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# A comparative atlas of the skull osteology of European lizards (Reptilia: Squamata)

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Skull osteology of European lizards

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ABSTRACT

The fossil record testifies for a very long evolutionary history of European lizards. Since fossil lizards are regularly represented by bone remains, the knowledge of the deep roots of extant taxa, as well as of their distribution in time and space, is hindered by the fact that their comparative osteology is still not adequately known as a whole. Even if a rising interest in this topic is evident since the end of XX century, a gap in our knowledge is still present. We here report the first broad-scale comparative osteological analysis of the skull of extant European lizards, focused at highlighting significant differences that could be used in the identification of their bones. This comparative study, including as much European species as possible, lead to the creation of a detailed diagnostic key for each single bone. Also, the new data herein reported significantly improve the recognisability of extant European non-snake squamates, with the 54% of the current diversity that can be recognised based on the new results contra the previously-estimated 31%. This recognisability is expected to further increase in the future, with new studies focused on species that are either missing or poorly represented here or applying promising advanced methodologies.

Keywords: comparative anatomy - skull - non-snake squamates - identification - diagnostic key

## INTRODUCTION

Interest in the osteology of European lizards is rising since the last decades of the XX century (Villa *et al.*, 2017). As a matter of fact, a distinctly increasing number of papers giving information related to this topic was published since then, being them directly focused on the comparative osteology of these reptiles (e.g., Klemmer, 1957; Arnold, 1989; Barahona & Barbadillo, 1997, 1998; Arnold, Arribas & Carranza, 2007; Klembara *et al.*, 2014; Klembara *et al.*, 2017; Villa *et al.*, 2018a, b) or just mentioning significant osteological features of taxa of interest (e.g., Blain, 2009; Čerňanský et al., 2016; Čerňanský & Smith, 2018; Klembara & Rummel, 2018). Nevertheless, we still face a significant gap in our knowledge of the comparative skeletal anatomy of these animals (Villa *et al.*, 2017). This is rather surprising, given that lizards represent a major component of the extant European herpetofauna (Arnold & Ovenden, 2002; Sillero *et al.*, 2014; Speybroeck *et al.*, 2016) and their remains are commonly found in European palaeontological and archaeological localities (see e.g., Rage 2013; Villa & Delfino, 2018).

Currently, members of eight lizard families are present in Europe, accounting for more than half of all reptile species present in the continent. These families are Agamidae, Chamaeleonidae, Sphaerodactylidae, Gekkonidae, Phyllodactylidae, Lacertidae, Scincidae, and Anguidae. To these, a single family of amphisbaenians (i.e., worm lizards) can be added: Blanidae. In the past, this diversity at high taxonomic level was even greater: mentioning only post-Mesozoic taxa, fossil representatives of extant families that are locally extirpated from Europe nowadays such as iguanids, cordylids, and varanids are known (among others, Estes, 1983; Augé, 2005; Rage, 2013; Villa & Delfino, 2018), as well as now completely extinct families such as eolacertid lizards (Čerňanský & Smith, 2018) and polyodontobaenid amphisbaenians (Folie *et al.*, 2013). In this context, comparative osteology stands out as the main tool available to clearly understand the composition of past European lizards assemblages by correctly identifying their fossil remains, but it is also the main, and often the only, source of data that can be used to infer the relationships between extinct and extant taxa.

In order to fill as much as possible the gap of knowledge we have of the comparative osteology of European lizards, we here provide precise descriptions and figures of the skull bones for five families of these animals, the Agamidae, Chamaeleonidae, Lacertidae, Scincidae, and Anguidae. The three European gekkotan families, Sphaerodactylidae, Gekkonidae, and Phyllodactylidae, were already dealt with in detail by Villa *et al.* (2018a). Given that, they are included only in the key up to the level of infraorder Gekkota here. The descriptions are presented in a comparative fashion, in order to highlight differences and similarities both within different families and different species of a same family. The resulting data are then used to create a diagnostic key for each single bone and to review the osteology-based recognisability of European non-snake squamates.

## MATERIAL AND METHODS

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 was directly studied (see the Supplementary Information for a list of all studied specimens and the institutions where they are stored, including institutional abbreviations). The definition of Europe and the list of European species of lizards follow Villa *et al.* (2017). Therefore we included all the species listed by Sillero *et al.* (2014) plus the lizards living on the Greek islands along the coast of Asiatic Turkey as reported by Speybroeck *et al.* (2016). The complete list counts 75 species on the whole. Of these, we here describe the cranial and lower jaw osteology of 46 taxonomic units (species or species complexes), adding also information taken from the literature about other, non-directly studied species when available. *Psammodromus hispanicus* is here considered in a broad sense, thus including also the recently described *Psammodromus occidentalis* and the recently revalidated *Psammodromus edwarsianus*, because no specimen of these species were available to us for study and most of the data about the skeletal morphology of *Ps. hispanicus* we retrieved from literature predated the works of Fitze *et al.* (2011, 2012) about the other two species of small European

*Psammodromus*. *Anguis fragilis* was recently split 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. Since there is currently no evidence for discrete morphological differences among the skeleton of these species, we considered the morphology of the available specimens of *A. veronensis* as representative of the *Anguis* gr. *A. fragilis* species complex pending a detailed comparative osteological analysis of the extant species of the genus. 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 was possible to obtain only few data on the precise morphology of its bones. A similar problem comes up with one of the two studied *Trachylepis aurata*, MNHN 1887-863, which is represented only by an isolated left lower jaw.

Some of the species included in the species list of European lizards on which this study is based 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*. It has to be said that all the missing species are lacertids, most of which with very limited distribution, and most of them belong to *Podarcis,* a genus with a skeletal morphology that appears quite uniform. When available, osteological data related to these species were obtained from the bibliography. Worth mentioning is that details about the osteology of European non-snake squamates have been at least mentioned or fully described in more than 100 papers. For a complete list of these works, see the Supplementary Information. A detailed study of the skull osteology of European gekkotans was recently published by Villa *et al.* (2018a). To avoid redundancy, descriptions of the bones of this lizard group are not included here and the reader is referred to the related paper. A certain degree of repetition is however unavoidable in the description of the general structures of the bones. From a nomenclatural perspective, some changes were recently made in the generic attribution of some European lizard (e.g., *Laudakia stellio* was moved to its own genus *Stellagama* by Baig *et al.*, 2012, whereas *Trachylepis aurata* was referred to *Heremites* by Karin *et al.*, 2016). To avoid confusion in the reader, however, we herein maintain the same taxon names used in the most up-to-date compendia of extant European lizards (namely, the atlas by Sillero *et al.*, 2014, and the field guide by Speybroeck *et al.*, 2016).

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), Klembara *et al.* (2010, 2014), and Rage & Augé (2010) when they were lacking in the above mentioned work. The bones are 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 were photographed with the following sets: 1) Leica M205 microscope equipped with the Leica application suite V 3.3.0 or V 4.10 at the University of Torino; 2) Canon EOS 50D camera mounted on a Leica M420 microscope at the Natural History Museum of Vienna; 3) Samsung WB252F Digital Camera.

## RESULTS

### NASAL

The nasal (Fig. 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. 1A-C)*

In *Laudakia 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 in the specimens we studied (in contrast with the short process reported by Smith *et al.*, 2016), whereas the anterolateral one is very short (slightly longer in MDHC 245; Fig. 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. 1A). The lappet, however, is not distinctly developed in MDHC 245 (Fig. 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. 1C) or absent (e.g., HUJ.OST-Z-424; Fig. 1B) and it is therefore possible that they are susceptible to some kind of variation.

*Chamaeleonidae (Fig. 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. 1D). The anterior end displays a moderately wide, moderately long and pointed anteromedial process. The anterolateral process is not clearly recognisable, 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.

### *Lacertidae (Fig. 1F-M)*

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 well-developed dermal ornamentation (Fig. 1H, J), at least in adults. The ornamentation is less marked in *Acanthodactylus erythrurus* (Fig. 1F), *Dalmatolacerta oxycephala*, *Iberolacerta bonnali* and *Iberolacerta horvathi*, almost absent in *Ophisops elegans* (Fig. 1L), and restricted to the posterior half in *Algyroides* (Fig. 1H) and *Psammodromus hispanicus*. In the largest specimens of *Algyroides nigropuctatus* (e.g., MDHC 243), however, the ornamentation can reach also the anterior margin on the lateral side of the bone. Barahona (1996) reported that the dermal cover can overstep the anterior margin of the bone in adults of *Iberolacerta monticola*, *Lacerta schreiberi*, *Lacerta viridis* (= *Lacerta bilineata*), *Podarcis muralis* and *Timon lepidus*, hiding also the anteromedial process in the largest species. This holds true also for other medium- or large-sized species, such as *Lacerta trilineata* and *Podarcis 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*, *Dinarolacerta mosorensis, I. bonnali* (according to Barahona, 1996, but UAM.R.Lm28A shows it), *Iberolacerta cyreni*, *I. horvathi*, *I. monticola cantabrica*, *O. elegans*, *Podarcis bocagei*, *Podarcis carbonelli* and *Podarcis hispanicus*.

### *Scincidae (Fig. 1N-R)*

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 *Trachylepis aurata*; Fig. 1Q-R), 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 *Chalcides chalcides* (Fig. 1N-O), *Chalcides striatus* and *Ophiomorus punctatissimus*, whereas it is slightly irregular and rounded in *Ablepharus kitaibelii*, *Chalcides ocellatus* (Fig. 1P) and *T. aurata* (Fig. 1Q-R). 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 1O-P). In *A. kitaibelii*, *C. ocellatus* (Fig. 1P), *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. 1N) and *C. striatus* and more developed in *C. ocellatus*, covers a small area in the middle of the dorsal surface. The ornamentation seems to be subject to a certain degree of individual variation, since the dorsal surface of smaller specimens of *C. ocellatus* is smooth. Moreover, the ornamentation is not present in *A. kitaibelii*, *O. punctatissimus* and in the single examined specimen of *T. aurata* (Fig. 1Q).

*Anguidae (Fig. 1S-V)*

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 does not project anteriorly. The anteromedial process, on the other hand, is rather long and slender in *Anguis* gr. *A. fragilis* (Fig. 1S-T) and moderately short and wide in *Pseudopus apodus* (Fig. 1U-V). The articulation surface with the premaxilla covers only the dorsal surface of the latter process (Fig. 1S). The posterior margin can either be straight and oblique (in both *Anguis* gr. *A. fragilis* and *P. apodus*; Fig. 1V) or present a small and roughly V-shaped notch in the middle (only in *Anguis* gr. *A. fragilis*; Fig. 1S-T). In *P. apodus*, the posterolateral corner is strongly developed, forming a long and pointed process (Fig. 1V). 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. 1U). 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 specimens 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. 1U). 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. 2, 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 end 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 postfrontal/postorbitofrontal can be present laterally near 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. 2A-D, 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 midlength 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. 2C-D). Smith *et al.* (2016; see their Supplementary Information) reported that this expansion can be already well developed in young individuals. 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. 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. 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 is visible (Fig. 3G). Cristae cranii are not developed and are represented only by weak ventral swellings along the lateral margins (Fig. 2B, D, 3G). The swellings 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. 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. 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. 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 MNHN 1887-875. 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. 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. 2F). Some specimens (e.g., NHMW 611; Fig. 2F) display also the articulation surfaces 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.

*Lacertidae (Fig. 2G-Q, 3H)*

Frontals of lacertids are paired, but they can fuse during ontogeny. Only in *A. erythrurus*, *Eremias 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. 2G-H); in this case, the suture line is not visible on the ventral surface. The medial constriction, which is always well evident in juveniles (Fig. 4), varies among different species in the adults: frontals of *A. erythrurus*, *E. arguta* and *O. elegans* are very strongly constricted (Fig. 2G-H), those of *Archaeolacerta bedriagae, Algyroides, D. oxycephala, D. mosorensis, Hellenolacerta graeca, I. bonnali, I. cyreni, I. horvathi, I. monticola, P. bocagei, P. carbonelli, Podarcis filfolensis, Po. hispanicus, Podarcis lilfordi, Podarcis melisellensis, Podarcis milensis, P. muralis, Podarcis pityusensis, Podarcis siculus, Podarcis tauricus, P. tiliguerta, Podarcis waglerianus, Psammodromus, T. lepidus* and *Zootoca vivipara* are slightly constricted (Fig. 2K-Q), and those of *Lacerta* have roughly parallel margins (Fig. 2I-J). As a rule, the posterior end is twice as large as the anterior one, giving a shape that roughly resembles an L to the unfused bone and a T to 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. 2I-J, M-N). 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. 4; 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 (*Algyroides marchi*, *Algyroides moreoticus*, *I. bonnali*, *I. cyreni*, *I. horvathi*, *I. monticola*, *Lacerta*, *T. lepidus* and *Z. vivipara*; Fig. 2I, M, P). Articulation surfaces with the prefrontal and the postfrontal are distinctly far from each other (Fig. 3H). 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. 2G-H). Except for *A. erythrurus* and *O. elegans*, this margin also shows little (*A. marchi*, *A. moreoticus*, *I. bonnali*, *I. horvathi*, *P. filfolensis*, *P. lilfordi* and *Z. vivipara*; Fig. 2P-Q) or strongly (other species; Fig. 2I-N) developed interdigitations, which are less marked in very young individuals (Fig. 4). 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. 2G, K). In some specimens of *T. lepidus*, this sulcus is located at midlength (Fig. 2O; see also Čerňanský, 2010), 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. 2I). 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. 2G). This condition approaches the one seen in juveniles of other, small-sized species. Measurements of the frontal of lacertid species are given in the Supplementary Information.

*Scincidae (Fig. 2R-Y, 3A-B, I-L)*

In European scincids, the frontal can be either unfused, showing no clear constriction in the middle (*Chalcides* and *O. punctatissimus*; Fig. 2T-Y) or fused, with a weak (*T. aurata*; Fig. 3A-B) or stronger (*A. kitaibelii*; Fig. 2R-S) 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 L-shaped in dorsal view. Because of the poor development of the posterolateral process, the frontal of *O. punctatissimus* widens only slightly posteriorly (Fig. 2X-Y). When fused, the suture line is still visible in ventral view on the anterior half of the resulting bone (Fig. 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. 3A-B). In *A. kitaibelii* and *O. punctatissimus*, the lateral processes are very little developed, in contrast with distinctly developed medial ones (Fig. 2R-S, X-Y). Very low (strongly more distinct in *T. aurata*; Fig. 3A) ridges mark the margins of the articulation surface with the nasal, which is subtrapezoidal (*A. kitaibelii*, *C. chalcides* and *O. punctatissimus*; Fig. 2R, X) or rounded (*C. ocellatus*, *C. striatus* and *T. aurata*; Fig. 2T, V, 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. 3L), but it does not touch the smaller and shorter (very short in *A. kitaibelii*; Fig. 3I) articulation surface with the postfrontal. In *C. ocellatus* and *O. punctatissimus*, however, these two articulation surfaces are very close to each other (Fig. 3K-L); they can also contact each other in the latter species (e.g., MDHC 427; Fig. 3L). The posterolateral process is moderately short (even shorter in *O. punctatissimus*; Fig. 2X-Y) and wide, with a rounded or pointed distal end (in dorsal view); the process is slightly longer and more slender in *A. kitaibelii* (Fig. 2R-S) and *T. aurata* (Fig. 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. 2S, 3A, I). The ventral surface is smooth, whereas a weak (*C. chalcides* and *C. striatus*; Fig. 2V) or well developed (*C. ocellatus*; Fig. 2T) 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 the ornamentation. In this case also, *T. aurata* is an exception, since it has a moderately developed ornamentation that reaches the posterior margin (Fig. 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. 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). Maximum lengths of the frontal in European species of scincids are summarized in the Supplementary Information.

### *Anguidae (Fig. 3C-F, M-N)*

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 recognisable in *Anguis* gr. *A. fragilis* (Fig. 3C), but more clearly visible in *P. apodus* (Fig. 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. 3M) or fifth (*P. apodus*; Fig. 3N) 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 either 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. 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 recognisable medially to the lappet of the posterolateral process (Fig. 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. 3M-N). 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. 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. 3C). The ornamentation reaches the lateral margin of the bone in adults of *P. apodus* (Fig. 3E), but not in *Anguis* gr. *A. fragilis* (Fig. 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. 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. 3E). Anyway, Klembara *et al.* (2017) showed that sometimes a very small interfrontal shield might be present in the latter species also. The maximum length of the frontal ranges 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. 5, 6) are quadrangular bones that can be either paired (only in gekkotans; Villa *et al.*, 2018a) or fused in a single element. They are composed by a straight parietal table, which develops the anterolateral processes by the anterolateral corners and the supratemporal processes (postparietal processes in Evans, 2008, and Villa *et al.*, 2018a) by the posterolateral corners. The former are usually anterolaterally directed, whereas the latter are posterolaterally directed and ventrally curved. The table can be pierced by the parietal foramen.

*Agamidae (Fig. 5A-B, 6D)*

*Laudakia stellio* has an unpaired parietal with a short and wide quadrangular table. 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. 5A-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. 2C-D). Laterally to the notch, the anterior margin is dorsoventrally expanded and forms a moderately deep, anteriorly concave surface (Fig. 6D). The anterolateral processes are large and pointed. They are strongly laterally projected, but they do not develop in anterior direction. The supratemporal 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 supratemporal process, starting from the middle of the medial margin (Fig. 5A). 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 table. The ventral surface is smooth and a very small parietal fossa is present in the middle of the posterior margin (Fig. 5B). No parietal notch is clearly visible in dorsal view in our specimens, but it was sometimes present in those studied by Smith *et al.* (2016), particularly in the youngest specimen. 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. 5C-D, 6E)*

The parietal of *C. chamaeleon* is an unpaired bone that differs from the above-described 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. 5C) and wide in lateral view (Fig. 6E). 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. 6E), 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. Dorsally, 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. 5C, 6E). 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. 5D). 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. Supratemporal processes are not present, nor it is the opening of the parietal foramen. The anterior and anterolateral margins of the laminar body are represented by interdigitated sutures (Fig. 5C). Two wide and anteriorly rounded parietal tabs develop from each lateral corner of the anterior margin (Fig. 5C-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.

### *Lacertidae (Fig. 5E-N, 6F)*

Lacertids have an unpaired parietal, with a weakly (*A. marchi*, *I. bonnali*, *I. horvathi*, *P. filfolensis*, and *Z. vivipara*; Fig. 5M-N) or strongly interdigitated (other species; Fig. 5G-H, K-L) anterior margin. The interdigitations are absent in *A. erythrurus* and generally in *O. elegans*, whose anterior margin is wavy and presents a concavity in the middle (Fig. 5E-F, I-J). The table is larger than it is long in *A. erythrurus*, *E. arguta*, *I. horvathi*, *O. elegans* and *Z. vivipara* (Fig. 5E-F, I-J, M-N), whereas it is longer in the other species (Fig. 5G-H, K-L). 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. 5E-F, I-J). The morphology of the long supratemporal 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. 5E-F, I-J, M-N), whereas they widen proximally in *Algyroides 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*, *Psammodromus algirus* and *T. lepidus* (Fig. 5G-H, K-L). A well-developed dermal ornamentation, the development of which increases in older individuals and larger species, is present on the dorsal surface of the table, but not on the processes. The two frontoparietal (anteriorly), the interparietal (in the middle of the table), the two lateral (laterally), and the occipital (posteriorly) shields are recognisable 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. 5E, I). The two former species lack the occipital shield, whereas a very small one is present in *O. elegans* (Fig. 5I). In *T. lepidus*, on the other hand, the latter shield is very large (Fig. 5K, 7). An area levis devoid of ornamentation is present on the parietal table of *A. erythrurus*, *I. horvathi*, *O. elegans*, *Ps. hispanicus*, and *Z. vivipara* (Fig. 5E, I, M), 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 table, two anterolateral ones running posteromedially from each anterolateral corner of the table, and two posterolateral ones running anteromedially along the ventral surface of the supratemporal processes. The crests are moderately low in small species (Fig. 5F, J, N) and in juveniles of the largest ones, but they can grow to become sharp and very well developed in adults of the latter (Fig. 5H, L). 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 was stated by Barahona, 1996, and Barahona & Barbadillo, 1997), *P. pityusensis*, *P. siculus*, *P. tauricus*, *P. tiliguerta*, *P. waglerianus*, *P. algirus*, and *T. lepidus* (Fig. 5H, L) and present in juveniles of the previously cited species as well as in both adults and juveniles of other ones (Fig. 5F, J, N). It has to be noted, however, that the contact is also present in some adult specimens of *Lacerta 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 parietal 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. 5F, J, N), 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. 5H, L). *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. 5E, I, M), whereas in adults of the other species the posterior margin is straight (Fig. 5G, K). A wide and either subcircular or subelliptical parietal foramen is present in the middle of the table. Measurements are given in the Supplementary Information.

### *Scincidae (Fig. 5O-X, 6G-I)*

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. 5S-T). A moderate lateral development is visible in *T. aurata* too (Fig.

5W-X). 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. 5S-T). The supratemporal processes are long, thin and pointed in *C. chalcides*, *C. striatus*, and *T. aurata* (Fig. 5Q-R, W-X, 6I), long, slender and posteriorly rounded in *O. punctatissimus* (Fig. 5U-V, 6H), and long, robust and posteriorly rounded in *C. ocellatus* (Fig. 5S-T, 6G). In the latter species, moreover, they show a distinct angle at midlength in dorsal view. *Ablepharus kitaibelii*, on the other hand, presents short, slender and pointed supratemporal processes (Fig. 5O-P). On the dorsal surface, a weak dermal ornamentation is present in the middle of the anterior half of the table, 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. 5Q). In *C. ocellatus*, the ornamentation covering the lateral areas is very poorly developed (barely recognisable), but it reaches the lateral margins of the table (Fig. 5S). On the other hand, the ornamentation is slightly more developed and reaches both the lateral and the anterior margins in *T. aurata* (Fig. 5W), whereas in *A. kitaibelii* and *O. punctatissimus* it is represented only by very light grooves (sometimes completely absent in the former; Fig. 5Q, U). 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. 5P, R, V, X). *Chalcides ocellatus*, on the other hand, shows robust ventral crests, all of which are always in contact (Fig. 5T). The parietal fossa is very narrow and shallow in *C. chalcides* (Fig. 5R), larger and deeper in *C. ocellatus* (Fig. 5T) and *T. aurata* (Fig. 5X), and moderately large and shallow in *A. kitaibelii* (Fig. 5P) 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. 5V). A suture line is distinctly visible longitudinally in the middle of the ventral surface of the parietal of *O. punctatissimus* MDHC 427 (Fig. 5V). The posterior margin of the parietal is characterized by the presence of two pointed processes (forked in *C. chalcides* MDHC 398; Fig. 5Q-R), which develop posteriorly and define a wide (narrow in *O. punctatissimus*; Fig. 5U-V) parietal notch. These processes are wide and moderately short in *C. chalcides* and *C. striatus* (Fig. 5Q-R), very long and wide in *O. punctatissimus* (Fig. 5U-V), long and thin in *C. ocellatus* (Fig. 5S-T). *Ablepharus kitaibelii* and *T. aurata* show only two wide and posteriorly rounded tabs, which are very short in the latter (Fig. 5W-X) and slightly longer in the former (Fig. 5O-P). The notch is U-shaped or, exceptionally (*C. chalcides* MDHC 398 and *C. striatus* MDHC 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. 6G-H). In the two aforementioned species the same process is short and triangular (Fig. 6I). The parietal foramen is wide, subcircular and located in the middle of the table; it can be partially or completely obliterated by the dermal ornamentation (e.g., in *T. aurata* MDHC 208; Fig. 5W-X). Measurements are given in the Supplementary Information.

### *Anguidae (Fig. 5Y-Z, 6A-C, J-K)*

The parietal of anguids is unpaired and presents a rectangular table, which is longer than it is wide. 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 table and a similar small and anteriorly developed ventral lappet is present medially to this surface. The anterolateral processes are poorly developed. The long supratemporal 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. 6J-K). A well-developed dermal ornamentation is present on the dorsal surface of the table and the frontoparietal, interparietal, lateral, and occipital shields are recognisable (Fig. 5Y, 6A, C). The interparietal shield is very large and reaches the anterior margin of the table, 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. 5Y) than in *P. apodus* (Fig. 6A). Linked to this difference in width, the anterior end of each groove separating the interparietal shield from the related frontoparietal shield is directed toward the anterolateral corner of the ornamented surface in *Anguis* gr. *A. fragilis*, whereas it is located more medially in *P. apodus* (see also Klembara *et al.*, 2017, and Klembara & Rummel, 2018). In *Anguis* gr. *A. fragilis*, moreover, the dermal ornamentation is usually less marked on the frontoparietal shields compared to the rest of the table (Fig. 5Y). The occipital shield is small in *Anguis* gr. *A. fragilis* (Fig. 5Y) and large in *P. apodus* (Fig. 6A). Posteriorly, the ornamentation does not reach the posterior margin of the parietal table, because of the presence of a large and smooth area levis (Fig. 5Y, 6A, C). According to Klembara (2012), Klembara *et al.* (2017), and Klembara & Rummel (2018), the area levis is shorter than the occipital shield in *Anguis*, whereas it is as long as the shield in *Pseudopus*. However, a certain degree of variation of this feature is clear based our specimens, which include *Anguis* gr. *A. fragilis* with an occipital shield that is as long as the area levis (Fig. 5Z) and *P. apodus* with a shield that is distinctly longer than the area levis (Fig. 6A). 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. 6B), since in *Anguis* gr. *A. fragilis* the posterior ends of the anterolateral ventral crests is shifted towards the posterior margin of the bone (Fig. 5Z). The contact of the anterolateral ventral crest with the medial ventral crest in *P. apodus* splits the margin of the parietal fossa into two sections, respectively called crista juxtafovealis (anterior to the contact) and crista postfovealis (posterior to the contact) by Klembara *et al.* (2010). Due to the posterior shifting of the posterior end of the anterolateral ventral crest, the crista postfovealis is not present in *Anguis* gr. *A. fragilis*. The medial ventral crest (lamina medialis in Klembara *et al.*, 2010) is moderately wide, the posterolateral ventral crests (ventrolateral ridge in Klembara *et al.*, 2010) can be robust or sharp and the anterolateral ventral crests (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. The parietal table of *P. apodus* extends laterally beyond the anterolateral ventral crests, forming a wide facies muscularis on each side of the bone. This facies is not developed in *Anguis* gr. *A. fragilis*. A narrow and smooth ventrolateral surface located laterally to the posterolateral ventral crest versus a crest that marks the lateral margin of the supratemporal process is commonly used to distinguish *Pseudopus* from *Anguis* (see e.g., Klembara *et al.*, 2010, 2017; Klembara, 2012; Klembara & Rummel, 2018). However, it seems that, at least among the herein-studied specimens, *Anguis* gr. *A. fragilis* can also display such a narrow surface in some cases (Fig. 5Z). 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. 5Z). In juveniles of *Anguis* and in *P. apodus*, on the other hand, the posterior portion of the wide fossa is visible in ventral view (Fig. 6B). 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. 6A). The carina is not developed posteriorly in *Anguis* gr. *A. fragilis* (Fig. 5Y-Z). 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. 6K), by the contact of the anterolateral and posterolateral ventral crests, but not in *Anguis* gr. *A. fragilis* (Fig. 6J). A wide and elliptical (*Anguis* gr. *A. fragilis*; Fig. 5Y-Z) or circular (*P. apodus*; Fig. 6A-B) parietal foramen is present in the middle of the table, even though sometimes it can be obliterated by the dermal ornamentation (Fig. 6C). 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. 8, 9) is composed of a ventral alveolar plate and of an ascending nasal process that projects posterodorsally from the middle portion of latter. Posteriorly, the alveolar plate extends into 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 teeth are supported by the alveolar margin of the alveolar plate. By the junction between the ascending nasal process and the alveolar plate, the foramina of the longitudinal canals are visible by the sides of the process. A septonasal crest runs medially along the posterior surface of the nasal process.

*Agamidae (Fig. 8A-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. 8B-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., four 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. 8A). The septonasal crest is robust and well developed (Fig. 8C); 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. 8D)*

*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 either two or three. Maximum width of the alveolar plate varies from 0.5 mm to 1 mm.

*Lacertidae (Fig. 8E-U)*

The premaxilla of lacertids present a long (usually shorter in *Lacerta*, *T. lepidus*, and *Z. vivipara*; Fig. 8M-N, U) 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. 8Q-R), arrow-shaped (*E. arguta*, *I. cyreni*, *I. galani*, and *I. monticola*; Fig. 8I-J), stocky and leaf-shaped (*Lacerta*, *T. lepidus*, and *Z. vivipara*; Fig. 8M-N, U) or moderately narrow and slightly leaf-shaped at the dorsal end (*A. erythrurus*; Fig. 8E-F) 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 *A. nigropunctatus*, *D. oxycephala*, *D. mosorensis*, and *P. muralis*, since some adult or subadult specimens (e.g., *A. nigropunctatus* MDHC 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. 8U). 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. 8M, P-Q). The notch between the palatal processes is deep, wide and V-shaped (Fig. 8H). 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. 8M-N, 10). Some specimens of *I. monticola* can present a second pair of foramina of the longitudinal canals (Barahona, 1996; Fig. 8I). *Acanthodactylus erythrurus* UAM.R.ACVII (Fig. 8E) 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, are given in the Supplementary Information.

*Scincidae (Fig. 8V-Y, 9A-D)*

European scincids differ from other European lizards in having paired premaxillae, both provided with a laminar and subquadrangular palatal process (Fig. 8Y, 9C). 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 (Villa *et al.*, 2018a). 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 (Villa *et al.*, 2018a), being pleurodont, cylindrical, slender and provided with a labial and a lingual cusps (morphotype F sensu Kosma, 2004). However, tooth crown is slightly curved posteriorly and shows a light striation on the lingual surface in scincids. Teeth of *C. ocellatus* differ from those of the other species because they are robust and provided with a blunt and mediolaterally enlarged crown (Fig. 9A-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 recognisable. The external surface of the premaxillae is smooth, with no traces of dermal ornamentation (Fig. 8V, 9A). Measurements and number of tooth positions are given in the Supplementary Information.

*Anguidae (Fig. 9E-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. 9E-F). In *P. apodus,* on the other hand, it is moderately wide, with straight and parallel lateral margins and a rounded dorsal end (Fig. 9I-J). According to Klembara *et al.* (2017), however, the process of young *P. apodus* is slightly widened at midlength. The anterior surface of the process is smooth (Fig. 9E, I), whereas only in *Anguis* gr. *A. fragilis* a low but distinct septonasal crest runs along the posterior one (Fig. 9F). The development of the crest increases during growth, being unrecognisable in juveniles. Each palatal process is split into two portions by a deep notch (Fig. 9H): 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. 9F). These ridges are present also in *P. apodus*, even if the crest is not present in this species (Fig. 9J). 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. 9H). 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. 9E-F). Teeth of *P. apodus* have a blunter tip (Fig. 9I-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 nine in *Anguis* gr. *A. fragilis* and goes from six to seven (seven to nine 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. 11, 12) 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 maxilla is crossed by the superior alveolar canal, which runs through the base of the facial process. Its anterior opening, the vomeronasal foramen, is located on the dorsal surface of the premaxillary process. The posterior opening, on the other hand, is the wide superior dental foramen (infraorbital foramen in Barahona, 1996) and opens on the dorsal surface of the palatal shelf. Lateral openings of the canal are represented by the ventrolateral (labial) foramina, whose number is highly variable, even in the two maxillae of the same specimen.

*Agamidae (Fig. 11A-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. 11A-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 spur 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. 11C), whereas acrodont and triangular teeth are present posteriorly. According to Smith *et al.* (2016), the second subpleurodont tooth is larger than the first one in males of *L. stellio*. Acrodont teeth are closely spaced and extend towards the medial surface of the alveolar shelf (Fig. 11B). 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. We observed four or five ventrolateral foramina on the otherwise smooth lateral surface, but Smith *et al.* (2016) reported six of them in the left maxilla of one of the specimens they examined (see Supplementary Information in Smith *et al.*, 2016). 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. 11B). Both the lateral and the medial surface of the process are smooth. Including the subpleurodont ones, a number of nine 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. 11D-E)*

The anterior premaxillary process of the maxilla of *C. chamaeleon* is strongly curved medially (Fig. 11E), 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 recognisable 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. 11E). Teeth are acrodont, triangular and tricuspid. They are well spaced (though exceptions may occur; e.g., NHMW 611, Fig. 11E, but see also Čerňanský, 2011) and larger in the posterior portion of the alveolar border. The lateral surface of the bone is smooth (Fig. 11D). Usually only one ventrolateral foramen is present (Fig. 11E), but rarely two 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. 11D). 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.

*Lacertidae (Fig. 11F-O, 12A-B, Q-R)*

The anterior premaxillary process of the maxilla of lacertids shows a deep anterior concavity, since both anteromedial and anterolateral processes are well developed (Fig. 12Q-R). The two processes are similar in size, but the anteromedial one can develop a lappet on its dorsal surface (Fig. 11H-O, 12A-B, R): the lappet is present in all species but *A. erythrurus* (Fig. 11F-G, 12Q), *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. 11H-J, 12R). 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. 11K-L), 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. 11J) or a simple step (Fig. 11H-I). 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. 11K-L, O, 13). 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. 11F-G) or large (other species; Fig. 11H-O, 12A-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. 12A-B), and in some specimens of *L. schreiberi* and *T. lepidus*. A well-developed dermal ornamentation is present on the lateral surface of the facial process (Fig. 11H, J-K, M), 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. 11F, 12A). 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 midlength, 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. 11I), *L. schreiberi*, and *Z. vivipara* (Fig. 12B), and is not visible in *A. erythrurus* (Fig. 11G). 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. 11N). Measurements, number of tooth positions and of ventrolateral foramina are given in the Supplementary Information.

### *Scincidae (Fig. 12C-L, S-U)*

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. 12S-U). 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. 12I-J), its posterior tip is slightly shifted in dorsal direction (Fig. 12C-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. 12G-H) and *T. aurata* (Fig. 12K-L) and well developed in *A. kitaibelii* (Fig. 12C-D), *C. chalcides* (Fig. 12E-F), *C. striatus*, and *O. punctatissimus* (Fig. 12I-J). In the latter four species, moreover, the ridge 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. 12U). 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 (Villa *et al.*, 2018a), but they have a slightly posterolingually curved crown provided with light striae on the lingual surface. Teeth 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. 12G-H). Even if not as much as in *C. ocellatus*, more robust teeth are present in *O. punctatissimus* too (Fig. 12I-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. 12K-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. 12I-J). In *C. chalcides*, *C. striatus*, and *T. aurata*, the dorsal margins are similar in length (Fig. 12E-F, K-L), whereas in *A. kitaibelii* and *C. ocellatus* the anterodorsal one is longer than the posterodorsal one (Fig. 12C-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. 12C-D). The anterior, dorsal and posterior corners of the process are pointed in *Chalcides* (Fig. 12E-H), but they do not develop projections. *Trachylepis aurata* shares a similar morphology, but the dorsal corner is rounded (Fig. 12K-L), whereas all corners are rounded in *A. kitaibelii* and *O. punctatissimus* (Fig. 12C-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 recognisable in *A. kitaibelii*, *C. ocellatus*, *O. punctatissimus*, and *T. aurata*). The Supplementary Information include measurements, number of tooth positions and number of ventrolateral foramina.

### *Anguidae (Fig. 12M-P, V)*

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. 12V). 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. 12V). The posterior process is long, slender and pointed in lateral view, lacking any step. The vomeronasal 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. 12M-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. 12O-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. 12M-N) and slightly oblique in *P. apodus* (Fig. 12O-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. 12M), whereas a very light one is visible in *P. apodus* (Fig. 12O). 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 nine in *Anguis* gr. *A. fragilis* and goes from nine to 14 in *P. apodus*. Three or four ventrolateral foramina are present in *Anguis* gr. *A. fragilis,* three, four or five in *P. apodus*.

### PREFRONTAL

The paired prefrontal (Fig. 14) has an anteriorly concave body, named the orbitonasal flange. The large and pointed dorsal process starts from the medial side of the dorsal margin of the flange, extending in posterodorsal direction. The laminar anterodorsal process develops in anterior direction from 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 of the lacrimal foramen is located between the anterodorsal and the posteroventral processes.

#### *Agamidae (Fig. 14A-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 recognisable on the ventromedial corner of the flange (Fig. 14B). 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. 14A-B). The notch of the lacrimal foramen is very wide and deep (Fig. 14B). 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. 14B).

*Chamaeleonidae (Fig. 14C-E)*

Prefrontals of *C. chamaeleon* have a subrectangular orbitonasal flange, with a moderately shallow ventral concavity (Fig. 14C). They are anteroposteriorly elongated in dorsal view (Fig. 14E), 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. 14C): 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. 15). This lateral 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 the lateral margin of the orbitonasal flange. The dorsal process is laminar, posteriorly rounded and strongly mediolaterally expanded (Fig. 14D-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. 14D-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. 14E).

*Lacertidae (Fig. 14F-N)*

In lacertids, the prefrontal shows a distinct and size-linked dermal ornamentation on the dorsal surface (Fig. 14F, L), 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. 14I). The anterodorsal process is covered by this ornamentation on its posterior half, whereas the anterior half 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. 14I-J). A similar, but proportionally smaller process can be present in *T. lepidus* too (Fig. 14L-M). 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. 14K), but it is shorter (roughly as long as the flange or even shorter than it) in the other species (Fig. 14G, N). 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. 14O-T)*

A subquadrangular orbitonasal flange projection is present also in the prefrontal of scincids (Fig. 14P, S). As in gekkotans (Villa *et al.*, 2018a), 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. 14O-Q), except for *C. striatus* and *T. aurata,* in which it is more easily recognisable (Fig. 14R-T). A deep notch for the lacrimal foramen is present. This notch is particulartly deep in *A. kitaibelii,* in which, moreover, it is partially covered dorsolaterally by an osseous projection of the bone (Fig. 14O-Q). The dorsal process is slender and slightly shorter than the rest of the bone in lateral view in all species (Fig. 14R, T) but *A. kitaibelii*, in which it can be slightly longer (Fig. 14O, Q). A low (*A. kitaibelii*, *Chalcides*, and *O. punctatissimus*; Fig. 14O, Q) or sharp (*T. aurata*; Fig. 14R, T) palpebral crest is visible on its base, except maybe for the prefrontals of *C. bedriagai*.

*Anguidae (Fig. 14U-Z)*

Anguids have a subtriangular orbitonasal flange projection, which is wider but very slightly shorter than the slender and truncated posteroventral process (Fig. 14V, Y). There is no ornamentation in *Anguis* gr. *A. fragilis* (Fig. 14U), whereas very mild rugosities are visible dorsally in *P. apodus*, on the base of the dorsal process (Fig. 14X). A distinct posterolateral projection is absent and the notch for the lacrimal foramen is very wide and moderately (*Anguis* gr. *A. fragilis*, Fig. 14U-W) or very (*P. apodus*; Fig. 14X-Z) 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 recognisable.

JUGAL

Jugals (Fig. 16) 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. 16A-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. 16A). A short palatal process is present, but it lacks any sign of a medial one (Fig. 16B). 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 midlength. This angle seems to be less marked in juveniles (Smith *et al.*, 2016). The distal end of the posterodorsal process 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. 16B). Large foramina are present on the lateral surface.

*Chamaeleonidae (Fig. 16C-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. 16C): 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. 16D), whereas a developed quadratojugal process is not present. The anterior end of the jugal forms part of the lateral margin of the lacrimal foramen.

