütz	Vaskapu Cave	Voroncha	Csarnóta 2	Bad Deutsch-Altenburg 4B	Sansan	Lazaret Cave	Baume Moula-Guercy	Abri des Pêcheurs	Issoire	Poncenat	Montaigu-le-Blin	Poncenat	Wiesbaden-Amöneburg	Oberdorf	Csarnóta 2	Rousillon	Poggio Schinaldo	Contrada Fusco
										Lacerta cf. L. viridis ; Lacerta viridis		Lacerta cf. L. viridis										
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Lacerta cf. L. agilis	Lacerta cf. L. agilis	Lacerta cf. L. agilis	Lacerta cf. L. agilis	Lacerta cf. L. agilis	Lacerta cf. L. agilis	Lacerta cf. L. agilis	Lacerta aff. L. agilis	Lacerta altenburgensis	Lacerta bifidentata	Lacerta bilineata	Lacerta bilineata	Lacerta cf. L. bilineata	Lacerta crassidens	Lacerta filholi	Lacerta s.l. filholi	Lacerta poncenatensis	Lacerta poncenatensis	Lacerta cf. L. poncenatensis	Lacerta ruscinensis	Lacerta ruscinensis	Lacerta siculimelitensis	Lacerta siculimelitensis

accridae Wied Incita Quarty Malta Upp Creece Piet accridae metrolae derece Malta Piet accridae metroland Cave Greece Piet Piet accridae metroland Cave Greece Piet Piet accridae metroland Deutsch-Altenburg 20 Austria Pio accridae Bad Deutsch-Altenburg 20A Austria Low accridae Bad Deutsch-Altenburg 4B Austria Low accridae Bad Deutsch-Altenburg 2C1 Austria Low accridae Metrola Bad Deutsch-Altenburg 4B Austria Low accridae Metrola Bad Deutsch-Altenburg 4B Austria Low accridae Metrola Bad Deutsch-Altenburg 4B Austria Low accridae <
accrtidae Wied Incia Quarry M accrtidae Vraoma Cave Gr accrtidae Petralona Cave Gr accrtidae Bad Deutsch-Altenburg 20 A accrtidae Bad Deutsch-Altenburg 30A A accrtidae Bad Deutsch-Altenburg 20A B accrtidae Bad Deutsch-Altenburg 20A B accrtidae Deutsch-Altenburg 20A B accrtid
acertidae acertidae

?Lacerta viridis	Lacertidae	Lacerta cf. L. virids	Rębielice Królewskie 1A	Poland	Upper Pliocene (Piacenzian, MN	Młynarski 1977; Estes 1983; Młynarski et al. 1984: Böhme & Ilø 2003: Ivanov 2007
?Lacerta viridis	Lacertidae	Lacerta cf. L. virids	Rębielice Królewskie 2	Poland	Upper Pliocene (Piacenzian, MN 16)	Młynarski 1977; Estes 1983; Młynarski et al. 1984; Böhme & Ilg 2003; Ivanov 2007
Lacerta cf. L. viridis	Lacertidae		Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Böhme & Ilg 2003; Tempfer 2005; Čerňanský 2010b
Lacerta cf. L. viridis	Lacertidae		Polgárdi 4	Hungary	Miocene (Messinian, MN 13)	Młynarski 1962; Böhme & Ilg 2003; Venczel 2006; Čerňanský 2010b
Lacerta cf. L. viridis	Lacertidae		Nogaisk	Ukraine	Pliocene (Zanclean/Piacenzian)	Böhme & Ilg 2003
Lacerta cf. L. viridis	Lacertidae	?Lacerta viridis	W ęże II	Poland	Upper Pliocene (Piacenzian, MN 16)	Młynarski et al. 1984; Böhme & Ilg 2003; Ivanov 2007; Čerňanský 2011b; Čerňanský et al. 2016c
Lacerta cf. L. viridis	Lacertidae		Zalesiaki B	Poland	Upper Pliocene	Młynarski 1977
Lacerta cf. L. viridis	Lacertidae		Novaya Etulia 2	Moldova	Pliocene/Pleistocene (Piacenzian/Gelasian, MN 16)	Böhme & Ilg 2003
Lacerta cf. L. viridis	Lacertidae		Kotlovina, middle level	Ukraine	Lower Pleistocene (Gelasian, MN 17)	Böhme & Ilg 2003
Lacerta cf. L. viridis	Lacertidae		Sitia 2, Crete	Greece	Lower Pleistocene	Böhme & Ilg 2003; Bailon 2004
Lacerta cf. L. viridis	Lacertidae		Beremend 16/17	Hungary	Lower Pleistocene	Böhme & Ilg 2003
Lacerta cf. L. viridis	Lacertidae	Lacerta viridis	Villány 5 and 8	Hungary	Lower Pleistocene	Estes 1983; Jánossy 1986; Holman 1998; Venczel 1998; Böhme & Ilg 2003
Lacerta cf. L. viridis	Lacertidae		Somssich Hill 2	Hungary	Late early Pleistocene	Pazonyi et al. 2017
Lacerta cf. L. viridis	Lacertidae		Kozi Grzbiet	Poland	Middle Pleistocene	Szyndlar 1981; Holman 1998; Böhme & Ilg 2003
Lacerta cf. L. viridis	Lacertidae		Tarko	Hungary	Middle/Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
Lacerta cf. L. viridis	Lacertidae	Lacerta viridis	Artenac	France	Upper Pleistocene (middle Paleolithic)	Blain & Bailon 2003; Böhme & Ilg 2003; Blain & Villa 2006
Lacerta cf. L. viridis	Lacertidae		Vaskapu Cave	Hungary	Upper Pleistocene	Virág et al. 2013
Lacerta cf. L. viridis	Lacertidae		Baume Claire/Baume Sourde	France	Holocene (middle Neolithic)	Bailon 1991
Lacerta gr.L. viridis	Lacertidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Čerňanský 2010b; Čerňanský 2016
Lacerta gr.L. viridis	Lacertidae		Capo Mannu D1 Local Fauna (= Mandriola)	Italy	Late Pliocene (Piacenzian)	Böhme & Ilg 2003; Delfino & Rook 2008; Delfino et al. 2011
Lacerta gr.L. viridis	Lacertidae		Rivoli Veronese	Italy	Early Pleistocene (Gelasian; MN 17)	Delfino et al. 2008a; Villa et al. 2017; this work
Lacerta gr.L. viridis	Lacertidae	Lacerta sp.	Riparo Mezzena, Avesa	Italy	Earliest Middle Pleistocene	Bon et al. 1991; Delfino et al. 2008a
Lacerta gr.L. viridis	Lacertidae	Lacerta sp.	San Vito di Leguzzano 2, Val Grande	Italy	Earliest Middle Pleistocene	Bon et al. 1991; Delfino 2002; Böhme & Ilg 2003; Delfino et al. 2008a
Lacerta gr.L. viridis	Lacertidae		Scivolone, Brecce di Soave	Italy	Earliest Middle Pleistocene	Delfino et al. 2008a

Lacerta gr. L. viridis	Lacertidae		Fondo Cattie	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2013
Lacerta gr. L. viridis	Lacertidae		Riparo di Visogliano	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003
Lacerta gr. L. viridis	Lacertidae	Lacerta sp.	Valdemino Cave	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2004c
Lacerta gr. L. viridis	Lacertidae	Lacerta viridis	Viatelle, Brecce di Soave	Italy	Middle Pleistocene	Bon et al. 1991; Delfino et al. 2008a
Lacerta gr. L. viridis	Lacertidae		Caverna Generosa	Italy	Upper Pleistocene	Böhme & Ilg 2003; Bona et al. 2009
Lacerta gr. L. viridis	Lacertidae	Lacerta viridis	Grotta della Volpe, Val d'Avesa	Italy	Late Pleistocene	Bon et al. 1991; Delfino et al. 2008a
Lacerta gr. L. viridis	Lacertidae		Grotta Romanelli	Italy	Pleistocene	Delfino 2013
Lacerta gr.L. viridis	Lacertidae	Lacerta viridis	Sternatia	Italy	Pleistocene	Holman 1998; Böhme & Ilg 2003; Delfino 2013
Lacerta gr. L. viridis	Lacertidae		Gabrovizza	Italy	Late Pleistocene/Holocene	Delfino 2002; Böhme & Ilg 2003
Lacerta gr. L. viridis	Lacertidae		Lova, Campagna Lupia	Italy	Holocene (I cent. AD)	Delfino 2002; Böhme & Ilg 2003; Delfino et al. 2008a
Lacerta gr. L. viridis	Lacertidae		Tenuta Zuccarello, Marcon	Italy	Holocene (I cent. AD)	Delfino et al. 2008a; Villa et al. 2015; this work
Lacerta gr. L. viridis	Lacertidae		Grotta delle Mura	Italy	Holocene	Delfino 2013
Lacerta gr. L. viridis	Lacertidae	Lacerta sp.	Grotta dell'Edera	Italy	Holocene	Bon et al. 1991; Delfino & Bressi 2000; Delfino 2002; Böhme & Ilg 2003
Lacerta gr. L. viridis	Lacertidae		Vallone Inferno	Italy	Holocene	Forgia et al. 2013
cf. Lacerta gr. L. viridis	Lacertidae		Grotta della Fata Nana, Bosco Chiesanuova	Italy	Earliest Middle Pleistocene	Delfino et al. 2008a
Lacerta sp. (Lacerta viridis group)	Lacertidae	Lacerta viridis	Pellegrino breach, Monte Pellegrino	Italy	Lower Pleistocene	Estes 1983; Holman 1998; Delfino 2002; Böhme & Ilg 2003; Bailon 2004
Lacerta sp. (Lacerta viridis group)	Lacertidae	Lacerta viridis	Castellana	Italy	Middle/Upper Pleistocene	Delfino 2002; Böhme & Ilg 2003; Bailon 2004
Lacerta sp. (agilis size)	Lacertidae		Erd	Hungary	Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
Lacerta sp. ("viridis - ocellata group")	Lacertidae		Menorca	Spain	Pleistocene	Kotsakis 1981; Böhme & Zammit-Maempel 1982: Böhme & Corti 1993
Lacerta sp. 1	Lacertidae		Lautern 2	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae	Lacerta sp.	Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Forsthart	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Langenau 1	Germany	Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Offingen 2	Germany	Miocene (Burdigalian, MN 4b/5)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Lacerta sp. 1	Lacertidae		Adelschlag	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003

						Schlaich 1085h: Böhma 2003: Böhma & Ila 2003.
Lacerta sp. 1	Lacertidae	Lacerta sp.	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Miklas-Tempfer 2003; Abdul Aziz et al. 2008;
						Böhme 2010b
Lacerta sp. 1	Lacertidae		Bodman	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Ichenhausen 3	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Lacerta sp. 1	Lacertidae		Puttenhausen A	Germany	Miocene (Burdigalian)	Schleich 1985b; Böhme & Ilg 2003; Abdul Aziz et al. 2008
Lacerta sp. 1	Lacertidae		Puttenhausen E	Germany	Miocene (Burdigalian)	Schleich 1985b; Böhme & Ilg 2003; Abdul Aziz et al. 2008
Lacerta sp. 1	Lacertidae		Untereichen-Altenstadt 540m	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010
Lacerta sp. 1	Lacertidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		San Roque 2	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Untereichen-Altenstadt 565m	Germany	Miocene (Langhian)	Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010
Lacerta sp. 1	Lacertidae		Caseton 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		La Col C	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Las Planas 4B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Las Umbrias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Las Umbrias 19	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Valdemoros 7A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Valdemoros 7F	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Tăşad	Romania	Middle Miocene (Serravallian, MN 8)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Borjas	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Las Planas 5H	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Paje 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Toril 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Toril 3B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003

Lacerta sp. 1	Lacertidae		Furth 460 m	Germany	Middle Miocene	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Lacerta sp. 1	Lacertidae		Petersbuch 10	Germany	Miocene (Serravallian/Tortonian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Hammerschmiede 1	Germany	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Crevillente 2	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		La Roma 1	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		La Roma 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Los Aguanaces	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Los Aguanaces 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Vivero de Pinos	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Concud 98'	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Peralejos E	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Valdecebro 5	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Villastar	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		El Arquillo 0	Spain	Miocene/Pliocene (Messian/Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Aldehuela 2 (La Calera 2)	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Barranca de Cuevas	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		El Arquillo 3	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Escorihuela B	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		La Gloria 4	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Orrios rio (base of profile)	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Villalba Alta 3	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Villalba Alta Rio 2	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Villalba Alta Rio 4	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Escorihuela C	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Gea 1	Spain	Pliocene (Piacenzian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		La Recueja	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Varshets	Bulgaria	Pleistocene (Gelasian)	Böhme & Ilg 2003
Lacerta sp. 1	Lacertidae		Valdeganga 7	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Lautern 2	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Lacerta sp.	Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Schleich 1985b; Böhme 2003
Lacerta sp. 2	Lacertidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Forsthart	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Langenau 1	Germany	Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Offingen 2	Germany	Miocene (Burdigalian, MN 4b/5)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Lacerta sp. 2	Lacertidae		Adelschlag	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003

Lacerta sp. 2	Lacertidae		Massendorf	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Lacerta sp.	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Miklas-Tempfer 2003; Böhme 2010b
Lacerta sp. 2	Lacertidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Fuente Sierra 1	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		San Roque 1	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		San Roque 5	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Vargas 4B	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Vargas 4BB	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Caseton 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Caseton 2B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Fuente Sierra 2	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Fuente Sierra 3	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Fuente Sierra 4	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		La Col C	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Las Umbrias 2	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Las Umbrias 7	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Las Umbrias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Las Umbrias 16	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Las Umbrias 18	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Las Umbrias 19	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Regajo 2	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Vargas 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Valdemoros 3E	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Valdemoros 3F	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Valdemoros 7A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Valdemoros 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Valdemoros 8C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003

Lacerta sn 2	Lacertidae	Villafeliche 4B	Snain	Miocene (Lanohian)	Böhme & Ilo 2003
Lacerta sp. 2	Lacertidae	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Tăşad	Romania	Middle Miocene (Serravallian, MN 8)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Alcocer 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Borjas	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Las Planas 5C	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Las Planas 5H	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Las Umbrias 20	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Paje 1	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Paje 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Toril 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Toril 3B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Valalto 1A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Valalto 1B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Valalto 2C	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Furth 460 m	Germany	Middle Miocene	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Lacerta sp. 2	Lacertidae	Petersbuch 10	Germany	Miocene (Serravallian/Tortonian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Hammerschmiede 1	Germany	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Crevillente 2	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	La Roma 1	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	La Roma 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Los Aguanaces	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Los Aguanaces 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Nombrevilla 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Vivero de Pinos	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Concud 98'	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	La Gloria 6	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	El Arguillo 3	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae	Escorihuela B	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003

Lacerta sp. 2	Lacertidae		La Gloria 4	Spain	Early Pliocene (Zanclean)	Böhme & IIg 2003
Lacerta sp. 2	Lacertidae		Villalba Alta Rio 2a	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Villalba Alta Rio 4	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 2	Lacertidae		Varshets	Bulgaria	Pleistocene (Gelasian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae	Lacerta sp.	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Miklas-Tempfer 2003; Böhme 2010b
Lacerta sp. 3	Lacertidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Fuente Sierra 1	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		San Roque 2	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Caseton 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Las Umbrias 7	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Las Umbrias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Las Umbrias 14	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Las Umbrias 19	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Regajo 2	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valdemoros 3B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valdemoros 3F	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valdemoros 7A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valdemoros 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valdemoros 8C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Vargas 5	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Vargas 7	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Alcocer 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Las Planas 5H	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Paje 1	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Paje 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Toril 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003

Lacerta sp. 3	Lacertidae		Toril 3B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valalto 1A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valalto 1B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Valalto 2C	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Crevillente 2	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Los Aguanaces	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		La Gloria 6	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Velillia 1a+1b	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Escorihuela B	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		La Gloria 4	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		Villalba Alta Rio 2a	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Lacerta sp. 3	Lacertidae		La Recueja	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003
Lacerta sp. 4	Lacertidae		Muela Alta	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Lacerta sp. 4	Lacertidae		Vargas 7	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 4	Lacertidae		Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp. 4	Lacertidae		Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp. 4	Lacertidae		Crevillente 2	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Lacerta sp. morphotype I	Lacertidae		Unknown locality, Asturias	Spain	Pleistocene	Roček 1984
Lacerta sp. morphotype II	Lacertidae		Unknown locality, Asturias	Spain	Pleistocene	Roček 1984
Lacerta sp. (large species)	Lacertidae		Kärlich G	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003; Holman & van Kolfschoten 2011
Lacerta sp. large size	Lacertidae	Lacerta sp. A	Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Böhme & Ilg 2003; Tempfer 2005
Lacerta sp. large size	Lacertidae	Lacerta sp. 1	Obergänserndorf, Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003: Tempfer 2005
Lacerta sp. large size	Lacertidae	Lacerta sp. 1	Teiritzberg (T1 = 001/D/C), Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003; Tempfer 2005
Lacerta sp. (small form)	Lacertidae		1/2001 Turtle Joint, Mokrá- Western Quarry	Czech Republic	Early Miocene (MN 4)	Ivanov et al. 2006
Lacerta sp. (small form)	Lacertidae		2/2003 Reptile Joint, Mokrá- Western Quarry	Czech Republic	Early Miocene (MN 4)	Ivanov et al. 2006
Lacerta sp. small size	Lacertidae	<i>Lacerta</i> sp. B	Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Böhme & Ilg 2003; Tempfer 2005
Lacerta sp. small size	Lacertidae	Lacerta sp. 2	Obergänserndorf, Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003; Tempfer 2005
Lacerta sp. small size	Lacertidae	Lacerta sp. 2	Teiritzberg (T2/3), Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003; Tempfer 2005

Lacerta sp. small size	Lacertidae		Subpiatră 2/1R	Romania	Miocene (MN 6)	Böhme & Ilg 2003; Hír & Venczel 2005
Lacerta sp. (small)	Lacertidae		Petralona Cave	Greece	Middle Pleistocene	Kretzoi & Poulianos 1981
Lacerta sp.	Lacertidae		Oschiri	Italy	Lower Miocene (Aquitanian, MN 1/MN 2b)	Böhme & Ilg 2003; Venczel & Sanchíz 2006; Zoboli & Pillola 2017
Lacerta sp.	Lacertidae		Poncenat	France	Lower Miocene (Aquitanian, MN2a)	Augé 1988b; Augé & Rage 2000
Lacerta sp.	Lacertidae		Ulm Westtangente	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Cetina de Aragon	Spain	Lower Miocene (Aquitanian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		San Roque 4A	Spain	Early Miocene (Burdigalian, MN 3)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003; Kosma 2004
Lacerta sp.	Lacertidae		Petersbuch 7	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Petersbuch 28	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1980; Roček 1984; Augé & Rage 2000; Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Venczel & Sanchiz 2006; Čerňanský 2016
Lacerta sp.	Lacertidae		Erkertshofen 1	Germany	Miocene (MN 4b)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Langenau 2	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & 11g 2003
Lacerta sp.	Lacertidae		Rauscheröd	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Lacerta sp. 1; Lacerta sp. 2	Rembach, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Kosma 2004
Lacerta sp.	Lacertidae		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Lacerta sp.	Lacertidae		Petersbuch 4	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Petersbuch 36 II	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Petersbuch 38-Boden	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Adelschlag	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Ambach near Pöttmes	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Arth 1a	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Aumühle - Oben (bei Walda)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003

Lacerta sp.	Lacertidae	B	odman 2	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	<u>M</u>	ieshof b. Pöttmes - unterer lergel	Germany	Early Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	E	itensheim	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	H	esselohe bei Neuburg/Donau	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Н	itzhofen 1	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	H	itzhofen 1+2	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	H	itzhofen 2	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Lá	angenmosen	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	M	lassendorf	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Z	iederaichbach	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	N	iederaichbach (links)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	P. (=	uttenhausen classic -Puttenhausen 1)	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Abdul Aziz et al. 2010
Lacerta sp.	Lacertidae	Sc	chiessen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Sc	chönenberg	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	ū	nterempfenbach la	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	n	interempfenbach 1b	Germany	Early Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Ū	interempfenbach 1d	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Ū	nterhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	n	/alda 1 (unten)	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	0	ggenhausen 2	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	<u>a</u>	andecker Maar	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	B	uñol	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	C	órcoles	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	R	ubielos de Mora	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003

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Lacerta sp.	Lacertidae		San Roque 3	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Villafeliche 2A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Aresing	Germany	Miocene (Burdigalian/Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Gaimersheim 2	Germany	Miocene (Burdigalian/Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Rothenstein 1/13	Germany	Miocene (Burdigalian/Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Dürrenäsch-Höhenrain	Switzerland	Miocene (Burdigalian/Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Pfaffengrund I. Bittenbrunn- Grube b. Neuburg/Donau	Germany	Miocene (Burdigalian/Langhian, MN 5/6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Giggenhausen	Germany	Miocene (Burdigalian/Langhian)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Allier	France	Lower Miocene	Estes 1983; Miklas-Tempfer 2003
Lacerta sp.	Lacertidae		Bouzigues	France	Early Miocene	Augé 1988b
Lacerta sp.	Lacertidae		Paulhiac	France	Early Miocene	Augé 1988b
Lacerta sp.	Lacertidae		Vieux-Collonges	France	Lower Miocene	Augé 1988b; Augé & Rage 2000
Lacerta sp.	Lacertidae		Anried 5	Germany	Miocene (Langhian, MN 5)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Denkendorf Nord (Westwand)	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Edelbeuren Maurerkopf	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Lacerta s.l.	Griesbeckerzell 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Ivanov & Böhme 2011; Čerňanský et al. 2016c
Lacerta sp.	Lacertidae		Petersbuch 41	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Altenstadt	Germany	Miocene (MN 5)	Böhme 2003
Lacerta sp.	Lacertidae		Derching 1a	Germany	Miocene (Langhian, MN 6)	Böhme 2003
Lacerta sp.	Lacertidae		Gallenbach 2b	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Gallenbach 2c	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Goldberg 9	Germany	Miocene (Langhian, MN 6)	Schleich 1985a; Schleich 1985b
Lacerta sp.	Lacertidae		Laimering 2a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & IIg 2003
Lacerta sp.	Lacertidae		Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Petersbuch 32 B	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Petersbuch 39	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Wannenwaldtobel 2	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Sámsonháza	Hungary	Miocene (Langhian, MN 6)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Derching (blauer Mergel ca. 2- 3m über BH)	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Georgensgmünd	Germany	Miocene (Langhian)	Böhme & Ilg 2003

Lacerta sp.	Lacertidae	Oberschöneberg 2D	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Petersbuch 68	Germany	Miocene (Langhian)	Böhme & IIg 2003
Lacerta sp.	Lacertidae	La Col B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	 Olmo Redondo 9	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Regajo 2	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Vargas 11	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Goldberg 2	Germany	Miocene (Langhian/Serravallian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Goldberg (without number)	Germany	Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Steinberg (Ries)	Germany	Middle Miocene (Langhian/Serravallian, MN 6)	Schleich 1985b; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Mühlrüti Pt. 806	Switzerland	Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Rümikon	Switzerland	Middle Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Uzwil-Nutzenbuech	Switzerland	Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Belomechetskaya	Russia	Miocene (Langhian/Serravallian, MN 6)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Göttschlag 1b	Germany	Miocene (MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Felsötárkány-Felnémet 2/3	Hungary	Miocene (Astaracian, MN7+8)	Böhme & Ilg 2003; Venczel & Hir 2013
Lacerta sp.	Lacertidae	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Tauț	Romania	Late middle Miocene (Serravallian, MN 8)	Böhme & Ilg 2003; Venczel & Știucă 2008
Lacerta sp.	Lacertidae	Anwil (Grabung 1968)	Switzerland	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	 Imenberg	Switzerland	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Las Planas 5K	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Las Planas 5L	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Petersbuch 35	Germany	Miocene (Serravallian/Tortonian, MN 8)	Böhme 2003; Böhme & Ilg 2003

an, Böhme 2003; Böhme & Ilg 2003	an, Böhme 2003; Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	an) Böhme & Ilg 2003	Böhme & Ilg 2003; Venczel & Hir 2013	Böhme & Ilg 2003; Venczel & Hir 2013	Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Böhme & Ilg 2003; Čerňanský 2011b	Papp et al. 1953; Estes 1983; Böhme & Ilg 2003; Miklas-Tempfer 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & IIg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & IIg 2003	Böhme & Ilg 2003	Böhme & IIg 2003	Böhme & Ilg 2003	Böhme & IIo 2003				
Miocene (Serravallian/Tortoni MN 8)	Miocene (Serravallian/Tortoni MN 8/9)	Miocene (Serravallian/Tortonian)	Miocene (Serravallian/Tortonian)	Miocene (Serravallian/Tortonian)	Late middle Miocene	Miocene (Burdigalian/Tortonia	Miocene (Vallesian, MN9)	Miocene (Vallesian, MN9)	Miocene (Tortonian, MN 9)	Miocene (Tortonian, MN 9)	Miocene (Tortonian, MN 9)	Miocene (Tortonian, MN 9)	Miocene (Tortonian, MN 9)	Miocene (Tortonian, MN 10)	Miocene (Tortonian)																
Germany	Germany	Spain	Spain	Spain	Austria	Spain	Hungary	Hungary	Germany	Germany	Hungary	Hungary	Slovakia	Austria	Russia	Spain															
Petersbuch 48	Unggenried (Autobahnanschnitt)	Escobosa de Calatañazor	Villafeliche 4	Villafeliche 6	Gratkorn	Valtorres 4-6	Felsötárkány 1	Felsötárkány 3/2	Hammerschmiede 3	Petersbuch 46	Rudabanya (black clay 5B)	Rudabanya (grey marl 6A)	Borský Svätý Jur	Vösendorf (= Vösendorf-Brunn)	Maykop	Casas Altas 75/76	Cascante 4	La Gloria 10	Los Aguanaces 1	Los Aguanaces 5B	Masada Ruea 3	Masada Ruea 4	Masia de la Roma 3	Masia de la Roma 4B	Masia de la Roma 4C	Masia de la Roma 9	Masia de la Roma 11	Nombrevilla	Puente Minero 2	Puente Minero 3	Puente Minero 8A
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.

I acouta en	I accentid as	Duente Minero 8B	Croin	Miccana (Toutonian)	Böhma & IIa 2002
Lacerta sp.	Lacertidae	Fucility Minero 00 Priente Minero 10	Snain	Miocene (Tortonian)	Bohme & IIg 2003 Böhme & IIg 2003
Lacerta sp	Lacertidae	Tortaiada B	Snain	Miocene (Tortonian)	Böhme & IIº 2003
Lacerta sp.	Lacertidae	Beluška and Prevalac, Veles	Macedonia	Late Miocene (MN 11+12)	Jovanović et al. 2002
Lacerta sp.	Lacertidae	Polgárdi 2	Hungary	Miocene (Messinian, MN 13)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Maramena	Greece	Late Miocene (MN 13/14)	Richter 1995; Georgalis et al. 2017a
Lacerta sp.	Lacertidae	Bunker de Vallecebro 3	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Bunker de Vallecebro 5	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Concud 3	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Concud B	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	La Fontana 1 A	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Lomas de Casares 2	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Los Mansuetos	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Tortajada C	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Valdecebro 3	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Villalba Baja 2B	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Biancone, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Bosco, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Cantatore, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Cava Fina, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Chirò, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Pepo, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Rinascita, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	San Giovannino, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Kamenjak, Bukulja	Serbia	Early Pliocene (MN 14)	Jovanović et al. 2002
Lacerta sp.	Lacertidae	Osztramos 1	Hungary	Pliocene (Zanclean, MN 14)	Venczel 2001; Böhme & Ilg 2003

iclean, MN Młynarski 1962; Estes 1983; Böhme & Ilg 2003	WN 15) Venczel & Gardner 2005	MN 15) Młynarski 1956; Młynarski 1962; Estes 1983; Böhme & Ilg 2003; Ivanov 2007	Böhme & Ilg 2003	Böhme & Ilg 2003	, MN 15) Böhme & Ilg 2003	15) Böhme & Ilg 2003	Młynarski 1960; Młynarski 1962; Estes 1983	uzian, MN Mörs 2002	uzian, MN Mörs 2002	enzian, MN Młynarski 1962; Estes 1983; Młynarski et al. 1984; Böhme & Ilg 2003; Ivanov 2007; Čerňanský et al. 2016c	6) Blain 2005	iacenzian) Böhme & Ilg 2003	Redkozubov 2003	N 17) Młynarski 1962; Estes 1983	elasian) Böhme & Ilg 2003;	elasian) Böhme & Ilg 2003	Hoek Ostende & Vos 2006; Villa et al. 2014; Schouten 2016; Villa et al. 2016a; this work	Calabrian) Redkozubov 2003	Calabrian) Redkozubov 2003	Böhme & Ilg 2003; Ivanov 2007	Holman 1998; Böhme & Ilg 2003	Ivanov 1996; Holman 1998; Böhme & Ilg 2003; Ivanov 2007	Böhme & Ilg 2003; Ivanov 2007	Ivanov 1995; Holman 1998; Böhme & Ilg 2003	
Lower Pliocene (Zan 14)	Pliocene (Zanclean, 1	Pliocene (Zanclean, 1	Pliocene (Zanclean)	Pliocene (Zanclean)	Pliocene (Piacenzian	Early Pliocene (MN	Lower Pliocene	Late Pliocene (Piacen 16b)	Late Pliocene (Piacen 16)	Upper Pliocene (Piac 16)	Late Pliocene (MN 1	Pliocene (Zanclean/P	Pliocene	Early Pleistocene (M	Early Pleistocene (Ge	Early Pleistocene (Ge	Early Pleistocene (G	Lower Pleistocene (C	Lower Pleistocene (C	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	
Poland	Hungary	Poland	Spain	Spain	Ukraine	Greece	Poland	Germany	Germany	Poland	Spain	Ukraine	Moldova	Poland	Spain	Spain	The Netherlands	Moldova	Moldova	Austria	Czech Republic	Czech Republic	Czech Republic	Czech	K P D D D C
Podlesice	Csarnóta 2	Węże I	Orrios 3	Orrios 7	Vinogradovka	Notio 1 (= Ptolemais 6C)	Rębielice Królewskie	Frechen	Hambach 11	W ęże II	Zújar	Nogaisk	Unknown locality, Moldova	Kadzielnia	Almenara Casablanca 1	Almenara Casablanca 4	Russel-Tiglia-Egypte pit, Tegelen	Chismikioi	Unknown locality, Moldova	Bad Deutsch-Altenburg 2A	Holstejn	Malá Dohoda Quarry	Mladeč Caves - excavation II	Stránská Skála Hill	
		?Lacerta sp.																							
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	
Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	-

y 1986; Holman 1998; Böhme & Ilg 2003	y 1986	y 1986; Holman 1998; Venczel 1998; . & Ilg 2003	& Ilg 2003; Ivanov 2007	ski 1962; Estes 1983; Holman 1998; & Ilg 2003	1997; Holman 1998; Böhme & Ilg 2003	et al. 2016	al. 1991	lio & Insacco 1992; Bonfiglio et al. 2002; & Ilg 2003; Bailon 2004	: Sanchiz 1980; Estes 1983; Holman 1998	n 1998; Böhme & Ilg 2003	n 1998; Böhme & Ilg 2003	n et al. 1990; Holman 1992; Holman Holman 1993b; Benton & Spencer 1995; n 1998; Böhme & Ilg 2003	n 1998; Böhme & Ilg 2003	972a; Holman 1998; Böhme & Ilg 2003	et al. 1997; Böhme & Ilg 2003; Bailon 3ailon & Rage 2012	al. 1976; Estes 1983; Holman 1998; & Ilg 2003	e & Ilg 2003	983; Holman 1998; Böhme & Ilg 2003	n 1998; Böhme & Ilg 2003	983; Caloi et al. 1986; Holman 1998; & Ilg 2003	2004	y 1986	y 1986	& Ilg 2003; Rook et al. 2003; Abbazzi et 4; Delfino & Rook 2008	o 2002; Böhme & Ilg 2003; Bailon 2004	lio & Insacco 1992; Holman 1998;
Jánoss	Jánoss	Jánoss Böhme	Böhme	Młynai Böhme	Ivanov	Vasile	ne Bon et	stocene Bonfig Böhme	11) Sanz &	Holma	Holma	Holma 1993a; Holma	Holma	Rage 1	Salotti 2004;]	Clot et Böhme	Böhme	Estes 1	Holma	Estes 1 Böhme	Bailon	Jánoss	Jánoss	Böhme al. 200	Delfino	Bonfig
Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Earliest Middle Pleistoce	Lower/early Middle Pleis	Middle Pleistocene (MIS	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	
Hungary	Hungary	Hungary	Poland	Poland	Poland	Romania	Italy	Italy	Spain	Croatia	Croatia	England	England	France	France	France	Germany	Germany	Germany	Greece	Greece	Hungary	Hungary	Italy	Italy	
Koevesvarad	Osztramos 2	Villány 5 and 8	Jaskinia Żabia	Kamyk	Zabia Cave	Copăceni	Zoppega 2, Brecce di Soave	Contrada Cozzo del Re	Áridos-1	Dubci	Podumci	Cudmore Grove, Mersea Island	East Farm	Abimes de la Fage	Castiglione 3, Corsica	Montoussé 3	Bilzingsleben	Breitenburg Cave (Breitenberghohle)	Miesenheim I	Chios	Latomi 1, Chios	Hórvőlgy Cave	Vértesszőlős	Cava XI 3, Monte Tuttavista	Contrada Annunziata, Ragusa	
															Lacerta n.sp.			Lacerta agilis ; Timon lepidus								
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	
Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.	

a sp.	Lacertidae		Koziy Ovrag	Russia	Middle Pleistocene	Böhme & Ilg 2003
	Lacertidae		Kuznetsovka, left board of Dodgornyi Buarak	Russia	Middle Pleistocene	Böhme & Ilg 2003
	Lacertidae		Vol'naya Vershina-3	Russia	Middle Pleistocene	Böhme & Ilg 2003
	Lacertidae		Arriaga	Spain	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
	Lacertidae		Cova d'Olopte	Spain	Middle Pleistocene	Böhme & Ilg 2003
	Lacertidae		Grajas Cave	Spain	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
	Lacertidae		Madrid	Spain	Middle Pleistocene	Crespo 2001
	Lacertidae		Trinchera Dolina TD8b, Gran Dolina	Spain	Middle Pleistocene	Blain 2005
	Lacertidae		Nagyharsanyhegy 3 and 6	Hungary	Lower/Middle Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Sitia 1, Crete	Greece	Lower or Middle Pleistocene	Böhme & Ilg 2003; Bailon 2004
	Lacertidae		Santa Catalina	Spain	Upper Pleistocene (upper/latest Magdalenian)	Bailon & Garcia-Ibaibarriaga 2014
	Lacertidae		Marie-Jeanne cave	Belgium	Late Pleistocene	Blain et al. 2014d
	Lacertidae	Lacerta fossilis	Brèche de Coudes	France	Upper Pleistocene	Pomel 1853; Estes 1983; Roček 1984; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Hortus Cave	France	Upper Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Jaurens Cave	France	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
	Lacertidae	Lacerta fossilis	Neschers	France	Upper Pleistocene	Pomel 1853; Estes 1983; Roček 1984; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Bad Langensalza	Germany	Upper Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Burgtonna, Hystrix-Horizont	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
	Lacertidae		Gamsenberg (fissure top)	Germany	Upper Pleistocene	Böhme & Ilg 2003
	Lacertidae		Grabschütz	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
	Lacertidae	Zootoca vivipara	Siegmannsbrunn	Germany	Upper Pleistocene	Estes 1983
	Lacertidae		Kalman Lambrecht Cave	Hungary	Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Rejtek 1	Hungary	Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Subalyuk	Hungary	Upper Pleistocene	Jánossy 1986
	Lacertidae		Süttö Upper Pleistocene strata	Hungary	Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
	Lacertidae		Brecce di Montorio, Monte Marseghina	Italy	Late Pleistocene	Bon et al. 1991
	Lacertidae		Pocket B, Contrada Pianetti	Italy	Upper Pleistocene	Bonfiglio et al. 1997; Bailon 2004
	Lacertidae		Riparo Zampieri	Italy	Upper Pleistocene	Bon et al. 1991
	Lacertidae		Valdiporro	Italy	Upper Pleistocene	Bon et al. 1991
	Lacertidae		Cueva de Cualventi	Spain	Upper Pleistocene	Sanchiz & Martín Albaladejo 2016
	Lacertidae		Laminak II Cave	Spain	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003

Lacerta sp.	Lacertidae		Málaga	Spain	Upper Pleistocene	Crespo 2001
Lacerta sp.	Lacertidae		Paloma Cave	Spain	Upper Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Unknown locality, Vizcaia	Spain	Upper Pleistocene	Crespo 2001
Lacerta sp.	Lacertidae	Lacerta viridis	Monte Pellegrino	Italy	Upper Pleistocene (?)	Estes 1983; Holman 1998; Bailon 2004
Lacerta sp.	Lacertidae		Gamsenberg (fissure basis)	Germany	Middle/Upper Pleistocene	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Tarko	Hungary	Middle/Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Cueva del Agua	Spain	Middle/Upper Pleistocene	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Unesic	Croatia	Lower/Upper Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Steinbruch Biedermann, Stuttgart (Stuttgart quarry Biedermann)	Germany	Lower/Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Undesignated caves, Malta	Malta	Lower/Upper Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Unknown locality, Mallorca	Spain	Lower/Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae	Lacerta melitensis	Benghisa Gap	Malta	Pleistocene	Adams 1866; Gulia 1912; Gulia 1913; Böhme & Zammit-Maempel 1982; Savona Ventura 1984; Bailon 2004
Lacerta sp.	Lacertidae	Lacerta melitensis	Ta' Gandja	Malta	Pleistocene	Adams 1866; Gulia 1912; Gulia 1913; Böhme & Zammit-Maempel 1982; Savona Ventura 1984; Bailon 2004
Lacerta sp.	Lacertidae		Vraona Cave	Greece	Pleistocene/Holocene	Rauscher 1995
Lacerta sp.	Lacertidae		Ozyornoye-1, east bank of Jalpug Lake	Ukraine	Middle Pleistocene/Holocene	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Függö-Kö Cave	Hungary	Upper Pleistocene/Holocene	Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Petenyi Cave	Hungary	Upper Pleistocene/Holocene	Holman 1998; Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Cueva de Cobrante	Spain	Holocene (MIS 1)	Martín et al. 2009
Lacerta sp.	Lacertidae		Kabyle	Bulgaria	Holocene	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Hortus Cave	France	Holocene	Rage 1972b; Estes 1983
Lacerta sp.	Lacertidae		Oberrohn bei Bad Salzungen	Germany	Holocene	Böhme & Ilg 2003
Lacerta sp.	Lacertidae		Grotta di Trebiciano	Italy	Holocene	Bon et al. 1991
Lacerta sp.	Lacertidae		Grotta Lonza o della Ciotola	Italy	Holocene	Bon et al. 1991
Lacerta sp.	Lacertidae		Su Guanu Cave	Italy	Holocene	Kotsakis 1980; Böhme & Ilg 2003; Bailon 2004
Lacerta s.s.	Lacertidae		Seynes	France	Late Pliocene (MN 16)	Bailon 1991
Lacerta s.s.	Lacertidae		La Combe Grenal	France	Upper Pleistocene (lower Palaeolithic)	Bailon 1991
Lacerta s.s.	Lacertidae	Lacerta sp.	Lazaret Cave	France	Middle Pleistocene/Holocene	Rage 1969; Estes 1983; Bailon 1991

Lacerta s.s.	Lacertidae		Baume Claire/Baume Sourde	France	Holocene (middle Neolithic)	Bailon 1991
?Lacerta sp.	Lacertidae		Teufelshöhle (Devil's Cave)	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
cf. Lacerta sp.	Lacertidae		Weisenau	Germany	Lower Miocene	Schleich 1988b
cf. Lacerta sp.	Lacertidae		Mühlbach am Manhartsberg	Austria	Miocene (Langhian, MN 5)	Böhme & Ilg 2003; Miklas-Tempfer 2003
cf. <i>Lacerta</i> sp.	Lacertidae	Lacertidae indet.	Moncucco Torinese	Italy	Latest Miocene (Messinian, p- ev2)	Colombero et al. 2014b; Colombero et al. 2017; this work
cf. <i>Lacerta</i> sp.	Lacertidae		Sète	France	Middle Pliocene (MN 15)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007
cf. Lacerta sp.	Lacertidae		Găvănoasa (Gavanosy)	Moldova	Pliocene (MN 15)	Nadachowski et al. 2006
cf. Lacerta sp.	Lacertidae		Lucești 2	Moldova	Pliocene (MN 15)	Nadachowski et al. 2006
cf. Lacerta sp.	Lacertidae		Tătărești	Moldova	Pliocene (MN 15)	Nadachowski et al. 2006
cf. Lacerta sp.	Lacertidae		Lucești	Moldova	Pliocene (MN 15/16)	Nadachowski et al. 2006
cf. Lacerta sp.	Lacertidae	Lacerta gr. L. viridis	Tourkobounia 2	Greece	earliest early Pleistocene	Delfino 2004b; this work
cf. Lacerta sp.	Lacertidae		Salcia 2	Moldova	Early Pleistocene (MN 17)	Nadachowski et al. 2006
cf. Lacerta sp.	Lacertidae	Lacerta gr. L. viridis	Tourkobounia 5	Greece	latest early/earliest Middle Pleistocene	Delfino 2004b; this work
cf. Lacerta sp.	Lacertidae		Praileaitz 1	Spain	Upper Pleistocene	Garcia-Ibaibarriaga et al. 2017
aff. Lacerta sp.	Lacertidae		Cueva Horá	Spain	Upper Pleistocene	Bailon 1986
Lacerta s.l. sp. 1	Lacertidae		Gratkorn	Austria	Late middle Miocene	Böhme & Ilg 2003; Böhme & Vasilyan 2014
Lacerta s.l. sp. 2	Lacertidae		Gratkorn	Austria	Late middle Miocene	Böhme & Ilg 2003; Böhme & Vasilyan 2014
Lacerta s.l. sp. 3	Lacertidae		Gratkorn	Austria	Late middle Miocene	Böhme & Ilg 2003; Böhme & Vasilyan 2014
Lacerta s.l. large size	Lacertidae	Lacerta sp.	Grotta di Luparello	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Bailon 2004
Lacerta s.l. large size	Lacertidae	Lacerta sp.	Grotta Marasà	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003
Lacerta s.l. large size	Lacertidae		Marosa Cave	Italy	Middle Pleistocene	Bailon 2004
Lacerta s.l. large size	Lacertidae	Lacerta siculimelitensis; Lacerta sp.	Spinagallo	Italy	Middle Pleistocene	Kotsakis 1977; Böhme & Zammit-Maempel 1982; Estes 1983; Caloi et al. 1986; Bonfiglio & Insacco 1992; Böhme & Corti 1993; Bonfiglio et al. 1997; Holman 1998; Delfino & Bailon 2000; Delfino 2001; Delfino 2002; Böhme & Ilg 2003; Bailon 2004
Lacerta s.l. large size	Lacertidae		K 22, San Vito lo Capo	Italy	Middle/late Pleistocene	Delfino 2002; Böhme & Ilg 2003
Lacerta s.l.	Lacertidae		Balaruc II	France	Middle/late Pliocene (MN 15/16)	Bailon 1989; Bailon 1995
Lacerta s.l.	Lacertidae		Miniera della Polveriera, Monte Argentario	Italy	Lower Pleistocene	Böhme & Ilg 2003; Siori et al. 2014
Lacerta s.l.	Lacertidae	Lacerta s.s.	Medas Islands	Spain	Early Pleistocene	Bailon 1991; Agustí et al. 2009; Blain et al. 2016a

"Lacerta" ponsortiana	Lacertidae	Lacerta ponsortiana	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Lartet 1851; Gervais 1859; Młynarski 1956; Estes 1983; Roček 1984; Augé & Rage 2000
Ligerosaurus pouiti	Lacertidae	Pseudeumeces pouti	Pontbrault-en-Lasse	France	Middle Miocene (MN5)	Augé 1993; Augé et al. 2003; Böhme & Ilg 2003
Ligerosaurus pouiti	Lacertidae		Pontigné	France	Middle Miocene (MN5)	Augé et al. 2003; Böhme & Ilg 2003
Maioricalacerta rafelinensis	Lacertidae		Caló den Rafelino, Mallorca	Spain	Earliest early Pliocene	Böhme & Ilg 2003; Bailon et al. 2014; Bover et al. 2014
Mediolacerta sp.	Lacertidae	cf. Amblyolacerta sp.	Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Miolacerta tenuis	Lacertidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1984; Augé & Rage 2000; Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Rage & Bailon 2005; Tempfer 2005; Böhme 2010b; Čerňanský 2016
Miolacerta tenuis	Lacertidae		Gratkorn	Austria	Late middle Miocene	Böhme & Ilg 2003; Böhme & Vasilyan 2014
Miolacerta tenuis	Lacertidae		Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Tempfer 2005; Böhme 2010b
cf. Miolacerta tenuis	Lacertidae	Miolacerta tenuis	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2005; Abdul Aziz et al. 2008; Böhme 2010b; Čerňanský et al. 2016c
<i>Miolacerta</i> sp.	Lacertidae		Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003; Kosma 2004
Miolacerta sp.	Lacertidae		Petersbuch 28	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003
Miolacerta sp.	Lacertidae		Günzburg 2/1 Umgehungsstrasse Sande	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
<i>Miolacerta</i> sp.	Lacertidae		Rauscheröd	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Miolacerta sp.	Lacertidae		Rembach, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4b)	Böhme 2003; Kosma 2004
Miolacerta sp.	Lacertidae		Laimering 2a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Miolacerta sp.	Lacertidae		Litke 1	Hungary	Miocene (Langhian, MN 6)	Böhme & Ilg 2003; Čerňanský et al. 2016c
Miolacerta sp.	Lacertidae		Goldberg (without number)	Germany	Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
<i>Miolacerta</i> sp.	Lacertidae		Rümikon	Switzerland	Middle Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
cf. <i>Miolacerta</i> sp.	Lacertidae	<i>Miolacerta</i> sp.	Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
cf. <i>Miolacerta</i> sp.	Lacertidae	<i>Miolacerta</i> sp.	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme & Ilg 2003; Villa & Delfino 2017; this work
cf. Miolacerta sp.	Lacertidae		Anwil (Grabung 1968)	Switzerland	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003

