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University of Fribourg (Switzerland)

# Fossil Reptiles from the Aegean Region

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# Table of Contents

**Appendix 1**

**Appendix 2**

**Appendix 3**

**Appendix 4**

**Appendix 5**

**Appendix 6**

**Appendix 7**

**Appendix 8**

**Appendix 9**

**Appendix 10**

**Appendix 11**

## Summary

Although fossil reptiles can offer valuable insights into several fields of the geosciences and biological sciences, the palaeoherpetofaunas of many regions remain virtually unexplored. The Aegean Region (comprised of Greece and western and central Turkey) is one of these areas, although it is situated at a geographic meeting point, at the boundaries of southeastern Europe with southwestern Asia and Africa. Fossil reptiles from the area were first described during the 1850's and important discoveries were subsequently made during the course of the 19th and 20th centuries. The history of discoveries of fossil reptiles from the Aegean Region is herein presented in detail. All previously named taxa are revised and their taxonomic status is evaluated. New finds from several Neogene and Quaternary localities from Greece and Turkey are described. Some reptile clades are recorded for the first time from the region, whereas the geographic and stratigraphic distributions of others significantly expanded. Fossil reptiles from the area provide important implications into biogeography and biostratigraphy, the evolution of modern taxa, taxonomy, faunal turnover and extinction, and palaeoenvironmental reconstructions.

## Zusammenfassung

Obwohlfossile Reptilien wertvolle Einblicke in mehrere Teilbereiche der Geowissenschaften und Biowissenschaften bieten können, verbleibenviele paläoherpetologische Faunen noch unerforscht. Die Ägäisregion (bestehend aus Griechenland und der West- und der Zentraltürkei) ist einer dieser Gebiete, obwohl sie an einem geografischen Treffpunkt liegt, an den Grenzen Südosteuropas mit Südwestasien und Afrika. Fossile Reptilien aus dieser Gegend wurden erstmals in den 1850er Jahren beschrieben und einige wichtige Entdeckungen wurden seitdem im Laufe des 19. und 20. Jahrhunderts gemacht. Die Entdeckungsgeschichte der fossilen Reptilien aus der Ägäis wird hier detailliert dargestellt. Alle zuvor benannten Taxa werden überarbeitet und ihr taxonomischer Status wird ausgewertet. Neue Funde aus mehreren neogenen und quartären Fundorten aus Griechenland und der Türkei werden beschrieben. Diverse neue Reptiliengruppen werdenzuersten Mal in der Region dokumentiert und die geographischen und stratigraphischen anderer Gruppen signifikant erweitert. Fossile Reptilien aus der Region liefern wichtige Hinweise für die Biogeographie und Biostratigraphie, die Evolution moderner Taxa, Taxonomie, Faunenwechsel und -sterben sowie Paläoumwelt-Rekonstruktionen.

# Introduction

> "*Yet, as the strange and gigantic Reptiles that have been restored, and, as it were, called again to life, from times vastly more ancient, realise in some measure the fabulous dragons of mediaeval romance*"
> (Richard Owen 1850:68).

## General Background

Besides the obvious attraction to palaeoherpetologists and many times also to the general audience, fossil reptile remains have long played an important role in understanding and estimating various geological phenomena, geographical transformations, ecological and palaeoenvironmental perturbations, stratigraphic correlations, biogeographic origins, and, of course, the evolution, and origin of extant taxa. In fact, certain cases of what appear to constitute "common knowledge" in geology were envisaged and supported by fossil reptile finds. Among the most characteristic of these cases is the identification of continental drift, as strong evidence for this phenomenon was first provided by the recovery of fossil finds of the Permian reptile *Mesosaurus tenuidens* Gervais, 1864–1866 in coeval strata in southern Africa and South America (Wegener 1912). The geological importance of fossil reptiles is also supported by the fact that many genera and species are known to pertain solely to specific time intervals, with their fossils often denoting more accurate ages than coeval and syntopic mammal taxa. As such, they are quintessential for biostratigraphy and on many occasions, the only means for deciphering exact geological ages, providing, however, that their alpha-level taxonomy has already been well resolved (e.g., Hutchison 1980; Rage 1983; Schleich 1985; Rage and Szyndlar 1986). Additionally, presence of related or even congeneric reptile taxa across different continents can imply the existence of land corridors which enabled dispersals of animals from one land mass to the other, providing thus important clues for palaeogeographic reconstruction through time. For example, the identification of closely related reptile taxa in the Paleogene of both North America and Western Europe provides substantial evidence for the emergence of a land corridor(s) and subsequent dispersal events between the two land masses, as this has been independently suggested on the basis of distant groups, such as pan-trionychids (Georgalis and Joyce 2017 [**Appendix 1**]), glyptosaurines (Sullivan 1979; Augé 2005), iguanids (Smith 2009), varanids (Augé 2005; Rage 2013), and amphisbaenians (Augé 2012). All such data extracted from reptile finds are crucial for the comprehension of the biogeographic origins of extant clades. The ability of certain terrestrial reptile groups to survive marine transport over large distances and eventually disperse and colonize islands has yielded insight for the evolution of modern insular faunas (e.g., Pregill and Steadman 2004; Zug et al. 2011). Moreover, the ectothermic nature and physiology of most reptiles render several clades as rather accurate and reliable indicators of palaeoclimatic reconstructions and this fact has been applied to estimate palaeotemperatures (e.g., Böhme 2003, 2010; Head et al. 2009; Blain et al. 2014). Ecological alterations, faunal turnovers, and extinction events, such as the K/Pg extinction event that wiped out the dinosaurs, have been also supported by fossil reptile finds (e.g., Lyson et al. 2011; Longrich et al. 2012). Study of fossil reptiles also enhances the understanding of palaeoecological and palaeoenvironmental responses of faunal ecosystems after severe extinction events. Characteristically, the so called "Grande Coupure," an extinction event that took place at the Eocene/Oligocene transition and long suggested to have extirpated several mammal clades (Stehlin 1909; Hooker et al. 2004), is now known to have had a significantly different impact on reptiles (Rage 1984a, 2006, 2013; Augé 2005), challenging the severity of that event on each clade and the explanations around its mechanisms (Augé and Smith 2009). Additionally, estimation of divergence dates of extant reptile clades can only be safely calibrated through fossil specimens attributed to the respective groups (e.g., Joyce et al. 2013; Head 2015; Head et al. 2016). Finally, in the case of the medicinally important venomous reptiles, such as elapid and viperid snakes, their identification in the fossil record, and especially of their venom delivery apparatus (i.e., maxillary) can imply significant clues about the evolution of this predatory strategy (Kuch et al. 2006).