*Lacertidae (Fig. 16E-L)*

In the jugal of lacertids, the anterior process can be narrow and pointed (most species; Fig. 16I-L), moderately large, flattened and more rounded anteriorly (*A. erythrurus*; Fig. 16E-F), or moderately large, flattened and anteriorly forked (*O. elegans*; Fig. 16G-H). 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. 16I, K), except for *A. erythrurus* and *O. elegans*, in which this surface is narrow and the bone is more laterally exposed (Fig. 16E, G). 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 weakly developed in *A. erythrurus* (Fig. 16F), *E. arguta*, and *O. elegans* (Fig. 16H) and moderately to well developed in other species (Fig. 16J, L). A distinct medial process is present in *O. elegans* (Fig. 16H) and *Psammodromus* (Fig. 16J, 17A), but a little developed one (Fig. 17B) 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 differ 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. 16G-J), the posterodorsal one is the longest in *A. erythrurus* and *E. arguta* (Fig. 16E-F), 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. 16K-L). 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. 18). The quadratojugal process can be absent (*A. erythrurus* and *O. elegans*; Fig. 16E-H), weakly developed (*I. horvathi*, *P. pityusensis*, *P. tiliguerta*, and *P. algirus*; Fig. 16I-J) or well developed (other species; Fig. 16K-L). 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. 16M-R)*

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. 16O-P), pointed (*C. bedriagai*) or rounded (*A. kitaibelii*, *C. ocellatus*, and *O. punctatissimus*; Fig. 16M-N, Q-R) dorsal end. The length of the two processes is similar in *C. chalcides* (Fig. 16O-P), whereas in *C. ocellatus* and *O. punctatissimus* the posterodorsal process is roughly twice as long as the anterior one (Fig. 16Q-R) and in *A. kitaibelii*, *C. striatus*, and *T. aurata* the former is slightly longer than the latter (Fig. 16M-N). 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. punctatissimus*, the medial opening of this foramen is located more dorsally, roughly at midlength of the posterodorsal process.

### *Anguidae (Fig. 16S-V)*

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. 16T, 17C), but a small hint of it is visible in *P. apodus* (Fig. 16V). 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. 16S-T) or pointed (*P. apodus*; Fig. 16U-V) 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. 16S-T), though it can be less marked in juveniles. *Pseudopus apodus*, on the other hand, shows a very little developed (almost absent) quadratojugal process (Fig. 16U-V). 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. 16S), but it presents an ornamentation made up by mild rugosities in *P. apodus* (Fig. 16U).

## POSTFRONTAL AND POSTORBITAL

Postfrontal and postorbital (Fig. 19) 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. 19A-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. 19B) and that with the posterolateral process of the frontal on the anterior one (Fig. 19A). The lateral margin contacts the jugal and squamosal and articulation surfaces are visible by its anterior (Fig. 19A) and posterior (Fig. 19B) ends. No articulation surface with the ectopterygoid is recognisable 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. 19C-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. 19C-D) and by a strongly mediolaterally expanded and laminar anterior process (Fig. 19E) 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. 19E). The posterodorsal and the ventral corner of the triangular posterior portion (posterior and ventral processes, respectively) are pointed (Fig. 19C-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. 19C, E), but it is lacking in MNHN 1942-103 and 1887-875. The medial surface is smooth.

*Lacertidae (Fig. 19F-P)*

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. 19O-P) 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. 19F-K). 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. 19F-G) and pointed. The anteromedial process is expanded in *Lacerta* (Fig. 19F-I) 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. 19J-K). 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. 19I). 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. 19F, H). This ornamentation is moderately or well developed in all species, except for *A. erythrurus*, *A. marchi*, *I. bonnali*, *I. horvathi*, and *O. elegans* (Fig. 19J). Traces left by supraocular scales can be visible. The free postorbital is L-shaped and narrow (Fig. 19L-N). 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. 19L). 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 named the missing process as the anterolateral one in the main text, but then marked 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. 19M).

*Scincidae (Fig. 19Q-AD)*

Scincids have usually separate postfrontal and postorbital too, but Evans (2008) stated 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 find it in the studied specimens of *T. aurata*. Nevertheless, 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. 19W-X) processes on the anterior corners and a concave anterior margin (Fig. 19Q-Z). In dorsal view, the body is slender and triangular in *A. kitaibelii* (Fig. 19Q-R), slender and subrectangular in *C. chalcides, C. striatus,* and *O. punctatissimus* (Fig. 19S-T, W-X), wider and laterally expanded in the posterior half in *C. ocellatus* (Fig. 19U-V), wider and provided with a moderately developed and pointed posterior projection by the posterolateral corner in *T. aurata* (Fig. 19Y-Z). A similar projection is present in *O. punctatissimus* too (Fig. 19W-X). 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. 19S-T). 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. 19U-V, Y-Z). 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. 19Q-R, W-X). 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. 19AA-AD) 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. 19AC-AD). The articulation surfaces with the postfrontal and the squamosal are recognisable 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. 19AE-AI)*

Free postfrontal and postorbital are present in anguids. The former is roughly T-shaped in dorsal view, with a slightly concave anterior margin and a straight and slender body (Fig. 19AE-AH). 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. 19AE-AF). *Pseudopus apodus*, on the other hand, shows a triangular body with a pointed end in dorsal view (Fig. 19AG-AH). A long anteromedial process develops from the medial corner of the anterior margin: it is moderately (*Anguis* gr. *A. fragilis*; Fig. 19AE-AF) or distinctly (*P. apodus*; Fig. 19AG-AH) 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. These 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. 19AI) 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 also 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. 19AI).

### SQUAMOSAL

The squamosal (Fig. 20) 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. 20A-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. 20A). 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 supratemporal 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. 20B), which is otherwise smooth; the ridge 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 of the bone is smooth.

#### *Chamaeleonidae (Fig. 20C-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. 20D); 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. 20C). However, no tubercles are present on MNHN 1887-875.

*Lacertidae (Fig. 20E-H)*

The squamosal is small in lacertids, recalling a small rod that curves ventrally at the posterior end. The latter end is represented by a single posterior process. The anterior process is pointed, whereas the posterior one is wider. Morphologically, the squamosal of lacertids is similar to the one of gekkotans (Villa *et al.*, 2018a), but with a longer anterior process. The posterior process is expanded in *Lacerta* (Fig. 20G-H), *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 & Odierna (2004) described a triangular medial process that frequently occurs on the squamosal of *I. martinezricai*.

*Scincidae and Anguidae (Fig. 20I-N)*

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. 20I-J), the anterior end is pointed, whereas in anguids it is a flattened lamina (Fig. 20K-N). *Anguis* gr. *A. fragilis* has a rounded and subhorizontal end (Fig. 20K-L), whereas in *P. apodus* the end is pointed and more dorsally concave (Fig. 20M-N).

QUADRATE

The main body of the paired quadrate (Fig. 21, 22) is a posteriorly curved pillar structure. From this pillar, an osseous lamina develops laterally forming a large and deep conch, which usually is strongly posteriorly concave. The lateral margin of the conch is defined by the slightly expanded tympanic crest. Another similar but much smaller lamina can be present on the medial side of the pillar, developing in anteromedial direction. The pillar bears the dorsally flattened cephalic condyle dorsally and the mandibular condyle ventrally. The mandibular condyle is composed by two portions, which are separated 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. One or two quadrate foramina may pierce the lateral lamina, dorsally to the mandibular condyle. However, the quadrate foramen can sometimes be absent.

*Agamidae (Fig. 21A-B)*

The quadrate of *L. stellio* is quadrangular and mediolaterally expanded in anterior view. The conch is not strongly concave (Fig. 21B), 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. 21B). The cephalic condyle is strongly expanded in an anteromedial to posterolateral direction and presents a rectangular, elongated and flattened articular surface dorsally (Fig. 21B). 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. 21C-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. 21C), whereas the posterior one is slightly convex (Fig. 21D). 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.

*Lacertidae (Fig. 22A-I)*

The quadrate of lacertids is roughly straight and rectangular in anterior view. In medial view, its anterior outline is rounded (Fig. 22F, I), except for *A. erythrurus*, *E. arguta*, and *O. elegans*, in which it is more angular (Fig. 22C). 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. 22A-B), 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. 22D-E). 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. 22G). 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 recognisable. The medial portion of the mandibular condyle is slightly more ventrally developed than the lateral one. Maximum length is given in the Supplementary Information.

*Scincidae (Fig. 22J-U)*

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. 22J-K, P-Q), whereas those of *C. ocellatus* and *T. aurata* are wider (Fig. 22M-N, S-T). 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. 22S-T) and well developed in *C. ocellatus* (Fig. 22M-N), 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. 22P-Q). An anterodorsally convex osseous swelling is present on the dorsal half of the lateral lamina in *C. ocellatus* and *O. punctatissimus* (Fig. 22M, O-P, R). In the former species, a low ridge runs in dorsoventral direction medially to the swelling (Fig. 22M), 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. 22R). 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 recognisable 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. Maximum length is given in the Supplementary Information.

### *Anguidae (Fig. 22V-AA)*

The quadrate of European anguids is a straight and subrectangular bone in anterior view. Only a very low to moderately developed lamina is present along the lateral margin of the pillar. The degree of development of this lamina is higher in *P. apodus* (Fig. 22Y-Z) than in *Anguis* gr. *A. fragilis* (Fig. 22V-W). Because of this, *Anguis* gr. *A. fragilis* lacks a real conch (Fig. 22W), whereas the conch of *P. apodus* is narrow and very shallow (Fig. 22Z). 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 recognisable 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. 22X). In *P. apodus*, the same expansion does not bend ventrally and the anterior outline of the bone appears angular in lateral view (Fig. 22AA). 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 recognisable 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. 23) is a rod-like paired bone.

#### *Agamidae (Fig. 23A)*

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).

#### *Lacertidae (Fig. 23B)*

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

#### *Scincidae (Fig. 23C-D)*

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. 23D).

*Anguidae (Fig. 23E)*

This bone is slightly arched, moderately robust and slightly twisted in anguids, with similar-sized dorsal and ventral ends. The epipterygoid 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. 24) are laminar, anteroposteriorly elongated and dorsally concave. They are pointed anteriorly and wider posteriorly. The medial margin of the vomeronasal fenestra is marked by a lateral notch on the anterior half of the bone.

*Agamidae (Fig. 24A-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. 24B).

*Chamaeleonidae (Fig. 24C-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. 24C-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. 24E) or two laminar tabs with a wavy posterior margin and a small U-shaped notch between them (Fig. 24C-D). Its ventral surface is distinctly concave, whereas the dorsal one is convex.

*Lacertidae (Fig. 24F-I)*

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. 24F-G). 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. 24H). 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. 24J-Q)*

In European scincids, the vomers are usually fused in a single, unpaired element, which reaches its maximum width at midlength (Fig. 24J-M). Only *T. aurata* and *O. punctatissimus* show separate vomers (Fig. 24N-Q). 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 recognisable on the anterior tip of the bone. A posterodorsally directed process is present, as in gekkotans (Villa *et al.*, 2018a), 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 posterior end 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. 24J). 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 midlength. The latter start from each lateral margin, but reach the longitudinal ridge only in *T. aurata* (Fig. 24P), 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. 24J, P), low in *C. ocellatus* (Fig. 24L), and almost indistinct in *O. punctatissimus* (Fig. 24N). 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. 24J, N), 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 ridge and touching it medially (Fig. 24L, P). The ventral surface of the vomer 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. 24K). *Ophiomorus punctatissimus* lacks any sign of ventral groove (Fig. 24O), but some foramina are present near the anterior end.

### *Anguidae (Fig. 24R-T)*

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. 24R) than in *P. apodus* (Fig. 24T). Anteriorly, a groove-like 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. 54R, T), 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. 24R); these ridges are separated by a groove and a second groove 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. 24T). 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. 25) 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).

*Lacertidae (Fig. 25A-F)*

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. 25E-F), short in *A. marchi*, *A. moreoticus*, *A. bedriagae*, and *I. bonnali* (Fig. 25A-B), and moderately long in the other species (Fig. 25C-D). 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. 25E), whereas the latter is directed laterally. The tip of the posterolateral process is more angular in *A. erythrurus* and *O. elegans* (Fig. 25E-F) than in other species (Fig. 25A-D). 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. 25G-J)*

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. 25I-J). Moreover, in scincids, the posterolateral process is usually more rounded than in lacertids. The same process is more developed in *C. ocellatus* (Fig. 25I-J) than in *A. kitaibelii*, *C. chalcides*, *C. striatus*, and *O. punctatissimus* (Fig. 25G-H). 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. 25I). This is not true, however, for *A. kitaibelii* (Fig. 25G). 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. 25K-N)*

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. 25K-L; slightly longer in juveniles), but distinctly longer in *P. apodus* (Fig. 25M-N). The anterolateral one is not distinctly developed, in particular in *P. apodus*, whose septomaxilla has a subtriangular aspect in dorsal view (Fig. 25M-N). 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. 26) 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. 26A-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. 26B). There are no palatine teeth.

*Chamaeleonidae (Fig. 26C-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 recognisable 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. 26D). The pterygoid process is large and has smooth dorsal and ventral surfaces, without palatine teeth. A foramen is visible at midlength, 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. 26C; 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. 26D). The infraorbital foramen is not present since the palatine is excluded from its formation by the prefrontal and the jugal.

*Lacertidae (Fig. 26E-H)*

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. 26G-H) and poorly developed in other species (Fig. 26E-F). According to Barahona (1996), the projection 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. 26G-H), except for *A. erythrurus* and *O. elegans*, in which the inclination is distinctly less marked (Fig. 26E-F). 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. 26I-P)*

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 duct appears therefore very deep. The expansion of the medial margin is absent in *A. kitaibelii* and *T. aurata* (Fig. 26I-J, O-P) and poorly developed and ventrolaterally directed in *Chalcides* and *O. punctatissimus* (Fig. 26K-N). 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. 26K-N), long and narrow in *A. kitaibelii* and *C. ocellatus* (Fig. 26I-J), and long and wider in *T. aurata* (Fig. 26O-P). The anterior projection is not well individualized in *Chalcides* (Fig. 26K-L), slightly more recognisable in *A. kitaibelii* and *T. aurata* (Fig. 26I-J, O-P), and distinctly recognisable in *O. punctatissimus* (Fig. 26M-N). 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. 26I-J, O-P). 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*, being also almost closed laterally in the former species. Only *O. punctatissimus* displays a complete and moderately wide infraorbital foramen (Fig. 26M-N). 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. 26I). A long and pointed process, slender in *C. chalcides* and *C. striatus* (Fig. 26K-L) and wider in *A. kitaibelii*, *C. ocellatus*, *O. punctatissimus,* and *T. aurata* (Fig. 26I-J, M-P), 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 recognisable on the ventral surface (marked anteromedially by a low and arched ridge in *C. chalcides*; Fig. 26L). 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. 26Q-T)*

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. 26R). 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. 26Q-R), which is therefore split into two pointed and equally long portions. In contrast, the notch is very small or absent in *P. apodus* (Fig. 26S-T). The articulation surface with the palatine process of the pterygoid covers the entire medial half of the ventral surface of the bone (Fig. 26R, T), 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. 26Q, S). 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. 26R), but a single row of them is present on the lateral half of the ventral surface of the pterygoid process in *P. apodus* (Fig. 26T).

### PTERYGOID

The paired pterygoid (Fig. 27, 28) is composed by three branches: the anteromedial palatine process, the anterolateral pterygoid flange, and the posterior quadrate process. Anteriorly, the pterygoid recess separates the palatine process and the pterygoid flange. The palatine process is laminar, but strengthen towards the medial margin. The pterygoid flange is usually pointed and slender and bears two ridges that runs along its dorsal and ventral surfaces respectively. 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 basipterygoid fossa continues posteriorly in a concave surface for the insertion of the pterygoideus muscle. Pterygoid teeth can be present on the ventral surface of the palatine process.

#### *Agamidae (Fig. 27A-B, U-V)*

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. 27U). On the dorsal surface, a robust and well-developed dorsal ridge is visible (Fig. 27A), but the ventral ridge is not developed on the opposed side (Fig. 27B). Because of the unique shape of the pterygoid flange, a real pterygoid recess is not distinctly recognisable. 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. 27U-V). A very narrow notch can be visible by the step, cutting the flange longitudinally. The presence of this very distinct step in the adult specimens studied by us is in contrast with the smoother ventral margin of the quadrate process reported by Smith *et al.* (2016), implying the possibility of intraspecific variation for this feature. Both the basipterygoid fossa and the concave surface for the pterygoideus muscle are wide (Fig. 27V). Neither a pterygoid ridge nor pterygoid teeth are present. Maximum length varies from 5.6 mm to 14 mm.

*Chamaeleonidae (Fig. 27W-X)*

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. 27X). 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 the 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. 27W). The ridge is more developed in its dorsal portion and the articulation surface with the ectopterygoid is recognisable on its anterolateral surface. The slender palatine process is straight and triangular 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.

*Lacertidae (Fig. 27C-F, 28A-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. 27F, 28D), 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 ridge 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. 27E) 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. 27C). The ventral ridge is poorly developed in *A. erythrurus*, *A. fitzingeri* (Fig. 27D), *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. waglerianus*, 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: 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. 27E-F) or deeper (other species; Fig. 27C-D). Juveniles of *T. lepidus* show a deeper recess, but its depth decreases 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. 27E, 28C) 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. 27C, 28A). 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 Supplementary Information.

*Scincidae (Fig. 27G-P, 28E-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. 27G-H), long and subrectangular in *C. chalcides, C. striatus,* and *T. aurata* (Fig. 27I-J, O-P), short and subtriangular in *C. ocellatus* and *O. punctatissimus* (Fig. 27K-N). The medial margin of the process can be straight (*T. aurata*; Fig. 27O-P), slightly convex (*A. kitaibelii, C. chalcides, C. striatus,* and *O. punctatissimus*; Fig. 27G-J, M-N) or strongly convex (*C. ocellatus*; Fig. 27K-L). 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 either a V-shaped (most specimens of *C. chalcides*; Fig. 27I-J) or U-shaped (*C. ocellatus, C. striatus,* and *C. chalcides* MDHC 398; Fig. 27K-L) notch in the middle, flanked by two small and pointed processes. The palatine process 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. 27O-P). *Ablepharus kitaibelii* has an anteriorly pointed palatine process (Fig. 27G-H), whereas that of *O. punctatissimus* has a wavy anterior margin (Fig. 27M-N). Pterygoid teeth are absent in *A. kitaibelii* and *Chalcides* (Fig. 27H, J, L), but present in very low number (just one or two in *T. aurata* MDHC 280, three in all specimens of *O. punctatissimus*) in *T. aurata* and *O. punctatissimus* (Fig. 27N, P). The moderately wide pterygoid recess is very deep and roughly V- or U-shaped in *C. chalcides* (Fig. 27I-J), shallow and U-shaped in *C. ocellatus* and *O. punctatissimus* (Fig. 27K-N), and deep and U-shaped in *A. kitaibelii*, *C. striatus*, and *T. aurata* (Fig. 27G-H, O-P). 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. 27G-H), but their proportions are the same. In *O. punctatissimus*, on the other hand, both the dorsal and the ventral ridges are well developed (Fig. 27M-N). 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. 27I, O, 28G, M). The ridge is completely absent in *C. ocellatus* and *O. punctatissimus* (Fig. 27K, M, 28I, K), whereas only a hint near the fossa is present in *A. kitaibelii* (Fig. 27G, 28E). 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 the Supplementary Information.

### *Anguidae (Fig. 27Q-T, 28O-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. 27R), but well developed in *P. apodus* (Fig. 27T). 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. 27S-T). The pterygoid ridge can be low or moderately developed. Pterygoid teeth are absent in *Anguis* gr. *A. fragilis* (Fig. 27R), but present in *P. apodus* (Fig. 27T). 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. 29) is a small and paired bone, the morphology of which varies greatly among different groups.

#### *Agamidae (Fig. 29A-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. 29E). 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. 29D). A short medial expansion is present by the dorsal end of this surface (Fig. 29B), covering dorsally the pterygoid flange.

#### *Chamaeleonidae (Fig. 29F-J)*

*Chamaeleo chamaeleon* has an ectopterygoid that 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. 29J). Moreover, the medial surface of the posteromedial process is narrow and subrectangular and shows a concave and rough articulation surface (Fig. 29I).

*Lacertidae (Fig. 29K-P)*

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. 29K-L), and for *Z. vivipara*, in which they can be similar in length or the longest process may even be the anterolateral one (Fig. 29O-P). The dorsal surface of the bone is smooth.

*Scincidae (Fig. 29Q-X)*

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 the posterolateral process (Fig. 29W-X). 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. 29U-V). Moreover, a distinct anteromedial lappet seems not to be developed in *A. kitaibelii* (Fig. 29Q-R). The ventral lappet of the posteromedial process of *C. ocellatus* shows a small anteromedially-developed projection (Fig. 29S-T), which contacts the palatine process of the pterygoid.

Anterolateral and posteromedial processes are similar in length in *A. kitaibelii*, *Chalcides*, and *O. punctatissimus* (Fig. 29Q-V), whereas the latter process is longer than the former in *T. aurata* (Fig. 29W-X). Both dorsal and ventral surfaces are smooth.

*Anguidae (Fig. 29Y-AB)*

Anguids have a crescent-shaped and medially concave ectopterygoid, similar to that of gekkotans (Villa *et al.*, 2018a). 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. 29AA). The mediodorsal surface of the bone is smooth.

## GENERAL FEATURES OF THE BRAINCASE

The sphenoid, the basioccipital, the prootics, the supraoccipital, and the otooccipitals fuse together to form the braincase (Fig. 30, 31, 32, 33, 34). The fusion is generally linked to ontogeny, with separated bones in juveniles that fuse in older individuals. On the posterior side of the region, the foramen magnum is defined by the basioccipital ventrally, the supraoccipital dorsally, and the otooccipitals laterally. Moreover, the otooccipitals and the basioccipital form the occipital condyle. On each side, the recessus scalae tympani is enclosed by the basioccipital and each otooccipital. The recessus 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 external opening of the cochlear cavity is the wide fenestra ovalis, located between the prootics and otooccipitals. The paired anterior, horizontal and posterior semicircular canals are present on each side of the ossified braincase. The anterior canal passes through the prootic and the supraoccipital, the horizontal canal goes from the dorsal portion of the prootic to the base of the paraoccipital process of the otooccipital, and the posterior canal develops between the supraoccipital and the otooccipital.

### *Agamidae*

The braincase 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 braincase 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. 35). The occipital condyle is composed mainly by otooccipitals, but a small portion of the posterior end of the basioccipital is also part of it (Fig. 35). 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. Because of this, the basioccipital forms the 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 recognisable.

### *Lacertidae (Fig. 30, 31A-E)*

Similarly to gekkotans (see Villa *et al.*, 2018a), lacertids have an ossified braincase that is roughly as long as wide and either slightly or not distinctly dorsoventrally compressed. They display a wide and subcircular foramen magnum and a condyle that is composed equally by the three bones that concur in its formation. In contrast with geckos, the U-shaped notch on the occipital condyle is wider and shallower or even absent in lacertids, 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. 31F-J, 32, 33)*

In scincids, the braincase 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. 33B). 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. 34)*

Anguids have a braincase 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. 34D-E) or rather straight (*P. apodus*; Fig. 34I-J), in dorsal and ventral view. The recessus scalae tympani is moderately reduced in *Anguis* gr. *A. fragilis* (Fig. 34B), but larger in *P. apodus* (Fig. 34G). It opens externally with an anteroposteriorly elongated lateral opening, which is narrow in *Anguis* gr. *A. fragilis* (Fig. 34B). 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 basioccipital (Fig. 36) is unpaired, subhexagonal, and roughly as long as it is wide. It has a dorsally concave body, with a central cranial depression and two moderately developed lateral wings. In dorsal view, it has a roughly straight or concave anterior margin. Posteriorly, it forms the medial portion of the occipital condyle. The ends of the lateral wings develop the sphenooccipital tubercles and constitute the ventral wall of the recessus scalae tympani. The crista tuberalis marks the posterior wall of the recessus. The basioccipital is smooth, both dorsally and ventrally. The bones that fuse with this bone are the sphenoid anteriorly, the prootics anterolaterally, and the otooccipitals posterolaterally.

*Agamidae (Fig. 36A-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. 36C-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.

*Lacertidae (Fig. 30, 31A-E, 36E)*

The basioccipital of lacertids is similar to that of gekkotans (see Villa *et al.*, 2018a). 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, the tubercles are ventrally pointed.

*Scincidae (Fig. 31F-J, 32, 33, 36F)*

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. 31G-H, 32A-C, 33A-C) and very well developed in *C. ocellatus* and *T. aurata* (Fig. 32F-H). The developed ones become subtriangular in lateral view.

*Anguidae (Fig. 34, 36G)*

The basioccipital is slightly longer than it is wide in *Anguis* gr. *A. fragilis* too (Fig. 34E, 36G). In *P. apodus*, on the other hand, length and width of this bone are roughly similar (Fig. 34J). Posteriorly, the basioccipital of anguids composes more than one third of the occipital condyle. Sphenooccipital tubercles are moderately or well developed in *Anguis* gr. *A. fragilis* (Fig. 34B-C) and always well developed in *P. apodus* (Fig. 34F-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 increases with growth, but they are as a rule larger in *P. apodus* than in *Anguis* gr. *A. fragilis*.

SPHENOID

The complete fusion of parasphenoid and basisphenoid results in the unpaired sphenoid (Fig. 37). This bone has a roughly quadrangular body, from which two basipterygoid processes develop anterolaterally from the anterolateral corners. Two posterolaterally directed cristae ventrolaterales (parasphenoid wings in Daza *et al.*, 2008) can be also present by the posterolateral corners. On the dorsal surface of the body of the bone, there are two cylindrical trabeculae cranii, the sella turcica (including the hypophysial fossa), and the transverse crista sellaris. The trabeculae, located between the basipterygoid processes, are continued posteriorly by two low cristae trabeculares that border the sella turcica laterally. A parasphenoid rostrum (cultriform process in Daza *et al.*, 2008) can be present between the trabeculae, on the anterior margin of the bone. The crista sellaris composes the posterior margin of the sella turcica and contacts the prootics laterally, with the alar processes. The crista can develop anterodorsally to form a dorsum sellae that covers the sella turcica. Moreover, it is pierced anteroposteriorly by two abducens foramina. The dorsal surface of the posterior portion of the sphenoid, located posteriorly to the crista sellaris, is smooth. Ventrally, the sphenoid can present a sunken area in the middle. The Vidian canals open anteriorly medial to the base of the basipterygoid process, medially in the sella turcica (with the internal carotid foramina), and posterolaterally towards the contact with the prootics. Both sides of the sphenoid display the recessus vena jugularis extending in posterodorsal direction starting from the latter openings. The recessus continues on the prootics. The sphenoid contacts the basioccipital posteriorly and the prootics posterolaterally.

*Agamidae (Fig. 37A-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. 37A-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. 37A). The medial openings of the Vidian canals are located close to each other in adults (Fig. 37B), but they are more spaced in juveniles. The ventral surface is only slightly sunken (Fig. 37D). The recessus vena jugularis is deep (Fig. 37C). 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. 37E-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 the basipterygoid processes are moderately long, moderately thick and roughly triangular. The processes enlarge distally and are tilted mediolaterally at an angle of 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. 37E). The crista sellaris is well developed and projects slightly anteriorly, creating a short dorsum sellae (Fig. 37E). 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. 37H). The recessus vena jugularis is very shallow (Fig. 37G).

*Lacertidae (Fig. 30, 31A-E, 37I-M)*

In lacertids, the 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. 30D-E) or enlarged for their entire length (adults of other species; Fig. 30I-J, 31D-E, 37I-J, L). 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. Well-developed (shorter in *A. marchi*, *A. moreoticus*, and *A. nigropunctatus*; Fig. 37J) cristae ventrolaterales and a long, narrow and laminar parasphenoid rostrum are present. The cristae reach the sphenooccipital tubercles. The trabeculae cranii are dorsoventrally flattened. They are small and well separated from one another in small-sized animals (e.g., *A. erythrurus*; Fig. 30D), but they grow bigger and tend to come in contact in adults of larger ones (e.g., *L. bilineata* and *T. lepidus*; Fig. 30I). 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 (Villa *et al.*, 2018a). 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 process from the related basipterygoid process. A low transverse ridge is present on the dorsolateral surface of the latter process 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 sphenoid shows a moderately to strongly sunken area in the middle (Fig. 30E). 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 suggests 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. 31F-J, 32, 33, 37N-Q)*

The sphenoid of scincids has axe-shaped and moderately short basipterygoid processes. The proximal half of these processes 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. 31J), each posterolateral corner of the sphenoid shows a short and pointed crista ventrolateralis (Fig. 32E, J, 33E). The trabeculae cranii (very poorly developed in *A. kitaibelii*, *T. aurata*, and *O. punctatissimus*; Fig. 31I, 33D, 37N) are not in contact (the only exceptions are *C. bedriagai* and *O. punctatissimus*; Fig. 33D) and, except for *O. punctatissimus*, they 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. 31I, 32D, 33D) or well developed (*C. ocellatus* and *T. aurata*; Fig. 32I, 37P) 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. 31G). 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 recognisable 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 slightly more 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. 32E, J).

### *Anguidae (Fig. 34, 37R-S)*

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 this process can be considered 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. 34B), whereas they are larger and more squared in *P. apodus* (Fig. 34G). 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. 38) includes the epiotic of Jollie (1960). This bone is elongated transversely and posteriorly inclined. It can be separated into three portions: a thin medial portion and two wide lateral portions. The latter form the roof of each cavum capsularis. Posteriorly the supraoccipital represents the dorsal margin of the foramen magnum. Anteriorly, it can carry an anterodorsally developed processus ascendens or other different structures. The anterior margin of the bone hosts the dorsal portions of the anterior semicircular canals. The dorsal portions of the posterior semicircular canals, on the other hand, run from the posterolateral corners to the middle of the dorsal surface of the bone. Anterior and posterior canals merge in the common crus, which in turn opens in the cavum capsularis. The endolymphatic foramina are present near the contact with the prootic, on the medial surface of each lateral portion of the supraoccipital. This foramina opens posterodorsally and are moderately wide. The supraoccipital is fused with the prootics and the otooccipitals.

#### *Agamidae (Fig. 38A)*

*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. 39).

*Chamaeleonidae (Fig. 38B-C)*

The supraoccipital is the largest bone of the braincase of *C. chamaeleon*. In the middle of the dorsal surface of the bone, there is the very well developed processus ascendens, developed in anterodorsal direction and strongly expanded dorsally to form a tall median crest (Fig. 38B). The dorsal expansion of the processus contacts the parietal crest of the parietal. On both sides of the processus ascendens, two well-developed and anteriorly projecting cylindrical processes are present. The common crus is absent and the semicircular canals enter directly the cavum capsularis.

*Lacertidae (Fig. 30, 31A-D, 38D)*

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. 30I, 31D, 38D), but in *A. erythrurus* they are roughly parallel (Fig. 30D).

*Scincidae (Fig. 31F-I, 32, 33, 38E)*

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. 32F-I), whereas *C. chalcides* and *C. striatus* have a short and more slender processus, which does not produce a crest posteriorly (Fig. 32A-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. 31F-I, 33A-D, 38E), 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. 32A-D). These processes are not recognisable in *C. ocellatus* and *C. striatus*, but the more expanded processus ascendens of the former could suggest that they are fused with it (Fig. 32F-I). The processus of *T. aurata* is flanked by two well-developed ridges, running along the anterior margin of the supraoccipital (Fig. 38E). Similar, but less developed ridges are visible in *C. striatus* too. Small marginal processes are recognisable by the anterior end of the contact with the prootics in *Chalcides* and *O. punctatissimus*.

### *Anguidae (Fig. 34)*

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 paired prootic (Fig. 40) includes a posterior process (posteriorly), an alar process (anterodorsally), and an anterior inferior process (ventrally). The horizontal semicircular canal and, anterodorsally to the latter, the anterior semicircular canal occupy the posterior process. Posteriorly, this process develops a projection that extends to cover the anterior surface of the paroccipital process of the otooccipital. The alar process extends from the anterodorsal end of the anterior semicircular canal, bearing the articulation surface with the epipterygoid on its anterior margin, which is named crista alaris. The anterior inferior process display the incisura prootica, the facial foramen, and the laminar crista prootica. 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. Two other large foramina are visible medially, opening in a concave acoustic recess. These foramina are the smaller anterior acoustic foramen and the very large posterior acoustic foramen. The former is located dorsally to the facial foramen and opens in the ampullary recess, whereas the latter 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 prootic encloses the anterior portion of the inner ear. Its inner structures include the anterior portions of the cavum capsularis dorsally, that of the cochlear cavity ventrally, and the cochlear crest between them. The opening of the anterior semicircular canal flanks dorsally the cavum capsularis, whereas laterally to the latter there is the opening of the horizontal semicircular canal. The opening of the ampullary recess is visible at the medioventral corner of the cavum. The dorsal half of the anterior wall of the cochlear cavity houses the wide groove for the perilymphatic duct. The prootic fuses with the sphenoid anteroventrally, the basioccipital posteroventrally, the supraoccipital posterodorsally, and the otooccipital posteriorly.

*Agamidae (Fig. 40A-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. 40A). 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. 40B). 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. 39, 40B-C).

*Chamaeleonidae (Fig. 40D-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. 40D). The inner structures are poorly ossified and therefore they are not closed medially (Fig. 40E). There is no distinct groove for the perilymphatic duct and the cochlear crest is very poorly defined.

*Lacertidae (Fig. 30, 31A-E, 40F-I)*

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. 31B, 40F) 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. 30B, G, 40H). 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. 30B) and longer in other species (Fig. 30G, 31B, 40F, H). 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. 30B), whereas a low one is present in other species. Usually, neither a clearly distinguishable recessus vena jugularis nor an entocarotid fossa are recognisable.

### *Scincidae (Fig. 31F-J, 32, 33, 40J-K)*

The prootics of scincids have a short paroccipital projection and an anteriorly rounded alar process, which is very short in *A. kitaibelii* (Fig. 31G), moderately short in *C. bedriagai*, *C. chalcides*, *C. striatus*, and *T. aurata* (Fig. 32B, 40J) and long in *C. ocellatus* and *O. punctatissimus* (Fig. 32G, 33B). The incisura prootica is deep (very deep in *C. ocellatus*; Fig. 32G) and moderately wide (even wider in *A. kitaibelii*; Fig. 31G). The facial foramen is also moderately wide, except for the one of *A. kitaibelii*. In *Chalcides* and *T. aurata*, the margins of this foramen 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 poorly developed (sometimes even absent) in *A. kitaibelii* and *O. punctatissimus* (Fig. 31G, 33B) and well developed in the other species (Fig. 32B, 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. 34, 40L-M)*

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. 34B) or moderately developed (*P. apodus*; Fig. 34G) and moderately robust; it can also be slightly irregular. The anteriormost and posteriormost portions of the crista are almost unrecognisable. 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. 41) is a paired bone made up by the complete fusion of exoccipital and opisthotic, which are not recognisable as separate elements. Each otooccipital takes part in composing the occipital condyle. The posterior semicircular canal is visible on the posterior surface of the bone, running vertically and continuing dorsally on the supraoccipital. Few foramina are located between the ventral end of the posterior semicircular canal and the occipital condyle. The vagus foramen is the largest and most dorsally located of these foramina. The other ones are the hypoglossal foramina, whose number is highly variable. On the lateral side of the otooccipital there is the well-developed paroccipital process, which is roughly rectangular in posterior view. The posterior portion of the horizontal semicircular canal is visible by the base of this process. The crista interfenestralis marks the dorsal margin of the lateral opening of the recessus scalae tympani, running anteroventrally from the paroccipital process on the lateral surface of the otooccipital. The posterior portion of the inner ear is enclosed by this bone. It houses the posterior walls of the cavum capsularis and of the cochlear cavity, located dorsally and ventrally respectively. There are no ridges or grooves separating the two cavities, but the openings of the ampullary recess ventrally and of the utricular recess dorsally are visible inside the cavum capsularis. Moreover, the openings of the horizontal semicircular canal and the posterior semicircular canal are present laterally and dorsally to the cavum, respectively. Inside the cochlear cavity, on the other hand, there is the perilymphatic foramen, opening in the recessus scalae tympani. The otooccipital contacts the basioccipital ventrally, the prootic anteriorly, and the supraoccipital dorsally, fusing with them.

#### *Agamidae (Fig. 41A-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 laminar ridge is present on the proximal half of its ventral surface (Fig. 41A, 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. 41A). It opens posteriorly on the ventromedial wall of the cavum capsularis.

*Chamaeleonidae (Fig. 41E-H)*

In *C. chamaeleon*, the portion of the occipital condyle composed by each otooccipital corresponds to almost its half (Fig. 35, 41G-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. 41F). 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 remnant of the lateral opening of the recessus scalae tympani (Fig. 41F). The paroccipital process (Fig. 41H) 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. 41E). Because of the reduction of the recessus scalae tympani, the perilymphatic foramen opens on the medial surface of the bone.

*Lacertidae (Fig. 30, 31A-E, 41I-J)*

As in gekkotans (Villa *et al.*, 2018a), the otooccipital of lacertids composes a third of the occipital condyle and the number of hypoglossal foramina is variable (see the Supplementary Information). 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. 31A-E, 41I). The process is slightly dorsoventrally enlarged by its distal end.

*Scincidae (Fig. 31F-J, 32, 33, 41K-L)*

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 two, but there can also be three or four of them. The paroccipital process is very short (*A. kitaibelii* and *O. punctatissimus*; Fig. 31F-J, 33), short (*C. chalcides*, *C. striatus*, and *T. aurata*; Fig. 32A-E, 41K) or moderately long (*C. ocellatus*; Fig. 32F-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. 34, 41M-N)*

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 recognisable 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. 34A-E, 41O) and long in *P. apodus* (Fig. 34F-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. 42) 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. 42A)*

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

### *Lacertidae (Fig. 42B)*

The footplate of the stapes of lacertids is subcircular. No stapedial foramen is present.

### *Scincidae (Fig. 42C)*

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

### *Anguidae (Fig. 42D)*

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

## DENTARY

The dentary (Fig. 43) is a long, paired bone. It is straight in both dorsal and medial view, but the anterior end bends moderately in medial direction. The mandibular symphysis covers the medial surface of the anterior end. The Meckelian fossa stands out on the medial surface of the bone, housing the anterior portion of the Meckel's cartilage. Dorsally to the fossa, there is an alveolar shelf (parapet in Rage & Augé, 2010) supporting the teeth. The bony structures separating the Meckelian fossa from the alveolar shelf were differently named by different authors in the past (including the authors of the present paper: see e.g., Villa *et al.*, 2018a, b), generating a certain degree of ambiguity on how to correctly define some terms. We herein follow the terminology proposed by Rage & Augé (2010), updating it with a single addition (the subdental ridge; see below). We choose this terminology because it gives clear definitions of the terms used. Teeth are supported ventrally by a subdental table. This table more or less extends medially to form a subdental shelf, which is not covered dorsally by the tooth bases. Dorsally, the subdental shelf can present a subdental ridge, which marks the medial margin of the sulcus dentalis. The alveolar canal is present between the Meckelian fossa and the subdental table, 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 inferior posterior process and the superior posterior process develop at the posterior end of the dentary. They are laminar and posteriorly directed. The lateral surface of the dentary is smooth in extant European lizards, except for a variable number of anteroposteriorly aligned mental foramina.

Before describing the dentaries of the different lizard groups herein considered, it is worth to briefly revise the descriptions of the groups that were formerly treated by Villa *et al.* (2018a, b) using a terminology different to those of Rage & Augé (2010). In gekkotans, the subdental table strongly develops medially to form a subdental shelf that is extensively expanded ventrally and contributes to the enclosure of the Meckelian fossa. Dorsally, a distinct subdental ridge and the related sulcus dentalis are visible. In *Blanus*, the subdental shelf is rather high in medial view, but not strongly extended in medial direction. Posteriorly, the subdental shelf displays a wide V-shaped notch in medial view. A low subdental ridge and a shallow sulcus dentalis are present dorsally. The reader is still referred to the original papers for the rest of the description of the dentary in these two groups.

*Agamidae (Fig. 43A-B)*

The dentary of *L. stellio* is stocky and its mandibular symphysis is large and subcircular or subelliptical in medial view (Fig. 43A). The Meckelian fossa is narrow, but widens slightly in its posterior half (Fig. 43A). The subdental table develops a short subdental shelf, which is high in medial view. The shelf displays a low ventral expansion in its posterior portion (Fig. 43A). A low subdental ridge is present, marking a shallow sulcus dentalis. 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 seventh and eight 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 recognisable 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. The dorsal one can be shorter than the ventral one in juveniles (Smith *et al.*, 2016). In medial and lateral views, only a small U-shaped notch separates the posterior processes. In posterior view, a recess similar to the one present in *C. chamaeleon* (see below) is present (Fig. 43B), but it is very narrow in *L. stellio*. 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. 43B). 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 four to eight.