Ophisops elegans	Lacertidae		Bad Deutsch-Altenburg 30B	Austria	Plio-Pleistocene	Rauscher 1992
Ophisops elegans	Lacertidae		Bad Deutsch-Altenburg 4B	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007
Podarcis cf. P. erhardii	Lacertidae	Lacerta cf. L. (Podarcis) erhardii	Bate Cave, Crete	Greece	Holocene	Estes 1983; Holman 1998; Böhme & Ilg 2003; Bailon 2004
Podarcis cf. P. hispanicus	Lacertidae		Almenara Casablanca 1	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005
Podarcis cf. P. hispanicus	Lacertidae		Gorham's Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001
Podarcis cf. P. hispanicus	Lacertidae		Cueva del Boquete de Zafarraya	Spain	Upper Pleistocene	Böhme & Ilg 2003
Podarcis lilfordi	Lacertidae		Unknown locality, Mallorca	Spain	Early Pleistocene	Crespo 2001
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta (Podarcis) sp.; Lacerta sp.	Cova Son Bauça, Mallorca	Spain	Middle Pleistocene	Alcover & Mayol 1981; Kotsakis 1981; Holman 1998; Böhme & Ilg 2003; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi	Cova de La Barxa, Mallorca	Spain	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta sp.	Cova de Llenaire, Mallorca	Spain	Upper Pleistocene	Kotsakis 1981; Holman 1998; Böhme & Ilg 2003; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta sp.	Cova des Pilar, Mallorca	Spain	Upper Pleistocene	Kotsakis 1981; Holman 1998; Böhme & Ilg 2003; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta sp.	Cova de sa Bassa Blanca, Mallorca	Spain	Upper Pleistocene	Kotsakis 1981; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta sp.	Cova de Son Maiol, Mallorca	Spain	Upper Pleistocene	Kotsakis 1981; Holman 1998; Böhme & Ilg 2003; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae		Unknown locality, Mallorca	Spain	Upper Pleistocene	Crespo 2001
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta sp.	Cova de Canet, Mallorca	Spain	Upper Pleistocene/Holocene	Kotsakis 1981; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae		Unknown locality, Mallorca	Spain	Upper Pleistocene/Holocene	Crespo 2001
Podarcis lilfordi	Lacertidae		Unknown locality, Mallorca	Spain	Pleistocene	Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi	Sa Naveta de Sa Cova, Menorca	Spain	Holocene (800 BC)	Kotsakis 1981; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi	Sa Torre dem Gaumes, Menorca	Spain	Holocene (500 BC)	Kotsakis 1981; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta (Podarcis) sp.; Lacerta sp.	Binicalaf, Menorca	Spain	Holocene (300 BC)	Alcover & Mayol 1981; Kotsakis 1981; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta (Podarcis) sp.	Torralba den Salort, Menorca	Spain	Holocene (III/II century BC)	Kotsakis 1981; Sanders 1984; Bailon 2004; Bailon et al. 2014
Podarcis lilfordi	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta sp.	Avenc de l'Hospital, Mallorca	Spain	Holocene (II century BC)	Kotsakis 1981; Bailon 2004; Bailon et al. 2014

Alcover & Mayol 1981; Kotsakis 1981; Bailon et al. 2014	Kotsakis 1981; Bailon 2004; Bailon et al. 2014	Böhme & Ilg 2003; Bailon 2004; Bailon et al. 2005; Bailon et al. 2014; Bover et al. 2014	Böhme & Ilg 2003; Bailon 2004; Bailon et al. 2005; Bailon et al. 2014; Bover et al. 2014	Kotsakis 1981; Holman 1998; Bailon 2004; Bailon et al. 2014	Crespo 2001	Delfino 2013	Rauscher 1995	Młynarski 1962; Młynarski 1977; Böhme & Ilg 2003; Ivanov 2007	Młynarski 1962; Młynarski 1977; Böhme & Ilg 2003; Ivanov 2007	Bailon 2004; Bailon et al. 2014	Bailon 2004	Rauscher 1992	Rauscher 1992	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007	Bailon & Rage 2012	Młynarski 1962; Böhme & Ilg 2003; Ivanov 2007	Młynarski 1962; Młynarski 1977; Estes 1983; Böhme & Ilg 2003; Ivanov 2007				
Holocene (II century BC)	Holocene	Between upper Miocene and Pleistocene	Between upper Miocene and Pleistocene	Pliocene/Pleistocene boundary	Plio-Pleistocene	Pleistocene	Pleistocene/Holocene	Upper Pliocene (Piacenzian, MN 16)	Upper Pliocene (Piacenzian, MN 16)	Upper Pleistocene	Upper Pleistocene	Holocene (1700 BC)	Holocene (before 700 BC)	Holocene (before 700 BC)	Pliocene	Plio-Pleistocene	Plio-Pleistocene	Lower Pleistocene	Lower Pleistocene	Holocene (Middle Age)	Upper Pliocene (Zanclean, MN 15)	Upper Pliocene (Piacenzian, MN 16)
Spain	Spain	Spain	Spain	Spain	Spain	Italy	Greece	Poland	Poland	Spain	Spain	Spain	Spain	Spain	Spain	Austria	Austria	Austria	Austria	France	Poland	Poland
Hospitalet, Mallorca	Rafal-Rubí, Menorca	Punta Nati 3, Menorca	Punta Nati 12, Menorca	Pedrera de S'Ònix, Mallorca	Unknown locality, Mallorca	Grotta Romanelli	Vraona Cave	Rębielice Królewskie 1A	Rębielice Królewskie 2	Santa Agnés de Corona, Ibiza	Santa Eulalia, Ibiza	Ca Na Costa, Ibiza	Cova des Cuiram, Ibiza	Es Pouas, Ibiza	Saint Antoni de Portmany, Ibiza	Bad Deutsch-Altenburg 3	Bad Deutsch-Altenburg 30A	Bad Deutsch-Altenburg 2C1	Bad Deutsch-Altenburg 4B	Unknown locality, Corsica	Węże I	Rębielice Królewskie 1A
Lacerta (Podarcis) lilfordi; Lacerta (Podarcis) sp.; Lacerta sp.	Lacerta (Podarcis) lilfordi; Lacerta sp.			Lacerta aff. L. (Podarcis) lilfordi; Lacerta sp.				Lacerta sp. (cf. muralis); Lacerta (Podarcis) sp.	Lacerta sp. (cf. muralis); Lacerta (Podarcis) sp.												Lacerta cf. L. sicula	Lacerta cf. L. sicula; Podarcis cf. P. siculus
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Podarcis lilfordi	Podarcis lilfordi	Podarcis aff. P. lilfordi	Podarcis aff. P. lilfordi	Podarcis aff. P. lilfordi	Podarcis aff. P. lilfordi	Podarcis muralis	Podarcis muralis	?Podarcis muralis	?Podarcis muralis	Podarcis pityusensis	Podarcis pityusensis (or ancestor)	Podarcis praemuralis	Podarcis praemuralis	Podarcis praemuralis	Podarcis praemuralis	Podarcis siculus	?Podarcis siculus	?Podarcis siculus				
cf. Podarcis siculus	Lacertidae		Monte di Tuda T1	France	Holocene (Middle Age/Present)	Böhme & Ilg 2003; Bailon 2004																
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Podarcis cf. P. siculus	Lacertidae	Lacerta cf. L. (Podarcis) sicula	Breitenburg Cave (Breitenberghohle)	Germany	Middle Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003																
Podarcis cf. P. siculus	Lacertidae		Fuchsloch	Germany	Middle Pleistocene	Estes 1983																
Podarcis cf. P. siculus	Lacertidae		Tortoreto	Italy	Holocene (Iron Age)	Delfino & Ragazzini 2010																
Podarcis tauricus	Lacertidae		Vraona Cave	Greece	Pleistocene/Holocene	Rauscher 1995																
Podarcis cf. P. tauricus	Lacertidae		Magura Cave	Bulgaria	Late Pleistocene	Ivanova et al. 2016																
Podarcis tiliguerta	Lacertidae		Castiglione 3, Corsica	France	Middle Pleistocene	Salotti et al. 1997; Böhme & Ilg 2003; Bailon 2004; Bailon & Rage 2012																
Podarcis tiliguerta	Lacertidae		Gritulu GR 1	France	Late Pleistocene (Tardiglacial)	Vigne et al. 2002; Böhme & Ilg 2003; Bailon 2004																
Podarcis tiliguerta	Lacertidae		Castiglione 1, Corsica	France	Upper Pleistocene	Ferrandini et al. 1995; Vigne et al. 1997; Böhme & Ilg 2003; Bailon 2004																
Podarcis tiliguerta	Lacertidae		A Teppa di U Lupinu Cave, Corsica	France	Latest Pleistocene/earliest Holocene	Salotti et al. 2008																
Podarcis tiliguerta	Lacertidae		Monte Leone ML1	France	Holocene (Preneolithic)	Vigne et al. 1997; Böhme & Ilg 2003; Bailon 2004																
Podarcis tiliguerta	Lacertidae		Monte Leone ML2	France	Holocene (early Neolithic)	Vigne et al. 1997; Böhme & Ilg 2003; Bailon 2004																
Podarcis tiliguerta	Lacertidae		Monte di Tuda T3	France	Holocene (Iron Age/Present)	Vigne et al. 1997; Böhme & Ilg 2003; Bailon 2004																
Podarcis tiliguerta	Lacertidae		Monte di Tuda T2	France	Holocene (Roman Age)	Vigne et al. 1997																
Podarcis tiliguerta	Lacertidae		Monte di Tuda T1	France	Holocene (Middle Age/Present)	Vigne et al. 1997																
Podarcis tiliguerta	Lacertidae		Su Guanu Cave	Italy	Holocene	Böhme & Ilg 2003; Bailon 2004																
?Podarcis tiliguerta	Lacertidae	Podarcis tiliguerta	Santa Maria Lavezzi, Lavezzi islands	France	Holocene (XIV-XVII century)	Bailon 1994; Vigne et al. 1997; Böhme & Ilg 2003; Bailon 2004																
Podarcis cf. P. tiliguerta	Lacertidae		Grotta Corbeddu	Italy	Upper Pleistocene/Holocene	Böhme & Ilg 2003; Bailon 2004																
Podarcis sp. (lilfordi/pityusensis group)	Lacertidae	Lacerta (Podarcis) sp.; Lacerta sp.	Barranc de Binigaus, Menorca	Spain	Lower Pleistocene	Kotsakis 1981; Estes 1983; Holman 1998; Böhme & Ilg 2003; Bailon 2004																
Podarcis sp.	Lacertidae		Crulls de Cap Farrutx, Mallorca	Spain	Late Pliocene	Bover et al. 2014																
Podarcis sp.	Lacertidae		Punta Nati 17, Menorca	Spain	Pliocene	Bailon 2004																
Podarcis sp.	Lacertidae		Punta Nati 20, Menorca	Spain	Pliocene	Bailon 2004																
Podarcis sp.	Lacertidae		Ca Na Reia, Ibiza	Spain	Late Pliocene/early Pleistocene	Bover et al. 2008; Bover et al. 2014																
Podarcis sp.	Lacertidae		Guadix-Baza	Spain	Plio-Pleistocene	Barbadillo et al. 1997; Crespo 2001																
Podarcis sp.	Lacertidae		Venta Micena-1	Spain	Plio-Pleistocene	Félix & Montori 1987																

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Podarcis sp.	Lacertidae		Cava dell'Erba, Pirro Nord	Italy	Lower Pleistocene	Delfino & Bailon 2000; Böhme & Ilg 2003; Delfino & Atzori 2013: Rlain et al 2016c
Podarcis sp.	Lacertidae		Cava Pirro, Pirro Nord	Italy	Lower Pleistocene	Delfino & Bailon 2000; Böhme & Ilg 2003; Delfino & Atzori 2013; Blain et al. 2016c
Podarcis sp.	Lacertidae	cf. Podarcis sp.	Medas Islands	Spain	Early Pleistocene	Bailon 1991; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain et al. 2016a
Podarcis sp.	Lacertidae		Almenara Casablanca 3	Spain	Late early Pleistocene (Calabrian)	Bailon & Blain 2007
Podarcis sp.	Lacertidae		Cúllar de Baza 1	Spain	Middle Pleistocene (close to 600 ka)	Barbadillo 1989; Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009; Blain 2009
Podarcis sp.	Lacertidae		Cava IV 20, Monte Tuttavista	Italy	Middle Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008
Podarcis sp.	Lacertidae		Cava XI - Canidae, Monte Tuttavista	Italy	Middle Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008
Podarcis sp.	Lacertidae		Cava XI Dic.2001, Monte Tuttavista	Italy	Middle Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008
Podarcis sp.	Lacertidae		Cava XI 3, Monte Tuttavista	Italy	Middle Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008
Podarcis sp.	Lacertidae		Cretone	Italy	Middle Pleistocene	Di Canzio et al. 2003
Podarcis sp.	Lacertidae	Lacerta (Podarcis) lilfordi; Lacerta sp.	Cala Morlanda, Mallorca	Spain	Middle Pleistocene	Kotsakis 1981; Bailon 2004
Podarcis sp.	Lacertidae		Trinchera Elefante TE19, Sima del Elefante	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain et al. 2011
Podarcis sp.	Lacertidae		Cueva del Angel	Spain	Middle/Upper Pleistocene (MIS 5e)	Barroso Ruíz et al. 2011
Podarcis sp.	Lacertidae		Artenac	France	Upper Pleistocene (middle Paleolithic)	Böhme & Ilg 2003
Podarcis sp.	Lacertidae		Gruta da Figueira Brava	Portugal	Upper Pleistocene (middle Paleolithic)	Crespo 2001; Crespo 2002; Böhme & Ilg 2003
Podarcis sp.	Lacertidae		Cava VI Banco 6, Monte Tuttavista	Italy	Upper Pleistocene	Delfino 2002; Böhme & Ilg 2003; Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Bailon 2004: Delfino & Rook 2008
Podarcis sp.	Lacertidae		Cava VII 2, Monte Tuttavista	Italy	Upper Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008
Podarcis sp.	Lacertidae		San Teodoro	Italy	Late Pleistocene	Bonfiglio et al. 2001; Delfino 2002; Böhme & Ilg 2003; Bailon 2004
Podarcis sp.	Lacertidae	Lacerta sp.	Avenc de Na Corna, Mallorca	Spain	Upper Pleistocene	Kotsakis 1981; Bailon 2004
Podarcis sp.	Lacertidae	Lacerta sp.	Cova de Son Berenguer, Mallorca	Spain	Upper Pleistocene	Kotsakis 1981; Bailon 2004
Podarcis sp.	Lacertidae	Lacerta sp.	Cova de Son Vida, Mallorca	Spain	Upper Pleistocene	Kotsakis 1981; Bailon 2004
Podarcis sp.	Lacertidae		COLT locality, Illa Grossa, Islas Columbretes	Spain	Holocene	Marquina et al. 2014

cf. Podarcis sp.	Lacertidae		Sète	France	Middle Pliocene (MN 15)	Bailon 1991; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007
cf. Podarcis sp.	Lacertidae		Grotta della Fata Nana, Bosco Chiesanuova	Italy	Earliest Middle Pleistocene	Delfino et al. 2008a
cf. Podarcis sp.	Lacertidae	Lacertidae type <i>Podarcis</i> - <i>Psammodromus</i> ; <i>Podarcis</i> sp.	Lazaret Cave	France	Middle Pleistocene (MIS 6)	Bailon 1991; Hanquet et al. 2010; Blain et al. 2017a
cf. Podarcis sp.	Lacertidae		La Coscia CO1	France	Middle Pleistocene	Böhme & Ilg 2003; Bailon 2004
cf. Podarcis sp.	Lacertidae	cf. Podarcis/Psammodromus sp.	Cova del Gegant	Spain	Upper Pleistocene	Böhme & Ilg 2003; López-García et al. 2012
cf. Podarcis sp.	Lacertidae		Galls Carboners Cave	Spain	Upper Pleistocene	Böhme & Ilg 2003; López-García et al. 2014
cf. Podarcis sp.	Lacertidae		Antoliñako Koba	Spain	Upper Pleistocene/Holocene	Zubeldia et al. 2007
cf. Podarcis sp.	Lacertidae		Gritulu GR2	France	Holocene (Neolithic)	Böhme & Ilg 2003; Bailon 2004
cf. Podarcis sp.	Lacertidae		Vallone Inferno	Italy	Holocene	Forgia et al. 2013
aff. Podarcis sp.	Lacertidae		Cueva Horá	Spain	Upper Pleistocene	Bailon 1986; Holman 1998; Böhme & Ilg 2003
Psammodromus algirus	Lacertidae		Quibas	Spain	Early Pleistocene (Calabrian)	Montoya et al. 1999; Montoya et al. 2001; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009
Psammodromus algirus	Lacertidae		Gruta da Figueira Brava	Portugal	Upper Pleistocene (middle Paleolithic)	Crespo 2001; Crespo 2002; Böhme & Ilg 2003
Psammodromus algirus	Lacertidae		La Salema	Spain	Upper Pleistocene	Marquina et al. 2016b
Psammodromus algirus	Lacertidae		La Ventana Cave	Spain	Upper Pleistocene/Holocene	Sánchez et al. 2005
Psammodromus cf. P. algirus	Lacertidae		Barranco de Cañuelas	Spain	Pliocene/Pleistocene	Barbadillo 1989; Blain 2005
Psammodromus cf. P. algirus	Lacertidae		Cueva de Alfarero 1	Spain	Pliocene/Pleistocene	Barbadillo 1989
Psammodromus cf. P. algirus	Lacertidae		Guadix-Baza	Spain	Plio-Pleistocene	Barbadillo et al. 1997; Crespo 2001
Psammodromus cf. P. algirus	Lacertidae		Almenara Casablanca 1	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005
Psammodromus cf. P. algirus	Lacertidae		Valdocarros	Spain	Middle Pleistocene (MIS 8/7)	Blain et al. 2012
Psammodromus cf. P. algirus	Lacertidae		Higueral de Valleja Cave	Spain	Upper Pleistocene (late Paleolithic)	Jennings et al. 2009
Psammodromus cf. P. algirus	Lacertidae		Vanguard Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001; Böhme & Ilg 2003
Psammodromus cf. P. algirus	Lacertidae		Cueva del Boquete de Zafarraya	Spain	Upper Pleistocene	Böhme & Ilg 2003

Psammodromus cf. P. algirus	Lacertidae		PRERESA	Spain	Upper Pleistocene	Böhme & Ilg 2003; Panera et al. 2014
cf. Psammodromus hispanicus	Lacertidae		Áridos-1	Spain	Middle Pleistocene (MIS 11)	Böhme & Ilg 2003; Blain et al. 2014e; Blain et al. 2015
Psammodromus sp.	Lacertidae		Higueral de Valleja Cave	Spain	Upper Pleistocene (late Paleolithic)	Böhme & Ilg 2003; Jennings et al. 2009
Psammodromus sp.	Lacertidae	Psammodromus cf. P. algirus	Gorham's Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001; Böhme & Ilg 2003; Blain et al. 2013
Psammodromus sp.	Lacertidae	Þ	Vanguard Cave, Gibraltar	England	Upper Pleistocene	Böhme & Ilg 2003
Psanmodromus sp.	Lacertidae		Guia	Portugal	Upper Pleistocene	Crespo 2001; Crespo 2002; Böhme & Ilg 2003
cf. Psammodromus sp.	Lacertidae		Galls Carboners Cave	Spain	Upper Pleistocene	López-García et al. 2014
Timon lepidus	Lacertidae		Almenara Casablanca 1	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003
Timon lepidus	Lacertidae	Timon cf. T. lepidus	Cueva Victoria	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008a; Agustí et al. 2009; Blain 2009; Blain 2012. 2014
Timon lepidus	Lacertidae	Lacerta lepida	Quibas	Spain	Early Pleistocene (Calabrian)	Montoya et al. 1999; Montoya et al. 2001; Böhme & Ilg 2003; Bailon & Blain 2007
Timon lepidus	Lacertidae	Lacerta aff. L. siculimelitensis; Lacerta sp.	Cava dell'Erba, Pirro Nord	Italy	Lower Pleistocene	Delfino & Bailon 2000; Delfino 2001; Böhme & Ilg 2003; Delfino & Atzori 2013; Blain et al. 2016c; Tschopp et al. 2016
Timon lepidus	Lacertidae	Lacerta aff. L. siculimelitensis ; Lacerta sp.	Cava Pirro, Pirro Nord	Italy	Lower Pleistocene	Delfino & Bailón 2000; Delfino 2001; Böhme & Ilg 2003; Delfino & Atzori 2013; Blain et al. 2016c; Tschopp et al. 2016
Timon lepidus	Lacertidae		Medas Islands	Spain	Early Pleistocene	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Agustí et al. 2009; Blain et al. 2016a
Timon lepidus	Lacertidae		Venta Micena-1	Spain	Lower Pleistocene	Böhme & Ilg 2003
Timon lepidus	Lacertidae	Lacerta aff. L. lepida; Lacerta cf. L. lepida; Timon aff. T. lepidus	Áridos-1	Spain	Middle Pleistocene (MIS 11)	Sanz & Sanchiz 1980; Estes 1983; Holman 1998; Böhme & Ilg 2003; Blain et al. 2014e; Blain et al. 2015
Timon lepidus	Lacertidae		Valdocarros	Spain	Middle Pleistocene (MIS 8/7)	Blain et al. 2012
Timon lepidus	Lacertidae	Lacerta cf. L. lepida	Lazaret Cave	France	Middle Pleistocene (MIS 6)	Bailon 1991; Hanquet et al. 2010; Bailon & Rage 2012; Blain et al. 2017a
Timon lepidus	Lacertidae		Sala de los Huesos, Maltravieso Cave	Spain	Middle Pleistocene (MIS 6)	Blain et al. 2017a
Timon lepidus	Lacertidae	Lacerta lepida	Lunel-Viel, Mas des Caves	France	Middle Pleistocene	Gervais 1859; Estes 1983; Holman 1998; Böhme & Ilg 2003
Timon lepidus	Lacertidae	Lacerta aff. L. lepida; Lacerta lepida	Arriaga	Spain	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Timon lepidus	Lacertidae	Lacerta lepida	Grajas Cave	Spain	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Timon lepidus	Lacertidae		Madrid	Spain	Middle Pleistocene	Crespo 2001
Timon lepidus	Lacertidae		Málaga	Spain	Middle Pleistocene	Crespo 2001

Timon lepidus	Lacertidae		Cueva del Angel	Spain	Middle/Upper Pleistocene (MIS 5e)	Barroso Ruíz et al. 2011
Timon lepidus	Lacertidae		Cova del Rinoceront	Spain	Middle/Upper Pleistocene	Böhme & Ilg 2003; Daura et al. 2015
Timon lepidus	Lacertidae		Cueva del Camino (= Pinilla del Valle) Secteur Central	Spain	Upper Pleistocene (MIS 5b)	Böhme & Ilg 2003; Laplana et al. 2013; Blain et al. 2014b
Timon lepidus	Lacertidae		Cueva del Camino (= Pinilla del Valle) Secteur Nord	Spain	Upper Pleistocene (MIS 5b)	Böhme & Ilg 2003; Laplana et al. 2013; Blain et al. 2014b
Timon lepidus	Lacertidae	Lacerta lepida	Cueva de los Torrejones	Spain	Upper Pleistocene (MIS 4/3)	Arribas Herrera et al. 1997
Timon lepidus	Lacertidae	Lacerta lepida	Gruta da Figueira Brava	Portugal	Upper Pleistocene (middle Paleolithic)	Crespo 2001; Crespo 2002; Böhme & Ilg 2003
Timon lepidus	Lacertidae		Sala de las Chimeneas, Maltravieso Cave	Spain	Upper Pleistocene (MIS 2)	Bañuls Cardona et al. 2012
Timon lepidus	Lacertidae		Peña de Estebanvela Cave	Spain	Upper Pleistocene (MIS 1)	Sanchiz & Barbadillo 2007
Timon lepidus	Lacertidae		Gorham's Cave, Gibraltar	England	Upper Pleistocene	Böhme & Ilg 2003; Blain et al. 2013
Timon lepidus	Lacertidae	Lacerta lepida	Vanguard Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001; Böhme & Ilg 2003
Timon lepidus	Lacertidae	Lacerta lepida	Guia	Portugal	Upper Pleistocene	Crespo 2001; Crespo 2002; Böhme & Ilg 2003
Timon lepidus	Lacertidae		Cueva del Boquete de Zafarraya	Spain	Upper Pleistocene	Böhme & Ilg 2003
Timon lepidus	Lacertidae	Lacerta lepida	Cueva Horá	Spain	Upper Pleistocene	Bailon 1986; Holman 1998; Böhme & Ilg 2003
Timon lepidus	Lacertidae		Hat, Jarama Valley	Spain	Upper Pleistocene	Böhme & Ilg 2003
Timon lepidus	Lacertidae		Málaga	Spain	Upper Pleistocene	Crespo 2001
Timon lepidus	Lacertidae		PRERESA	Spain	Upper Pleistocene	Böhme & Ilg 2003; Panera et al. 2014
Timon lepidus	Lacertidae		Bize	France	Pleistocene	Estes 1983
Timon lepidus	Lacertidae		Burgos	Spain	Pleistocene	Barbadillo 1989
Timon lepidus	Lacertidae		Caverna dei Parmorari	Italy	Upper Pleistocene/Holocene	this work
Timon lepidus	Lacertidae	Lacerta lepida	La Ventana Cave	Spain	Upper Pleistocene/Holocene	Böhme & Ilg 2003; Sánchez et al. 2005
Timon lepidus	Lacertidae		Valdavara-1 Cave	Spain	Upper Pleistocene/Holocene	Böhme & Ilg 2003; López-García et al. 2011
Timon lepidus	Lacertidae		La Roberte, Châteauneuf-du- Rhône	France	Holocene (middle Neolithic)	Bailon 1991
Timon lepidus	Lacertidae		Font Juvenal	France	Holocene (Neolithic)	Bailon 1991
Timon lepidus	Lacertidae		Jaén	Spain	Holocene (Neolithic)	Barbadillo 1989
Timon lepidus	Lacertidae		Cueva de Las Orcillas 1	Spain	Holocene (Epipalaeolithic/Copper Age)	Fernández Eraso et al. 2010
Timon lepidus	Lacertidae	Lacerta lepida	La Balsa la Tamariz	Spain	Holocene (MIS 1, Bronze Age)	Laplana Conesa & Cuenca Bescós 1995
Timon lepidus Timon lepidus	Lacertidae I acertidae	Lacerta lepida	Lloma de Betxí Castilleio del Bonete	Spain Snain	Holocene (Bronze Age) Holocene	Tormo Cuñat & de Pedro Michó 2013 Benítez de Lugo Enrich et al. 2015
THRUE ADDARD			Cusures we serve			

Estes 1983	Crespo 2001	Estes 1983	Martínez-Sánchez et al. 2010, 2012	Barbadillo et al. 1997; Crespo 2001	Böhme & IIg 2003; Blain 2005; Agustí et al. 2009; Blain 2009	Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009; Blain 2009	Blain 2003; Bölmæ & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agusti et al. 2009; Blain 2009; Agustí et al. 2010; Blain & Bailon 2010; Blain et al. 2011; Blain et al. 2016d	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009; Blain & Railon 2010: Rlain et al. 2016d	Barbadillo 1989; Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009: Blain 2009	Böhme & Ilg 2003	Böhme & Ilg 2003	Bailon 1991	Barbadillo 1989; Crespo 2001	this work	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; Delfino et al. 2008b; this work	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; this work	Böhme & Ilg 2003; Blain 2005; Blain 2009	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; this work	this work	Böhme & IIg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; this work	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008; this work
Holocene	Holocene	Holocene	Upper Pleistocene (MIS 3)	Plio-Pleistocene	Early Pleistocene (Gelasian)	Early Pleistocene (Gelasian)	Early Pleistocene (Calabrian)	Early Pleistocene (Calabrian)	Middle Pleistocene (close to 600 ka)	Upper Pleistocene	Late Pleistocene	Middle Pleistocene	Middle Pleistocene	Pleistocene (Calabrian)	Pleistocene (Calabrian)	Pleistocene (Calabrian)	Early Pleistocene (Calabrian)	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene
Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	France	Spain	Italy	Italy	Italy	Spain	Italy	Italy	Italy	Italy
Los Palacios (Ciudad Real)	Pontones	Villena	Sima de Abraham	Guadix-Baza	Almenara Casablanca 1	Almenara Casablanca 4	Barranco León	Fuente Nueva 3	Cúllar de Baza 1	Cova del Gegant	Cova dels Musclos	Terra Amata	Madrid	Cava IV <i>Macaca</i> , Monte Tuttavista	Cava VI 3, Monte Tuttavista	Cava VII blocco strada, Monte Tuttavista	Fuente Nueva 2	Cava IX <i>Prolagus</i> , Monte Tuttavista	Cava X 3 uccelli, Monte Tuttavista	Cava XI - Canidae, Monte Tuttavista	Cava XI Dic.2001, Monte Tuttavista
				Timon lepidus			Lacerta cf. L. lepida ; Timon lepidus	Lacerta cf. L. lepida; Timon lepidus							Lacerta sp.	Lacerta sp.	Lacerta sp.	Lacerta sp.		<i>Lacerta</i> sp.	Lacerta sp.
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Timon lepidus	Timon lepidus	Timon lepidus	cf. Timon lepidus	Timon cf. T. lepidus	Timon cf. T. lepidus	Timon cf. T. lepidus	Timon cf. T. lepidus	Timon cf. T. lepidus	Timon cf. T. lepidus	Timon cf. T. lepidus	Timon cf. T. lepidus	Timon aff. T. lepidus	Timon aff. T. lepidus	Timon sp.	Timon sp.	Timon sp.	Timon sp.	Timon sp.	Timon sp.	Timon sp.	Timon sp.

Timon en	I acertidae	I acerta en	Cava VI Banco 6, Monte	Italy	I Inner Dleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et
.de noun		racena sp.	Tuttavista	fran	Opport I totalo	al. 2004; Delfino & Rook 2008; this work
Timon sp.	Lacertidae		Cava X G3, Monte Tuttavista	Italy	Pleistocene	this work
Timon on	T acompidate		Corro VI C2 Monto Tuttorifoto	Teo b.	Distances	dais accords
t mon sp.	דמרכו ווחמכ		Cava Al UJ, MUINE LUNAVISIA	fran		
Zootoca vivipara	Lacertidae		Bad Deutsch-Altenburg 3	Austria	Plio-Pleistocene	Rauscher 1992
Zootoca vivipara	Lacertidae		Bad Deutsch-Altenburg 2A	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007
Zootoca vivipara	Lacertidae		Bad Deutsch-Altenburg 2C1	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007
Zootoca vivipara	Lacertidae		Bad Deutsch-Altenburg 4B	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Ivanov 2007
Zootoca vivipara	Lacertidae	Lacerta vivipara	Boxgrove	England	Middle Pleistocene	Holman 2000
Zootoca vivipara	Lacertidae	cf. L. vivipara	Cudmore Grove, Mersea Island	England	Middle Pleistocene	Benton & Spencer 1995; Stuart 1995; Gleed- Owen 1998
Zootoca vivipara	Lacertidae		Hunas	Germany	Middle Pleistocene	Böhme 2011
Zootoca vivipara	Lacertidae	Lacerta vivipara	Kärlich G	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003; Holman & van Kolfschoten 2011
Zootoca vivipara	Lacertidae	Lacerta vivipara	Maastricht-Belvedere 4	The Netherlands	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003; Schouten 2016
Zootoca vivipara	Lacertidae	Lacerta vivipara	Miesenheim II	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Zootoca vivipara	Lacertidae	Lacerta vivipara	Steinheim an der Murr	Germany	Upper Pleistocene	Bloos et al. 1991; Holman 1998; Böhme & Ilg 2003
Zootoca vivipara	Lacertidae		Weimar-Ehringsdorf Site Complex, Black Colluvial Unit	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Zootoca vivipara	Lacertidae	Lacerta vivipara	Oblazowa 2	Poland	Upper Pleistocene	Nadachowski et al. 1993; Holman 1998; Böhme & Ilg 2003
Zootoca vivipara	Lacertidae	cf. L. viviypara ; Lacerta cf. L. vivipara ; Lacerta vivipara	Nazeing III	England	Lower Pleistocene/Holocene	Holman 1990; Holman 1993a; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Zootoca vivipara	Lacertidae	Lacerta vivipara	Pisede	Germany	Upper Pleistocene/Holocene	Holman 1998; Böhme & Ilg 2003
Zootoca vivipara	Lacertidae	cf. Lacerta vivipara; Lacerta cf. L. vivipara	Badger Cave, Creag nan Uamh Caves	Scotland	Holocene	Gleed-Owen 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Zootoca vivipara	Lacertidae	cf. Lacerta vivipara; Lacerta cf. L. vivipara	Bone Cave, Creag nan Uamh Caves	Scotland	Holocene	Gleed-Owen 1998; Gleed-Owen 1999; Böhme & Ilg 2003
cf. Zootoca vivipara	Lacertidae		Rivoli Veronese	Italy	Early Pleistocene (Gelasian; MN 17)	Villa et al. 2017; this work

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Zootoca cf. Z. vivipara	Lacertidae	Lacerta cf. L. vivipara	Boxgrove	England	Middle Pleistocene	Holman 1992; Holman 1993b; Benton & Spencer 1995; Holman 1998; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	Lacerta cf. L. vivipara	Kärlich H	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	cf. Lacerta vivipara; Lacerta cf. L. vivipara	Roger's Cave (Symonds Yat East Cave No.14), Wye Valley	England	Upper Pleistocene	Gleed-Owen 1998; Gleed-Owen 1999; Böhme & lg 2003
Zootoca cf. Z. vivipara	Lacertidae	cf. L. vivipara; Lacerta cf. L. vivipara	Shropham Pit (Interglacial Component)	England	Upper Pleistocene	Holman 1993a; Stuart 1995; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	cf. Lacerta vivipara ; Lacerta cf. L. vivipara	Tornewton Cave (Hyaena stratum), Torbryan Caves	England	Upper Pleistocene	Gleed-Owen 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	Lacerta cf. L. vivipara	Burgtonna, Deckschichten	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	Lacerta cf. L. vivipara	Villa Seckendorf, Stuttgart	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	cf. Lacerta vivipara ; Lacerta cf. L. vivipara	Kent's Cavern (Wolf Den)	England	Middle Pleistocene/Holocene	Gleed-Owen 1999; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	cf. Lacerta vivipara; Lacerta cf. L. vivipara; Lacerta vivipara	Broken Cavern, Torbryan Caves	England	Upper Pleistocene/Holocene	Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	Lacerta cf. L. vivipara	Ightham fissures near Sevenoaks	England	Upper Pleistocene/Holocene	Gleed-Owen 1999
Zootoca cf. Z. vivipara	Lacertidae	cf. Lacerta vivipara; Lacerta cf. L. vivipara; Lacerta vivipara	Three Holes Cave, Torbryan Caves	England	Upper Pleistocene/Holocene	Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	Lacerta cf. L. vivipara	Raj Cave	Poland	Upper Pleistocene/Holocene	Holman 1998; Böhme & Ilg 2003
Zootoca cf. Z. vivipara	Lacertidae	cf. Lacerta vivipara ; Lacerta cf. L. vivipara	Smoo Cave	England	Holocene	Gleed-Owen 1998; Gleed-Owen 1999; Böhme & Ilg 2003
cf. Lacerta or Podarcis sp. indet.	Lacertidae		Kärlich H	Germany	Middle Pleistocene	Holman & van Kolfschoten 2011
Edlartetia sp. vel Miolacerta sp.	Lacertidae	Edlartetia sansaniensis	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Böhme & Ilg 2003; Ivanov & Böhme 2011; Villa & Delfino 2017; this work
Eremiadini indet.	Lacertidae	Lacertidae indet.	Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Villa et al. 2016b; this work
Lacertidae indet. 1	Lacertidae	Lacerta sp.	Hambach 6C	Germany	Early middle Miocene (Langhian, MN 5)	Mörs 2002; Böhme 2003; Böhme & Ilg 2003; Čerňanský et al. 2016c
Lacertidae indet. 2	Lacertidae	Lacerta sp.	Hambach 6C	Germany	Early middle Miocene (Langhian, MN 5)	Mörs 2002; Böhme 2003; Böhme & Ilg 2003; Čerňanský et al. 2016c
Lacertidae indet. sp. 1	Lacertidae		Béon 1 (= Montréal-du-Gers)	France	Lower Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Rage & Bailon 2005

ene (Langhian) Böhme & Ilg 2003; Bastir et al. 2014	ene (Langhian) Böhme & Ilg 2003	taracian, MN7+8) Böhme & Ilg 2003; Venczel & Hir 2013	taracian, MN7+8) Böhme & Ilg 2003; Venczel & Hir 2013	llesian. MN9) Böhme & Ilg 2003: Venczel & Hir 2013	llesian, MN9) Böhme & Ilg 2003; Venczel & Hir 2013	Ilesian, MN9) Böhme & Ilg 2003; Venczel & Hir 2013	Ilesian, MN9) Böhme & Ilg 2003; Venczel & Hir 2013	rtonian, MN 9) Böhme & Ilg 2003	e (Messinian, MN Marquina et al. 2016a	ene (Burdigalian, Böhme & Ilg 2003; Rage & Bailon 2005	ene (Langhian) Böhme & Ilg 2003; Bastir et al. 2014	ene (Langhian) Böhme & Ilg 2003	llesian, MN9) Böhme & Ilg 2003; Venczel & Hir 2013	rtonian, MN 9) Böhme & Ilg 2003	e (Messinian, MN Marquina et al. 2016a	ene (Langhian) Böhnne & Ilg 2003; Bastir et al. 2014	ssinian, MN 13) Böhme & Ilg 2003; Venczel 2006	ssinian, MN 13) Böhme & Ilg 2003; Venczel 2006	ssinian, MN 13) Venczel 2006	ocene (middle Blain & Bailon 2003	cene (upper Clot et al. 1984; Bailon 1991	
MINUTAL DINNER	Middle Mioco	Miocene (Ast	Miocene (Ast	Miocene (Va	Miocene (Va.	Miocene (Va	Miocene (Va	Miocene (To	Late Miocene 13)	Lower Mioce MN 4b)	Middle Mioc	Middle Mioc	Miocene (Va	Miocene (To	Late Miocene 13)	Middle Mioc	Miocene (Me	Miocene (Me	Miocene (Me	Upper Pleistc Paleolithic)	Upper Pleistc Palaeolithic)	Upper Pleisto
Spain	Spain	Hungary	Hungary	Hungary	Hungary	Hungary	Hungary	Slovakia	Spain	France	Spain	Spain	Hungary	Slovakia	Spain	Spain	Hungary	Hungary	Hungary	France	France	
Moratilla 2	Valdemoros 3B	Felsötárkány-Felnémet 2/3	Felsötárkány-Felnémet 2/7	Felsötárkánv 1	Felsötárkány 2	Felsötárkány 3/2	Felsötárkány 3/10	Borský Svätý Jur	Venta del Moro	Béon 1 (= Montréal-du-Gers)	Moratilla 2	Valdemoros 3B	Felsötárkány 1	Borský Svätý Jur	Venta del Moro	Moratilla 2	Polgárdi 4	Polgárdi 5	Polgárdi 4	Artenac	Bois du Cantet	
Lacerta sp. 1											Lacerta sp. 2					Lacerta sp. 3					Lacerta sp.	
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	
Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 1	Lacertidae indet. sp. 2	Lacertidae indet. sp. 2	Lacertidae indet. sp. 2	Lacertidae indet. sp. 2	Lacertidae indet. sp. 2	Lacertidae indet. sp. 2	Lacertidae indet. sp. 3	Lacertidae indet. A	Lacertidae indet. A	Lacertidae indet. B	Lacertidae type Podarcis- Lacerta sensu stricto	Lacertidae type Podarcis- Psammodromus	Lacertidae type Podarcis-

лk	лк	лк	лrk	лrk	& Ilg 2003	& Ilg 2003	ain 2005; Blain et al. 09; Blain 2009; Blain 2012.	dríguez et al. 2011; Cuenca-	dríguez et al. 2011; Cuenca-	ain et al. 2010a; Rodríguez sscós et al. 2015	ain et al. 2010a; Rodríguez sscós et al. 2015	ain et al. 2010a; Rodríguez sscós et al. 2015	ain et al. 2010a; Rodríguez sscós et al. 2015	ain et al. 2010a; Rodríguez sscós et al. 2015		& Ilg 2003	ain 2005; Blain et al. 9; Agustí et al. 2009; Blain 2011; Cuenca-Bescós et al.
Delfino 2004b; this we	Delfino 2002; Böhme	Delfino 2002; Böhme	Böhme & Ilg 2003; Bl 2008a; Agustí et al. 20 2014	Blain et al. 2010a; Roo Bescós et al. 2015	Blain et al. 2010a; Roo Bescós et al. 2015	Böhme & Ilg 2003; Bl et al. 2011; Cuenca-Be	Böhme & Ilg 2003; Bl et al. 2011; Cuenca-Bε	Böhme & Ilg 2003; Bl et al. 2011; Cuenca-Be	Böhme & Ilg 2003; Bl et al. 2011; Cuenca-Be	Böhme & Ilg 2003; Bl et al. 2011; Cuenca-Be	Bailon 2010	Delfino 2002; Böhme	Böhme & Ilg 2003; Bl 2008b; Blain et al. 20(2009; Rodríguez et al. 2015				
Late Pliocene	Late Pleistocene	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene	Late Pleistocene	Early Pleistocene	Early Pleistocene (Calabrian)	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Lower Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene
Greece	Greece	Greece	Greece	Greece	Italy	Italy	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	France	Italy	Spain
Spilia 3 (1976)	Arnissa	Liko A	Liko BA	Liko C	Contrada Pianetti - Ragusa - Lato Est 1994	Gervasio 5	Cueva Victoria	Trinchera Elefante TE9a, Sima del Elefante	Trinchera Elefante TE9a+, Sima del Elefante	Trinchera Elefante TE9b, Sima del Elefante	Trinchera Elefante TE10, Sima del Elefante	Trinchera Elefante TE11, Sima del Elefante	Trinchera Elefante TE13, Sima del Elefante	Trinchera Elefante TE14, Sima del Elefante	Romain-la-Roche	Contrada Annunziata, Ragusa	Trinchera Dolina TD5up, Gran Dolina
"Lacertilia" indet.	Lacerta gr. L. viridis	Lacerta gr. L. viridis	Lacertidae indet.	"Lacertilia" indet.						Lacerta sp. small size	<i>Lacerta</i> sp. small size	<i>Lacerta</i> sp. small size	<i>Lacerta</i> sp. small size	Lacerta sp. small size			
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Lacertidae indet. (large-sized taxon)	Lacertidae indet. (<i>Podarcis</i> size)	Lacertidae indet. (small Podarcis size)	Lacertidae indet. small size (Podarcis /Psammodromus sp.)	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size	Lacertidae indet. small size				

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Lacertidae indet. small size	Lacertidae		Trinchera Dolina TD6up, Gran Dolina	Spain	Middle Pleistocene	bonne & ug 2005; biam 2005; biam et al. 2008b; Blain et al. 2009; Agustí et al. 2009; Blain 2009; Rodríguez et al. 2011; Cuenca-Bescós et al. 2015
Lacertidae indet. small size	Lacertidae		Trinchera Dolina TD7, Gran Dolina	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008b; Blain et al. 2009; Agustí et al. 2009; Blain 2009; Rodríguez et al. 2011; Cuenca-Bescós et al. 2015
Lacertidae indet. small size	Lacertidae		Trinchera Dolina TD8a, Gran Dolina	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008b; Blain et al. 2009; Blain 2009; Rodríguez et al. 2011; Cuenca-Bescós et al. 2015
Lacertidae indet. small size	Lacertidae		Trinchera Dolina TD8b, Gran Dolina	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008b; Blain et al. 2009; Blain 2009; Cuenca- Bescós et al. 2015
Lacertidae indet. small size	Lacertidae		Trinchera Dolina TD10, Gran Dolina	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008b; Blain et al. 2009; Blain 2009; Rodríguez et al. 2011; Blain et al. 2015
Lacertidae indet. small size	Lacertidae		Artenac	France	Upper Pleistocene (middle Paleolithic)	Blain & Bailon 2003; Böhme & Ilg 2003
Lacertidae indet. small size	Lacertidae	cf. Podarcis sp.	Abri des Pêcheurs	France	Upper Pleistocene	Moncel et al. 2010
Lacertidae indet.	Lacertidae		Grafenmühle 2	Germany	Miocene (Aquitanian, MN 1/2)	Schleich 1985b
Lacertidae indet.	Lacertidae		Oschiri	Italy	Lower Miocene (Aquitanian, MN 1/MN 2b)	Böhme & Ilg 2003; Bailon 2004
Lacertidae indet.	Lacertidae		Chavroches P1C2	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Chavroches P1C11	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Montaigu-le-Blin P23	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Montaigu-le-Blin 87 a Sorex	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Montaigu-le-Blin, Le Vendant	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Montaigu-le-Blin, Le Vendant a Sorex	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Poncenat	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003
Lacertidae indet.	Lacertidae		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b
Lacertidae indet.	Lacertidae		Wallenried	Switzerland	Early Miocene (MN 2a)	Mennecart et al. 2016
Lacertidae indet.	Lacertidae		Schaffhausen (Harburg) 1 (A)	Germany	Miocene (MN 2)	Schleich 1985b
Lacertidae indet.	Lacertidae		Treuchtlingen 2	Germany	Miocene (MN 2)	Schleich 1985b