Despite this obvious importance of fossil reptiles for evolutionary studies, many gaps still exist. Among "terrae incognitae" for fossil reptiles, is the Aegean region. For simplicity and convenience purposes, the Aegean region is herein defined as being comprised of Greece, European part of Turkey, and western and central Anatolia in Turkey (*Figure 1*). Therefore, as this region does not encompass the whole of Anatolia, but only the western and central parts of that peninsula, important finds such as a booid snake from the Oligo-Miocene of eastern Anatolia (Szyndlar and Hoşgör 2012) are here not taken into consideration. The same applies also for certain important reptile finds from the southern Balkans that originate from the adjacent countries northern of Greece and Turkey. These include the types of the pan-trionychid turtle *Trionyx capellinii bulgaricus* Khosatzky et al., 1983 from the late Eocene of Bulgaria, the crocodylian *Diplocynodon levantinicum* Huene and Nikoloff, 1963 from the Miocene or Pliocene of Bulgaria, and the pan-testudinoid turtle *Temnoclemmys mazedonica* Pašić and Klinčarski, 1959, from the late Eocene of the Former Yugoslav Republic of Macedonia. Furthermore, there are also few, sporadic, but nevertheless important Mesozoic records of reptiles from Turkey, that lie geographically within the herein studied area, but considering that the all other material in this paper are of post-Eocene age, they will thus not be taken into further consideration. These include a mosasaurid from the Late Cretaceous of Beyler Dam, near Kastamonu in central Anatolia (Bardet and Tunoğlu 2002), fragments of a phytosaur from the Triassic of the Lycian Taurus in southern Anatolia (Buffetaut et al. 1988),

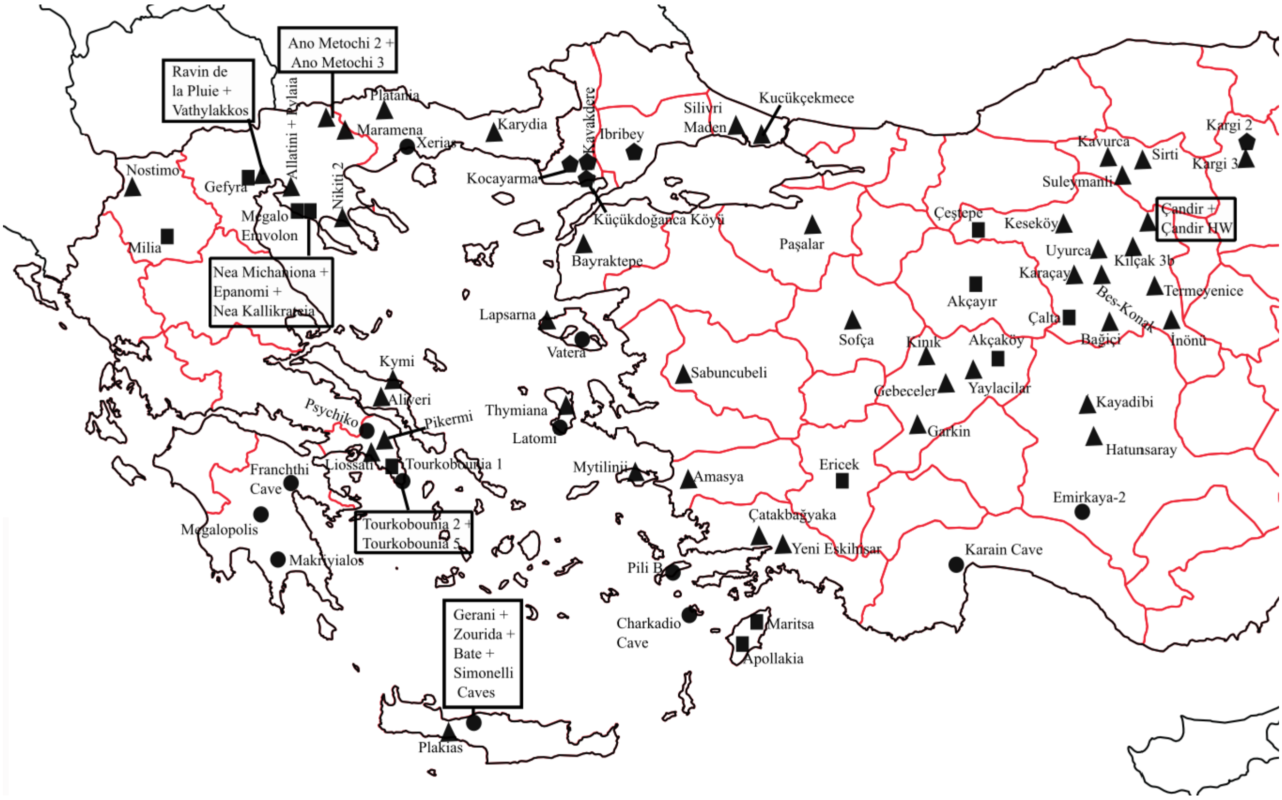

**Figure 1.** Map of the Aegean region, indicating the localities that have yielded fossil reptiles. See Appendix II for ages and reptile taxa of all localities. Pentagones represent Oligocene, triangles Miocene, squares Pliocene, and circles Quaternary localities. The locality of Korydallos, near Athens, is omitted as its age is not determined.

and the newly described crocodyliform *Turcosuchus okani* Jouve et al., 2017, from the early Cretaceous of Zonguldak near the Black Sea. In total, 85 localities from the Aegean region have so far yielded fossil reptile remains (see Appendix II for full details about their names, exact ages, and taxa). Few of these localities are of Oligocene age and the rest pertain to the Miocene, Pliocene, and Quaternary, with the Miocene ones representing the vast majority (*Figure 2*). Note that I am taking into consideration only material that has been formally published and includes descriptions, figures, or at least precise repository numbers. Preliminary mentions without any descriptions or figures that can be reevaluated, as well as abstracts, unpublished theses, or reports are herein omitted.

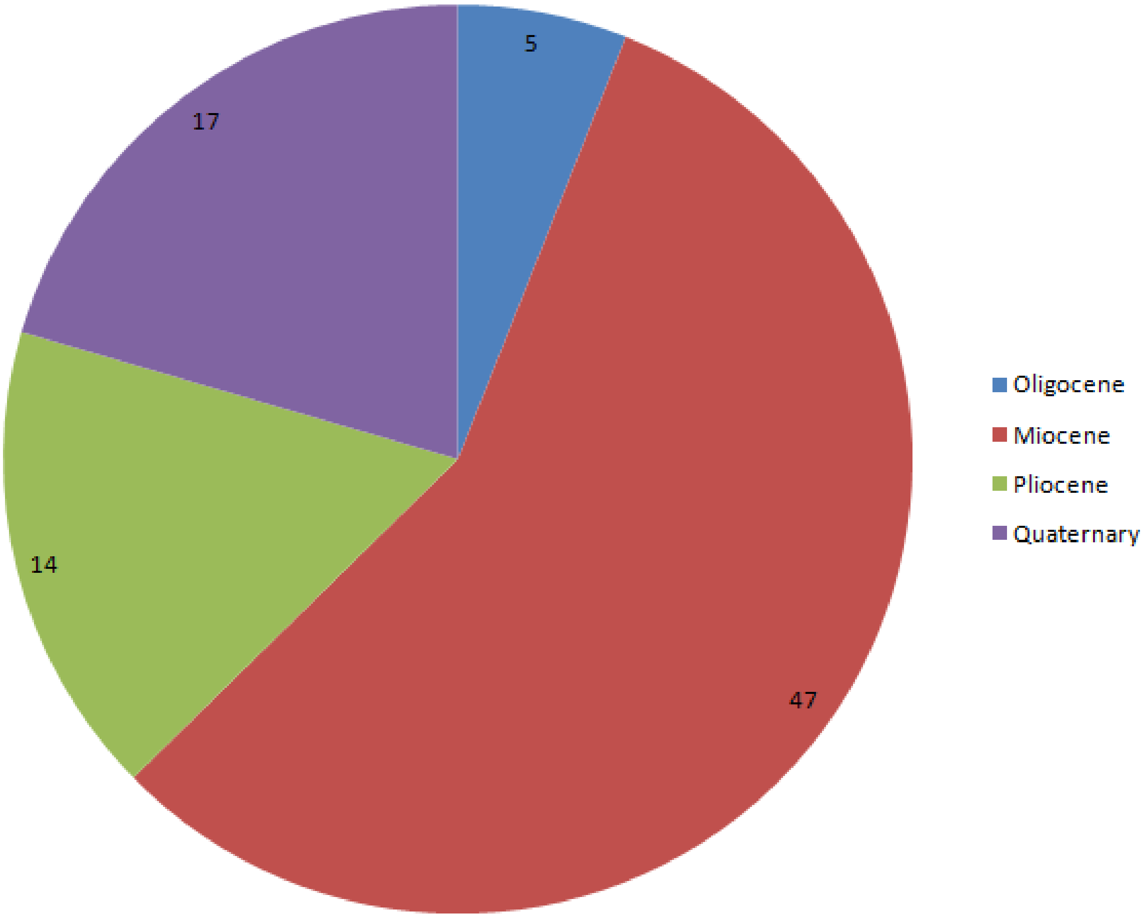

**Figure 2.** Pie chart indicating the numbers of fossil reptile bearing localities from the Aegean region per age. The locality of Korydallos and the unknown type locality of *Testudo sloanei* are not included in the graph, as their ages are not accurately known.