*Chamaeleonidae (Fig. 43C-D)*

In *C. chamaeleon*, the dentary is stocky and presents a moderately wide mandibular symphysis (Fig. 43C), which is almost vertical (it shows only a low inclination of less than 25° in anteroposterior direction). The Meckelian fossa and the subdental table are similar to the ones of *L. stellio*, but the anterior half of the former opens in ventral direction (Fig. 43C). 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. 43C). 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, they clearly 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. 43C). 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. 43D). 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 three, four or five.

*Lacertidae (Fig. 43E-H)*

Lacertids have a narrow and almost horizontal mandibular symphysis. The Meckelian fossa is wide, but narrows towards the anterior end of the bone. In lacertids, the subdental shelf protrudes more medially than in *L. stellio* and *C. chamaeleon*. It is rather narrow in medial view and can display a very little ventral expansion towards its anterior end. The subdental ridge and the sulcus dentalis are well distinct. 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. 43G-H), 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. 43E-F). 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 Supplementary Information.

*Scincidae (Fig. 43I-P)*

The mandibular symphysis is narrow and almost horizontal in the dentaries of European 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 shelf covers it medially. The remaining portion of the shelf is rather narrow, as in lacertids. Caputo (2004) stated that some specimens of *C. ocellatus* can present a partly closed fossa, probably because of a very strong ventral development of the subdental shelf. This happens also in *T. aurata* (e.g., MDHC 280; Fig. 43O). *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. 43I). European scincids display well-distinct subdental ridge and sulcus dentalis, as in lacertids. As in other tooth-bearing bones of this family, teeth are morphologically similar to those of gekkotans (see above and Villa *et al.*, 2018a), except for a slightly posteriorly curved crown provided with a light striation on the lingual surface. Exceptions are *C. ocellatus*, whose teeth are robust and provided with a blunt and enlarged crown (Fig. 43K-L), 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. 43M-N). The morphology of the posterior processes is usually similar to the one presented by gekkotans (i.e., inferior process long and pointed, superior process smaller and composed by two pointed projections; Villa *et al.*, 2018a), but the notch separating the projections of the superior one is very shallow and roughly U-shaped. Moreover, the largest projection of the superior process 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. 43I-J). *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. 43M-N). Moreover, 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. 43M-N). 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 Supplementary Information.

### *Anguidae (Fig. 43Q-T)*

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 recognisable (Fig. 44). 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. The subdental ridge is not present and the dorsomedial surface of the shelf is therefore smooth. The sulcus dentalis is also absent. Roughly by the beginning of the posterior fourth (*Anguis* gr. *A. fragilis*; Fig. 43Q) or third (*P. apodus*; Fig. 43S) 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. 43Q), but fused with the wall of the bone in *P. apodus* (Fig. 43S). The opening of the alveolar canal is located by the end of the ninth tooth position in *Anguis* gr. *A. fragilis* (near the last tooth position, as stated by Klembara *et al.*, 2014; Fig. 43Q) and between the ninth and the 11th tooth position in *P. apodus* (Fig. 43S). 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 species, teeth are monocuspid, trenchant, well-spaced, unstriated and distinctly posterolingually bent by their tip (Fig. 43Q-R), whereas the latter species 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. 43S-T). 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 a moderately wide and deep U-shaped notch (coronoid incisure in Klembara *et al.*, 2014). They are similar in size in *Anguis* gr. *A. fragilis* (Fig. 43Q-R), but the dorsal one is distinctly shorter than the ventral one in *P. apodus* (Fig. 43S-T). The surangular process of *P. apodus* bears an opening for the anterior surangular foramen (Fig. 43T), 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 (eight or nine in the specimens studied by Edmund, 1969) and three or four mental foramina, whereas in *P. apodus* they range from 12 to 18 and from four to seven respectively.

### SPLENIAL

The paired splenial (Fig. 45) is a blade-like bone, pierced by two foramina: the anterior inferior foramen anterodorsally and the anterior mylohyoid foramen posteroventrally.

### *Agamidae and Chamaeleonidae*

According to our observations, the splenial is absent in both *L. stellio* and *C. chamaeleon*, as previously reported for some agamids and chamaeleons in general by other authors (e.g., Jollie, 1960; Evans, 2008). The same authors stated 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. Baig *et al.* (2012) reported a small splenial in *Laudakia* s.l. However, the presence of articulated specimens in the herein-studied material (HUJ.OST-Z-5) seems to confirm its absence in the European species (Fig. 46), even though a variable condition could still be considered as possible due to the fact that this bone is easily lost during preparation.

*Lacertidae (Fig. 45A-F)*

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. 45E-F). 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 crest extends longitudinally in the middle of the surface. The splenial of *A. erythrurus* is expanded ventrally (Fig. 45A-B).

*Scincidae (Fig. 45G-N)*

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. 45K-L) 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. 45K). The ventral margin is straighter in medial view than the one of lacertids (which is rather convex) and the posterior portion of the dorsal margin is wavy in *Chalcides* (Fig. 45I-J), straight in *O. punctatissimus* (Fig. 45K-L), and convex in *T. aurata* (Fig. 45M-N). 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. 45G-H). 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 midlength of the ventral margin. Both the medial and the lateral surfaces of the splenial of *A. kitaibelii* are smooth.

*Anguidae (Fig. 45O-R)*

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 process and two longer, slender and pointed ventral ones. Only the small anterior mylohyoid foramen is clearly visible at midlength, 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. 45Q-R). The anterior mylohyoid foramen is located ventrally to the posterior margin of the notch of the anterior inferior foramen in *P. apodus* (Fig. 45Q-R), whereas it is shifted more posteriorly in *Anguis* gr. *A. fragilis* (Fig. 45O-P). 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. 47) is composed by five processes. The dorsally developed and subtriangular coronoid process stands out in the middle of the bone. Adding to this process, there 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. 47A-B)*

In *L. stellio*, the coronoid is robust and roughly straight in dorsal view. It has a well-developed, 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. 47A). 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. 47B). The ridge is less developed in juveniles.

*Chamaeleonidae (Fig. 47C-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 and 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 process (Fig. 47D).

*Lacertidae (Fig. 47E-H)*

If compared with that of gekkotans (Fig. 48A; see also Villa *et al.*, 2018a), the coronoid is only moderately concave in medial direction in lacertids (Fig. 48B). 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. 47E-F). 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 the medial surface of the latter process, 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. 47I-N)*

Scincids have a moderately crescent-shaped coronoid (Fig. 48C), provided with an anteromedial process that is morphologically similar to the one of gekkotans (Villa *et al.*, 2018a). However, in contrast with the latter group, this process does not show foramina. The labial process is strongly reduced in *O. punctatissimus* (Fig. 47M). 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 (Villa *et al.*, 2018a). 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 process (Fig. 47K-L).

*Anguidae (Fig. 47O-R)*

The coronoid of anguids is rather straight (very slightly medially concave) in dorsal view (Fig. 48D). The coronoid process is moderately thin (*Anguis* gr. *A. fragilis*; Fig. 47O-P) or distinctly robust (*P. apodus*; Fig. 47Q-R), dorsally rounded and posteriorly directed. In the articulated lower jaw, this process is covered more extensively by the superior posterior process of the dentary in *P. apodus* than it is in *Anguis* gr. *A. fragilis* (see Klembara *et al.*, 2014): as a matter of fact, the process of the dentary runs up to half the height of the coronoid process in the former taxon, whereas it only covers a short part of it in the latter. 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. 47O-P). In *P. apodus*, the anterior end of this process contributes in defining the anterior inferior foramen, as can bee clearly seen in articulated specimens (Klembara *et al.*, 2014). In *Anguis* gr. *A. fragilis*, the process is excluded from the foramen by the dentary and the splenial (Klembara *et al.*, 2014). The labial process is short in *P. apodus* (Fig. 47Q), but distinctly longer in *Anguis* gr. *A. fragilis* (Fig. 47O). 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. 47Q-R) than in *Anguis* gr. *A. fragilis* (Fig. 47O-P). The posteromedial process is very long, slender and can be lobe-shaped or pointed. In anguids, this process develops more posteriorly than ventromedially. A well-developed and laminar coronoid ridge, very similar to the lamina of gekkotans (Villa *et al.*, 2018a), is present between the coronoid and the posteromedial processes. The laminar ridge of *P. apodus* (Fig. 47Q-R) is thicker and slightly less developed than the one of *Anguis* gr. *A. fragilis* (Fig. 47O-P), being also less distinguishable from the coronoid process.

### ANGULAR, SURANGULAR, PREARTICULAR, AND ARTICULAR

These four bones (Fig. 49, 50, 51) 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, it is expanded and displays 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 and the posterior surangular foramen. The former is located near the dorsal margin of the bone by the anterior expanded area, whereas the latter is placed near the ventral margin by the posterior expansion. The prearticular and the 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 or subquadrangular; 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 near the anteroventral corner of the medial surface. An angular process can develop in medial direction ventrally to the condyle. Medially, the broad adductor fossa is present anteriorly to the articular condyle. The fossa is defined by the surangular dorsally and by the prearticular/articular complex ventrally.

*Agamidae (Fig. 49A-B, 50A-D, 51A)*

In *L. stellio*, only the prearticular and the articular are fused together, whereas angular and surangular remain free. The angular (Fig. 49A-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 midlength; it continues in a shallow groove on the medial concave surface of the bone, but does not open dorsally. The lateral surface of the angular is smooth, except for a sharp and sigmoid-shaped ridge running along its entire length. The surangular of *L. stellio* (Fig. 50A-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. 50A). The dorsal ridge is less developed than the other and marks the ventral margin of the anterior expanded area, whereas the more developed ventral ridge 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. 50B). The imprints of the posterior processes of the latter bone are recognisable 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. 50C-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. 50C). The articular condyle is subquadrangular in dorsal view and roughly flat (Fig. 51A). 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. 49C-D, 50E-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. 49C-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 midlength. The surangular and prearticular portions of the compound bone are clearly recognisable as distinct branches separated by a notch where the inferior posterior process of the dentary inserts (Fig. 50E-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. 50E). 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. 50E).

*Lacertidae (Fig. 49E-H, 50G-J, 51B)*

The angular of lacertids (Fig. 49E-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. 49E). 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. 49H). The lateral surface is smooth, except for the articulation surface with the dentary, which covers its anterior half (Fig. 49E-F). The other bones fuse to form a compound bone (Fig. 50G-J, 51B) that can be separated in two portions in juveniles. The articular condyle is subquadrangular in dorsal view and rather flattened. A stocky tubercle develops in medial direction from its anteromedial corner (Fig. 51B). The retroarticular process is straight and subtriangular in medial view, given that it narrows posteriorly. Its 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. 50G). In other European lacertids, the margin is usually straight in medial view (Fig. 50H-I), but a strong ventral development is visible also in both compound bones of MRAC 91-077-R-76 (Fig. 50J) and in the left one of NHMW 663 (Fig. 52), 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. 50I). In *L. agilis*, *L. bilineata*, *L. viridis*, and *T. lepidus*, a distinct and rather sharp longitudinal ridge runs dorsally to the articulation surface (Fig. 50I). 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. 49I-J, 50K-R, 51C)*

In scincids, all the bones but the angular fuse to form a compound bone. The latter (Fig. 49I-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. 50K-R, 51C) 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. 50K-L). Nevertheless, the concavity is well distinct in the small *O. punctatissimus* (Fig. 50O-P). 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. 51C) 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. 50K-L, O-P). The process is more anteroposteriorly elongated in *A. kitaibelii*, *C. chalcides*, and *C. striatus* (Fig. 50K-L) and more dorsoventrally expanded in *C. ocellatus*, *O. punctatissimus*, and *T. aurata* (Fig. 50M-R). 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.

*Anguidae (Fig. 49K-N, 50S-V, 51D-E)*

Anguids have a free angular, whereas the other bones are fused in a compound bone. The angular (Fig. 49K-N) is very slender, with pointed anterior and posterior ends. The latter end 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. 49K-L) than in *P. apodus* (Fig. 49M-N). The angular ridge runs along the ventral margin, showing a thickening roughly at midlength. 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. 50S-V, 51D-E) 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. 51D-E). 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. 50T, V). The articulation surface with the angular is visible on the lateral surface of the bone, reaching roughly midlength (Fig. 50T, V). 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. 50S), but can be moderately or well developed in *P. apodus* (Fig. 50U). 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*.

## DISCUSSION

### DIAGNOSTIC KEY

The main goal of comparative osteological analyses like the one presented here is to highlight similarities and differences between different species or groups. The resulting data can be then used in a number of different studies, going from phylogenetic analysis to morphofunctional investigations. However, one of the most intuitive ways of using these data is for the identification of bones whose original owner is not known. This is mainly the case with fossil/subfossil remains (e.g., Bochaton *et al.*, 2018), but examples are also present in zoological studies focused on extant animals (e.g., to identify prey remains; see, for example, Kupriyanov *et al.*, 2012, and Grano & Cattaneo, 2017). To ease bone identification, diagnostic keys based on osteological features were created in the past by some authors, dealing with different groups (e.g., Bailon, 1999, for French anurans; Szyndlar, 1984, for European snakes; Barahona & Barbadillo, 1997, for Iberian lacertids). Our comparative analysis gives the opportunity to create a similar tool covering the skull bones of European lizards on the whole. Following the rationale of Villa *et al.* (2018a), size is not considered directly in the key, even though we acknowledge that it can still be of help in absence of clearly diagnostic morphological features. Given that amphisbaenians are often treated together with lizards in palaeontological works, we included also data on European amphisbaenians (genus *Blanus*) in the key. These data come from the comparative description of the *Blanus* skull by Villa *et al.* (2018b), to which the reader is referred for diagnostic differences that possibly allow to discriminate between the different species of the genus. Similarly, the reader is referred to the work of Villa *et al.* (2018a) for a detailed key of European gekkotans skull bones. In the end, when a feature is still considered useful for the identification despite being variable within a taxon, the variability is signaled in the key.

*Nasal* (Fig. 1)

1. Nasal short…………………………………………………………………………...*Blanus*

- Nasal anteroposteriorly elongated……………………………………………………………..2

2. Nasal slender in dorsal view…………………………………………………...*C. chamaeleon*

- Nasal wider in dorsal view…………………………………………………………………….3

3. Nasal shrinking towards the posterior end; well-defined articular surface 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………………………………………………….....8

5. Anterolateral process present; lateral laminar expansion absent…………………………..Gekkota

- Anterolateral process absent; lateral laminar expansion present……………………………………...6

6. Lateral expansion clearly recognisable…………………………………………………*T. aurata*

- Lateral expansion very short and poorly individualized……………………………………………7

7. Posterior margin rounded…………………………………………………………….*A. kitaibelii*

- Posterior margin oblique and roughly straight……………………………………*O. punctatissimus*

8. Ornamentation restricted to the posterior half of the dorsal surface…………………….*Algyroides* (but variable in *A. nigropunctatus*), *Ps. hispanicus*

- Ornamentation located in the middle of the dorsal surface…………………………………………9

- Ornamentation largely occupying the dorsal surface……………………………………………...11

9. Lateral laminar expansion clearly recognisable………………………………………..*C. chalcides*

- Lateral laminar expansion poorly individualized……………………………………………….10

10. Weak ornamentation; posterior margin oblique and roughly straight………………….*C. striatus*

- Stronger ornamentation; posterior margin rounded……………………………………..*C. ocellatus*

11. Posterior margin straight and oblique, sometimes provided with a small, V-shaped notch in the middle……………………………………………………………………………..12 (Anguidae)

- Posterior margin convex………………………………………………………………………..13

12. Anteromedial process long and slender; posterolateral corner not developed in a pointed process………………………………………………………………...*Anguis* gr. *A. fragilis*

- Anteromedial process short and wide; posterolateral corner developing a long and pointed process…………………………………………………………………………………*P. apodus*

13. In adults, ornamentation almost absent……………………………………………...*O. elegans*

- In adults, ornamentation poorly developed…..*A. erythrurus*, *D. oxycephala*, *I. bonnali*, *I. horvathi*

- In adults, ornamentation strongly developed……………………………………………...14

14. Sulcus not visible on the ornamented surface…………………………………..*D. mosorensis*, *I. cyreni*, *I. monticola cantabrica*, *P. bocagei*, *P. carbonelli*, *Po. hispanicus*

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

*Frontal* (Fig. 2-4)

1. Frontal unpaired……………………………………………………………………………2

- Frontal paired and, if fused in a single element, fusion occurs only in old individuals and the suture line is visible in ventral view…………………………………………………………....8

2. Frontal composed of a subtriangular anterior portion and a subpentagonal posterior portion; all margins represented by interdigitated sutures…………………………………………*C. chamaeleon*

- Frontal T-shaped; interdigitated sutures, if present, located by the posterior margin only…………3

3. Cristae cranii forming a tubular structure……………………………………………….Gekkota

- Cristae cranii not fused in a tubular structure…………………………………………………4

4. Cristae cranii poorly or not developed; anterior processes absent………………………………...5

- Cristae cranii more developed and originating well-developed anterior processes anteriorly……..7

5. Lateral processes moderately large; dorsal surface sunken along midline; articular surfaces with the nasals large, deep and U-shaped……………………………………………………….*L. stellio*

- Lateral processes short or very short; dorsal surface unsunken; articular surfaces with the nasals less deep and less distinct…………………………………………………………………………6

6. Strong middle constriction; pointed and very little developed lateral processes; articular surface with the nasals subtrapezoidal; no distinct ornamentation on the dorsal surface…………*A. kitaibelii*

- 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*

7. Posterior margin interdigitated……………………………………………………………*E. arguta*

- Posterior margin wavy, with a posterior expansion in the middle and no interdigitations…………………………………………………………...*A. erythrurus*, *O. elegans*

8. 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 corner of the bone; articular surface with the postfrontal not present…………………………………………………………………….*Blanus*

- Frontal anteroposteriorly elongated; posterolateral process present; articular surface with the premaxilla not present; crista cranii running along the lateral margin; articular surface with the postfrontal present……………………………………………………………………………9

9. Lateral process absent; presence of a ventral lappet of the posterolateral process; crista cranii laminar and well developed, without a distinct anterior process………………………10 (Anguidae)

- Lateral process present; ventral lappet of the posterolateral process absent; crista cranii posteriorly low, but originating a well-developed anterior process……………………………………………..11

10. 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 present………………………...*Anguis* gr. *A. fragilis*

- 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 small…………………………………..*P. apodus*

11. Lateral process never bifurcated; posterior margin without interdigitations; anterior process large in lateral view and distally pointed……………………………………………………………12

- Lateral process usually bifurcated; posterior margin interdigitated; anterior process thin, with an irregular ventral margin……………………………………………………………………..15

12. 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 light grooves……………………*O. punctatissimus*

- Posterior end twice as large as the anterior one; lateral process short but distinct; articular surface with the prefrontal reaching midlength; dermal ornamentation present in the middle of the dorsal surface, at least in adults…………………………………………………………………………13

13. 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……………………………………………………………………………………14

14. Articular surface with the nasal subtrapezoidal………………………………………*C. chalcides*

- Articular surface with the nasal rounded…………………………………………………*C. striatus*

15. Frontal with parallel lateral and medial margins in adults……………………………………...16

- Frontal with a slight medial constriction in adults…………………………………………………...17

16. 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*

17. Articular surface with the maxilla reduced or absent…………………………………………...18

- Articular surface with the maxilla larger, not reduced……………………………………………20

18. Posterior end less than twice as large as the anterior one, at least in adults; sulcus between frontal and frontoparietal shields located at midlength or at 3/5 of the total length………..*T. lepidus*

- Posterior end twice as large as the anterior one; sulcus between frontal and frontoparietal shields located at the beginning of the posterior third of the total length…………………………………..19

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

- Interdigitations on the posterior margin strongly developed…………………*I. cyreni, I. monticola*

20. Posterior end less than twice as large as the anterior one, at least in adults…………….*H. graeca*

- Posterior end twice as large as the anterior one…………………………………………………...21

21. Interdigitations on the posterior margin little developed…………………*P. filfolensis, P. lilfordi*

- Interdigitations on the posterior margin strongly developed…………………………Other lacertids

*Parietal* (Fig. 5-7)

1. Parietal paired……………………………………………………………………………...Gekkota

- Parietal unpaired……………………………………………………………………………………….2

2. Supratemporal processes absent…………………………………………………………………...3

- Supratemporal processes present…………………………………………………………………...4

3. 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; presence of posterior plates; parietal fossa small and moderately deep……………………………………………………*Blanus*

4. 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 the parietal table………………………………………………………………………………………………..5

5. When present, dermal ornamentation covering only the anterior half of the parietal table; presence of two processes on the posterior margin……………………………………...6 (Scincidae)

- Dermal ornamentation covering most of or entirely the dorsal surface of the table; posterior margin devoid of processes…………………………………………………………………………11

6. Anterolateral processes strongly developed laterally; supratemporal processes robust and provided with a distinct angle at midlength; 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; supratemporal processes slender and straight; medial ventral crest not in contact with the lateral ones; processes on the posterior margin wide…………………………………………………………………………..7

7. Processes on the posterior margin reduced to rounded tabs; epipterygoid processes short and triangular…………………………………………………………………………………..8

- Processes on the posterior margin pointed and not reduced; epipterygoid processes long…………9

8. Supratemporal processes short; dermal ornamentation absent or represented only by light grooves; parietal fossa shallow; posterior tabs very short……………………………..*A. kitaibelii*

- Supratemporal processes long; dermal ornamentation distinctly developed; parietal fossa deep; posterior tabs slightly longer……………………………………………………………...*T. aurata*

9. Supratemporal processes with a rounded end; dermal ornamentation represented only by light grooves; parietal notch narrow; processes on the posterior margin very long……..*O. punctatissimus*

- Supratemporal processes pointed; light dermal ornamentation present; parietal notch wide; processes on the posterior margin moderately short………………………………………………..10

10. Parietal fossa very narrow………………………………………………………………*C. chalcides*

- Parietal fossa moderately large…………………………………………………………*C. striatus*

11. 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 margin…………12 (Anguidae)

- Articular surface for the ventral lappet of the posterolateral process of the frontal absent; interparietal shield not reaching the anterior margin…………………………………13 (Lacertidae)

12. Groove between interparietal and frontoparietal shields directed toward the anterolateral corner of the ornamented surface; occipital shield small; facies muscularis absent; anterolateral ventral crest not in contact with the medial one (crista juxtafovealis absent); medial ventral crest completely covering the parietal fossa in adults; carina arcuata not extending posteriorly to cover parietal notch; epipterygoid process absent…………………………………………………..*Anguis* gr. *A. fragilis*

- Groove between interparietal and frontoparietal shields located more medially; occipital shield large; facies muscularis present; anterolateral ventral crest touching medial one (crista juxtafovealis present); 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*

13. Dermal ornamentation poorly developed; parietal tabs laterally expanded……………………14

- Dermal ornamentation well developed; parietal tabs not expanded laterally……………………..16

14. Presence of a very small occipital shield……………………………………………*O. elegans*

- Occipital shield absent…………………………………………………………………………15

15. Anterior margin without interdigitations, wavy and provided with a concavity in the middle; area levis retained in adults……………………………………………………..*A. erythrurus*

- Anterior margin with well-developed interdigitations; ornamentation reaching posterior margin, at least in adults……………………………………………………………………...*E. arguta*

16. Occipital shield very large…………………………………………………………*T. lepidus*

- Occipital shield moderately small………………………………………………………………17

17. Supratemporal processes thin………………………………………………………………...18

- Supratemporal processes distinctly widened proximally…………………………………………23

18. Parietal notch retained in adults…………………………………………………………...19

- In adults, no parietal notch………………………………………………………………...21

19. Ornamentation reaching posterior margin in adults……………………………………*A. marchi*

- Area levis present in adults……………………………………………………………………..20

20. Anterior margin with little-developed interdigitations; parietal table larger than long…………………………………………………………………………………...*Z. vivipara*

- Anterior margin strongly interdigitated; parietal table longer………………………..*Ps. hispanicus*

21. Contact between anterolateral and posterolateral ventral crests absent in adults……….*P. siculus*

- Contact between anterolateral and posterolateral ventral crests present in adults………………...22

22. Poorly developed interdigitations on the anterior margin……………………………….*I. bonnali*

- Strongly developed interdigitations on the anterior margin………….*A. moreoticus, D. mosorensis*

23. Parietal table larger than long; area levis retained in adults……………………………*I. horvathi*

- Parietal table longer; ornamentation reaching the posterior margin in adults……………………..24

24. Contact between anterolateral and posterolateral ventral crests present in adults….*A. bedriagae*, *D. oxycephala*, *I. cyreni*, *I. monticola*, *P. bocagei*, *Po. hispanicus*, *P. lilfordi*

- Contact between anterolateral and posterolateral ventral crests absent in adults…………………25 (variable in *L. agilis*, *P. melisellensis,* and *P. muralis*)

25. Poorly developed interdigitations on the anterior margin……………………………*P. filfolensis*

- Strongly developed interdigitations on the anterior margin……………………………*A. fitzingeri*, *A. nigropunctatus*, *H. graeca*, *Lacerta*, *P. melisellensis, P. milensis*, *P. muralis*, *P. pityusensis*, *P. tauricus*, *P. tiliguerta*, *P. waglerianus*, *P. algirus*

*Premaxilla* (Fig. 8, 9)

1. Premaxillae paired and, if fused, fusion present only in old individuals by the ventral margin of the bones……………………………………………………………………………….Scincidae

- Premaxilla unpaired………………………………………………………………………...2

2. Premaxilla very small and slender; palatal processes absent………………………*C. chamaeleon*

- Premaxilla larger, not reduced; palatal processes present…………………………………………..3

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 of real palatal processes…………………………………………………………………………………...*L. stellio*

- Alveolar plate wider than the base of the ascending nasal process; palatal processes distinct and more developed……………………………………………………………………………4

4. Palatal processes split in maxillary and vomerine processes…………………………5 (Anguidae)

- Palatal processes undivided……………………………………………………………………6

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 midlength lateral margins; septonasal crest never developed………………………………*P. apodus*

6. Notch between the palatal processes shallow and more or less rounded…………………………7

- Notch between the palatal processes deep and V-shaped……………………………..8 (Lacertidae)

7. Second pair of foramina by the base of the ascending nasal process present………………*Blanus*

- Second pair of foramina by the base of the ascending nasal process absent………………..Gekkota

8. In adults, ascending nasal process long, moderately narrow and slightly leaf-shaped at the distal end……………………………………………………………………………………*A. erythrurus*

- In adults, ascending nasal process shorter, stocky and leaf-shaped…………………………*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* (Fig. 11, 12)

1. Anterior premaxillary process strongly curved medially; presence of an anterior dorsal process, provided with tubercular ornamentation……………………………………………*C. chamaeleon*

- Anterior premaxillary process slightly or not curved medially; anterior dorsal process absent; tubercular ornamentation absent……………………………………………………………………...2

2. Maxilla short, with a very short posterior process; anteromedial process very well developed, wide, squared and ventrally concave…………………………………………………………...*Blanus*

- Maxilla anteroposteriorly elongate, with a long posterior process; anteromedial process usually less developed and not ventrally concave…………………………………………………………3

3. Anteromedial process developed in dorsal direction; anterior margin of the facial process bending medially………………………………………………………………………………*L. stellio*

- Anteromedial process not dorsally developed; anterior margin of the facial process not bending medially…………………………………………………………………………………4

4. Facial process subtrapezoidal……………………………………………………………...5

- Facial process pentagonal……………………………………………………...7 (Scincidae)

- Facial process subtriangular………………………………………………………11 (Lacertidae)

5. Presence of a lappet on the anteromedial process; vomeronasal foramen located in an anteriorly concave area; presence of an arched ridge on the medial surface of the facial process…6 (Anguidae)

- Lappet on the anteromedial process absent; vomeronasal foramen located on the dorsal surface of the premaxillary process, not in an anteriorly concave area; arched ridge on the medial surface of the facial process absent………………………………………………………………………Gekkota

6. Anteromedial and anterolateral processes similar in size; lappet on the anteromedial process projecting anteriorly with a pointed tip and slightly medially bending; posterior margin of the facial process almost vertical; lateral surface devoid of dermal ornamentation……….*Anguis* gr. *A. fragilis*

- Anteromedial process slightly shorter than the anterolateral one; lappet not projecting anteriorly and not bending; posterior margin of facial process slightly oblique; light dermal ornamentation present on the lateral surface……………………………………………………………..*P. apodus*

7. 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 clearly distinguishable…….8

8. Medial ridge of the anteriorly concave area well developed, originating a distinct lappet on the anteromedial process…………………………………………………………………………9

- Medial ridge of the anteriorly concave area low, not originating a lappet………………………...10

9. 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 facial process rounded……………………………………………………………………………….*A. kitaibelii*

10. Posterodorsal margin roughly straight and shorter than the anterodorsal one; all corners of the facial process pointed……………………………………………………………..*C. ocellatus*

- Posterodorsal margin strongly concave and as long as the anterodorsal one; dorsal corner of the facial process rounded……………………………………………………………….*T. aurata*

11. Dorsal margin of the posterior process stepped………………………………………………...12

- Dorsal margin of the posterior process not stepped………………………………………………13

12. 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*

13. Anteromedial process devoid of lappet…………………………………………………………14

- Lappet on the anteromedial process present………………………………………………………17

14. Projections of the facial process scarcely developed……………………...*A. fitzingeri*, *A. marchi*

- Projections of the facial process more developed…………………………………………………15

15. Projections of the facial process large……………………………………….*E. arguta*, *H. graeca*

- Projections of the facial process narrow……………………………………………………….16

16. Dorsoventral ridge on the medial surface absent…………………………………….*A. erythrurus*

- Dorsoventral ridge on the medial surface present…………………………………….*..O. elegans*

17. In adults, dermal ornamentation on the lateral surface absent or poorly developed……………18

- In adults, dermal ornamentation on the lateral surface well developed…………………………...19

18. Projections of the facial process scarcely developed…………………………………..*Z. vivipara*

- Projections of the facial process more developed…………………………………….*A. moreoticus*, *A. nigropunctatus*, *D. oxycephala*, *D. mosorensis*, *I. bonnali*, *I. horvathi*

19. Projections of the facial process scarcely developed…………*A. bedriagae*, *T. lepidus* (variable)

- Projections of the facial process more developed……………………………………Other lacertids

*Prefrontal* (Fig. 14, 15)

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*

- Dorsal process pointed and not mediolaterally expanded; suture not present by the posterior end of the process; tubercular ornamentation not present………………………………………………...2

2. Presence of a very robust tubercle on the dorsolateral corner……………………………..*L. stellio*

- Tubercle on the dorsolateral corner not present…………………………………………………3

3. Orbitonasal flange projection present…………………………………………………………...4

- Orbitonasal flange projection absent…………………………………………………………..9

4. Orbitonasal flange projection more developed than the posteroventral process…………..Gekkota

- Orbitonasal flange projection shorter than the posteroventral process……………………………..5

5. Orbitonasal flange projection subtriangular……………………………………………..6 (Anguidae)

- Orbitonasal flange projection subquadrangular………………………………………..7 (Scincidae)

6. Ornamentation not present; notch of the lacrimal foramen deep……………..*Anguis* gr. *A. fragilis*

- Ornamentation made up of mild rugosities; notch of the lacrimal foramen very deep……*P. apodus*

7. Osseous projection covering the notch of the lacrimal foramen dorsolaterally; dorsal process slightly longer than the orbitonasal flange……………………………………………...*A. kitaibelii*

- Notch of the lacrimal foramen not covered dorsolaterally; dorsal process slightly shorter than the flange………………………………………………………………………………………8

8. Palpebral crest sharp……………………………………………………………………*T. aurata*

- Palpebral crest low………………………………………………*Chalcides*, *O. punctatissimus*

9. Dorsal process very short; palpebral crest absent………………………………………...*Blanus*

- Dorsal process longer; palpebral crest well distinct…………………………………10 (Lacertidae)

10. Dorsal process as long as or shorter than the orbitonasal flange in lateral view……………………………Other lacertids not mentioned below (variable in *A. nigropunctatus*)

- Dorsal process slightly longer than the orbitonasal flange in lateral view………………………...11

11. Presence of a projection dorsally to the notch of the lacrimal foramen………………..*O. elegans*

- Projection dorsally to the notch of the lacrimal foramen not present…………………*A. erythrurus, A. marchi, A. moreoticus, Psammodromus*

*Jugal* (Fig. 16-18)

1. Jugal absent………………………………………………………………………………*Blanus*

- Jugal present……………………………………………………………………………...2

2. Jugal reduced to a small and straight bone…………………………………………...Gekkota

- Jugal L-shaped, composed of an anterior and a posterior processes………………………………..3

3. Posterodorsal process massive or expanded……………………………………………………4

- Posterodorsal process narrow or slender………………………………………………………5

4. 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 midlength; tubercles not present…………………………………………………………...*L. 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………………………………………………………………………………*C. chamaeleon*

5. Jugal very slender…………………………………………...……………………………..6

- Jugal less slender…………………………………………………………………11 (Lacertidae)

6. Palatal process poorly developed; articular surface with the maxilla twisted in ventral direction……………………………………………………………………………7 (Anguidae)

- Palatal process absent; articular surface with the maxilla not twisted ventrally……….8 (Scincidae)

7. Medial process absent; posterior end of the posterodorsal process rounded; posterodorsal process slightly shorter than the anterior one; quadratojugal process distinctly developed; lateral surface smooth...……………………………………………………………………*Anguis* 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 rugosities………………………………………*P. apodus*

8. Medial opening of the canal passing through the middle of the bone located at midlength of the posterodorsal process………………………………………………………………*O. punctatissimus*

- Medial opening of the canal passing through the middle of the bone not shifted dorsally…………9

9. Posterodorsal process as long as the anterior one……………………………………...*C. chalcides*

- Posterodorsal process roughly twice as long as the anterior one………………………..*C. ocellatus*

- Posterodorsal process slightly longer than the anterior one……………………………………….10

10. Dorsal end of the posterodorsal process rounded……………………………………..*A. kitaibelii*

- Dorsal end of the posterodorsal process truncated……………………………*C. striatus*, *T. aurata*

11. Palatal process poorly developed……………………………………………………………….12

- Palatal process moderately or well developed…………………………………………………….14

12. Quadratojugal process well developed; anterior process narrow and pointed; articular surface with the maxilla largely covering the lateral surface………………………………………...*E. arguta*

- Quadratojugal process absent; anterior process large and flattened; lateral surface more exposed laterally……………………………………………………………………………………...13

13. Anterior process rounded anteriorly; medial process absent; posterodorsal process longer than the anterior one……………………………………………………………………..*A. erythrurus*

- Anterior process forked anteriorly; medial process distinct; anterior process longer than the posterodorsal one…………………………………………………………………………...*O. elegans*

14. Quadratojugal process weakly developed………………………………………………………15

- Quadratojugal process well developed…………………………………………………………….18

15. Medial process distinct………………………………………………………………*P. algirus*

- Medial process absent or little developed………………………………………………………16

16. Articular surface with the maxilla not stepped……………………………………………*I. horvathi*

- Articular surface with the maxilla stepped……………………………………………………...17

17. Anterior and posterodorsal processes similar in length……………………………..*P. pityusensis*

- Anterior process longer than the posterodorsal one……………………………………..*P. tiliguerta*

18. Medial process distinct……………………………………………………………..*Ps. hispanicus*

- Medial process absent or little developed………………………………………………………19

19. Articular surface with the maxilla stepped or spurred……………………………………..20

- Articular surface with the maxilla not stepped/spurred……………………………………...22

20. Mark of a well-developed spur present……………………………………...*P. melisellensis*

- Mark of a well-developed spur not present……………………………………………………..21

21. Anterior process longer than posterodorsal one…………………………………………*L. agilis*, *L. bilineata*, *L. schreiberi*, *L. viridis*, *P. siculus*, *P. tauricus*, *P. muralis* (variable), *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* (variable)

22. Anterior process longer than posterodorsal one………………………………………*Algyroides*, *D. oxycephala*, *D. mosorensis*, *Z. vivipara*

- 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* (Fig. 19)

1. Postfrontal absent……………………………………………..*L. stellio*, *C. chamaeleon*, *Blanus*

- Postfrontal present……………………………………………………………………………..2

2. Dorsal surface smooth…………………………………………………………………………..3

- Dorsal surface ornamented……………………………………………………..10 (Lacertidae)

3. Postfrontal T-shaped; anterior margin poorly concave; anteromedial process strongly longer than the anterolateral one……………………………………………………………………..4 (Anguidae)

- Postfrontal Y-shaped; anterior concavity more developed; difference in length between anteromedial and anterolateral processes absent or less developed……………………..5 (Scincidae)

4. Body roughly subrectangular; anteromedial process moderately robust…….*Anguis* gr. *A. fragilis*

- Body subtriangular; anteromedial process distinctly robust………………………………*P. apodus*

5. Body wide…………………………………………………………………………………………6

- Body slender……………………………………………………………………………………...7

6. Posterior end of the bone laterally expanded……………………………………….*C. ocellatus*

- Posterior end of the bone provided with a pointed projection……………………………..*T. aurata*

7. Body subtriangular; medial margin not expanded……………………………………...*A. kitaibelii*

- Body subrectangular; medial margin distinctly enlarged……………………………………...8

8. Anterolateral process similar in length to the anteromedial one and slightly curved in posterior direction distally………………………………………………………………………*C. chalcides*

- Anterolateral process shorter than the anteromedial one and straight……………………………...9

9. Anterior processes pointed; projection on the posterior end absent……………………..*C. striatus*

- Anterior processes rounded; pointed projection present on the posterior end……*O. punctatissimus*

10. Anterolateral process absent……………………………………………………...*A. bedriagae, I. aurelioi, I. bonnali* (variable), *I. horvathi, O. elegans*

- Anterolateral process present……………………………………………………………………...11

11. Anteromedial process expanded (at least in adults)……………………………………………12

- Anteromedial process not expanded…………………………………………………Other lacertids

12. Anterolateral process short………..*L. bilineata, L. schreiberi, L. trilineata, L. viridis, T. lepidus*

- Anterolateral process longer…………………………………………………………...*L. agilis*

*Postfrontal and postorbital - Postorbital* (Fig. 19)

1. Postorbital absent…………………………………*A. kitaibelii*, *Blanus*, and maybe also *T. aurata*

- Postorbital present……………………………………………………………………………..2

2. Postorbital large……………………………………………………………………………3

- Postorbital small and slender……………………………………………………………….4

3. Presence of a laminar anterior process and of tubercular ornamentation…………...*C. chamaeleon*

- Anterior process and tubercular ornamentation absent……………………………………..*L. stellio*

4. Anteromedial process absent………………………………………………………….Scincidae, Anguidae, *D. oxycephala*, *I. aurelioi, I. bonnali*, *P. filfolensis, P. pityusensis, L. trilineata* (variable)

- Anteromedial process present………………………………………………………...Other lacertids

*Postfrontal and postorbital - Postorbitofrontal* (Fig. 19)

1. Postorbitofrontal anteroposteriorly elongated and laminar; postfrontal and postorbital portions clearly recognisable………………………………………………………………………*E. arguta, L. schreiberi*, *Psammodromus,* older individuals of *A. nigropunctatus,* other species of *Lacerta*, *P. siculus,* and *T. lepidus*

- Postorbitofrontal small and V- or Y-shaped; postfrontal and postorbital portions not clearly recognisable………………………………………………………………………………..Gekkota

*Squamosal* (Fig. 20)

1. Squamosal strongly reduced………………………………………………………………*Blanus*

- Squamosal not reduced……………………………………………………………………..2

2. Squamosal large; posterior end composed by quadrate process and dorsal parietal process……...3

- Squamosal small; posterior end composed by a single posterior process…………………………..4

3. Anterior process dorsally concave; dorsal parietal process subtriangular; lateral surface smooth……………………………………………………………………………………..*L. stellio*

- Anterior process laminar and dorsoventrally expanded; dorsal parietal process very long and slender; tubercles usually present on the lateral surface………………………………*C. chamaeleon*

4. Anterior process very long………………………………………………………………...5

- Anterior process short or moderately long……………………………………………………7

5. Anterior end provided with a pointed tip.....……………………………………………...Scincidae

- Anterior end represented by a flattened lamina……………………………………..6 (Anguidae)