Lacertidae indet.	Lacertidae		Mont Merle	France	Miocene (Aquitanian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Bargota	Spain	Early Miocene (Aquitanian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Rage 2013
Lacertidae indet.	Lacertidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Lacertidae indet.	Lacertidae		Gögglingen	Germany	Miocene (Burdigalian, MN 3)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Sant Andreu de la Barca, Vallès Penedès Basin	Spain	Early Miocene (MN 3)	this work
Lacertidae indet.	Lacertidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1984
Lacertidae indet.	Lacertidae		Béon 1 (= Montréal-du-Gers)	France	Lower Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Rage & Bailon 2005; Venczel & Sanchíz 2006; Böhme 2010b
Lacertidae indet.	Lacertidae		Forsthart	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1985b
Lacertidae indet.	Lacertidae		Günzburg 2/3 Umgehung mittlere Bereiche der Sande	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Günzburg 2/6 Umgehung Sande im Norden Aufschluss	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Lacertidae indet.	Lacertidae	Lacerta sp.	Aliveri	Greece	Early Miocene (MN 4)	Böhme & Ilg 2003; Delfino 2004b; this work
Lacertidae indet.	Lacertidae		Els Casots, Vallès Penedès Basin	Spain	Early Miocene (MN 4)	this work
Lacertidae indet.	Lacertidae		Sant Mamet, Vallès Penedès Basin	Spain	Early Miocene (MN 4)	this work
Lacertidae indet.	Lacertidae		Teiritzberg (T2/6 = 001/Z/C/4), Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Attenfeld	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme 2003; Böhme & Ilg 2003; Čerňanský et al. 2016c
Lacertidae indet.	Lacertidae		Ateca 1	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Ateca 3	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Olmo Redondo 4A	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Vargas 4A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Schmiedrued-Pyffrüti level 618, Swiss Molasse Basin	Switzerland	Late Early Miocene (Burdigalian)	Böhme & Ilg 2003; Jost et al. 2015

I acertidae indet	I acertidae		Budenheim	Garmany	I otter Miccene	Schlaich 1088h
Lacertidae indet.	Lacertidae		Mainz - Sonnenbrauerei	Germany	Lower Miocene	Schleich 1988b
Lacertidae indet.	Lacertidae		Lapsarna, Lesvos Petrified Forest, Lesvos	Greece	Early Miocene	Vasileiadou et al. 2017
Lacertidae indet.	Lacertidae	Lacerta sp.	Burtenbach 1b (b. Thannhausen)	Germany	Early Miocene (MN 5)	Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2010
Lacertidae indet.	Lacertidae		Derching 1b (unten)	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Eberstetten 2 (unter Weg)	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae	Lacerta sp.	Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Lacertidae indet.	Lacertidae	Lacerta sp.	Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Lacertidae indet.	Lacertidae		Dinkelscherben	Germany	Miocene (MN 5/6)	Schleich 1985b
Lacertidae indet.	Lacertidae	Lacerta s.l.; Lacerta sp.	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Böhme & Ilg 2003; Ivanov & Böhme 2011; Čerňanský et al. 2016c; Villa & Delfíno 2017; this work
Lacertidae indet.	Lacertidae		Laimering 2a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Petersbuch 33 B	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Petersbuch 39 II	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Litke 1	Hungary	Miocene (Langhian, MN 6)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Caseton 2B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Las Planas 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Las Umbrias 9	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Las Umbrias 10	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Somosaguas Sur	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Valdemoros 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Valdemoros 7B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Vargas 6	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Schmiedrued-Pyffrüti level 642, Swiss Molasse Basin	Switzerland	Early Middle Miocene (Langhian)	Böhme & Ilg 2003; Jost et al. 2015
Lacertidae indet.	Lacertidae		Gündlkofen	Germany	Miocene (MN 6)	Schleich 1985b
Lacertidae indet.	Lacertidae		La Gornal 1, Vallès Penedès Basin	Spain	Middle Miocene (MN 6)	this work
Lacertidae indet.	Lacertidae		Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000
Lacertidae indet.	Lacertidae		Abocador de Can Mata, Vallès Penedès Basin	Spain	Middle Miocene (MN 6/MN 7+8)	Böhme & Ilg 2003; this work
Lacertidae indet.	Lacertidae		Moneva	Spain	Middle/upper Miocene (MN 6/7)	Benito & Bolet 2016

Jovanović et al. 2002	this work	Böhme 2003; Villa & Delfino 2017; this work	Böhme & Ilg 2003; Venczel & Știucă 2008	Böhme & Ilg 2003	Böhme & Ilg 2003; Böhme & Vasilyan 2014	this work	Böhme & Ilg 2003	Böhme & Ilg 2003	Schleich 1985b	this work	this work	this work	this work	this work	this work	this work	Delfino 2004b; this work	this work	this work	this work	this work	Böhme & Ilg 2003
Middle Miocene (MN 7+8)	Middle Miocene (MN 7+8)	Miocene (Serravallian, MN 8)	Late middle Miocene (Serravallian, MN 8)	Middle Miocene (Serravallian)	Late middle Miocene	Middle/late Miocene (MN 7+8/MN 9)	Late Miocene (Serravallian/Tortonian, MN 9)	Miocene (Tortonian, MN 9)	Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 10)	Late Miocene (MN 10)	Late Miocene (MN 10)	Late Miocene (MN 10)	Late Miocene (MN 9 or MN 10)	Miocene (Tortonian)
Serbia	Spain	Germany	Romania	Spain	Austria	Spain	Ukraine	Austria	Germany	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Greece	Spain	Spain	Spain	Spain	Spain
Vračević, near Bogovadje monastery	Sant Quirze, Vallès Penedès Basin	Kleineisenbach	Taut	Borjas	Gratkorn	Els Hostalets de Pierola, Vallès Penedès Basin	Gritsev	Götzendorf	Markt Rettenbach	Autovía Orbital de Barcelona B- 40, Vallès Penedès Basin	Can Llobateres, Vallès Penedès Basin	Can Missert, Vallès Penedes Basin	Can Poncic, Vallès Penedes Basin	Can Sant Feliu, Vallès Penedes Basin	Castell de Barberà, Vallès Penedes Basin	Ecoparc de Can Mata, Vallès Penedès Basin	indet. small size Lefkon 1	Can Perellada, Vallès Penedes Basin	Sant Miquel del Toudell, Vallés- Penedés Basin	Trinxera Nord Autopista, Vallès Penedès Basin	El Repetidor, Vallès Penedès Basin	Masia de la Roma 7
ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae	ertidae
Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet. Lac

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Lacertidae indet.	Lacertidae		Nombrevilla 1	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Morskaya 2	Russia	Miocene (Tortonian/Messinian, MN 12)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Ano Metochi 2	Greece	Late Miocene (Messinian, MN 13)	Georgalis et al. 2017a; this work
Lacertidae indet.	Lacertidae		Ano Metochi 3	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; Georgalis et al. 2017a; this work
Lacertidae indet.	Lacertidae	"Lacertilia" indet.	Tomea Eksi - TO 1 (= Ptolemais 1a)	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	"Lacertilia" indet.; Lacerta sp.	Tomea Eksi - TO 2 (= Ptolemais 1b)	Greece	Late Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Delfino 2004b; this work
Lacertidae indet.	Lacertidae		Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Delfino 2002; Böhme & Ilg 2003; Rook et al. 2005; Rook & Delfino 2007; Rook et al. 2015; Villa et al. 2016b; this work
Lacertidae indet.	Lacertidae	Lacerta sp.	Maramena 1	Greece	Late Miocene (MN 13/14)	Böhme & Ilg 2003; Delfino 2004b; this work
Lacertidae indet.	Lacertidae		Maramena 3	Greece	Late Miocene (MN 13/14)	this work
Lacertidae indet.	Lacertidae		Moncucco Torinese	Italy	Latest Miocene (Messinian, p- ev2)	Colombero et al. 2014b; Colombero et al. 2017; this work
Lacertidae indet.	Lacertidae		Verduno	Italy	Miocene (Messinian)	Böhme & Ilg 2003; Colombero et al. 2014a
Lacertidae indet.	Lacertidae	Lacertidae indet. small size	Rema Marmara 2	Greece	Late Miocene	Delfino 2004b; this work
Lacertidae indet.	Lacertidae		Biancone, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
Lacertidae indet.	Lacertidae		Bosco, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
Lacertidae indet.	Lacertidae		Cantatore, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
Lacertidae indet.	Lacertidae		Cava Fina, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
Lacertidae indet.	Lacertidae		Cava Pirro, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
Lacertidae indet.	Lacertidae		Chirò, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
Lacertidae indet.	Lacertidae		Gargano "Terre Rosse" (F - Coll. Firenze)	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002

Delfino 2002	Delfino 2004b; this work	Böhme & Ilg 2003; Bover et al. 2014	Blain et al. 2016a	Bailon et al. 2010	Delfino 2004b; this work	Blain 2005	Blain 2005	Blain 2005	Böhme & Ilg 2003; Bailon & Blain 2007	Böhme & Ilg 2003; Bailon & Blain 2007	Delfino 2004b; this work	Kotsakis 1980; Estes 1983; Böhme & Ilg 2003; Bailon 2004; Delfino et al. 2011	Delfino 2004b; this work	Bailon 2004	Böhme & Ilg 2003	Rithme & IIo 2003: Blain 2005: Blain 2009				
Upper Miocene (Messinian)/lower Pliocene	Miocene/Pliocene	Miocene/Pliocene (Messian/Zanclean)	Latest Miocene/Middle Pleistocene	Earliest early Pliocene	Early Pliocene (MN 15)	Lower Pliocene	Middle Pliocene (MN15)	Middle Pliocene (MN15)	Middle/late Pliocene (MN 15/16)	Late Pliocene (MN 16)	Late Pliocene (MN 16)	Late Pliocene (Piacenzian)	Late Pliocene	Pliocene	Late Pliocene/early Pleistocene (MN 16)	Pliocene/Pleistocene				
Italy	Italy	Italy	Italy	Italy	Greece	Spain	Spain	Spain	Greece	Spain	Spain	Spain	France	France	Greece	Italy	Greece	Spain	Spain	Snain
Gervasio, Gargano "Terre Rosse"	Pizzicoli, Gargano "Terre Rosse"	San Giovannino, Gargano "Terre Rosse"	San Nazario, Gargano "Terre Rosse"	Tre Fossi, Gargano "Terre Rosse"	Trilofon	Na Burguesa-1, Mallorca	Canal Negre 1	Caló den Rafelino, Mallorca	Notio 1 (= Ptolemais 6C)	Baza	Galera 1C	Gorafe 27	Balaruc II	Seynes	Tourkobounia 1	Capo Mannu D1 Local Fauna (= Mandriola)	Spilia 4	Punta Nati 6, Menorca	Cova Bonica	Barranco del Agua-6
							Acanthodactylus cf. A. erythrurus ; Lacerta sp.; Podarcis cf. P. taurica; Psammodromus cf. P. algirus; Timon cf. T. lepidus		Lacertidae indet. small size						Lacertidae indet. small size	cf. Podarcis sp.				
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.				

I acertidae indet.	I.acertidae		Barranco de Cañuelas	Snain	Pliocene/Pleistocene	Barhadillo 1989
Lacertidae indet.	Lacertidae		Huéscar 7/3	Spain	Pliocene/Pleistocene	Barbadillo 1989
Lacertidae indet.	Lacertidae		Rambla del Conejo 3	Spain	Pliocene/Pleistocene	Barbadillo 1989
Lacertidae indet.	Lacertidae	Lacertidae indet. small size	Tourkobounia 2	Greece	earliest early Pleistocene	Delfino 2004b; this work
Lacertidae indet.	Lacertidae		Rivoli Veronese	Italy	Early Pleistocene (Gelasian; MN 17)	Villa et al. 2017; this work
Lacertidae indet.	Lacertidae		Montoussé 5	France	Early Pleistocene (MN 17)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007
Lacertidae indet.	Lacertidae		Fuente Nueva 1	Spain	Early Pleistocene (MN 17)	Böhme & Ilg 2003; Blain 2005; Blain 2009
Lacertidae indet.	Lacertidae		Galera-2	Spain	Early Pleistocene (MN 17)	Böhme & Ilg 2003; Blain 2005; Blain 2009
Lacertidae indet.	Lacertidae		Almenara Casablanca 1	Spain	Early Pleistocene (Gelasian)	Bailon & Blain 2007; Agustí et al. 2009; Blain 2009
Lacertidae indet.	Lacertidae		Almenara Casablanca 4	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009; Blain 2009
Lacertidae indet.	Lacertidae		Calella-Y	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005; Blain 2009
Lacertidae indet.	Lacertidae		Fonelas P-1	Spain	Lower Pleistocene (Gelasian)	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Vallirana	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009
Lacertidae indet.	Lacertidae	cf. Podarcis sp.	Russel-Tiglia-Egypte pit, Tegelen	The Netherlands	Early Pleistocene (Gelasian)	Villa et al. 2014; Schouten 2016; Villa et al. 2016a; this work
Lacertidae indet.	Lacertidae		Barranco Conejos	Spain	Early Pleistocene (ca 1.6 ma)	Böhme & Ilg 2003; Agustí et al. 2009
Lacertidae indet.	Lacertidae		Trinchera Elefante TE9c, Sima del Elefante	Spain	Early Pleistocene (ca 1.2 ma)	Agustí et al. 2009; Blain et al. 2010a; Rodríguez et al. 2011
Lacertidae indet.	Lacertidae	Acanthodacrylus cf. A. erythrurus ; Lacertidae indet. 1; Lacertidae indet. 2; Podarcis cf. P. hispanicus ; Psanmodronus cf. P. algirus	Almenara Casablanca 3	Spain	Late early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Blain et al. 2007; Augustí et al. 2009; Blain 2009
Lacertidae indet.	Lacertidae		Barranco León	Spain	Early Pleistocene (Calabrian)	Blain 2003; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009; Agustí et al. 2010; Blain & Bailon 2010; Blain et al. 2011; Blain et al. 2016d
Lacertidae indet.	Lacertidae		Cal Guardiola	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009
Lacertidae indet.	Lacertidae		Can Altisench	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Blain 2009

Lacertidae indet.	Lacertidae		Fuente Nueva 3	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009; Blain & Bailon 2010: Blain et al. 2016d
Lacertidae indet.	Lacertidae		Bagur 2	Spain	Early Pleistocene	Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009: Blain 2009
Lacertidae indet.	Lacertidae		Medas Islands	Spain	Early Pleistocene	Agustí et al. 2009
Lacertidae indet.	Lacertidae		Quibas	Spain	Early Pleistocene	Montoya et al., 1999; Montoya et al., 2001; Böhme & IIg 2003
Lacertidae indet.	Lacertidae		Sierra del Chaparral	Spain	Lower Pleistocene	Böhme & Ilg 2003; Pacheco et al. 2011
Lacertidae indet.	Lacertidae	Lacertidae indet. small size	Tourkobounia 3	Greece	latest early/earliest Middle Pleistocene	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	Lacertidae indet. small size	Tourkobounia 4	Greece	latest early/earliest Middle Pleistocene	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	Lacertidae indet. small size	Tourkobounia 5	Greece	latest early/earliest Middle Pleistocene	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	Lacerta sp.	Cava Nord, Brecce di Soave	Italy	Earliest Middle Pleistocene	Bon et al. 1991; Delfino et al. 2008a
Lacertidae indet.	Lacertidae		Cengelle, Brecce di Soave	Italy	Earliest Middle Pleistocene	Delfino et al. 2008a
Lacertidae indet.	Lacertidae		Cúllar de Baza 1	Spain	Middle Pleistocene (close to 600 ka)	Barbadillo 1989; Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009; Blain 2009
Lacertidae indet.	Lacertidae		Ambrona	Spain	Middle Pleistocene (MIS 11)	Blain et al. 2015
Lacertidae indet.	Lacertidae		Cuesta de la Bajada	Spain	Middle Pleistocene (MIS 9/8)	Blain et al. 2017b
Lacertidae indet.	Lacertidae		Valdocarros	Spain	Middle Pleistocene (MIS 8/7)	Blain et al. 2012
Lacertidae indet.	Lacertidae		Lazaret Cave	France	Middle Pleistocene (MIS 6)	Hanquet et al. 2010
Lacertidae indet.	Lacertidae		H-02, Estanque de Tormenta de Butarque	Spain	Late Middle Pleistocene (MIS 6)	Blain et al. 2017a
Lacertidae indet.	Lacertidae		Beeches Pit	England	Middle Pleistocene	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Cudmore Grove, Mersea Island	England	Middle Pleistocene	Gleed-Owen 1999
Lacertidae indet.	Lacertidae		Abimes de la Fage	France	Middle Pleistocene	Estes 1983
Lacertidae indet.	Lacertidae		Montoussé 3	France	Middle Pleistocene	Bailon 1991
Lacertidae indet.	Lacertidae		Contrada Frategianni, Comiso	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Bailon 2004
Lacertidae indet.	Lacertidae		Rifreddo, Bacino di San Lorenzo	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Masini et al. 2005
Lacertidae indet.	Lacertidae		Riparo di Visogliano	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae		Valdemino Cave	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2004c
Lacertidae indet.	Lacertidae		Koziy Ovrag	Russia	Middle Pleistocene	Böhme & IIg 2003
Lacertidae indet.	Lacertidae		Krolatnik	Russia	Middle Pleistocene	Böhme & Ilg 2003

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Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Agustí et al. 2009; Blain 2009	Böhme & Ilg 2003	Barroso Ruíz et al. 2011	Delfino 2002; Böhme & Ilg 2003	Böhme & Ilg 2003	Delfino et al. 2008a	Bon et al. 1991; Delfino et al. 2008a	Böhme & Ilg 2003; Laplana et al. 2013; Blain et al. 2014b	Böhme & Ilg 2003; Laplana et al. 2013; Blain et al. 2014b	Böhme & Ilg 2003; Laplana et al. 2013; Blain et al. 2014b	Martínez-Sánchez et al. 2010, 2012	Bañuls Cardona et al. 2012	Bailon & Garcia-Ibaibarriaga 2014	this work	Böhme & Ilg 2003; Jennings et al. 2009	Gleed-Owen 1998; Böhme & Ilg 2003	Gleed-Owen 2001; Böhme & Ilg 2003	Böhme & Ilg 2003; Blain & Villa 2006	Ferrandini et al. 1995; Böhme & Ilg 2003	Delfino 2004b; this work	Gasparik 1993	Virág et al. 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2004a
Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle/Upper Pleistocene (MIS 5e)	Middle/late Pleistocene	Middle/Upper Pleistocene	Earliest late Pleistocene	?earliest late Pleistocene	Upper Pleistocene (MIS 5b)	Upper Pleistocene (MIS 5b)	Upper Pleistocene (MIS 5a)	Upper Pleistocene (MIS 3)	Upper Pleistocene (MIS 2)	Upper Pleistocene (upper/latest Magdalenian)	Upper Pleistocene (Upper Paleolithic)	Upper Pleistocene (late Paleolithic)	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene	Late Pleistocene	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene
Russia	Russia	Spain	Spain	Ukraine	Spain	Italy	Spain	Italy	Italy	Spain	Spain	Spain	Spain	Spain	Spain	Italy	Spain	England	England	France	France	Greece	Hungary	Hungary	Italy
Kuznetsovka, left board of Podgornvi Buerak	Vol'naya Vershina-3	Cova d'Olopte	Trinchera Dolina TD4, Gran Dolina	Nagornoye-2, east shore of Kagul Lake	Cueva del Angel	K 22, San Vito lo Capo	Cueva del Agua	Riparo Mezzena, Avesa	La Curva, Monte Tondo, Soave	Cueva del Camino (= Pinilla del Valle) Secteur Central	Cueva del Camino (= Pinilla del Valle) Secteur Nord	Cueva del Camino (= Pinilla del Valle) Secteur Sud	Sima de Abraham	Sala de las Chimeneas, Maltravieso Cave	Santa Catalina	Riparo dell'Aquila	Higueral de Valleja Cave	Tornewton Cave (Hyaena stratum), Torbryan Caves	Vanguard Cave, Gibraltar	Bois Roche Cave	Castiglione 1, Corsica	Arnissa	Tokod	Vaskapu Cave	Buco del Frate
									Lacerta sp.										Lacertilia indet. sp. 1; Lacertilia indet. sp. 2			Lacertidae indet. small size			
Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae	Lacertidae
Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.	Lacertidae indet.

Lacertidae indet.	Lacertidae	 Contrada Tabuna, Ragusa	Italy	Late Pleistocene	Delfino 2002; Böhme & Ilg 2003; Bailon 2004
Lacertidae indet.	Lacertidae	Grotta di Veja (A), S. Anna d'Alfaedo	Italy	Late Pleistocene	Delfino et al. 2008a
Lacertidae indet.	Lacertidae	Pocket B, Contrada Pianetti	Italy	Upper Pleistocene	Bonfiglio et al. 1997
Lacertidae indet.	Lacertidae	Abric Romanì	Spain	Late Pleistocene	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae	Canyars, Gavá	Spain	Upper Pleistocene	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae	Cova dels Musclos	Spain	Upper Pleistocene	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae	 Cova dels Xaragalls	Spain	Upper Pleistocene	Böhme & Ilg 2003; López-García et al. 2012a
Lacertidae indet.	Lacertidae	El Portalón, Cueva Mayor, Atapuerca	Spain	Upper Pleistocene	Böhme & Ilg 2003; López-García et al. 2010
Lacertidae indet.	Lacertidae	 Galls Carboners Cave	Spain	Upper Pleistocene	Böhme & Ilg 2003; López-García et al. 2014
Lacertidae indet.	Lacertidae	Hat, Jarama Valley	Spain	Upper Pleistocene	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae	La Salema	Spain	Upper Pleistocene	Marquina et al. 2016b
Lacertidae indet.	Lacertidae	Teixoneres II Cave	Spain	Upper Pleistocene	Böhme & Ilg 2003
Lacertidae indet.	Lacertidae	Kaiafa	Greece	Pleistocene	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	Karpathos	Greece	Pleistocene	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	 Tal Guiem (or Tal Gniem)	Malta	Pleistocene	Böhme & Zammit-Maempel 1982; Bailon 2004
Lacertidae indet.	Lacertidae	La Escala, Cala Montgò	Spain	Pleistocene	Böhme & Ilg 2003; Blain 2005; Blain 2009
Lacertidae indet.	Lacertidae	Anabussos	Greece	Pleistocene (?)	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	Milatos 3	Greece	Pleistocene (?)	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	Xeros	Greece	Pleistocene (?)	Delfino 2004b; this work
Lacertidae indet.	Lacertidae	K 22, San Vito lo Capo	Italy	Late Pleistocene (or Holocene)	Delfino 2002; Böhme & Ilg 2003
Lacertidae indet.	Lacertidae	Askondo Cave	Spain	Upper Pleistocene/Holocene (MIS3/1)	García-Ibaibarriaga et al. 2015
Lacertidae indet.	Lacertidae	Macinaggio	France	Upper Pleistocene/Holocene	Vigne et al. 1997
Lacertidae indet.	Lacertidae	Antoliñako Koba	Spain	Upper Pleistocene/Holocene	Rofes et al. 2015
Lacertidae indet.	Lacertidae	Valdavara-1 Cave	Spain	Upper Pleistocene/Holocene	Böhme & Ilg 2003; López-García et al. 2011
Lacertidae indet.	Lacertidae	 Caverna dell'Aurera	Italy	?Upper Pleistocene/Holocene	this work
Lacertidae indet.	Lacertidae	Cova Colomera CE12, Sierra de Montsec	Spain	Holocene (Neolithic)	Böhme & Ilg 2003; Blain et al. 2016b
Lacertidae indet.	Lacertidae	Cova Colomera CE13-14, Sierra de Montsec	Spain	Holocene (Neolithic)	Böhme & Ilg 2003; Blain et al. 2016b
Lacertidae indet.	Lacertidae	Peña Larga	Spain	Holocene (MIS 1, Atlantic to Sub-boreal, Neolithic to Bronze Age)	Murelaga et al. 2009

Lacertidae indet.	Lacertidae		Santimamiñe Cave	Spain	Holocene (MIS 1, Chalcolithic/Bronze Age)	Murelaga Bereikua et al. 2011
Lacertidae indet.	Lacertidae		Cova Colomera A sup., Sierra de Montsec	Spain	Holocene (Bronze Age)	Böhme & Ilg 2003; Blain et al. 2016b
Lacertidae indet.	Lacertidae		Cova Colomera EE1, Sierra de Montsec	Spain	Holocene (Bronze Age)	Böhme & Ilg 2003; Blain et al. 2016b
Lacertidae indet.	Lacertidae		Tenuta Zuccarello, Marcon	Italy	Holocene (I cent. AD)	Villa et al. 2015; this work
Lacertidae indet.	Lacertidae		Steetley Cave	England	Holocene	Gleed-Owen 1998; Gleed-Owen 1999
?Lacertidae indet.	Lacertidae	Lacertidae indet.	Stubersheim 2	Germany	Miocene (Burdigalian, MN 3b)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
?Lacertidae indet.	Lacertidae		Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	this work
?Lacertidae indet.	Lacertidae		Schönenberg	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b
?Lacertidae indet.	Lacertidae		Punta Nati 2, Menorca	Spain	Middle Miocene	Bailon 2004
Ablepharus kitaibelii	Scincidae		Vraona Cave	Greece	Pleistocene/Holocene	Rauscher 1995
Bavariascincus mabuyaformis	Scincidae		Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme & Ilg 2003; Kosma 2004; Böhme 2010b; Čerňanský 2016
Bavariascincus mabuyaformis	Scincidae	Scincidae indet.	Forsthart	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Bavariascincus mabuyaformis	Scincidae	'35cincidae indet. (cf. Mabuya sp.); Scincidae indet.	Rembach, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Kosma 2004; Böhme 2010b; Čerňanský 2016
Chalcides bedriagai	Scincidae	Chalcides cf. C. bedriagai	Cueva Victoria	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Blain et al. 2007; Blain et al. 2008a; Agustí et al. 2009; Blain 2009; López-García et al. 2011; Blain 2012-2014
Chalcides bedriagai	Scincidae	Chalcides sp.	Gorham's Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001; Böhme & Ilg 2003; Blain et al. 2013
Chalcides bedriagai	Scincidae		Cueva del Boquete de Zafarraya	Spain	Upper Pleistocene	Böhme & Ilg 2003
Chalcides bedriagai	Scincidae		La Salema	Spain	Upper Pleistocene	Marquina et al. 2016b
Chalcides bedriagai	Scincidae		El Salt	Spain	Upper Pleistocene/Holocene (middle Palaeolithic, MIS 3)	Marquina et al. 2017
Chalcides bedriagai	Scincidae		COLT locality, Illa Grossa, Islas Columbretes	Spain	Holocene	Marquina et al. 2014
Chalcides cf. C. bedriagai	Scincidae		Cueva de Alfarero 1	Spain	Pliocene/Pleistocene	Barbadillo 1989
Chalcides cf. C. bedriagai	Scincidae		Guadix-Baza	Spain	Plio-Pleistocene	Crespo 2001
Chalcides cf. C. bedriagai	Scincidae		Almenara Casablanca 1	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Blain et al. 2007; Agustí et al. 2009; Blain 2009; López-García et al. 2011

					Dellegance	Claurance of.
Barbadillo 1989 Barbadillo 1989	Pliocene/Pleistocene Pliocene/Pleistocene	Spain	Bacocnas 1 Ramhla del Coneio 3		Scincidae	Chalcides sp. Chalcides sn
Böhme & IIg 2003	Early Pliocene (Zanclean)	Spain 2 ·	La Gloria 4		Scincidae	Chalcides sp.
Alcover & Mayol 1981; Kotsakis 1981; Carranza et al. 2008	Late Miocene/early Pliocene	Spain	Unknown locality, Menorca		Scincidae	Chalcides sp.
Böhme & Ilg 2003	Miocene (Tortonian, MN 9)	Germany	Hammerschmiede 1		Scincidae	Chalcides sp.
Böhme & Ilg 2003; Venczel & Hir 2013	Miocene (Vallesian, MN 9)	Hungary	Felsötárkány 1		Scincidae	Chalcides sp.
Böhme & Ilg 2003; López-García et al. 2011	Upper Pleistocene/Holocene	Spain	Valdavara-1 Cave		Scincidae	Chalcides striatus
Rofes et al. 2015	Upper Pleistocene/Holocene	Spain	Antoliñako Koba		Scincidae	Chalcides striatus
Gleed-Owen 2001; Böhme & Ilg 2003; Blain et al. 2013	Upper Pleistocene	England	Gorham's Cave, Gibraltar	Chalcides sp.	Scincidae	Chalcides striatus
Bailon & Garcia-Ibaibarriaga 2014	Upper Pleistocene (upper/latest Magdalenian)	Spain	Santa Catalina		Scincidae	Chalcides striatus
Blain et al. 2012	Middle Pleistocene (MIS 8/7)	Spain	Valdocarros		Scincidae	Chalcides striatus
Böhme & Ilg 2003; Venczel & Hir 2013	Miocene (Vallesian, MN 9)	Hungary	Felsötárkány 3/10		Scincidae	Chalcides cf. C. ocellatus
Böhme & Ilg 2003; Venczel & Hir 2013	Miocene (Astaracian, MN7+8)	Hungary	Felsötárkány-Felnémet 2/3		Scincidae	Chalcides cf. C. ocellatus
Kotsakis 1980; Delfino 2002; Delfino & Rook 2008	Holocene	Italy	Su Guanu Cave	Chalcides sp.	Scincidae	Chalcides ocellatus
Delfino 2002; Böhme & Ilg 2003; Delfino & Rook 2008	Late Pleistocene	Italy	Porto Leccio		Scincidae	Chalcides ocellatus
Bailon 1991	Middle Pleistocene/Holocene	France	Lazaret Cave		Scincidae	Chalcides cf. C. chalcides
Delfino 2002; Böhme & Ilg 2003; Delfino 2006	Middle Pleistocene	Italy	Fondo Cattie		Scincidae	Chalcides chalcides
Delfino 2002; Böhme & Ilg 2003; Delfino 2006; Delfino 2013	Middle Pleistocene	Italy	Dolina Maglie		Scincidae	Chalcides chalcides
Barbadillo 1989; Bailon 1991; Böhme & Ilg 2003; Blain 2005; Agustí et al. 2009; Blain 2009; López. García et al. 2011	Middle Pleistocene (close to 600 ka)	Spain	Cúllar de Baza 1		Scincidae	Chalcides cf. C. bedriagai
Böhme & IIg 2003; Blain 2005; Bailon & Blain 2007; Blain et al. 2007; Agustí et al. 2009; Blain 2009; Blain & Bailon 2010; López-García et al. 2011; Blain et al. 2016d	Early Pleistocene (Calabrian)	Spain	Fuente Nueva 3	Chalcides bedriagai	Scincidae	Chalcides cf. C. bedriagai
Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Blain et al. 2007; Augustí et al. 2009; Blain 2009; López-García et al. 2011	Late early Pleistocene (Calabrian)	Spain	Almenara Casablanca 3		Scincidae	Chalcides cf. C. bedriagai
Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Blain et al. 2007; Agustí et al. 2009; Blain 2009; López-García et al. 2011	Early Pleistocene (Gelasian)	Spain	Vallirana		Scincidae	Chalcides cf. C. bedriagai

Chalcides sp.	Scincidae		Guadix-Baza	Spain	Plio-Pleistocene	Crespo 2001; Blain et al. 2007
Chalcides sp.	Scincidae		Cueva Victoria	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003
Chalcides sp.	Scincidae		Cúllar de Baza 1	Spain	Middle Pleistocene (close to 600 ka)	Barbadillo 1989
Chalcides sp.	Scincidae		Valdocarros	Spain	Middle Pleistocene (MIS 8/7)	Blain et al. 2012
Chalcides sp.	Scincidae		Cueva del Angel	Spain	Middle/Upper Pleistocene (MIS 5e)	Barroso Ruíz et al. 2011
Chalcides sp.	Scincidae		Higueral de Valleja Cave	Spain	Upper Pleistocene (late Paleolithic)	Böhme & Ilg 2003; Jennings et al. 2009
Chalcides sp.	Scincidae		Vanguard Cave, Gibraltar	England	Upper Pleistocene	Gleed-Owen 2001; Böhme & Ilg 2003
Chalcides sp.	Scincidae		Cueva del Boquete de Zafarraya	Spain	Upper Pleistocene	Böhme & Ilg 2003
Chalcides sp.	Scincidae		Unknown locality, Mallorca	Spain	Lower/Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Chalcides sp.	Scincidae		Unknown locality, Menorca	Spain	Pleistocene	Estes 1983; Caputo 2004
cf. Chalcides sp.	Scincidae		Na Burguesa-1, Mallorca	Spain	Miocene/Pliocene (Messian/Zanclean)	Böhme & Ilg 2003; Bover et al. 2014
cf. Chalcides sp.	Scincidae	Chalcides bedriagai	Barranco Conejos	Spain	Early Pleistocene (ca 1.6 ma)	Böhme & Ilg 2003; Agustí et al. 2009
cf. Chalcides sp.	Scincidae	Chalcides bedriagai: Chalcides cf. C. bedriagai	Barranco León	Spain	Early Pleistocene (Calabrian)	Blain 2003; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Blain et al. 2007; Agustí et al. 2009; Blain 2009; Agustí et al. 2010; Blain & Bailon 2010; Blain et al. 2011; López-García et al. 2011; Blain et al. 2016d
Eumeces sp.	Scincidae		Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003
Eumeces sp.	Scincidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme & Ilg 2003
Eumeces sp.	Scincidae		Erkertshofen 1	Germany	Miocene (MN 4b)	Böhme & Ilg 2003
aff. <i>Eumeces</i> sp.	Scincidae		Stubersheim 2	Germany	Miocene (Burdigalian, MN 3b)	Villa & Delfino 2017; this work
aff. <i>Eumeces</i> sp.	Scincidae	Scincidae indet.	Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Mabuya sp.	Scincidae		Paje 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Mabuya sp.	Scincidae		Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Mabuya sp.	Scincidae		Varshets	Bulgaria	Pleistocene (Gelasian)	Böhme & Ilg 2003
cf. Mabuya sp.	Scincidae		Notio 1 (= Ptolemais 6C)	Greece	Early Pliocene (MN 15)	Böhme & Ilg 2003
cf. Mabuya sp.	Scincidae		Medas Islands	Spain	Early Pleistocene	Bailon 1991; Kage & Augé 1993; Augé & Rage 2000, Böhme & Ilg 2003; Bailon & Blain 2007; Agustí et al. 2009; Bolet et al. 2015; Blain et al. 2016a
aff. Mabuya sp.	Scincidae		San Roque 5	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003

att. Mabuya sp.	Scincidae		Las Planas 4B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
att. Mabuya sp.	Scincidae		Las Umbrias 3	Spain	Miocene (Langhian)	Böhme & Ilg 2003
aff. Mabuya sp.	Scincidae		Valalto 1A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
aff. Ophiomorus sp.	Scincidae	Scincidae indet.	Kaiafa	Greece	Pleistocene	Delfino 2004b; this work
Trachylepis cf. T. aurata	Scincidae	Mabuya cf. M. aurata	Varshets	Bulgaria	Pleistocene (Gelasian)	Böhme & Ilg 2003
Tropidophorus bavaricus	Scincidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003; Böhme 2010b; Čerňanský et al. 2016c
Tropidophorus bavaricus	Scincidae		Oggenhausen 2	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003
?Tropidophorus bavaricus	Scincidae		Oggenhausen 2	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Oschiri	Italy	Lower Miocene (Aquitanian, MN 1/MN 2b)	Böhme & Ilg 2003; Venczel & Sanchíz 2006; Zoboli & Pillola 2017
Scincidae indet. sp. 1	Scincidae		Offingen 2	Germany	Miocene (Burdigalian, MN 4b/5)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Scincidae indet. sp. 1	Scincidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003; Abdul Aziz et al. 2008; Böhme 2010b; Čerňanský et al. 2016c
Scincidae indet. sp. 1	Scincidae		Ichenhausen 3	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Scincidae indet. sp. 1	Scincidae		Puttenhausen D	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Scincidae indet. sp. 1	Scincidae		Puttenhausen E	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Scincidae indet. sp. 1	Scincidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		San Roque 2	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Vargas 1A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Caseton 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Caseton 2B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Las Umbrias 19	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Moratilla 2	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003; Bastir et al. 2014
Scincidae indet. sp. 1	Scincidae		Valdemoros 3B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Valdemoros 7A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Valdemoros 7F	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Vargas 7	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae		Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003

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Scincidae indet. sp. 1	Scincidae	Las Planas JU	Spain 5 i	Milocene (Serravallian)	bonne & lig 2003
Scincidae indet. sp. 1	Scincidae	Las Planas 5H	Spain	Miocene (Serravallian)	Bohme & Ilg 2005
Scincidae indet. sp. 1	Scincidae	Las Planas 5L	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Las Umbrias 20	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Las Umbrias 21	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Paje 1	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Paje 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Toril 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Toril 3B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Valalto 1A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Valalto 1B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Valalto 2C	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Crevillente 2	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Crevillente 3	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	El Arquillo 3	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
Scincidae indet. sp. 1	Scincidae	Sarrión 1	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Oschiri	Italy	Lower Miocene (Aquitanian, MN 1/MN 2b)	Böhme & Ilg 2003; Venczel & Sanchíz 2006; Zoboli & Pillola 2017
Scincidae indet. sp. 2	Scincidae	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003; Böhme 2010b; Čerňanský et al. 2016c
Scincidae indet. sp. 2	Scincidae	Puttenhausen E	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Scincidae indet. sp. 2	Scincidae	Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Artesilla	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	San Roque 2	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Vargas 4A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Vargas 4B	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Vargas 4BB	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Caseton 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Caseton 2B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	La Col C	Spain	Miocene (Langhian)	Böhme & IIg 2003
Scincidae indet sn 2	Scincidae	I as Planas 4B	Snain	Miccene (I anohian)	Böhme & IIo 2003
Scincidae indet sp. 2 Crimaidae indet sn. 3	Sciincides	Las Flattas +12 Los T1mhrine Q	Spain	MIOCEIIC (Lauguan)	Dillic & II 2000 Dillic & II 2000
SCITICIDAE ILIUCI. Sp. 2	ocilicidae	Las Uilibilas o	opani		DUILIDE & LIE 2002

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Scincidae indet. sp. 2	Scincidae	Las Umbrias 12	Spain 5 ·	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Las Umbrias 19	spain	Muocene (Langnian)	Bonne & lig 2005
Scincidae indet. sp. 2	Scincidae	Moratilla 2	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003; Bastir et al. 2014
Scincidae indet. sp. 2	Scincidae	Valdemoros 3F	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Valdemoros 7A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Valdemoros 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Valdemoros 8C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Vargas 7	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Vargas 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Vargas 8C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Alcocer 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Las Planas 5H	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Las Planas 5L	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Las Umbrias 20	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Paje 1	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Paje 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Toril 2	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Toril 3B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Valalto 1A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Valalto 1B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Valalto 2C	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Crevillente 2	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Crevillente 3	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Nombrevilla 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Viverro de la Rambla	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Valdecebro 5	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Villalba Alta 1	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Villalba Alta Rio 4	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Scincidae indet. sp. 2	Scincidae	Loma del Castillo 3	Spain	Pliocene (Piacenzian)	Böhme & Ilg 2003

Bonme & 11g 2003	MIOCENE (BURUIGANAN)	opain	Fuence Sterra 1		Scincidae	Scincidae indet.
Bohme & IIg 2003	Miocene (Burdigalian)	Spain	Banon 3		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian)	Spain 2	Ateca 3		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian)	Spain	Ateca 1		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Early Miocene (Burdigalian)	Greece	Aliveri		Scincidae	Scincidae indet.
Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010	Miocene (Burdigalian)	Germany	Untereichen-Altenstadt 540m		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian)	Germany	Randecker Maar		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Miocene (Burdigalian, MN 5)	Germany	Walda 1 (unten)		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Miocene (Burdigalian, MN 5)	Germany	Unterhausen		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Early Miocene (Burdigalian, MN 5)	Germany	Unterempfenbach 1b		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Miocene (Burdigalian, MN 5)	Germany	Niederaichbach (links)		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Miocene (Burdigalian, MN 5)	Germany	Niederaichbach		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian, MN 5)	Germany	Massendorf		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Early Miocene (Burdigalian, MN 5)	Germany	Dieshof b. Pöttmes - unterer Mergel		Scincidae	Scincidae indet.
Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003; Tempfer 2005	Miocene (Burdigalian, MN 5)	Austria	Teiritzberg (T1 = 001/D/C), Korneuburg Basin		Scincidae	Scincidae indet.
Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003; Tempfer 2005	Miocene (Burdigalian, MN 5)	Austria	Obergänserndorf, Korneuburg Basin		Scincidae	Scincidae indet.
this work	Early Miocene (MN 4)	Spain	Els Casots, Vallès Penedès Basin		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Miocene (MN 4b)	Germany	Erkertshofen 1		Scincidae	Scincidae indet.
Roček 1984; Bailon 1991; Böhme 2003; Böhme & Ilg 2003; Tempfer 2005	Early Miocene (Burdigalian, MN 4b)	Czech Republic	Dolnice	cf. Scincidae indet.	Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Lower Miocene (Burdigalian, MN 4a)	Germany	Petersbuch 2		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Miocene (Burdigalian, MN 3)	Germany	Gögglingen		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Lower Miocene (Aquitanian)	Spain	Cetina de Aragon		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Lower Miocene (Aquitanian, MN 2a)	France	Poncenat		Scincidae	Scincidae indet.
Böhme 2003; Böhme & Ilg 2003	Lower Miocene (Aquitanian, MN 2a)	France	Montaigu-le-Blin P23		Scincidae	Scincidae indet.
Böhme & Ilg 2003	Late Miocene (Tortonian)	Spain	Crevillente 3		Scincidae	Scincidae indet. sp. 3
Böhme & Ilg 2003	Middle Miocene (Langhian)	Spain	Vargas 7		Scincidae	Scincidae indet. sp. 3
Böhme & Ilg 2003	Late Pliocene (Piacenzian)	Spain	Sarrión 1		Scincidae	Scincidae indet. sp. 2

Scincidae indet.	Scincidae	Olmo Redondo 4A	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	San Roque 3	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Ainertshofen	Germany	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Eberstetten 2 (unter Weg)	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Scincidae indet.	Scincidae	Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Scincidae indet.	Scincidae	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Ivanov & Böhme 2011; Čerňanský et al. 2016c
Scincidae indet.	Scincidae	Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Scincidae indet.	Scincidae	Georgensgmünd	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Oberschöneberg 2H	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Petersbuch 68	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Untereichen-Altenstadt 565m	Germany	Miocene (Langhian)	Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010
Scincidae indet.	Scincidae	La Col C	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Las Umbrias 1	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Las Umbrias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Somosaguas Sur	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Valdemoros 8C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Vargas 6	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Villafeliche 4B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Steinberg (Ries)	Germany	Middle Miocene (Langhian/Serravallian, MN 6)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Rümikon	Switzerland	Middle Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Scincidae indet.	Scincidae	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Borjas	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Las Planas 5K	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Las Umbrias 20	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Toril 3A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Toril 3B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003

Scincidae indet.	Scincidae		Valalto 1A	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Gratkorn	Austria	Late middle Miocene	Böhme & Ilg 2003; Böhme & Vasilyan 2014
Scincidae indet.	Scincidae		Furth 460 m	Germany	Middle Miocene	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Gritsev	Ukraine	Late Miocene (Serravallian/Tortonian, MN 9)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Felsötárkány 2	Hungary	Miocene (Vallesian, MN9)	Böhme & Ilg 2003; Venczel & Hir 2013
Scincidae indet.	Scincidae		Felsötárkány 3/10	Hungary	Miocene (Vallesian, MN9)	Böhme & Ilg 2003; Venczel & Hir 2013
Scincidae indet.	Scincidae		Hammerschmiede 3	Germany	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Can Missert, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
Scincidae indet.	Scincidae		Castell de Barberà, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
Scincidae indet.	Scincidae		Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Böhme & Ilg 2003; Tempfer 2005
Scincidae indet.	Scincidae		Richardhof - Golfplatz	Austria	Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		La Roma 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Los Aguanaces	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Los Aguanaces 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Villa et al. 2016b; this work
Scincidae indet.	Scincidae		Venta del Moro	Spain	Late Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Marquina et al. 2016a
Scincidae indet.	Scincidae		Concud 98'	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		El Regajo 3	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Lomas de Casares 2	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Villastar	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Orrios 3	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Orrios rio (base of profile)	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Villalba Alta Rio 2a	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Scincidae indet.	Scincidae	Scincidae indet. large size	Notio 1 (= Ptolemais 6C)	Greece	Early Pliocene (MN 15)	Delfino 2004b; this work
Scincidae indet.	Scincidae		Valdeganga 7	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003
Scincidae indet.	Scincidae		Cúllar de Baza 1	Spain	Middle Pleistocene (close to 600 ka)	Barbadillo 1989
?Scincidae indet. sp. 1	Scincidae		Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Böhme & Ilg 2003
?Scincidae indet. sp. 2	Scincidae		Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Böhme & Ilg 2003