*Abbreviations*: AMNH, American Museum of Natural History, New York, USA; AMPG; Athens Museum of Palaeontology and Geology, University of Athens, Athens, Greece; BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; GR, Greece; IPUW, Institut für Paläontologie, University of Vienna, Vienna, Austria; LGPUT, Laboratory of Geology and Palaeontology, University of Thessaloniki, Thessaloniki, Greece; Ma, million years ago; MN, Mammifères Neogène (standard level zone); MNHN, Muséum national d'Histoire naturelle, Paris, France; MP, Mammifères Paléogène (standard level zone); NHMUK, Natural History Museum, London, United Kingdom; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMP, Nostimo Museum of Palaeontology, Nostimo Kastorias, Greece; TR, Turkey.

## Palaeogeographic reconstruction of the Aegean region throughout the Cenozoic

The Aegean region, situated at the boundaries of southeastern Europe with southwestern Asia and Africa, is a geographically complex and constantly changing area with new emerging landmasses, sea level fluctuations, and island formations (*Figure 3*). The exact palaeogeography of the Aegean region is rather poorly known for the Paleogene, with different suggestions and reconstructions proposed in different studies (e.g., Dermitzakis and Papanikolaou 1981; Rögl 1999; Meulenkamp and Sissingh 2003; Popov et al. 2004; Tranos et al. 2010; Kilias et al. 2013), especially for the earlier parts of this epoch. Paleocene and early Eocene fossil vertebrates from the region are rather poorly known (Sen 2013). A relatively clearer, though still inadequate, view emerges for the middle Eocene, where it seems that a large part of Anatolia was an isolated island (the Anatolian Land; Popov et al. 2004), as is supported by insular mammal faunas from Central Anatolia (Maas et al. 2001; Maaga and Beck 2017). During the middle and late Eocene, the southeastern Balkans were part of another large island, the Rhodope High (Popov et al. 2004), a fact demonstrated by geological data (Zagorchev 1998) and large mammal finds from northeastern Greece (Métais and Sen 2017). This situation is also concordant with the Eocene palaeogeography of the rest of Europe, which at that time consisted also an Archipelago of large and small islands (Rögl 1999). Also, the Mesohellenic Trough occuring in northwestern Greece from the middle Eocene up to the middle Miocene (Kilias et al. 2013) provided additional evidence for the existence of another emerging landmass in the area, the so called Pindos Cordillera (Dermitzakis and Papanikolaou 1981; Tranos et al. 2010), though its possible connection(s) with the Rhodope High is not known. In any case, possible land connections that may have appeared between the Eocene islands of Anatolia and Rhodope are difficult to evaluate on the basis of current evidence (Métais and Sen 2017). During the Oligocene, large parts of Europe and Western Asia were covered by the epicontinental Paratethys sea (Rögl 1999). Fluctuations in the sea levels of the Paratethys and the Western Tethys across the Oligocene drastically altered the shape, landscape, and overall geography of the southern Balkan and western Anatolian land masses. However, the scarceness of geological studies and fossil remains hinder an exact comprehension of Oligocene land masses in the Aegean region (Popov et al. 2004). The palaeogeographical understanding of the region appears significantly better for the Neogene. During the early Miocene, a large and continuous landmass, called Ägäis, was present, spanning from western Greece to Anatolia (Lymberakis and Poulakakis 2010) (*Figure 3*). Ägäis was in fact only part of a vast land corridor, which ranged from Central Europe to Anatolia (Meulenkamp and Sissingh 2003). The emergence of Ägäis was likely the result of a combination of the movements of the African plate and the Anatolian subplate, along with intense tectonic and volcanic activity (Lymberakis and Poulakakis 2010; Poulakakis et al. 2015). Ägäis persisted in the area also during the middle Miocene, although achieving a relatively smaller surface, especially at its Anatolian part. By the late middle Miocene (Serravallian), a sea barrier, known as the mid-Aegean Trench, began to gradually split the formerly continuous landmass of Ägäis (Dermitzakis and Papanikolaou 1981; Lymberakis and Poulakakis 2010; Poulakakis et al. 2015). The mid-Aegean Trench commenced at around 12 Ma, with a breakage at the southern edge of Ägäis, between Crete and the area of modern Kasos and Karpathos islands, resulting into the full isolation of Crete. The so-called Tortonian Transgression (11–9 Ma) divided the Aegean region into two (eastern and western) parts (Rogl 1999; Lymberakis and Poulakakis 2010; Poulakakis et al. 2015). However, during the end phase of the Messinian Salinity Crisis event, which occurred

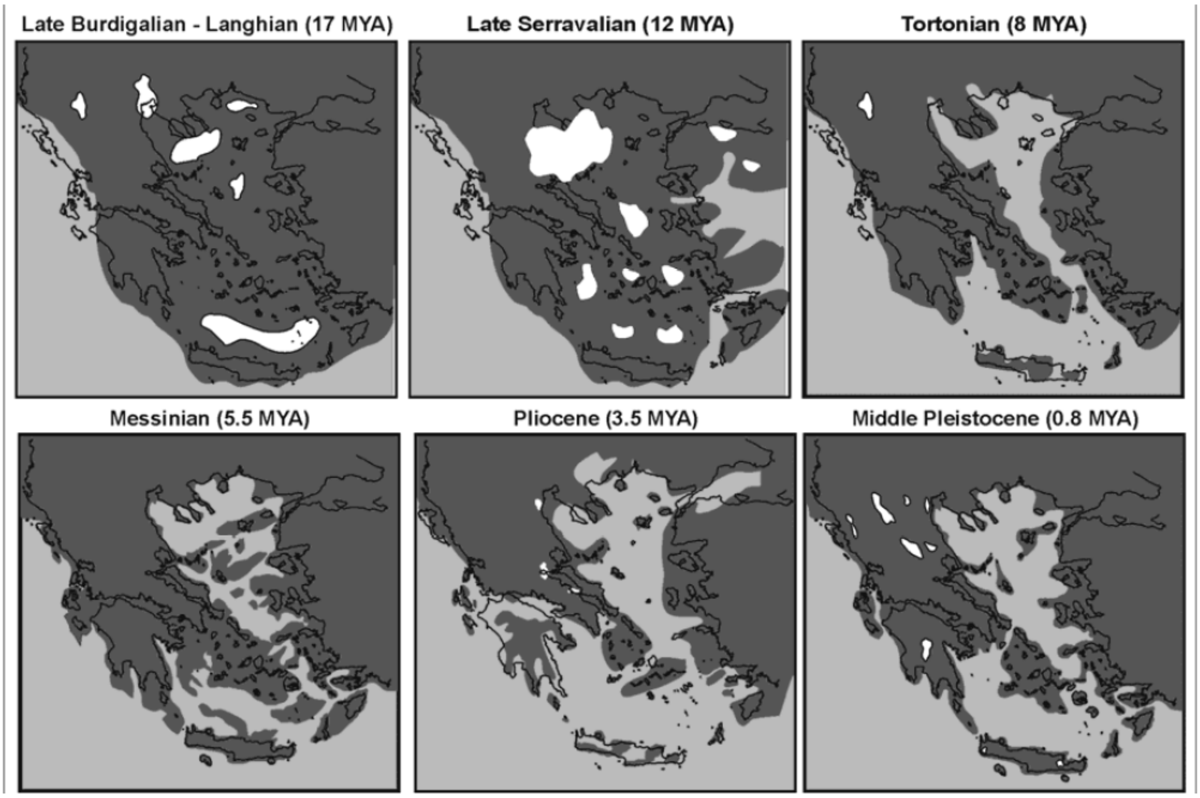

**Figure 3.** Palaeogeographic reconstructions of the Aegean Region during the Neogene and Quaternary. Maps adapted from Lymberakis and Poulakakis (2010). Dark grey and light grey colours indicate landmass and sea respectively, white colour indicates lakes.