6. Anterior end rounded and subhorizontal……………………………………..*Anguis* gr. *A. fragilis*

- 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* (variable)

- Medial process absent………………………………………………………………………………9

9. Posterior process expanded…………………………………………………………...*Lacerta*, *O. elegans*, *P. tauricus, P. tiliguerta*, *Psammodromus, T. lepidus* (variable)

- Posterior process not expanded……………………………………………………Other lacertids

*Quadrate* (Fig. 21, 22)

1. Lateral lamina absent (quadrate rod-like); cephalic condyle composed by three portions……………………………………………………………………………...*C. chamaeleon*

- Lateral lamina present; cephalic condyle single…………………………………………………2

2. Lateral lamina projecting anteriorly……………………………………………………*Blanus*

- Lateral lamina not projecting anteriorly……………………………………………………….3

3. Quadrate mediolaterally expanded in anterior view; medial lamina very well developed, being also more developed in its dorsal portion; cephalic condyle strongly expanded in anteromedial to posterolateral direction; mandibular condyle very distinctly enlarged in posterior view……*L. 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……………4

4. Rounded outline (bean-like shape) in anterior view; medial lamina absent……………….Gekkota

- Quadrate subrectangular in anterior view; medial lamina present…………………………………….5

5. Lateral lamina distinctly developed (well-developed conch present)……………………………..6

- Lateral lamina less developed (conch either absent or shallow)……………………………………..11

6. Cephalic condyle expanded posteroventrally; pterygoid flange present…………….7 (Lacertidae)

- Cephalic condyle slightly expanded to the sides; pterygoid flange absent…………………………9

7. Anterior outline angular in medial view……………………...*A. erythrurus, E. arguta, O. elegans*

- Anterior outline rounded in medial view………………………………………………………..8

8. Anterior platform concave………………………………………………………….*T. lepidus*

- Anterior platform flat………………………………………………………………...Other lacertids

9. Quadrate narrow in anterior view; medial lamina reduced to a hint…………………...*A. kitaibelii, C. chalcides, C. striatus*

- Quadrate wider in anterior view; medial lamina more developed………………………………...10

10. Medial lamina well developed……………………………………………………..*C. ocellatus*

- Medial lamina moderately developed…………………………………………………...*T. aurata*

11. Quadrate narrow in anterior view; medial lamina reduced to a hint……………*O. punctatissimus*

- Quadrate wider in anterior view; medial lamina more developed……………………12 (Anguidae)

12. Conch absent; anterior outline rounded; notch on the cephalic condyle small………………………………………………………………………..*Anguis* gr. *A. fragilis*

- Conch shallow; anterior outline angular; notch on the cephalic condyle deep……………*P. apodus*

*Epipterygoid* (Fig. 23)

1. Epipterygoid absent……………………………………………………………*C. chamaeleon*

- Epipterygoid present………………………………………………………………………..2

2. Epipterygoid small and mediolaterally compressed…………………………………………*Blanus*

- 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 than the dorsal one…………...*L. stellio*

- Dorsal end bending posteriorly; ventral end narrower than the dorsal one……………………......6

6. Epipterygoid short; posterior curve poorly marked……………………………...*O. 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* (Fig. 24)

1. Vomer unpaired……………………………………………………………………………2

- Vomer paired……………………………………………………………………………..5

2. Vomer dorsally convex and subrectangular, not expanded at midlength; notch of the vomeronasal fenestra shallow; posterodorsal process absent……………………………………..*C. chamaeleon*

- Vomer dorsally concave, with maximum width at midlength; notch of the vomeronasal fenestra moderately deep; posterodorsal process present……………………………………………..3

3. Posterodorsal process very little developed; on the ventral surface, foramina near the anterior end not present; posterior end of the ventral groove closed…………………………………...*A. kitaibelii*

- Posterodorsal process well developed; on the ventral surface, foramina near the anterior end present; ventral groove completely open……………………………………………………….4

4. Transverse ridges low…………………………………………………………..*C. ocellatus*

- Transverse ridges well developed……………………………………….*C. chalcides*, *C. striatus*

5. Finger-like lateral wing present………………………………………………………...*Blanus*

- Finger-like lateral wing absent…………………………………………………………...6

6. Posterodorsal process absent……………………………………………………………7

- Posterodorsal process present……………………………………………………………..10

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 end…..*L. 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 (Lacertidae)

8. Difference in width between anterior and posterior portions low……………………………………9

- Difference in width between anterior and posterior portions strong…………………Other lacertids

9. Lateral margin of the posterior half rounded………………………………………*Psammodromus*

- Lateral margin of the posterior half angular………………………………*A. erythrurus, O. elegans*

10. Posterodorsal process shifted medially, covering partially the posterior end…………………..11

- Posterodorsal process not shifted medially…………………………………………………Gekkota

11. Notch of the vomeronasal fenestra moderately deep; lateral margin of the posterior half straight; posterodorsal process posteriorly truncated…………………………………………………………...12

- Notch of the vomeronasal fenestra shallow; lateral margin of the posterior half convex; posterodorsal process displaying a notch on the posterior end………………………...13 (Anguidae)

12. Transverse ridge almost indistinct; ventral groove absent……………………...*O. punctatissimus*

- Transverse ridge well developed, reaching the longitudinal medial ridge; ventral groove present………………………………………………………………………………………..*T. aurata*

13. Medial ridge present; vomerine teeth never present………………………...*Anguis* gr. *A. fragilis*

- Medial ridge absent; vomerine teeth sometimes present………………………………….*P. apodus*

*Septomaxilla* (Fig. 25)

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)……………………………………......5

4. Process by the posterolateral corner short; laterally directed triangular process absent…..*L. stellio*

- Process by the posterolateral corner long; presence of a laterally directed triangular process……………………………………………………………………………………...Gekkota

5. Ventral expansion by the anterior end not present……………………………………………...6

- Ventral expansion by the anterior end present……………………………………………………...8

6. Posterolateral process bending dorsally……………………………………*Anguis* gr. *A. fragilis*

- Posterolateral process not bending dorsally…………………………………………7 (Scincidae)

7. Small ventral expansion by the posterior margin present………………………………..*Chalcides*

- Small ventral expansion by the posterior margin not present………………………...Other scincids

8. Anterolateral process anteriorly developed…………………………………………………*Blanus*

- Anterolateral process dorsally or anterodorsally developed…………………………..9 (Lacertidae)

9. Posteromedial process lacking; tip of the posterolateral process angular……………*A. erythrurus*, *O. elegans*

- Posteromedial process present; tip of the posterolateral process quadrangular…………………...10

10. Anterolateral process anterodorsally directed……………………………………*Psammodromus*

- Anterolateral process dorsally directed…………………………………………………………11

11. Posteromedial process short…………………*A. marchi*, *A. moreoticus*, *A. bedriagae*, *I. bonnali*

- Posteromedial process moderately long…………………………………………...Other lacertids

*Palatine* (Fig. 26)

1. Pterygoid process laminar; on the ventral surface of the pterygoid process, choanal duct represented by a very shallow trough; distinct palatine ridge not present……………………Gekkota

- Pterygoid process more robust; on the ventral surface of the pterygoid process, choanal duct deep and distinct; palatine ridge present……………………………………………………………...2

2. Palatine gutter-shaped; presence of a pointed process in the middle of the posterior end…………………………………………………………………………….3 (Scincidae)

- Palatine not gutter-shaped; posterior pointed process not present…………………………………7

3. Expansion of the medial margin absent; expansion of the lateral margin very well developed…..4

- Expansion of the medial margin present; expansion of the lateral margin less developed…………5

4. Vomerine process narrow; pterygoid process very narrow…………………………….*A. kitaibelii*

- Vomerine process wider; pterygoid process wide………………………………………*T. aurata*

5. Anterior projection of the vomerine process distinctly recognisable; infraorbital foramen complete………………………………………………………………………*O. punctatissimus*

- Anterior projection of the vomerine process not well individualized; infraorbital foramen represented by a notch……………………………………………………………………….6

6. Vomerine process short and small; process on the posterior end slender…*C. chalcides*, *C. striatus*

- Vomerine process long and narrow; process on the posterior end wider……………….*C. ocellatus*

7. Infraorbital foramen absent or represented by a notch…………………………………………8

- Infraorbital foramen complete……………………………………………………………..10

8. Vomerine process massive; posterolateral corner of the maxillary process provided with a long projection; infraorbital foramen represented by a moderately deep notch…………………...*L. stellio*

- Vomerine process slender; posterolateral corner of the maxillary process not projecting posterolaterally; no signs of infraorbital foramen…………………………………………………9

9. 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 absent……………………………………..*C. chamaeleon*

- Interdigitated articular surface not present on the vomerine process; maxillary process long and slender; palatine ridge well developed and not interdigitated; choanal duct very deep and wide; presence of a finger-like expansion on the lateral margin……………………………………...*Blanus*

10. Vomerine process slender; maxillary process slender and T-shaped in dorsal view; palatine ridge moderately developed; sulcus dorsalis present on the dorsal surface……………11 (Anguidae)

- Vomerine process moderately wide; maxillary process wide and subtrapezoidal in dorsal view; palatine ridge well developed; sulcus dorsalis absent…………………………………12 (Lacertidae)

11. Notch on the posterior end very deep; palatine teeth absent………………...*Anguis* gr. *A. fragilis*

- Notch on the posterior end very small or absent; palatine teeth present…………………..*P. apodus*

12. Anterolateral margin of the maxillary process poorly inclined………..*A. erythrurus, O. elegans*

- Anterolateral margin of the maxillary process strongly oblique……………………..Other lacertids

*Pterygoid* (Fig. 27, 28)

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…………………………………………………………………*Blanus*

- 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 concave…………………………………………………………………………….Gekkota

- Quadrate process straight; medial margin of the palatine process straight or convex……………...4

4. Pterygoid flange laterally directed and ending with an expanded surface; in adults, presence of a step on the ventral margin of the quadrate process (at least in some specimens)……………*L. stellio*

- Pterygoid flange anterolaterally directed and pointed; no step on the ventral margin of the quadrate process…………………………………………………………………………………..5

5. Basipterygoid fossa marked by flanges both dorsally and ventrally…………………6 (Anguidae)

- Basipterygoid fossa not marked by flanges……………………………………………………...7

6. Ventral ridge on the pterygoid flange poorly developed; ventral flange moderately developed and rounded; pterygoid teeth absent…………………………………………………*Anguis* gr. *A. fragilis*

- Ventral ridge on the pterygoid flange well developed; ventral flange longer and thumb-like; pterygoid teeth present…………………………………………………………………...*P. apodus*

7. Palatine process provided with a thicker area in the middle…………………………8 (Scincidae)

- Palatine process provided with a robust medial margin……………………………..12 (Lacertidae)

8. Palatine process short; pterygoid recess shallow; pterygoid ridge absent…………………………9

- Palatine process long; pterygoid recess deep; pterygoid ridge present……………………………10

9. 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…………………………………………………………………………….*C. ocellatus*

- 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 developed……..*O. punctatissimus*

10. Medial margin of the palatine process straight; pterygoid teeth present………………...*T. aurata*

- Medial margin of the palatine process slightly convex; pterygoid teeth absent…………………..11

11. Palatine process subtriangular; anterior end of the palatine process pointed; pterygoid ridge reduced to a hint…………………………………………………………………...*A. kitaibelii*

- Palatine process subrectangular; anterior end of the palatine process bifurcated; pterygoid ridge distinctly developed……………………………………………………*C. chalcides*, *C. striatus*

12. Pterygoid ridge moderately developed………………………………………………………13

- Pterygoid ridge well developed…………………………………………………………………15

13. Pterygoid recess moderately shallow (at least in adults)………………...*A. erythrurus*, *T. lepidus*

- Pterygoid recess deep………………………………………………………………………...14

14. Pterygoid teeth present (at least in adults)……………………………………….*A. moreoticus*, *D. oxycephala* (variable), *P. milensis*

- Pterygoid teeth absent…………………………………………………..*D. oxycephala* (variable), *D. mosorensis*, *I. monticola*, *P. filfolensis*, *P. muralis*

15. Pterygoid teeth present (at least in adults)……………………………………..*A. nigropunctatus*, *E. arguta*, *Lacerta*, *P. melisellensis* (variable), *P. siculus* (variable), *P. tauricus*, *P. algirus*

- Pterygoid teeth absent…………………………………………………………….*A. fitzingeri*, *A. marchi*, *A. bedriagae*, *H. graeca*, *I. bonnali*, *I. cyreni*, *I. horvathi*, *O. elegans*, *P. bocagei*, *Po.*

*hispanicus, P. lilfordi, P. melisellensis* (variable), *P. pityusensis, P. siculus* (variable), *P. tiliguerta, P. waglerianus, Z. vivipara*

*Ectopterygoid* (Fig. 29)

1. Ectopterygoid small and subtriangular in dorsal view……………………………………*Blanus*

- Ectopterygoid thick and rod-like in dorsal view…………………………………………………2

- Ectopterygoid crescent- or L-shaped, with a medial concavity in dorsal view……………………..3

2. Medial end kidney-shaped in lateral view; posterolateral process slightly longer than the similar-sized anterolateral and ventral processes…………………………………………………..*L. stellio*

- Medial end narrow and subrectangular in lateral view; ventral process shorter than the similar-sized anterolateral and posterolateral processes………………………………………*C. chamaeleon*

3. Ectopterygoid L-shaped………………………………………………………………………4

- Ectopterygoid crescent-shaped……………………………………………………………………...5

4. Articular surface with the maxilla covering the ventral surface of the anterolateral process…………………………………………………………………………...Lacertidae

- Articular surface with the maxilla limited to the lateral margin of the anterolateral process………………………………………………………………………………*T. aurata*

5. Posterior end provided with three lappets……………………………………………………6

- Posterior end forked in lateral view, with two projections/lappets………………………………7

6. Anteromedial projection of the ventral lappet present………………………………*C. ocellatus*

- Anteromedial projection of the ventral lappet absent….*C. chalcides, C. striatus, O. punctatissimus*

7. Articular surface with the maxilla limited to the lateral margin of the anterolateral process………………………………………………………………………………*A. kitaibelii*

- Articular surface with the maxilla covering the lateral margin of the ventral surface of the anterolateral process…………………………………………………………………..Gekkota

- Articular surface with the maxilla represented by a concave area on the lateral surface…………………………………………………………………………...8 (Anguidae)

8. Anterior end not forked…………………………………………………….*Anguis* gr. *A. fragilis*

- Anterior end slightly forked……………………………………………………………*P. apodus*

*Tabulosphenoid*

1. Tabulosphenoid present……………………………………………………………...*Blanus*

- Tabulosphenoid absent………………………………………………………………….Lizards

*General features of the braincase* (Fig. 30-35)

1. Presence of the elements-X; region distinctly dorsoventrally compressed; fenestra ovalis very wide, shifted ventrally to touch sphenoid and basioccipital and opening in an inner concave area connected to the cochlear cavity; lateral opening of the recessus scalae tympani not present……………………………………………………………………………………….*Blanus*

- Elements-X not present; region only slightly or not compressed; fenestra ovalis not shifted ventrally and opening directly in the cochlear cavity; lateral opening of the recessus scalae tympani present……………………………………………………………………………………...2

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 fenestra ovalis……………………………………………*C. chamaeleon*

- 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 composed by the sphenooccipital tubercles……..3

3. Portion of the occipital condyle made by each otooccipital reduced compared to the basioccipital portion……………………………………………………………………………………...4

- Portion of the occipital condyle made by each otooccipital equal to the basioccipital portion…….6

4. Posterior margin of the occipital condyle very slightly concave………………………….*L. stellio*

- Posterior margin of the occipital condyle straight or convex………………………….5 (Anguidae)

5. Posterior margin of the condyle convex; lateral opening of the recessus scalae tympani narrow; medial opening of the recessus scalae tympani anteroposteriorly elongated……*Anguis* gr. *A. fragilis*

- 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*

6. Posterior notch on the occipital condyle deep (paired condyle)…………………………...Gekkota

- Posterior notch on the occipital condyle shallow or absent……………………………………...7

7. 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 margin...……………………………………………………………………………….8 (Scincidae)

8. 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* (Fig. 36)

1. Sphenooccipital tubercles absent…………………………………………………………*Blanus*

- Sphenooccipital tubercles present……………………………………………………………..2

2. Basioccipital participating only slightly in the formation of the occipital condyle…*C. chamaeleon*

- Basioccipital composing more than a third of the occipital condyle……………*L. stellio,* Anguidae

- Basioccipital composing a third of the occipital condyle…………..Gekkota, Lacertidae, Scincidae

*Sphenoid* (Fig. 37)

1. Basipterygoid processes very short and subrectangular; crista sellaris not present…………*Blanus*

- Basipterygoid processes longer and subtriangular or axe-shaped; crista sellaris present…………..2

2. Parasphenoid rostrum thick……………………………………………………………*C. chamaeleon*

- Parasphenoid rostrum thin or absent…………………………………………………………..3

3. Supravenous processes absent…………………………………………………………..*L. stellio*

- Supravenous processes present………………………………………………………………..4

4. Supravenous processes horizontal; groove of the lateral head vein narrow……………….Gekkota

- Supravenous processes vertical; groove of the lateral head vein wide……………………………..5

5. Trabeculae cranii projecting beyond the anterior margin; posterolateral openings of the Vidian canals located on prootics………………………………………………………………6 (Anguidae)

- 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………………………7

6. Supravenous processes narrow……………………………………………….*Anguis* gr. *A. fragilis*

- Supravenous processes larger……………………………………………………..*P. apodus*

7. Parasphenoid rostrum present………………………………………………………..8 (Lacertidae)

- Parasphenoid rostrum absent…………………………………………………………..9 (Scincidae)

8. Basipterygoid processes narrowing proximally……………………………..*A. erythrurus*, *O. elegans*, juveniles of other lacertids

- Basipterygoid processes enlarged for their entire length…………………..Adults of other lacertids

9. Dorsum sellae well developed…………………………………………………………………10

- Dorsum sellae short or not developed…………………………………………………………..11

10. Trabeculae cranii very poorly developed…………………………………………..*T. aurata*

- Trabeculae cranii more developed……………………………………………………*C. ocellatus*

11. Cristae ventrolaterales absent; supravenous processes very narrow…………………..*A. kitaibelii*

- Cristae ventrolaterales short; supravenous processes less narrow………………………………...12

12. Trabeculae cranii not in contact……………………………………………………………...13

- Trabeculae cranii contacting each other………………………………………………………...14

13. Ventral surface displaying a shallow sunken area……………………………………*C. chalcides*

- Ventral surface flat………………………………………………………………………..*C. striatus*

14. Trabeculae cranii very poorly developed; distinct cristae trabeculares not present……………………………………………………………………………*O. punctatissimus*

- Trabeculae cranii more developed; cristae trabeculares low but distinct………………*C. bedriagai*

*Supraoccipital* (Fig. 38, 39)

1. Processus ascendens absent…………………………………………………………..Gekkota

- Processus ascendens present…………………………………………………………………..2

2. Processus ascendens originating a tall median crest dorsally………………………*C. chamaeleon*

- Processus ascendens not originating a median crest………………………………………………..3

3. Presence of a notch of the sphenoccipital foramen………………………………………..*L. stellio*

- Notch of the sphenoccipital foramen not present…………………………………………………...4

4. Anterior margin without ridges…………………………………………………………………5

- Presence of ridges on the anterior margin…………………………………………………………..9

5. Processus ascendens not compressed………………………………………………………...6

- Processus ascendens more dorsoventrally compressed……………………………………………..7

6. Processus ascendens short and slender; supraoccipital crest absent…………………...*C. chalcides*

- Processus ascendens stocky and moderately ossified; supraoccipital crest well developed………………………………………………………………………………*C. ocellatus*

7. Supraoccipital crest well developed in adults………………………………………………*Blanus*

- Supraoccipital crest always absent…………………………………………………………………8

8. Processus ascendens very short; marginal processes absent…………………………...*A. kitaibelii*

- Processus ascendens longer; marginal processes present…………………………*O. punctatissimus*

9. Supraoccipital crest present……………………………………………………………………10

- Supraoccipital crest absent……………………………………………………………………...12

10. Processus ascendens not compressed……………………………………………...11 (Lacertidae)

- Processus ascendens more dorsoventrally compressed……………………………………Anguidae

11. Anterolateral margins roughly parallel……………………………………………...*A. erythrurus*

- Anterolateral margins convergent…………………………………………………Other lacertids

12. Processus ascendens not compressed……………………………………………..*C. striatus*

- Processus ascendens more dorsoventrally compressed………………………………………*T. aurata*

*Prootic* (Fig. 40)

1. Anterior inferior process reduced and widely occupied by the fenestra ovalis……………...*Blanus*

- Anterior inferior process not reduced and not widely occupied by the fenestra ovalis…………….2

2. Alar process absent…………………………………………………………………………...3

- Alar process present…………………………………………………………………………...4

3. Crista prootica very well developed, at least in adults; notch of the sphenoccipital foramen present……………………………………………………………………………………...*L. stellio*

- Crista prootica very poorly developed; notch of the sphenoccipital foramen absent……………………………………………………………………………..*C. chamaeleon*

4. Crista alaris mediolaterally expanded; incisura prootica usually closed dorsally…………Gekkota

- Crista alaris not mediolaterally expanded; incisura prootica not closed dorsally…………………..5

5. Posterior opening of the Vidian canal located on the anterior inferior process………6 (Anguidae)

- Posterior opening of the Vidian canal not located on the prootic…………………………………..7

6. Crista prootica low…………………………………………………………*Anguis* gr. *A. fragilis*

- Crista prootica moderately developed……………………………………………………..*P. apodus*

7. Recessus vena jugularis shallow and very wide………………………………………8 (Scincidae)

- Recessus vena jugularis not distinguishable…………………………………………12 (Lacertidae)

8. Margins of the facial foramen not raised; crista prootica low developed or absent………………9

- Margins of the facial foramen raised; crista prootica well developed……………………………10

9. Alar process very short; crista prootica continuing posteriorly………………………...*A. kitaibelii*

- Alar process long; crista prootica ending by the facial foramen…………………*O. punctatissimus*

10. Crista prootica continuing posteriorly…………………………………………………...*T. aurata*

- Crista prootica ending by or near to the facial foramen……………………………………………...11

11. Alar process moderately short; crista prootica ending by the facial foramen………*C. bedriagai*, *C. chalcides*, *C. striatus*

- Alar process long; crista prootica extending slightly beyond the facial foramen………*C. ocellatus*

12. Paroccipital projection short in adults……………………………………………………………..13

- Paroccipital projection long in adults…………………………………………………………...16

13. Alar process moderately short in adults………………………………………………………...14

- Alar process longer in adults……………………………………………………………………15

14. Posterior portion of the crista prootica absent……………………………*A. fitzingeri, A. marchi*

- Posterior portion of the crista prootica present………………*A. moreoticus, I. horvathi, O. elegans*

15. Posterior portion of the crista prootica absent……………..*P. filfolensis, P. muralis, P. tiliguerta*

- Posterior portion of the crista prootica present………………………………………..*A. bedriagae, I. cyreni, I. monticola cantabrica, P. bocagei, P. carbonelli, Po. hispanicus, P. lilfordi, P. melisellensis, P. milensis, P. tauricus, Ps. hispanicus, Z. vivipara*

16. Alar process moderately short in adults………………………………………………………...17

- Alar process longer in adults……………………………………………………………………18

17. Posterior portion of the crista prootica absent………………………………………*A. erythrurus*

- Posterior portion of the crista prootica present………………………………………*D. mosorensis*

18. Posterior portion of the crista prootica absent…………………………………*A. nigropunctatus, L. agilis, P. siculus, P. waglerianus*

- Posterior portion of the crista prootica present………………………………………*D. oxycephala, E. arguta, H. graeca, I. bonnali, I. monticola monticola, L. bilineata, L. schreiberi, L. trilineata, L. viridis, P. algirus, T. lepidus*

*Otooccipital* (Fig. 41)

1. Paroccipital process very poorly developed, ridge-like……………………………………..*Blanus*

- Paroccipital process more developed, not ridge-like……………………………………………….2

2. Otooccipital composing more or less than a third of the occipital condyle……………………….3

- Otooccipital composing a third of the occipital condyle……………………………………………..6

3. Otooccipital composing almost a half of the occipital condyle; presence of a foramen representing the remnant of the reduced lateral opening of the recessus scalae tympani……………………………………………………………………………..*C. chamaeleon*

- Otooccipital composing less than a third of the occipital condyle; lateral opening of the recessus scalae tympani not reduced to a foramen……………………………………………………………4

4. Paroccipital process very long; very well-developed ridge present on the proximal half of the ventral surface of the paroccipital process………………………………………………...*L. stellio*

- Paroccipital process shorter; ridge on the ventral surface of the paroccipital process not present……………………………………………………………………………...5 (Anguidae)

5. Paroccipital process moderately short………………………………………...*Anguis* gr. *A. fragilis*

- Paroccipital process long…………………………………………………………….*P. apodus*

6. Distal end of paroccipital process not enlarged ………………………………………...Gekkota

- Distal end of paroccipital process more or less enlarged ……………………………………..7

7. Paroccipital process very short……………………………………*A. kitaibelii, O. punctatissimus*

- Paroccipital process short…………………………………………………………*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, Z. vivipara*, juveniles of other lacertids, *C. chalcides, C. striatus, T. aurata*

- Paroccipital process long…………………………………..Adults of other lacertids, *C. ocellatus*

*Stapes* (Fig. 42)

1. Footplate very large; shaft very short……………………………………………………..*Blanus*

- 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 pointed……………………..*L. stellio*, Lacertidae, Scincidae, Anguidae

*Dentary* (Fig. 43, 44)

1. Meckelian fossa entirely or almost entirely closed……………………………………………..2

- Meckelian fossa open (if present, closure reduced to a small portion of it)………………………..3

2. Ventral projection of the superior posterior process not recognisable; rounded expansion sometimes present on the dorsal margin of the inferior posterior process………………..*A. kitaibelii*

- Ventral projection of the superior posterior process present; rounded expansion never present on the dorsal margin of the inferior posterior process………………………………………...Gekkota

3. Presence of a smooth subdental shelf, with no subdental ridge; splenial spine present………………………………………………………………………...4 (Anguidae)

- Subdental ridge present; splenial spine absent………………………………………………...5

4. 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 surangular foramen………………………………*Anguis* gr. *A. fragilis*

- Splenial spine short and located by the beginning of the posterior third of the tooth row; posterior portion of the intramandibular septum fused 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 surangular process……………………………………...*P. apodus*

5. Subdental shelf high; presence of a posterior recess between the posterior processes; presence of interdental grooves on the lateral surface……………………………………………………………6

- Subdental shelf narrower; posterior recess not present between posterior processes; interdental grooves absent………………………………………………………………………………..7

6. Anterior half of the Meckelian fossa opening medially; posterior recess very narrow……*L. stellio*

- Anterior half of the Meckelian fossa opening ventrally; posterior recess large……...*C. chamaeleon*

7. Ventral margin straight……………………………………………………………………8

- Ventral margin convex……...…………………………………………………..10 (Lacertidae)

8. Meckelian fossa represented by a very narrow groove; subdental shelf moderately high; intramandibular septum originating a posterior portion fused to the wall of the bone………..*Blanus*

- Meckelian fossa widening in the posterior half; subdental shelf narrower; intramandibular septum not extending posteriorly……………………………………………………………………………..9

9. Two posterior processes present on the posterior end; superior posterior process directed posteriorly and composed by two projections………………………………….*..Chalcides*, *T. aurata*

- Three posterior processes present on the posterior end; superior posterior process directed posterodorsally and not composed by separated projections………………………*O. punctatissimus*

10. 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*

- Inferior posterior process longer than superior one……………………………………*...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,* juveniles of *I. bonnali*, *L. agilis*, *L. bilineata, L. schreiberi*, *P. bocagei*, *P. carbonelli*, *Po. hispanicus, P. muralis, P. algirus*

*Splenial* (Fig. 45, 46)

1. Splenial absent………………………………………………………*L. stellio, C. chamaeleon*

- Splenial present……………………………………………………………………………..2

2. Splenial small and thin……………………………………………………………………….3

- Splenial larger…………………………………………………………………………………5

3. Splenial pierced by a single foramen in the posterior half………………………………….*.Blanus*

- 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 sometimes represented by a notch………………….Gekkota

5. Splenial clearly divided into an slender anterior half and a wide posterior half; posterior end irregular, provided with three processes…………………………………………………...6 (Anguidae)

- Splenial not composed by two different-shaped halves; posterior end pointed……………………7

6. Anterior mylohyoid foramen located ventrally to the posterior margin of the notch for the anterior inferior foramen……………………………………………………………………..*P. apodus*

- Anterior mylohyoid foramen located posteroventrally to the posterior margin of the notch for the anterior inferior foramen……………………………………………………...*Anguis* gr. *A. fragilis*

7. Foramina shifted anteriorly; anterior inferior foramen not closed anteriorly; crests on the lateral surface shifted ventrally; ventral margin straight……………………………………………………8

- Foramina located roughly in the middle of the bone; anterior inferior foramen completely closed; crests on the lateral surface more dorsally located; ventral margin convex……………9 (Lacertidae)

8. Posterior portion of the dorsal margin wavy……………………………………………..*Chalcides*

- Posterior portion of the dorsal margin straight……………………………………*O. punctatissimus*

- Posterior portion of the dorsal margin convex……………………………………………..*T. aurata*

9. Splenial ventrally expanded……………………………………………………….*A. erythrurus*

- Splenial not ventrally expanded……………………………………………...Other lacertids

*Coronoid* (Fig. 47, 48)

1. Labial process absent or strongly reduced………………………………………………………2

- Labial process present, not reduced……………………………………………………………...5

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 ridge………………………...*Blanus*

- 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

3. Coronoid crescent-shaped in dorsal view; posterior process very small or absent; posteromedial process lappet-like……………………………………………………………………*O. punctatissimus*

- Coronoid straight in dorsal view; posterior process more developed; posteromedial process not lappet-like…………………………………………………………………………………………4

4. Posterior process moderately short; posteromedial process long, straight and distally rounded; coronoid ridge very thick……………………………………………………………………..*L. stellio*

- Posterior process well developed; posteromedial process shorter, triangular and distally pointed; coronoid ridge thinner………………………………………………………………*C. chamaeleon*

5. Posteromedial process very thin…………………………………………………………...Gekkota

- Posteromedial process wider……………………………………………………………………….6

6. Coronoid rather straight in dorsal view………………………………………………7 (Anguidae)

- Coronoid moderately medially concave in dorsal view……………………………………………8

7. Coronoid process moderately thin; anterior projection of the anteromedial process present; labial process long; laminar ridge thin…………………………………………………*Anguis* gr. *A. fragilis*

- Coronoid process distinctly robust; anterior projection of the anteromedial process absent; labial process short; laminar ridge thicker…………………………………………………...*P. apodus*

8. Posterior process present……………………………………………………………..9 (Lacertidae)

- Posterior process absent………………………………………………………………………...10

9. 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 process more dorsally directed………………..Adults of other lacertids

10. 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* (Fig. 49)

1. Free angular absent………………………………………………………………………...Gekkota

- Free angular present……………………………………………………………………………...2

2. Angular dorsoventrally enlarged……………………………………………………...Lacertidae

- Angular slender……………………………………………………………………………..3

3. On the medial surface, angular ridge present……………………………………………...4

- On the medial surface, angular ridge absent………………………………………………..5

4. Presence of a clear constriction at midlength…………………………………………….Anguidae

- Angular not constricted at midlength……………………………………………...Scincidae

5. Angular thin and laminar………………………………………………………………*Blanus*

- Angular thicker and dorsally or dorsolaterally concave…………………..*L. stellio, C. chamaeleon*

*Angular, surangular, prearticular and articular - Compound bone* (Fig. 50-52)

1. In adults, surangular free; two pointed projections present by the anterior end of the surangular; posterior end of the retroarticular process rod-like; presence of a thick and well-developed angular process……………………………………………………………………………..*L. stellio*

- In adults, surangular fused with the rest of the compound bone; anterior end of the surangular not displaying two pointed projections; posterior end of the retroarticular process not rod-like; angular process absent or represented only by a small tubercle………………………………………………2

2. Surangular and prearticular portions of the compound bone recognisable as distinct branches; presence of an anterior recess on the surangular branch; retroarticular process not present; small tubercle present ventrally to the articular condyle……………………………………..*C. chamaeleon*

- Surangular and prearticular portions of the compound bone not distinctly separated; anterior recess absent; retroarticular process present; tubercle not present ventrally to the articular condyle……….3

3. Articular surface with the angular absent………………………………………………….Gekkota

- Articular surface with the angular present………………………………………………………4

4. Compound bone moderately short; tubercle on the articular condyle not present…………..*Blanus*

- Compound bone long; presence of a tubercle by the anteromedial corner of the articular condyle………………………………………………………………………………………….5

5. Retroarticular process distinctly bending in ventral direction; ridge-like ventral expansion of the retroarticular process absent…………………………………………………………..6 (Scincidae)

- Retroarticular process posteriorly directed; ridge-like ventral expansion present ventrally to the retroarticular process…………………………………………………………………………..10

6. Retroarticular process more anteroposteriorly elongated…………………………………………7

- Retroarticular process more dorsoventrally expanded……………………………………………..8

7. Retroarticular process lobe-shaped; tympanic ridge well developed……..*C. chalcides*, *C. striatus*

- Retroarticular process subrectangular; tympanic ridge less developed………………….*A. kitaibelii*

8. Anterior surangular foramen very large…………………………………………………………..9

- Anterior surangular foramen smaller………………………………………………………*C. ocellatus*

9. Retroarticular process lobe-shaped; tympanic ridge well developed……………………..*T. aurata*

- Retroarticular process subrectangular; tympanic ridge less developed…………...*O. punctatissimus*

10. Retroarticular process subtriangular; adductor fossa very wide…………………..11 (Lacertidae)

- Retroarticular process quadrangular; adductor fossa reduced………………………..12 (Anguidae)

11. Ventral expansion of the retroarticular process well developed (ventral margin concave in lateral view)……………………………………………………………………*A. erythrurus*, *E. arguta*

- Ventral expansion of the retroarticular process less developed (ventral margin straight in lateral view)…………………………………………………………………………...Other lacertids

12. Anterior surangular foramen not shifted anteriorly…………………………*Anguis* gr. *A. fragilis*

- Anterior surangular foramen shifted anteriorly into the articular surface with the dentary……………………………………………………………………………………*P. apodus*

*Dentition*

1. Acrodont teeth present……………………………………………………………………………..2

- Acrodont teeth absent……………………………………………………………………………3

2. Premaxillary teeth and anteriormost maxillary and dentary teeth subpleurodont; acrodont teeth usually closely spaced and extending onto the medial surface of the alveolar shelf…………*L. stellio*

- All teeth acrodont; teeth carried on the edge of the tooth-bearing bones and usually well-spaced…………………………………………………………………………………*C. chamaeleon*

3. Bicuspid teeth with labial and lingual cusps……………………………………………………4

- Teeth monocuspid or with cusps longitudinally aligned……………………………………………7

4. Crown not curved and without striae……………………………………………………Gekkota

- Crown slightly curved posteriorly and provided with a light striation on the lingual surface…………………………………………………………………………...5 (Scincidae)

5. Teeth slender………………………*A. kitaibelii, C. bedriagai, C. chalcides, C. striatus, T. aurata*

- Teeth robust………………………………………………………………………………6

6. Teeth very robust; crown blunt and enlarged…………………………………………..*C. ocellatus*

- Teeth less robust; crown not blunt and not enlarged……………………………...*O. punctatissimus*

7. Teeth pleurodont; presence of mono-, bi- or even tricuspid teeth……………………….Lacertidae

- Teeth subpleurodont; all teeth monocuspid………………………………………………...8

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 five; number of dentary teeth seven, eight or nine…………………………………………………………………………………..*Blanus*

- In the premaxilla, all tooth similar in size; in the maxilla, maximum tooth size reached in the middle or by the end of the tooth row; number of maxillary teeth more than five; number of dentary teeth usually more than nine……………………………………………………..9 (Anguidae)

9. Teeth trenchant and well-spaced; striae not present; in both maxilla and dentary, maximum tooth size reached in the middle of the tooth row……………………………………..*Anguis* gr. *A. fragilis*

- Teeth cylindrical and closely spaced, slightly robust anteriorly and very large and stout posteriorly; striae present on both lingual and labial side of the crown; in both maxilla and dentary, maximum size of teeth reached more posteriorly…………………………………………...*P. apodus*

In a recent paper, Villa *et al.* (2017) presented an estimate of the recognisability of extant European lizards and worm lizards based on the morphology of their bones 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 is 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 units at 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; see the Supplementary Information). Scincidae are the group that benefits most from the new data in terms of recognisability, since almost all European species appear now to be recognisable, in contrast with the worse scenario of just three recognisable OTUs reported by Villa *et al.* (2017), with only *C. ocellatus* identifiable at the species level. According to our new data, only *C. bedriagai* is still not recognisable at the species level, being identifiable only as *Chalcides* sp. However, 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 is 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 at genus level of all the species belonging to *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 the Material and methods paragraph 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 morphology of isolated bones. Nevertheless, a specimen-level phylogenetic analysis has demonstrated that every single *Lacerta* species can be identified based on combinations of characters coming from different bones 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 significant change is observed in the amphisbaenians, due to the fact that the three European *Blanus* species are distinguishable based on the different development of a ridge present on the inner side of the quadrate (Villa *et al.*, 2018b). Other skull elements still bear no clear diagnostic features allowing to discriminate between the different species of European worm lizards, and only the premaxilla can be used to recognise the Western Group from the *B. strauchi* complex (Villa *et al.*, 2018b). Moreover, Smith *et al.* (2016) described some osteological features useful to distinguish *L. stellio* and *C. chamaeleon* from some other closely related agamids and chamalaeonids respectively.

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 (see the Supplementary Information): 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 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 reason is due to the fact that thanks to the improvement in the recognisability brought by this atlas, several now identifiable OTUs are now unknown in the fossil record.

The herein conducted comparative analysis corroborates the hypothesis that diagnostic osteological features might indeed be present in the bones of most if not all 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. As already highlighted by Delfino (2004) and Villa *et al.* (2017), 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 (Bochaton *et al.*, 2018; Villa *et al.*, 2018a, b; this work) and advanced methodologies such as specimen-level phylogenetic analysis (Villa *et al.*, 2017) and geometric morphometrics (Dollion *et al.*, 2015; Gray *et al.*, 2017; Paluh *et al.*, 2018).

## CONCLUSIONS

Comparative osteological analyses focused on a broad taxon sampling are significant resources when it comes to the identification of remains (either fossils or not) of animal groups showing a high degree of diversity such as lizards do. The osteological study we presented here exemplify this, allowing the creation of a detailed diagnostic key for the bones of European lizards. However, they also have some intrinsic limitations. First, the very large number of taxa included force the need of a compromise in terms of the amount of studied specimens per taxon. As a matter of fact, the number of specimens per taxon in a study focusing on a smaller subgroup of the large “European lizards” category (e.g., single families or lizards living in a specific European country) could inherently be higher than in our analysis. This is even more evident in works devoted to a single species. The second main issue is the different degree of availability of skeletonized specimens for different species in a wide geographic area such as Europe. This general problem was already highlighted by Bell & Mead (2014) and it is particularly evident for some European lizards, particularly when small Eastern European species such as *Darevskia* spp. are considered.

Still, our analysis is helpful to better understand the osteological diversity of European lizards as a whole, showing the presence of useful diagnostic features, and improves our ability to recognise the different taxa when only their bones are available, therefore aiding the study of fossil or archaeological remains and the diet of predators on the basis of the non-digested bones of their preys. Indeed, the new data enhance significantly the recognisability of European lizards, with a 13% improvement compared with previous estimates. Nevertheless, we prospect a further improvement in the future, following new studies dealing with the osteology of these European squamates. In this context, studies focusing more deeply on particular groups (such as *Anguis* spp., *Podarcis* spp., small *Psammodromus* spp.), adding species that are missing from our analysis (such as *Anatololacerta* spp. and *Darevskia* spp.) or applying promising methodologies (such as geometric morphometrics and specimen-level phylogenetic analysis) are highly desirable.