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?Scincidae indet. (cf. Mabuya sp.)	Scincidae		Rauscheröd	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1985b
?Scincidae indet.	Scincidae		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
?Scincidae indet.	Scincidae		Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	this work
?Scincidae indet.	Scincidae		Maramena 1	Greece	Late Miocene (MN 13/14)	Böhme & Ilg 2003; Delfino 2004b; this work
?Scincidae indet.	Scincidae		Sète	France	Middle Pliocene (MN 15)	Bailon & Blain 2007
aff. Scincidae indet.	Scincidae		Adelschlag	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003
aff. Scincidae indet.	Scincidae		Gallenbach 2b	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Bavaricordylus molassicus	Cordylidae		Puttenhausen 2	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003; Böhme 2010b; Čerňanský 2012
Bavaricordylus molassicus	Cordylidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003; Böhme 2010b; Čerňanský et al. 2016c
Bavaricordylus cf. B. molassicus	Cordylidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003; Böhme 2010b
Bavaricordylus ornatus	Cordylidae		Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme & Ilg 2003; Kosma 2004; Böhme 2010b; Čerňanský 2011a; Čerňanský 2012; Čerňanský 2016
Bavaricordylus sp.	Cordylidae		Schmiedrued-Pyffrüti level 642, Swiss Molasse Basin	Switzerland	Early Middle Miocene (Langhian)	Böhme & Ilg 2003; Jost et al. 2015
Palaeocordylus bohemicus	Cordylidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1984; Augé 1987; Augé & Rage 2000; Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Čerňanský 2012; Čerňanský 2016
?Palaeocordylus bohemicus	Cordylidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003
aff. Palaeocordylus bohemicus	Cordylidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Čerňanský 2012; Rage 2013; Čerňanský et al. 2015b; Čerňanský 2016
Palaeocordylus ulmensis	Cordylidae		Haslach North Ulm	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003
Palaeocordylus ulmensis	Cordylidae	Ophisaurus ulmensis	Oberer Eselsberg	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003; Čerňanský et al. 2015b
Palaeocordylus sp.	Cordylidae		Lautern 2	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003
aff. Palaeocordylus sp.	Cordylidae	Scincidae indet.	Maramena 1	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
aff. Palaeocordylus sp.	Cordylidae	Scincidae indet.	Maramena 3	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Cordylidae indet.	Cordylidae		Petersbuch 2	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003
Cordylidae indet.	Cordylidae		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Cordylidae indet.	Cordylidae		Obergänserndorf, Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme 2003; Böhme & IIg 2003; Tempfer 2003; Böhme 2010b; Čerňanský 2012; Čerňanský 2016
Cordylidae indet.	Cordylidae		Puttenhausen 2	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003

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Scincomorpha indet.	Scincomorpha indet.	Schönenberg	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Offingen 4	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Scincomorpha indet.	Scincomorpha indet.	Oggenhausen 1	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Puttenhausen A	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Scincomorpha indet.	Scincomorpha indet.	Puttenhausen B	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Scincomorpha indet.	Scincomorpha indet.	Puttenhausen D	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Scincomorpha indet.	Scincomorpha indet.	Untereichen-Altenstadt 540m	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010
Scincomorpha indet.	Scincomorpha indet.	Aliveri	Greece	Early Miocene (Burdigalian)	this work
Scincomorpha indet.	Scincomorpha indet.	Quinta do Pombeiro	Portugal	Miocene (Burdigalian)	Antunes & Rage 1974; Crespo 2001
Scincomorpha indet.	Scincomorpha indet.	Vargas 2A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Vargas 2B	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	this work
Scincomorpha indet.	Scincomorpha indet.	Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	this work
Scincomorpha indet.	Scincomorpha indet.	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	this work
Scincomorpha indet.	Scincomorpha indet.	Oberschöneberg 2C	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Oberschöneberg 2E	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Oberschöneberg 2G	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Las Umbrias 17	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Valdemoros 6A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Valdemoros 7B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	this work
Scincomorpha indet.	Scincomorpha indet.	Solera	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Scincomorpha indet.	Scincomorpha indet.	Furth 460 m	Germany	Middle Miocene	Abdul Aziz et al. 2008

Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	this work	this work	Böhme & Ilg 2003	this work	Böhme & Ilg 2003	Böhme & Ilg 2003	this work	this work	this work	this work	Holman 1998; Böhme & Ilg 2003	this work	Jánossy 1986; Holman 1998; Böhme & Ilg 2003	this work	this work	this work	Jánossy 1986; Holman 1998; Böhme & Ilg 2003	Böhme & Ilg 2003; Tempfer 2005	Venczel 2001; Böhme & Ilg 2003
Miocene (Serravallian/Tortonian)	Miocene (Serravallian/Tortonian)	Miocene (Tortonian)	Late Miocene (MN 13/14)	Late Miocene (MN 13/14)	Miocene (Messinian)	Early Pliocene (MN 14)	Early Pliocene (Zanclean)	Pliocene (Zanclean)	Early Pliocene (MN 15)	Late Pliocene (MN 16)	earliest early Pleistocene	Early Pleistocene (Gelasian; MN 17)	Middle Pleistocene	Late Pleistocene	Upper Pleistocene	Pleistocene	Pleistocene (?)	Pleistocene (?)	Upper Pleistocene/Holocene	Upper Miocene (Tortonian, MN 11)	Pliocene (Zanclean, MN 14)
Spain	Spain	Hungary	Greece	Greece	Spain	Greece	Spain	Spain	Greece	Greece	Greece	Italy	Hungary	Greece	Hungary	Greece	Greece	Greece	Hungary	Austria	Hungary
Villafeliche 4	Villafeliche 6	Csákvár, Esterhźy Cave	Maramena 1	Maramena 3	Los Mansuetos	Maritsa A	La Gloria 3	Orrios 1	Notio 1 (= Ptolemais 6C)	Tourkobounia 1	Tourkobounia 2	Rivoli Veronese	Burgberg-Hilton	Arnissa	Süttö Upper Pleistocene strata	Kaiafa	Anabussos	Xeros	Remetehegy	Kohfidisch	Osztramos 1
													Sauria indet.		Sauria indet.				Lacertilia indet.; Sauria indet.		
Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Anguidae	Anguidae
Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Scincomorpha indet.	Anguis fragilis	Anguis fragilis

Anguis fragilis	Anguidae	Anguis cf. A. fragilis	Podlesice	Poland	Lower Pliocene (Zanclean, MN 14)	Młynarski 1962; Młynarski 1977; Estes 1983; Młynarski et al. 1984; Bailon 1991; Böhme & Ilg 2003
Anguis fragilis	Anguidae	Anguis cf. A. fragilis	Węże I	Poland	Upper Pliocene (Zanclean, MN 15)	Młynarski 1962, Młynarski 1977; Estes 1983; Bailon 1991; Böhme & Ilg 2003; Ivanov 2007; Klembara & Rummel 2016
Anguis fragilis	Anguidae		Ivanovce	Slovakia	Upper Pliocene (Zanclean, MN 15)	Klembara 1986a; Bailon 1991; Böhme & Ilg 2003; Ivanov 2007
Anguis fragilis	Anguidae	Anguis cf. A. fragilis	Rębielice Królewskie 1A	Poland	Upper Pliocene (Piacenzian, MN 16)	Estes 1983; Mtynarski 1977; Mtynarski et al. 1984; Bailon 1991; Böhme & Ilg 2003; Ivanov 2007
Anguis fragilis	Anguidae	Anguis cf. A. fragilis	Kadzielnia	Poland	Early Pleistocene (MN 17)	Młynarski 1962; Młynarski 1977; Młynarski et al. 1984
Anguis fragilis	Anguidae		Varshets	Bulgaria	Pleistocene (Gelasian)	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Bad Deutsch-Altenburg 2A	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Tempfer 2005; Ivanov 2007
Anguis fragilis	Anguidae		Bad Deutsch-Altenburg 4B	Austria	Lower Pleistocene	Rauscher 1992; Böhme & Ilg 2003; Tempfer 2005; Ivanov 2007
Anguis fragilis	Anguidae	Lacerta sp.	Malá Dohoda Quarry	Czech Republic	Lower Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Mladeč Caves - excavation II	Czech Republic	Lower Pleistocene	Böhme & Ilg 2003; Ivanov 2007
Anguis fragilis	Anguidae		Kalbsrieth	Germany	Lower Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Jaskinia Żabia	Poland	Lower Pleistocene	Böhme & Ilg 2003; Ivanov 2007
Anguis fragilis	Anguidae		Zabia Cave	Poland	Lower Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae	Anguis cf. A. fragilis	Zalesiaki A	Poland	Lower Pleistocene	Młynarski 1977; Młynarski et al. 1984; Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Betfia 2 (Püspökfürdö or Episcopia Biharuli)	Romania	Lower Pleistocene	Bolkay 1913; Młynarski 1962; Estes 1983
Anguis fragilis	Anguidae	Anguis sp.	Bagur 2	Spain	Early Pleistocene	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007: Agustí et al. 2009; Blain 2009
Anguis fragilis	Anguidae	Anguis sp.	Medas Islands	Spain	Early Pleistocene	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009; Bailon & Auoć 2017: Rlain et al. 2016a
Anguis fragilis	Anguidae		Trinchera Elefante TE14, Sima del Elefante	Spain	Lower Pleistocene	Böhme & IIg 2003; Blain et al. 2010a; Rodríguez et al. 2011; Cuenca-Bescós et al. 2015; Garcia- tudivariana et al. 2015
Anguis fragilis	Anguidae		Grotta della Fata Nana, Bosco Chiesanuova	Italy	Earliest Middle Pleistocene	Delfino et al. 2008a
Anguis fragilis	Anguidae		Balaruc VII	France	Middle Pleistocene (Isotopic Stage 9)	Bailon 1991; Bailon & Rage 2012
Anguis fragilis	Anguidae		Lazaret Cave	France	Middle Pleistocene (MIS 6)	Bailon 1991; Hanquet et al. 2010; Bailon & Rage 2012
Anguis fragilis	Anguidae		Barnham	England	Late Middle Pleistocene	Stuart 1995; Gleed-Owen 1998; Gleed-Owen 1999

Anguis fragilis	Anguidae		Baume Moula-Guercy	France	Pleistocene (Isotopic Stage 5)	Bailon & Rage 2012
Anguis fragilis	Anguidae		Beeches Pit	England	Middle Pleistocene	Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Anguis fragilis	Anguidae	Lacerta sp.	Boxgrove	England	Middle Pleistocene	Holman 1992; Holman 1993a; Holman 1993b; Benton & Spencer 1995; Stuart 1995; Gleed- Owen 1997; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Holman 2000; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Cudmore Grove, Mersea Island	England	Middle Pleistocene	Holman et al. 1990; Holman 1992; Holman 1993a; Holman 1993b; Benton & Spencer 1995; Stuart 1995; Gleed-Owen 1997; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & II <u>2</u> 2003
Anguis fragilis	Anguidae		East Farm	England	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Greenlands Pit, Purfleet	England	Middle Pleistocene	Holman 1993a; Gleed-Owen 1997; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Nightingale Estate, Hackney	England	Middle Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		West Runton Freshwater Bed	England	Middle Pleistocene	Holman 1989; Holman 1992; Holman 1993a; Holman 1993b; Benton & Spencer 1995; Stuart 1995; Gleed-Owen 1997; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003; Böhme 2010a
Anguis fragilis	Anguidae		Westbury-Sub-Mendip Cave	England	Middle Pleistocene	Holman 1992; Holman 1993a; Holman 1993b; Stuart 1995; Gleed-Owen 1997; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
Anguis fragilis	Anguidae	Anguis cf. A. fragilis	Montoussé 3	France	Middle Pleistocene	Clot et al. 1976; Estes 1983; Bailon 1991
Anguis fragilis	Anguidae		Orgnac III	France	Middle Pleistocene	Bailon & Rage 2012
Anguis fragilis	Anguidae		Terra Amata	France	Middle Pleistocene	Bailon 1991
Anguis fragilis	Anguidae		Trancarville	France	Middle Pleistocene	Bailon 2010
Anguis fragilis	Anguidae		Bilzingsleben	Germany	Middle Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae	Anguis stammeri	Breitenburg Cave (Breitenberghohle)	Germany	Middle Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Hunas	Germany	Middle Pleistocene	Böhme 1997; Holman 1998; Böhme & Ilg 2003; Böhme 2011
Anguis fragilis	Anguidae		Kärlich G	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003; Holman & van Kolfschoten 2011
Anguis fragilis	Anguidae		Kärlich H	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003; Holman & van Kolfschoten 2011
Anguis fragilis	Anguidae		Miesenheim I	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Mühlhausen	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003

Anguis fragilis	Anguidae		Mühlhausen, Travertin in der Marienkirche	Germany	Middle Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Steinbruch Schmid, Stuttgart (Stuttgart quarry Schimd)	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Weimar-Ehringsdorf Site Complex, Lower Travertine Unit	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Weimar-Ehringsdorf Site Complex, Pocket in the Lower Travertin	Germany	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Hórvőlgy Cave	Hungary	Middle Pleistocene	Jánossy 1986
Anguis fragilis	Anguidae		Riparo di Visogliano	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2006
Anguis fragilis	Anguidae		Valdemino Cave	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2004c; Delfino 2006
Anguis fragilis	Anguidae	Anguis cf. A. fragilis	Kozi Grzbiet	Poland	Middle Pleistocene	Młynarski 1977; Szyndlar 1981; Młynarski et al. 1984; Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Vol`naya Vershina-3	Russia	Middle Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Cova d'Olopte	Spain	Middle Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Trinchera Dolina TD5up, Gran Dolina	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008b; Blain et al. 2009; Agustí et al. 2009; Blain 2009; Rodríguez et al. 2011; Cuenca-Bescós et al. 2015
Anguis fragilis	Anguidae		Trinchera Dolina TD6up, Gran Dolina	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008b; Blain et al. 2009; Agustí et al. 2009; Blain 2009; Rodríguez et al. 2011; Cuenca-Bescós et al. 2015
Anguis fragilis	Anguidae		Trinchera Dolina TD10, Gran Dolina	Spain	Middle Pleistocene	Böhme & IIg 2003; Blain 2005; Blain et al. 2008b; Blain et al. 2009; Blain 2009; Rodríguez et al. 2011
Anguis fragilis	Anguidae		Trinchera Elefante TE19, Sima del Elefante	Spain	Middle Pleistocene	Böhme & Ilg 2003; Blain et al. 2011; Rodríguez et al. 2011; Garcia-Ibaibarriaga et al. 2015
Anguis fragilis	Anguidae		Maastricht-Belvedere 4	The Netherlands	Middle Pleistocene	Holman 1998; Böhme & Ilg 2003; Schouten 2016
Anguis fragilis	Anguidae		Scladina	Belgium	Middle/Upper Pleistocene (MIS 5/3)	Blain et al. 2014c; Blain et al. 2014d
Anguis fragilis	Anguidae		Gamsenberg (fissure basis)	Germany	Middle/Upper Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Cova del Rinoceront	Spain	Middle/Upper Pleistocene	Böhme & Ilg 2003; Blain 2005; Daura et al. 2015
Anguis fragilis	Anguidae		Pontnewydd Cave, Elwy Valley	Wales	Middle/Upper Pleistocene	Gleed-Owen 1997; Gleed-Owen 1998; Gleed- Owen 1999; Böhme & Ilg 2003
us fragilis	Anguidae		La Combe Grenal	France	Upper Pleistocene (lower Palaeolithic)	Bailon 1991; Tempfer 2005
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agilis	Anguidae		Cueva del Camino (= Pinilla del Valle) Secteur Nord	Spain	Upper Pleistocene (MIS 5b)	Böhme & Ilg 2003; Laplana et al. 2013; Blain et al. 2014b
iagilis	Anguidae		Cueva del Camino (= Pinilla del Valle) Secteur Sud	Spain	Upper Pleistocene (MIS 5a)	Böhme & Ilg 2003; Laplana et al. 2013; Blain et al. 2014b
iagilis	Anguidae		Artenac	France	Upper Pleistocene (middle Palaeolithic)	Blain & Bailon 2003; Böhme & Ilg 2003
iagilis	Anguidae		Santimamiñe Cave	Spain	Upper Pleistocene (MIS 2/MIS 1)	Murelaga Bereikua et al. 2011; García- Ibaibarriaga et al. 2015
ragilis	Anguidae		Santa Catalina	Spain	Upper Pleistocene (upper/latest Magdalenian)	Bailon & Garcia-Ibaibarriaga 2014
ragilis	Anguidae		Bois du Cantet	France	Upper Pleistocene (upper Palaeolithic)	Clot et al. 1984; Bailon 1991
ragilis	Anguidae		Milton Hill Cave	England	Upper Pleistocene	Gleed-Owen 1997; Gleed-Owen 1998; Gleed- Owen 1999; Böhme & Ilg 2003
iagilis	Anguidae		Roger's Cave (Symonds Yat East Cave No.14), Wye Valley	England	Upper Pleistocene	Gleed-Owen 1997; Gleed-Owen 1998; Gleed- Owen 1999; Böhme & Ilg 2003
ragilis	Anguidae		Tornewton Cave (Hyaena stratum), Torbryan Caves	England	Upper Pleistocene	Gleed-Owen 1998; Gleed-Owen 1999; Böhme & Ilg 2003
agilis	Anguidae		Wookey Hole (Hyaena Den)	England	Upper Pleistocene	Gleed-Owen 1997; Gleed-Owen 1998; Böhme & Ilg 2003
agilis -	Anguidae		Bois Roche Cave	France	Upper Pleistocene	Böhme & Ilg 2003; Blain & Villa 2006
agilis	Anguidae		Carrière Cave	France	Upper Pleistocene	Rage 1977; Estes 1983; Bailon 1991; Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Siréjol	France	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Burgtonna, Hystrix-Horizont	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Burgtonna, Travertinsand	Germany	Upper Pleistocene	Böhme & Ilg 2003
agilis	Anguidae		Gamsenberg (fissure top)	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Grabschütz	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Gröbern	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Grundfelsen Cave	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Llisen Cave	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Park Cave Travertine	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis.	Anguidae		Ranis Ilsenhöhle	Germany	Upper Pleistocene	Böhme 1997; Böhme & Ilg 2003
agilis	Anguidae		Saalfeld Roter Berg	Germany	Upper Pleistocene	Böhme & Ilg 2003
agilis	Anguidae		Schönfeld	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae		Steinheim an der Murr	Germany	Upper Pleistocene	Bloos et al. 1991; Holman 1998; Böhme & Ilg 2003
agilis	Anguidae	Anguis stammeri	Taubach	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
agilis	Anguidae	Anguis stammeri	Teufelshöhle (Devil's Cave)	Germany	Upper Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003

Anguis fragilis	Anguidae		Weimar-Ehringsdorf Site Complex, Black Colluvial Unit	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae	Anguis stammeri	Weimar-Ehringsdorf Site Complex, Pariser Unit	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Weimar-Ehringsdorf Site Complex, Upper Travertine Unit	Germany	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Kalman Lambrecht Cave	Hungary	Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Rejtek 1	Hungary	Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Süttö Upper Pleistocene strata	Hungary	Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Poroslyuk of Ballavölgy	Hungary	Upper Pleistocene	Jánossy 1986
Anguis fragilis	Anguidae		Caverna Generosa	Italy	Upper Pleistocene	Böhme & Ilg 2003; Bona et al. 2009
Anguis fragilis	Anguidae		Abric Romanì	Spain	Late Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Canyars, Gavá	Spain	Upper Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Cova dels Xaragalls	Spain	Upper Pleistocene	Böhme & Ilg 2003; López-García et al. 2012a
Anguis fragilis	Anguidae		Cueva de Cualventi	Spain	Upper Pleistocene	Sanchiz & Martín Albaladejo 2016
Anguis fragilis	Anguidae		Cueva de las Aguas	Spain	Upper Pleistocene	Sanchiz & Martín Albaladejo 2016
Anguis fragilis	Anguidae		Cueva del Conde	Spain	Upper Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Galls Carboners Cave	Spain	Upper Pleistocene	López-García et al. 2014
Anguis fragilis	Anguidae		Laminak II Cave	Spain	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Paloma Cave	Spain	Upper Pleistocene	Estes 1983; Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Teixoneres II Cave	Spain	Upper Pleistocene	Böhme & Ilg 2003
Anguis fragilis	Anguidae		Unknown locality, Asturias	Spain	Upper Pleistocene	Crespo 2001
Anguis fragilis	Anguidae		Unknown locality, Vizcaia	Spain	Upper Pleistocene	Crespo 2001
Anguis fragilis	Anguidae		Chilleurs-aux-Bois	France	Lower/Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Stuttgart Viadukt	Germany	Lower/Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Dog Holes	England	Pleistocene	Holman 1993a; Benton & Spencer 1995; Gleed- Owen 1997; Gleed-Owen 1998; Gleed-Owen
						1999
Anguis fragilis	Anguidae		Askondo Cave	Spain	Upper Pleistocene/Holocene (MIS3/1)	García-Ibaibarriaga et al. 2015
Anguis fragilis	Anguidae		Broken Cavern, Torbryan Caves	England	Upper Pleistocene/Holocene	Gleed-Owen 1997; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003
	-		- د د			Holman 1993a; Benton & Spencer 1995; Gleed-
Anguis fraguis	Anguidae		Ignmam fissures near Sevenoaks	England	Upper Pleistocene/Holocene	Owen 1997; Gieed-Owen 1998; Gieed-Owen 1999; Böhme & Ilg 2003
Anguis fragilis	Anguidae		Six Cave, Torbryan Caves	England	Upper Pleistocene/Holocene	Gleed-Owen 1997; Gleed-Owen 1998; Gleed- Owen 1999; Böhme & Ilg 2003

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eistocene/Holocene [1998; Gleed-Owen 1997; Gleed-Owen 1998; Holman [1998; Gleed-Owen 1999; Böhme & Ig 2003	eistocene/Holocene Holman 1998; Böhme & Ilg 2003	eistocene/Holocene Paunović & Dimitrijević 1990, Holman 1998; Böhme & Ilg 2003	eistocene/Holocene Zubeldia et al. 2007; Rofes et al. 2015	eistocene/Holocene Böhme & Ilg 2003; López-Garcia et al. 2011; Garcia-Ibaibarriaga et al. 2015	e (MIS 1, Sub-boreal, Murelaga et al. 2007 ker culture)	e (MIS 1, Atlantic to al, Neolithic to Bronze Sanchiz et al. 2012	e (MIS 1, Atlantic to Murelaga et al. 2009; García-Ibaibarriaga et al. al. Neolithic to Bronze 2015	e (MIS 1, Pre-boreal) Murelaga et al. 2008	e (middle Neolithic) Bailon 1991	e (Neolithic) Böhme & Ilg 2003; Blain et al. 2016b	e (MIS 1, Murelaga Bereikua et al. 2011; García- Bronze Age) Ibaibarriaga et al. 2015							
Upper P	Upper P	Upper P	Upper P	Upper P	Upper P	Upper P	Upper P	Upper P	Upper P	Upper P	Holocen Bell-Bea	Holocen Sub-bore Age)	Holocen Sub-bore Age)	Holocen	Holocen	Holocen	Holocen Azilian/I	Holocen
England	Germany	Germany	Germany	Germany	Germany	Hungary	Poland	Serbia	Spain	Spain	Spain	Spain	Spain	Spain	France	Spain	Spain	Snain
Three Holes Cave, Torbryan Caves	Dietfurt	Euerwanger Bühl	Malerfels	Pisede	Spitzbubenhöhle	Függö-Kö Cave	Raj Cave	Smolucka Pećina Cave	Antoliñako Koba	Valdavara-1 Cave	Dolmen de Errekatxuetako Atxa	El Mirón Cave	Peña Larga	Aizkoltxo Cave	Baume Claire/Baume Sourde	Cova Colomera CE12, Sierra de Montsec	Santimamiñe Cave	Cova Colomera A sup., Sierra de
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anchicae
Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anguis fragilis	Anauis fraailis

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Lartet 1851; Gervais 1859; Mtynarski 1962; Estes 1983; Augé & Rage 2000; Tempfer 2005	Middle Miocene (Langhian/Serravallian; MN 6)	France	Sansan	Anguis acutidentatus	Anguidae	Anguis? acutidentatus
Delfino et al. 2008a; Villa et al. 2015; this work	Holocene (I cent. AD)	Italy	Tenuta Zuccarello, Marcon	Anguis fragilis	Anguidae	Anguis gr. A. fragilis
Hoek Ostende & Vos 2006; Villa et al. 2014; Schouten 2016; Villa et al. 2016a; this work	Early Pleistocene (Gelasian)	The Netherlands	Russel-Tiglia-Egypte pit, Tegelen	Anguis fragilis	Anguidae	Anguis gr. A. fragilis
Delfino et al. 2008a; Villa et al. 2017; this work	Early Pleistocene (Gelasian; MN 17)	Italy	Rivoli Veronese	Anguis fragilis	Anguidae	Anguis gr. A. fragilis
Delfino et al. 2008a	Late Pleistocene	Italy	Brecce di Montorio, Monte Marseghina		Anguidae	cf. Anguis fragilis
Delfino et al. 2008a	Early Pleistocene	Italy	Monte La Mesa, Rivoli Veronese		Anguidae	cf. Anguis fragilis
Gleed-Owen 1998; Böhme & Ilg 2003	Upper Pleistocene/Holocene	England	Three Holes Cave, Torbryan Caves	cf. Anguis fragilis	Anguidae	Anguis cf. A. fragilis
Clot et al. 1976; Holman 1998; Böhme & Ilg 2003	Middle Pleistocene	France	Montoussé 4		Anguidae	Anguis cf. A. fragilis
Młynarski 1962; Estes 1983; Młynarski et al. 1984; Böhme & Ilg 2003; Ivanov 2007; Čerňanský 2011b; Čerňanský et al. 2016c	Upper Pliocene (Piacenzian, MN 16)	Poland	Węże II	Anguis fragilis	Anguidae	Anguis cf. A. fragilis
Bohme & IIg 2003; venczel & HII 2013 Böhme & IIg 2003; Venczel & Hir 2013	Miocene (Vallesian, MN9) Miocene (Vallesian, MN9)	Hungary	Felsotarkany 2 Felsötárkány 3/2		Anguidae Anguidae	Anguis ci. A. fraguis Anguis cf. A. fragilis
Böhme & Ilg 2003; Venczel & Hir 2013	Miocene (Vallesian, MN9)	Hungary	Felsötárkány 1		Anguidae	Anguis cf. A. fragilis
Böhme & Ilg 2003; Venczel & Hir 2013	Miocene (Astaracian, MN7+8)	Hungary	Felsötárkány-Felnémet 2/3		Anguidae	Anguis cf. A. fragilis
Böhme & Ilg 2003	Holocene	Spain	Kobeaga II		Anguidae	Anguis fragilis
Gleed-Owen 1997; Gleed-Owen 1998; Gleed- Owen 1999; Böhme & Ilg 2003	Holocene	Scotland	Bone Cave, Creag nan Uamh Caves		Anguidae	Anguis fragilis
Gleed-Owen 1997; Gleed-Owen 1998; Gleed- Owen 1999; Böhme & Ilg 2003	Holocene	Scotland	Badger Cave, Creag nan Uamh Caves		Anguidae	Anguis fragilis
Nadachowski et al. 1989	Holocene	Poland	Nad Mosurem Starym Duża Cave		Anguidae	Anguis fragilis
Delfino & Bressi 2000; Delfino 2006	Holocene	Italy	Grotta dell'Edera		Anguidae	Anguis fragilis
Böhme & Ilg 2003	Holocene	Germany	Oberrohn bei Bad Salzungen		Anguidae	Anguis fragilis
Böhme & Ilg 2003	Holocene	Germany	Gamsenberg (Vorderer)		Anguidae	Anguis fragilis
Jeannet & Cartonnet 2000	Holocene	France	La Chênelaz		Anguidae	Anguis fragilis
Gleed-Owen 1998; Gleed-Owen 1999; Böhme & Ilg 2003	Holocene	England	Wardey Hill, Coveney		Anguidae	Anguis fragilis
Gleed-Owen 1998; Gleed-Owen 1999; Böhme & Ilg 2003	Holocene	England	Madawg Rockshelter (& Cavell Shelter), Wye Valley		Anguidae	Anguis fragilis
Owen 1997; Gleed-Owen 1998; Holman 1998; Gleed-Owen 1999; Böhme & Ilg 2003	1101006116	England	COW Cave		Anguidae	Anguis fraguis
Holman 1993a; Benton & Spencer 1995; Gleed- Oricon 1007: Cloud Oricon 1000: Holmon 1000.	TI of control of the	Enclosed			Ammidao	A warrie free file

Anguis? bibronianus	Anguidae	Anguis bibronianus; Ophisaurus ? bibronianus	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Lattet 1851; Gervais 1859; De Stefano 1903; Młynarski 1962; Estes 1983; Augé & Rage 2000
Anguis ?polgardiensis	Anguidae		Vösendorf (= Vösendorf-Brunn)	Austria	Miocene (Tortonian, MN 10)	Papp et al. 1953
?Anguis polgardiensis	Anguidae	Anguis polgardiensis ; Ophisaurus pannonicus	Polgárdi 2	Hungary	Miocene (Messinian, MN 13)	Bolkay 1913; Młynarski 1962; Estes 1983; Klembara 2015; Klembara & Rummel 2016
Anguis rarus	Anguidae		Petersbuch 62	Germany	Miocene (MN 3)	Klembara & Rummel 2016
Anguis stammeri	Anguidae	Anguis fragilis	Fuchsloch	Germany	Middle Pleistocene	& IIg 2003; Klembara & Runnel 2016
Anguis sp.	Anguidae		Ugljevik	Bosnia and Herzegovina	Early Miocene (MN 1)	Jovanović et al. 2002
Anguis sp.	Anguidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme 2003
Anguis sp.	Anguidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003; Čerňanský 2016; Klembara & Rummel 2016
Anguis sp.	Anguidae	Anguidae indet.	Langenau 1	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Anguis sp.	Anguidae		Puttenhausen E	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Anguis sp.	Anguidae		Schmiedrued-Pyffrüti level 618, Swiss Molasse Basin	Switzerland	Late Early Miocene (Burdigalian)	Böhme & Ilg 2003; Jost et al. 2015
Anguis sp.	Anguidae		Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Villa & Delfino 2017; this work
Anguis sp.	Anguidae		Sámsonháza	Hungary	Miocene (Langhian, MN 6)	Böhme & Ilg 2003
Anguis sp.	Anguidae		Petersbuch 68	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguis sp.	Anguidae		Mátraszőlős 2	Hungary	Miocene (Langhian/Serravallian, MN 6)	Böhme & Ilg 2003
Anguis sp.	Anguidae		Petersbuch 35	Germany	Miocene (Serravallian/Tortonian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Anguis sp.	Anguidae		Gritsev	Ukraine	Late Miocene (Serravallian/Tortonian, MN 9)	Böhme & Ilg 2003
Anguis sp.	Anguidae	Anguidae indet.	Fosso della Fittaia 2013	Italy	Late Miocene (MN 11)	Cirilli et al. 2014; Cirilli et al. 2016; this work
Anguis sp.	Anguidae	Pseudopus sp./Ophisaurus sp.	Maramena 1	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Anguis sp.	Anguidae	Pseudopus sp./Ophisaurus sp.	Maramena 3	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Anguis sp.	Anguidae		Peralejos E	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Anguis sp.	Anguidae		Kamenjak, Bukulja	Serbia	Early Pliocene (MN 14)	Jovanović et al. 2002
Anguis sp.	Anguidae		Csarnóta 2	Hungary	Pliocene (Zanclean, MN 15)	Jánossy 1986

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Anguts sp.	Anguidae		Escorinuela B	Spain	Lower Phocene (Zanclean) Diocene (Zanclean)	Bonme & IIg 2003 Böhme & IIg 2003
Anguis sp.	Aliguidae		LUIIAS UE CASALES I	made		
Anguis sp.	Anguidae	Anguis fragilis	Sète	France	Middle Pliocene (MN 15)	Bailon 1991; Bohme & Ilg 2003; Bailon & Blain 2007
Anguis sp.	Anguidae	Anguidae indet.	Notio 1 (= Ptolemais 6C)	Greece	Early Pliocene (MN 15)	Böhme & Ilg 2003; Delfino 2004b; this work
Anguis sp.	Anguidae	Anguis fragilis	Balaruc II	France	Middle/late Pliocene (MN 15/16)	Bailon 1991; Bailon 1995; Böhme & Ilg 2003; Bailon & Blain 2007
Anguis sp.	Anguidae		Seynes	France	Late Pliocene (MN 16)	Böhme & Ilg 2003; Bailon & Blain 2007
Anguis sp.	Anguidae	Anguis cf. A. fragilis; Anguis fragilis	Montoussé 5	France	Early Pleistocene (MN 17)	Clot et al. 1976; Estes 1983; Bailon et al. 1988; Bailon 1991; Holman 1998; Böhme & Ilg 2003; Bailon & Blain 2007
Anguis sp.	Anguidae	Anguis fragilis	Vallirana	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009
Anguis sp.	Anguidae		Somssich Hill 2	Hungary	Late early Pleistocene	Pazonyi et al. 2017
Anguis sp.	Anguidae	?Anguis sp.	Holstejn	Czech Republic	Lower Pleistocene	Holman 1998; Böhme & Ilg 2003
Anguis sp.	Anguidae		21 Országház Str., Budapest Castle Hill	Hungary	Middle Pleistocene	Jánossy 1986
Anguis sp.	Anguidae		Tarko	Hungary	Middle/Upper Pleistocene	Jánossy 1986; Holman 1998; Böhme & Ilg 2003
Anguis sp.	Anguidae		Marie-Jeanne cave	Belgium	Late Pleistocene	Blain et al. 2014d
Anguis sp.	Anguidae		Arnissa	Greece	Late Pleistocene	Delfino 2004b; this work
Anguis sp.	Anguidae		Corund	Romania	Upper Pleistocene	Sos et al. 2011
Anguis sp.	Anguidae		Zeifen	Germany	Pleistocene	Schleich 1985b
?Anguis sp.	Anguidae		Abocador de Can Mata, Vallès Penedès Basin	Spain	Middle Miocene (MN 6/MN 7+8)	this work
?Anguis sp.	Anguidae		Furth 460 m	Germany	Middle Miocene	Böhme & Ilg 2003
?Anguis sp.	Anguidae		Castell de Barberà, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
?Anguis sp.	Anguidae		Trinxera Nord Autopista, Vallès Penedès Basin	Spain	Late Miocene (MN 10)	this work
?Anguis sp.	Anguidae		Rivoli Veronese	Italy	Early Pleistocene (Gelasian; MN 17)	this work
cf. Anguis sp.	Anguidae		Concud Estacion 2	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
cf. Anguis sp.	Anguidae		Lomas de Casares 2	Spain	Miocene (Messinian)	Böhme & Ilg 2003
cf. Anguis sp.	Anguidae		La Gloria 4	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
cf. Anguis sp.	Anguidae		Orrios 7	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
cf. Anguis sp.	Anguidae		Villalba Alta Rio 2	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Ophisaurus acuminatus	Anguidae		Höwenegg, near Öhningen	Germany	Upper Miocene (Tortonian)	Jörg 1965; Estes 1983; Schleich 1985b; Böhme & Ilg 2003; Klembara 2015; Klembara & Rummel 2016
Ophisaurus fejfari	Anguidae	Dopasia fejfari	Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus fejfari	Anguidae	Dopasia fejfari	Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Kosma 2004; Čerňanský 2016

Ophisaurus fejfari	Anguidae	Dopasia fejfari	Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Klembara 1979; Klembara 1981; Estes 1893; Roček 1984; Böhme 2003; Böhme & Ilg 2003; Miklas-Tempfer 2003; Böhme 2010b; Klembara 2015; Čerňanský 2016; Klembara & Rummel 2016
Ophisaurus fejfari	Anguidae	Dopasia fejfari ; Ophisaurus sp.	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Ivanov & Böhme 2011; Čerňanský et al. 2016c; Klembara & Rummel 2016
Ophisaurus fejfari	Anguidae	Dopasia fejfari	Petersbuch 31 - oben	Germany	Miocene (Langhian/Serravallian, MN 7)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus fejfari	Anguidae	Dopasia fejfari	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus cf. O. fejfari	Anguidae	Dopasia cf. D. fejfari	Oschiri	Italy	Lower Miocene (Aquitanian, MN 1/MN 2b)	Böhme & Ilg 2003; Venczel & Sanchíz 2006; Delfino & Rook 2008; Zoboli & Pillola 2017
Ophisaurus cf. O. fejfari	Anguidae	Dopasia cf. D. fejfari; Ophisaurus sp.	Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus cf. O. fejfari	Anguidae	Dopasia cf. D. fejfari	Petersbuch 28	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus cf. O. fejfari	Anguidae	Dopasia cf. D. fejfari	Petersbuch 36 II	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus cf. O. fejfari	Anguidae	Dopasia aff. D. fejfari	Unterhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus aff. O fejfari	Anguidae	Dopasia aff. D. fejfari ; Ophisaurus sp.	Obergänserndorf, Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003
Ophisaurus aff. O.fejfari	Anguidae	Dopasia aff. D. fejfari	Teiritzberg (T1 = 001/D/C), Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme & Ilg 2003; Tempfer 2003
Ophisaurus cf. O. fraasi	Anguidae		Sant Quirze de Galliners, Vallès Penedès Basin	Spain	Middle Miocene	Crusafont Pairó & Villalta 1952
Ophisaurus cf. 0 . fraasi	Anguidae		Els Hostalets de Pierola, Vallès Penedès Basin	Spain	Middle/late Miocene (MN 7+8/MN 9)	Crusafont Pairó & Villalta 1952
Ophisaurus holeci	Anguidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Klembara 2015; Klembara & Rummel 2016; Čerňanský & Klembara 2017
Ophisaurus holeci	Anguidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Villa & Delfino 2017; this work
Ophisaurus holeci	Anguidae		Petersbuch 62	Germany	Miocene (MN 3)	Klembara & Rummel 2016
Ophisaurus holeci	Anguidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Klembara & Rummel 2016
Ophisaurus holeci	Anguidae		Petersbuch 39 III	Germany	Miocene (MN 5)	Klembara & Rummel 2016
Ophisaurus holeci	Anguidae	Ophisaurus sp.	Ohningen (= Ohningen, oberer Bruch)	Germany	Miocene (Serravallian, MN 6/7)	Böhme & Ilg 2003; Čerňanský & Klembara 2017
Ophisaurus intermedius	Anguidae		Csarnóta 2	Hungary	Pliocene (Zanclean, MN 15)	lánossy 1986

Ophisaurus intermedius	Anguidae		Villány 6	Hungary	Lower Pleistocene	lánossy 1986
Ophisaurus moguntinus	Anguidae		Frankfurt	Germany	Lower Miocene	Młynarski 1956; Estes 1983
Ophisaurus moguntinus	Anguidae		Haslach North Ulm	Germany	Lower Miocene	Estes 1983
Ophisaurus moguntinus	Anguidae		Ulm	Germany	Lower Miocene	Estes 1983
Ophisaurus moguntinus	Anguidae	Ophisaurus cf. O. moguntinus; Propseudopus cf. P. fraasi	Opole 2 (= Nowa Wies Krółewska II)	Poland	Miocene (Serravallian, MN 7)	Mtynarski 1956; Mtynarski 1984; Mtynarski et al. 1982; Estes 1983
Ophisaurus moguntinus	Anguidae		Przeworno I	Poland	Miocene (late Vindobonian/lower Badenian)	Estes 1983; Mlynarski 1984
Ophisaurus moguntinus	Anguidae		Langenmosen	Germany	Upper Miocene	Estes 1983
Ophisaurus robustus	Anguidae		Petersbuch 62	Germany	Miocene (MN 3)	Klembara & Rummel 2016
Ophisaurus robustus	Anguidae	Anguis robustus; Ophisaurus (?) robustus (cf. Anguis)	Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Klembara 1979; Klembara 1981; Estes 1983; Roček 1984; Bailon 1991; Böhme 2003; Böhme & Ilg 2003; Böhme 2010b; Klembara 2015; Čerňanský 2016; Klembara & Rummel 2016
Ophisaurus robustus	Anguidae	Ophisaurus cf. O. spinari	Felsötárkány-Felnémet 2/3	Hungary	Miocene (Astaracian, MN7+8)	Böhme & Ilg 2003; Venczel & Hir 2013; Klembara & Rummel 2016
Ophisaurus aff. O. robustus	Anguidae	Ophisaurus sp.	Erkertshofen 1	Germany	Miocene (MN 4b)	Schleich 1985b; Böhme & Ilg 2003
Ophisaurus spinari	Anguidae		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b
Ophisaurus spinari	Anguidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Klembara 2015
Ophisaurus spinari	Anguidae		Petersbuch 62	Germany	Miocene (MN 3)	Klembara & Rummel 2016
Ophisaurus spinari	Anguidae	Ophisaurus aff. O. spinari; Ophisaurus cf. O. spinari; Ophisaurus holeci	Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Klembara 1979; Klembara 1981; Estes 1983; Roček 1984; Augé 1992; Augé & Rage 2000; Böhme 2003; Böhme & Ilg 2003; Miklas-Tempfer 2003; Böhme 2010b; Čerňanský et al. 2015b; Klembara 2016; Čerňanský 2016; Klembara & Rummel 2016; Georgalis et al. 2017a
Ophisaurus spinari	Anguidae		Petersbuch 39 III	Germany	Miocene (MN 5)	Klembara & Rummel 2016
Ophisaurus spinari	Anguidae		ZAPFE's fissure, Devínska Nová Ves	Slovakia	Middle Miocene	Klembara 1986b
Ophisaurus spinari	Anguidae	Dopasia spinari	Stockerau	Slovakia	Miocene	Blain 2009
Ophisaurus spinari	Anguidae	Anguinae indet.; <i>Dopasia</i> sp.	Capo Mannu D1 Local Fauna (= Mandriola)	Italy	Late Pliocene (Piacenzian)	Kotsakis 1980; Estes 1983; Böhme & Ilg 2003; Delfino & Rook 2008; Delfino et al. 2011; Klembara & Rummel 2016

Ophisaurus cf. O. spinari	Anguidae		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Ophisaurus cf. O. spinari	Anguidae		Felsötárkány-Felnémet 2/7	Hungary	Miocene (Astaracian, MN7+8)	Böhme & Ilg 2003; Venczel & Hir 2013
Ophisaurus cf. O. spinari	Anguidae		Felsötárkány 1	Hungary	Miocene (Vallesian, MN 9)	Böhme & Ilg 2003; Venczel & Hir 2013
Ophisaurus cf. O. spinari	Anguidae		Felsötárkány 2	Hungary	Miocene (Vallesian, MN 9)	Böhme & Ilg 2003; Venczel & Hir 2013
Ophisaurus cf. O. spinari	Anguidae		Felsötárkány 3/2	Hungary	Miocene (Vallesian, MN 9)	Böhme & Ilg 2003; Venczel & Hir 2013
Ophisaurus cf. O. spinari	Anguidae		Felsötárkány 3/8	Hungary	Miocene (Vallesian, MN 9)	Böhme & Ilg 2003; Venczel & Hir 2013
Ophisaurus cf. O. spinari	Anguidae		Felsötárkány 3/10	Hungary	Miocene (Vallesian, MN 9)	Böhme & Ilg 2003; Venczel & Hir 2013
cf. Ophisaurus spinari	Anguidae	Ophisaurus cf. O. spinari	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Böhme 2010b
Ophisaurus sp. 1	Anguidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme 2003; Böhme & Ilg 2003; Klembara 2015
Ophisaurus sp. 1	Anguidae	Ophisaurus sp.	Rembach, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003: Kosma 2004
Ophisaurus sp. 1	Anguidae		Massendorf	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp. 1	Anguidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme 2003; Böhme & Ilg 2003; Böhme 2010b
Ophisaurus sp. 1	Anguidae		Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Böhme & Ilg 2003; Böhme 2010b
Ophisaurus sp. 2	Anguidae	Pseudopus cf. P. moguntinus	Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme 2003; Böhme & Ilg 2003; Klembara 2015
Ophisaurus sp. 2	Anguidae	Ophisaurus sp.	Rembach, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Kosma 2004
Ophisaurus sp. 2	Anguidae		Massendorf	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp. 2	Anguidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp. 2	Anguidae		Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Böhme & Ilg 2003; Böhme 2010b
Ophisaurus sp. I	Anguidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1984; Klembara 2015; Čerňanský 2016
Ophisaurus sp. II	Anguidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1984; Klembara 2015
Ophisaurus sp. (morphotype 1)	Anguidae	Pseudopus sp./Ophisaurus sp.	Maramena 1	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work

Delfino 2004b; this work	Delfino 2004b; this work	Delfino 2004b; this work	Delfino 2004b; this work	Crusafont et al. 1955; Bergounioux 1958	Crusafont et al. 1955; Bergounioux 1958	2) Schleich 1985b	2) Schleich 1985b	2) Böhme 2003; Böhme & Ilg 2003	 Schleich 1988b; Böhme & Ilg 2003; Čerňansk; al. 2015b 	Mennecart et al. 2016	MN Schleich 1985b	Schleich 1985b	Schleich 1985b	Böhme & Ilg 2003	, Böhme & Ilg 2003	b) Schleich 1985b; Böhme 2003; Böhme & Ilg 20 Villa & Delfino 2017; this work	b) Villa & Delfino 2017; this work) Schleich 1985b; Böhme 2003; Böhme & Ilg 20	Schleich 1985b	Schleich 1985b	Schleich 1985b	Schleich 1985b	Schleich 1985b			
Late Miocene (MN 13/14)	Late Miocene (MN 13/14)	Late Miocene (MN 13/14)	Late Miocene (MN 13/14)	Early Miocene (Upper Burdigalian)	Miocene (lower Burdigalian)	Miocene (Aquitanian, MN 1/2	Miocene (Aquitanian, MN 1/2	Miocene (Aquitanian, MN 1/2	Miocene (Aquitanian, MN 2a	Early Miocene (MN 2a)	Early Miocene (Aquitanian, N 2)	Miocene (MN 2)	Miocene (MN 2)	Miocene (Aquitanian)	Miocene (Aquitanian)	Miocene (Aquitanian)	Lower Miocene (Aquitanian)	Lower Miocene (Burdigalian, MN 3a)	Miocene (Burdigalian, MN 31	Miocene (Burdigalian, MN 3	Miocene (Burdigalian, MN 3)	Miocene (MN 3/4)	Miocene (Burdigalian, MN 3a/4b)	Miocene (MN 3/5)	Miocene (MN 3/5)	Miocene (MN 3/5)
Greece	Greece	Greece	Greece	Spain	Spain	Germany	Germany	Germany	Germany	Switzerland	Germany	Germany	Germany	Germany	Germany	Germany	Spain	Czech Republic	Germany	Germany	Germany	Germany	Germany	Germany	Germany	Germany
Maramena 1	Maramena 1	Maramena 1	Maramena 1	Can Mas, Vallés-Penedés Basin	Moli Calopa	Grafenmühle 2	Grafenmühle 9	Grafenmühle 21	Wiesbaden-Amöneburg	Wallenried	Jungingen	Schaffhausen (Harburg) 1 (A)	Treuchtlingen 2	Lautern 2	Oberer Eselsberg	Ulm Westtangente	Cetina de Aragon	Merkur North	Stubersheim 2	Stubersheim 3	Bissingen 1 (Wütherich)	Haag 1	Schnaitheim 1	Altheim 1	Burgmagerbein 4	Weissenburg 10
Pseudopus sp./Ophisaurus sp.	Pseudopus sp./Ophisaurus sp.	Pseudopus sp./Ophisaurus sp.	Pseudopus sp./Ophisaurus sp.																							
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae
Ophisaurus sp. (morphotype 2)	Ophisaurus sp. (morphotype 3)	Ophisaurus sp. (morphotype 4)	Ophisaurus sp. (morphotype 5)	Ophisaurus sp. large size	Ophisaurus sp. small size	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.