at the latest Miocene, around 5.96–5.33 Ma, the Mediterranean Sea was dried up significantly due to the closure of the Gibraltar Straights at the west and its isolation from the Atlantic Ocean (Hsü 1972; Krijgsman et al. 1999). As such, several areas in the Aegean region that formerly formed a marine environment, were now transformed into extensive saline deserts interspersed with saline/hypersaline lakes (Poulakakis et al. 2015). At that time, Crete temporarily lost its isolation and insular nature by being united to southern mainland Greece. However, the reopening of the Gibraltar straights by the end of the Messinian Salinity Crisis, refilled the Mediterranean with water and permanently isolated Crete from the mainland, a situation persisting until today (Lymberakis and Poulakakis 2010; Poulakakis et al. 2015). During the Pliocene, the rising sea levels submerged several parts of Greece under water, including parts of the Peloponnese, Kythira Island, and most of Crete, whereas the Cyclades Islands were still forming a single landmass which was probably united with the mainland. Kasos and Karpathos were now isolated from Rhodes and Asia Minor (Lymberakis and Poulakakis 2010). During the culmination of the Pleistocene Glacial events, sea level fell by around 200 m (Beerli et al. 1996). Several of the Cyclades Islands were still united together with each other and many of the eastern Aegean Islands were still united with Asia Minor. Indeed, many of the Aegean Islands were only isolated from each other or adjacent mainland during the latest Pleistocene or even later (Sfenthourakis and Triantis 2017). The recent geographic image of the region is therefore extremely young.

### *History of discoveries*

The first description of fossil reptiles from the Aegean region dates back to the middle of the 19th century, with the original publication of the large snake *Laophis crotaloides* from the Pliocene of vicinity of Thessaloniki (Central Macedonia) by Owen (1857). Other scarce, but nevertheless important discoveries were subsequently made during the course of the 19th centrury, including the establishment of new "key" taxa (Gaudry 1862a, 1862–1867; Römer 1870; Weithofer 1888) (*Figure 4*). The situation was similar at the beginning of the 20th century, with few palaeoherpetological studies conducted in the area, though still important finds were described (e.g., Arambourg and Piveteau 1929; Szalai 1931). The second half of the 20th century witnessed a larger number of publications focusing on fossil reptiles from the Aegean region, however, the majority of the described material was rather fragmentary or only poorly documented (Paraskevaidis 1955; Bachmayer 1967; Bachmayer and Symeonidis 1970, 1976; Schneider 1975; Rage and Sen 1976; Szyndlar and Zerova 1990; Szyndlar 1995).

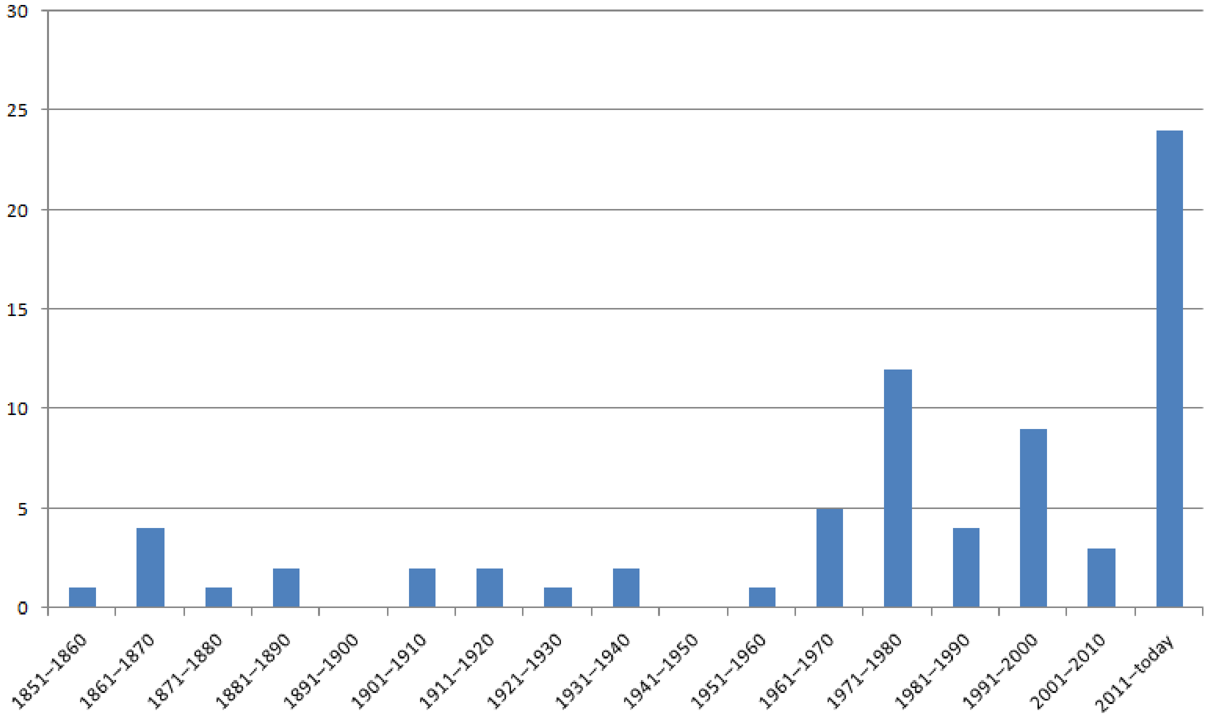

**Figure 4.** Number of publications describing and/or dealing with fossil reptiles from the Aegean region (1857–today) per decade. See Appendix I for a complete list of the papers.

The situation contrasts with the beginning of the 21st century. While there are only three studies on fossil reptiles from the region between 2001 and 2010 (Lapparent de Broin 2002; Lyras and Van der Geer 2007; Staesche et al. 2007), this number drastically increased since 2011 until today (Mueller-Töwe et al. 2011; Tsoukala et al. 2011; Conrad et al. 2012; Georgalis et al. 2013; Georgalis and Kear 2013; Vlachos and Tsoukala 2014, 2016; Vlachos et al. 2014, 2015a, 2015b; Hoek Ostende et al. 2015; Garcia et al. 2016; Georgalis et al. 2016a [**Appendix 4**], 2016b [**Appendix 5**], 2016c [**Appendix 6**], 2017a [**Appendix 7**], 2017b [**Appendix 8**], 2018a [**Appendix 9**], 2018b [**Appendix 10**], 2018c [**Appendix 11**]; Vlachos and Delfino 2016; Čerňanský et al. 2017; Sen et al. 2017; Vasileiadou et al. 2017), leading to a much better understanding of fossil Aegean herpetofaunas and their taxonomic diversity.