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## FIGURE CAPTIONS

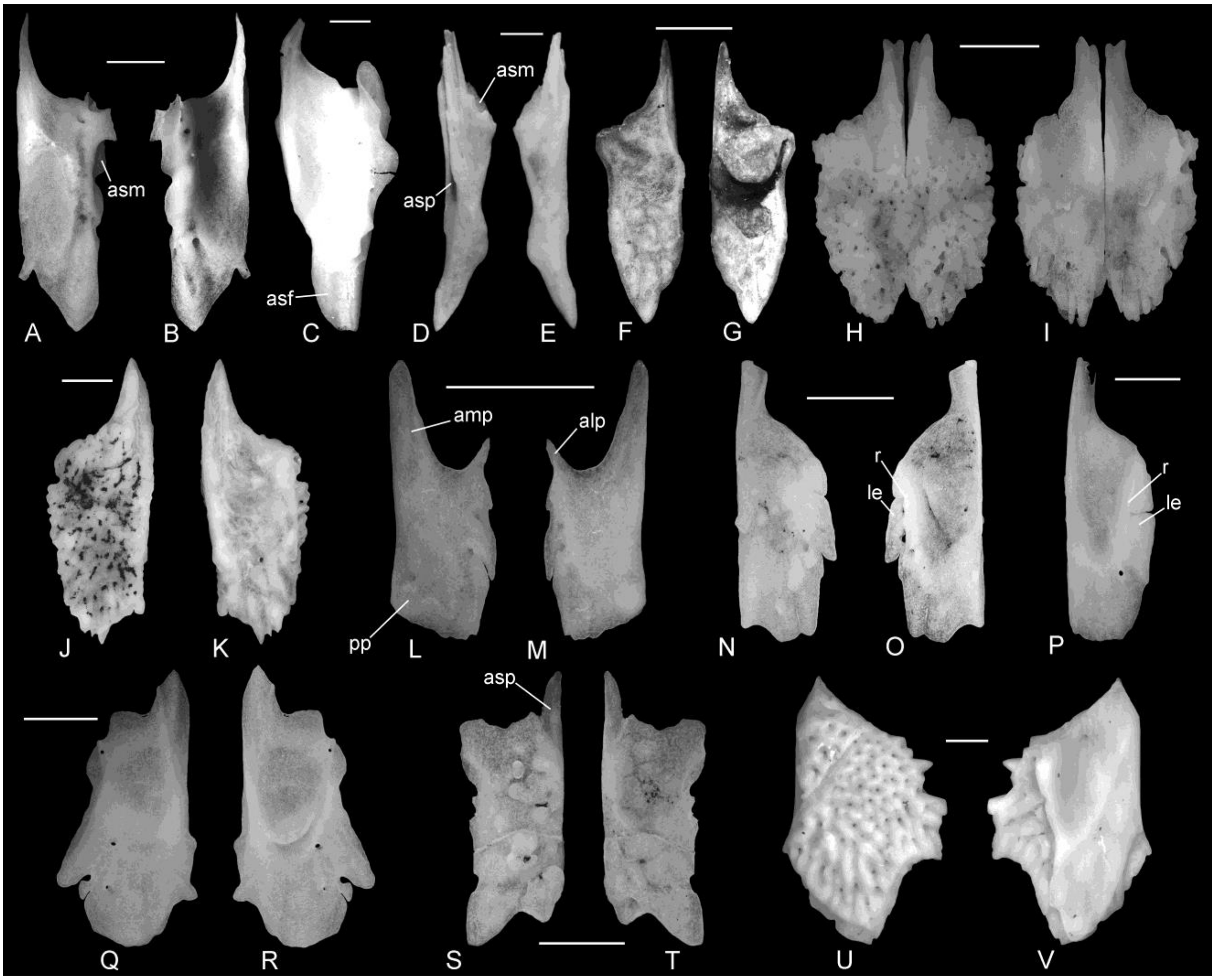

**Figure 1.** Nasals - A-B: *L. stellio* (HUJ.OST-Z-424), right nasal in dorsal (A) and ventral (B) views. C: *L. stellio* (MDHC 245), left nasal in ventral view. D-E: *C. chamaeleon* (NHMW 611), right nasal in dorsal (D) and ventral (E) views. F-G: *A. erythrurus* (UAM.R.ACVII), left nasal in dorsal (F) and ventral (G) views. H-I: *A. nigropunctatus* (MDHC 242), articulated nasals in dorsal (H) and ventral (I) views. J-K: *L. bilineata* (MDHC 381), left nasal in dorsal (J) and ventral (K) views. L-M: *O. elegans* (MDHC 281), right nasal in dorsal (L) and ventral (M) views. N-O: *C. chalcides* (MDHC 398), right nasal in dorsal (N) and ventral (O) views. P: *C. ocellatus* (MDHC 250), left nasal in ventral view. Q-R: *T. aurata* (MDHC 280), left nasal in dorsal (Q) and ventral (R) views. S-T: *Anguis* gr. *A. fragilis* (MDHC 221), left nasal in dorsal (S) and ventral (T) views. U-V: *P. apodus* (MDHC 214), right nasal in dorsal (U) and ventral (V) 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. Scale bars = 1 mm.

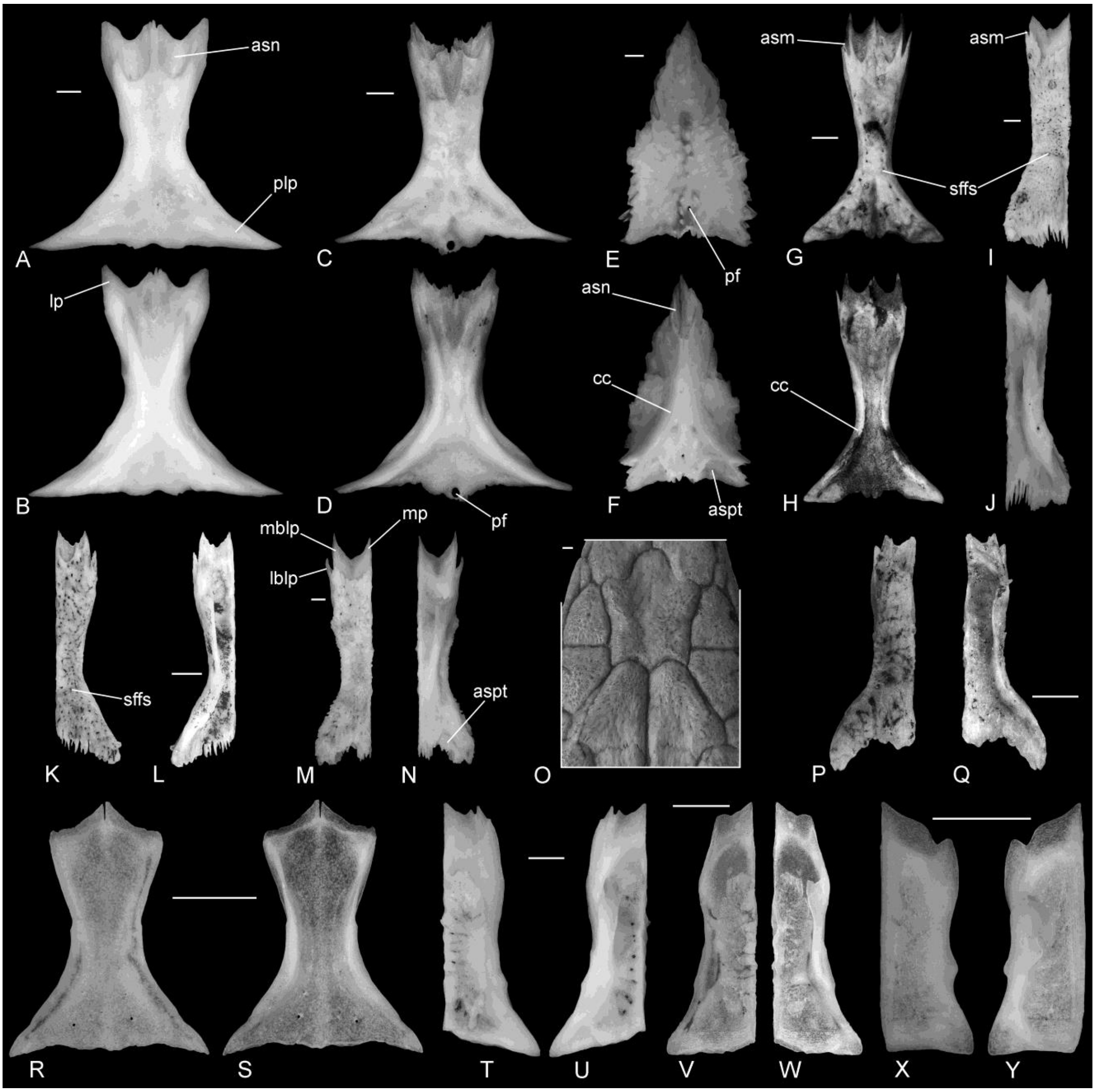

**Figure 2.** Frontals - A-B: *L. stellio* (MDHC 245), frontal in dorsal (A) and ventral (B) views. C-D: *L. stellio* (HUJ.OST-Z-423), frontal in dorsal (C) and ventral (D) views (the medial process is broken). E-F: *C. chamaeleon* (NHMW 611), frontal in dorsal (E) and ventral (F) views. G-H: *A. erythrurus* (UAM.R.ACVII), frontal in dorsal (G) and ventral (H) views. I-J: *L. viridis* (MRAC 91-077-R-76), left frontal in dorsal (I) and ventral (J) views. K-L: *P. muralis* (MDHC 311), right frontal in dorsal (K) and ventral (L) views. M-N: *T. lepidus* (MDHC 216), left frontal in dorsal (M)

and ventral (N) views. O: *T. lepidus* (MNHN 1991.4242), articulated frontals in dorsal view. P-Q: *Z. vivipara* (UAM.R.Lv24), left frontal in dorsal (P) and ventral (Q) views. R-S: *A. kitaibelii* (MDHC 239), frontal in dorsal (R) and ventral (S) views. T-U: *C. ocellatus* (MDHC 250), right frontal in dorsal (T) and ventral (U) views. V-W: *C. striatus* (MDHC 404), left frontal in dorsal (V) and ventral (W) views. X-Y: *O. punctatissimus* (MDHC 427), right frontal in dorsal (X) and ventral (Y) 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.

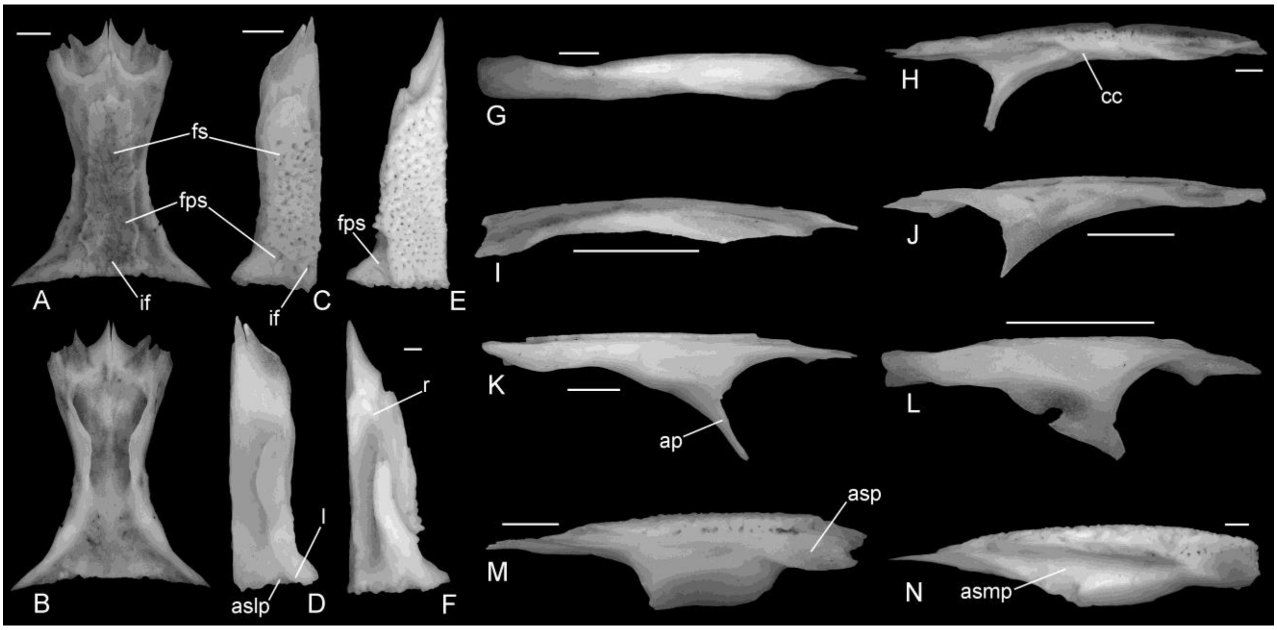

**Figure 3.** Frontals (continues) - A-B: *T. aurata* (MDHC 280), frontal in dorsal (A) and ventral (B) views. C-D: *Anguis* gr. *A. fragilis* (MDHC 102), left frontal in dorsal (C) and ventral (D) views. E-F: *P. apodus* (MDHC 214), left frontal in dorsal (E) and ventral (F) views. G: *L. stellio* (MDHC 245), frontal in right lateral view. H: *L. viridis* (MRAC 91-077-R-76), left frontal in lateral view. I: *A. kitaibelii* (MDHC 239), frontal in right lateral view. J: *C. striatus* (MDHC 404), left frontal in lateral view. K: *C. ocellatus* (MDHC 250), right frontal in lateral view. L: *O. punctatissimus* (MDHC 427), right frontal in lateral view. M: *Anguis* gr. *A. fragilis* (MDHC 102), left frontal in

lateral view. N: *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; l, lappet; r, ridge. Scale bars = 1 mm.

**Figure 4.** Right frontal of a juvenile of *T. lepidus* (NHMW 625) in dorsal (A) and ventral (B) views. Scale bar = 1 mm.

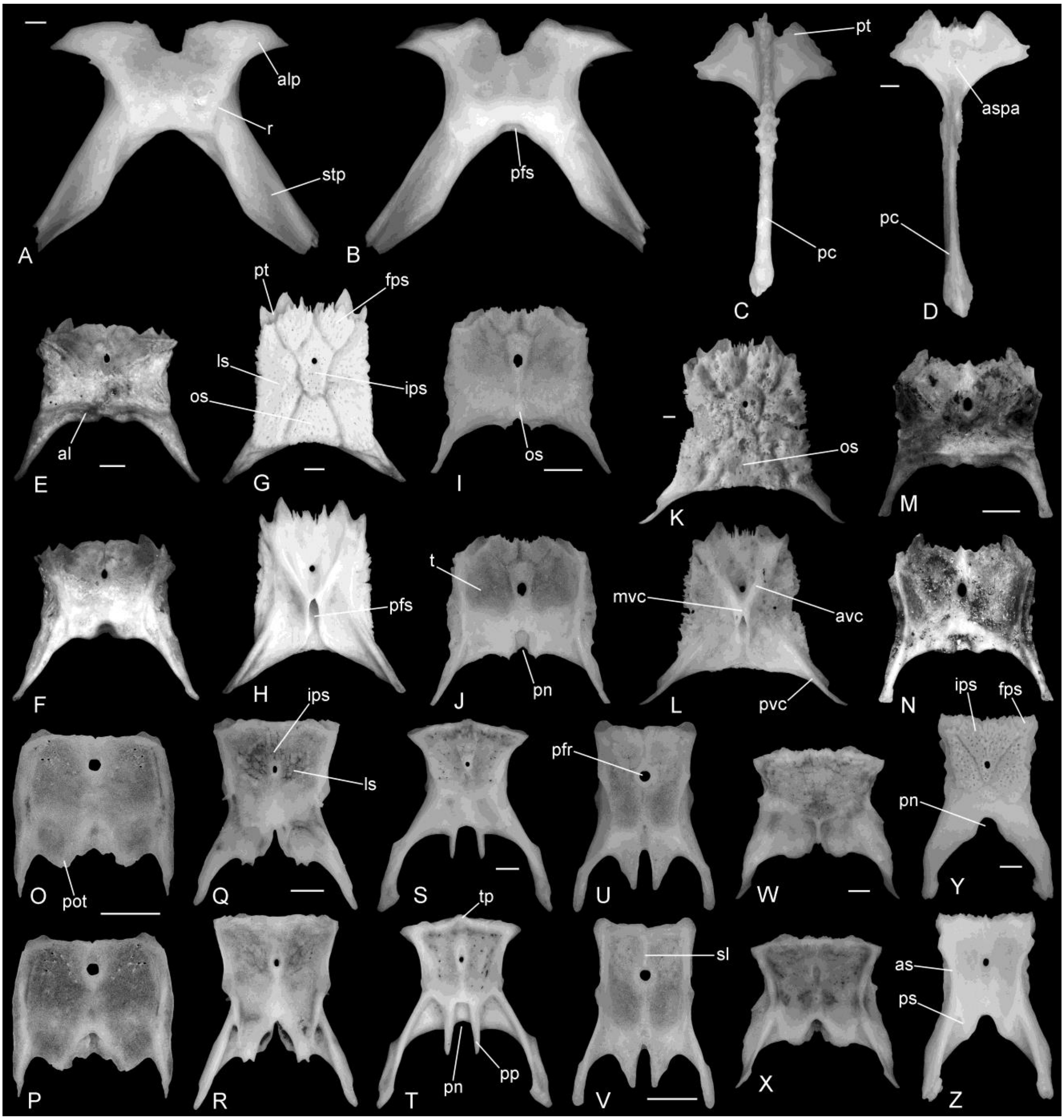

**Figure 5.** Parietals - A-B: *L. stellio* (MDHC 245), parietal in dorsal (A) and ventral (B) views. C-D: *C. chamaeleon* (NHMW 611), parietal in dorsal (C) and ventral (D) views. E-F: *A. erythrurus* (UAM.R.ACVII), parietal in dorsal (E) and ventral (F) views. G-H: *L. schreiberi* (UAM.R.S-6), parietal in dorsal (G) and ventral (H) views. I-J: *O. elegans* (MDHC 281), parietal in dorsal (I) and ventral (J) views. K-L: *T. lepidus* (MDHC 216), parietal in dorsal (K) and ventral (L) views. M-N: *Z. vivipara* (UAM.R.Lv24), parietal in dorsal (M) and ventral (N) views. O-P: *A. kitaibelii* (MDHC 239), parietal in dorsal (O) and ventral (P) views. Q-R: *C. chalcides* (MDHC 398), parietal in dorsal

(Q) and ventral (R) views. S-T: *C. ocellatus* (MDHC 250), parietal in dorsal (S) and ventral (T) views. U-V: *O. punctatissimus* (MDHC 427), parietal in dorsal (U) and ventral (V) views. W-X: *T. aurata* (MDHC 280), parietal in dorsal (W) and ventral (X) views. Y-Z: *Anguis* gr. *A. fragilis* (MDHC 102), parietal in dorsal (Y) and ventral (Z) 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; ls, lateral shield; mvc, medial ventral crest; os, occipital shield; pc, parietal crest; pfr, parietal foramen; pfs, parietal fossa; pn, parietal notch; pot, posterior tab; pp, posterior process; ps, posterior section of the posterolateral ventral crest; pt, parietal tab; pvc, posterolateral ventral crest; r, ridge; sl, suture line; stp, supratemporal process; t, parietal table; tp, triangular process. Scale bars = 1 mm.

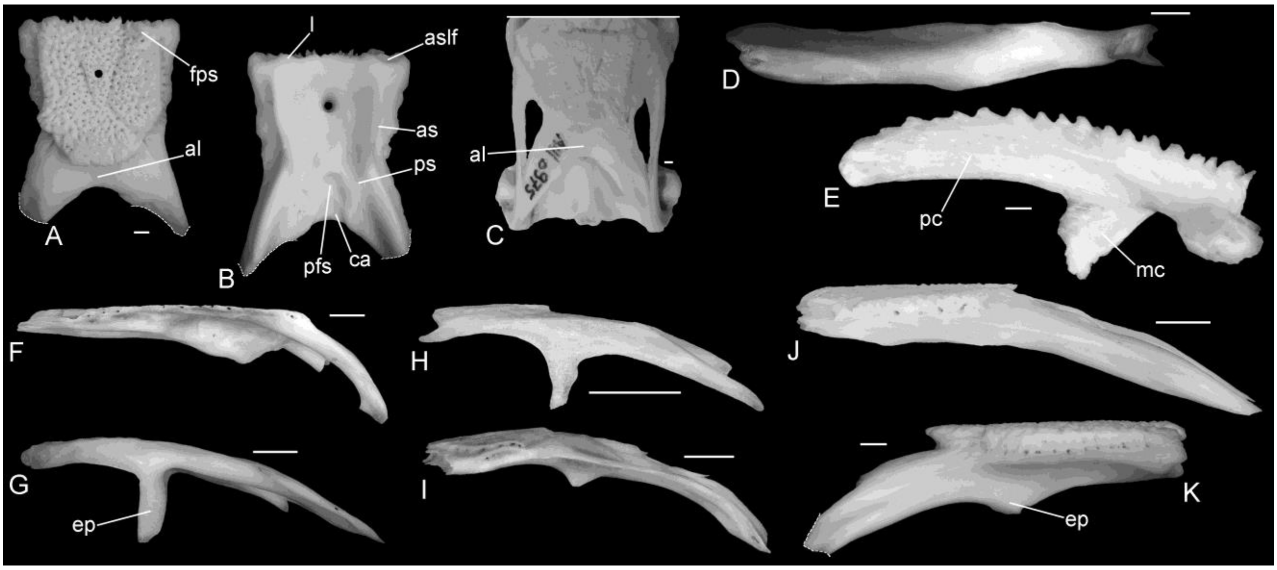

**Figure 6.** Parietals (continues) - A-B: *P. apodus* (MDHC 214), parietal in dorsal (A) and ventral (B) views (supratemporal processes are broken). C: *P. apodus* (PIMUZ A/III0975), parietal in dorsal view. D: *L. stellio* (MDHC 245) in right lateral view. E: *C. chamaeleon* (NHMW 611), parietal in right lateral view. F: *L. bilineata* (MDHC 381), parietal in left lateral view. G: *C. ocellatus* (MDHC 250), parietal in left lateral view. H: *O. punctatissimus* (MDHC 427), parietal in left lateral view. I: *T. aurata* (MDHC 280), parietal in left lateral view. J: *Anguis* gr. *A. fragilis* (MDHC 102), parietal in left lateral view. K: *P. apodus* (MDHC 214), parietal in right lateral view

(supratemporal 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; l, lappet; mc, median crest; pc, parietal crest; pfs, parietal fossa; ps, posterior section of the posterolateral ventral crest. Scale bars = 1 mm.

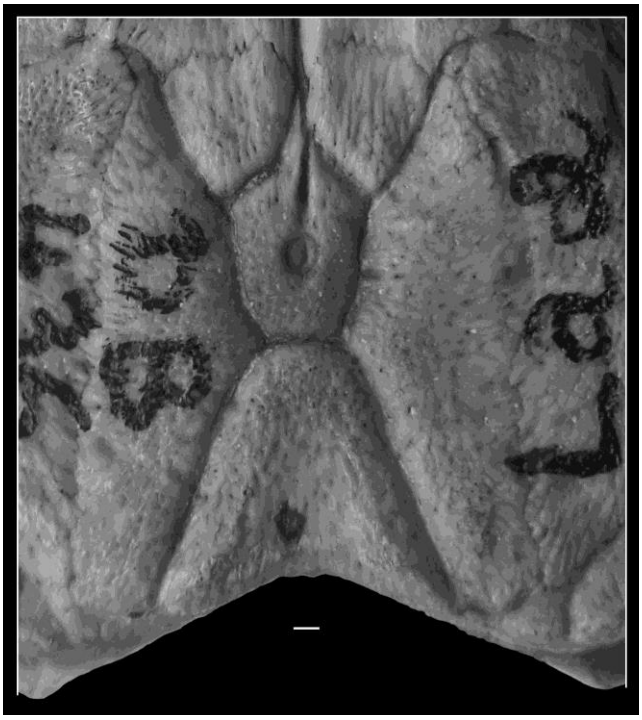

**Figure 7.** Articulated parietal of *T. lepidus* (MNHN 1991.4242) in dorsal view. Scale bar = 1 mm.

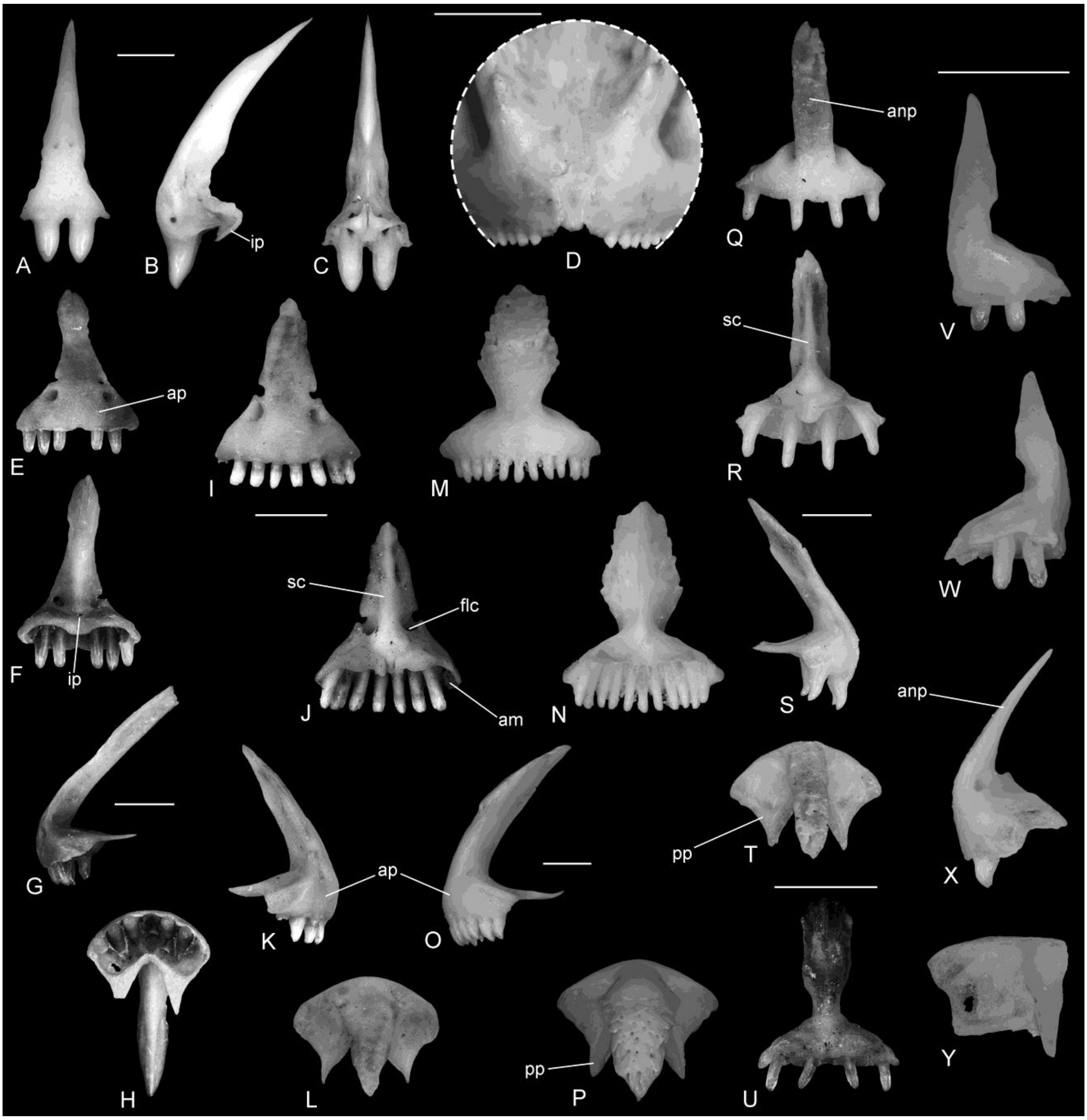

**Figure 8.** Premaxillae - A-C: *L. stellio* (HUJ.OST-Z-424), premaxilla in anterior (A), left lateral (B), and posterior (C) views. D: *C. chamaeleon* (NHMW 721), articulated premaxilla in anterior view. E-H: *A. erythrurus* (UAM.R.ACVII), premaxilla in anterior (E), posterior (F), left lateral (G), and ventral (H) views. I-L: *I. monticola monticola* (UAM.R.Lm77), premaxilla in anterior (I), posterior (J), right lateral (K), and dorsal (L) views. M-P: *L. bilineata* (MDHC 15), premaxilla in anterior (M), posterior (N), left lateral (O), and dorsal (P) views. Q-T: *P. waglerianus* (MDHC 390), premaxilla in anterior (Q), posterior (R), right lateral (S), and dorsal (T) views. U: *Z. vivipara* (UAM.R.Lv24), premaxilla in posterior view. V-Y: *C. chalcides* (MDHC 94), left premaxilla in

anterior (V), posterior (W), lateral (X), and dorsal (Y) 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.

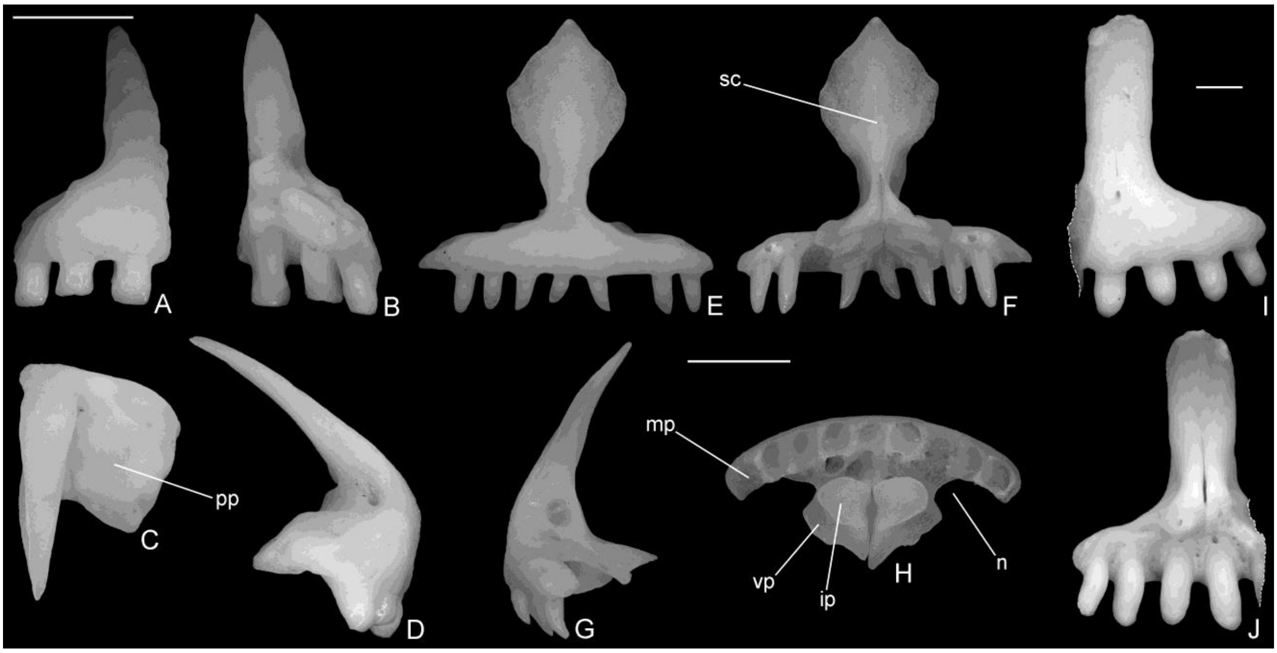

**Figure 9.** Premaxillae (continues) - A-D: *C. ocellatus* (MDHC 250), right premaxilla in anterior (A), posterior (B), dorsal (C), and lateral (D) views. E-H: *Anguis* gr. *A. fragilis* (MDHC 102), premaxilla in anterior (E), posterior (F), left lateral (G), and ventral (H) views. I-J: *P. apodus* (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.

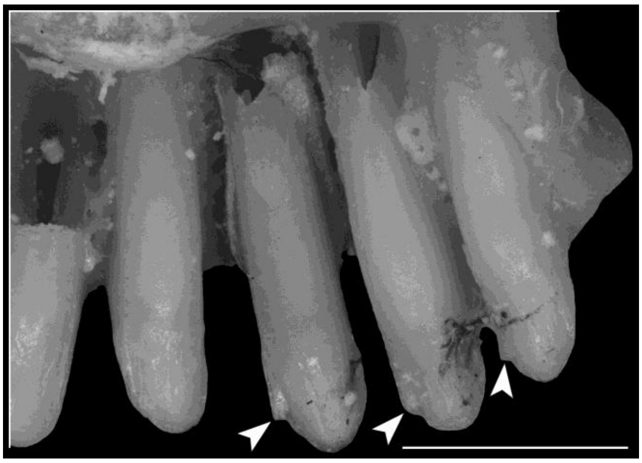

**Figure 10.** Detail of the premaxillary dentition of *T. lepidus* MRAC 92-050-R-1, showing bicuspid teeth (white arrows). Scale bar = 1 mm.

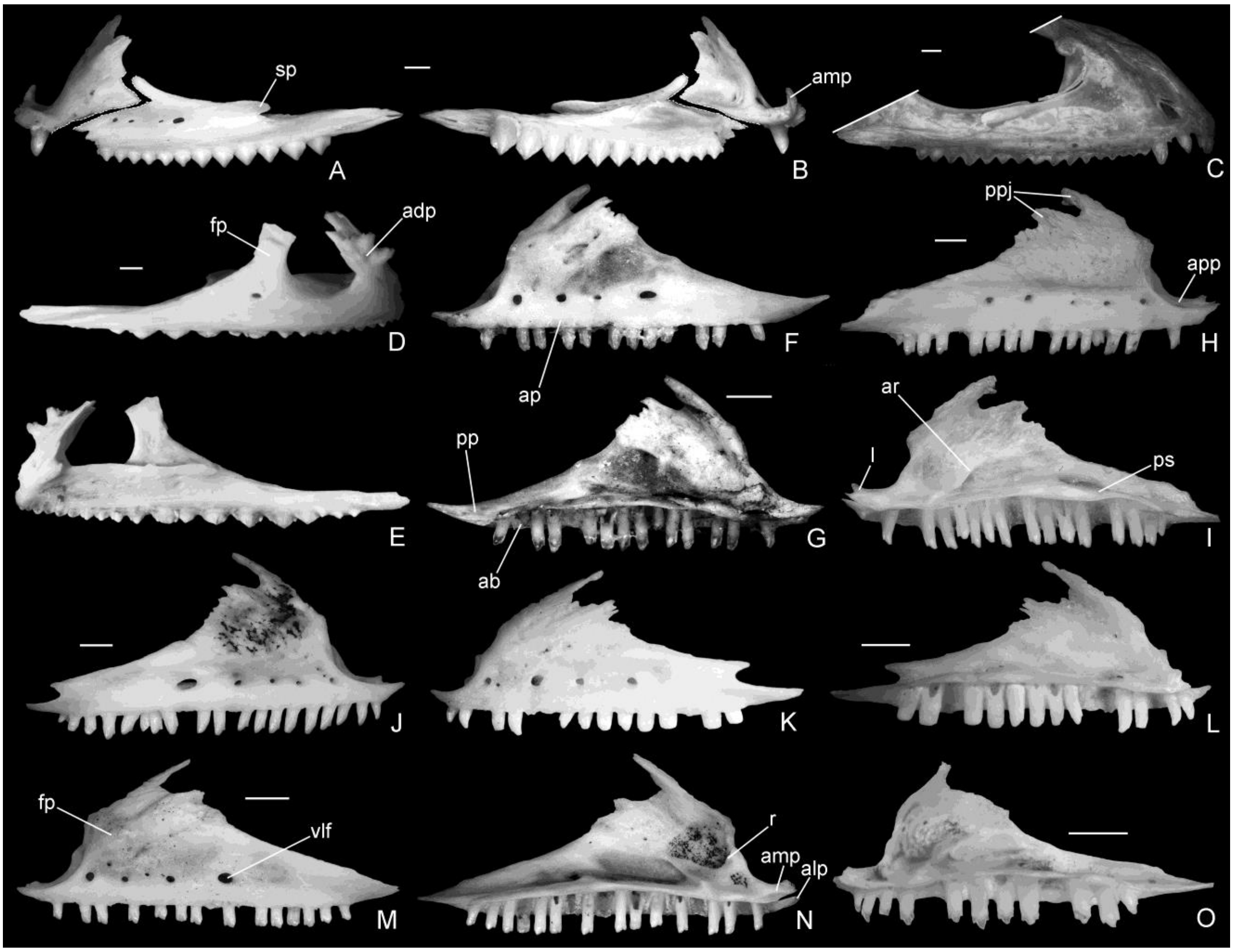

**Figure 11.** Maxillae - A-B: *L. stellio* (HUJ.OST-Z-423), left maxilla in lateral (A) and medial (B) views (the maxilla is broken and lacks part of the tooth row). C: *L. stellio* (HUJ.OST-Z-5), articulated right maxilla in lateral view. D-E: *C. chamaeleon* (NHMW 611), right maxilla in lateral (D) and medial (E) views. F-G: *A. erythrurus* (UAM.R.ACVII), left maxilla in lateral (F) and medial (G) views. H-I: *L. bilineata* (MDHC 15), right maxilla in lateral (H) and medial (I) views. J: *L. bilineata* (MDHC 381), right maxilla in lateral view. K-L: *P. melisellensis* (NHMW 628), left maxilla in lateral (K) and medial (L) views. M-N: *P. algirus* (UAM.R.Ps9), left maxilla in lateral (M) and medial (N) views. O: *T. lepidus* (NHMW 625), right maxilla of a juvenile individual in medial view. 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.

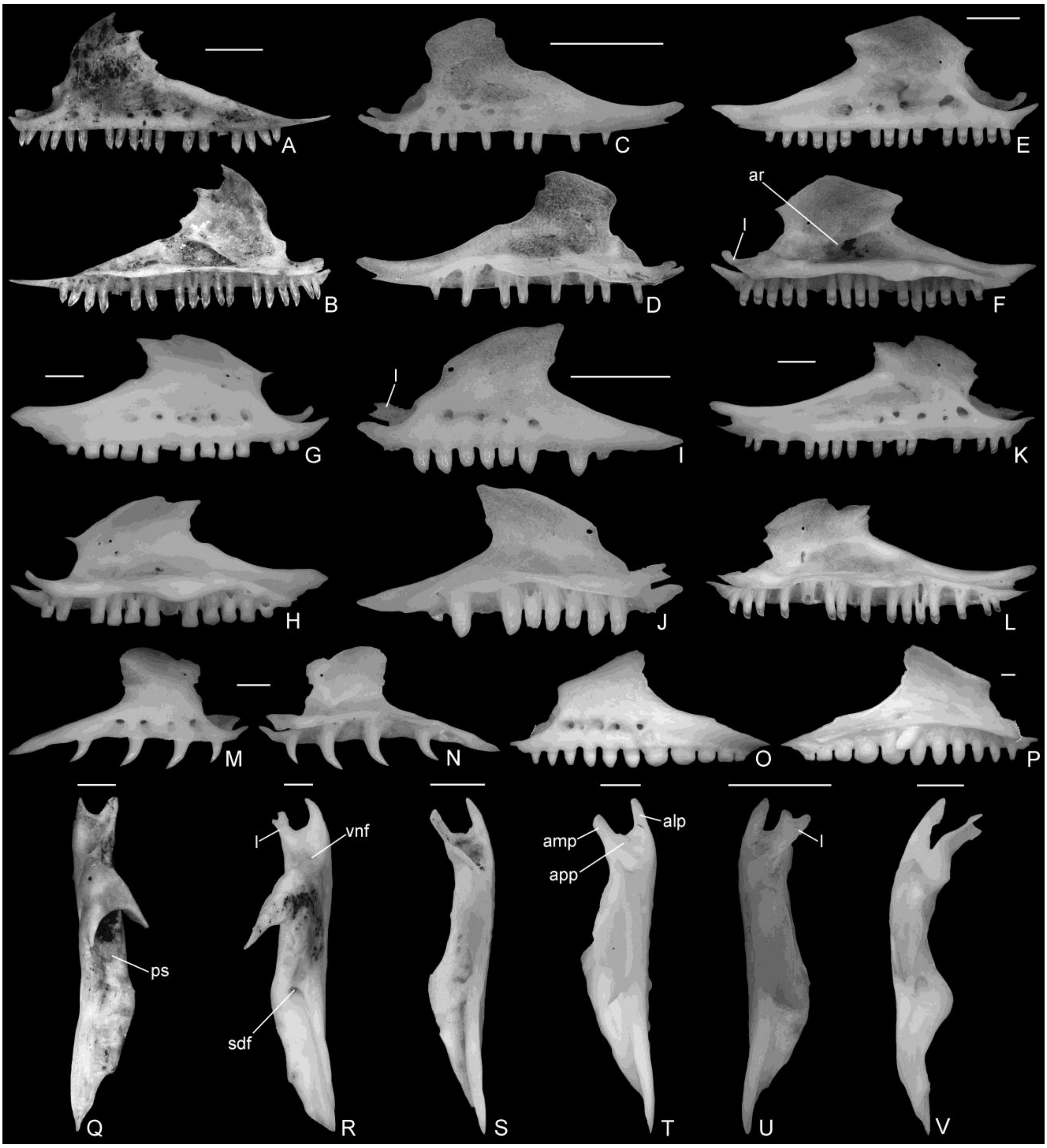

**Figure 12.** Maxillae (continues) - A-B: *Z. vivipara* (UAM.R.Lv24), left maxilla in lateral (A) and medial (B) views. C-D: *A. kitaibelii* (MDHC 239), left maxilla in lateral (C) and medial (D) views. E-F: *C. chalcides* (MDHC 398), right maxilla in lateral (E) and medial (F) views. G-H: *C. ocellatus* (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). Q: *A. erythrurus* (UAM.R.ACVII), left maxilla in dorsal view. R: *L. bilineata* (MDHC 381), right maxilla in dorsal view. S: *C. chalcides* (MDHC 398), right maxilla in medial view. T: *C. ocellatus* (MDHC 250), right maxilla in dorsal view. U: *O. punctatissimus* (MDHC 427), left maxilla in dorsal view. V: *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.