Ophisaurus sp.	Anguidae		Hermaringen 1	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003: Kosma 2004
Ophisaurus sp.	Anguidae	Anguinae indet. morphotype I; Anguinae indet. morphotype V; cf. <i>Ophisaurus</i> sp.	Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Klembara 1981; Roček 1984; Klembara 1986b; Böhme 2003; Böhme & Ilg 2003; Čerňanský et al 2015b; Klembara 2015
Ophisaurus sp.	Anguidae		Béon 1 (= Montréal-du-Gers)	France	Lower Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Rage & Bailon 2005
Ophisaurus sp.	Anguidae		Erkertshofen 2	Germany	Miocene (MN 4b)	Schleich 1985b
Ophisaurus sp.	Anguidae		Forsthart	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1985b
Ophisaurus sp.	Anguidae	Anguidae indet.	Langenau 1	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Langenau 2	Germany	Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Rauscheröd	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1985b
Ophisaurus sp.	Anguidae		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Ophisaurus sp.	Anguidae		Petersbuch 36 II	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Petersbuch 38-Boden	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Offingen 1 (graue Schneckenschicht)	Germany	Miocene (Burdigalian, MN 4b/5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Adelschlag	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Ambach near Pöttmes	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Arth (Coll. Seehuber)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Arth 1a	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Attenfeld	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Dieshof b. Pöttmes - oberer Mergel	Germany	Early Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Dieshof b. Pöttmes - unterer Mergel	Germany	Early Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Eitensheim	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Hitzhofen 1	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003

Ophisaurus sp.	Anguidae		Hitzhofen 1+2	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Hitzhofen 2	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Illertissen (=Betlingshausen)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Langenmosen	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b
Ophisaurus sp.	Anguidae		Niederaichbach	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Niederaichbach (links)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme & Ilg 2003; Böhme 2010b; Čerňanský et al. 2016c
Ophisaurus sp.	Anguidae		Schönenberg	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Unterempfenbach 1a	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Unterempfenbach 1b	Germany	Early Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Unterhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Unterneul 1a	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Walda 1 (unten)	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Walda 2 (oben)	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Oggenhausen 1	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Oggenhausen 2	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Puttenhausen A	Germany	Miocene (Burdigalian)	Schleich 1985b; Böhme & Ilg 2003; Abdul Aziz et al. 2008
Ophisaurus sp.	Anguidae		Puttenhausen B	Germany	Miocene (Burdigalian)	Schleich 1985b; Böhme & Ilg 2003; Abdul Aziz et al. 2008
Ophisaurus sp.	Anguidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Ophisaurus s.l.	Barranco de Tudela 3, Bardenas Reales, Navarra	Spain	Early Miocene (Burdigalian)	Murelaga et al. 2002; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Ophisaurus s.l.	Barranco del Fraile 1, Bardenas Reales, Navarra	Spain	Early Miocene (Burdigalian)	Murelaga et al. 2002; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Ophisaurus s.l.	La Nasa 1 (= Tripazul), Bardenas Reales, Navarra	Spain	Miocene (Burdigalian)	Murelaga et al. 2002; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Olmo Redondo 4A	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Ophisaurus s.l.	Rincón del Bu, Bardenas Reales, Navarra	Spain	Miocene (Burdigalian)	Murelaga et al. 2002; Böhme & Ilg 2003

Ophisaurus sp.	Anguidae		San Roque 2	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		San Roque 3	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Vargas 4A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Villafeliche 2A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Schmiedrued-Pyffrüti level 618, Swiss Molasse Basin	Switzerland	Late Early Miocene (Burdigalian)	Böhme & Ilg 2003; Jost et al. 2015
Ophisaurus sp.	Anguidae		Budenheim	Germany	Lower Miocene	Schleich 1988b
Ophisaurus sp.	Anguidae		Mainz - Sonnenbrauerei	Germany	Lower Miocene	Schleich 1988b
Ophisaurus sp.	Anguidae	Ophisaurus moguntinus	Weisenau	Germany	Lower Miocene	Estes 1983; Schleich 1988b
Ophisaurus sp.	Anguidae		Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Altenstadt	Germany	Miocene (MN 5)	Böhme 2003
Ophisaurus sp.	Anguidae		Appertshofen	Germany	Middle Miocene (MN 5)	Schleich 1985b
Ophisaurus sp.	Anguidae		Aresing	Germany	Miocene (Burdigalian/Langhian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Burtenbach 1b (b. Thannhausen)	Germany	Early Miocene (MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2010
Ophisaurus sp.	Anguidae		Burtenbach 1c (b. Thannhausen)	Germany	Early Miocene (MN 5)	Schleich 1985 b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Grafenmühle	Germany	Miocene (MN 5)	Schleich 1985b
Ophisaurus sp.	Anguidae		Rothenstein 1/13	Germany	Miocene (Burdigalian/Langhian, MN 5)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Regensburg - Prüfening	Germany	Miocene (MN 5?)	Schleich 1985b
Ophisaurus sp.	Anguidae		Mühlbach am Manhartsberg	Austria	Miocene (Langhian, MN 5)	Böhme & Ilg 2003; Miklas-Tempfer 2003
Ophisaurus sp.	Anguidae		Denkendorf Nord (Südwand)	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Denkendorf Nord (Westwand)	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Denkendorf Süd Westseite - Schneckenlage	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Derching 1b (unten)	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Eberstetten 2 (unter Weg)	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Eberstetten 2 (Wand Mitte)	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work
Ophisaurus sp.	Anguidae		Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work

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Ophisaurus sp.	Anguidae	Griesbeckerzell 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Oberbernbach 1	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Oberbernbach 2	Germany	Miocene (Langhian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Oberbernbach 3	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Aich	Germany	Middle Miocene (MN 5/6)	Schleich 1985b
Ophisaurus sp.	Anguidae	Berg im Gau	Germany	Middle Miocene (MN 5/6)	Schleich 1985b
Ophisaurus sp.	Anguidae	Buch	Germany	Middle Miocene (MN 5/6)	Schleich 1985b
Ophisaurus sp.	Anguidae	Dinkelscherben	Germany	Miocene (MN 5/6)	Schleich 1985b
Ophisaurus sp.	Anguidae	Mettenhausen	Germany	Miocene (MN 5/6)	Schleich 1985b
Ophisaurus sp.	Anguidae	Pöttmes	Germany	Miocene (MN 5/6)	Schleich 1985b
Ophisaurus sp.	Anguidae	Derching 1a	Germany	Early Miocene (Langhian, MN 6)	Böhme 2003
Ophisaurus sp.	Anguidae	Gallenbach 2a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Gallenbach 2b	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Gallenbach 2c	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Goldberg 4	Germany	Miocene (Langhian, MN 6)	Schleich 1985b
Ophisaurus sp.	Anguidae	Goldberg 10	Germany	Miocene (Langhian, MN 6)	Schleich 1985a; Schleich 1985b
Ophisaurus sp.	Anguidae	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Villa & Delfino 2017; this work
Ophisaurus sp.	Anguidae	Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Laimering 4b	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Laimering 5	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Petersbuch 39	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Litke 1	Hungary	Miocene (Langhian, MN 6)	Böhme & Ilg 2003; Čerňanský et al. 2016c
Ophisaurus sp.	Anguidae	Derching (blauer Mergel ca. 2- 3m über BH)	Germany	Early Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Oberschöneberg 2H	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Petersbuch 68	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Untereichen-Altenstadt 565m	Germany	Miocene (Langhian)	Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010
Ophisauru s sp.	Anguidae	Caseton 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Caseton 2B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Las Planas 4B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Las Umbrias 19	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Moratilla 2	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003; Bastir et al. 2014
Ophisaurus sp.	Anguidae	Valdemoros 3F	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Valdemoros 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Valdemoros 8C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003

Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Schleich 1985b	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Schleich 1985b	Schleich 1985b	Böhme & Ilg 2003; Hír & Venczel 2005	Benito & Bolet 2016	Villa & Delfino 2017; this work	Böhme 2003; Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003; Venczel & Știucă 2008	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003	0000			
Middle Miocene (Langhian)	Middle Miocene (Langhian)	Middle Miocene (Langhian)	Middle Miocene (Langhian)	Miocene (Langhian)	Miocene (Langhian/Serravallian, MN 6)	Middle Miocene (Langhian/Serravallian, MN 6)	Miocene (Langhian/Serravallian, MN 6)	Middle Miocene (Langhian/Serravallian, MN 6)	Miocene (MN 6)	Miocene (MN 6)	Miocene (MN 6)	Miocene (MN 6)	Middle/upper Miocene (MN 6/7)	Miocene (Serravallian, MN 8)	Miocene (Serravallian, MN 8)	Middle Miocene (Serravallian, MN 8)	Late middle Miocene (Serravallian, MN 8)	Middle Miocene (Serravallian)								
Spain	Spain	Spain	Spain	Spain	Germany	Germany	Switzerland	Switzerland	Germany	Germany	Germany	Romania	Spain	Germany	Germany	Romania	Romania	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	
Vargas 5	Vargas 6	Vargas 8B	Vargas 8C	Villafeliche 4A	Goldberg (without number)	Steinberg (Ries)	Mühlrüti Pt. 806	Rümikon	Göttschlag 1b	Gündlkofen	Häder	Subpiatră 2/1R	Moneva	Kleineisenbach	Laimering 1a	Tăşad	Tauț	Borjas	Las Planas 5C	Las Planas 5H	Las Planas 5K	Las Umbrias 20	Las Umbrias 21	Las Umbrias 22	Paje 1	
											Propseudopus aff. P. fraasi															
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Ameridae
Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Onhiemme en

n) Böhme & Ilg 2003	() Bachmayer & Mlynarski 1977	() Bachmayer & Mlynarski 1977	Klembara 1986b; Čerňanský & Klembara 20	Klembara 1986b; Čerňanský 2011b	Schleich 1985b	Schleich 1985b Schleich 1985b	Schleich 1985b	iian, Böhme 2003; Böhme & Ilg 2003	López Martínez et al. 1977; Böhme & Ilg 20	Böhme & Ilg 2003	Böhme & Ilg 2003	iian, Böhme 2003; Böhme & Ilg 2003	Crusafont Pairó & Villalta 1952; Bolet et al.	8) Böhme & Ilg 2003; Hír & Venczel 2005	Schleich 1985b	Schleich 1985b; Böhme & Ilg 2003	Schleich 1985b; Böhme & Ilg 2003					
Middle Miocene (Serravallia	Miocene (late Vindobonian/lower Badenian	Miocene (late Vindobonian/lower Badenian	Middle Miocene	Middle Miocene	Middle Miocene (MN 7+8)	Miocene (MN 7+8) Miocene (MN 7+8)	Miocene (MN 8)	Miocene (Serravallian/Tortor MN 8)	Miocene (Serravallian/Tortonian)	Miocene (Serravallian/Tortonian)	Miocene (Serravallian/Tortonian)	Miocene (Serravallian/Tortor MN 8/9)	Middle/late Miocene (MN 7+8/MN 9)	Miocene (Tortonian, MN 7+5	Miocene (MN 4/?8)	Miocene (Tortonian, MN 9)	Miocene (Tortonian, MN 9)					
Spain	Spain	Spain	Spain	Spain	Poland	Poland	Slovakia	Slovakia	Germany	Germany	Germany	Germany	Spain	Spain	Spain	Germany	Spain	Romania	Germany	Germany	Germany	
Toril 2	Toril 3A	Toril 3B	Valatto 1A	Valatto 2C	Przeworno I	Przeworno II	Bonanza, Devínska Nová Ves	ZAPFE's fissure, Devínska Nová Ves	Bitzenhofen	Onnugen Rennertshofen	Fröttmaning	Petersbuch 48	Escobosa de Calatañazor	Villafeliche 4	Villafeliche 6	Unggenried (Autobahnanschnitt)	Els Hostalets de Pierola, Vallès Penedès Basin	Subpiatră 2/2	Oberbirnbach 53, 56	Hammerschmiede 1	Hammerschmiede 3	
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	
Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp. Onhisaurus sn	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.	Ophisaurus sp.						

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Onhisaurus sn.	Anguidae		Marktl am Inn	Germany	Miocene (MN 9)	Schleich 1985b
Ophisaurus sp.	Anguidae		Felsötárkány 3/2	Hungary	Miocene (Vallesian, MN9)	Venczel & Hir 2013
Ophisaurus sp.	Anguidae		Gritsev	Ukraine	Late Miocene (MN 9)	Böhme & Ilg 2003; Vasilyan et al. 2016
Ophisaurus sp.	Anguidae		Vösendorf (= Vösendorf-Brunn)	Austria	Miocene (Tortonian, MN 10)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Sant Miquel del Toudell, Vallés- Penedés Basin	Spain	Late Miocene (MN 10)	Crusafont Pairó & Villalta 1952
Ophisaurus sp.	Anguidae		Viladecaballs (Can Purull)	Spain	Miocene (Vallesian)	Crusafont Pairó & Villalta 1952
Ophisaurus sp.	Anguidae		Viladecaballs (Can Trullàs)	Spain	Miocene (Vallesian)	Crusafont Pairó & Villalta 1952
Ophisaurus sp.	Anguidae		La Gloria 10	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		La Roma 1	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		La Roma 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Los Aguanaces	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Los Aguanaces 1	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Los Aguanaces 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Masada Ruea 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Masia de la Roma 9	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Nombrevilla 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Ano Metochi 2	Greece	Late Miocene (Messinian, MN 13)	Georgalis et al. 2017a; this work
Ophisaurus sp.	Anguidae	Pseudopus sp./Ophisaurus sp.	Ano Metochi 3	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; Georgalis et al. 2017a; this work
Ophisaurus sp.	Anguidae		Polgárdi 2	Hungary	Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Venczel 2006; Georgalis et al. 2017a
Ophisaurus sp.	Anguidae		Polgárdi 4	Hungary	Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Venczel 2006; Georgalis et al. 2017a
Ophisaurus sp.	Anguidae		Polgárdi 5	Hungary	Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Venczel 2006; Georgalis et al. 2017a
Ophisaurus sp.	Anguidae	Ophisaurus s.l.	Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Delfino 2002; Böhme & Ilg 2003; Rook et al. 2005; Rook & Delfino 2007; Rook et al. 2015; Villa et al. 2016b; this work
Ophisaurus sp.	Anguidae		Maramena	Greece	Late Miocene (MN 13/14)	Richter 1995; Georgalis et al. 2017a
Ophisaurus sp.	Anguidae	Pseudopus sp./Ophisaurus sp.	Maramena 1	Greece	Late Miocene (MN 13/14)	Böhme & Ilg 2003; Delfino 2004b; this work
Ophisaurus sp.	Anguidae		Aljezar B	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Concud 98'	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Los Mansuetos	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Tortajada C	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Valdecebro 5	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Villastar	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae		Los Valles de Fuentidueña	Spain	Late Miocene	Sanchiz 1981
Ophisaurus sp.	Anguidae		El Arquillo 0	Spain	Miocene/Pliocene (Messian/Zanclean)	Böhme & Ilg 2003
Ophisaurus sp.	Anguidae	Dopasia sp.	Na Burguesa-1, Mallorca	Spain	Miocene/Pliocene (Messian/Zanclean)	Böhme & Ilg 2003; Bover et al. 2014

sp.	Augurac	sp.	Caló den Rafelino, Mallorca	Spain	Earliest early Pliocene	al. 2014; Bover et al. 2014
	Anguidae		Kamenjak, Bukulja	Serbia	Early Pliocene (MN 14)	Jovanović et al. 2002
	Anguidae	Dopasia sp.	Csarnóta 2	Hungary	Pliocene (Zanclean, MN 15)	Böhme & Ilg 2003; Venczel & Gardner 2005
	Anguidae		Ivanovce	Slovakia	Upper Pliocene (Zanclean, MN 15)	Młynarski 1962; Böhme & Ilg 2003; Čerňanský 2011b
	Anguidae		El Arquillo 3	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
	Anguidae		Escorihuela B	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003
	Anguidae		La Gloria 4	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
	Anguidae		Orrios rio (base of profile)	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
	Anguidae		Peralejos 7	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
	Anguidae		Villalba Alta 1	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
	Anguidae		Villalba Alta 3	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
	Anguidae		Gorafe 27	Spain	Middle Pliocene (MN15)	Blain 2005
	Anguidae		Sarrión 1	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003
	Anguidae		Bad Deutsch-Altenburg 9	Austria	Pliocene	Bachmaver & Mlvnarski 1977
	Anguidae		Eichkogel bei Mödling	Austria	Pliocene	Bachmayer & Mlynarski 1977
	Anguidae	Dopasia sp.	Galera-2	Spain	Early Pleistocene (MN 17)	Böhme & Ilg 2003
	Anguidae	Dopasia sp.	Almenara Casablanca 4	Spain	Early Pleistocene (Gelasian)	Böhme & IIg 2003; Blain 2005; Agustí et al. 2009; Blain 2009; Blain & Bailon 2010; Blain et
						al. 2016a
	Anguidae	Anguis fragilis; Blanus cinereus; Dopasia sp.	Barranco León	Spain	Early Pleistocene (Calabrian)	Blain 2003; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; De Marfa 2007; Agustí et al. 2009; Blain 2009; Mancheño et al. 2009; Agustí et al. 2010; Blain & Bailon 2010; Blain et al. 2011; Blain et al. 2016d; Blain et al. 2016
						Bihuna % II.a 2003: Blain 2005: Bailan % Blain
	Anguidae	cf. Dopasia sp.; cf. Ophisaurus sp.	Fuente Nueva 3	Spain	Early Pleistocene (Calabrian)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009; Mancheño et al. 2009; Blain & Bailon 2010; Blain et al. 2016a; Blain et al. 2016d; Klembara & Rummel 2016
	Anguidae		Somssich Hill 2	Hungary	Late early Pleistocene	Jánossy 1986; Pazonyi et al. 2017
	Anguidae		Osztramos 8	Hungary	Lower Pleistocene	Jánossy 1986
	Anguidae		Villány 6	Hungary	Lower Pleistocene	Böhme & Ilg 2003
	Anguidae	Dopasia sp.	Quibas	Spain	Early Pleistocene	Mancheño et al. 2009; Blain et al. 2016a
	Anguidae		Bristie 2	Italy	Earliest Middle Pleistocene	Bon et al. 1991
	Anguidae		Adlerberg	Germany	Middle Pleistocene	Schleich 1985b
	Anguidae	Dopasia sp.	Canal Negre 1	Spain	Latest Miocene/Middle Pleistocene	Blain et al. 2016a
	Anguidae		Šandalja near Pula	Croatia	Upper Pleistocene	Holman 1998; Böhme & Ilg 2003
	Anguidae		Osztramos 7	Hungary	Pleistocene	Jánossy 1986
	Anguidae		Kadzielnia	Poland	Pleistocene	Bachmayer & Mlynarski 1977

?Ophisaurus sp.	Anguidae		Schaffhausen (Harburg) 1 (B)	Germany	Miocene (MN 2)	Schleich 1985b
?Ophisaurus sp.	Anguidae		Petersbuch 5	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
?Ophisaurus sp.	Anguidae		Anwil (Grabung 1968)	Switzerland	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003
?Ophisaurus sp.	Anguidae		Anwil (Grabung 1980)	Switzerland	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003
?Ophisaurus sp.	Anguidae	Ophisaurus sp.	Montoussé 5	France	Early Pleistocene (MN 17)	Clot et al. 1976; Estes 1983; Böhme & Ilg 2003; Bailon & Blain 2007
cf. Ophisaurus sp.	Anguidae		Untereichen-Altenstadt 540m	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010
cf. Ophisaurus sp.	Anguidae		Asseiceira/Rio Maior	Portugal	Middle Miocene	Crespo 2001
cf. Ophisaurus sp.	Anguidae		Amor	Portugal	Middle Miocene (MN5)	Antunes & Mein 1981; Crespo 2001; Böhme & Ilg 2003
cf. Ophisaurus sp.	Anguidae		Mühlbach am Manhartsberg	Austria	Miocene (Langhian, MN 5)	Böhme & Ilg 2003; Miklas-Tempfer 2003
cf. Ophisaurus sp.	Anguidae		Petersbuch 46	Germany	Miocene (Tortonian, MN 9)	Böhme 2003; Böhme & Ilg 2003
cf. Ophisaurus sp.	Anguidae		Sète	France	Middle Pliocene (MN 15)	Böhme & Ilg 2003; Bailon & Blain 2007
cf. Ophisaurus sp.	Anguidae		Galera 1C	Spain	Middle Pliocene (MN 15)	Blain 2005
cf. Ophisaurus sp.	Anguidae		Galera 1G	Spain	Late Pliocene (MN 16)	Blain 2005
cf. Ophisaurus sp.	Anguidae		Zújar	Spain	Late Pliocene (MN 16)	Blain 2005
cf. Ophisaurus sp.	Anguidae	cf. Dopasia sp.	Barranco del Agua-6	Spain	Pliocene/Pleistocene (Zanclean/Gelasian)	Böhme & Ilg 2003; Blain 2005; Blain 2009
cf. Ophisaurus sp.	Anguidae	cf. Dopasia sp.	Almenara Casablanca 1	Spain	Early Pleistocene (Gelasian)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009
aff. Ophisaurus sp.	Anguidae		Rudabanya (black clay 5B)	Hungary	Miocene (Tortonian, MN 9)	Böhme 2003; Böhme & Ilg 2003
aff. Ophisaurus sp.	Anguidae		Tortajada	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
"Ophisaurus" sp.	Anguidae		Balaruc II	France	Middle/late Pliocene (MN 15/16)	Bailon 1989; Bailon 1991; Bailon 1995; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Blain & Bailon 2010
?Ophisaurus s.l.	Anguidae		Montaigu-le-Blin	France	Lower Miocene (Aquitanian, MN 2a)	Müller 2001
Propseudopus sp.	Anguidae		La Grive-Saint-Alban	France	Miocene	Hoffstetter 1962
Pseudopus ahnikoviensis	Anguidae	Pseudopus cf. P. moguntinus	Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & IIg 2003; Klembara 2012; Rage 2013; Čerňanský et al. 2015b; Klembara 2015; Čerňanský et al. 2016a; Čerňanský et al. 2016c;
						Klembara & Rummel 2016
Pseudopus ahnikoviensis	Anguidae	Pseudopus sp.	Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Klembara 2012; Cerñanský 2016; Čerňanský et al. 2016c
Pseudopus cf. P. ahnikoviensis	Anguidae		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b; Čerňanský et al. 2016c
Pseudopus cf. P. ahnikoviensis	Anguidae	Ophisaurus sp.	Hambach 6C	Germany	Early middle Miocene (Langhian, MN 5)	Mörs 2002; Böhme 2003; Böhme & Ilg 2003; Čerňanský et al. 2016c

Pseudopus moguntinus Pseudopus moguntinus	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme & Ilg 2003; Abdul Aziz et
Pseudopus moguntinus				al. 2008; Bonme 20100; Cernansky et al. 2010c
	Walda 2 (oben)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Klembara et al. 2010
	Ichenhausen 3	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
	Offingen 4	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
	Randecker Maar	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
	Petersbuch 39 III	Germany	Miocene (MN 5)	Böhme & Ilg 2003; Klembara et al. 2010
	Griesbeckerzell 1b	Germany	Miocene (Langhian, MN 5)	Böhme & IIg 2003; Klembara et al. 2010; Ivanov & Böhme 2011; Čerňanský et al. 2016c
Pseudopus moguntinus	Sainbach	Germany	Miocene (MN 5/6)	Böhme 2003; Böhme & Ilg 2003; Klembara et al. 2010
	Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Böhme & IIg 2003; Klembara et al. 2010; Ivanov & Böhme 2011; Čerňanský et al. 2016c; Villa & Delfino 2017; this work
	Petersbuch 68	Germany	Miocene (MN 6)	Böhme & Ilg 2003; Klembara et al. 2010
Anguis laurillardi: Anguis ? laurillardi; Ophisaurus moguntinus: Ophisaurus ? Laurillardi	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Lartet 1851; Gervais 1859; De Stefano 1903; Młynarski 1962; Estes 1983; Augé & Rage 2000; Böhme & Ilg 2003; Rage & Bailon 2005; Tempfer 2005; Tempfer 2009; Klembara & Rummel 2016
	Petersbuch 73	Germany	Miocene (MN 7+8)	Böhme & Ilg 2003; Klembara et al. 2010
Pseudopus sp.	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003; Klembara et al. 2010; Klembara 2012
	Opole 2 (= Nowa Wies Królewska II)	Poland	Miocene (Serravallian, MN 7)	Böhme & Ilg 2003
	Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Villa & Delfino 2017; this work
	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
	Altenstadt	Germany	Miocene (MN 5)	Böhme 2003
	Laimering 2a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
	Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
	Hammerschmiede	Germany	Miocene (Tortonian, MN 9)	Böhme 2003
	Zhoften (=Petroviérovak)	Ukraine	Miocene (Tortonian/Messinian, MN 12/MN 13)	Alexejew 1912; Böhme & Ilg 2003
	Atzelsdorf	Austria	Miocene (Tortonian, MN 9)	Tempfer 2009; Böhme & Ilg 2003; Čerňanský et al. 2016c
	Anguis laurillardi ; Anguis ? laurillardi ; Ophisauras ? moguntinus ; Ophisauras ? Laurillardi Pseudopus sp.	Griesbeckerzell Ia Anguis laurillardi: Anguis? Anguis laurillardi: Ophisaurus? Baurillardi: Ophisaurus? Sansan Laurillardi Pseudopus sp. Kleineisenbach Opole 2 (= Nowa Wies Krokewska II) Gisseltshausen Ia Sandelzhausen Iamering 2a Laurillardi Laurillardi Pseudopus sp. Krokewska II) Gisseltshausen Ia Sandelzhausen Iamering 3 Iamering 3 Iamering 3 Iamering 3 Iamering 3 Iamering 3 Antenschmiede Iamering 3	Gresbeckerzell 1aGermany $ -$ <t< td=""><td>Germany Germany Miocene (Langhian, MN 6) Anguis laurillardi : Anguis ? Petersbuch 68 Germany Miocene (MN 6) Anguis laurillardi : Ophisaurus ? Sansan France Middle Miocene Iaurillardi : Ophisaurus ? Sansan France (Langhian, Serravallian, MN 6) Iaurillardi : Ophisaurus ? Sansan France (Langhian, Serravallian, MN 6) Iaurillardi : Ophisaurus ? Petersbuch 73 Germany Miocene (MN 7+8) Pseudopus sp. Kleineisenbach Germany Miocene (Janghian, MN 7) Pseudopus sp. Kleineisenbach Germany Miocene (Langhian, MN 7) Pseudopus sp. Germany Miocene (Langhian, MN 7) Miocene (Langhian, MN 7) Pseudopus sp. Kleineisenbach Germany Miocene (Langhian, MN 7) Pseudopus sp. Kalensen la Germany Miocene (Langhian, MN 5) Pseudopus sp. Sandelzhausen la Germany Miocene (Langhian, MN 5) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 5) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 5) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 9) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 9)</td></t<>	Germany Germany Miocene (Langhian, MN 6) Anguis laurillardi : Anguis ? Petersbuch 68 Germany Miocene (MN 6) Anguis laurillardi : Ophisaurus ? Sansan France Middle Miocene Iaurillardi : Ophisaurus ? Sansan France (Langhian, Serravallian, MN 6) Iaurillardi : Ophisaurus ? Sansan France (Langhian, Serravallian, MN 6) Iaurillardi : Ophisaurus ? Petersbuch 73 Germany Miocene (MN 7+8) Pseudopus sp. Kleineisenbach Germany Miocene (Janghian, MN 7) Pseudopus sp. Kleineisenbach Germany Miocene (Langhian, MN 7) Pseudopus sp. Germany Miocene (Langhian, MN 7) Miocene (Langhian, MN 7) Pseudopus sp. Kleineisenbach Germany Miocene (Langhian, MN 7) Pseudopus sp. Kalensen la Germany Miocene (Langhian, MN 5) Pseudopus sp. Sandelzhausen la Germany Miocene (Langhian, MN 5) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 5) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 5) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 9) Pseudopus sp. Altenstatt Germany Miocene (Langhian, MN 9)

Pseudopus pannonicus	Anguidae	Ophisaurus sp.	Götzendorf	Austria	Miocene (Tortonian, MN 9)	Bachmayer & Mlynarski 1977; Böhme 2003; Böhme & Ilg 2003; Tempfer 2005; Tempfer 2009
Pseudopus pannonicus	Anguidae		Hammerschmiede 1	Germany	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae		Hammerschmiede 3	Germany	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae		Vösendorf (= Vösendorf-Brunn)	Austria	Miocene (Tortonian, MN 10)	Tempfer 2005; Tempfer 2009
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Bachmayer & Mlynarski 1977; Estes 1983; Böhme & Ilg 2003; Miklas-Tempfer 2003; Tempfer 2005; Tempfer 2009
Pseudopus pannonicus	Anguidae		Tardosbánya 3	Hungary	Miocene (Tortonian, MN 12)	Klembara 1986a; Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae		Richardhof - Golfplatz	Austria	Miocene (Tortonian)	Böhme & Ilg 2003; Tempfer 2005; Tempfer 2009
Pseudopus pannonicus	Anguidae		Polgárdi 2	Hungary	Miocene (Messinian, MN 13)	Kormos 1911; Bolkay 1913; Młynarski 1956; Młynarski 1962; Młynarski et al. 1982; Estes 1983; Böhme & Ilg 2003; Tempfer 2009; Čerňanský et al. 2016c; Klembara & Rummel 2016
Pseudopus pannonicus	Anguidae		Polgárdi 3	Hungary	Miocene (Messinian, MN 13)	Tempfer 2005
Pseudopus pannonicus	Anguidae		Polgárdi 4	Hungary	Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Venczel 2006; Čerňanský et al. 2016c
Pseudopus pannonicus	Anguidae		Polgárdi 5	Hungary	Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Venczel 2006; Čerňanský et al. 2016c
Pseudopus pannonicus	Anguidae		Osztramos 1	Hungary	Pliocene (Zanclean, MN 14)	Venczel 2001; Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus; Ophisaurus sp.	Podlesice	Poland	Lower Pliocene (Zanclean, MN 14)	Młynarski 1962; Bachmayer & Mlynarski 1977; Młynarski 1977; Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Węże I	Poland	Upper Pliocene (Zanclean, MN 15)	Młynarski 1956; Młynarski 1962; Bachmayer & Młynarski 1977; Młynarski 1977; Estes 1893; Młynarski et al. 1984; Böhme & Ilg 2003; Ivanov 2007; Blain 2009
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Ivanovce	Slovakia	Upper Pliocene (Zanclean, MN 15)	Estes 1893; Klembara 1986a; Böhme & Ilg 2003; Ivanov 2007; Čerňanský 2011b; Čerňanský et al. 2016c
Pseudopus pannonicus	Anguidae		Arondelli	Italy	Late Pliocene (Piacenzian, MN 16a)	Delfino 2002; Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae		Frechen	Germany	Late Pliocene (Piacenzian, MN 16b)	Mörs 2002

Pseudopus pannonicus	Anguidae	Ophisarurus intermedius ; Ophisaurus pamonicus ; Varanus deserticolus	Beremend 1	Hungary	Pliocene (MN 16)	Bolkay 1913; Młynarski 1962; Estes 1983; Georgalis et al. 2017b
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Rębielice Królewskie 1A	Poland	Upper Pliocene (Piacenzian, MN 16)	Mynarski 1960; Mlynarski 1962; Bachmayer & Mlynarski 1977; Mlynarski 1977; Estes 1983; Mlynarski et al. 1984; Roček 1984; Böhme & Ilg 2003; Ivanov 2007; Blain 2009
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Węże II	Poland	Upper Pliocene (Piacenzian, MN 16)	Mynarski 1962; Estes 1983; Młynarski 1977; Młynarski et al. 1984; Böhme & Ilg 2003; Ivanov 2007; Blain 2009; Čerňanský 2011b; Čerňanský et al. 2016c
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus; Ophisaurus sp.	Bad Deutsch-Altenburg 20	Austria	Pliocene (Piacenzian)	Bachmayer & Mlynarski 1977; Estes 1983; Rauscher 1992; Böhme & Ilg 2003; Miklas- Tempfer 2003; Tempfer 2005; Ivanov 2007
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Bad Deutsch-Altenburg 21	Austria	Pliocene (Piacenzian)	Estes 1983; Rauscher 1992; Böhme & Ilg 2003; Tempfer 2005; Miklas-Tempfer 2003; Ivanov 2007
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Eichkogel bei Mödling	Austria	Pliocene	Thenius 1952; Estes 1983; Miklas-Tempfer 2003; Tempfer 2005; Tempfer 2009
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Csarnóta	Hungary	Pliocene	Estes 1983
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus; Ophisaurus sp.	Hajnáčka	Slovakia	Pliocene	Mtynarski 1962; Estes 1893
Pseudopus pannonicus	Anguidae		Villa Moffa, Bra	Italy	Upper Pliocene/lower Pleistocene (?)/Villafranchian (?)	Delfino 2002; Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Bad Deutsch-Altenburg 14	Austria	Pliocene/Pleistocene	Bachmayer & Miynarski 1977; Estes 1983; Rauscher 1992; Miklas-Tempfer 2003; Tempfer 2005
Pseudopus pannonicus	Anguidae	Ophisaurus cf. O. pamonicus; Ophisaurus pamonicus	Kadzielnia	Poland	Early Pleistocene (MN 17)	Mtynarski 1962; Mtynarski 1977; Estes 1983; Mtynarski et al. 1984
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Bad Deutsch-Altenburg 2C1	Austria	Lower Pleistocene	Bachmayer & Mlynarski 1977; Estes 1983; Rauscher 1992; Böhme & Ilg 2003; Miklas- Tempfer 2003; Tempfer 2005; Ivanov 2007
Pseudopus pannonicus	Anguidae		Villány 8	Hungary	Lower Pleistocene	Venczel 1998

Pseudopus pannonicus	Anguidae		Jaskinia Žabia	Poland	Lower Pleistocene	Böhme & Ilg 2003; Ivanov 2007
Pseudopus pannonicus	Anguidae	Ophisaurus intermedius ; Ophisaurus pannonicus	Betfia 2 (Púspökfürdő or Episcopia Biharuli)	Romania	Lower Pleistocene	Bolkay 1913; Młynarski 1962; Estes 1983
Pseudopus pannonicus	Anguidae		Včeláre	Slovakia	Lower Pleistocene	Klembara 1986a
Pseudopus pannonicus	Anguidae		Cengelle, Brecce di Soave	Italy	Middle Pleistocene	Delfino 2002; Böhme & Ilg 2003
Pseudopus pannonicus	Anguidae		Canal Negre 1	Spain	Latest Miocene/Middle Pleistocene	Blain et al. 2016a
Pseudopus pannonicus	Anguidae	Ophisaurus pannonicus	Koepecz	Hungary	Lower/Upper Pleistocene	Estes 1983
?Pseudopus pannonicus	Anguidae		Bushor 1	Moldova	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003
?Pseudopus pannonicus	Anguidae		Kalfa	Moldova	Miocene (Tortonian)	Böhme & Ilg 2003
Pseudopus cf. P. pannonicus type A	Anguidae		Vendargues	France	Upper Pliocene (MN 16)	Bailon 1991
Pseudopus cf. P. pannonicus type B	Anguidae		Vallee de la Canterrane	France	Pliocene	Bailon 1991
Pseudopus cf. P. pannonicus	Anguidae	Pseudopus pannonicus	Hambach 11	Germany	Late Pliocene (Piacenzian, MN 16)	Mörs 2002; Čerňanský et al. 2016c
Pseudopus cf. P. pannonicus	Anguidae		Hambach 13	Germany	Late Pliocene (Piacenzian, MN 16)	Čerňanský et al. 2016c
Pseudopus cf. P. pannonicus	Anguidae		Unknown locality, Moldova	Moldova	Pliocene	Redkozubov 2003
Pseudopus cf. P. pannonicus	Anguidae	Pseudopus sp.	Cova Bonica	Spain	Late Pliocene/early Pleistocene (MN 16)	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain 2009; Blain et al. 2016a
Pseudopus cf. P. pannonicus	Anguidae		Chismikioi	Moldova	Lower Pleistocene (Calabrian)	Redkozubov 2003
Pseudopus cf. P. pannonicus	Anguidae		Unknown locality, Moldova	Moldova	Lower Pleistocene (Calabrian)	Redkozubov 2003
Pseudopus cf. P. pannonicus	Anguidae		Somssich Hill 2	Hungary	Late early Pleistocene	Pazonyi et al. 2017
Pseudopus aff. P. pannonicus	Anguidae		Novoelizavetovka	Ukraine	Miocene (Tortonian, MN 12)	Böhme & Ilg 2003
Pseudopus aff. P. pannonicus	Anguidae		Cherevichnoje, lower level	Ukraine	Miocene (Tortonian/Messinian, MN 12)	Böhme & Ilg 2003
Pseudopus sp. 1	Anguidae	Ophisaurus sp.	Hambach 6C	Germany	Early middle Miocene (Langhian, MN 5)	Mörs 2002; Böhme 2003; Böhme & Ilg 2003; Čerňanský et al. 2016c
Pseudopus sp. 2	Anguidae	Pseudopus pannonicus	Hambach 11	Germany	Late Pliocene (Piacenzian, MN 16)	Mörs 2002; Čerňanský et al. 2016c

Pseudopus sp. 2	Anguidae		Hambach 13	Germany	Late Pliocene (Piacenzian, MN 16)	Čerňanský et al. 2016c
Pseudopus sp.	Anguidae		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b; Klembara & Rummel 2016
Pseudopus sp.	Anguidae		Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Böhme 2003
Pseudopus sp.	Anguidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Villa & Delfino 2017; this work
Pseudopus sp.	Anguidae		Petersbuch 28	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1984; Böhme 2003; Böhme & Ilg 2003; Klembara 2015
Pseudopus sp.	Anguidae		Forsthart	Germany	Miocene (Burdigalian, MN 4b)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Rembach	Germany	Lower Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003
Pseudopus sp.	Anguidae		1/2001 Turtle Joint, Mokrá- Western Quarry	Czech Republic	Early Miocene (MN 4)	Ivanov et al. 2006
Pseudopus sp.	Anguidae		2/2003 Reptile Joint, Mokrá- Western Quarry	Czech Republic	Early Miocene (MN 4)	Ivanov et al. 2006
Pseudopus sp.	Anguidae		Petersbuch 5	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Sibnica	Serbia	Early Miocene (MN 4)	Durić 2016
Pseudopus sp.	Anguidae		Teiritzberg (T1 = 001/D/C), Korneuburg Basin	Austria	Miocene (Burdigalian, MN 5)	Böhme 2003
Pseudopus sp.	Anguidae		Adelschlag	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Eitensheim	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Langenmosen	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Schönenberg	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Walda 2 (oben)	Germany	Miocene (Burdigalian, MN 5)	this work
Pseudopus sp.	Anguidae		Puttenhausen B	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Pseudopus sp.	Anguidae	Pseudopus laurillardi	Burtenbach 1b (b. Thannhausen)	Germany	Early Miocene (MN 5)	Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2010
Pseudopus sp.	Anguidae		Rothenstein 1/13	Germany	Miocene (Burdigalian/Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Edelstetten	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Gisseltshausen 1a	Germany	Miocene (Langhian, MN 5)	Villa & Delfino 2017; this work
Pseudopus sp.	Anguidae		Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Villa & Delfino 2017; this work

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Pseudonus sn.	Anguidae		Griesbeckerzell 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003: Böhme & Ilø 2003
Pseudopus sp.	Anguidae		Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Villa & Delfino 2017; this work
Pseudopus sp.	Anguidae		Laimering 5	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Petersbuch 33 B	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Petersbuch 68	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Pseudopus sp.	Anguidae	Pseudopus laurillardi	Untereichen-Altenstadt 565m	Germany	Miocene (Langhian)	Böhme & Ilg 2003; Prieto et al. 2009; Abdul Aziz et al. 2010
Pseudopus sp.	Anguidae		Uzwil-Nutzenbuech	Switzerland	Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae	cf. Pseudopus sp.	Abocador de Can Mata, Vallès Penedès Basin	Spain	Middle Miocene (MN 6/MN 7+8)	Böhme & Ilg 2003; this work
Pseudopus sp.	Anguidae		Petersbuch 31 - oben	Germany	Miocene (Langhian/Serravallian, MN 7)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Kirrberg b. Balzhausen - Tongrube	Germany	Miocene (Langhian/Serravallian)	Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Steinheim a. Albuch	Germany	Miocene (Serravallian, MN 7)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Villa & Delfino 2017; this work
Pseudopus sp.	Anguidae		Felsötárkány-Felnémet 2/3	Hungary	Miocene (Astaracian, MN7+8)	Böhme & Ilg 2003; Venczel & Hir 2013
Pseudopus sp.	Anguidae		Felsötárkány-Felnémet 2/7	Hungary	Miocene (Astaracian, MN7+8)	Böhme & Ilg 2003; Venczel & Hir 2013
Pseudopus sp.	Anguidae		Petersbuch 73	Germany	Miocene (MN 7+8)	Klembara & Rummel 2016
Pseudopus sp.	Anguidae		Sant Quirze, Vallès Penedès Basin	Spain	Middle Miocene (MN 7+8)	this work
Pseudopus sp.	Anguidae		Devínska Nová Ves	Slovakia	Middle Miocene	Klembara & Rummel 2016
Pseudopus sp.	Anguidae		Mörgen (b. Eppishausen)	Germany	Miocene (Serravallian/Tortonian)	Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Petersbuch 33	Germany	Miocene (Serravallian/Tortonian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Petersbuch 35	Germany	Miocene (Serravallian/Tortonian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Petersbuch 48	Germany	Miocene (Serravallian/Tortonian, MN 8)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Els Hostalets de Pierola, Vallès Penedès Basin	Spain	Middle/late Miocene (MN 7+8/MN 9)	this work
Pseudopus sp.	Anguidae		Petersbuch 18	Germany	Miocene (Tortonian, MN 8/9)	Böhme 2003; Böhme & Ilg 2003
Pseudopus sp.	Anguidae		Felsötárkány 3/2	Hungary	Miocene (Vallesian, MN 9)	Böhme & Ilg 2003; Venczel & Hir 2013
Pseudopus sp.	Anguidae		Felsötárkány 3/10	Hungary	Miocene (Vallesian, MN 9)	Böhme & Ilg 2003; Venczel & Hir 2013

Böhme & Ilg 2003	Böhme & Ilg 2003; Čerňanský 2011b	this work	this work	this work	this work	this work	Böhme & Ilg 2003	Böhme & Ilg 2003	Jovanović et al. 2002	Villa et al. 2016b; this work	Böhme & Ilg 2003; Marquina et al. 2016a	Delfino 2004b; this work	Delfino 2004b; this work	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013
Miocene (Tortonian, MN 9)	Miocene (Tortonian, MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Miocene (Tortonian, MN 10)	Late Miocene (MN 11+12)	Miocene (latest Messinian, MN 13)	Late Miocene (Messinian, MN 13)	Late Miocene (MN 13/14)	Late Miocene (MN 13/14)	Upper Miocene (Messinian)/lower Pliocene					
Moldova	Slovakia	Spain	Spain	Spain	Spain	Spain	Ukraine	Ukraine	Macedonia	Italy	Spain	Greece	Greece	Italy	Italy	Italy	Italy	Italy	Italy
Kainary	Borský Svätý Jur	Can Llobateres, Vallès Penedès Basin	Can Missert, Vallès Penedes Basin	Can Poncic, Vallès Penedes Basin	Castell de Barberà, Vallès Penedes Basin	Santiga, Vallès Penedès Basin	Gritsev	Krivoj Rog	Beluška and Prevalac, Veles	Cava Monticino, Brisighella	Venta del Moro	Maramena 1	Maramena 3	Biancone, Gargano "Terre Rosse"	Bosco, Gargano "Terre Rosse"	Cantatore, Gargano "Terre Rosse"	Cava Fina, Gargano "Terre Rosse"	Cava Pirro, Gargano "Terre Rosse"	Chirò, Gargano "Terre Rosse"
									Ophisaurus pannonicus; Pseudopus pannonicus	Ophisaurus sp.; Ophisaurus s.1.	Anguidae indet.								
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae
Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.

Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Delfino 2002; Böhme & Ilg 2003; Delfino 2013	Jovanović et al. 2002	Böhme & Ilg 2003	Böhme & Ilg 2003; Čerňanský 2011b) Böhme & Ilg 2003	Delfino 2004b; this work	Delfino 2004b; this work	Böhme & Ilg 2003	Bailon 1991; Böhme & Ilg 2003; Rage & Bailon 2005; Bailon & Blain 2007	Böhme & Ilg 2003
Upper Miocene (Messinian)/lower Pliocene	Early Pliocene (MN 14)	Pliocene (Zanclean, MN 14)	Pliocene (Zanclean, MN 15)	Pliocene (Piacenzian, MN 15	Late Pliocene (MN 16)	Pliocene	Pliocene/Pleistocene (Piacenzian/Gelasian, MN 16	Early Pleistocene (MN 17)	Lower Pleistocene (Gelasian,								
Italy	Serbia	Ukraine	Slovakia	Ukraine	Greece	Greece	Moldova	France	Ukraine								
Falcone, Gargano "Terre Rosse"	Gargano "Terre Rosse" (F - Coll. Firenze)	Gervasio, Gargano "Terre Rosse"	Pizzicoli, Gargano "Terre Rosse"	Rinascita, Gargano "Terre Rosse"	San Giovannino, Gargano "Terre Rosse"	San Nazario, Gargano "Terre Rosse"	Tre Fossi, Gargano "Terre Rosse"	Unknown locality, Gargano "Terre Rosse" (Coll. Torino)	Kamenjak, Bukulja	Kuchurgan	Ivanovce	Vinogradovka	Tourkobounia 1	Kastoria	Novaya Etulia 2	Montoussé 5	Kotlovina, middle level
													cf. Pseudopus sp.	Pseudopus sp./Ophisaurus sp.		Pseudopus cf. P. pannonicus type A	
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae								
Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.	Pseudopus sp.								