*Turtles*

Gaudry (1862a, 1862b, 1862–1867) made the first fossil turtle contribution from the Aegean region by describing and figuring his new testudinid species *Testudo marmorum* Gaudry, 1862a from the late Miocene of Pikermi, near Athens. Calvert and Neumayr (1880) mentioned the presence of *Emys* and *Trionyx* from the Neogene of the Hellespont (= Dardanelles) without, however, providing any figure or other information. Lydekker (1889) established his new taxon *Testudo sloanei* on the basis of an incomplete shell from Turkey, however, he neither provided figures of the material nor exact locality data. Woodward (1901) reported the presence of giant testudinid remains from Pikermi, but once again failed to provide figures or any further information that could verify his claim. Campana (1917, 1919) described a testudinid from the Neogene of Thessaloniki, which he referred to the Italian species *Testudo amiatae* Pantanelli, 1893, and also eggs that he assigned to a giant tortoise. Arambourg and Piveteau (1929) described testudinid remains from the Neogene of the Thessaloniki area. Among their finds, remains of a giant tortoise, including a relatively well preserved cranium, for which Arambourg and Piveteau (1929) suggested possible affinities with the French taxon *Testudo perpiniana* Depéret, 1885, and additionally a second, smaller form, which was though never figured. Taking the giant tortoise research one step further, Szalai (1931) described a gigantic tortoise from late Miocene (formerly thought to be Pliocene) of Samos Island, represented by a relatively complete cranium and a femur. In order to accommodate these specimens, he established the new species *Testudo schafferi* Szalai, 1931. Malik and Nafiz (1933) described an aquatic turtle, a small testudinid with affinities with *Testudo marmorum*, and a giant testudinid from the late Miocene of Kücükçekmece, in the European part of Turkey. Paraskevaidis (1955) described two testudinid specimens from the middle Miocene of Chios Island, whereas the same author later reported the presence of the same clade in indeterminate "Tertiary' sediments near Athens (Paraskevaidis 1961). Rückert-Ülkümen (1963) described fragmentary remains of a pan-trionychid from the Miocene of western Turkey, soon after followed by Lebküchner (1974) who described additional fragmentary material from the same clade in the Oligocene of the same region. Melentis (1966) documented the presence of a geoemydid in the Pleistocene of Megalopolis (Peloponnese). Bachmayer (1967) confirmed the presence of giant tortoises from Pikermi, by describing fragmentary remains that he attributed to *Testudo* cf. *schafferi*. Bachmayer and Symeonidis (1970) described additional finds of *Testudo marmorum* from its type locality, Pikermi and additionally referred another specimen from the late Miocene or Pliocene of Thessaloniki to *Testudo amiatae*. The same authors, a few years later, suggested the presence of *Testudo marginata* Schoepff, 1792, from Tilos Island (Bachmayer and Symeonidis 1975), whereas the following year, they described incomplete specimens of a small and a large-sized testudinid from the late Miocene or early Pliocene of Liossati, near Athens (Bachmayer and Symeonidis 1976). Bachmayer et al. (1975) established a new subspecies *Testudo marginata cretensis* in order to accommodate several relatively complete testudinid specimens from Pleistocene caves across Crete, and two years later, Kotsakis (1977) referred to the same taxon additional shell material. Kuss (1975) mentioned the presence of testudinid remains from a Pleistocene cave in Karpathos Island, without, however, providing any kind of description or figure of the material. Staesche (1975) mentioned the presence of several small and large Neogene testudinids, geoemydids, and pan-trionychids, but no figures, once again, accompany his reports. Paicheler et al. (1978) described the first known chelydrid fossil remains from Anatolia on the basis of beautifully preserved specimens from Bes-Konak, near Ankara. From the Quaternary of the Vraona cave, near Athens, Rauscher (1995) reported aquatic terrapin remains. Bachmayer et al. (1980) described incomplete remains of both a small and a large-sized testudinid from the Pliocene of Thessaloniki area. Schleich (1982) described the oldest remains attributed to the extant species *Testudo marginata* from the early Pleistocene of Peloponnese in southern Greece. Tuna (1988) described fragmentary shell elements of a pan-trionychid from the late Miocene of Bayraktepe in Turkey. Gad (1990) documented fragmentary remains from the latest Miocene of Maramena, Eastern Macedonia, which he referred to *Mauremys caspica*. Few years later, Schleich (1994) established two new aquatic testudinoid taxa, *Palaeochelys rueckerti* and *Palaeochelys turcica*, from the late Oligocene or early Miocene of Küçükdoğanca Köyü, near Kesan in the European part of Turkey, from where he also described fragmentary chelydrid remains which he referred to *Chelydropsis*, and also an indeterminate emydid. Zwick and Schleich (1994) described geoemydid and testudinid remains from the Pleistocene/Holocene Karain cave in southern Turkey. Brinkering (1996) made a short preliminary report on Cretan Pleistocene turtle finds. De Vos et al. (2002) preliminarily described and figured osteoderms and shell material pertaining to a giant tortoise and a much smaller-sized testudinids from the Pliocene of Vatera, Lesvos Island. The same year, Lapparent de Broin (2002) described this material in detail. She referred the latter form to cf. *Cheirogaster* aff. *schafferi* and provided a carapace length size estimation of 186 cm for that tortoise based on rather fragmentary remains that render this tortoise as one of the largest known tortoises globally (Lapparent de Broin 2002). From the same area in Lesvos, Lyras and van der Geer (2007) mentioned the presence of an additional small testudinid, however, without any figure or description to accompany their claim. The same year, Staesche et al. (2007) described multiple pan-trionychid, geoemydid, ptychogasterid, and testudinid specimens from several localities from Turkey, spanning from the Oligocene up to the Pleistocene. Mueller-Töwe et al. (2011) described large fossil eggs and shell fragments of a large-sized testudinid from the Pliocene of Rhodes Island. Tsoukala et al. (2011) described a small testudinid from the Pleistocene of Eastern Macedonia. Georgalis et al. (2013) established a new podocnemidoid taxon, *Nostimochelone lampra*, on the basis of a carapace and plastron from the early Miocene (Burdigalian) of Nostimo, in Western Macedonia. This was the first and so far only pleurodire turtle known from the Aegean region and it constitutes one of the youngest European occurrences of this clade for Europe. Georgalis and Kear (2013) provided a detailed overview of all fossil turtle specimens recovered from Greece. Vlachos et al. (2014) established *Cheirogaster bacharidisi* (currently placed in *Titanochelon*) on the basis of rather complete cranial and postcranial material from the Pliocene of Central Macedonia. Vlachos and Tsoukala (2014) described a testudinid from the late Miocene of the Drama region in Eastern Macedonia that they referred to *Testudo* cf. *graeca*. Vlachos et al. (2015a) described pan-trionychid remains from the Pliocene of Thessaloniki. The same year, Vlachos et al. (2015b) revised the testudinids from the late Miocene or early Pliocene of the east Thessaloniki area and described new specimens of a geoemydid, which they referred to *Mauremys*. Garcia et al. (2016) described a new testudinid specimen from the late Miocene of Nikiti in northern Greece which they referred to *Testudo* cf. *marmorum*. Georgalis et al. (2016c [**Appendix 6**]) described new remains of the geoemydid *Mauremys* and a pan-trionychid from the late Miocene of Crete. Vlachos and Delfino (2016) confirmed the presence of *Emys orbicularis* in the fossil record of the Aegean region, by describing Quaternary remains of that taxon from Peloponnese. Vlachos and Tsoukala (2016) described geoemydid and testudinid remains from the late Pliocene of Milia (Western Macedonia), large eggs that they attributed to a giant tortoise, and established their new taxon *Testudo brevitesta*. Georgalis et al. (2018c [**Appendix 11**]) described new indeterminate turtle remains from the early Miocene of Aliveri (Euboea) and Karydia (Eastern Macedonia and Thrace), which, despite being rather fragmentary, constitute among the earliest records of fossil chelonians from Greece.