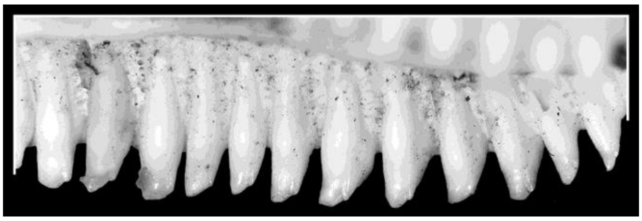

**Figure 13.** Detail of the hyperthrophied dentition of *T. lepidus* NHMW 681 (not to scale).

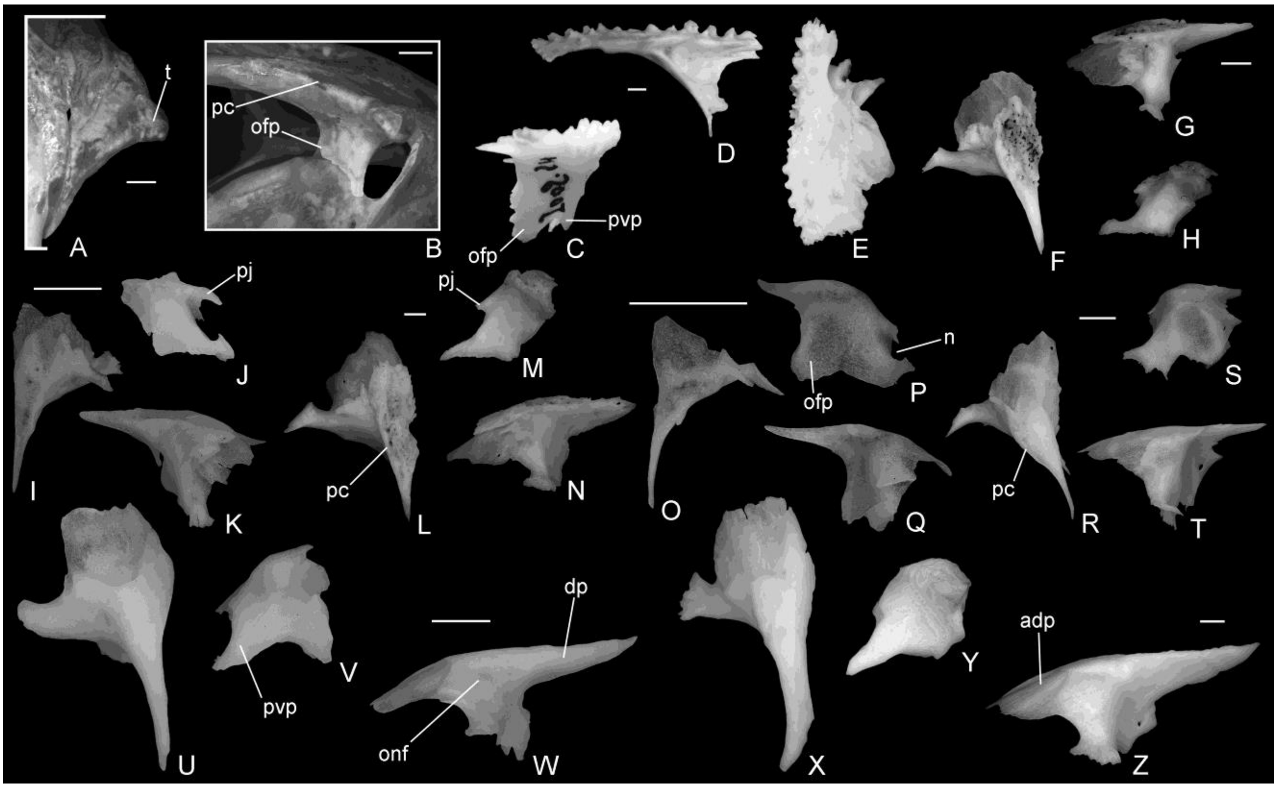

**Figure 14.** Prefrontals - A-B: *L. stellio* (HUJ.OST-Z-5), right prefrontal in dorsal (A) and dorsolateral (B) views. C: *C. chamaeleon* (MNHN 2002-24), right prefrontal in posterior view. D-E: *C. chamaeleon* (NHMW 611), left prefrontal in dorsal (D) and medial (E) views. F-H: *L. bilineata* (MDHC 381), left prefrontal in dorsal (F), lateral (G), and posterior (H) views. I-K: *O. elegans* (MDHC 281), right prefrontal in dorsal (I), posterior (J), and lateral (K) views. L-N: *T. lepidus* (MDHC 216), left prefrontal in dorsal (L), posterior (M), and lateral (N) views. O-Q: *A. kitaibelii* (MDHC 239), right prefrontal in dorsal (O), posterior (P), and lateral (Q) views. R-T: *T. aurata* (MDHC 280), left prefrontal in dorsal (R), posterior (S), and lateral (T) views. U-W: *Anguis* gr. *A. fragilis* (MDHC 102), left prefrontal in dorsal (U), posterior (V), and lateral (W) views. X-Z: *P. apodus* (MDHC 214), left prefrontal in dorsal (X), posterior (Y), and lateral (Z) 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.

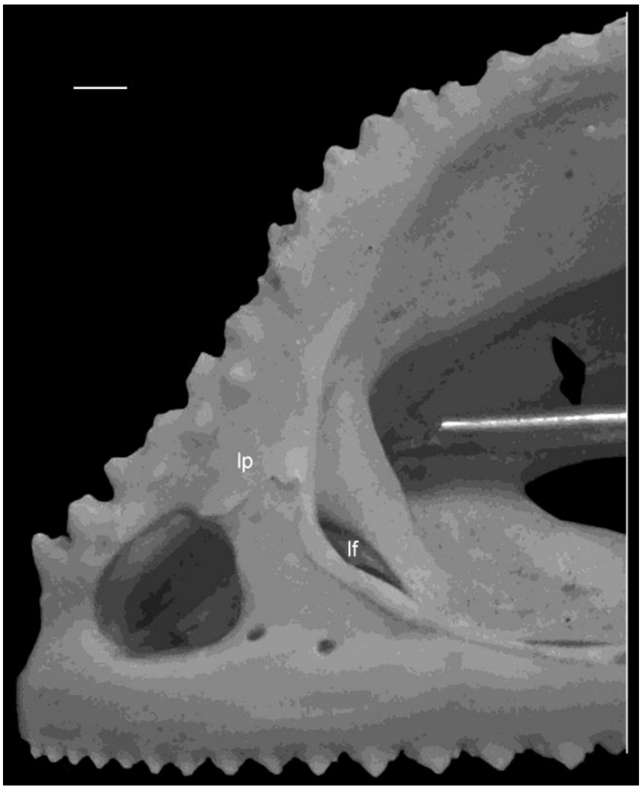

**Figure 15.** Articulated skull of *C. chamaeleon* (NHMW 721) in lateral view, showing the lateral process of the prefrontal (lp) and the lacrimal foramen (lf). Scale bar = 1 mm.

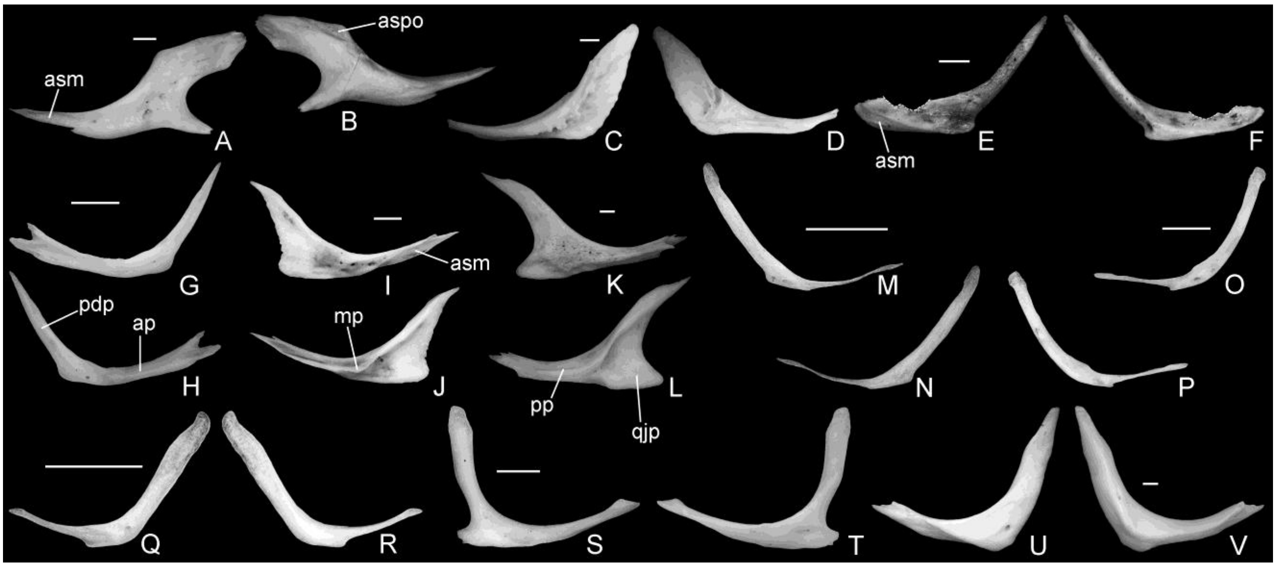

**Figure 16.** Jugals - A-B: *L. stellio* (HUJ.OST-Z-424), left jugal in lateral (A) and medial (B) views. C-D: *C. chamaeleon* (NHMW 611), left jugal in lateral (C) and medial (D) views. E-F: *A. erythrurus* (UAM.R.ACVII), left jugal in lateral (E) and medial (F) views (the dorsal margin of the anterior process is damaged). G-H: *O. elegans* (MDHC 281), left jugal in lateral (G) and medial (H) views. I-J: *P. algirus* (UAM.R.Ps9), right jugal in lateral (I) and medial (J) views. K-L: *T. lepidus* (MDHC 216), right jugal in lateral (K) and medial (L) views. M-N: *A. kitaibelii* (MDHC 239), right jugal in lateral (M) and medial (N) views. O-P: *C. chalcides* (MDHC 398), left jugal in lateral (O) and medial (P) views. Q-R: *O. punctatissimus* (MDHC 427), left jugal in lateral (Q) and medial (R) views. S-T: *Anguis* gr. *A. fragilis* (MDHC 102), right jugal in lateral (S) and medial (T) views. U-V: *P. apodus* (MDHC 215), left jugal in lateral (U) and medial (V) 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; qjp, quadratojugal process. Scale bars = 1 mm.

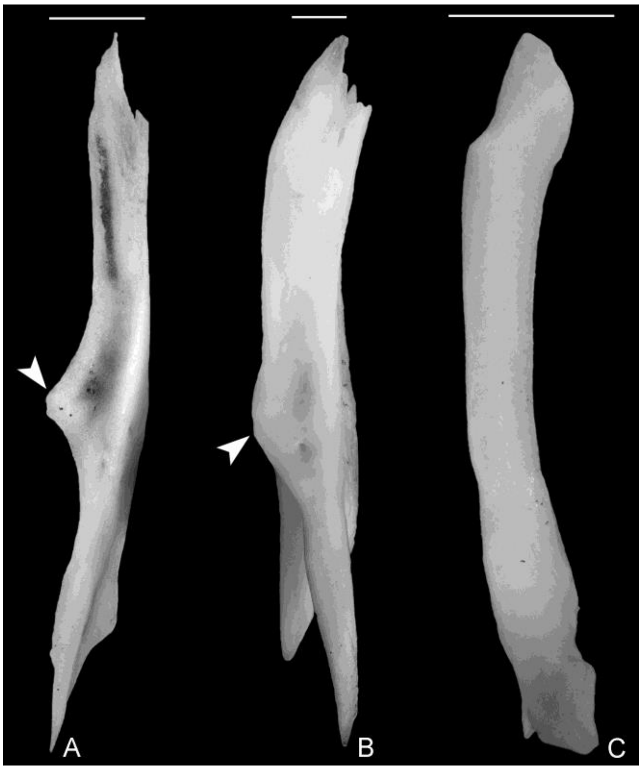

**Figure 17.** Dorsal view of the right jugal of *P. algirus* (UAM.R.Ps9; A), *T. lepidus* (MDHC 216; B) and *Anguis* gr. *A. fragilis* (MDHC 102; C), displaying different developments of the medial process (white arrows): well developed (A), poorly developed/almost indistinct (B) and absent (C). Scale bars = 1 mm.

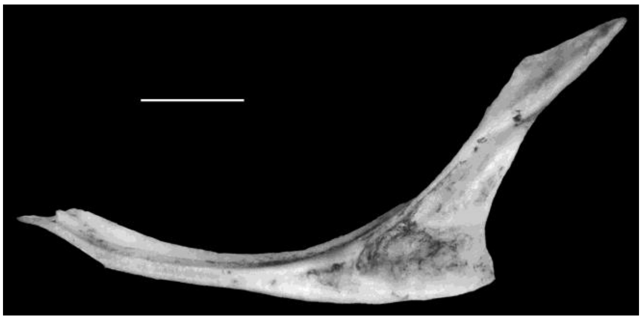

**Figure 18.** Right jugal of NHMW 625, a young individual of *T. lepidus,* in medial view. Note the anterior process, which is longer than the posterodorsal one. Scale bar = 1 mm.

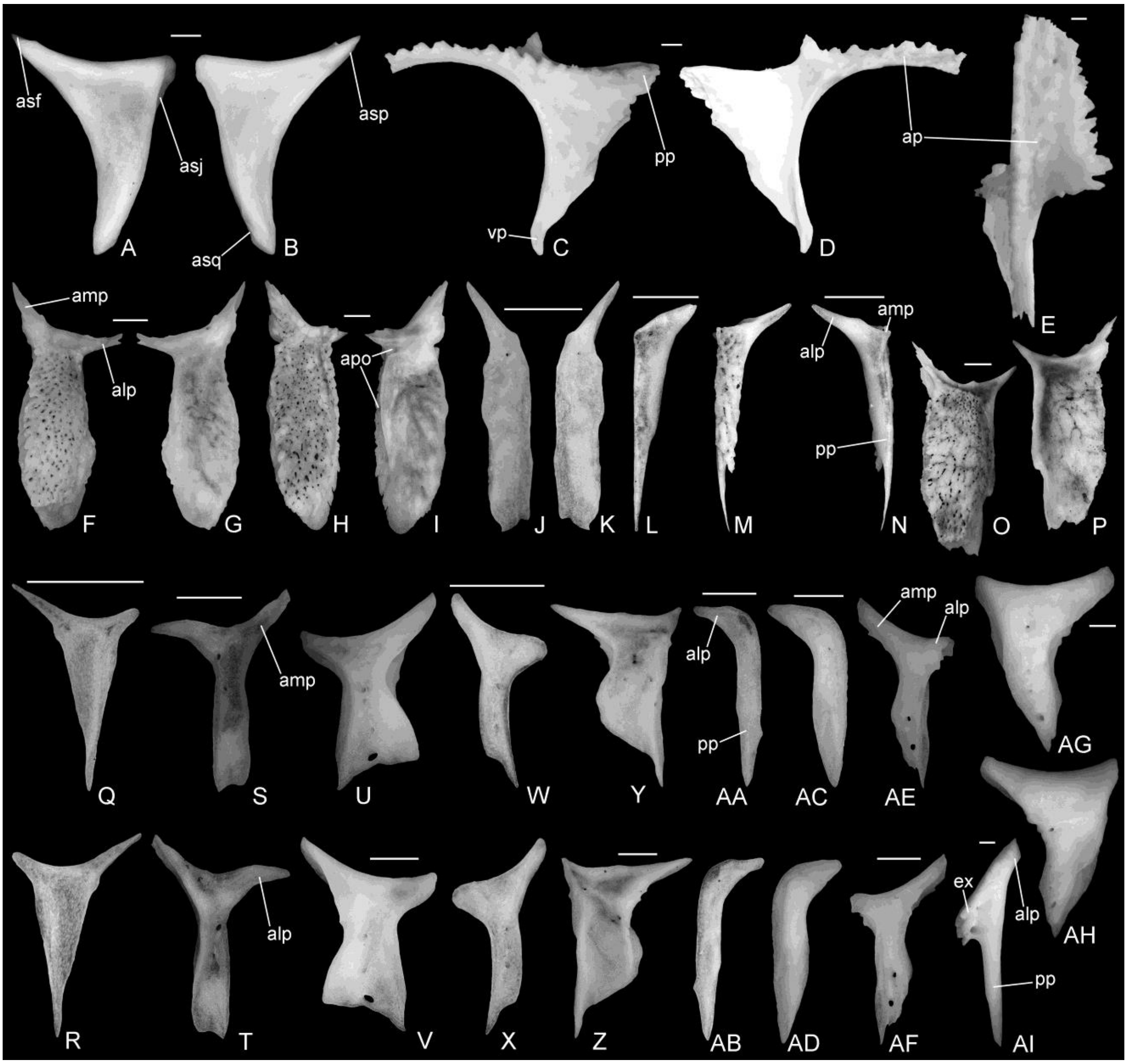

**Figure 19.** Postfrontals, postorbitals and postorbitofrontals - A-B: *L. stellio* (MDHC 245), right postorbital in dorsal (A) and ventral (B) views. C-D: *C. chamaeleon* (NHMW 611), left postorbital in lateral (C) and medial (D) views. E: *C. chamaeleon* (MNHN 2002-24), left postorbital in dorsal view. F-G: *L. agilis* (MDHC 176), right postfrontal in dorsal (F) and ventral (G) views. H-I: *L. bilineata* (MDHC 381), right postfrontal in dorsal (H) and ventral (I) views. J-K: *O. elegans* (MDHC 281), right postfrontal in dorsal (J) and ventral (K) views. L: *I. bonnali* (UAM.R.Lm28A), left postorbital in ventral view. M-N: *P. bocagei* (UAM.R.PB48), right postorbital in dorsal (M) and ventral (N) views. O-P: *P. algirus* (UAM.R.Ps9), right postorbitofrontal in dorsal (O) and ventral (P) views. Q-R: *A. kitaibelii* (MDHC 239), right postfrontal in dorsal (Q) and ventral (R) views. S-

T: *C. chalcides* (MDHC 398), left postfrontal in dorsal (S) and ventral (T) views. U-V: *C. ocellatus* (MDHC 250), left postfrontal in dorsal (U) and ventral (V) views. W-X: *O. punctatissimus* (MDHC 427), right postfrontal in dorsal (W) and ventral (X) views. Y-Z: *T. aurata* (MDHC 280), right prefrontal in dorsal (Y) and ventral (Z) views. AA-AB: *C. chalcides* (MDHC 398), left postorbital in dorsal (AA) and ventral (AB) views. AC-AD: *C. ocellatus* (MDHC 250), left postorbital in dorsal (AC) and ventral (AD) views. AE-AF: *Anguis* gr. *A. fragilis* (MDHC 102), right postfrontal in dorsal (AE) and ventral (AF) views. AG-AH: *P. apodus* (MDHC 214), left postfrontal in dorsal (AG) and ventral (AH) views. AI: *P. apodus* (MDHC 215), right postorbital 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; pp, posterior process; vp, ventral process. Scale bars = 1 mm.

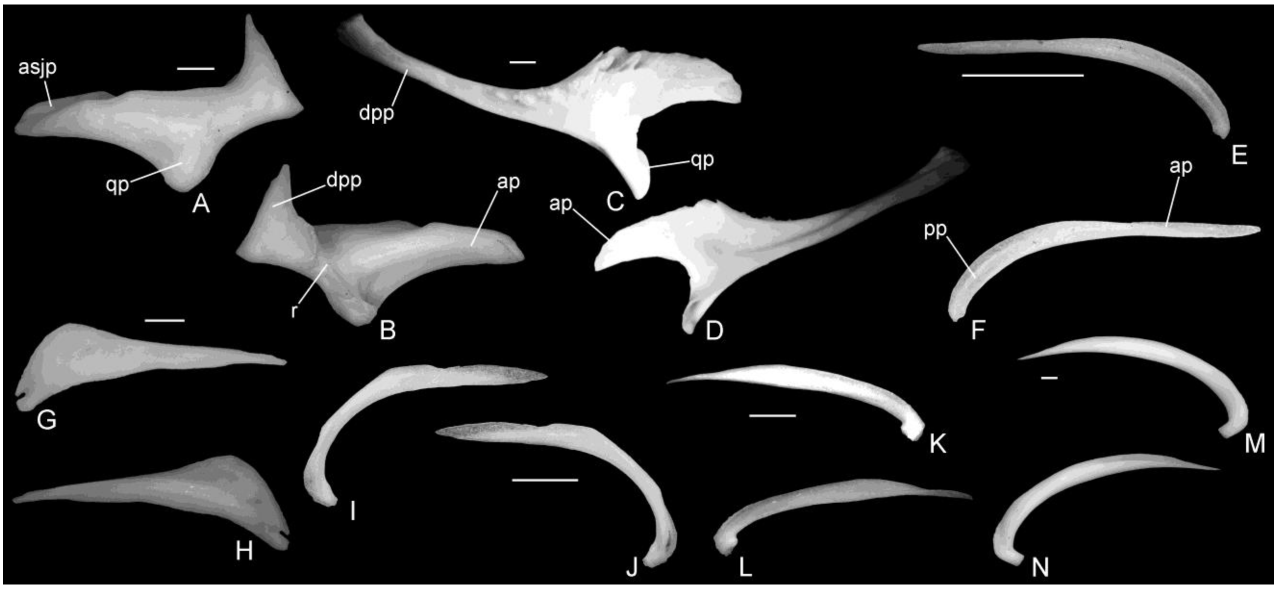

**Figure 20.** Squamosals - A-B: *L. stellio* (MDHC 245), left squamosal in lateral (A) and medial (B) views. C-D: *C. chamaeleon* (NHMW 611), right squamosal in lateral (C) and medial (D) views. E-F: *P. muralis* (MDHC 312), left squamosal in lateral (E) and medial (F) views. G-H: *L. viridis* (MRAC 91-077-R-76), right squamosal in lateral (G) and medial (H) views. I-J: *C. chalcides* (MDHC 398), right squamosal in lateral (I) and medial (J) views. K-L: *Anguis* gr. *A. fragilis* (MDHC 102), left squamosal in lateral (K) and medial (L) views. M-N: *P. apodus* (MDHC 215),

left squamosal in lateral (M) and medial (N) 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.

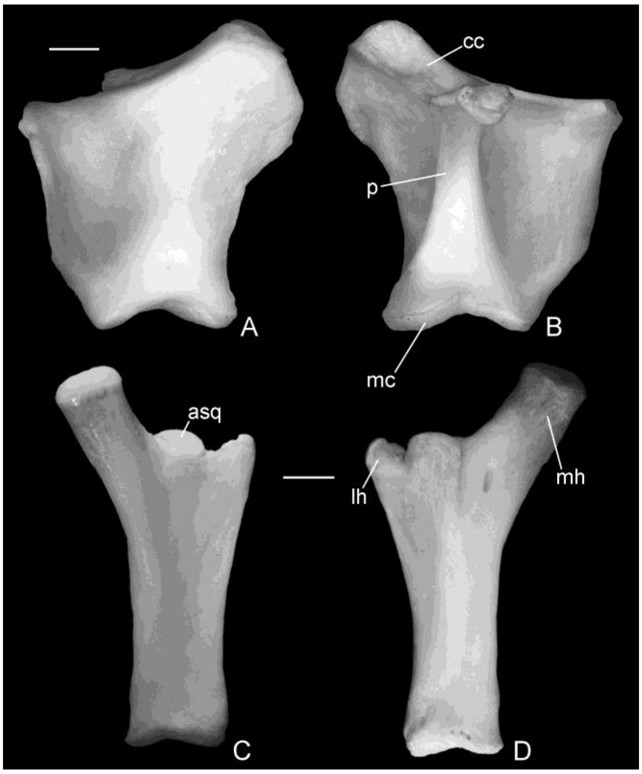

**Figure 21.** Quadrates - A-B: *L. stellio* (MDHC 245), right quadrate in anterior (A) and posterior (B) views. C-D: *C. chamaeleon* (NHMW 611), left quadrate in anterior (C) and posterior (D) views. Abbreviations: asq, articulation surface with the squamosal; cc, cephalic condyle; lh, lateral head; mc, mandibular condyle; mh, medial head; p, pillar. Scale bars = 1 mm.

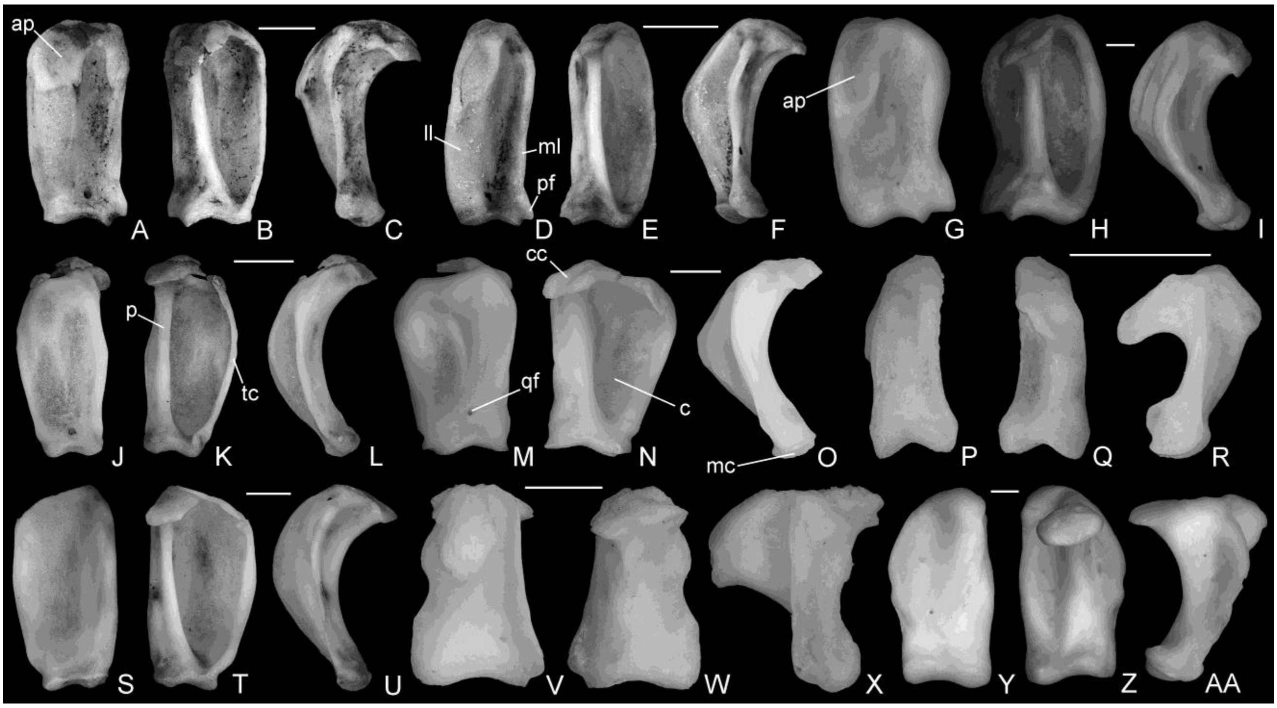

**Figure 22.** Quadrates (continues) - A-C: *A. erythrurus* (UAM.R.ACVII), right quadrate in anterior (A), posterior (B), and medial (C) views. D-F: *P. bocagei* (UAM.R.PB48), right quadrate in anterior (D), posterior (E), and medial (F) views. G-I: *T. lepidus* (MDHC 216), right quadrate in anterior (G), posterior (H), and medial (I) views. J-L: *C. chalcides* (MDHC 398), right quadrate in anterior (J), posterior (K), and medial (L) views. M-O: *C. ocellatus* (MDHC 250), right quadrate in anterior (M), posterior (N), and medial (O) views. P-R: *O. punctatissimus* (MDHC 427), left quadrate in anterior (P), posterior (Q), and medial (R) views. S-U: *T. aurata* (MDHC 280), right quadrate in anterior (S), posterior (T), and medial (U) views. V-X: *Anguis* gr. *A. fragilis* (MDHC 102), right quadrate in anterior (V), posterior (W), and medial (X) views. Y-AA: *P. apodus* (MDHC 214), left quadrate in anterior (Y), posterior (Z), and medial (AA) views. Abbreviations: ap, anterior platform; c, conch; cc, cephalic condyle; ll, lateral lamina; mc, mandibular condyle; ml, medial lamina; p, pillar; pf, pterygoid flange; qf, quadrate foramen; tc, tympanic crest. Scale bars = 1 mm.

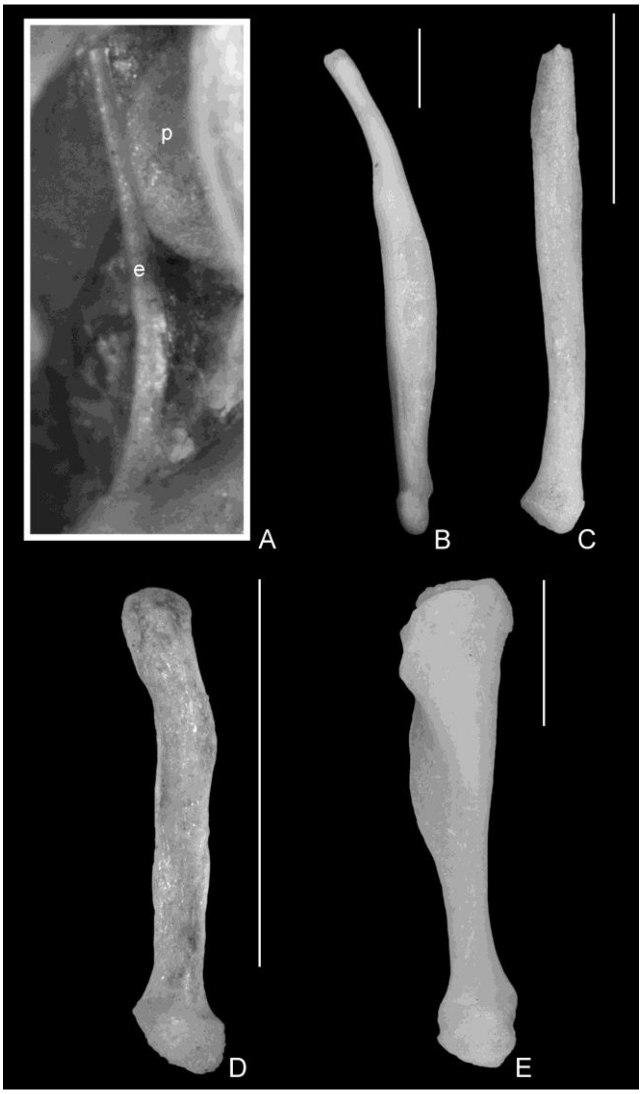

**Figure 23.** Epipterygoids - A: *L. stellio* (NHMW 570; not to scale). B: *L. bilineata* (MDHC 381). C: *C. chalcides* (MDHC 94). D: *O. punctatissimus* (MDHC 427; reversed for comparison). E: *Anguis* gr. *A. fragilis* (MDHC 102). Abbreviations: e, epipterygoid; p, prootic. Scale bars = 1 mm.

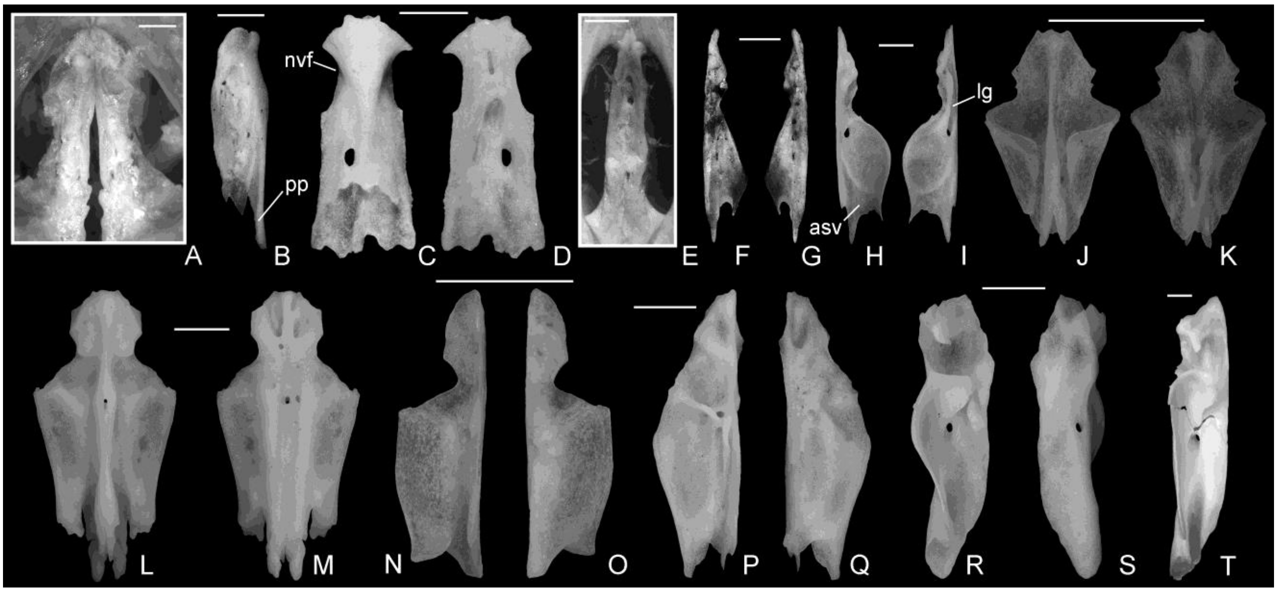

**Figure 24.** Vomers - A: *L. stellio* (HUJ.OST-Z-5), articulated vomers in ventral view. B: *L. stellio* (HUJ.OST-Z-424), right vomer in dorsal view. C-D: *C. chamaeleon* (NHMW 611), vomer in dorsal (C) and ventral (D) views. E: *C. chamaeleon* (NHMW 721), articulated vomers in ventral view. F-G: *A. erythrurus* (UAM.R.ACVII), right vomer in dorsal (F) and ventral (G) views. H-I: *L. bilineata* (MDHC 381), right vomer in dorsal (H) and ventral (I) views. J-K: *A. kitaibelii* (MDHC 239), fused vomers in dorsal (J) and ventral (K) views. L-M: *C. ocellatus* (MDHC 250), fused vomers in dorsal (L) and ventral (M) views. N-O: *O. punctatissimus* (MDHC 427), left vomer in dorsal (N) and ventral (O) views. P-Q: *T. aurata* (MDHC 280), left vomer in dorsal (P) and ventral (Q) views. R-S: *Anguis* gr. *A. fragilis* (MDHC 102), left vomer in dorsal (R) and ventral (S) views. T: *P. apodus* (MDHC 215), left vomer in dorsal view (the specimen is broken roughly at midlength). Abbreviations: asv, articulation surface with the vomerine process of the palatine; lg, lacrimal groove; nvf, notch of the vomeronasal fenestra; pp, posterior process. Scale bars = 1 mm.

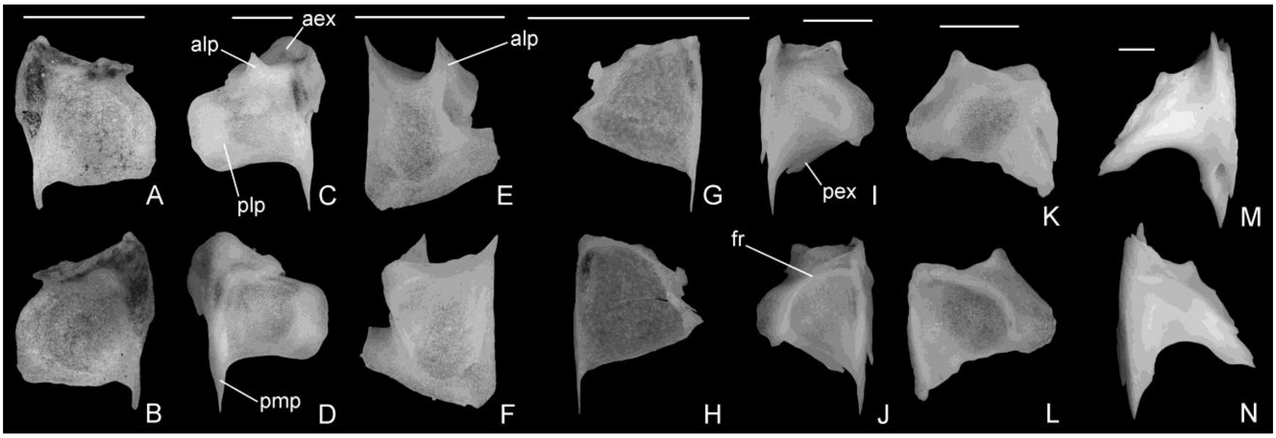

**Figure 25.** Septomaxillae - A-B: *I. bonnali* (UAM.R.Lm28A), right septomaxilla in dorsal (A) and ventral (B) views. C-D: *L. bilineata* (MDHC 381), left septomaxilla in dorsal (C) and ventral (D) views. E-F: *O. elegans* (MDHC 281), right septomaxilla in dorsal (E) and ventral (F) views. G-H: *A. kitaibelii* (MDHC 239), left septomaxilla in dorsal (G) and ventral (H) views. I-J: *C. ocellatus* (MDHC 250), right septomaxilla in dorsal (I) and ventral (J) views. K-L: *Anguis* gr. *A. fragilis* (MDHC 102), left septomaxilla in dorsal (K) and ventral (L) views. M-N: *P. apodus* (MDHC 215), left septomaxilla in dorsal (M) and ventral (N) views. Abbreviations: aex, anteroventral expansion; alp, anterolateral process; fr, forked ridge; pex, posteroventral expansion; plp, posterolateral process; pmp, posteromedial process. Scale bars = 1 mm.