Pseudopus sp.	Anguidae		Cava dell'Erba, Pirro Nord (reworked from "Terre Rosse")	Italy	Early Pleistocene	Delfino & Bailon 2000; Böhme & Ilg 2003; Delfino 2013; Delfino & Atzori 2013; Blain et al. 2016c
Pseudopus sp.	Anguidae		Monte La Mesa, Rivoli Veronese	Italy	Early Pleistocene	Delfino et al. 2008a
Pseudopus sp.	Anguidae		Canal Negre 3	Spain	Early/Middle Pleistocene	Blain et al. 2016a
Pseudopus sp.	Anguidae	Ophisaurus sp.	Zoppega 2, Brecce di Soave	Italy	Earliest Middle Pleistocene	Bon et al. 1991; Delfino et al. 2008a
Pseudopus sp.	Anguidae	cf. Pseudopus sp.; Ophisaurus sp.	Montoussé 3	France	Middle Pleistocene	Clot et al. 1976; Bailon 1991; Blain 2005; Blain 2009; Bailon & Rage 2012
Pseudopus sp.	Anguidae	Ophisaurus sp.; Pseudopus pannonicus; Varanus sp.	Viatelle, Brecce di Soave	Italy	Middle Pleistocene	Bon et al. 1991; Delfino 2002; Böhme & Ilg 2003; Delfino et al. 2008a
Pseudopus sp.	Anguidae	Pseudopus pannonicus	Grotta della Volpe, Val d'Avesa	Italy	Late Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino et al. 2008a
Pseudopus sp.	Anguidae	Pseudopus sp./Ophisaurus sp.	Kaiafa	Greece	Pleistocene	Delfino 2004b; this work
?Pseudopus sp.	Anguidae		Unterempfenbach 1a	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
?Pseudopus sp.	Anguidae		Anwil (Grabung 1980)	Switzerland	Miocene (Serravallian, MN 8)	Böhme 2003; Böhme & Ilg 2003
cf. Pseudopus sp.	Anguidae		Tășad	Romania	Middle Miocene (Serravallian, MN 8)	Böhme & Ilg 2003
cf. Pseudopus sp.	Anguidae		Sète	France	Middle Pliocene (MN 15)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007
cf. Pseudopus sp.	Anguidae		Balaruc II	France	Middle/late Pliocene (MN 15/16)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007
cf. Pseudopus sp.	Anguidae		Zújar	Spain	Late Pliocene (MN 16)	Bailon 1991; Blain 2005; Blain 2009; Blain et al. 2016a
cf. Pseudopus sp.	Anguidae	Pseudopus sp.	Rivoli Veronese	Italy	Early Pleistocene (Gelasian; MN 17)	Delfino et al. 2008a; Villa et al. 2017; this work
cf. Pseudopus sp.	Anguidae		Russel-Tiglia-Egypte pit, Tegelen	The Netherlands	Early Pleistocene (Gelasian)	this work
cf. Pseudopus sp.	Anguidae	Pseudopus sp.	Medas Islands	Spain	Early Pleistocene	Bailon 1991; Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Bailon & Augé 2012; Blain et al. 2016a
cf. Pseudopus sp.	Anguidae		Pili B	Greece	Upper Pleistocene	this work
Pseudopus sp./Ophisaurus sp.	Anguidae		Karydia 3	Greece	Middle Miocene (MN 4)	Delfino 2004b

Bailon 1991; Böhme & Ilg 2003, Blain 2005; Bailon & Blain 2007; Agustí et al. 2009; Blain & Bailon 2010; Bailon & Augé 2012; Blain et al. 2016a; Klembara & Rummel 2016	this work	this work	this work	Böhme & Ilg 2003; Delfino 2004b; this work	Böhme & Ilg 2003; Delfino 2004b; this work	this work	this work	this work	this work	this work	this work	this work	this work	this work	this work	this work	this work	this work
Early Pleistocene	Miocene (Burdigalian, MN 3b)	Miocene (Burdigalian, MN 3b)	Early Miocene (MN 3)	Early Miocene (MN 4)	Miocene (MN 4)	Early Miocene (MN 4)	Early Miocene (MN 4)	Early Miocene (MN 3 or MN 4)	Miocene (Langhian, MN 5)	Miocene (Langhian, MN 5)	Miocene (Langhian, MN 6)	Middle Miocene (MN 6)	Middle Miocene (MN 6)	Middle Miocene (MN 6/MN 7+8)	Middle Miocene (MN 7+8)	Middle Miocene (MN 7+8)	Miocene (Serravallian, MN 8)	Middle/late Miocene (MN 7+8/MN 9)
Spain	Germany	Germany	Spain	Greece	Greece	Spain	Spain	Spain	Germany	Germany	Germany	Spain	Spain	Spain	Spain	Spain	Germany	Spain
Medas Islands	Stubersheim 2	Stubersheim 3	Sant Andreu de la Barca, Vallès Penedès Basin	Aliveri	Karydia 2	Els Casots, Vallès Penedès Basin	Sant Mamet, Vallès Penedès Basin	Rubí-Papiol, Vallès Penedès Basin	Gisseltshausen 1a	Gisseltshausen 1b	Griesbeckerzell 1a	Ca n'Almirall, Vallès Penedès Basin	La Gornal 1, Vallès Penedès Basin	Abocador de Can Mata, Vallès Penedès Basin	Sant Quirze, Vallès Penedès Basin	Trinxera del Ferrocarril, Vallès Penedès Basin	Kleineisenbach	Els Hostalets de Pierola, Vallès Penedès Basin
aff. <i>Dopasia</i> sp.; aff. Ophisaurus sp.; Ophisaurus sp.				Anguidae indet., Ophisaurus sp.; Pseudopus sp./Ophisaurus sp.	Anguidae indet.; <i>Pseudopus</i> sp./ <i>Ophisaurus</i> sp.													
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae
Ragesaurus medasensis	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.	non-Anguis Anguinae indet.

non-Anguis Anguinae indet.	Anguidae	Anguidae indet.	Autovía Orbital de Barcelona B- 40, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	Böhme & Ilg 2003; Alba et al. 2010; this work
non-Anguis Anguinae indet.	Anguidae		Can Llobateres, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	this work
non-Anguis Anguinae indet.	Anguidae		Can Missert, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
non-Anguis Anguinae indet.	Anguidae		Can Poncic, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
non-Anguis Anguinae indet.	Anguidae		Castell de Barberà, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
non-Anguis Anguinae indet.	Anguidae		Creu Conill 22, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
non-Anguis Anguinae indet.	Anguidae		El Repetidor, Vallès Penedès Basin	Spain	Late Miocene (MN 9 or MN 10)	this work
non-Anguis Anguinae indet.	Anguidae	Pseudopus sp./Ophisaurus sp.	Lefkon 1	Greece	Late Miocene (MN 10)	Delfino 2004b; this work
non-Anguis Anguinae indet.	Anguidae		Sant Miquel del Toudell, Vallés- Penedés Basin	Spain	Late Miocene (MN 10)	this work
non-Anguis Anguinae indet.	Anguidae		Trinxera Nord Autopista, Vallès Penedès Basin	Spain	Late Miocene (MN 10)	this work
non-Anguis Anguinae indet.	Anguidae		Viladecavalls, Vallès Penedès Basin	Spain	Late Miocene (MN 10)	this work
non-Anguis Anguinae indet.	Anguidae	Anguidae indet.	Fosso della Fittaia 2013	Italy	Late Miocene (MN 11)	Cirilli et al. 2014; Cirilli et al. 2016; this work
non-Anguis Anguinae indet.	Anguidae	Ophisaurus sp.; Ophisaurus s.1.	Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Villa et al. 2016b; this work
non-Anguis Anguinae indet.	Anguidae	Pseudopus sp./Ophisaurus sp.	Maramena 1	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
non-Anguis Anguinae indet.	Anguidae	Pseudopus sp./Ophisaurus sp.	Maramena 2	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
non-Anguis Anguinae indet.	Anguidae	Anguinae indet.	Moncucco Torinese	Italy	Latest Miocene (Messinian, p- ev2)	Colombero et al. 2014b; Colombero et al. 2017; this work
non-Anguis Anguinae indet.	Anguidae	Anguidae indet.	Ciabòt Cagna	Italy	Late Miocene (late Messinian)	Cavallo et al. 1993; Böhme & Ilg 2003; this work
non-Anguis Anguinae indet.	Anguidae	Anguidae indet.; <i>Pseudopus</i> sp./ <i>Ophisaurus</i> sp.	Komanos 1 High A (= Ptolemais 2 high A)	Greece	Early Pliocene (MN 14)	Böhme & Ilg 2003; Delfino 2004b; this work
non-Anguis Anguinae indet.	Anguidae	Anguidae indet.	Spilia 4	Greece	Late Pliocene	Delfino 2004b; this work
Anguinae indet. morphotype 1	Anguidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Čerňanský et al. 2015b; Klembara 2015; Klembara & Rummel 2016
Anguinae indet. morphotype 2	Anguidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Klembara 2015; Georgalis et al. 2017a
Anguinae indet. morphotype 3	Anguidae		Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Klembara 2015

& Ilg 2003; Klembara 2015	& Ilg 2003; Klembara 2015	& Ilg 2003; Klembara 2015	1984	1984	& Ilg 2003	1984	1984	1984	& Ilg 2003; Čerňanský et al. 2015b	. Rage 2000	vić et al. 2002	& IIg 2003; Carnevale et al. 2014; bero et al. 2014a	1984	1999a	& Ilg 2003	& Ilg 2003	& IIg 2003	vić et al. 2002	& Ilg 2003; Böhme & Vasilyan 2014; ra & Rummel 2016	2010b	¥
Böhme	Böhme	Böhme	Roček 1	Roček 1	Böhme	Roček 1	Roček 1	Roček 1	Böhme	Augé &	Jovanov	Böhme . Colomb	Roček 1	Böhme	Böhme	Böhme	Böhme	Jovanov	Böhme Klemba	Böhme	this wor
Lower Miocene (Burdigalian, MN 3a)	Lower Miocene (Burdigalian, MN 3a)	Lower Miocene (Burdigalian, MN 3a)	Early Miocene (Burdigalian, MN 4b)	Miocene (Aquitanian, MN 2a)	Middle Miocene (Langhian/Serravallian; MN 6)	Middle Miocene (MN 7+8)	Miocene (Messinian)	Early Miocene (Burdigalian, MN 4b)	Miocene (Burdigalian, MN 5)	Early Miocene (Burdigalian, MN 4b)	Miocene (Burdigalian, MN 5)	Miocene (Langhian/Serravallian, MN 6)	Middle Miocene (MN 7+8)	Late middle Miocene	Miocene (Burdigalian, MN 5)	Early Miocene (MN 4)					
Czech Republic	Germany	France	Serbia	Italy	Czech Republic	Germany	Czech Republic	Germany	Switzerland	Serbia	Austria	Germany	Spain								
Merkur North	Merkur North	Merkur North	Dolnice	Dolnice	Dolnice	Dolnice	Dolnice	Dolnice	Wiesbaden-Amöneburg	Sansan	Vračević, near Bogovadje monastery	Verduno	Dolnice	Sandelzhausen	Dolnice	Sandelzhausen	Mühlrüti Pt. 806	Vračević, near Bogovadje monastery	Gratkorn	Sandelzhausen	Els Casots, Vallès Penedès Basin
Ophisaurus sp.																			Ophisaurus spinari		
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae								
Anguinae indet. morphotype 4	Anguinae indet. morphotype 5	Anguinae indet. morphotype 6	Anguinae indet. morphotype II	Anguinae indet. morphotype III	Anguinae indet. morphotype IV	Anguinae indet. morphotype VI	Anguinae indet. morphotype VII	Anguinae indet. morphotype VIII	Anguinae indet.	Anguinae indet.	Anguinae indet.	Anguinae indet.	cf. Xestops sp.	Glyptosaurini indet.	Melanosaurini indet.	Glyptosaurinae indet.	?Glyptosaurinae indet.	?Gerrhonotinae indet.	Anguidae indet. (new form?)	Anguidae indet. nov. sp.	Anguidae new taxon?

this work	this work	this work	this work	this work	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Roček 1984	Roček 1984	Mörs 2002; Böhme 2003; Böhme & Ilg 2003; Čerňanský et al. 2016c	Mörs 2002; Čerňanský et al. 2016c	Böhme 2003; Böhme & Ilg 2003	Böhme & Ilg 2003	this work	this work	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003			
Middle Miocene (MN 6/MN 7+8)	Middle/late Miocene (MN 7+8/MN 9)	Late Miocene (MN 9)	Late Miocene (MN 9)	Late Miocene (MN 10)	Lower Miocene (Aquitanian, MN 2a)	Lower Miocene (Aquitanian, MN 2a)	Early Miocene (Burdigalian, MN 4b)	Early Miocene (Burdigalian, MN 4b)	Early middle Miocene (Langhian, MN 5)	Late Pliocene (Piacenzian, MN 16)	Lower Miocene (Aquitanian, MN 2a)	Miocene (Aquitanian)	Miocene (Burdigalian, MN 3b)	Miocene (Burdigalian, MN 3b)	Miocene (Burdigalian, MN 3)	Miocene (Burdigalian, MN 3)	Miocene (Burdigalian, MN 4a)	Miocene (Burdigalian, MN 4b)	Miocene (Burdigalian, MN 4b)	Miocene (Burdigalian, MN 4b)	Miocene (Burdigalian, MN 4b)
Spain	Spain	Spain	Spain	Spain	France	France	Czech Republic	Czech Republic	Germany	Germany	France	France	Germany	Germany	Germany	Germany	Germany	Germany	Germany	Germany	Germany
Abocador de Can Mata, Vallès Penedès Basin	Els Hostalets de Pierola, Vallès Penedès Basin	Can Sant Feliu, Vallès Penedes Basin	Castell de Barberà, Vallès Penedes Basin	Sant Miquel del Toudell, Vallés- Penedés Basin	Montaigu-le-Blin P23	Montaigu-le-Blin P23	Dolnice	Dolnice	Hambach 6C	Hambach 11	Le Gondailly	Mont Merle	Stubersheim 2	Stubersheim 3	Bissingen 1 (Wütherich)	Gögglingen	Petersbuch 7	Günzburg 1/1 Umgehungsstrasse schwarze Lage West	Günzburg 1/3 US oberster schokoladenbrauner Mergel	Günzburg 2/2 Umgehungstr höhere Bereiche der Sande	Günzburg 2/4 Umgehung tiefere Bereiche der Sande
									Ophisaurus sp.	Pseudopus pannonicus											
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae
Anguidae new taxon?	Anguidae new taxon?	Anguidae new taxon?	Anguidae new taxon?	Anguidae new taxon?	Anguidae indet. sp. 1	Anguidae indet. sp. 2	Anguidae indet. I	Anguidae indet. II	Anguidae indet. 1	Anguidae indet. 2	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.

shme 2003; Böhme & Ilg 2003	shme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003	öhme & Ilg 2003	öhme 2003; Kosma 2004	öhme & Ilg 2003	5hme & Ilg 2003	erňanský 2016	öhme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003	5hme 2003; Böhme & Ilg 2003; Abdul Aziz et . 2010	öhme 2002; Böhme & Ilg 2003; Tempfer 2003	öhme 2002; Böhme & Ilg 2003; Tempfer 2003	5hme 2002; Böhme 2003; Böhme & Ilg 2003; 9mpfer 2003	shme 2002; Böhme 2003; Böhme & Ilg 2003; smpfer 2003	öhme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003	öhme 2003; Böhme & Ilg 2003
Miocene (Burdigalian, MN 4b) B	Miocene (Burdigalian, MN 4b) B	Miocene (Burdigalian, MN 4b) B	Miocene (Burdigalian, MN 4b) B	Miocene (Burdigalian, MN 4b) B	Lower Miocene (Burdigalian, BMN 4b)	Miocene (Burdigalian, MN 4b) B	Miocene (Burdigalian, MN 4b) B	Early Miocene (MN 4) Č	Miocene (Burdigalian, MN 4) B	Miocene (Burdigalian, MN 4) B	Miocene (Burdigalian, MN 4b/5) B	Miocene (Burdigalian, MN 5) B	Miocene (Burdigalian, MN 5) B	Miocene (Burdigalian, MN 5) $\frac{B}{T}$	Miocene (Burdigalian, MN 5) T	Miocene (Burdigalian, MN 5) B	Miocene (Burdigalian, MN 5) B	Miocene (Burdigalian, MN 5) B	Early Miocene (Burdigalian, MN B)	Miocene (Burdigalian, MN 5) B	Miocene (Burdigalian, MN 5) B
Germany	Germany	Germany	Germany	Germany	Germany	Switzerland	Switzerland	Austria	Germany	Germany	Germany	Austria	Austria	Austria	Austria	Germany	Germany	Germany	Germany	Germany	Germany
Günzburg 2/5 Umgehung Sande im Süden Aufschluss	Günzburg 2/6 Umgehung Sande im Norden Außchluss	Illerkirchberg Fp.18 (Ho 8)	Langenau 2	Rauscheröd	Rembach, Bavarian Freshwater Molasse	Mauensee (Layer 47)	Mauensee (Layer 52)	Oberdorf	Petersbuch 4	Petersbuch 36	Offingen 2	Obergänserndorf, Korneuburg Basin	Teiritzberg (T1 = 001/D/C), Korneuburg Basin	Teiritzberg (T2/3), Korneuburg Basin	Teiritzberg (T2/5 = 001/Z/C/3), Korneuburg Basin	Arth 1b	Aumühle - Mitte (bei Walda)	Aumühle - Oben (bei Walda)	Dieshof b. Pöttmes - Sand	Eitensheim	Hesselohe bei Neuburg/Donau
Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae	Anguidae
Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.	Anguidae indet.

Anguidae indet.	Anguidae		Puttenhausen 2	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae		Puttenhausen classic (=Puttenhausen 1)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Abdul Aziz et al. 2010
Anguidae indet.	Anguidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme 2003; Böhme & Ilg 2003; Böhme 2010b
Anguidae indet.	Anguidae		Schiessen	Germany	Miocene (Burdigalian, MN 5)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Unterempfenbach 1d	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae		Teiritzberg (001/Z/D), Korneuburg Basin	Austria	Miocene (Burdigalian)	Böhme 2002; Böhme & Ilg 2003; Tempfer 2003
Anguidae indet.	Anguidae		Teiritzberg (001/Z/D/250-280), Korneuburg Basin	Austria	Miocene (Burdigalian)	Böhme 2002; Böhme & Ilg 2003; Tempfer 2003
Anguidae indet.	Anguidae		Ichenhausen 3	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Anguidae indet.	Anguidae		Ichenhausen 7	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Anguidae indet.	Anguidae		Offingen 4	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2010
Anguidae indet.	Anguidae		Puttenhausen C	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Anguidae indet.	Anguidae		Puttenhausen D	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Anguidae indet.	Anguidae		Puttenhausen E	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Anguidae indet.	Anguidae		Quinta das Pedreiras	Portugal	Miocene (Burdigalian)	Antunes & Rage 1974; Crespo 2001
Anguidae indet.	Anguidae		Quinta do Pombeiro	Portugal	Miocene (Burdigalian)	Antunes & Rage 1974; Crespo 2001
Anguidae indet.	Anguidae		Artesilla	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Ateca 1	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Ateca 3	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Banon 4	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Córcoles	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		San Roque 1	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Vargas 1A	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Vargas 4BB	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Bergheim	Germany	Miocene (Burdigalian/Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Ophisaurus sp.	Gaimersheim 2	Germany	Miocene (Burdigalian/Langhian, MN 5)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Ophisaurus sp.	Giggenhausen	Germany	Miocene (Burdigalian/Langhian)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae		Goldern bei Landshut	Germany	Miocene (Burdigalian/Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003

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Anguidae indet.	Anguidae	Caseton 3	/4	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Muela Alt	ta	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Grund nea	ar Hollabrunn, GRU-F-	Austria	Miocene (Langhian, MN 5)	Böhme & Ilg 2003; Miklas-Tempfer 2003
Anguidae indet.	Anguidae	Anried 2		Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Anried 4		Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Eberstette Sand)	sn 2 (Gastropoden-	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Edelbeure	en Maurerkopf	Germany	Early Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Gisseltsha	ausen 1a	Germany	Miocene (Langhian, MN 5)	this work
Anguidae indet.	Anguidae	Gisseltsha	ausen 1b	Germany	Miocene (Langhian, MN 5)	this work
Anguidae indet.	Anguidae	Petersbuc	h 41	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Ziemetsha	ausen 1f	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Mala Mili	iva, Despotovac	Serbia	Middle Miocene (MN 5)	Jovanović et al. 2002
Anguidae indet.	Anguidae	Bonlander	n	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Griesbeck	cerzell la	Germany	Miocene (Langhian, MN 6)	this work
Anguidae indet.	Anguidae	Laimering	5 4a	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Sallmanns	sberg	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Wannenw	aldtobel 2	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Ziemetsha	ausen 1b	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Ziemetsha	ausen 1g	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Anguidae indet.	Anguidae	Biberach-	Jordanbad	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Burgerbac	chtobel 1	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Georgens	gmünd	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Heggbach	1 am Buchhaldenberg	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Oberschöi	neberg 2B	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Oberschör	neberg 2C	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Oberschöt	neberg 2D	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Oberschör	neberg 2G	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Unterzell	la	Germany	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Fuente Sie	erra 2	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	La Col B		Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	La Col C		Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Las Umbr	ias 2	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Las Umbr	rias 7	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Las Umbr	ias 8	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Las Umbr	ias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Las Umbr	ias 16	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Moratilla	3	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Regajo 2		Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae	Somosaguas Sur	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
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Anguidae indet.	Anguidae	Valdemoros 1A	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Valdemoros 3B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Valdemoros 3E	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Valdemoros 7B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Valdemoros 7C	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Valdemoros 7E	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Valdemoros 9	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Valdemoros 11	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Vargas 6	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Vargas 8B	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Schmiedrued-Pyffrüti level 640, Swiss Molasse Basin	Switzerland	Early Middle Miocene (Langhian)	Böhme & Ilg 2003; Jost et al. 2015	
Anguidae indet.	Anguidae	Schmiedrued-Pyffrüti level 642, Swiss Molasse Basin	Switzerland	Early Middle Miocene (Langhian)	Böhme & Ilg 2003; Jost et al. 2015	
Anguidae indet.	Anguidae	Mühhrüti Pt. 806	Switzerland	Miocene (Langhian/Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Ornberg	Switzerland	Miocene (Serravallian, MN 6)	Böhme 2003; Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Lazarevac, Trstenik	Serbia	Middle Miocene (MN 6)	Jovanović et al. 2002	
Anguidae indet.	Anguidae	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme 2003; this work	
Anguidae indet.	Anguidae	Borjas	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Las Planas 5D	Spain	Miocene (Serravallian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Las Umbrias 20	Spain	Miocene (Serravallian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Furth 460 m	Germany	Middle Miocene	Abdul Aziz et al. 2008	
Anguidae indet.	Anguidae	Petersbuch 14	Germany	Miocene (Serravallian/Tortonian, MN 8/9)	Böhme 2003; Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Hillenloh	Germany	Miocene (Tortonian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Barrachina	Spain	Miocene (Tortonian)	Böhme & Ilg 2003	
Anguidae indet.	Anguidae	Casas Altas 75/76	Spain	Miocene (Tortonian)	Böhme & Ilg 2003	

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Anguidae indet.	Anguidae		Cascante 4	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Crevillente 2	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Crevillente 3	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Los Aguanaces 5B	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Masada Ruea 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Masia de la Roma 4B	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Masia de la Roma 4C	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Masia de la Roma 7	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Masia de la Roma 11	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Nombrevilla	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Puente Minero 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Puente Minero 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Puente Minero 8A	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Puente Minero 10	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Tortajada A	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Vivero de Pinos	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Viverro de la Rambla	Spain	Late Miocene (Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Valtorres 4-6	Spain	Miocene (Burdigalian/Tortonian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Morskaya 2	Russia	Miocene (Tortonian/Messinian, MN 12)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Ano Metochi 2	Greece	Late Miocene (Messinian, MN 13)	Georgalis et al. 2017a; this work
Anguidae indet.	Anguidae	Pseudopus sp./Ophisaurus sp.	Ano Metochi 3	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; Georgalis et al. 2017a; this work
Anguidae indet.	Anguidae	Pseudopus sp./Ophisaurus sp.	Maramena 1	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Anguidae indet.	Anguidae	Pseudopus sp./Ophisaurus	Maramena 2	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Anguidae indet.	Anguidae	Pseudopus sp./Ophisaurus	Maramena 3	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Anguidae indet.	Anguidae		Bunker de Vallecebro 3	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Concud 3	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		El Regajo 3	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		La Fontana 1 C	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		La Gloria 6	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Lomas de Casares 3	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Velillia 1a+1b	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Villalba Baja 2B	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Quinta da Silvéria	Portugal	Miocene	Antunes & Rage 1974; Crespo 2001
Anguidae indet.	Anguidae		Notio 1 (= Ptolemais 6C)	Greece	Early Pliocene (MN 15)	Böhme & Ilg 2003; Delfino 2004b; this work
Anguidae indet.	Anguidae		Ptolemais 97' 2	Greece	Pliocene (Zanclean)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Celadas 5	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Escorihuela D	Spain	Lower Pliocene (Zanclean)	Böhme & IIg 2003
0	0					0

Anguidae indet	Anonidae		I a Gloria 3	Snain	Farly Plincene (Zanclean)	Böhme & IIa 2003
Anguidae indet.	Anguidae		Orrios 1	Spain	Pliocene (Zanclean)	Böhme & IIg 2003
Anguidae indet.	Anguidae		Orrios 3	Spain	Pliocene (Zanclean)	Böhme & IIg 2003
Anguidae indet.	Anguidae		Orrios 9c	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Teruel desvio	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Velilia 3	Spain	Lower Pliocene (Zanclean)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Villalba Alta Rio 2a	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Villalba Alta Rio 4	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Escorihuela	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		La Recueja	Spain	Late Pliocene (Piacenzian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Loma del Castillo 3	Spain	Pliocene (Piacenzian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Fonelas P-1	Spain	Lower Pleistocene (Gelasian)	Böhme & Ilg 2003
Anguidae indet.	Anguidae		Tourkobounia 3	Greece	latest early/earliest Middle Pleistocene	this work
Anguidae indet.	Anguidae		Hitzlohe 1	Germany	Pleistocene	Schleich 1985b
Anguidae indet.	Anguidae		Schernfeld 1	Germany	Pleistocene	Schleich 1985b
Anguidae indet.	Anguidae		Weissenburg 7	Germany	Pleistocene	Schleich 1985b
Anguidae indet.	Anguidae	Pseudopus sp./Ophisaurus sp.	Kaiafa	Greece	Pleistocene	Delfino 2004b; this work
aff. Shinisaurus sp.	Shinisauridae		Wintershof West	Germany	Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003
Merkurosaurus ornatus	Shinisauria indet.		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b
Merkurosaurus ornatus	Shinisauria indet.	cf. Shinisaurus sp.	Merkur North	Czech Republic	Lower Miocene (Burdigalian, MN 3a)	Böhme & Ilg 2003; Klembara 2008; Rage 2013; Čerňanský et al. 2015b
cf. Merkurosaurus ornatus	Shinisauria indet.		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b
Merkurosaurus sp.	Shinisauria indet.	aff. Shinisaurus sp.	Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme & Ilg 2003; Villa & Delfino 2017; this work
Shinisauria indet.	Shinisauria indet.		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Böhme & Ilg 2003; Čerňanský et al. 2015b
Varanus (Varaneades) amnhophilis	Varanidae		Q1, Samos	Greece	Miocene (Turolian)	Conrad et al. 2012; Pérez-Ramos et al. 2016; Georgalis et al. 2017b; Ivanov et al. 2017
Varanus deserticolus	Varanidae		Csarnóta 2	Hungary	Pliocene (Zanclean, MN 15)	Jánossy 1986
Varanus deserticolus	Varanidae	Monitor deserticolus	Villány 6	Hungary	Lower Pleistocene	Jánossy 1986
Varanus hofmanni	Varanidae		Petersbuch 2, Bavarian Freshwater Molasse	Germany	Lower Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003; Kosma 2004; Ivanov et al. 2017
Varanus hofmanni	Varanidae		Petersbuch 28	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus hofmanni	Varanidae		Stätzling	Germany	Miocene (Langhian, MN 6)	Roger 1898; Hoffstetter 1943; Hoffstetter 1969; Estes 1983; Schleich 1985b; Böhme & Ilg 2003; Tempfer 2005; I'vanov et al. 2017

Varanus hofmanni	Varanidae		Unterzell 1a	Germany	Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus cf. V. hofmanni	Varanidae		Petersbuch 36	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus cf. V. hofmanni	Varanidae		Artenay	France	Early Miocene (Burdigalian)	Hoffstetter 1969; Estes 1983; Rage & Bailon 2005; Tempfer 2005; Ivanov et al. 2017
Varanus cf. V. hofmanni	Varanidae		Córcoles	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003; Rage & Bailon 2005; Ivanov et al. 2017
Varanus cf. V. hofmanni	Varanidae		Petersbuch 39	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus cf. V. hofmanni	Varanidae		Sant Miquel del Toudell, Vallés- Penedés Basin	Spain	Late Miocene (MN 10)	Hoffstetter 1969; Estes 1983
Varanus cf. V. hofmanni	Varanidae		Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Böhme 2003; Böhme & Ilg 2003; Tempfer 2005; Ivanov et al. 2017
Varanus cf. V. hofmanni	Varanidae		Polgárdi 5	Hungary	Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Venczel 2006
Varanus aff. V. hofmanni	Varanidae		Kalfa	Moldova	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus marathonensis	Varanidae		Batallones-3, Cerro de los Batallones	Spain	Late Miocene (Vallesian, MN 10)	Pérez-Ramos et al. 2016; Ivanov et al. 2017
Varanus marathonensis	Varanidae	Varanus atticus ; Varanus ?	Pikermi	Greece	Late Miocene	Gaudry 1862; Weithofer 1888; Nopcsa 1908; Hoffstetter 1943; Estes 1893; Pérez-Ramos et al. 2016; Georgalis et al. 2017b; Ivanov et al. 2017
Varanus marathonensis	Varanidae	Varanus deserticolus	Beremend 1	Hungary	Pliocene (MN 16)	Estes 1983; Rage 2013; Georgalis et al. 2017b; Ivanov et al. 2017
Varanus marathonensis	Varanidae		Csarnóta	Hungary	Pliocene	Sanz 1977; Estes 1983; Ivanov et al. 2017
Varanus aff. V. marathonensis	Varanidae	Varanus ex. aff. marathonis ; Varanus intermedius	Petralona Cave	Greece	Middle Pleistocene	Sickenberg 1971; Kretzoi & Poulianos 1981; Georgalis et al. 2017b
Varanus mokrensis	Varanidae	Varanus sp.	1/2001 Turtle Joint, Mokrá- Western Quarry	Czech Republic	Early Miocene (MN 4)	Ivanov et al. 2006; Ivanov et al. 2017
Varanus mokrensis	Varanidae	Varanus sp.	2/2003 Reptile Joint, Mokrá- Western Quarry	Czech Republic	Early Miocene (MN 4)	Ivanov et al. 2006; Ivanov et al. 2017
Varanus tyrasiensis	Varanidae	Varanus hofmanni	Varnitza	Moldova	Miocene (Tortonian, MN 9)	Lungu et al. 1983; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		San Roque 4A	Spain	Early Miocene (Burdigalian, MN 3)	Böhme & Ilg 2003; Delfino et al. 2013b; Bolet Mercadal 2014; Ivanov et al. 2017
Varanus sp.	Varanidae		Petersbuch 8	Germany	Miocene (Burdigalian, MN 4a)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Béon 1 (= Montréal-du-Gers)	France	Lower Miocene (Burdigalian, MN 4b)	Böhme & Ilg 2003; Rage & Bailon 2005; Delfino et al. 2013b; Bolet Mercadal 2014; Ivanov et al. 2017
Varanus sp.	Varanidae		Erkertshofen 2	Germany	Miocene (MN 4b)	Böhme & Ilg 2003; Ivanov et al. 2017

Varanus sp.	Varanidae		Petersbuch 5	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Petersbuch 36 (Coll. Rummel)	Germany	Miocene (Burdigalian, MN 4)	Böhme 2003; Böhme & Ilg 2003
Varanus sp.	Varanidae	cf. Testudo sp.?; Iberovaranus catalaunicus ; Ophisaurus sp.	Can Mas, Vallés-Penedés Basin	Spain	Early Miocene (Upper Burdigalian)	Hoffistetter 1969; Estes 1983; Böhme & Ilg 2003; Delfino et al. 2013b; Bolet Mercadal 2014; Ivanov et al. 2017
Varanus sp.	Varanidae	Iberovaranus cf. I. catalaunicus	Quinta das Pedreiras	Portugal	Miocene (Burdigalian)	Antunes & Rage 1974; Estes 1983; Crespo 2001; Böhme & Ilg 2003
Varanus sp.	Varanidae	Iberovaranus cf. I. catalaunicus	Quinta do Pombeiro	Portugal	Miocene (Burdigalian)	Antunes & Rage 1974; Estes 1983; Crespo 2001; Böhme & Ilg 2003
Varanus sp.	Varanidae	aff. Iberovaranus sp.	Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003; Delfino et al. 2013b; Bolet Mercadal 2014; Ivanov et al. 2017
Varanus sp.	Varanidae	Iberovaranus cf. I. catalaunicus	Ateca 1	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003; Delfino et al. 2013b; Bolet Mercadal 2014; Ivanov et al. 2017
Varanus sp.	Varanidae	cf. Iberovaranus sp.	San Marcos	Spain	Early Miocene (Burdigalian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae	cf. Iberovaranus sp.	Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Varanus sp.	Varanidae		Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Petersbuch 41	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Ziemetshausen	Germany	Miocene (Langhian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae	Iberovaranus cf. I. catalaunicus	Amor	Portugal	Middle Miocene (MN 5)	Antunes & Mein 1981; Crespo 2001; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Hohenraunau b. Krumbach	Germany	Miocene (Langhian, MN 6)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Laimering 3	Germany	Middle Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Litke 2	Hungary	Miocene (Langhian, MN 6)	Böhme & Ilg 2003; Čerňanský et al. 2016c; Ivanov et al. 2017
Varanus sp.	Varanidae		Häder	Germany	Miocene (MN 6)	Böhme 2003
Varanus sp.	Varanidae		Petersbuch 68	Germany	Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Las Umbrias 11	Spain	Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Las Umbrias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Las Umbrias 18	Spain	Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Las Umbrias 19	Spain	Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae	aff. Iberovaranus sp.	Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Petersbuch 31 - oben	Germany	Miocene (Langhian/Serravallian, MN 7)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Gratkorn	Austria	Late middle Miocene (MN 7+8)	Böhme & Ilg 2003; Böhme & Vasilyan 2014; Ivanov et al. 2017

Varanus sp.	Varanidae		Toril 3B	Spain	Middle Miocene (Serravallian)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Petersbuch 18	Germany	Miocene (Tortonian, MN 8/9)	Böhme 2003; Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae	Varanus lungui	Bujor	Moldova	Miocene (MN 9b)	Zerova & Chkhikvadze 1986; Ivanov et al. 2017
Varanus sp.	Varanidae		Bushor 1	Moldova	Miocene (Tortonian, MN 9)	Böhme & Ilg 2003
Varanus sp.	Varanidae		Can Llobateres, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae		Mytilinii-3, Samos	Greece	Miocene (MN 12)	Koufos 2006
Varanus sp.	Varanidae	Varanidae indet.	Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Delfino 2002; Böhme & Ilg 2003; Rook et al. 2005; Rook & Delfino 2007; Delfino et al. 2013a; Rook et al. 2015; Villa et al. 2016b; Ivanov et al. 2017; this work
Varanus sp.	Varanidae		El Arquillo 1	Spain	Late Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Ivanov et al. 2017
Varanus sp.	Varanidae	Varanus semjonovi	Cherevichnoje	Ukraine	Late Miocene (MN 13)	Zerova & Chkhikvadze 1986; Ivanov et al. 2017
Varanus sp.	Varanidae		Maramena 1	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Varanus sp.	Varanidae		Maramena 3	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
Varanus sp.	Varanidae		Verduno	Italy	Miocene (Messinian)	Böhme & Ilg 2003; Carnevale et al. 2014; Colombero et al. 2014a: Ivanov et al. 2017
Varanus sp.	Varanidae	Lacertilia indet.	Goriach	Germany	Upper Miocene	Estes 1983
Varanus sp.	Varanidae	cf. Varanus type B	Sète	France	Middle Pliocene (MN 15)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Ivanov et al. 2017
Varanus sp.	Varanidae		Layna	Spain	Middle Pliocene (MN 15)	Sanz 1977; Estes 1983; Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Ivanov et al. 2017
Varanus sp.	Varanidae	cf. Varanus type A	Moreda	Spain	Middle Pliocene (MN15)	Bailon 1991; Bailon 1992; Böhme & Ilg 2003; Bailon & Blain 2007; Ivanov et al. 2017
Varanus sp.	Varanidae	cf. Varanus type B	Balaruc II	France	Middle/late Pliocene (MN 15/16)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007; Rage 2013; Ivanov et al. 2017
Varanus sp.	Varanidae		Granada	Spain	Middle/late Pliocene	Crespo 2001
Varanus sp.	Varanidae		Kotlovina, middle level	Ukraine	Lower Pleistocene (Gelasian, MN 17)	Böhme & Ilg 2003
Varanus sp.	Varanidae		Tourkobounia 5	Greece	latest early/earliest Middle Pleistocene	Delfino 2004b; Georgalis et al. 2017b; Ivanov et al. 2017; this work
?Varanus sp.	Varanidae		Rauscheröd	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1985b
?Varanus sp.	Varanidae		Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Schleich 1985b
?Varanus sp.	Varanidae		Vargas 11	Spain	Middle Miocene (Langhian)	Böhme & Ilg 2003; Ivanov et al. 2017

Pomel 1835; monstener 1944; Estes 1965	Lower Ivilocene	France	Langy		Laceruna inder.	Sauromorus tacertmus
POMEL 1000; FIOUSICHUEL 1744, ESUES 1700 Domoi 1062: Understation 1044: Estas 1002	Lower Miccene	France	Marcoun r		"T accertitia" indet	Sauromorus amorgaus
Pomel 1853; Hoffstetter 1944; Estes 1983	Lower Miocene	France	Langy		"Lacertilia" indet.	Sauromorus ambiguus
this work	Late Miocene (MN 13/14)	Greece	Maramena 1		Anguimorpha indet.	Anguimorpha indet.
Augé & Rage 2000	Middle Miocene (Langhian/Serravallian; MN 6)	France	Sansan		Anguimorpha indet.	Anguimorpha indet.
this work	Miocene (Langhian, MN 5)	Germany	Gisseltshausen 1a		Anguimorpha indet.	Anguimorpha indet.
Böhme & Ilg 2003	Miocene (Langhian, MN 5)	Germany	Anried 1		Anguimorpha indet.	Anguimorpha indet.
Böhme & Ilg 2003	Miocene (Burdigalian, MN 5)	Germany	Sandelzhausen		Anguimorpha indet.	Anguimorpha indet.
this work	Miocene (Burdigalian, MN 3b)	Germany	Stubersheim 3		Anguimorpha indet.	Anguimorpha indet.
Böhme & Ilg 2003; Čerňanský et al. 2015b	Miocene (Aquitanian, MN 2a)	Germany	Wiesbaden-Amöneburg		Platynota indet.	Platynota indet.
Böhme & Ilg 2003; Abdul Aziz et al. 2008	Middle Miocene	Germany	Furth 460 m	?Varanidae indet.	Varanidae	aff. Varanidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian/Langhian)	Spain	Muela Alta		Varanidae	aff. Varanidae indet.
Delfino 2004b; this work	Late Pliocene	Greece	Spilia 4	Varanus sp.	Varanidae	cf. Varanidae indet.
Böhme & Ilg 2003; Villa & Delfino 2017; this work	Miocene (Serravallian, MN 8)	Germany	Kleineisenbach		Varanidae	Varanidae indet.
Hoffstetter 1943; Hoffstetter 1969; Estes 1893; Bailon 1991; Rage & Bailon 2005; Ivanov et al. 2017	Middle Miocene (MN 7+8)	France	La Grive-Saint-Alban	Necrosaurus cayluxi ; "Palaeovaranus" cayluxi ; Varanus cf. V. hofmanni; Varanus sp.	Varanidae	Varanidae indet.
Böhme & Ilg 2003; Hír & Venczel 2005; Ivanov et al. 2017	Miocene (Tortonian, MN 6)	Romania	Subpiatră 2/1R		Varanidae	Varanidae indet.
Hoffstetter 1969	Middle Miocene (MN 5)	France	Pontigné		Varanidae	Varanidae indet.
Hoffstetter 1969; Estes 1983; Bailon 1991; Rage & Bailon 2005; Ivanov et al. 2017	Lower Miocene	France	Vieux-Collonges	Varanus cf. V. hofmanni	Varanidae	Varanidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian)	Spain	Artesilla		Varanidae	Varanidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian, MN 5)	Germany	Schiessen		Varanidae	Varanidae indet.
this work	Early Miocene (MN 4)	Spain	Els Casots, Vallès Penedès Basin		Varanidae	Varanidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian, MN 3)	Germany	Bissingen 1 (Wütherich)		Varanidae	Varanidae indet.
Böhme 2003; Böhme & Ilg 2003	Miocene (Langhian, MN 6)	Germany	Petersbuch 39	aff. Iberovaranus sp.; cf. Iberovaranus sp.	Varanidae	aff. Varanus sp.
Böhme 2003; Böhme & Ilg 2003	Miocene (Burdigalian, MN 4)	Germany	Petersbuch 38-Boden	cf. Iberovaranus sp.	Varanidae	cf. Varanus sp.
Böhme 2003; Böhme & Ilg 2003	Miocene (Burdigalian, MN 4)	Germany	Petersbuch 36 II	cf. Iberovaranus sp.	Varanidae	cf. Varanus sp.
Schleich 1985b; Böhme 2003; Böhme & Ilg 2003; Kosma 2004	Lower Miocene (Burdigalian, MN 4a)	Germany	Petersbuch 2, Bavarian Freshwater Molasse	?Varanus sp.; cf. Iberovaranus sp.	Varanidae	cf. Varanus sp.

Roček 1984	Roček 1984	Roček 1984	Jánossy 1986	Jánossy 1986	Benítez de Lugo Enrich et al. 2015	Félix & Montori 1987	Schleich 1985b	Schleich 1985b	this work	this work	Schleich 1985b	Schleich 1985b	Schleich 1985b	Schleich 1985b	Delfino 2004b; this work	Delfino 2004b	this work	this work	Murelaga et al. 2002	Murelaga et al. 2002	Schleich 1988b	Schleich 1988b	this work	this work	Schleich 1985b	this work	Böhme & Ilg 2003	Augé & Rage 2000	this work	Jovanović et al. 2002
Early Miocene (Burdigalian, MN 4b)	Early Miocene (Burdigalian, MN 4b)	Early Miocene (Burdigalian, MN 4b)	Lower Pleistocene	Lower Pleistocene	Holocene	Plio-Pleistocene	Miocene (MN 2)	Miocene (MN 2/3)	Miocene (Burdigalian, MN 3b)	Miocene (Burdigalian, MN 3b)	Miocene (MN 4b)	Miocene (MN 4)	Miocene (MN 4)	Miocene (MN 4)	Early Miocene (MN 4)	Middle Miocene (MN 4)	Early Miocene (MN 4)	Early Miocene (MN 4)	Early Miocene (Burdigalian)	Early Miocene (Burdigalian)	Lower Miocene	Lower Miocene	Miocene (Langhian, MN 5)	Miocene (Langhian, MN 5)	Miocene (MN 5/6)	Middle Miocene (MN 6)	Miocene (Langhian)	Middle Miocene (Langhian/Serravallian; MN 6)	Middle Miocene (MN 6/MN 7+8)	Middle Miocene (MN 7+8)
Czech Republic	Czech Republic	Czech Republic	Hungary	Hungary	Spain	Spain	Germany	Germany	Germany	Germany	Germany	Germany	Germany	Germany	Greece	Greece	Spain	Spain	Spain	Spain	Germany	Germany	Germany	Germany	Germany	Spain	Germany	France	Spain	Serbia
Dolnice	Dolnice	Dolnice	Beremend 11	Beremend 11	Castillejo del Bonete	Venta Micena-2	Mauren 1	Übermatzhofen 1	Stubersheim 2	Stubersheim 3	Erkertshofen 2	Erkertshofen 3	Erkertshofen 4	Raithenbuch 2	Aliveri	Karydia 3	Els Casots, Vallès Penedès Basin	Sant Mamet, Vallès Penedès Basin	Barranco de Tudela 3, Bardenas Reales, Navarra	Rincón del Bu, Bardenas Reales, Navarra	Budenheim	Weisenau	Gisseltshausen 1a	Gisseltshausen 1b	Rothenstein 1	La Gornal 1, Vallès Penedès Basin	Biberach-Jordanbad	Sansan	Abocador de Can Mata, Vallès Penedès Basin	Crnča village, Levač
							Sauria indet.	Sauria indet.			Sauria indet.	Sauria indet.	Sauria indet.	Sauria indet.											Sauria indet.					Sauria indet.
"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.
"Lacertilia" indet. I	"Lacertilia" indet. II	"Lacertilia" indet. III	"Lacertilia" indet. sp. I	"Lacertilia" indet. sp. II	"Lacertilia" indet. sp. B	"Lacertilia" indet. medium size	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.	"Lacertilia" indet.