### *Crocodylians*

Until relatively recently, crocodylians were not known from the fossil record of the Aegean region. The presence of fossils of these reptiles was preliminarily mentioned already by Lebküchner (1974), but the first formal description was only provided by Schleich (1994) on the basis of isolated teeth from the late Oligocene or early Miocene of Küçükdoğanca Köyü in the European part of Turkey. More recently, Georgalis et al. (2016c [**Appendix 6**]) described the first crocodylian finds from Greece, on the basis of isolated teeth from the late Miocene (Tortonian) of Plakias in Crete. Soon after, early Miocene crocodylian remains were also described from Lesvos (Vasileiadou et al. 2017), and more recently from Aliveri in Euboea Island (Central Greece) (Georgalis et al. 2018c [**Appendix 11**]).

### *Squamates*

Richard Owen was the first to describe a fossil squamate from the Aegean region by establishing his new taxon *Laophis crotaloides*, on the basis of 13 large vertebrae from the Pliocene of Megalo Emvolon (formerly Karabournou), near Thessaloniki (Owen 1857). The author referred *L. crotaloides* to Viperidae, provided a preliminary size estimation of this animal, and regarded it as the largest known viperid snake (Owen 1857). A few years later, Gaudry (1862a, 1862b, 1862–1867) described fossil material of a varanid from the late Miocene of Pikermi. Although he only had access to a single, large vertebra, Gaudry (1862a, 1862b, 1862–1867) nevertheless accurately identified it as a varanid. This was the first documentation of a fossil monitor lizard from Europe. The locality of Pikermi later yielded varanid cranial material which was used by Weithofer (1888) to define a new species, *Varanus marathonensis*. Curiously, the original Gaudry's Pikermi vertebra served much later as the holotype of another varanid species, *Varanus atticus* by Nopcsa (1908), who did not mention Weithofer's (1888) taxon and material. Römer (1870) established the second named fossil snake species from the Aegean region, the rather large pythonid *Python euboicus*, on the basis of a rather complete skeleton, including cranial elements, from the early Miocene of Kymi in Euboea Island. After a rather long absence of fossil squamate descriptions from the Aegean region, Schneider (1975) described the herpetofauna of the Middle Pleistocene locality of Latomi in Chios Island, with lacertids, colubrines, erycids, natricines, viperids, and an elapid. The identification of elapids from that locality was rejected though later (Szyndlar 1991b; Georgalis et al. 2018b [**Appendix 10**]). Rage and Sen (1976) conducted the first description of fossil squamates from Anatolia, with incomplete remains of anguids, lacertids, varanids, amphisbaenians, colubrids, elapids, erycids, and scolecophidians from the Piocene of Çalta, near Ankara. Kotsakis (1977) described fragments of a lacertid and a colubrine from the Pleistocene of a Cretan cave. From another, nearby, Pleistocene Cretan cave, Mangilli (1980) mentioned the presence of the large agamid lizard *Uromastyx*, on the basis of a single, non-figured, tibia, however, this identification was subsequently rejected by Georgalis et al. (2016b [**Appendix 5**]) who considered it as a probable lacertid. Paicheler et al. (1978) mentioned the presence of a colubroid snake from the early Miocene of Bes-Konak, near Ankara, without, however, any figuring of that material. Szyndlar and Zerova (1990) documented the first presence of cobras from Greece, describing large vertebrae from the Pliocene of Tourkobounia 1 near Athens, which they referred to the genus *Naja* Laurenti, 1768. In his two large compendia on Neogene and Quaternary snakes from Central and Eastern Europe, Szyndlar (1991a, 1991b) described several specimens from multiple Greek localities, including scolecophidians, booids, elapids, colubrines, natricines, and viperids. Venczel and Sen (1994) reported the presence of a large anguid (with affinities with the extant *Pseudopus apodus* [Pallas, 1775]), a lacertid, and several snakes from the Middle Pleistocene of the Emirkaya-2, near Konya. Zwick and Schleich (1994) described remains of lizards and snakes from the Late Pleistocene/Holocene Karain cave, near Antalya. The rich micromammal fauna of Maramena in Central Macedonia yielded also squamates, with lizards (agamids, anguids, lacertids, and scincoids) briefly described by Richter (1995) and snakes (colubrines, natricines, elapids, and viperids) by Szyndlar (1995). Rauscher (1995) briefly documented fragmentary remains of lizards and snakes from the Late Pleistocene/Holocene of the Vraona cave, near Athens, however, without any figure provided, his identifications cannot be verified. Conrad et al. (2012) established another varanid taxon from Greece, *Varanus amnhophilis*, this time from the late Miocene of Samos Island, on the basis of cranial and postcranial remains. Hoek Ostende et al. (2015) described fragmentary remains from Ericek, in Denizli Province. Georgalis et al. (2016a [**Appendix 4**]) described new material of the giant viperid *Laophis crotaloides* from its type locality near Thessaloniki. Considering that the original type material of this species is considered lost, the new finds provided important information about this taxon, including a detailed description and an emended diagnosis, and further confirmed its rather large size (Georgalis et al. 2016a [**Appendix 4**]). The same year, Georgalis et al. (2016b [**Appendix 5**]) described the first known fossil chamaeleonids from the region, providing biogeographic implications for this lizard clade and how they dispersed from Africa to Europe. In another paper, Georgalis et al. (2016c [**Appendix 6**]) described the late Miocene herpetofauna of Plakias (Crete), identifying a probable natricine snake and the first documentation of an amphisbaenian from Greece. The following year, Georgalis et al. (2017a [**Appendix 7**]) described a diverse squamate fauna from the late Miocene of Ano Metochi, in northern Greece, comprising anguid, lacertid, and cordylid lizards and scolecophidian, colubrine, and natricine snakes. It is worth noting that the cordylids from Ano Metochi represented the youngest record of this clade in Europe. Meanwhile, Georgalis et al. (2017b [**Appendix 8**]) described new cranial material of *Varanus* from the Middle Pleistocene of the Tourkobounia 5 locality, near Athens, which represented the youngest varanid remains from Europe and implied a significant stratigraphic expansion for this lizard clade and a much later extinction date than what was previously thought. Čerňanský et al. (2017) described several cranial and postcranial remains of anguine lizards from the Oligocene and Miocene of numerous Turkish localities, providing thus the first records of Paleogene squamates from the Aegean region. Sen et al. (2017) described lizard (anguid, lacertid, and varanid) remains from the Pliocene of Çeştepe, near Ankara. Vasileiadou et al. (2017) described fragmentary lizard and snake remains from the early Miocene of Lapsarna (Lesvos Island). Georgalis et al. (2018a [**Appendix 9**]) described the first record of the amphisbaenian *Blanus strauchi* complex, on the basis of a dentary from the middle Miocene of Gebeceler in Afyon region. Georgalis et al. (2018b [**Appendix 10**]) described the fossil lizards and snakes from the late Miocene hominoid-bearing locality Ravin de la Pluie, near Thessaloniki, with anguid and varanid lizards and elapid and colubrine snakes, suggesting also that Neogene European varanids possessed comparatively short and robustly built limbs. Finally, Georgalis et al. (2018c [**Appendix 11**]) described lizards and snakes from the early Miocene of two Greek localities, Aliveri (Euboea) and Karydia (Eastern Macedonia and Thrace), providing also implications about the biogeography of early Neogene herpetofaunas of southeastern Europe.

## Taxonomic evaluation and review of named reptile taxa from the Aegean region (sorted by publication date)

*Laophis crotaloides* Owen, 1857.