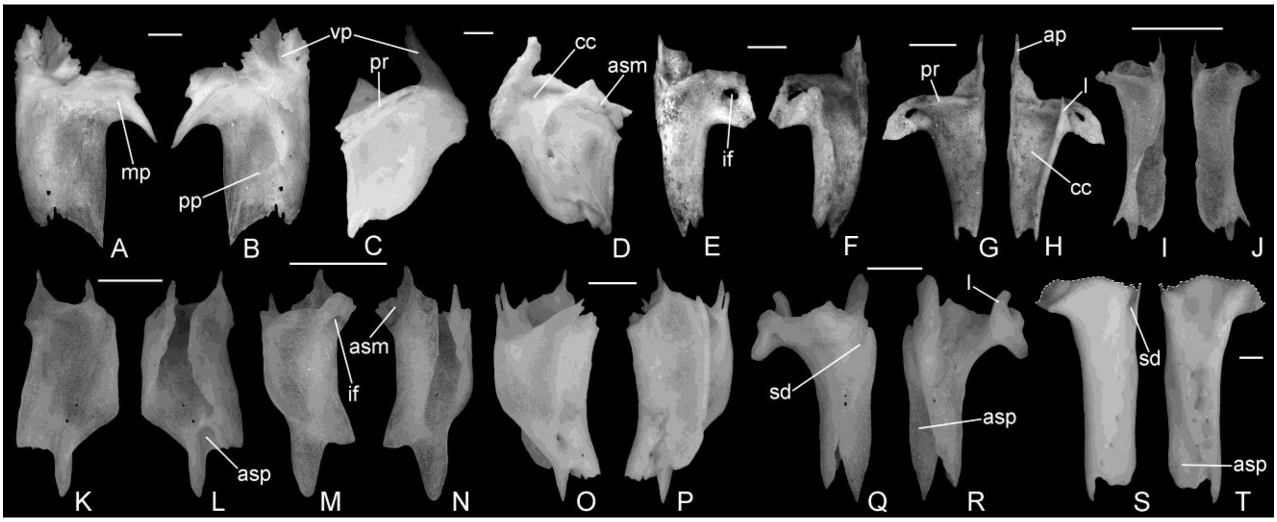

**Figure 26.** Palatines - A-B: *L. stellio* (HUJ.OST-Z-424), right palatine in dorsal (A) and ventral (B) views. C-D: *C. chamaeleon* (NHMW 611), left palatine in dorsal (C) and ventral (D) views. E-F: *A. erythrurus* (UAM.R.ACVII), right palatine in dorsal (E) and ventral (F) views. G-H: *I. monticola*

*cantabrica* (UAM.R.Lm92), left palatine in dorsal (G) and ventral (H) views. I-J: *A. kitaibelii* (MDHC 239), left palatine in dorsal (I) and ventral (J) views. K-L: *C. chalcides* (MDHC 398), left palatine in dorsal (K) and ventral (L) views. M-N: *O. punctatissimus* (MDHC 427), right palatine in dorsal (M) and ventral (N) views. O-P: *T. aurata* (MDHC 280), right palatine in dorsal (O) and ventral (P) views. Q-R: *Anguis* gr. *A. fragilis* (MDHC 102), left palatine in dorsal (Q) and ventral (R) views. S-T: *P. apodus* (MDHC 215), left palatine in dorsal (S) and ventral (T) 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.

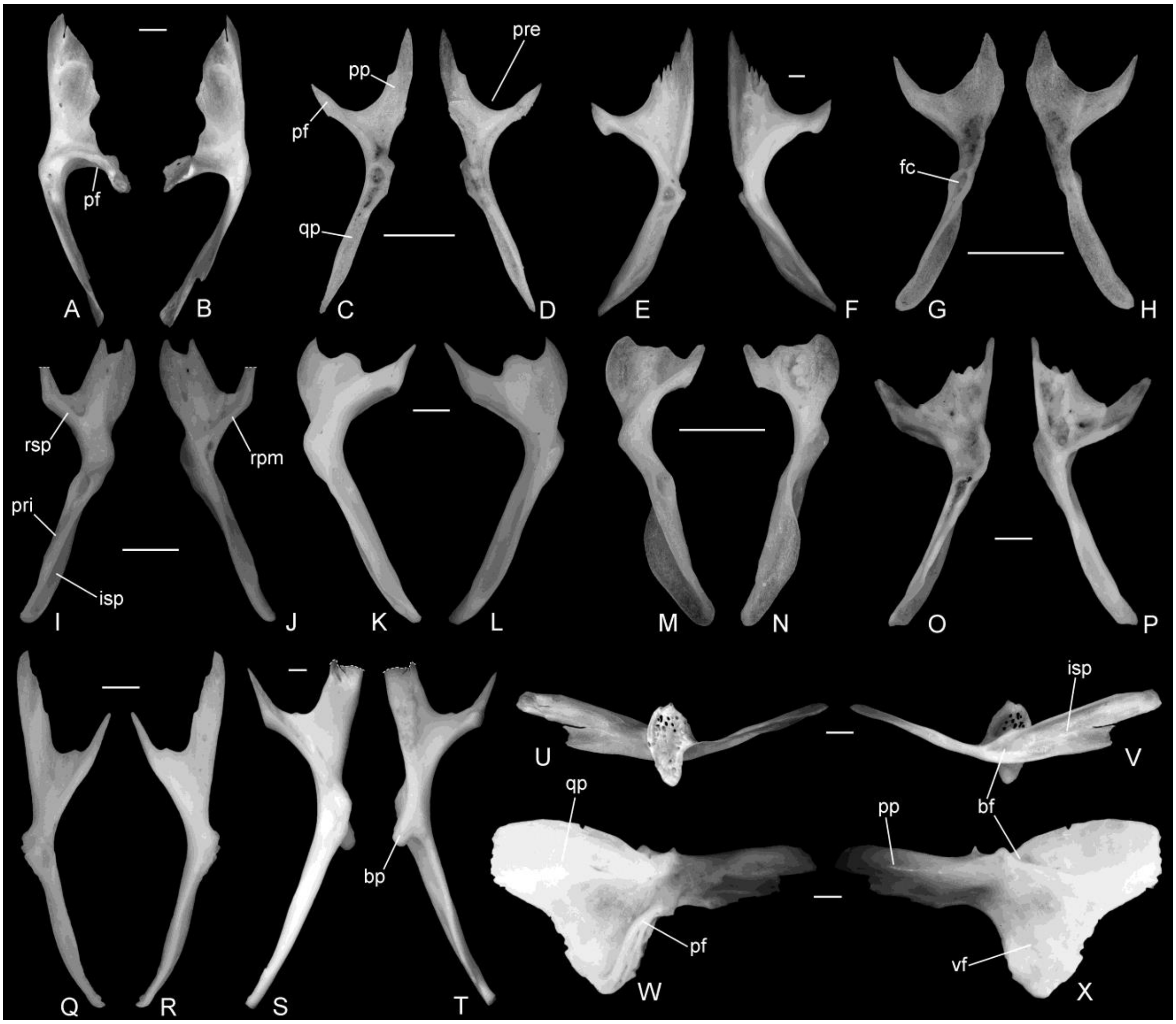

**Figure 27.** Pterygoids - A-B: *L. stellio* (HUJ.OST-Z-423), right pterygoid in dorsal (A) and ventral (B) views. C-D: *A. fitzingeri* (MDHC 351), left pterygoid in dorsal (C) and ventral (D views. E-F: *T. lepidus* (MDHC 216), left pterygoid in dorsal (E) and ventral (F) views. G-H: *A. kitaibelii* (MDHC 239), left pterygoid in dorsal (G) and ventral (H) views. I-J: *C. chalcides* (MDHC 94), left pterygoid in dorsal (I) and ventral (J) views (the tip of the pterygoid flange is broken). K-L: *C. ocellatus* (MDHC 250), right pterygoid in dorsal (K) and ventral (L) views. M-N: *O. punctatissimus* (MDHC 427), right pterygoid in dorsal (M) and ventral (N) views. O-P: *T. aurata* (MDHC 280), left pterygoid in dorsal (O) and ventral (P) views. Q-R: *Anguis* gr. *A. fragilis* (MDHC 102), right pterygoid in dorsal (Q) and ventral (R) views. S-T: *P. apodus* (MDHC 215), left pterygoid in dorsal (S) and ventral (T) views (the anterior end of the palatine process is broken). U-V: *L. stellio* (HUJ.OST-Z-423), right pterygoid in lateral (U) and medial (V) views. W-X: *C. chamaeleon* (NHMW 611), right pterygoid in lateral (W) and medial (X) 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 = 1 mm.

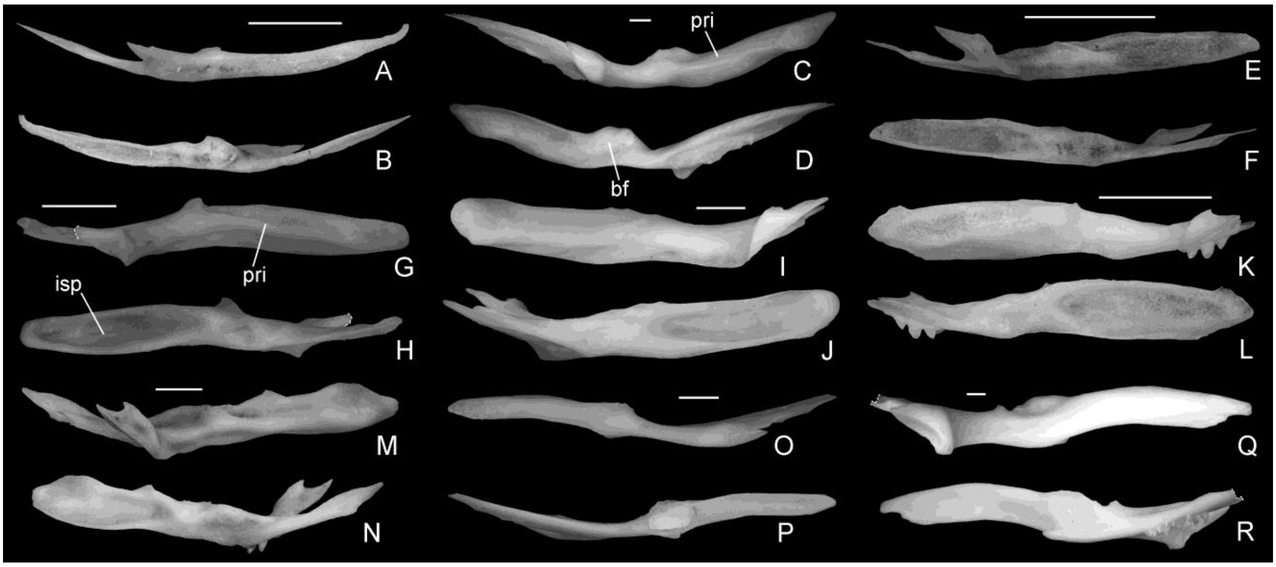

**Figure 28.** Pterygoids (continues) - A-B: *A. fitzingeri* (MDHC 351), left pterygoid in lateral (A) and medial (B) views. C-D: *T. lepidus* (MDHC 216), left pterygoid in lateral (C) and medial (D) views.

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.

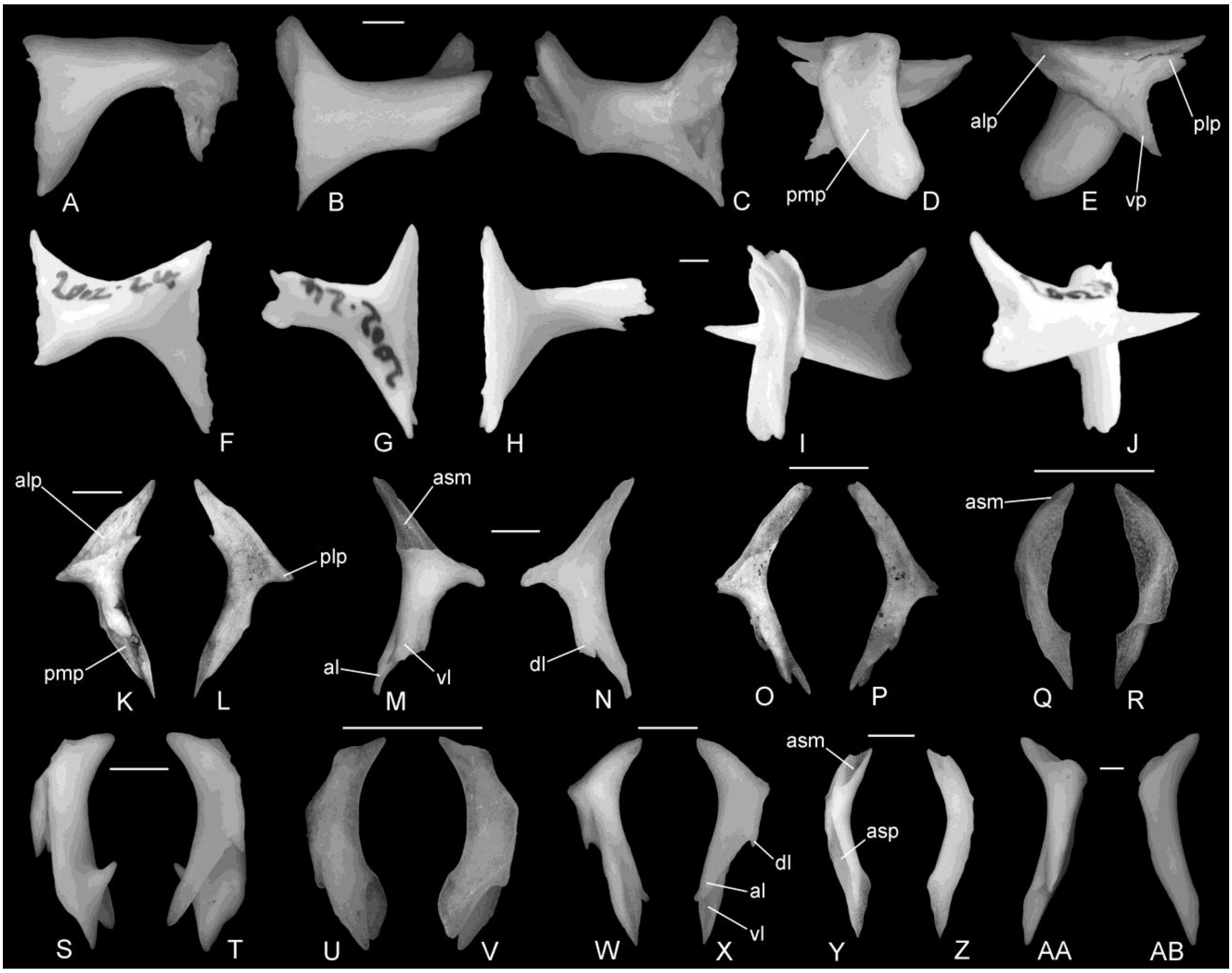

**Figure 29.** Ectopterygoids - A-E: *L. stellio* (MDHC 245), left ectopterygoid in anterior (A), dorsal (B), ventral (C), medial (D), and lateral (E) views. F-J: *C. chamaeleon* (MNHN 2002-24), right ectopterygoid in anterior (F), dorsal (G), ventral (H), medial (I), and lateral (J) views. K-L: *A.*

*erythrurus* (UAM.R.ACVII), right ectopterygoid in ventral (K) and dorsal (L) views. M-N: *L. agilis* (MDHC 176), left ectopterygoid in ventral (M) and dorsal (N) views. O-P: *Z. vivipara* (UAM.R.Lv24), right ectopterygoid in ventral (O) and dorsal (P) views. Q-R: *A. kitaibelii* (MDHC 239), right ectopterygoid in ventral (Q) and dorsal (R) views. S-T: *C. ocellatus* (MDHC 250), right ectopterygoid in ventral (S) and dorsal (T) views. U-V: *O. punctatissimus* (MDHC 427), right ectopterygoid in ventral (U) and dorsal (V) views. W-X: *T. aurata* (MDHC 280), right ectopterygoid in ventral (W) and dorsal (X) views. Y-Z: *Anguis* gr. *A. fragilis* (MDHC 102), right ectopterygoid in ventral (Y) and dorsal (Z) views. AA-AB: *P. apodus* (MDHC 215), left ectopterygoid in ventral (AA) and dorsal (AB) 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.

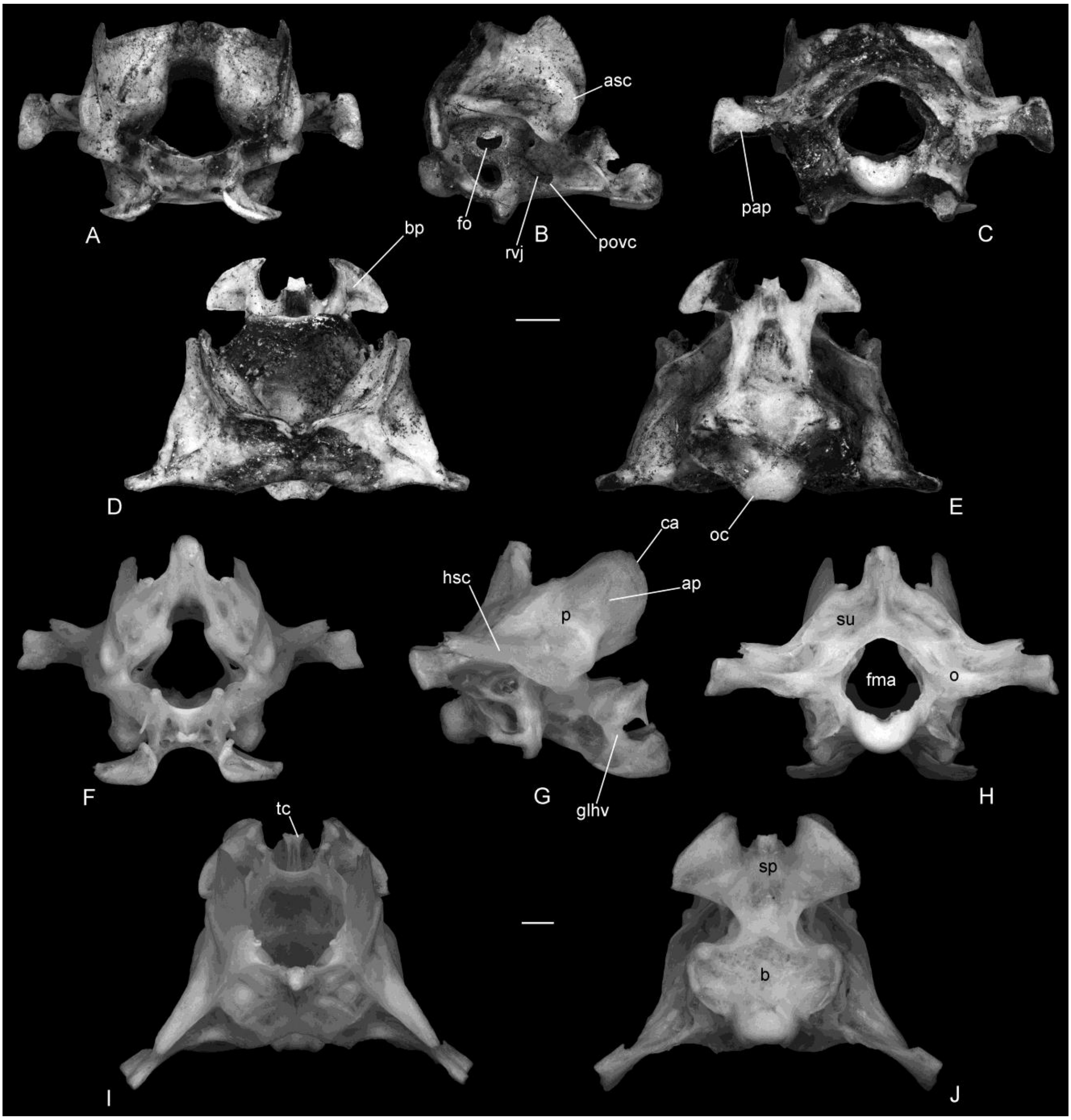

**Figure 30.** Braincases - A-E: *A. erythrurus* (UAM.R.ACVII), braincase in anterior (A), right lateral (B), posterior (C), dorsal (D), and ventral (E) views. F-J: *L. bilineata* (MDHC 15), braincase in anterior (F), right lateral (G), posterior (H), dorsal (I), and ventral (J) views. The parasphenoid rostrum is broken in both specimens. Abbreviations: ap, alar process; asc, anterior semicircular canal; b, basioccipital; bp, basipterygoid process; ca, crista alaris; fma, foramen magnum; fo, fenestra ovalis; glhv, groove of the lateral head vein; hsc, horizontal semicircular canal; o, otooccipital; oc, occipital condyle; p, prootic; pap, paroccipital process; povc, posterior opening of

the Vidian canal; rvj, recessus vena jugularis; sp, sphenoid; su, supraoccipital; tc, trabecula cranii. Scale bars = 1 mm.

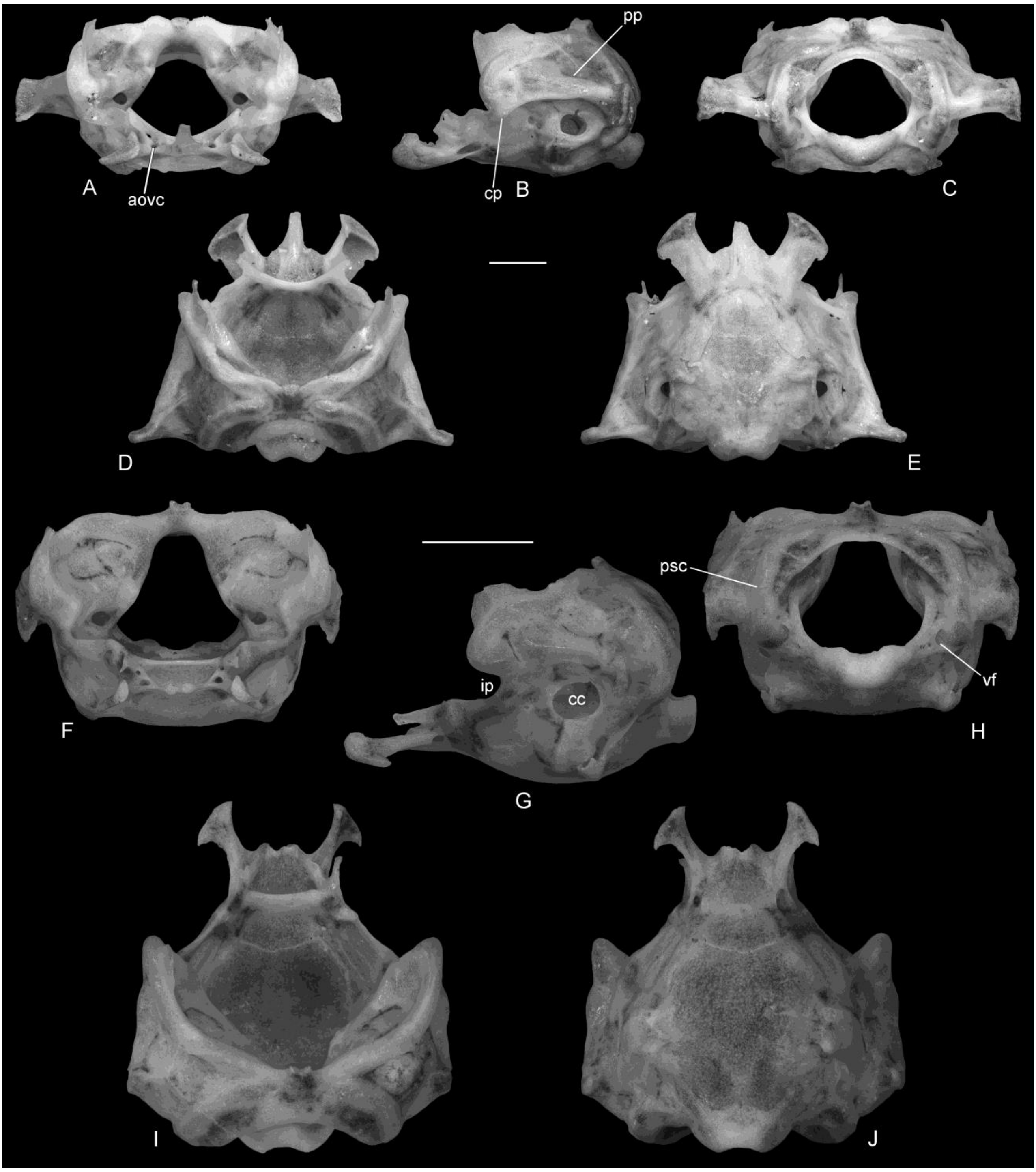

**Figure 31.** Braincases (continues) - A-E: *P. bocagei* (UAM.R.PB48), braincase in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. F-J: *A. kitaibelii* (MDHC 239), braincase in anterior (F), right lateral (G), posterior (H), dorsal (I), and ventral (J) views. Abbreviations: aovc, anterior opening of the Vidian canal; cc, cochlear cavity; cp, crista prootica;

ip, incisura prootica; pp, posterior process of the prootic; psc, posterior semicircular canal; vf, vagus foramen. Scale bars = 1 mm.

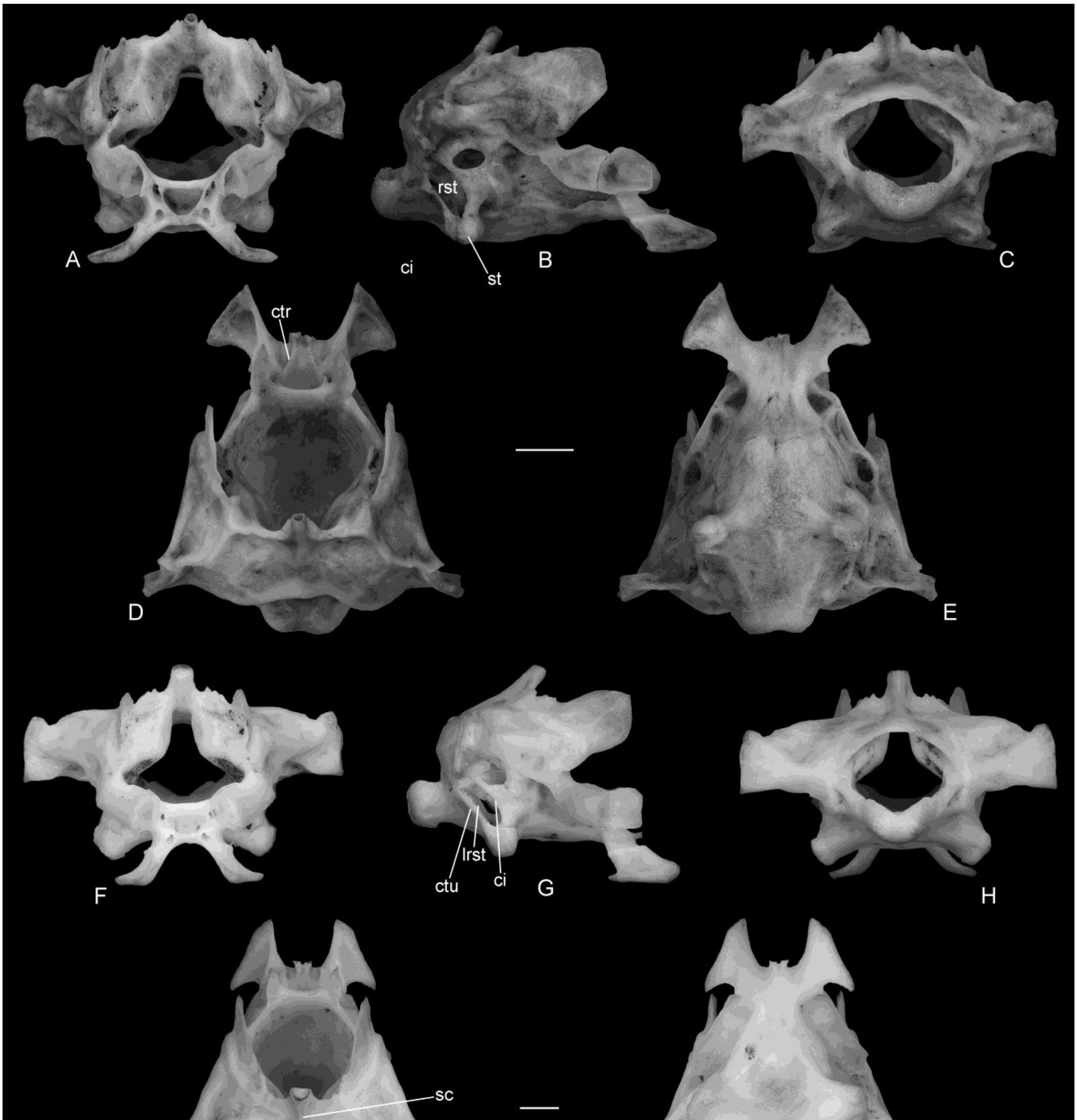

**Figure 32.** Braincases (continues) - A-E: *C. chalcides* (MDHC 398), braincase in anterior (A), right lateral (B), posterior (C), dorsal (D), and ventral (E) views. F-J: *C. ocellatus* (MDHC 250), braincase in anterior (F), right lateral (G), posterior (H), dorsal (I), and ventral (J) views. Abbreviations: ci, crista interfenestralis; ctr, crista trabecularis; ctu, crista tuberalis; lrst, lateral

opening of the recessus scalae tympani; rst, recessus scalae tympani; sc, supraoccipital crest; st, sphenooccipital tubercle. Scale bars = 1 mm.

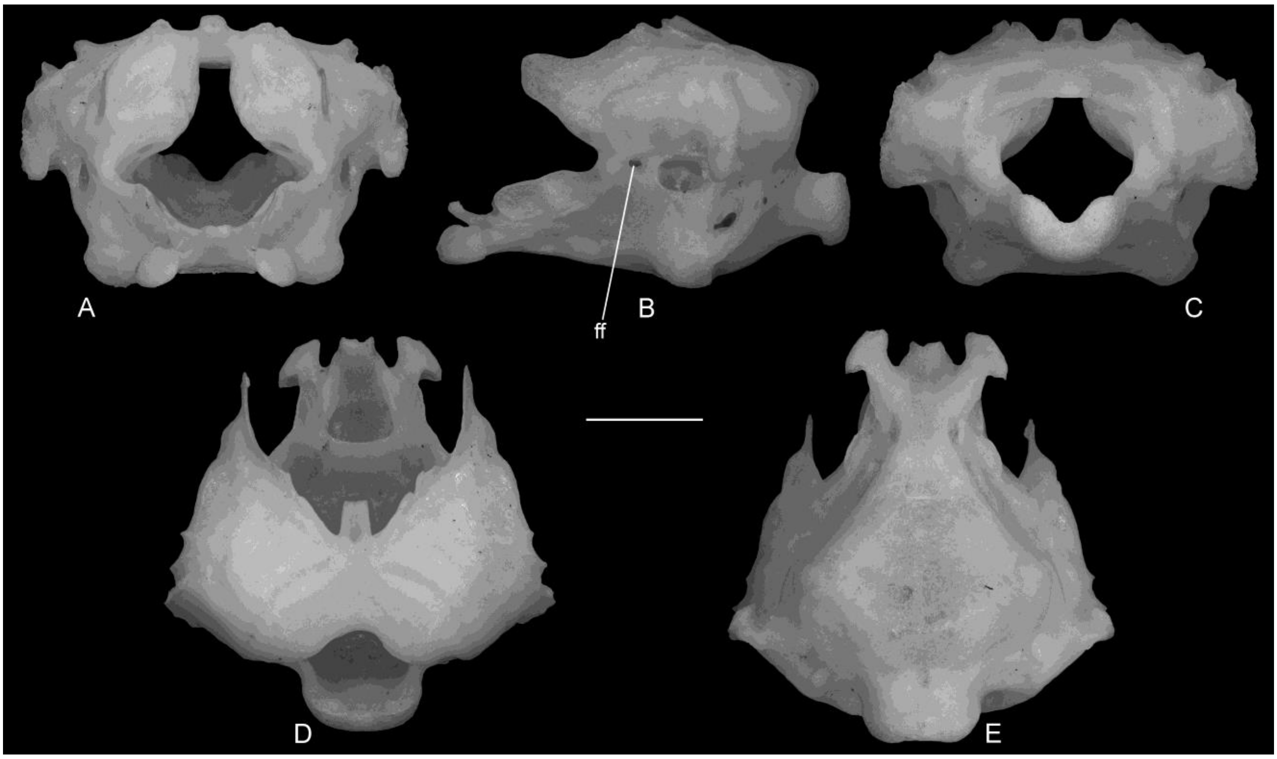

**Figure 33.** Braincases (continues) - A-E: *O. punctatissimus* (MDHC 427), braincase in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. Abbreviations: ff, facial foramen. Scale bars = 1 mm.

**Figure 34.** Braincases (continues) - A-E: *Anguis* gr. *A. fragilis* (MDHC 102), braincase 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), braincase 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 35.** 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.

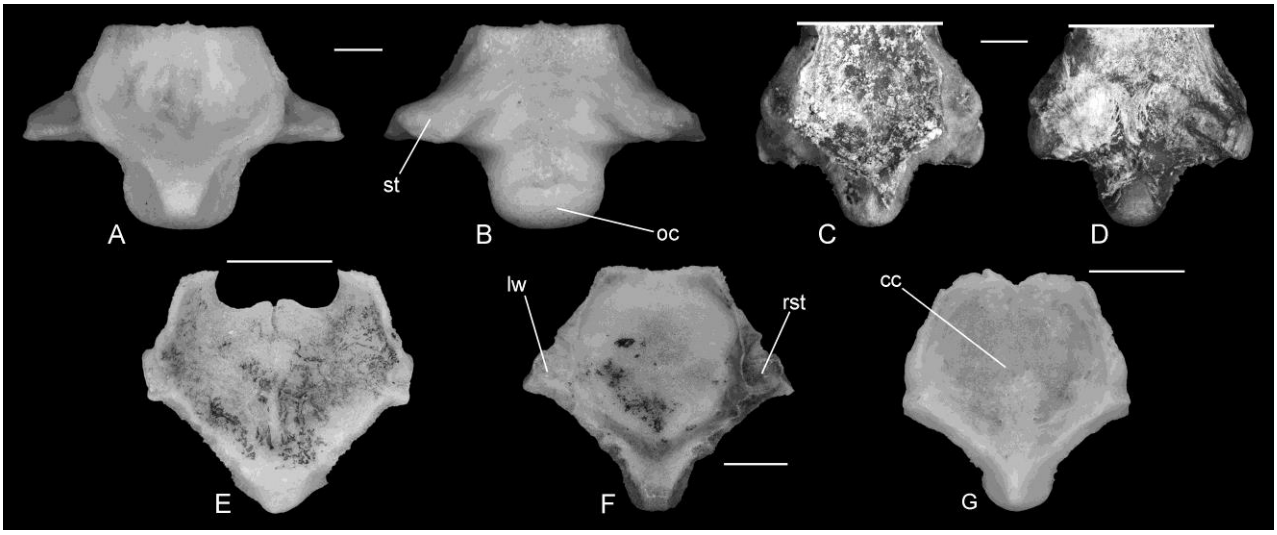

**Figure 36.** Basioccipitals - A-B: *L. stellio* (MDHC 245), basioccipital in dorsal (A) and ventral (B) views. C-D: *C. chamaeleon* (HUJ.OST-Z-380), basioccipital in dorsal (C) and ventral (D) views. E: *P. muralis* (MDHC 312), basioccipital in dorsal view. F: *T. aurata* (MDHC 280), basioccipital in dorsal view. G: *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.

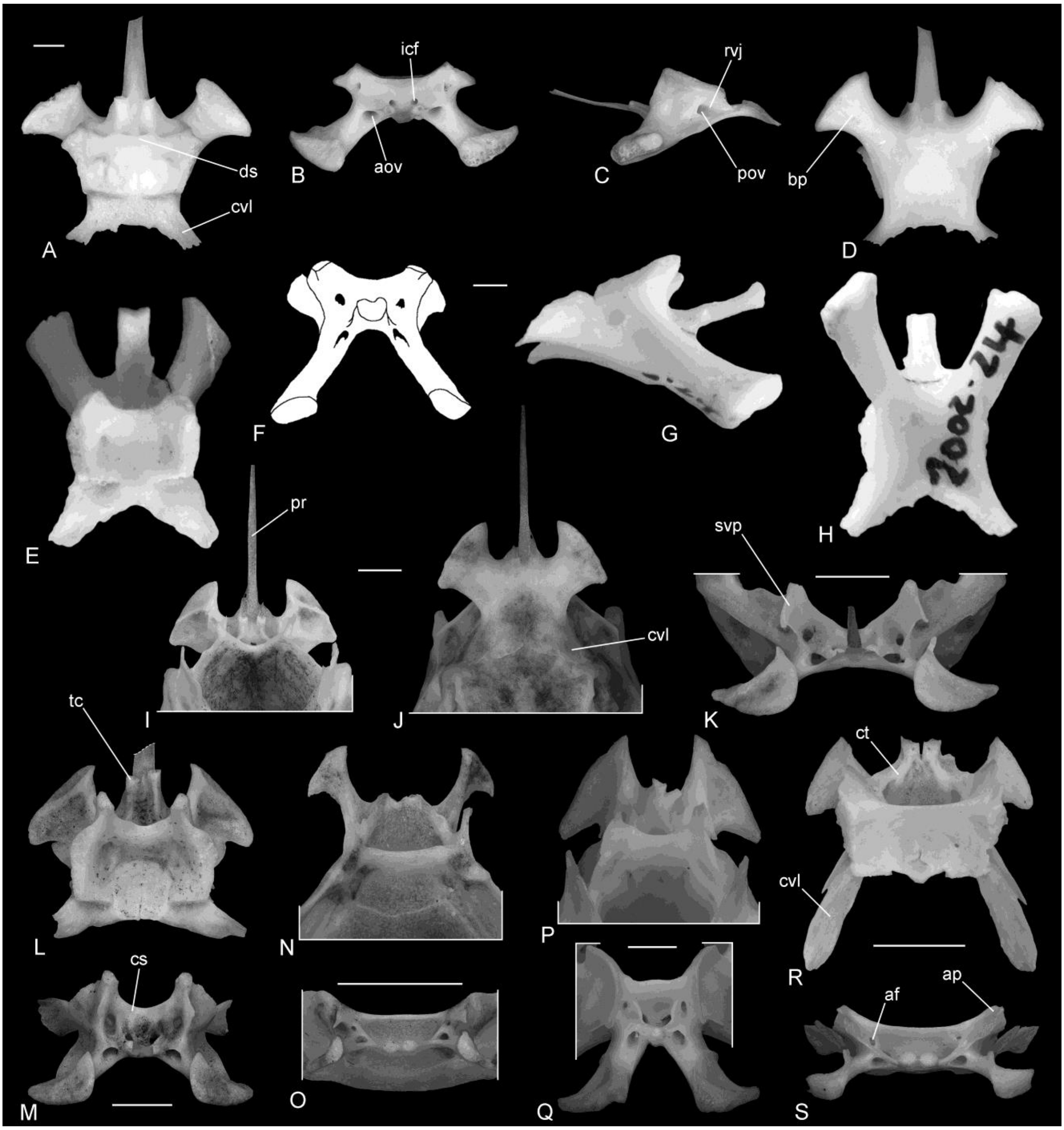

**Figure 37.** Sphenoids - A-D: *L. stellio* (MDHC 245), sphenoid in dorsal (A), anterior (B), left lateral (C), and ventral (D) views. E-H: *C. chamaeleon* (MNHN 2002-24), sphenoid in dorsal (E), anterior (F), right lateral (G), and ventral (H) views. I-K: *A. nigropunctatus* (MDHC 242), articulated sphenoid in dorsal (I), ventral (J), and anterior (K) views. L-M: *L. agilis* (MDHC 231), sphenoid in dorsal (L) and anterior (M) views (the parasphenoid rostrum is broken). N-O: *A.*

*kitaibelii* (MDHC 239), articulated sphenoid in dorsal (N) and anterior (O) views. P-Q: *C. ocellatus* (MDHC 193), articulated sphenoid in dorsal (P) and anterior (Q) views. R-S: *Anguis* gr. *A. fragilis* (MDHC 49), sphenoid in dorsal (R) and anterior (S) 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; svp, supravenous process; tc, trabecula cranii. Scale bars = 1 mm.