"Lacertilia" indet.	"Lacertilia" indet.		Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Can Llobateres, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Can Missert, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Can Sant Feliu, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Castell de Barberà, Vallès Penedes Basin	Spain	Late Miocene (MN 9)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Ecoparc de Can Mata, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Biodrak	Greece	Late Miocene (MN 10)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Lefkon 1	Greece	Late Miocene (MN 10)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Sant Miquel del Toudell, Vallés- Penedés Basin	Spain	Late Miocene (MN 10)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Kohfidisch	Austria	Upper Miocene (Tortonian, MN 11)	Tempfer 2005
"Lacertilia" indet.	"Lacertilia" indet.	Lacertidae indet.	Fosso della Fittaia 2013	Italy	Late Miocene (MN 11)	Cirilli et al. 2014; Cirilli et al. 2016; this work
"Lacertilia" indet.	"Lacertilia" indet.	Sauria indet.	Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Delfino 2002; Rook et al. 2005; Rook & Delfino 2007; Villa et al. 2016b; this work
"Lacertilia" indet.	"Lacertilia" indet.	Squamata indet.	Ano Metochi 2	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; Georgalis et al. 2017a
"Lacertilia" indet.	"Lacertilia" indet.	Squamata indet.	Ano Metochi 3	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; Georgalis et al. 2017a
"Lacertilia" indet.	"Lacertilia" indet.		Monasteri	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Tomea Eksi - TO 1 (= Ptolemais 1a)	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Tomea Eksi - TO 2 (= Ptolemais 1b)	Greece	Late Miocene (Messinian, MN 13)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Ciabòt Cagna	Italy	Late Miocene (late Messinian)	Cavallo et al. 1993; Böhme & Ilg 2003; this work
"Lacertilia" indet.	"Lacertilia" indet.		Moncucco Torinese	Italy	Latest Miocene (Messinian, p- ev2)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Maramena 1	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Maramena 2	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Maramena 3	Greece	Late Miocene (MN 13/14)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Biancone, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Bosco, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002

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"Lacertilia" indet.	"Lacertilia" indet.		Cantatore, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Cava Fina, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Cava Pirro, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Chirò, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Falcone, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Gargano "Terre Rosse" (F - Coll. Firenze)	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Pizzicoli, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Rinascita, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		San Giovannino, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		San Nazario, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Tre Fossi, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Ses Fontanelles, Ibiza	Spain	Late Miocene/early Pliocene	Bover et al. 2014
"Lacertilia" indet.	"Lacertilia" indet.		Rema Aslan 1	Greece	Miocene/Pliocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Trilofon	Greece	Miocene/Pliocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Maritsa A	Greece	Early Pliocene (MN 14)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Vorio 3 (VOR 3/3A)	Greece	Early Pliocene (MN 14)	Delfino 2004b
"Lacertilia" indet.	"Lacertilia" indet.		Notio 1 (= Ptolemais 6C)	Greece	Early Pliocene (MN 15)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.	Sauria indet.	Musaitu (Musaid, Musait)	Moldova	Pliocene (MN 15)	Nadachowski et al. 2006
"Lacertilia" indet.	"Lacertilia" indet.		Apolakkia 2	Greece	Pliocene (Ruscinian)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Tourkobounia 1	Greece	Late Pliocene (MN 16)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Capo Mannu D1 Local Fauna (= Mandriola)	Italy	Late Pliocene (Piacenzian)	Böhme & Ilg 2003; Delfino et al. 2011
"Lacertilia" indet.	"Lacertilia" indet.		Spilia 4	Greece	Late Pliocene	Delfino 2004b; this work

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"I acertilia" indet	"I acertilia" indet		Kastoria	Greece	Plincene	this work
"Lacertilia" indet.	"Lacertilia" indet.		Linni 6	Greece	Pliocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Venta Micena-1	Spain	Plio-Pleistocene	Félix & Montori 1987
"Lacertilia" indet.	"Lacertilia" indet.		Tourkobounia 2	Greece	earliest early Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Rivoli Veronese	Italy	Early Pleistocene (Gelasian; MN 17)	this work
"Lacertilia" indet.	"Lacertilia" indet.		Russel-Tiglia-Egypte pit, Tegelen	The Netherlands	Early Pleistocene (Gelasian)	this work
"Lacertilia" indet.	"Lacertilia" indet.	Sauria indet.	Cava VI 3, Monte Tuttavista	Italy	Pleistocene (Calabrian)	Rook et al. 2003; Abbazzi et al. 2004
"Lacertilia" indet.	"Lacertilia" indet.		Almenara Casablanca 3	Spain	Late early Pleistocene (Calabrian)	Blain et al. 2007
"Lacertilia" indet.	"Lacertilia" indet.		Osztramos 8	Hungary	Lower Pleistocene	Jánossy 1986
"Lacertilia" indet.	"Lacertilia" indet.		Cava dell'Erba, Pirro Nord	Italy	Lower Pleistocene	Delfino & Bailon 2000
"Lacertilia" indet.	"Lacertilia" indet.		Cava Pirro, Pirro Nord	Italy	Lower Pleistocene	Delfino & Bailon 2000
"Lacertilia" indet.	"Lacertilia" indet.		Miniera della Polveriera, Monte Argentario	Italy	Lower Pleistocene	Böhme & Ilg 2003; Siori et al. 2014
"Lacertilia" indet.	"Lacertilia" indet.		Tourkobounia 3	Greece	latest early/earliest Middle Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Tourkobounia 5	Greece	latest early/earliest Middle Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Castle Hill-Hilton, Budapest Castle Hill	Hungary	Middle Pleistocene	Jánossy 1986
"Lacertilia" indet.	"Lacertilia" indet.		Rock shelter no. 1, Uppony	Hungary	Middle Pleistocene	Jánossy 1986
"Lacertilia" indet.	"Lacertilia" indet.	Sauria indet.	Cava XI - Canidae, Monte Tuttavista	Italy	Middle Pleistocene	Rook et al. 2003; Abbazzi et al. 2004
"Lacertilia" indet.	"Lacertilia" indet.	Sauria indet.	Cava XI 3, Monte Tuttavista	Italy	Middle Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004
"Lacertilia" indet.	"Lacertilia" indet.		Riparo di Visogliano	Italy	Middle Pleistocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Valdemino Cave	Italy	Middle Pleistocene	Delfino 2002; Delfino 2004c
"Lacertilia" indet.	"Lacertilia" indet.		Alcamo Cappuccini	Italy	Middle/late Pleistocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		K 22, San Vito lo Capo	Italy	Middle/late Pleistocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Higueral de Valleja Cave	Spain	Upper Pleistocene (late Paleolithic)	Böhme & Ilg 2003; Jennings et al. 2009
"Lacertilia" indet.	"Lacertilia" indet.		Vanguard Cave, Gibraltar	England	Upper Pleistocene	Böhme & Ilg 2003
"Lacertilia" indet.	"Lacertilia" indet.		Arnissa	Greece	Late Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.	Lacertidae indet.	Liko A	Greece	Upper Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.	Lacertidae indet.	Liko BA	Greece	Upper Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Pili B	Greece	Upper Pleistocene	this work
"Lacertilia" indet.	"Lacertilia" indet.	?Agama sp.; Uromastyx aegyptia ; Uromastyx spinipes	Simonelli Cave, Crete	Greece	Late Pleistocene	Mangili 1980; Estes 1983; Delfino et al. 2008b; Georgalis et al. 2016a
"Lacertilia" indet.	"Lacertilia" indet.		Porlyuk	Hungary	Upper Pleistocene	Jánossy 1986
"Lacertilia" indet.	"Lacertilia" indet.		Poroslyuk of Ballavölgy	Hungary	Upper Pleistocene	Jánossy 1986

"Lacertilia" indet.	"Lacertilia" indet.	Varanus marathonensis; Varanus sp.	Arene Candide Cave	ltaly	Upper Pleistocene	Morelli 1891; Estes 1983; Holman 1998; Delfino 2002; Böhme & Ilg 2003; Georgalis et al. 2017b
"Lacertilia" indet.	"Lacertilia" indet.		Cava VI Banco 6, Monte Tuttavista	ltaly	Upper Pleistocene	Abbazzi et al. 2004
"Lacertilia" indet.	"Lacertilia" indet.	Sauria indet.	Cava VII 2, Monte Tuttavista	ltaly	Upper Pleistocene	Rook et al. 2003; Abbazzi et al. 2004
"Lacertilia" indet.	"Lacertilia" indet.		Porto Leccio	Italy	Late Pleistocene	Delfino 2002
"Lacertilia" indet.	"Lacertilia" indet.		Kaiafa	Greece	Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.	Lacertidae indet.	Karpathos	Greece	Pleistocene	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Agia Loucas (Evia)	Greece	Pleistocene (?)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		Anabussos	Greece	Pleistocene (?)	Delfino 2004b; this work
"Lacertilia" indet.	"Lacertilia" indet.		K 22, San Vito lo Capo	ltaly	Late Pleistocene (or Holocene)	Delfino 2002; Böhme & Ilg 2003
"Lacertilia" indet.	"Lacertilia" indet.		Caverna dei Parmorari	ltaly	Upper Pleistocene/Holocene	this work
"Lacertilia" indet.	"Lacertilia" indet.		Riparo del Castello	ltaly	Late Pleistocene/Holocene	Delfino 2002
Squamata indet. 1	Squamata indet.		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Squamata indet. 2	Squamata indet.		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Squamata indet. 3	Squamata indet.		Oberdorf	Austria	Early Miocene (MN 4)	Čerňanský 2016
Squamata indet.	Squamata indet.		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian, MN 2a)	Čerňanský et al. 2015b
Squamata indet.	Squamata indet.		Lapsarna, Lesvos Petrified Forest, Lesvos	Greece	Early Miocene	Vasileiadou et al. 2017

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	Bibliography	Böhme 1999b; Böhme 2003; Böhme & Ilg 2003; Miklas-Tempfer 2003	Böhme & Ilg 2003; Miklas-Tempfer 2003	Böhme 2003; Böhme & Ilg 2003	Böhme 2003; Böhme & Ilg 2003	Schleich 1985a; Schleich 1985b; Böhme 1999b; Böhme & Ilg 2003; Miklas-Tempfer 2003	Böhme 2003; Böhme & Ilg 2003	Böhme & Ilg 2003	Böhme & Ilg 2003; Miklas-Tempfer 2003	Bailon 1991; García-Porta et al. 2002; Böhme & Ilg 2003; Bailon & Blain 2007	Bailon 1991; García-Porta et al. 2002; Blain 2005; Blain 2009	Barbadillo et al. 1997	Böhme & Ilg 2003; Blain 2005; Blain 2009	Crespo 2001; García-Porta et al. 2002	Böhme & IIg 2003; Blain 2005; Bailon & Blain 2007; Blain 2009; Čerňanský et al. 2015a	Böhme & Ilg 2003; Blain 2005; Čerňanský et al. 2015a	Böhme & Ilg 2003	Böhme & Ilg 2003; Blain 2005; Blain 2009	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007; Blain et al. 2007; Blain 2009; Čerňanský et al. 2015a	Böhme & Ilg 2003; Blain 2005; Bailon & Blain 2007	Böhme & Ilg 2003; Blain 2005; Blain et al. 2008a; Blain 2009; Blain 2012-2014
	Age	Miocene (Burdigalian, MN 3b)	Middle Miocene (Langhian, MN 5)	Miocene (Langhian, MN 5)	Miocene (Langhian, MN 6)	Miocene (Langhian, MN 6)	Miocene (Langhian, MN 6)	Miocene (Langhian/Serravallian)	Middle Miocene (Langhian, MN 5)	Middle Pliocene (MN 15)	Late Pliocene (MN 16)	Late Pliocene (MN 16)	Late Pliocene/early Pleistocene (MN 16)	Plio-Pleistocene	Early Pleistocene (Gelasian)	Early Pleistocene (Gelasian)	Pleistocene (Gelasian)	Early Pleistocene (Gelasian)	Late early Pleistocene (Calabrian)	Early Pleistocene (Calabrian)	Early Pleistocene (Calabrian)
	Country	Germany	Austria	Germany	Germany	Germany	Germany	Germany	Austria	France	France	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain
Amphisbaenia	Locality	Stubersheim 3	Mühlbach am Manhartsberg	Derching 1b (unten)	Gallenbach 2b	Goldberg 9	Laimering 2a	Steinberg	Mühlbach am Manhartsberg	Sète	Seynes	Rosellón	Cova Bonica	Guadix/Granada	Almenara Casablanca 1	Almenara Casablanca 4	Galera-2	Vallirana	Almenara Casablanca 3	Barranco León 5	Cueva Victoria
	Previous identifications								cf. Blanus cf. B. antiquus	Blanus cf. B. cinereus					Blanus sp.						
	Family	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae
	Taxon	Blanus antiquus	Blanus antiquus	Blanus antiquus	Blanus antiquus	Blanus antiquus	Blanus antiquus	Blanus antiquus	Blanus cf. B. antiquus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus

 Bailon 1991; Barbadillo et al. 1997; García-Porta et al. 2002; Böhme & Ilg 2003; Blain 2005; Albert et al. 2007; Bailon & Blain 2007; Blain 2009; Čerňanský & Venczel 2011; Bolet Mercadal 2014; Bolet et al. 2014; Blain et al. 2016; Čerňanský et al. 2016a 	Böhme & Ilg 2003; Pacheco et al. 2011	Barbadillo 1989; Holman 1998; Crespo 2001; Böhme & Ilg 2003; Blain 2005; Agusti et al. 2009: Blain 2009	Holman 1998; Böhme & Ilg 2003	Crespo 2001; García-Porta et al. 2002	Böhme & Ilg 2003; Blain 2005; Blain 2009; Rodríguez et al. 2011; Cuenca-Bescós et al. 2015	Barroso Ruíz et al. 2011	Böhme & Ilg 2003	Crespo 2001; Crespo 2002; García-Porta et al. 2002; Böhme & Ilg 2003	Gleed-Owen 2001; Böhme & Ilg 2003	Crespo 2001; Crespo 2002; Böhme & Ilg 2003	Böhme & Ilg 2003	Crespo 2001; García-Porta et al. 2002	Barbadillo 1989; Holman 1998; Crespo 2001; Böhme & Ilg 2003	Sánchez et al. 2005	Blain 2005	Böhme & Ilg 2003; Blain 2005; Blain 2009	Böhme & Ilg 2003; Blain 2005; Blain 2009	Holman 1998; Böhme & Ilg 2003	Crespo 2001	Crespo 2001	Crespo 2001	Marquina et al. 2017
Early Pleistocene	Lower Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle Pleistocene	Middle/Upper Pleistocene (MIS 5e)	Middle/Upper Pleistocene	Upper Pleistocene (middle Paleolithic)	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene	Upper Pleistocene/Holocene	Middle Pliocene (MN 15)	Pliocene/Pleistocene (Zanclean/Gelasian)	Pleistocene (Gelasian)	Middle Pleistocene	Middle Pleistocene	Upper Pleistocene	Holocene	Upper Pleistocene/Holocene (middle Palaeolithic, MIS 3)
Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Portugal	England	Portugal	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain
Medas Islands	Sierra del Chaparral	Cúllar de Baza 1	Grajas Cave	Málaga	Trinchera Dolina TD8b, Gran Dolina	Cueva del Angel	Cueva del Agua	Gruta da Figueira Brava	Vanguard Cave, Gibraltar	Guia	Cueva del Boquete de Zafarraya	Málaga	Pontones	La Ventana Cave	Gorafe 27	Barranco del Agua-6	Calella-Y	Ponton	Madrid	Madrid	Pontones	El Salt
									cf. Blanus cinereus									cf. Blanus cinereus				
Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae	Blanidae
Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cinereus	Blanus cf. B. cinereus	Blanus cf. B. cinereus	Blanus cf. B. cinereus	Blanus cf. B. cinereus	cf. Blanus cinereus	cf. Blanus cinereus	cf. Blanus cinereus	Blanus cinereus s.l.

Blanus gracilis	Blanidae		Oschiri	Italy	Miocene (Aquitanian, MN 1/MN 2b)	Böhme & Ilg 2003; Venczel & Sanchíz 2006; Delfino & Rook 2008; Zoboli & Pillola 2017
Blanus gracilis	Blanidae	Blanus antiquus ; Blanus sp.; Omoiotyphlops gracilis	Dolnice	Czech Republic	Early Miocene (Burdigalian, MN 4b)	Roček 1984; Böhme 1999b; Böhme 2003; Böhme & Ilg 2003; Venczel & Sanchíz 2006; Bolet Mercadal 2014; Bolet et al. 2014
Blanus cf. B. gracilis	Blanidae		Tauț	Romania	Late middle Miocene (Serravallian, MN 8)	Böhme & Ilg 2003; Venczel & Știucă 2008; Georgalis et al. 2016c
Blanus mendezi	Blanidae		Abocador de Can Mata, Vallès Penedès Basin	Spain	Middle Miocene (MN 6/MN 7+8)	Böhme & Ilg 2003; Bolet Mercadal 2014; Bolet et al. 2014
Blanus thomaskelleri	Blanidae		Wiesbaden-Amöneburg	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003; Čerňanský et al. 2015c
Blanus thomaskelleri	Blanidae	Blanus sp.	Merkur North	Czech Republic	Lower Miocene (Burdigalian)	Böhme & Ilg 2003; Čerňanský & Venczel 2011; Rage 2013; Čerňanský et al. 2015c
Blanus sp. 1	Blanidae		Caseton 2B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Las Umbrias 1	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Valdemoros 3F	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Valdemoros 8B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Valdemoros 8C	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Vargas 6	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Las Planas 5C	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Paje 1	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Paje 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Toril 2	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Toril 3A	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		Toril 3B	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 1	Blanidae		La Gloria 4	Spain	Early Pliocene (Zanclean)	Böhme & Ilg 2003
Blanus sp. 2	Blanidae		Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Blanus sp. 2	Blanidae		Las Umbrias 12	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp. 2	Blanidae		Las Umbrias 20	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 2	Blanidae		Toril 3A	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp. 2	Blanidae		Toril 3B	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Chavroches P1	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Blanus sp.	Blanidae		Chavroches P1C2	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Blanus sp.	Blanidae		Montaigu-le-Blin, Le Vendant a Sorex	France	Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Blanus sp.	Blanidae		Montaigu-le-Blin P23	France	Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Blanus sp.	Blanidae		Treuchtlingen 1	Germany	Miocene (Aquitanian/Burdigalian)	Böhme & Ilg 2003
Blanus sp.	Blanidae	?Blanus sp.	Rembach	Germany	Miocene (Burdigalian, MN 4b)	Schleich 1985b; Böhme 2003; Böhme & Ilg 2003

Blanus sp.	Blanidae		2/2003 Reptile Joint, Mokrá- Western Quarry	Czech Republic	Early Miocene (MN 4)	Ivanov et al. 2006
Blanus sp.	Blanidae		Els Casots, Vallès Penedès Basin	Spain	Early Miocene (MN 4)	this work
Blanus sp.	Blanidae		Sant Mamet, Vallès Penedès Basin	Spain	Early Miocene (MN 4)	this work
Blanus sp.	Blanidae		Niederaichbach (links)	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Buñol	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Córcoles	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Retama Loranca Basin	Spain	Miocene (Burdigalian/Langhian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Laimering 3	Germany	Miocene (Langhian, MN 6)	Böhme 2003; Böhme & Ilg 2003
Blanus sp.	Blanidae		Caseton 1A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Caseton 2B	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Las Umbrias 11	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Las Umbrias 19	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Valdemoros 7F	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Vargas 7	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Villafeliche 4A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Diamesen	Dlonidoo	Blowne antionne	Concorn	Eronoo	Middle Miocene	Böhme 1999b; Augé & Rage 2000; Böhme & Ilg
Dianus sp.	Dialituae	Dianus anu iquus	Dallsall	riance	(Langhian/Serravallian; MN 6)	2003; Bolet Mercadal 2014; Bolet et al. 2014
Blanus sp.	Blanidae		Moneva	Spain	Middle/upper Miocene (MN 6/7)	Benito & Bolet 2016
<i>Blanus</i> en	Blanidae		Abocador de Can Mata, Vallès	Snain	Middle Miocene (MN 6/MN	this work
de comma			Penedès Basin	mde	7+8)	
Blanus sp.	Blanidae		Borjas	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Las Planas 5H	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Las Planas 5L	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Valalto 1A	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Valalto 2C	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Can Missert, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	this work
Blanus sp.	Blanidae		La Roma 2	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Los Aguanaces	Spain	Miocene (Tortonian)	Sanchiz 1998; Böhme & Ilg 2003
Blanus sp.	Blanidae		Los Aguanaces 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Masada Ruea 4	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Puente Minero 3	Spain	Miocene (Tortonian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Bunker de Vallecebro 3	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Concud 98'	Spain	Late Miocene (Messinian)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Los Mansuetos	Spain	Miocene (Messinian)	Böhme & Ilg 2003
Blanus sp.	Blanidae	Amphisbaenidae indet.	Ciabòt Cagna	Italy	Late Miocene (late Messinian)	Cavallo et al. 1993; Böhme & Ilg 2003; Delfino 2003: this work
Blanus sp.	Blanidae		El Arguillo 3	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003
Blanus sp.	Blanidae		Punta Nati-Cala's Pous (= Punta Nati 12), Menorca	Spain	Pliocene (Zanclean)	García-Porta et al. 2002; Böhme & Ilg 2003; Bailon et al. 2010; Bover et al. 2014

Blanus sp.	Blanidae	cf. Blanus sp.	Balaruc II	France	Middle/late Pliocene (MN 15/MN 16)	Bailon 1989; Bailon 1991; García-Porta et al. 2002; Böhme & Ilg 2003; Bailon & Blain 2007
Blanus sp.	Blanidae		Las Higueruelas	Spain	Pliocene (Piacenzian)	Böhme & Ilg 2003
Blanus sp.	Blanidae	cf. Blanus sp.	Balaruc VI	France	Late Pliocene (MN 16)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007
Blanus sp.	Blanidae	cf. Blanus sp.	Mas Genegals	France	Late Pliocene (MN 16)	Bailon 1991; Böhme & Ilg 2003; Bailon & Blain 2007
Blanus sp.	Blanidae		Quibas	Spain	Early Pleistocene (Calabrian)	Montoya et al. 1999; Montoya et al. 2001; Böhme & Ilg 2003; Bailon & Blain 2007
Blanus sp.	Blanidae	Blanus cf. B. strauchi	Cava dell'Erba, Pirro Nord	Italy	Early Pleistocene	Holman 1998; Delfino & Bailon 2000; García- Porta et al. 2002; Böhme & Ilg 2003; Delfino 2003: Delfino 2013: Delfino & Atzori 2013; Blain
						et al. 2016c
Blanus sp.	Blanidae		Murcia	Spain	Lower Pleistocene	García-Porta et al. 2002
Blanus sp.	Blanidae		Hat, Jarama Valley	Spain	Upper Pleistocene	Böhme & Ilg 2003
Blanus sp.	Blanidae		PRERESA	Spain	Upper Pleistocene	Panera et al. 2014
Blanus sp.	Blanidae		Jaén	Spain	Holocene (Neolithic)	García-Porta et al. 2002
cf. Blanus sp.	Blanidae	Blanus sp.	Kleineisenbach	Germany	Miocene (Serravallian, MN 8)	Böhme & Ilg 2003; Villa & Delfino 2017; this work
Palaeoblanus tobieni	Blanidae		Budenheim	Germany	Miocene (Aquitanian)	Schleich 1988a; Schleich 1988b; Böhme 1999b; Böhme & Ilg 2003; Čerňanský et al. 2015c
Palaeoblanus tobieni	Blanidae		Mainz-Weisenau (quarry, Fp.19)	Germany	Miocene (Aquitanian)	Schleich 1988a; Schleich 1988b; Böhme 1999b; Böhme & Ilg 2003; Čerňanský et al. 2015c; Čerňanský et al. 2016a
Palaeoblanus tobieni	Blanidae		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Böhme 1999b; Böhme 2003; Böhme & Ilg 2003; Miklas-Tempfer 2003
Palaeoblanus cf. P. tobieni	Blanidae		Unterempfenbach 1b	Germany	Early Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003
Palaeoblanus nov. sp.	Blanidae	Palaeoblanus cf. P. tobieni	Sandelzhausen	Germany	Miocene (Burdigalian, MN 5)	Böhme 1999a; Böhme 1999b; Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Böhme 2010b; Bolet Mercadal 2014; Bolet et al. 2014; Čerňanský et al. 2016c
Palaeoblanus sp.	Blanidae		Chavroches P1	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Palaeoblanus sp.	Blanidae		Chavroches P1C2	France	Lower Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Palaeoblanus sp.	Blanidae		Montaigu-le-Blin 85	France	Miocene (Aquitanian, MN 2a)	Böhme 2003; Böhme & Ilg 2003
Palaeoblanus sp.	Blanidae		Agramon	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Palaeoblanus sp.	Blanidae		San Roque 5	Spain	Miocene (Burdigalian)	Böhme & Ilg 2003
Palaeoblanus sp.	Blanidae		Caseton 1A	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Palaeoblanus sp.	Blanidae		La Col C	Spain	Miocene (Langhian)	Böhme & Ilg 2003
Palaeoblanus sp.	Blanidae		Valdemoros 3F	Spain	Miocene (Langhian)	Böhme & Ilg 2003

Palaeoblanus sp.	Blanidae	Amphisbaenidae indet.	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Augé & Rage 2000; Bolet Mercadal 2014; Bolet et al. 2014
Palaeoblanus sp.	Blanidae		Cantatore, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
Palaeoblanus sp.	Blanidae		Cava Fina, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
Palaeoblanus sp.	Blanidae		Cava Pirro, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; García-Porta et al. 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
Palaeoblanus sp.	Blanidae	cf. Blanus sp.	Cava Rodisano, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; García-Porta et al. 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
Palaeoblanus sp.	Blanidae		Chirò, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
Palaeoblanus sp.	Blanidae		Falcone, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
Palaeoblanus sp.	Blanidae		Gargano "Terre Rosse" (F - Coll. Firenze)	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
Palaeoblanus sp.	Blanidae		Tre Fossi, Gargano "Terre Rosse"	Italy	Upper Miocene (Messinian)/lower Pliocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2003; Delfino 2013
aff. Palaeoblanus sp.	Blanidae		Las Planas 5L	Spain	Miocene (Serravallian)	Böhme & Ilg 2003
Blanidae indet.	Blanidae		Venta del Moro	Spain	Late Miocene (Messinian, MN 13)	Marquina et al. 2016a
Omoiotyphlops edwardsi	Amphisbaenidae	Typhlops edwardsi	Sansan	France	Middle Miocene (Langhian/Serravallian; MN 6)	Hoffstetter 1942; Estes 1983; Roček 1984; Schleich 1985a
Omoiotyphlops edwardsi	Amphisbaenidae	Typhlops edwardsi	La Grive-Saint-Alban	France	Miocene	Hoffstetter 1942; Estes 1983; Roček 1984; Schleich 1985a
Omoiotyphlops edwardsi	Amphisbaenidae	Typhlops edwardsi	Saint-Gérand-le-Puy	France	Miocene	Hoffistetter 1942; Estes 1983; Roček 1984; Schleich 1985a
Amphisbaenidae indet.	Amphisbaenidae		Ulm Westtangente	Germany	Miocene (Aquitanian)	Böhme & Ilg 2003
Amphisbaenidae indet.	Amphisbaenidae		Teiritzberg (T1 = 001/D/C), Korneuburg Basin	Austria	Lower Miocene (Burdigalian, MN 5)	Böhme 2002; Böhme 2003; Böhme & Ilg 2003; Tempfer 2003
Amphisbaenidae indet.	Amphisbaenidae		Puttenhausen classic (=Puttenhausen 1)	Germany	Miocene (Burdigalian, MN 5)	Böhme 2003; Böhme & Ilg 2003; Abdul Aziz et al. 2008; Abdul Aziz et al. 2010
Amphisbaenidae indet.	Amphisbaenidae		Schmiedrued-Pyffrüti level 618, Swiss Molasse Basin	Switzerland	Late Early Miocene (Burdigalian)	Böhme & Ilg 2003; Jost et al. 2015
Amphisbaenidae indet.	Amphisbaenidae		Obergänserndorf, Korneuburg Basin	Austria	Lower Miocene (Burdigalian)	Böhme 2002; Böhme & Ilg 2003; Tempfer 2003

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Villa & Delfino 2017; this work	Miocene (Burdigalian, MN 3b)	Germany	Stubersheim 2	Amphisbaenia indet.	Amphisbaenia indet.
Böhme & Ilg 2003	Miocene (Aquitanian)	France	Mont Merle	Amphisbaenia indet.	Amphisbaenia indet.
Roček 1984	Miocene (Aquitanian)	France	Limagne	Amphisbaenia indet.	Amphisbaenia indet.
Böhme & Ilg 2003	Miocene (Serravallian/Tortonian, MN 9)	Ukraine	Gritsev	Amphisbaenidae	?Amphisbaenidae indet.
Crespo 2001	Plio-Pleistocene	Spain	Guadix/Granada	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Pliocene (Zanclean)	Spain	Villalba Alta 1	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Pliocene (Zanclean)	Spain	Peralejos 7	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Messinian)	Spain	Valdecebro 5	Amphisbaenidae	Amphisbaenidae indet.
Böhme & IIg 2003	Miocene (Messinian)	Spain	La Gloria 6	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Tortonian)	Spain	Viverro de la Rambla	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Tortonian)	Spain	Masia de la Roma 3	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Tortonian)	Spain	Los Aguanaces 5B	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Tortonian)	Spain	La Roma 1	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Tortonian)	Spain	Crevillente 3	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Tortonian)	Spain	Barrachina	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Tortonian)	Germany	Hammerschmiede 1	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Serravallian)	Spain	Las Umbrias 21	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Serravallian)	Spain	Las Planas 5K	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Serravallian)	Spain	Borjas	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Middle Miocene (Serravallian)	Spain	Alcocer 2	Amphisbaenidae	Amphisbaenidae indet.
Augé & Rage 2000	Middle Miocene (Langhian/Serravallian; MN 6)	France	Sansan	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Villafeliche 4A	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Valdemoros 7B	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Valdemoros 3B	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Regajo 2	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Moratilla 3	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003; Bastir et al. 2014	Middle Miocene (Langhian)	Spain	Moratilla 2	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Las Umbrias 16	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Las Umbrias 14	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Spain	Las Umbrias 8	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Germany	Petersbuch 68	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Germany	Oberschöneberg 2B	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003; Abdul Aziz et al. 2008	Miocene (Langhian)	Germany	Furth 460m	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Langhian)	Germany	Anried 2	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003; Bolet Mercadal 2014; Bolet et al. 2014	Early Miocene	Spain	Córcoles	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian)	Spain	Artesilla	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003; Abdul Aziz et al. 2008	Miocene (Burdigalian)	Germany	Puttenhausen E	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003; Abdul Aziz et al. 2008	Miocene (Burdigalian)	Germany	Puttenhausen B	Amphisbaenidae	Amphisbaenidae indet.
Böhme & Ilg 2003	Miocene (Burdigalian)	Germany	Erkertshofen 1	Amphisbaenidae	Amphisbaenidae indet.

Amphisbaenia indet.	Amphisbaenia indet.		Stubersheim 3	Germany	Miocene (Burdigalian, MN 3b)	Villa & Delfino 2017; this work
Amphisbaenia indet.	Amphisbaenia indet.		Béon 1 (= Montréal-du-Gers)	France	Lower Miocene (Burdigalian, MN 4)	Böhme & Ilg 2003; Rage & Bailon 2005
Amphisbaenia indet.	Amphisbaenia indet.		Els Casots, Vallès Penedès Basin	Spain	Early Miocene (MN 4)	this work
Amphisbaenia indet.	Amphisbaenia indet.	Amphisbaenidae indet.	Puttenhausen A	Germany	Miocene (Burdigalian)	Böhme & Ilg 2003; Abdul Aziz et al. 2008
Amphisbaenia indet.	Amphisbaenia indet.	Amphisbaenidae indet.	Cabezo Vaquero, Bardenas Reales, Navarra	Spain	Miocene (Burdigalian)	Murelaga et al. 2002; Böhme & Ilg 2003
Amphisbaenia indet.	Amphisbaenia indet.	Amphisbaenidae indet.	La Nasa 1 (= Tripazul), Bardenas Reales, Navarra	Spain	Miocene (Burdigalian)	Murelaga et al. 2002; Böhme & Ilg 2003
Amphisbaenia indet.	Amphisbaenia indet.		Gisseltshausen 1b	Germany	Miocene (Langhian, MN 5)	Villa & Delfino 2017; this work
Amphisbaenia indet.	Amphisbaenia indet.		Griesbeckerzell 1a	Germany	Miocene (Langhian, MN 6)	Villa & Delfino 2017; this work
Amphisbaenia indet.	Amphisbaenia indet.		Abocador de Can Mata, Vallès Penedès Basin	Spain	Middle Miocene (MN 6/MN 7+8)	this work
Amphisbaenia indet.	Amphisbaenia indet.		Tarazona de Aragón	Spain	Middle Miocene	Bolet Mercadal 2014; Bolet et al. 2014
Amphisbaenia indet.	Amphisbaenia indet.		Plakias	Greece	Earliest late Miocene (Tortonian, MN 9)	Delfino 2004b; Georgalis et al. 2016b; Georgalis et al. 2016c; this work
Amphisbaenia indet.	Amphisbaenia indet.		Can Missert, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	Bolet Mercadal 2014; Bolet et al. 2014; this work
Amphisbaenia indet.	Amphisbaenia indet.		Can Poncic, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	this work
?Amphisbaenia indet.	Amphisbaenia indet.		Castell de Barberà, Vallès Penedès Basin	Spain	Late Miocene (MN 9)	this work
Amphisbaenia indet.	Amphisbaenia indet.		Sant Miquell del Toudell, Vallès Penedès Basin	Spain	Late Miocene (MN 10)	this work
Amphisbaenia indet.	Amphisbaenia indet.		Trinxera Nord Autopista, Vallès Penedès Basin	Spain	Late Miocene (MN 10)	this work
Amphisbaenia indet.	Amphisbaenia indet.		Moncucco Torinese	Italy	Latest Miocene (Messinian, p- ev2)	Colombero et al. 2014b; Colombero et al. 2017; this work
Amphisbaenia indet.	Amphisbaenia indet.		Cava Monticino, Brisighella	Italy	Miocene (latest Messinian, MN 13)	Delfino 2002; Böhme & Ilg 2003; Delfino 2003; Rook & Delfino 2007; Rook et al. 2015; Villa et al. 2016b; this work
Amphisbaenia indet.	Amphisbaenia indet.		Verduno	Italy	Miocene (Messinian)	Böhme & Ilg 2003; Carnevale et al. 2014; Colombero et al. 2014a
Amphisbaenia indet.	Amphisbaenia indet.	Amphisbaenidae indet.	Bacochas	Spain	Late Miocene	Barbadillo 1989; Bolet Mercadal 2014; Bolet et al. 2014
Amphisbaenia indet.	Amphisbaenia indet.		Can Llobateres	Spain	Late Miocene	Bolet Mercadal 2014; Bolet et al. 2014
Amphisbaenia indet.	Amphisbaenia indet.	Amphisbaenidae indet.	Los Valles de Fuentidueña	Spain	Late Miocene	Sanchiz 1981; Barbadillo 1989; Bolet Mercadal 2014; Bolet et al. 2014
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Апривоаения писе.	Ашривоаста шист.	Ашршу ваеннае шаег.	V HAUCCADALIS (CALL FULULI)	unade		Estes 1963; Barbauno 1969; Botet Mercauat 2014; Bolet et al. 2014
Amphisbaenia indet.	Amphisbaenia indet.		Lomas de Casares 1	Spain	Pliocene (Zanclean)	Böhme & Ilg 2003

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		Conc Manni DI I cool Forme (-			Kotsakis 1980; Estes 1983; Schleich 1985a;
Amphisbaenia indet.	Amphisbaenia indet.	Capo Maninu DI LOCAI Fauna (Italy	Late Pliocene (Piacenzian)	Böhme & Ilg 2003; Delfino 2003; Delfino &
		INTALIGIT (DIA)			Rook 2008; Delfino et al. 2011
Amphisbaenia indet.	Amphisbaenia indet.	Spilia 4	Greece	Late Pliocene	Delfino 2004b; this work
					Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et
Amphisbaenia indet.	Amphisbaenia indet.	Cava VI 3, Monte Tuttavista	Italy	Pleistocene (Calabrian)	al. 2004; Delfino & Rook 2008; Delfino et al.
					2008b
Amphisbaenia indet.	Amphisbaenia indet.	Quibas	Spain	Early Pleistocene	Mancheño et al. 2009
Amhichaania indat	A muhicha ania indat	Const Name 1	Snain	Latest Miocene/Middle	Blain at al 2016
лиршеластиа шисе.	инривоаеща шаст.		Jpaur	Pleistocene	DIALLI CL 41. 2010
Amphisbaenia indet.	Amphisbaenia indet.	K 22, San Vito lo Capo	Italy	Middle/late Pleistocene	Delfino 2002; Böhme & Ilg 2003; Delfino 2003
Amphisbaenia indet.	Amphisbaenia indet.	Cava VI Banco 6, Monte Tuttavista	Italy	Upper Pleistocene	Böhme & Ilg 2003; Rook et al. 2003; Abbazzi et al. 2004; Delfino & Rook 2008
Amphisbaenia indet.	Amphisbaenia indet.	Castillejo del Bonete	Spain	Holocene	Benítez de Lugo Enrich et al. 2015

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Taxon	Family	Previous identifications	Locality	Country	Age	Bibliography
Barbus sp.	Cyprinidae	Agamidae indet.	Tokod	Hungary	Upper Pleistocene	Meszoely & Gasparik 2002; Rage 2013
Cyprinidae indet.	Cyprinidae	Agama sp.; Agama s.l.	Ano Metochi 3	Greece	Late Miocene (Messinian, MN 13)	Böhme & Ilg 2003; Delfino 2004b; Delfino et al. 2008b; Blain et al. 2016a; Georgalis et al. 2017a
Serpentes indet.	Serpentes indet.	cf. Anguis sp.	Węże I	Poland	Pliocene (Zanclean, MN 15)	Młynarski 1956
Squamata indet.	Squamata indet.	?Agamidae indet.	Węże I	Poland	Pliocene (Zanclean, MN 15)	Młynarski 1956; Młynarski 1962; Böhme & Ilg 2003
Squamata indet.	Squamata indet.	?Gekkonidae indet.	Węże I	Poland	Pliocene (Zanclean, MN 15)	Młynarski 1956; Młynarski 1962; Böhme & Ilg 2003

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Appendix 6

List of characters considered in the phylogenetic analysis conducted in chapter 4.

- 1. Premaxilla, number of teeth: 7 or less (0); 8 or more (1). (Barahona & Barbadillo 1997; Villa et al. 2017 (C1))
- Maxilla, number of labial foramina: 6 or less (0); >6 (1). ((Rauscher 1992); Villa et al. 2017 (C2), wording modified; does not count the smaller foramina above the level of the large ones)
- 3. Teeth, crown complexity, maximum number of cusps in single tooth: 4 or more (0); 3 (1);2 or less (2). ((Müller 1996))
- 4. Teeth, number of maxillary teeth: <16 (0); 16 or more (1). ((Rauscher 1992); Villa et al. 2017 (C6))
- 5. Teeth, number of dentary teeth: <13 (0); 13 or more (1). ((Rauscher 1992); Villa et al. 2017 (C7))
- 6. Presacral vertebrae, number: <27 (0); 27 or more (1). (Arnold 1973 (C8); Estes et al. 1988 (C104-106); Müller 2001 (C48); Arnold et al. 2007 (C13); state boundary adapted to taxon sampling by Villa et al. 2017 (C8))
- 7. Presacral vertebrae, number of posterior elements with short ribs: 5 or fewer (0); 6 (1); 7 or more (2). ((Siebenrock 1894); Arnold 1989; Arnold et al. 2007 (C14); modified by Villa et al. 2017 (C9))
- 8. Cervical intercentra, number: < 7 (0); 7 or more (1). ((Al-Hassawi 2004))
- 9. Anterior caudal vertebrae, number of non-autotomic elements: 4 or less (0); 5 (1); 6 (2);7 or more (3). ((Arnold 1973); Villa et al. 2017 (C17), modified)
- 10. Premaxilla, ascending nasal process, cross section at base, minimum transverse width to anteroposterior length ratio: > 1.1 (0); 0.9-1.1 (1); < 0.9 (2). ((Rauscher, 1992); Villa et al. 2017 (C22), modified)
- 11. Premaxilla, angle of ascending nasal process to horizontal plane: > 70° (0); 50°-70° (1);
 < 50° (2). (Čerňanský et al. 2016 (C5); wording modified)
- 12. Nasal, length relative to frontal length: < 0.40 (0); 0.40-1.00 (1); > 1.00 (2). (Čerňanský et al. 2016 (C17); modified)
- 13. Frontal, dorsal surface, anteroposterior length of frontoparietal shield to anteroposterior length of ornamented portion: 0.40 or less (0); > 0.40 (1). ((Čerňanský 2010); Čerňanský et al. 2016 (C24); modified)

- 14. Frontal, transverse width posterior end compared to midlength width: narrow, <1.8 (0); intermediate, 1.8-3.0 (1); widely expanded, >3.0 (2). ((Estes et al. 1988); Gauthier et al. 2012 (C49); Villa et al. 2017 (C52), added quantitative boundaries)
- 15. Frontals, anterior transverse width/minimum transverse width: > 1.20 (0); 1.20 or less (1). ((Rauscher 1992); Barahona & Barbadillo 1997; Villa et al. 2017 (C51), added quantitative state boundaries)
- 16. Postfrontal, maximum anteroposterior length to maximum anteroposterior length of postorbital: longer to subequal (0); distinctly shorter (1). ((Arribas 1998); Villa et al. 2017 (C3))
- 17. Postorbital, length of contact with squamosal, compared to total anteroposterior length: > 0.41 (0); 0.41 or less (1). ((Arribas 1998); Villa et al. 2017 (C4))
- 18. Parietal, length to width of ornamented part of dorsal surface: longer (0): equal to wider (1). (Arnold 1989 (C9); wording modified by Villa et al. 2017 (C5))
- 19. Parietal, interparietal shield, length compared to occipital shield: < 0.95 (0); 0.95-1.05 (1); > 1.05 (2). (Čerňanský et al. 2016 (C30); modified)
- 20. Parietal, width of occipital shield compared to posterior width of ornamented portion: narrow, < 0.40 (0); intermediate, 0.40-0.60 (1); wide, > 0.60 (2). (Barahona & Barbadillo (1997, C2.6, fig. 2); Villa et al. 2017 (C71), modified)
- 21. Presacral vertebrae, dorsoventral height to centrum length ratio: 1.1 or less (0); 1.2-1.3 (1); 1.4 or greater (2). (Villa et al. 2017 (C10))
- 22. Presacral vertebrae, width across postzygapophyses to greatest length: 0.7 or less (0);
 0.8 (1); 0.9 or greater (2). ((Barbadillo & Sanz 1983); Villa et al. 2017 (C11))
- 23. Axial neural arch pedicels, minimum anteroposterior length to height of posterior edge:< 1 (0); 1-1.4 (1); > 1.4 (2). (Villa et al. 2017 (C12))
- 24. Axis, neural spine height (without pedicel) to greatest height: < 0.5 (0); 0.5 or greater(1). ((Barbadillo & Sanz 1983); Villa et al. 2017 (C13))
- 25. Postaxial presacral centrum length/posterior condyle height: < 2.5 (0); 2.5-3.5 (1); > 3.5 (2). (Villa et al. 2017 (C14))
- 26. Sacral vertebra 1, greatest height to width across pleurapophyses: less than or equal to 0.38 (0); > 0.38 (1). ((Barbadillo & Sanz 1983); Villa et al. 2017 (C16))
- 27. Interclavicle, length of anterior process compared to posterior process: < 0.40 (0); 0.40 or greater (1). ((Arribas 1998); Villa et al. 2017 (C18))

- 28. Humerus, greatest length/maximum shaft diameter at midlength: < 10 (0); 10 or greater(1). ((Lécuru 1969))
- 29. Humerus, proximal transverse width/distal transverse width: < 0.95 (0); 0.95-1.05 (1); >
 1.05 (2). ((Lécuru 1969))
- 30. Humerus, minimum/maximum shaft diameter at midlength: < 0.82 (0); 0.82 or greater(1). ((Lécuru 1969))
- 31. Tibia/femur length ratio: <0.70 (0); 0.70 or greater (1).
- 32. Premaxilla, shape: two bilaterally symmetric elements (0); single, midline bone (1). (Estes et al. 1988 (C1); Müller 2001 (C1))
- 33. Premaxilla, tooth-bearing portion, shape in dorsal view: tapering laterally, anterior and lateral edges form an acute angle (0); retaining width along curvature, angle between anterior and lateral edges approaching 90° (1). ((Rauscher, 1992); Villa et al. 2017 (C19))
- 34. Premaxilla, tooth-bearing portion, dorsal surface: pierced by a circular pit close to origin of nasal process (0); no pits present (1). ((Rauscher, 1992); Villa et al. 2017 (C20))
- 35. Premaxilla, tooth-bearing portion, maxillary facet, size: small to absent (0); large, reaching almost base of nasal process (1).
- 36. Premaxilla, ascending nasal process, lateral margins: parallel (0); expanding transversely around midlength (1). ((Rauscher 1992); Barahona & Barbadillo 1997 (C3.1), modified after Gauthier et al. 2012 (C13; Appendix 2, fig. 13) by Villa et al. 2017 (C21), wording modified)
- 37. Premaxilla, ascending nasal process, ethmoidal foramen at base: situated within fossa (0); without fossa around foramen (1).
- 38. Premaxilla, fossa around ethmoidal foramen (if present), delimitation: with distinct ridge posteriorly (0); with distinct ridge anteriorly (1).
- 39. Premaxilla, ascending nasal process, shape in lateral view: relatively straight (0); convex (1). ((Rauscher 1992); Villa et al. 2017 (C24))
- 40. Premaxilla, ascending nasal process, dorsoventral constriction, in lateral view: present (0); absent (1). ((Rauscher 1992); Villa et al. 2017 (C25))
- 41. Premaxilla, ascending nasal process, ventral surface, longitudinal medial ridge, development: extending nearly throughout entire length (0); restricted to posterior

portion, accompanied laterally by two shallow fossae (1). ((Rauscher, 1992); Villa et al. 2017 (C26))