Based on 13 large vertebrae from the Pliocene of Megalo Emvolon, near Thessaloniki, this species was already considered to be a rather large viperid snake in its original description, with a total length “between 10 and 12 feet in length” (Owen 1857:199). *Laophis crotaloides* was in fact one of the first fossil snakes to be named. Owen (1857) figured only one of these

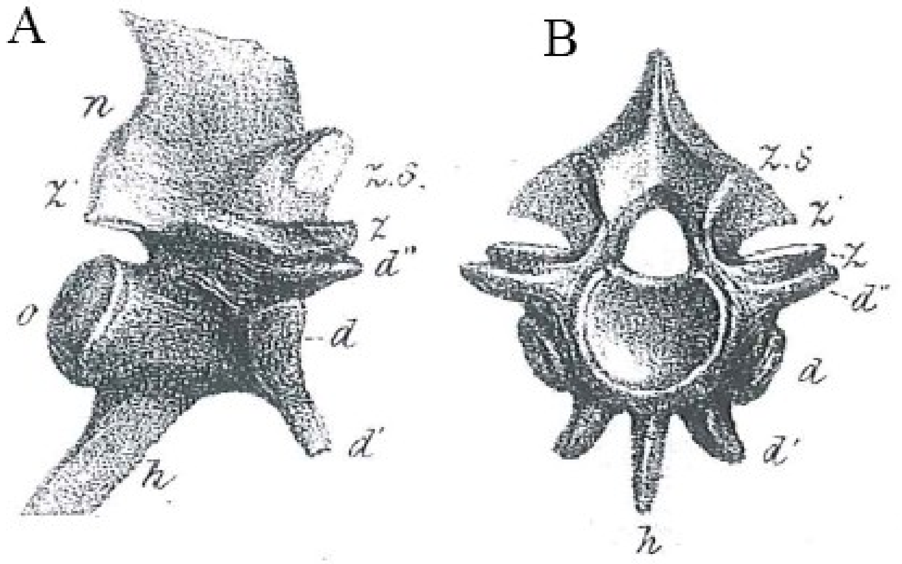

**Figure 5.** Original lithograph of the type trunk vertebra (currently lost) of *Laophis crotaloides* from the Pliocene of Megalo Emvolon, near Thessaloniki. Image modified from Owen (1857). Specimen depicted in lateral (A) and anterior (B) views.

vertebrae (and only in lateral and anterior views) (*Figure 5*), compared the Greek material with various specimens of the giant aquatic snake *Palaeophis* Owen, 1841, that were previously described by him few years earlier from the Eocene of the United Kingdom (Owen 1841, 1842, 1850), but also with extant forms, and concluded that *L. crotaloides* belonged to viperids. Unfortunately the fact that the type and only known material was subsequently lost hindered the exact taxonomic affinities within viperids, with either crotaline or viperine relationships variously suggested (e.g., Kuhn 1939, 1963; Hoffstetter 1955). Rage (1984) concluded that due to the inaccurate original lithograph of the type material and its inadequate description, this taxon should be considered a nomen dubium. The taxonomic uncertainty about the affinities and even the validity of *L. crotaloides* was subsequently followed by other workers (Szyndlar 1991b; Szyndlar and Rage 1999, 2002; Wallach et al. 2014). Nevertheless, Georgalis et al. (2016a [**Appendix 4**]) recently described new material (a single, large vertebra) of *Laophis crotaloides* from its type locality and on the basis of this specimen they redescribed the taxon in detail, revalidated it, and provided a new diagnosis confirming its species distinctiveness. They additionally provided a detailed overview of the taxonomic history of this taxon (Georgalis et al. 2016a [**Appendix 4**]). Regarding that the new specimen is the largest viperid vertebra ever described (centrum length more than 15 mm), the already suggested large size of *Laophis crotaloides* was confirmed (Georgalis et al. 2016a [**Appendix 4**]). Nevertheless, the following year, Codrea et al. (2017) considered again that *L. crotaloides* was an invalid taxon and treated it as a nomen dubium. However, the rationale which these authors provided for acting so was inaccurate. More specifically, Codrea et al. (2017) suggested that this Greek snake taxon was invalid because of the loss of the type material, the inaccuracies of Owen's (1857) original lithograph, and the fact that a neotype was not designated based on the new material described by Georgalis et al. (2016a [**Appendix 4**]), citing ICZN (1999:Article 75.3). However, Georgalis et al. (2016a [**Appendix 4**]) discussed extensively the inaccuracies of Owen's lithograph and further mostly based their new diagnosis on the basis of their new material. Furthermore, the ICZN (1999:Article 75.3) clearly states that neotypes should be only designated "when there is an exceptional need". As such, the fact that the new vertebra of *Laophis crotaloides* from Megalo Emvolon described by Georgalis et al. (2016a [**Appendix 4**]) is the only currently available material of this taxon but was not formally designated as a neotype, cannot invalidate the status of the species. Regarding the loss of the type material, I further confirm that during my last visit (March 2017) in NHMUK I was unable to locate it. Yet, I have to note that the fact that *Laophis crotaloides* is not mentioned at all in Lydekker's (1888) extensive catalogue of fossil reptile specimens of the NHMUK (then British Museum), makes me wonder if indeed Owen's (1857) original material was ever curated in the new buliding that was constructed during the 1880's. Alternatively, the type material of *L. crotaloides* could be in the collections of the Hunterian Museum of the Royal College of Surgeons in London, another Institution that Richard Owen was affiliated, earlier in his career, but still there is no clear indication about such a case. Whatever the whereabouts of this enigmatic type material may have been, I here follow the detailed description of Georgalis et al. (2016a [**Appendix 4**]) and consider *Laophis crotaloides* as a valid viperid species.

*Testudo marmorum* Gaudry, 1862a.

Gaudry (1862a) originally established *Testudo marmorum* on the basis of shell material from the late Miocene of Pikermi, by describing and figuring one carapace and plastron (MNHN PIK 3683). He also detemined its sex as male, judging from the shape of its posterior portion (*Figure 6*). The same author provided comparisons with both extant and extinct taxa and noted resemblance with *Testudo marginata*, which is a common element of the modern Greek herpetofauna (Gaudry 1862a). The same year, he provided further brief comments about *T. marmorum* (Gaudry 1862b), whereas in his large manuscript on the Pikermi fossils, he further described the taxon and figured an additional shell (Gaudry 1862–1867). Since then, *Testudo marmorum* became a rather important taxon in early fossil chelonian literature, with multiple studies discussing it or using it for comparisons with new testudinid finds across Europe (e.g., Maack 1869; Hoernes 1892; Zittel 1887–1890; Reinach 1900; De Stefano 1902; Koch 1904; Dacque 1912; Arambourg and Piveteau 1929). Bachmayer and Symeonidis (1970) described new shell material of *T. marmorum* from its type locality, Pikermi. Unfortunately, no skull elements have been found. Similar or even conspecific forms have been described from Kücükçekmece, near Istanbul (Malik and Nafiz 1933) and Nikiti-2 in northern Greece (Garcia et al. 2016). Jiménez Fuentes (1981) erroneously mentioned the presence of *T. marmorum* in Crete, citing Bachmayer and Symeonidis (1970). However, there is no mention of specimens of that species from Crete in that or any other paper, and as such, Jiménez Fuentes's (1981) claim should be regarded as an error. *Testudo marmorum* is characterized by the presence of the hypo–xiphiplastral hinge, a narrow nuchal, and a widening in the posterior part of the carapace (Auffenberg 1974; Lapparent de Broin 2002; Lapparent de Broin et al. 2006; Georgalis and Kear 2013; Vlachos and Tsoukala 2014). Recent phylogenetic analyses have placed *T. marmorum* as the sister taxon of either the European *Testudo marginata* (Corsini et al. 2014) or the North African *Testudo kleinmanni* Lortet, 1883 (Vlachos and Tsoukala 2016; Vlachos and Rabi 2018). In any case, *Testudo marmorum* has been always treated as a valid taxon, even though its exact affinities within the genus *Testudo* are not yet fully resolved, awaiting a full redescription of the type and referred material using modern standards and a more comprehensive phylogenetic analysis (Georgalis and Kear 2013). The validity of *Testudo marmorum* is uncontroversial. Pending a redescription of its type material, I am confining the species solely to its type locality, Pikermi. Accordingly, I follow the previously published opinions and consider the Kücükçekmece and Nikiti-2 material mentioned above are tentatively referred to as *Testudo* cf. *marmorum*.