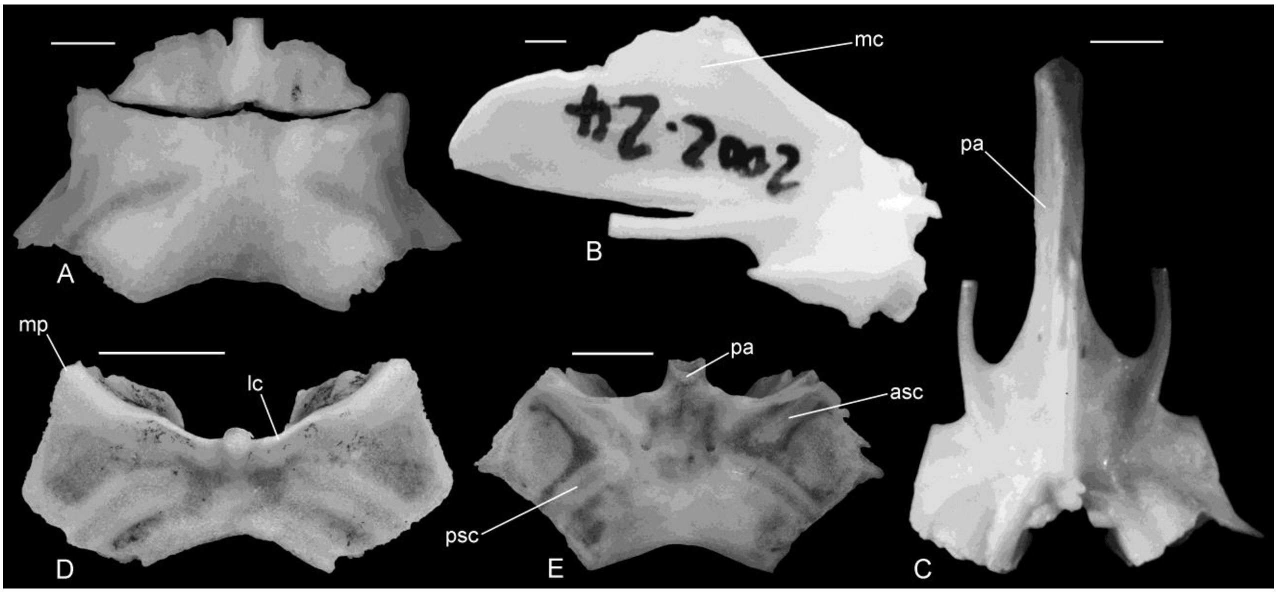

**Figure 38.** Supraoccipitals - A: *L. stellio* (MDHC 245), supraoccipital (broken) in dorsal view. B: *C. chamaeleon* (MNHN 2002-24), supraoccipital in left lateral view. C: *C. chamaeleon* (NHMW 611), supraoccipital in dorsal view. D: *P. muralis* (MDHC 312), supraoccipital in dorsal view. E: *T. aurata* (MDHC 280), supraoccipital in dorsal view. Abbreviations: asc, anterior semicircular canal; lc, lateral crest; mc, median crest; mp, marginal process; pa, processus ascendens; psc, posterior semicircular canal. Scale bars = 1 mm.

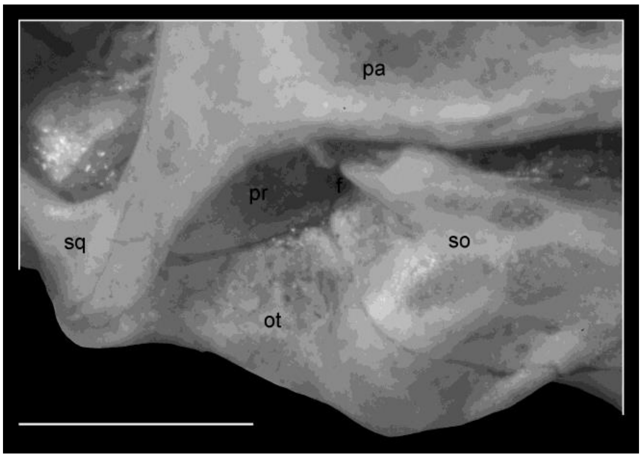

**Figure 39.** Posterodorsal view of an articulated skull of *L. stellio* (NHMW 570), showing the position of the sphenoccipital foramen. Abbreviations: f, sphenoccipital foramen; ot, otooccipital; pa, parietal; pr, prootic; so, supraoccipital; sq, squamosal. Scale bar = 1 mm.

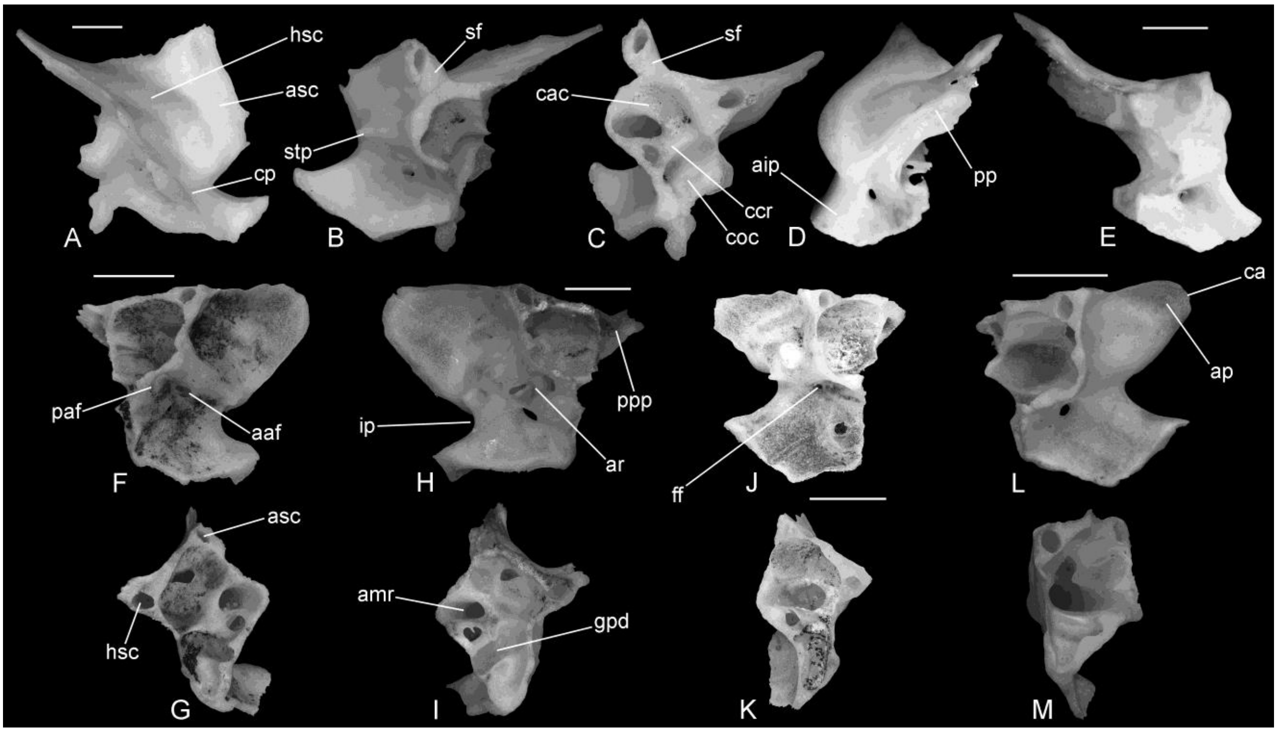

**Figure 40.** Prootics - A-C: *L. stellio* (MDHC 245), right prootic in lateral (A), medial (B), and posterior (C) views. D-E: *C. chamaeleon* (NHMW 611), left prootic in lateral (D) and medial (E) views. F-G: *P. muralis* (MDHC 312), left prootic in medial (F) and posterior (G) views. H-I: *H. graeca* (MDHC 423), right prootic in medial (H) and posterior (I) views. J-K: *C. striatus* (MDHC 404), right prootic in medial (J) and posterior (K) views. L-M: *Anguis* gr. *A. fragilis* (MDHC 49), left prootic in medial (L) and posterior (M) 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.

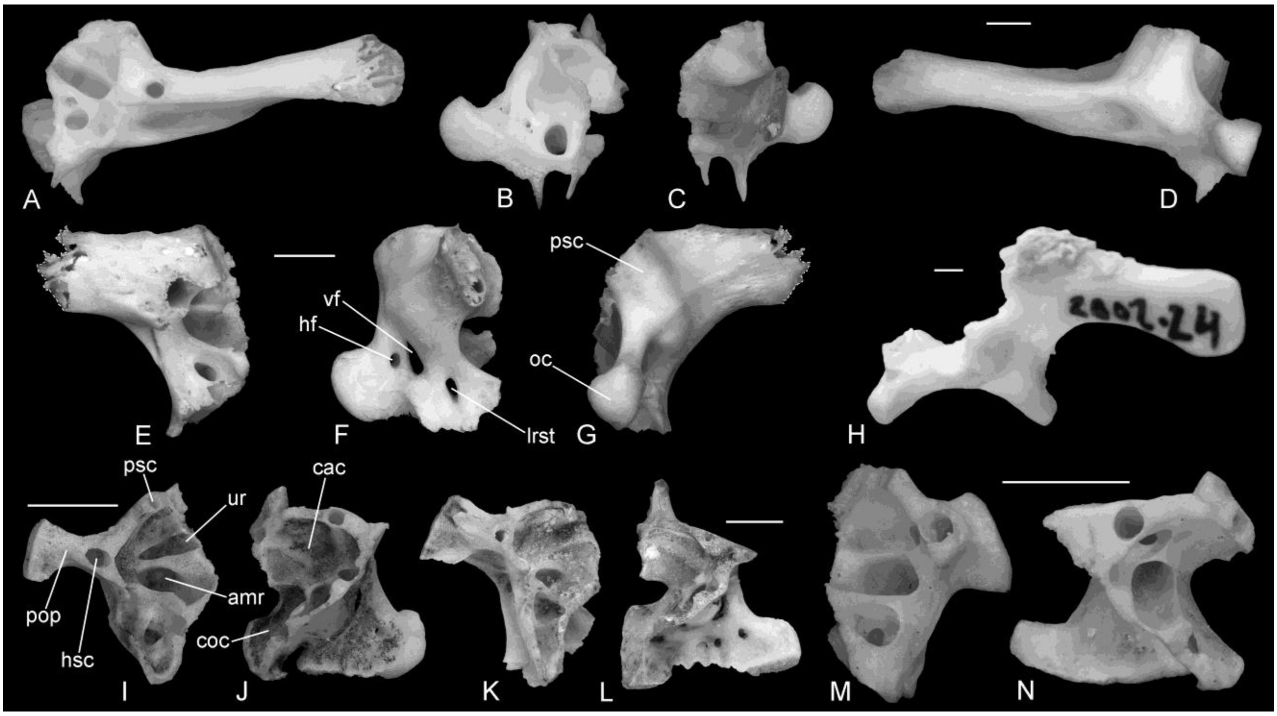

**Figure 41.** Otooccipitals - A-D: *L. stellio* (MDHC 245), left otooccipital in anterior (A), medial (B), lateral (C), and posterior (D) views. E-G: *C. chamaeleon* (HUJ.OST-Z-425), right otooccipital in anterior (E), lateral (F), and posterior (G) views (the distal portion of the paroccipital process is broken). H: *C. chamaeleon* (MNHN 2002-24), right otooccipital articulated with the basioccipital in posterior view. I-J: *P. muralis* (MDHC 312), right otooccipital in anterior (I) and medial (J) views. K-L: *T. aurata* (MDHC 280), right otooccipital in anterior (K) and medial (L) views. M-N: *Anguis* gr. *A. fragilis* (MDHC 49), left otooccipital in anterior (M) and medial (N) views. Abbreviations: amr, ampullary recess; cac, cavum capsularis; coc, cochlear cavity; 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; ur, utricular recess; vf, vagus foramen. Scale bars = 1 mm.

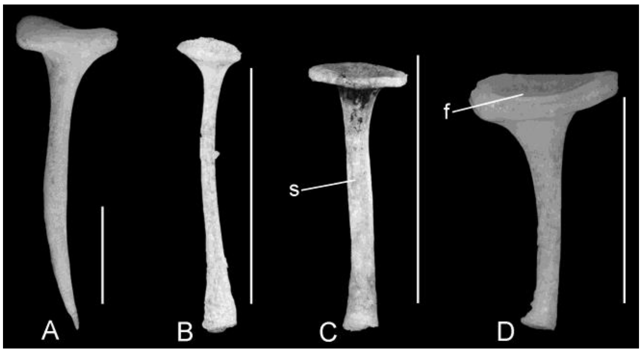

**Figure 42.** Stapes - A: *C. chamaeleon* (NHMW 611), stapes. B: *A. nigropunctatus* (MDHC 242), stapes. C: *C. chalcides* (MDHC 398), stapes. D: *Anguis* gr. *A. fragilis* (MDHC 102), stapes. Abbreviations: f, footplate; s, shaft. Scale bars = 1 mm.

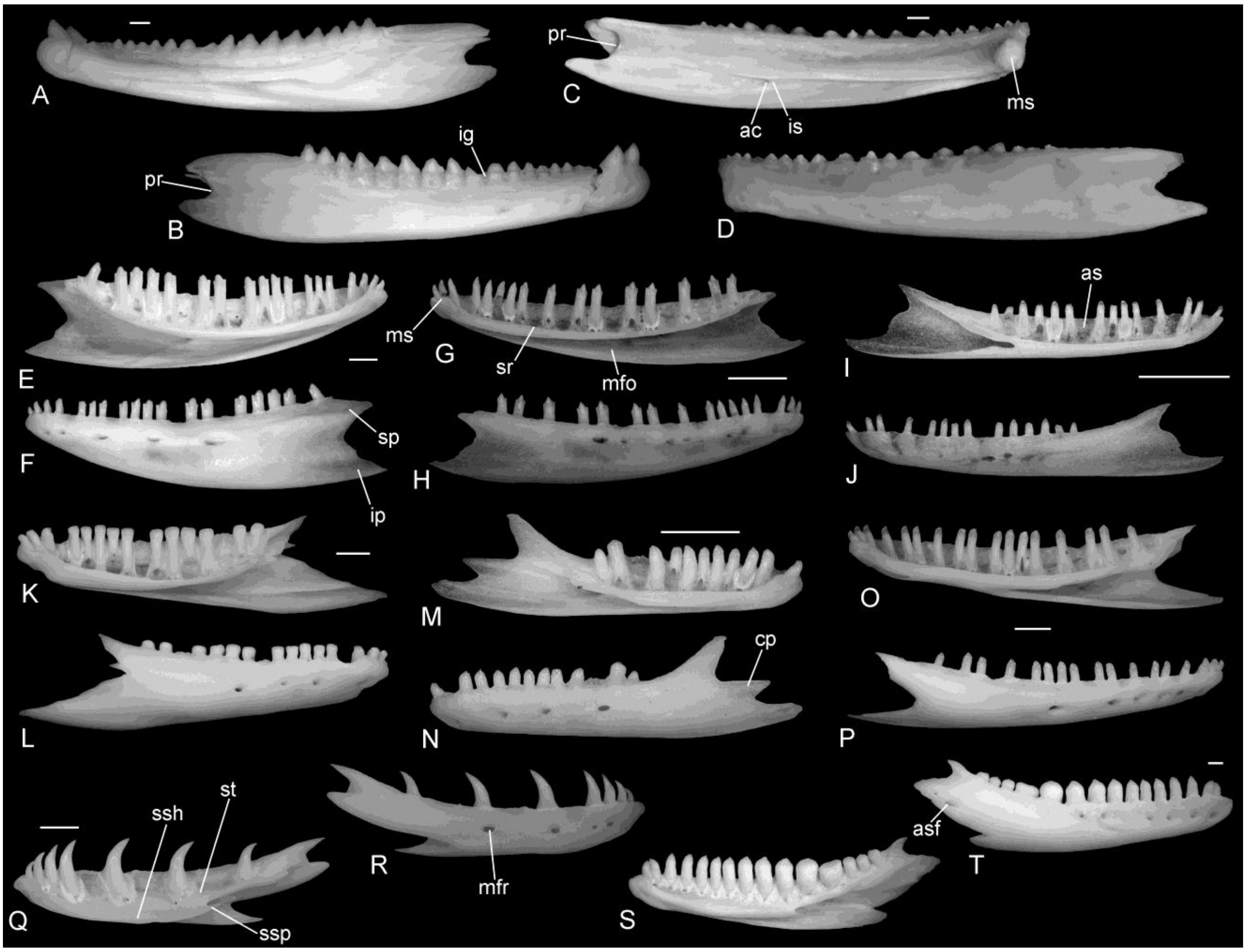

**Figure 43.** Dentaries - A-B: *L. stellio* (MDHC 245), right dentary in medial (A) and lateral (B) views. C-D: *C. chamaeleon* (NHMW 611), left dentary in medial (C) and lateral (D) views. E-F: *L.*

*bilineata* (MDHC 84), left dentary in medial (E) and lateral (F) views. G-H: *Z. vivipara* (MDHC 179), right dentary in medial (G) and lateral (H) views. I-J: *A. kitaibelii* (MDHC 239), left dentary in medial (I) and lateral (J) views. K-L: *C. ocellatus* (MDHC 250), right dentary in medial (K) and lateral (L) views. M-N: *O. punctatissimus* (MDHC 427), left dentary in medial (M) and lateral (N) views. O-P: *T. aurata* (MDHC 280), right dentary in medial (O) and lateral (P) views. Q-R: *Anguis* gr. *A. fragilis* (MDHC 102), right dentary in medial (Q) and lateral (R) views. S-T: *P. apodus* (MDHC 214), right dentary in medial (S) and lateral (T) 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; st, subdental table. Scale bars = 1 mm.

**Figure 44.** 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.

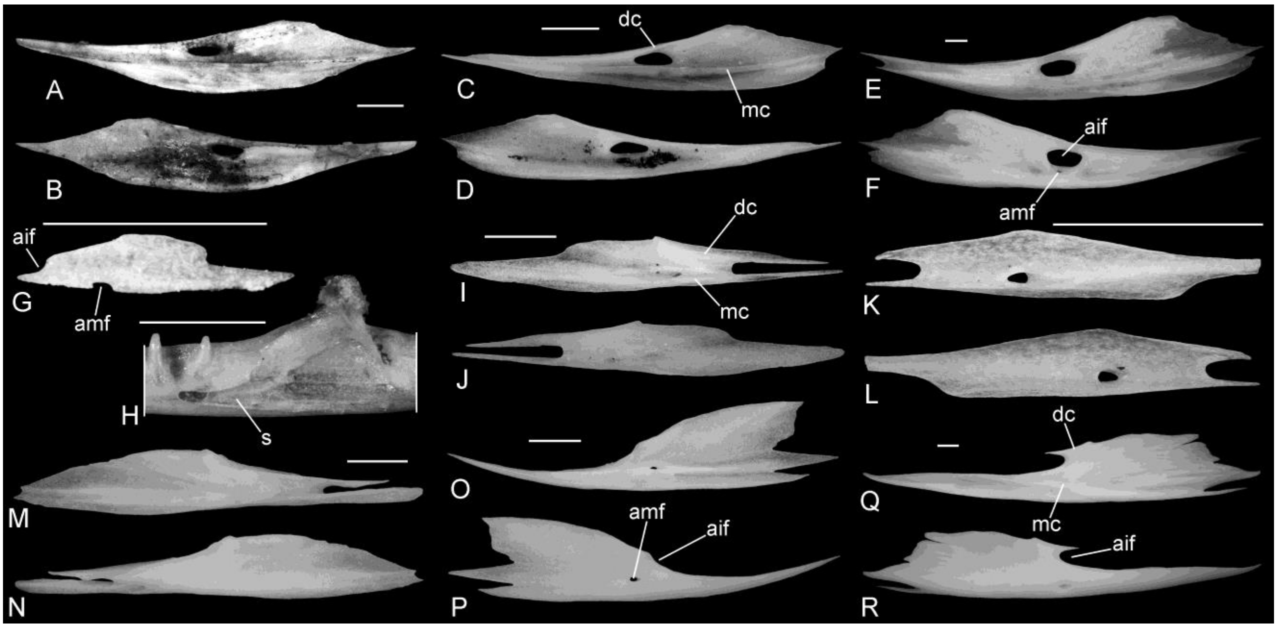

**Figure 45.** Splenials - A-B: *A. erythrurus* (UAM.R.ACVII), left splenial in lateral (A) and medial (B) views. C-D: *P. tauricus* (MDHC 153), left splenial in lateral (C) and medial (D) views. E-F: *T. lepidus* (MDHC 216), left splenial in lateral (E) and medial (F) views. G: *A. kitaibelii* (NHMW 751b), right splenial in medial view. H: *A. kitaibelii* (NHMW 751a), articulated right splenial in medial view. I-J: *C. chalcides* (MDHC 398), right splenial in lateral (I) and medial (J) views. K-L: *O. punctatissimus* (MDHC 427), left splenial in lateral (K) and medial (L) views. M-N: *T. aurata* (MDHC 280), right splenial in lateral (M) and medial (N) views. O-P: *Anguis* gr. *A. fragilis* (MDHC 102), left splenial in lateral (O) and medial (P) views. Q-R: *P. apodus* (MDHC 215), left splenial in lateral (Q) and medial (R) views. Abbreviations: aif, anterior inferior foramen; amf, anterior mylohyoid foramen; dc, dorsal crest; mc, medial crest; s, splenial. Scale bars = 1 mm.

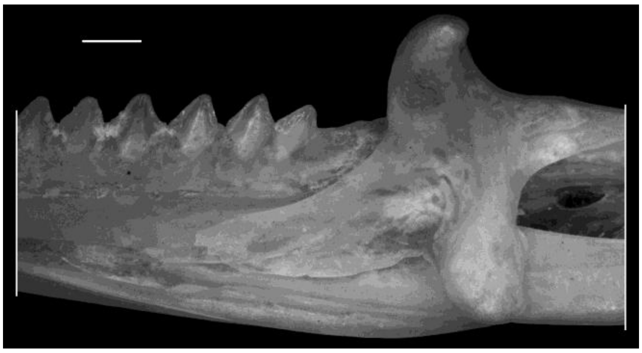

**Figure 46.** Median portion of the right lower jaw of *L. stellio* (HUJ.OST-Z-5) in medial view, showing the absence of the splenial. Scale bar = 1 mm.

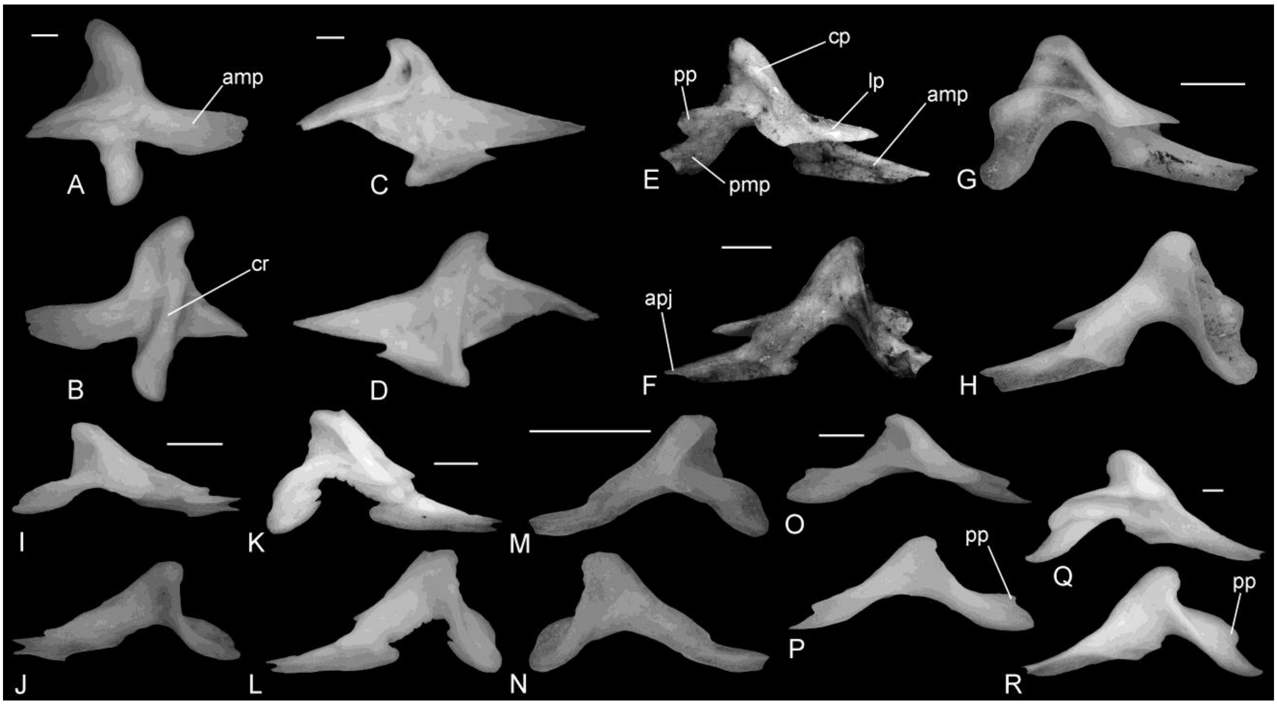

**Figure 47.** Coronoids - A-B: *L. stellio* (MDHC 245), right coronoid in lateral (A) and medial (B) views. C-D: *C. chamaeleon* (NHMW 611), right coronoid in lateral (C) and medial (D) views. E-F: *A. erythrurus* (UAM.R.ACVII), right coronoid in lateral (E) and medial (F) views. G-H: *P. muralis* (MDHC 311), right coronoid in lateral (G) and medial (H) views. I-J: *C. chalcides* (MDHC 398), right coronoid in lateral (I) and medial (J) views. K-L: *C. ocellatus* (MDHC 250), right coronoid in lateral (K) and medial (L) views. M-N: *O. punctatissimus* (MDHC 427), left coronoid in lateral (M) and medial (N) views. O-P: *Anguis* gr. *A. fragilis* (MDHC 102), right coronoid in lateral (O) and medial (P) views. Q-R: *P. apodus* (MDHC 214), right coronoid in lateral (Q) and medial (R) views. Abbreviations: amp, anteromedial process; apj, anterior projection of the anteromedial process; cp, coronoid process; cr, coronoid ridge; lp, labial process; pmp, posteromedial process; pp, posterior process. Scale bars = 1 mm.

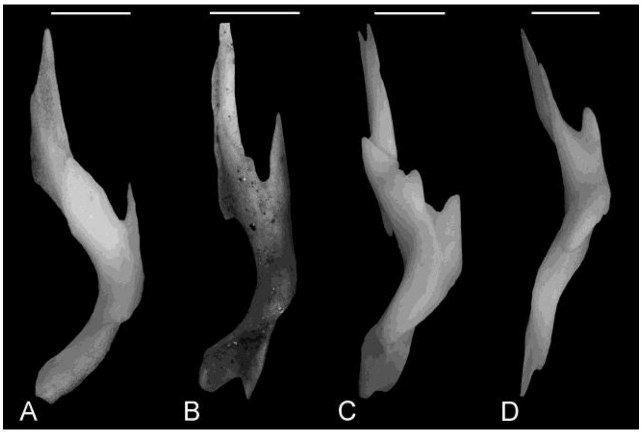

**Figure 48.** Coronoids of *Tarentola mauritanica* (MDHC 302; A), *I. monticola cantabrica* (UAM.R.Lm92; B), *C. ocellatus* (MDHC 250; C) and *Anguis* gr. *A. fragilis* (MDHC 102; D) in dorsal view, showing the difference in the degree of medial concavity of the bones. Scale bars = 1 mm.

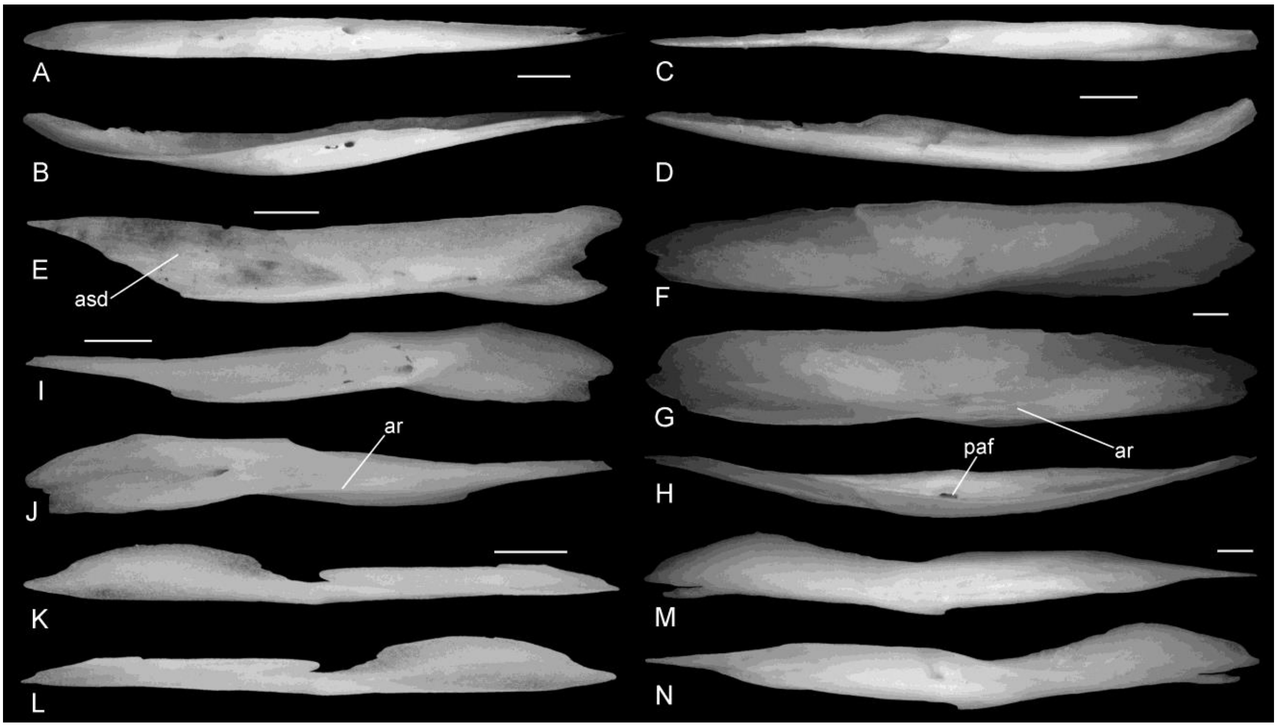

**Figure 49.** Angulars - A-B: *L. stellio* (HUJ.OST-Z-423), left angular in dorsal (A) and medial (B) views. C-D: *C. chamaeleon* (HUJ.OST-Z-425), right angular in dorsal (C) and medial (B) views. E: *P. algirus* (UAM.R.Ps9), left angular in lateral view. F-H: *T. lepidus* (MDHC 216), left angular in 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.

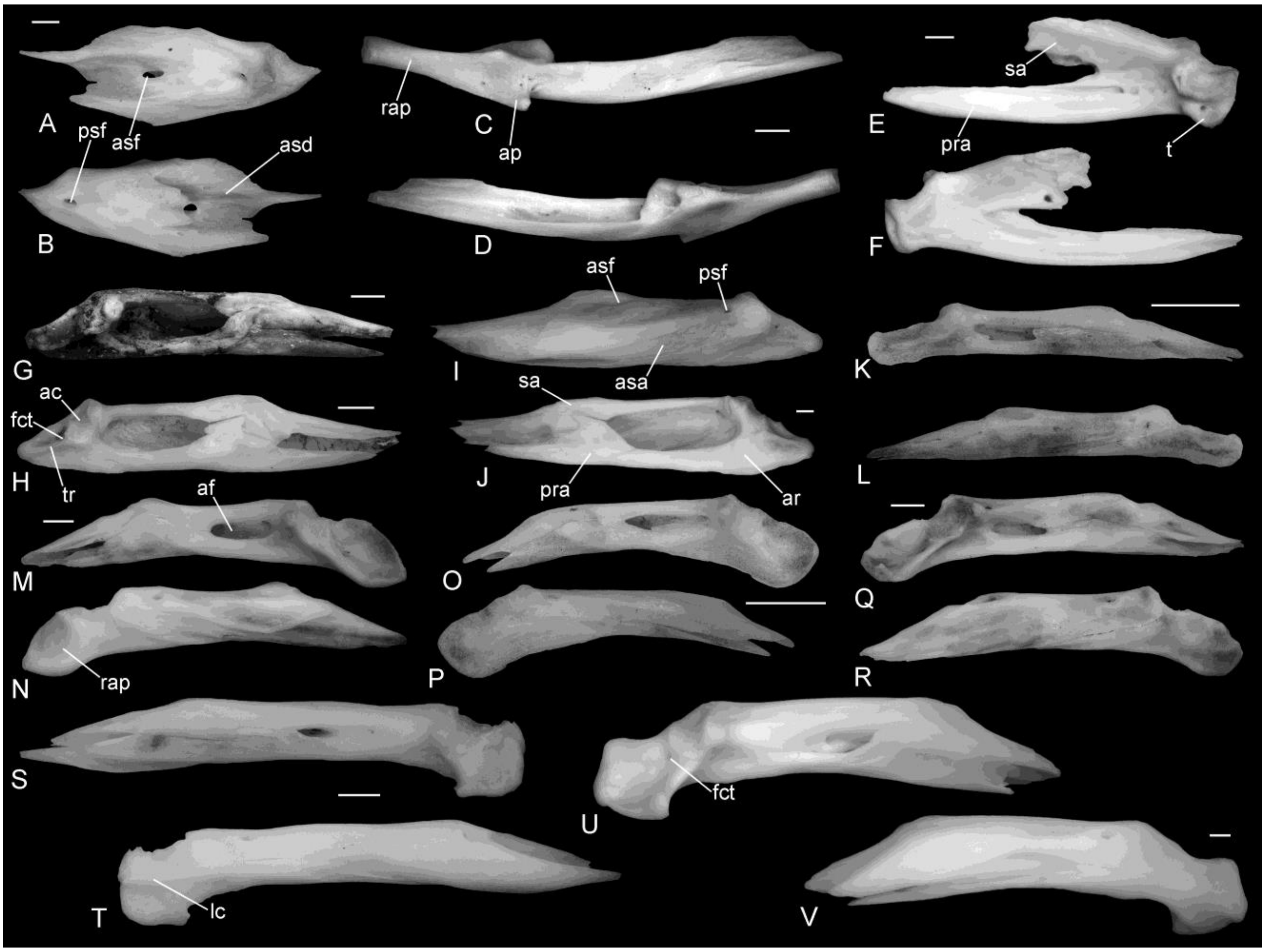

**Figure 50.** Compound bones - A-B: *L. stellio* (MDHC 245), right surangular in medial (A) and lateral (B) views. C-D: *L. stellio* (HUJ.OST-Z-424), fused left prearticular and articular in medial (C) and lateral (D) views. E-F: *C. chamaeleon* (NHMW 611), right compound bone in medial (E) and lateral (F) views. G: *A. erythrurus* (UAM.R.ACVII), left compound bone in medial view. H-I: *L. agilis* (MDHC 176), left compound bone in medial (H) and lateral (I) views. J: *L. viridis* (MRAC 91-077-R-76), right compound bone in medial view. K-L: *A. kitaibelii* (MDHC 239), left compound bone in medial (K) and lateral (L) views. M-N: *C. ocellatus* (MDHC 250), right compound bone in medial (M) and lateral (N) views. O-P: *O. punctatissimus* (MDHC 427), right compound bone in medial (O) and lateral (P) views. Q-R: *T. aurata* (MDHC 280), left compound bone in medial (Q)

and lateral (R) views. S-T: *Anguis* gr. *A. fragilis* (MDHC 102), right compound bone in medial (S) and lateral (T) views. U-V: *P. apodus* (MDHC 214), left compound bone in medial (U) and lateral (V) views. 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.

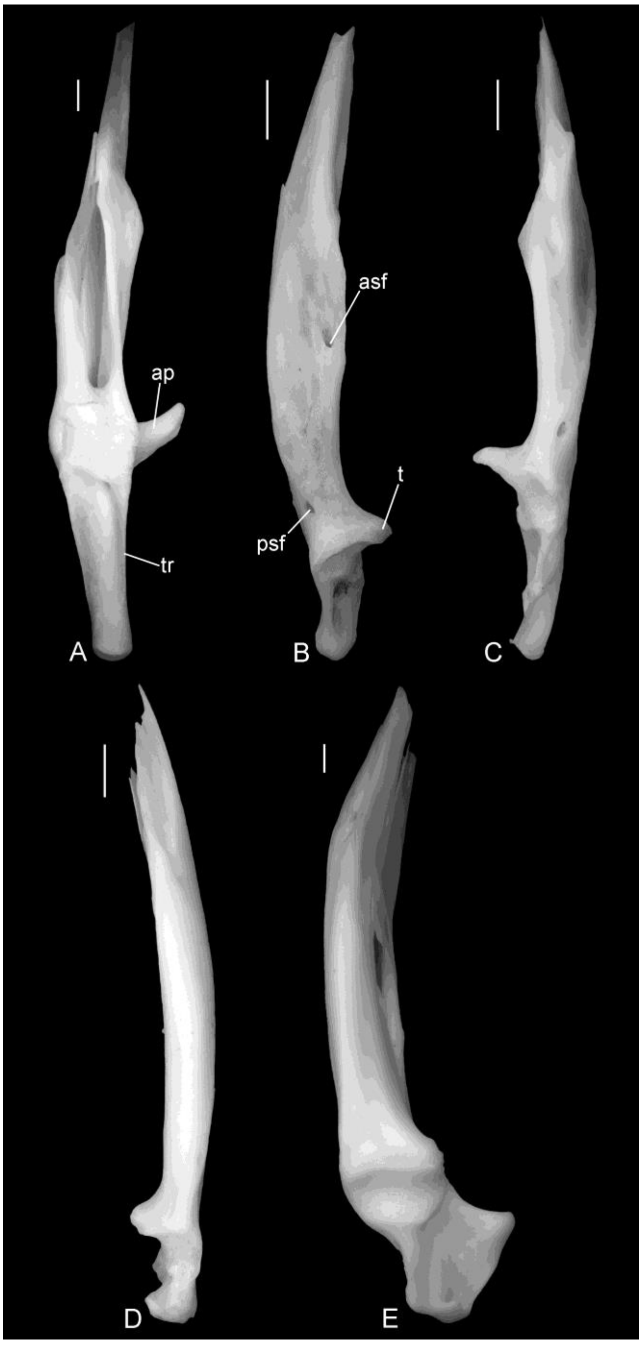

**Figure 51.** Compound bones (continues) - A: *L. stellio* (MDHC 245), left compound bone in dorsal view. B: *L. agilis* (MDHC 176), left compound bone in dorsal view. C: *C. ocellatus* (MDHC 250), right compound bone in dorsal view. D: *Anguis* gr. *A. fragilis* (MDHC 102), right compound bone in dorsal view. E: *P. apodus* (MDHC 214), left compound bone in dorsal view. Abbreviations: ap, angular process; asf, anterior surangular foramen; psf, posterior surangular foramen; t, tubercle; tr, tympanic ridge. Scale bars = 1 mm.

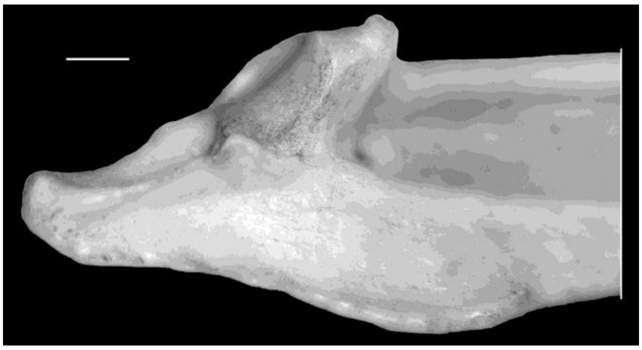

**Figure 52.** Posterior end of the left compound bone of *L. viridis* NHMW 663 in medial view, showing the strong expansion of the ventral margin. Scale bar = 1 mm.