- 42. Premaxilla, ascending nasal process, ventral surface, longitudinal medial ridge, posterior end: fading (0); distinct (1). ((Rauscher 1992); Villa et al. 2017 (C27))
- 43. Premaxilla, ascending nasal process, posterior end of medial ridge, shape in lateral view: bifid, with dorsal and ventral spurs (0); single (1). ((Rauscher 1992); Villa et al. 2017 (C28))
- 44. Premaxilla, posterolaterally projecting palatine processes on horizontal plate: absent (0); present (1). ((Rauscher, 1992); Villa et al. 2017 (C29), wording modified)
- 45. Premaxilla, horizontal plate, medial depression: absent, plate straight (0); present, depression bordered by ridges that extend onto palatine processes (1).
- 46. Premaxilla-maxilla contact: continuous (0); incomplete, with opening between premaxillary processes of maxilla (1). (Villa et al. 2017 (C30))
- 47. Snout, medial depression around premaxilla-nasal contact: present (0); absent (1). (Barahona & Barbadillo 1997 (C23), wording modified by Villa et al. 2017 (C31))
- Maxilla, external surface of facial process: uniform, without distinct subdivisions (0); subdivided into dorsal and ventral halves by horizontal groove (1). ((Rauscher 1992); Villa et al. 2017 (C32), wording modified)
- 49. Maxilla, dermal ornamentation: absent to weak (0); well-developed (1).
- 50. Maxilla, anterolateral premaxillary process, shape of ventral edge in lateral view: straight to convex (0); concave (1). (Villa et al. 2017 (C33))
- 51. Maxilla, anterior margin of facial process, orientation relative to dental crest: posteriorly inclined throughout (0); perpendicular for some distance (1).
- 52. Maxilla, anterior margin of facial process, distinct, subtriangular process projecting anteriorly or anterodorsally: absent (0); present (1).
- 53. Maxilla, prefrontal process on dorsal end of facial process: weakly developed (0); develops two distinct posterodorsally projecting spurs (1). ((Rauscher 1992); Villa et al. 2017 (C34))
- 54. Maxilla, bifid prefrontal process (if present), in lateral view: anterodorsal projection reaching considerably dorsal to posteroventral projection (0); both projections at subequal height (1). ((Rauscher 1992); Villa et al. 2017 (C35))

55. Maxilla, facial process: straight, flat (0); curves considerably medially towards dorsal tip (1). (Villa et al. 2017 (C36))

56. Maxilla, nasal recess: absent (0); present (1). ((Rauscher 1992); Villa et al. 2017 (C37))

- 57. Maxilla, dorsal margin of anteromedial premaxillary process: smooth (0); bears a dorsally or anterodorsally projecting spur close to anterior end (1). ((Rauscher 1992), Barahona & Barbadillo 1997, wording modified after Villa et al. 2017 (C38))
- 58. Maxilla, transition from orbital margin into posterior process: smooth (0); separated by step or spur (1). (Arnold 1989 (C17, fig. 6); Barahona & Barbadillo 1997; modified after Müller 2001 (C42) and Villa et al. 2017 (C39))
- 59. Maxilla, morphology of separation of orbital margin and posterior process (if present): incipient step (0); distinct step, forming right angle (1); posteriorly projecting spur (2). ((Rauscher 1992); Villa et al. 2017 (C40), modified)
- 60. Maxilla, posterior process, posterior extent: reaches mid-orbit (0); posterior to mid-orbit
 (1). (Müller 2001 (C17); Lee & Scanlon, 2002 (C23); modified by Čerňanský et al. 2016 (C12))
- 61. Maxilla, facial process, medial surface, anteroposterior ridge on supradental shelf connecting anterior margin of facial process with carina maxillaris: absent (0); present (1).
- 62. Maxilla, supradental shelf, articulation facet for palatine, shape in dorsal view: slight medial extension (0); distinctly offset from crest (1).
- 63. Maxilla, tooth row, shape in ventral view: curves laterally at distal end (0); straight (1).(Villa et al. 2017 (C41))
- 64. Septomaxilla, anterolateral process: distinct (0); reduced (1). (Arnold 1989 (C2; fig. 4), modified after Barahona & Barbadillo 1997, by Villa et al. 2017 (C42))
- 65. Septomaxilla, posteromedial process, length: scarcely developed (0); long (1). (Arnold 1989 (C2; fig. 4), modified after Barahona & Barbadillo 1997, split in two by Villa et al. 2017 (C43))
- 66. Septomaxilla, posterolateral corner: angular, projecting posterolaterally (0); rounded (1).
 (Arnold 1989 (C2; fig. 4), modified after Barahona & Barbadillo 1997 by Villa et al. 2017 (C44))
- 67. Nasals, ventral contact beneath premaxillary nasal process: broad contact below (0); not in contact except near apex (1). (Gauthier et al. 2012 (C24); Villa et al. 2017 (C45))

- 68. Prefrontal, dorsal process length compared to length of orbitonasal flange: longer (0); equal to shorter (1).
- 69. Frontals: paired (0); fused (1). ((Boulenger 1920; Camp 1923); Estes et al 1988 (C6);
 Arnold 1989 (C4; figs 2, 3); Müller 2001 (C1); wording modified by Villa et al. 2017 (C46))
- 70. Frontal, anterior processes: reduced (0); long, distinct (1). (Estes et al. 1988 (C9); Gauthier et al. 2012 (C38); Villa et al. 2017 (C47); wording modified)
- 71. Frontal, nasal margin: rather straight (0); highly irregular (1). ((Rauscher 1992); Villa et al. 2017 (C48))
- 72. Frontal, medial and lateral processes: well developed (0); reduced or absent (1). (Arnold 1989 (C6); Arnold et al. 2007 (C8); Villa et al. 2017 (C49), wording modified)
- 73. Frontal, facet to accommodate dorsal process of maxilla: conspicuous (0); weak to absent(1). (Barahona & Barbadillo 1997 (C1.4), wording modified by Villa et al. 2017
 - (C50))
- 74. Frontal, prefrontal shield, impression: absent (0); present (1).
- 75. Frontal, prefrontal shield, impression, shape: connected anteromedially (0); medially separated (1).
- 76. Frontal, suture with parietal: interdigitating (0); rather straight (1). (Arnold 1989 (C7, figs 2, 3); Müller 2001 (C65); wording modified after Barahona & Barbadillo 1997 by Villa et al. 2017 (C53))
- 77. Postfrontal, anteromedial process: expanded (0); not expanded (1). (Barahona & Barbadillo 1997 (C7.2), modified by Villa et al. 2017 (C54))
- Postfrontal, short, subtriangular, anterior projection close to suture with postorbital: absent (0); present (1).
- 79. Postorbital-postfrontal suture: fused (0); separate (1). ((Siebenrock 1894); Arnold 1973 (C7, fig. 2); Estes et al. 1988 (C14); Arnold 1989 (C12; figs 2, 3); Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C55))
- 80. Postorbital, anteromedial process: absent (0); present (1). (Barahona & Barbadillo 1997;Villa et al. 2017 (C56))
- Postorbital-postfrontal, impression of lateral shield, location: does not reach lateral margin (0); reaches lateral margin posteriorly (1); reaches lateral margin along most of its length (2). ((Arnold et al. 2007))

- 82. Postorbital anterolateral process, ventral extension compared to level of quadrate cephalic condyle: ventral (0); same level (1); dorsal (2). ((Estes et al. 1988); Gauthier et al. 2012 (C82), wording modified)
- 83. Jugal, quadratojugal process: absent (0); distinct (1). ((Siebenrock 1894); Arnold 1989 (C15, fig. 6); polarity reversed by Barahona & Barbadillo 1997; Villa et al. 2017 (C57))
- 84. Jugal, quadratojugal process, shape: acute (0); forms nearly a 90° angle (1).
- 85. Jugal, posterodorsal process, posterior margin, shape: distinctly curving posteriorly towards tip (0); nearly straight (1).
- 86. Jugal, medial process on medial ridge: present (0); absent (1). (Barahona & Barbadillo 1997 (C6.2); Villa et al. 2017 (C58))
- 87. Jugal, posterodorsal process, position of medial ridge: on anterior half (0); on posterior half (1). ((Čerňanský et al., 2014); Čerňanský et al., 2016 (C22); modified)
- 88. Jugal, maxillary facet on anterior process: small (0); large (1). (Estes et al. 1988 (C31); modified by Arnold 1989 (C16, fig. 6); polarity reversed by Barahona & Barbadillo 1997 (C6.3); Gauthier et al. 2012 (C149); modified after Arnold 1989 by Villa et al. 2017 (C59))
- 89. Lacrimal, orbital margin: forked, with posterodorsal process (0); posterodorsal process absent, tapering to a pointed posteroventral end (1). (Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C60))
- 90. Quadrate, anterior surface, pit above mandibular condyle: absent (0); present (1). ((Rauscher 1992); Villa et al. 2017 (C61))
- 91. Quadrate, anterior margin in medial view: angular (0); rounded (1). (Barahona & Barbadillo 1997 (C9.1); Villa et al. 2017 (C62))
- 92. Quadrate, anterior platform: concave (0); flat (1). (Barahona & Barbadillo 1997; Villa et al. 2017 (C63))
- 93. Quadrate, medial edge, pterygoid process: distinct (0); small to absent (1). (Estes et al. 1988 (C37); Müller 2001 (C24); Gauthier et al. 2012 (C182), modified after Estes et al. 1988)
- 94. Quadrate, central pillar, position: at medial border, only laterally accompanied by a flange (0); inset, with flanges medially and laterally (1). ((Rauscher 1992); Villa et al. 2017 (C64))

- 95. Quadrate, cephalic condyle, medial edge: straight (0); with distinct expansion, accompanied by a short vertical ridge extending ventrally on medial surface of central pillar (1). (Villa et al. 2017 (C65), wording modified)
- 96. Squamosal, posterior end: medially expanded (0); slender, curving laterally (1). (Estes et al. 1988 (C34); Arnold 1989 (C14; fig. 5); Barahona & Barbadillo 1997 (C8); Müller 2001 (C21); wording modified by Villa et al. 2017 (C66))
- 97. Parietal, anterior margin: small concavity near midline (0); straight (1). (Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C67))
- 98. Parietal, parietal tabs: well-developed, projecting far anteriorly (0); reduced to absent(1). (Estes et al. 1988 (C22); Müller 2001 (C13); Villa et al. 2017 (C68))
- 99. Parietal lappets lateral expansion: present (0); absent (1). (Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C69))
- 100. Parietal, dorsal ornamentation: irregular (0); symmetrically subdivided by distinct grooves (1). ((Rauscher 1992); Villa et al. 2017 (C70))
- 101. Parietal, facies dorsalis, outline shape: strongly diverging anteriorly (0); subquadrangular to subrectangular (1); converging anteriorly (2).
- 102. Parietal, posterior edge of parietal fossa: concave transversely (0); straight (1). (Barahona & Barbadillo 1997 (C2.1), modified by Villa et al. 2017 (C72))
- 103. Parietal, posterior margin, extension in dorsal view: not exceeding anterior margin of supraoccipital (0); extending over anterior margin of supraoccipital (1). (Estes et al. 1988 (C24); modified after Barahona & Barbadillo 1997 by Villa et al. 2017 (C73))
- 104. Parietal, posterior margin, single or bifid projection near midline: absent (0); present(1). (Gauthier et al. 2012 (C95), wording modified)
- 105. Parietal, posterior margin, midline projection: single (0); bifid (1). ((Rauscher 1992, fig. 23.3); Gauthier et al. 2012 (C97), Villa et al. 2017 (C74), wording modified)
- 106. Parietal, postparietal processes: straight (0); twisted (1). ((Rauscher 1992); Villa et al. 2017 (C75))
- 107. Parietal, ventral surface, anterolateral and posterolateral ventral crests, contact: absent (0); present (1). (Barahona & Barbadillo 1997, modified after Villa et al. 2017 (C76))

- 108. Parietal, ventral surface, anterolateral ventral crests, orientation: forming V-shape (0); forming U-shape, being subparallel anteriorly (1).
- 109. Parietal, epipterygoid processes: absent (0); present (1). (Estes et al. 1988 (C23);Müller 2001 (C14); Gauthier et al. 2012 (C108), modified to include only the transformational component, following Estes et al. 1988)
- 110. Parietal, ventral surface, bony structure between facies triangularis and parietal fossa, shape: wide shelf (0); narrow ridge (1).
- 111. Parietal, ventral surface, parietal fossa, anterior end, shape: U-shaped to rectangular (0); triangular to trapezoid (1). ((Barahona 1996); Villa et al. 2017 (C77), wording modified)
- 112. Parietal foramen, shape: circular (0); pear-shaped (1). ((Rauscher 1992); Villa et al. 2017 (C78))
- 113. Paroccipital process, length: long, exceeding posterior margin of otoccipital in lateral view (0); short (1). (Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C79))
- 114. Supraoccipital, lateral margins of processus ascendens: parallel (0); converging (1).(Barahona & Barbadillo 1997; Villa et al. 2017 (C80), wording modified)
- 115. Supraoccipital, supraoccipital crest, shape: distinct crest (0); wide ridge (1). ((Al-Hassawi 2004))
- 116. Basioccipital, shape in ventral view: subtriangular, exoccipital margin straight (0); mushroom-shaped, exoccipital margin concave (1). ((Rauscher 1992); Villa et al. 2017 (C81))
- 117. Basioccipital, cornua basisphenoidea: medially separated (0); medially co-ossified (1).((Rauscher 1992); Villa et al. 2017 (C82))
- 118. Basioccipital, occipital condyle, shape in ventral view: continuously rounded (0); bears weak recess (1). ((Rauscher 1992); Villa et al. 2017 (C83))
- 119. Basioccipital, posterior process on lateral sinuses: absent (0); present, separating lateral sinus from exoccipital margin (1). ((Rauscher 1992); Villa et al. 2017 (C84))
- 120. Basioccipital, dorsal surface, texture: smooth (0); ornamented (1). ((Rauscher 1992); Villa et al. 2017 (C85))
- 121. Sphenoid, ventral surface, depression close to base of basipterygoid processes: present(0); absent (1). (Barahona & Barbadillo 1997, modified by Villa et al. 2017 (C86))

- 122. Sphenoid, ventral surface, depression close to base of basipterygoid processes, shape: rounded (0); longitudinal trough (1).
- 123. Sphenoid, ventral surface, distinct longitudinal ridges or bosses at base of basipterygoid processes: absent (0); present (1). (Villa et al. 2017 (C87))
- 124. Basipterygoid processes, shape at base: narrow, margins strongly concave (0); widened, margins nearly parallel (1). (Barahona & Barbadillo 1997 (C15.2), modified by Villa et al. 2017 (C88), wording modified)
- 125. Prootic, alar process, development: weak, scarcely developed (0); well developed (1).(Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C89))
- 126. Prootic, posterior process, length: long (0); reduced (1). (Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C90))
- 127. Prootic-epipterygoid contact: absent (0); present, alar process of prootic reaches dorsal end of epipterygoid (1). (Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C91))
- 128. Palatine, anterolateral process, shape: rounded margins (0); straight margins (1).(Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C92))
- 129. Palatine-ectopterygoid contact: absent (0); present, anterolateral process of ectopterygoid reaches posterior extension of lateral process of palatine (1). (Barahona & Barbadillo 1997 (C24), wording modified by Villa et al. 2017 (C93))
- 130. Pterygoid recess, development: weak, angle between posteriormost point of recess and anteriormost points of anteromedial and -lateral processes > 90° (0); deep, angle 90° or less (1). (Barahona & Barbadillo 1997, modified by Villa et al. 2017 (C94))
- 131. Pterygoid, palatine processes, orientation in articulated skulls: parallel (0); convergent(1). (Barahona & Barbadillo 1997, wording modified by Villa et al. 2017 (C95), wording modified)
- 132. Pterygoid, dorsal surface, crest separating concave area between columellar crest and transverse crest: absent (0); present (1).
- 133. Pterygoid, quadrate process, pterygoid ridge on dorsolateral surface, development: weakly developed (0); laminar crest (1).
- 134. Pterygoid, ventral surface, distinct ridge on transverse crest: present (0); absent (1).(Villa et al. 2017 (C96), wording modified)

- 135. Pterygoid teeth: present (0); absent (1). ((Boulenger 1916); (Pregill et al. 1986); Müller2001 (C40); modified by Gauthier et al. 2012 (C267); Villa et al. 2017 (C97))
- 136. Pterygoid teeth, arrangement (if present): patch (0); mostly in single line (1). (Müller 2001 (C40); modified by Villa et al. 2017 (C98))
- 137. Ectopterygoid posterolateral process, length: long process (0); short knob (1). ((Smith 2009); Gauthier et al. 2012 (C283), modified to adapt to restricted taxon sampling)
- 138. Dentary, shape: continuously broadening dorsoventrally towards distal (0); sickleshaped, subparallel in distal half, tapering mesially (1).
- 139. Dentary, splenial facet on subdental ridge, development: weak (0); well-developed (1).((Bailon et al. 2014))
- 140. Dentary, symphysis, distinct articular facet: absent (0); present (1).
- 141. Dentary, Meckelian fossa, anterior portion, shape: closed, open portion restricted posteriorly (0); open portion nearly reaching symphysis (1). ((Hoffstetter 1944); Müller 2001 (C30); modified)
- 142. Dentary, tooth row, differences in tooth size: significant (0); minimal (1).
- 143. Dentary, tooth row, orientation in lateral view: rather straight (0); curves distinctly dorsally towards distal end (1).
- 144. Dentary, coronoid process, dorsal expansion: level with tooth row (0); strongly expanded above distal-most teeth (1).
- 145. Dentary, coronoid process, length: shorter than angular process (0); equally long to longer than angular process (1). ((Rauscher 1992), Barahona & Barbadillo 1997, modified by Villa et al. 2017 (C99))
- 146. Dentary, coronoid facet on labial surface, shape: shallow, with indistinct margins (0); distinct (1).
- 147. Dentary, surangular process: absent (0); present (1). ((Rauscher 1992); Villa et al. 2017 (C100))
- 148. Dentary, angular process, posterior end: blunt (0); pointed (1). ((Rauscher 1992; figs 16-19); Villa et al. 2017 (C101))
- 149. Dentary, angular process, posterior extension; reaches below or exceeds coronoid apex (0); restricted anterior to coronoid apex (1); restricted anterior to entire coronoid bone (2). ((Gauthier 1982); Čerňanský et al. 2016 (C39))
- 150. Splenial, anterior extension relative to dentary tooth row: around one-third (or less) (0); about one-half (1); about two-third (2); three-fourth (or more) (3). (Müller 2001 (C31); Gauthier et al. 2012, wording modified by Villa et al. 2017 (C102))
- 151. Splenial, anterior end: single (0); bifid (1). ((Barahona 1996); Villa et al. 2017 (C103))
- 152. Splenial, medial surface anterior to splenial anterior inferior alveolar foramen: flat or weakly concave (0); strongly concave dorsoventrally (1). (Villa et al. 2017 (C104), wording modified)
- 153. Splenial, posterior end, shape: single (0); bifid (1). (Villa et al. 2017 (C105), wording modified)
- 154. Coronoid, anteromedial process, anterior end, shape: pointed (0); blunt (1). (Villa et al. 2017 (C106))
- 155. Coronoid, angle between anteromedial process and posteromedial process in medial view: more open, > 50° (0); more acute, 50° or less (1). (Čerňanský et al. 2016 (C42), wording adapted to terminology proposed by Rauscher (1992))
- 156. Surangular, labial surface, distinct horizontal crest: absent (0); present, delimits adductor fossa ventrally (1).
- 157. Surangular adductor fossa on labial face of mandible: shallow, not extending further ventrally than midheight (0); deep, extending nearly to angular (1). ((Gauthier 1984); Estes et al. 1988 (C81); Gauthier et al. 2012 (C399), wording modified)
- 158. Articular, dorsal margin of anterior ramus: with distinct bulge (0); straight (1).(Barahona & Barbadillo 1997 (C18), wording modified by Villa et al. 2017 (C107))
- 159. Retroarticular process, dorsal surface posterior to articular facet: flat to weakly concave transversely (0); strongly concave transversely (1). (Estes et al. 1988 (C74); Müller 2001 (C34); wording modified)
- 160. Retroarticular process breadth (greatest width) relative to mandibular condyle (glenoid): narrower (0); wider (1). ((Estes et al. 1988); Müller 2001 (C37); Gauthier et al. 2012 (C401))
- 161. Palpebral, posterior margin: strongly concave, with elongate dorsoposterolateral process (0); relatively straight, palpebral outline subtriangular (1). (Barahona & Barbadillo 1997 (C19), wording modified by Villa et al. 2017 (C108))
- 162. Ossification of temporal scales: little or none (0); extensive (1). (Arnold 1973 (C5), 1989 (C19); Arnold et al. 2007 (C12); wording modified by Villa et al. 2017 (C109))

- 163. Teeth, premaxillary, crown morphology: biscupid teeth present (0); absent (1). (Barahona & Barbadillo 1997, modified by Villa et al. 2017 (C111))
- 164. Teeth, maxillary, size compared to premaxillary teeth: significantly larger (0); similar (1). (Barahona & Barbadillo 1997; Villa et al. 2017 (C112), wording modified)
- 165. Teeth, maxillary, crown morphology in majority of teeth: monocuspid (0); bicuspid (1);
 tricuspid (2); > 3 cusps (3). ((Siebenrock 1894); Barahona & Barbadillo 1997, modified by Villa et al. 2017 (C113))
- 166. Teeth, maxilla and dentary, location of most robust teeth: anterior half (0); central (1); distal half (2); distal-most (3). ((De Stefano 1903); Villa et al. 2017 (C114))
- 167. Teeth, maxilla and dentary, distal transition from larger to smaller teeth (if present): gradual (0); distinct (1). (Villa et al. 2017 (C115))
- 168. Teeth, dentary, crown morphology in majority of teeth: monocuspid (0); bicuspid (1); tricuspid (2); > 3 cusps (3). (Villa et al. 2017 (C116))
- 169. Teeth, crown surface: smooth (0); with longitudinal striae (1).
- 170. Tooth crowns, striae spacing (if present): wide (0); narrow (1).
- 171. Teeth, dentary tooth crowns overtop dental crest: by less than half their height (0); by half their height or more (1). ((Böhme 2010); Villa et al. 2017 (C117))
- 172. Atlas, foramen on lateral surface: absent (0); present (1). (Villa et al. 2017 (C118))
- 173. Atlas, foramen on lateral surface, position: centrum (0); neural arch (1). ((Calori 1858); Villa et al. 2017 (C119))
- 174. Atlas, intercentrum, ventral keel, dorsoventral height in comparison to centrum: subequal to smaller (0); considerably larger (1). (Villa et al. 2017 (C120))
- 175. Atlantal intercentrum, ventral keel anteroposterior length compared to centrum length: shorter to subequal (0); considerably longer (1). (Villa et al. 2017 (C121))
- 176. Atlas, ventral keel, shape: confluent with centrum anteriorly and posteriorly (0); separated from centrum by transverse grooves (1). (Villa et al. 2017 (C122))
- 177. Atlantal neural arches, anterior and posterior articular facets on base, dorsal separation: present (0); absent (1). (Villa et al. 2017 (C123))
- 178. Atlantal neural arch, posterolateral projection on base: small tubercle (0); distinct projection (1). (Villa et al. 2017 (C124))
- 179. Atlantal neural arch, dorsal process, width to length: wider than long (0); subequal to narrower (1). (Villa et al. 2017 (C125))

- 180. Atlantal neural arch, dorsal process, medial edge, dorsoventral height: high, with distinct medial surface (0); tapering to a thin edge (1). (Villa et al. 2017 (C126))
- 181. Atlantal neural arch, indentation of posterior margin of dorsal process: deep, forming distinct posterior extension (0); shallow (1). (Villa et al. 2017 (C127))
- 182. Axial centrum, articular surface with odontoid process, dorsoventral midline groove, width: narrow (0); wide, approximately 1/3 of facet (1). (Villa et al. 2017 (C128))
- 183. Axial centrum, depression on posterior articular condyle: absent (0); present (1). (Villa et al. 2017 (C129))
- 184. Axial centrum, longitudinal ventral crest: absent (0); present (1). (Villa et al. 2017 (C130))
- 185. Axial centrum, neural canal floor, longitudinal median ridge, shape: continuous (0); interrupted at midlength (1). (Villa et al. 2017 (C131))
- 186. Axial intercentrum, ventral keel, anterior extension: absent (0); present (1). (Villa et al. 2017 (C132))
- 187. Axial intercentrum, ventral keel, collateral posterior projections on proximal base: absent (0); present (1). (Villa et al. 2017 (C133))
- 188. Axis, postzygapophyseal facets, shape in posterior view: straight (0); concave (1).(Villa et al. 2017 (C134))
- 189. Axial neural spine, posterior extension: terminates anterior to or at posterior end of centrum (0); exceeds posterior end of centrum (1). (Villa et al. 2017 (C135))
- 190. Axial neural spine, sprl, shape: simple (0); bifurcates ventrally, forming transverse ridge posterior to prezygapophyseal facet (1). (Villa et al. 2017 (C136); can have bilateral asymmetry)
- 191. Axis, posteriorly projecting process dorsal to postzygapophysis: absent (0); present (1).(Villa et al. 2017 (C137), wording modified)
- 192. Presacral centrum, posterior articular condyle, transverse expansion compared to centrum: wider (0); narrower, condyle circumscribed by distinct groove dorsally and laterally (1). ((Hoffstetter & Gasc 1969); Villa et al. 2017 (C138))
- 193. Cervical neural spine, dorsal edge, shape: simple (0); with longitudinal groove, resulting in slight bifurcation (1). (Villa et al. 2017 (C139))

- 194. Postaxial presacral neural spine, shape in lateral view: subparallel anterior and posterior edges (0); anterior edge much more inclined than posterior edge (1). (Villa et al. 2017 (C140))
- 195. Postaxial presacral neural arch, zygosphene-zygantrum articulation: absent (0); present (1). ((Hoffstetter & Gasc 1969); Estes et al. 1988 (C96), polarity reversed due to limited taxon sampling)
- 196. Anterior postaxial cervical neural spines, inclination of anterior edge in relation to neural canal floor: weak, < 40° (0); strong, 40° or greater (1). (Villa et al. 2017 (C141))
- 197. Cervical vertebra 3, ossified cervical ribs: absent (0); present (1). ((Arribas 1998); Villa et al. 2017 (C142))
- 198. Cervical ribs, expansion of distal end of anterior elements: wide (0); narrow, not significantly wider than anterior end (1). (Villa et al. 2017 (C143))
- 199. Cervical intercentra, lateral crests: absent (0); present (1). ((Al-Hassawi 2004))
- 200. Dorsal synapophyses, foramen on dorsolateral portion: absent (0); present (1). (Villa et al. 2017 (C145))
- 201. Dorsal vertebrae, posterior centrosynapophyseal lamina: absent (0); present (1). (Villa et al. 2017 (C146))
- 202. Dorsal vertebral spines, foramina on lateral surface of spol: absent (0); present (1). (Villa et al. 2017 (C147))
- 203. Posterior dorsal vertebral centra, ventral keel: absent (0); present (1). (Villa et al. 2017 (C144), modified)
- 204. Posterior dorsal neural spines, development: distinct, elevated (0); reduced to a ridge (1). (Villa et al. 2017 (C148))
- 205. Sacral vertebra 2, pleurapophyses, shape in dorsal view: curved (0); straight (1). (Villa et al. 2017 (C149), wording modified)
- 206. Sacral vertebra 2, pleurapophyses, posterolateral projection on posterior edge: present (0); absent (1).
- 207. Caudal, autotomic vertebrae, transverse processes on posterior portion: absent (0); present (1). ((Etheridge 1967); Arnold 1973 (C12, fig. 4), 1989 (C31, fig. 11); Arnold et al. 2007 (C19); modified by Villa et al. 2017 (C150))

- 208. Caudal, autotomic vertebrae, transverse processes on posterior portion, length compared to anterior process: shorter (0); longer (1). ((Etheridge 1967); Arnold 1973 (C12, fig. 4), 1989 (C31, fig. 11); Arnold et al. 2007 (C19); modified by Villa et al. 2017 (C151))
- 209. Caudal centra, pedicels for haemal arches: present (0); absent (1). ((Pregill et al. 1986); Gauthier et al. 2012 (C475), modified to adapt to restricted taxon sampling)
- 210. Chevrons, articulation with caudal vertebrae: entirely with more anterior element (0); between anterior and posterior caudal centrum (1). ((Hoffstetter & Gasc 1969))
- 211. Scapulacoracoid, secondary, ventral coracoid emargination: absent (0); present (1). ((Lecuru 1968); Estes et al. 1988 (C113); Müller 2001 (C51); wording modified)
- 212. Clavicle, medial loop: complete (0); interrupted posteriorly (1). ((Boulenger 1920); Arnold 1973 (C9, fig. 3); 1989 (C22, fig. 9); Arnold et al. 2007 (C15); modified by Villa et al. 2017 (C152))
- 213. Interclavicle, transverse arms orientation: perpendicular to sagittal axis or slightly curving forward (0); directed obliquely backwards (1). (Arnold 1973 (C11, fig. 3), 1989 (C24, fig. 10); Arnold et al. 2007 (C16); wording modified by Villa et al. 2017 (C153))
- 214. Sternal fontanelle: absent (0); present (1). (Estes et al. 1988 (C121); Gauthier et al. 2012 (C481))
- 215. Sternal fontanelle, shape: heart-shaped (0); oval (1). ((Siebenrock 1894); Arnold 1973 (C10, fig. 3), 1989 (C26, fig. 10); Arnold et al. 2007 (C17); polarity reversed by Villa et al. 2017 (C154))
- 216. Xiphisternal fontanelle: absent (0); present (1). (Gauthier et al. 2012 (C485))
- 217. Inscriptional ribs: absent (0); present (1). ((Arnold 1973); Arnold 1989 (C30); Arnold et al. 2007 (C18); polarity reversed by Villa et al. 2017 (C155))
- 218. Humerus, area dorsal to deltopectoral crest: concave (0); flat to convex (1).
- 219. Humerus, subcondylar and subtrochlear fossae, shape: form an m-shape, with a deep dorsal incision between them (0); conjoined completely medially (1). ((Lécuru 1969))
- 220. Manus and pes, distal-most non-ungual phalanx, length compared to preceding phalanx: equal to shorter (0); longer (1). ((Arnold 1998); Villa et al. 2017 (C157))

- 221. Ilium, preacetabular process: present (0); absent (1). ((Lee 1998); Gauthier et al. 2012 (C521), wording modified)
- 222. Ischium, posterior process, shape: subtriangular (0); pointed process, posteroventral edge of ischium is concave (1). (Villa et al. 2017 (C158))
- 223. Ischium, posterodorsal edge, shape: straight to slightly concave (0); convex, or somewhat sinuous (1). (Villa et al. 2017 (C159))

Appendix 7

List of specimens studied for the phylogenetic analysis conducted in chapter 4. Abbreviations: CIPA - Osteoteca, Laboratorio Arqueociencias, Lisbon, Portugal; CMGR -Collezione Mauro Grano, Roma, Italy; HUJ.OST - Osteological collection of the Hebrew University of Jerusalem, Israel; ICP - Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; MDHC - Massimo Delfino Herpetological Collection, Departement of Earth Sciences, University of Torino, Italy; MNCN - Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN - Muséum national d'Histoire naturelle, Paris, France; MRAC -Royal Museum for Central Africa, Tervuren, Belgium; NHMUK - Natural History Museum, London, UK; NHMW - Naturhistorisches Museum Wien, Austria; PIMUZ -Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SRK - Ralf Kosma's personal collection; UAM - Universidad Autonoma de Madrid, Spain; ZZSiD -Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.

Lacertidae

Acanthodactylus boskianus: MDHC 276. Acanthodactylus erythrurus: UAM.R Ac-VII. Algyroides fitzingeri: MDHC 351. Algyroides nigropunctatus: NHMW 797. Archaeolacerta bedriagae: MDHC 167; SRK 00.120. Eremias velox: NHMW 822. Gallotia caesaris: SRK 00.346. Gallotia stehlini: MNCN-22226. Iberolacerta cyreni: UAM.R Lm-4. Iberolacerta monticola: UAM.R Lm77, 92. Lacerta agilis: CIPA 1550; MDHC 176, 177, 178, 230, 231; MNCN-15979; MNHN 1963-49; NHMW 802; PIMUZ A/III 0902. Lacerta bilineata: MDHC 15, 48, 73, 77, 84, 381, 420; MNCN-16505; UAM Q-21. Lacerta media: NHMW 34809; HUJ-OST-Z-299, 396. Lacerta schreiberi: CIPA 778, 1045, 1256, 1511, 1517; NHMUK 1906.10.30.14; UAM S-6. Lacerta strigata: MDHC 304; NHMW 10918.

Lacerta trilineata: MDHC 240, 241, 295, 356; NHMUK 1914.1.12.1; ZZSiD R/235/76.

Lacerta viridis: MNCN-16504; MNHN 1887-813, 1888-139; NHMW 887, 906, 32879:3;

PIMUZ A/III 1276; ZZSiD R/287/80, 463/87.

Podarcis hispanicus: UAM R H30.

Podarcis muralis: MDHC 311, 312, 313.

Podarcis siculus: MDHC 25, 125.

Podarcis tiliguerta: MDHC 153.

Podarcis waglerianus: MDHC 390.

Psammodromus algirus: NHMW 788; UAM R PS-9.

Pseudeumeces cadurcensis; MNHN PFR 11004, QU 17169, QU 17180, QU 17749.

Timon kurdistanicus: NHMW 18545.

Timon lepidus: CIPA 761; MDHC 216; MNCN-41021; MNHN 1887-545; MRAC 3390, 92-050-R-1; NHMW 699; PIMUZ A/III 0965.

Timon pater: NHMUK 1920.1.20.1259, 1920.1.20.2722.

Timon princeps: NHMW 32881.

Zootoca vivipara: MDHC 179.

Teiidae

Salvator merianae: COMGR 235.

Scincidae

Chalcides ocellatus: MDHC 193.

Varanidae

Varanus exanthematicus: MDHC 335.

Additional sources taken from the literature.

Acanthodactylus boskianus, Timon princeps, Zootoca vivipara:

Arnold E.N. (1989). Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. Bulletin of the British Museum, Natural History. Zoology, 55: 209-257.

Algyroides fitzingeri, Chalcides ocellatus:

Lécuru S. (1968). Remarques sur le scapulo-coracoïde des lacertiliens. Annales des Sciences Naturelles, Zoologie, Paris, 10: 475-510.

Gallotia caesaris, Gallotia stehlini:

- Barahona F., López-Jurado L.F., Mateo J.A. (1998). Estudio anatómico del esqueleto en el género *Gallotia* (Squamata: Lacertidae). Revista Española de Herpetología, 12: 68-89.
- Barahona F., Evans S.E., Mateo J.A., García-Márquez M., López-Jurado L.F. (2000). Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary Islands. Journal of Zoology, 250: 373-388.

Janosikia ulmensis, Podarcis muralis, Pseudeumeces cadurcensis:

Čerňanský A., Klembara J., Smith K.T. (2016). Fossil lizard from central Europe resolves the origin of large body size and herbivory in giant Canary Island lacertids. Zoological Journal of the Linnean Society, 176 (4): 861-877.

Varanus exanthematicus:

Gauthier J.A., Kearney M., Maisano J.A., Rieppel O., Behlke A.D.B. (2012). Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History, 53: 3-308.

Appendix 8

Character matrix used in the phylogenetic analysis conducted in chapter 4.

Standard Categorical Data (compacted) Number of characters: 223 Number of taxa: 36 Number of characters excluded: 0 Proportion of missing data: 0.22421525 Proportion of inapplicable codings: 0.01706527

Varanus_exanthematicus

112001?130 21-11101-- 0121210010 1100101-01 010001?000 000-01010? 0011111100 1010-11011 -?0-110110 1110011100 0101000000 1001100000 1-0110?1?1 ?0011-1001 00000100?1 000000?100 ??10030011 10-0111010 01011??100 100001??11 000010--00 1110-0?00? 000

Chalcides_ocellatus

102011?000 21-01??1-- 1121101121 0011101-01 00110??000 110-0100-? 011010?101 0110-1?0?? -?0-110001 0110001110 00?1101010 00110??000 0100110??1 ?1101-1011 01010001?1 10001???01 ??10020011 111???0101 0?01001110 111101?110 0000011100 0000-??01? 100

Salvator_merianae

Gallotia_caesaris

Gallotia_stehlini

11011???11????0?????????0?????111?0??110111???00???101110-?????????01100??01?????1100?0?011?1????11????00????0?1?100001-??10?1?0???100?0??11001?01????0????110?11031?3??01101000010??1?0101101?1?????111011??????01????????0?

Psammodromus_algirus

 1011101?10/1
 1/20010010/120
 1101111111
 1110/100/10000
 0111000000
 10101110-0

 110/1010?011
 00010/10/1010/11
 2110/10000/111
 0/10/100001011
 1100-00100

 10/11100/110/10
 000110/10100/1
 00/11000/110?0
 1100010102/3
 00/100010110

 01101/2201/20/10
 0/10-000?10?
 0?00/1100011
 0/110100/110
 100/101010?

 00011?1011
 0/10-000?10?
 0?00/1100011
 0/110100/110
 100/101010?

Acanthodactylus_boskianus

102110??20 2102010111 0211201??1 110101010 01110??000 001011010? 011????011 0000-1010? 2?0-1100?1 0100100100 10?1101100 0011111100 000000?1?1 ?0111-01?0 11000001?? 0100001010 0?1111010- 10-0000111 1?01111000 010110?111 1001101111 00010??00? 000

Acanthodactylus_erythrurus

001111??20 2?120101-- 0211101101 1101010101 01110??001 10101100-? 111001?011 0000-11111 2?111100?1 01001?0100 10?1101100 01111?11?0 000000?1?0 ?0010101?0 1100?00??? 0100100010 ??1111/2010- 110??00111 1?01111000 010110?110 1001101111 000????00? 000

Eremias_velox

0021102?31 20020001-- ????????? ?11101??01 ???1?0000? 0010100100 ?00????011 0?00-1?011 010-0?0010 1100110??0 1001101?0? ?01101111? 1-00000?10 0?1?1-01?1 11000?0103 0100101010 ?0101201?? 1??000?10? ???0?00?11 0101?001?? 1001100-?? ?011011??0 00?

Mesalina_guttulata

102111??11 2102000120 020020???1 1101000101 01110??000 000-1100-? 101101?010 0110-11?10 ??0-1101?0 1100011011 10?1101100 101110?100 010001?1?1 ?0111-11?0 11000001?? 0000011010 0?1103-00- 0110000011 0?00110000 011100?101 0001001111 01?????10? 000

Ophisops_elegans

002110??20 2002011120 0/10/2001/211??1 110100/10001 01110??000 10100100-? 101001?010 1010-11111 ??0-1001?1 1100000111 10?1101100 00/110001100 010001?1?1 ?0111-11?0 11000101?3 0000011110 1?1112-10- 00-0100001 1?00110010 011100?100 0001101111 000????10? 001

Algyroides_fitzingeri

10111????0 2?????020 02??20???1 1111000000 10110??001 11011100-? 101????1?? ????0???? ??111001?0 1100011111 11?0-01100 101010?100 1-0101?1?0 ?0111?1100 11000001?? ???001?010 ??1012010- 1??001???? ?????????? ?10110???0 0001001?1? 0??11??10? 011

Algyroides_nigropunctatus

Archaeolacerta_bedriagae

101/2110??00/1 1101000020 0201200101 1111000000 01110?1000 0000/10/1110/101 111100/1?101 0001101010 2210110110/1 1110111110/1 1100/1001100 001110?0/100 0000/1011111 00/10/111-1101 1100001102 00/100/1101110 ??10120/1111 10-0010101 1?00110100 010110?1?1 000111101? 010????10? 000

Iberolacerta_cyreni

Iberolacerta_monticola

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 0/1111010001
 11110??000
 10010110-?

 101100/1?101
 0111001011
 ??10110101
 1100110/1111
 21?0-01100
 1-11000100
 1

 00/100?0?1
 ?0/1011-10?0
 11000110??
 010010/11110
 1?00210211
 1110000/1001

 0/1?000/1100/111
 010110?101
 000110/10-11
 010????00?
 011

Podarcis_hispanicus

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Podarcis_muralis

00111???1/20 0001000020 0/11/20110/11101 1110010001 00110?1000 001111111? 101101?101 0001101011 ??101101?1 1100001011 11?0-00100 1011110110 000111?1?1 ?0101-0000 11000001?? 0110001110 0/1?0/10/112010- 00/10000/10101 1?00/110/100/110 11010/10/1?101 0000/1111111 010????10? 010

Podarcis_siculus

001110/1?00/10 110/110010/120 110/11211111 1110/1010001 00/1110?0000 0101100010/1 0/1010/111111/21 101010/11101 ??10/10/100111 11000/111111 10/1?0/1110/1100 001110?0/10/10 00010/10/1?0/100/1 10/110/10/110/10/110 1100000/1102 001010/1?0/110 ??10/112/3010-10-00100/101 1?0/10/1000/1110/1 0/110110/1?010/1 0000111111 010????10? 011

Podarcis_tiliguerta

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 110100?021
 01/21020/11111
 1111000000
 00/10/110??010

 00/10/10110/111/2?
 1110/100/1?101
 1101000/1110/1
 ??111001?0/1
 110/100/11111
 11?

 00/10/10110/111/2?
 1110/100/1?101
 1101000/1110/1
 ??111001?0/1
 110/100/11111
 11?

 00/1100
 101101?110
 000101?0?1
 ?0101-0000
 110010/111?
 0100/101?110
 ??0013-10

 00/10/10101
 1?01000/10/110/1
 0/110111?0/101
 000000/10/11111
 010????00/1?
 010/1

Podarcis_waglerianus

002111??20 110100?020 1121111111 1110000001 00110??010 101011111? 100101?101 1001101011 ??100001?1 1001011011 11?0-01100 001100?100 000110?1?1 ?0101-1000 11000111?? 010001?110 1?1012010- 1110010111 1?11010111 11111?101 100011111? 010????11? 010

Zootoca_vivipara

001111??00 011101?120 0201101121 1101010010 00110??001 100-0100-? 101101?101 1100-1100? ??101101?1 01101?0001 10?1001100 011110?100 1-0001?1?0 ?0101-0101 11000011?? 111101?110 0?10220210 10-1011101 1?00100111 010111??10 0001?0??1? 0??1???01? 011

Timon_pater_sspp

1111112?1?0?1010?0?1?????????0/1111010?010011?000?0/10???01110??00/101???010????0??0??2101??1111?01?01??1?010-0/10001?000?1?010010/11101?100/10?0/10010?111000?0/11?3100/10?10/1??0?1101002100/10-01?00101??1?01?111111?100?0100011101??0/100/1?111?1011

Timon_princeps_sspp

Timon_lepidus_sspp

 1111112111
 1111101002
 1021101111
 1111010010
 0111000110
 1001011100/1

 1001101101
 000/11100001
 01/210100011
 0001001011
 2110-00001
 1000011110

0101101010 1000010011 1100101113 1000110010 110/10100111 01101100/111 1?01011111 1101110011 1010111010 010/1

Lacerta_agilis

 1011112?00
 0101100/1120
 010/11101101
 1110010001
 0111101000
 1010111120

 101111?0/101
 00111000/111
 0210000111
 1101101011
 1100-01100
 0011000100

 000110110/11
 0011010100
 1100101113
 010010/11110
 1010110111
 1100100101

 1?00000011
 1101110/10/100
 0001011011
 01011110/100
 011

Lacerta_bilineata

 101111?021
 1101101020
 111/21111111
 1110010001
 01110??111
 101011111?

 001110?101
 0110-00011
 ??10010111
 1101011011
 1110-00001
 1011000000
 010110?1?0

 ?001000010
 1100111103
 1001101110
 ??10120110
 1111110101
 1101100011
 110111?011

 101011101
 0001111000
 011
 0111000011
 110111?011

Lacerta_media

101111??10/1 2??110?020 ?10/11000111 0111?01111 1010111121 ??00/1110?01 ?01??00?11 11?1111011 1110-00??? ?00100/1?0?0 ?11010?111 0101101111 1??001?0?? ?1001?1103 011?1100?0 ?10/1012011? 00-????111 010/110/1000/110 0/1?01?????0 10101????? ?00??????? ???

Lacerta_schreiberi

 1011112?10
 1110101020/1
 2101110101
 1111010011
 0111000011
 101111110?

 0/1010/10/10/12101
 0011000100
 2010100111
 1000/1011011
 1110-000/101
 101000/10000

 01011010/111
 0101010021
 1100001123
 110010/11110
 2110120110
 0/10-0011100/1

 01000000/1011
 0/10101111120
 1000101011
 01011110
 2110120110
 0/10-0011100/1

Lacerta_strigata

Lacerta_trilineata

 101/21111?20
 01100/101020
 211111111
 1111010000
 1011000011
 101011112?

 0001101101
 0001100011
 10100/110111
 1100/1001011
 1/20/110-00001
 000100000/10

 0101101110
 0000/1010010
 1100000/11?3
 1110111110
 0110120110/1
 1110100111

 1001101111
 110111011
 000111000
 0110120110/1
 1110100111

Lacerta_viridis

 101/21111020
 0100100020
 211111111
 1111010010/1
 110100010
 1010111121

 0/10111010/101
 1010/10/100011
 0?10000111
 1101000/1011
 1/2110-100/101

 0/10/11100/11110
 0001101110/1
 0/10010100?0
 1100001103
 1100111010
 1110120110

 0/1110110110/1
 1101001011
 1101110110
 110010101
 1110120110

Janosikia_ulmensis

Monte_Tuttavista

Pseudeumeces_cadurcensis

Maioricalacerta_rafelinensis

Appendix 9

Data included in some of the chapters composing this thesis have been partly published. Here, a list of the related papers is reported.

Chapter 2

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