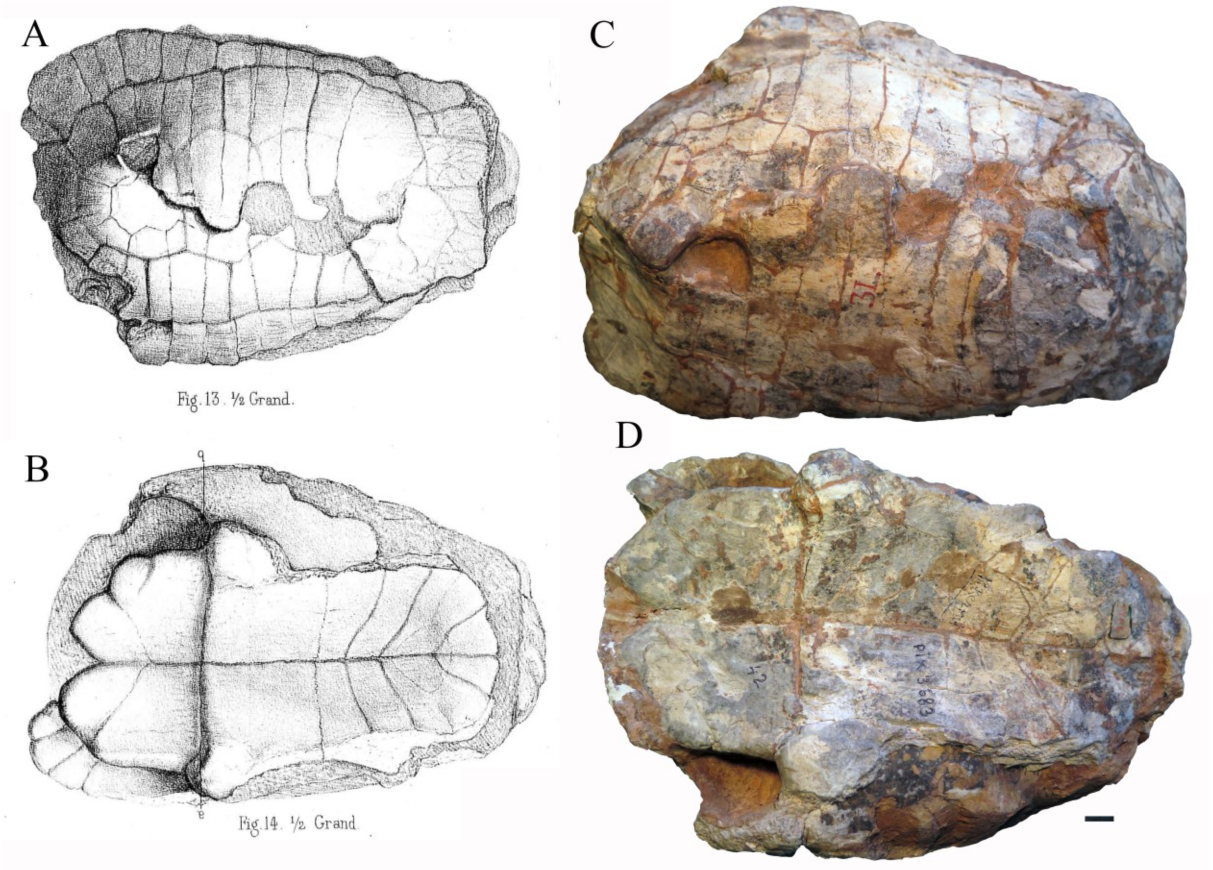

**Figure 6.** Original lithograph (A, B) and photographs (C, D) of the type carapace and plastron (MNHN.PIK 3683) of *Testudo marmorum* from the late Miocene of Pikermi, near Athens. Image modified from Gaudry (1862a) (A, B) and photographs (C, D) of the specimens by GLG (courtesy of MNHN). Specimen depicted in dorsal (A, C) and ventral (B, D) views. Note that the original figure of Gaudry (1862a) appears to be a reverse image of the actual photograph, a case that is a common fact for 19th century's lithographs. Scale bar = 1 cm.

*Python euboicus* Römer, 1870.

This species was established upon a beautifully preserved, articulated, though incomplete, skeleton on a slab from the early Miocene (?MN 3) of Kymi, Euboea Island (Römer 1870) (*Figure 7*). Around 25 large vertebrae, several ribs, and a partial dentary are preserved, pertaining to a rather large individual, and on the basis of this material, the species was assigned to the extant pythonid genus *Python* (Römer 1870). A few years later, Rochebrune (1880) recombined the pythonid from Euboea in his new, monotypic genus *Heteropython*, as he considered it to be rather different from *Python* Daudin, 1803, and more similar to the Paleogene European *Palaeopython* Rochebrune, 1880. The same author further provided an emended diagnosis for the Greek species (Rochebrune 1880). Gilmore (1938) followed that generic placement, but he erroneously mentioned that this taxon is from Sardinia and not from Euboea, apparently confusing it with the purported "pythonid" *Palaeopython sardus* Portis, 1901a, which is now known to pertain to an indeterminate acanthomorph fish (Delfino et al. 2014). With the exception of Kuhn (1939, 1963), this generic placement and the validity of the genus *Heteropython* did not meet wide acceptance, with most subsequent authors returning the large snake from Euboea back to its original genus, *Python* (e.g., Rage 1984b; Szyndlar 1991a; Szyndlar and Schleich 1993; Szyndlar and Rage 2003; Head 2005; Rage and Szyndlar 2005; Schleip and O'Shea 2010; Wallach et al. 2014; Georgalis et al. 2016b

[**Appendix 5**], 2018c [**Appendix 11**]). In fact, Rage (1984) even casted doubt about the validity of *Python euboicus*, considering that the holotype and only known specimen is probably lost, and that the original Römer's (1870) description was inadequate. Accordingly, he considered *P. euboicus* to be a nomen dubium. Szyndlar and Rage (2003) continued to accept this taxonomic opinion, they further described the anatomy of this species, and noted strong similarity of its vertebral anatomy with another European pythonid, their *Python europaeus* Szyndlar and Rage, 2003. Nevertheless, these authors provided for the first time an estimation of the vertebral dimensions of *Python euboicus*, stating that "the length of the vertebral centra apparently exceeds 10 mm, whereas their width is 13 to 14 mm" (Szyndlar and Rage 2003:68). Accordingly, they considered this species to be one of the largest known snakes from Europe (Szyndlar and Rage 2003), although it has to be noted that certain palaeophiid specimens from the Paleogene of the continent were significantly larger (e.g., Owen 1841, 1842, 1850; Rage 1984). Regarding the loss of the material, I confirm that I was unfortunately unable to locate the holotype at the collections of the University of Wrocław, where it was originally kept. I am herein tentatively keeping *Python euboicus* as a valid taxon, taking into consideration the completeness of the specimen with adequate characters observed on the vertebrae and the dentary but also on the basis of a biogeographic rationale, as this is the first recorded member of *Python* from the Neogene of Europe. I further agree with Szyndlar and Rage (2003) about the strong vertebral resemblance among *Python euboicus* and their new species *Python europaeus*, but I am noting that in the case of probable synonymy, the Greek taxon should have nomenclatural priority, especially in the case that the holotype would eventually turn up or if new, diagnostic material from its type locality is recovered.

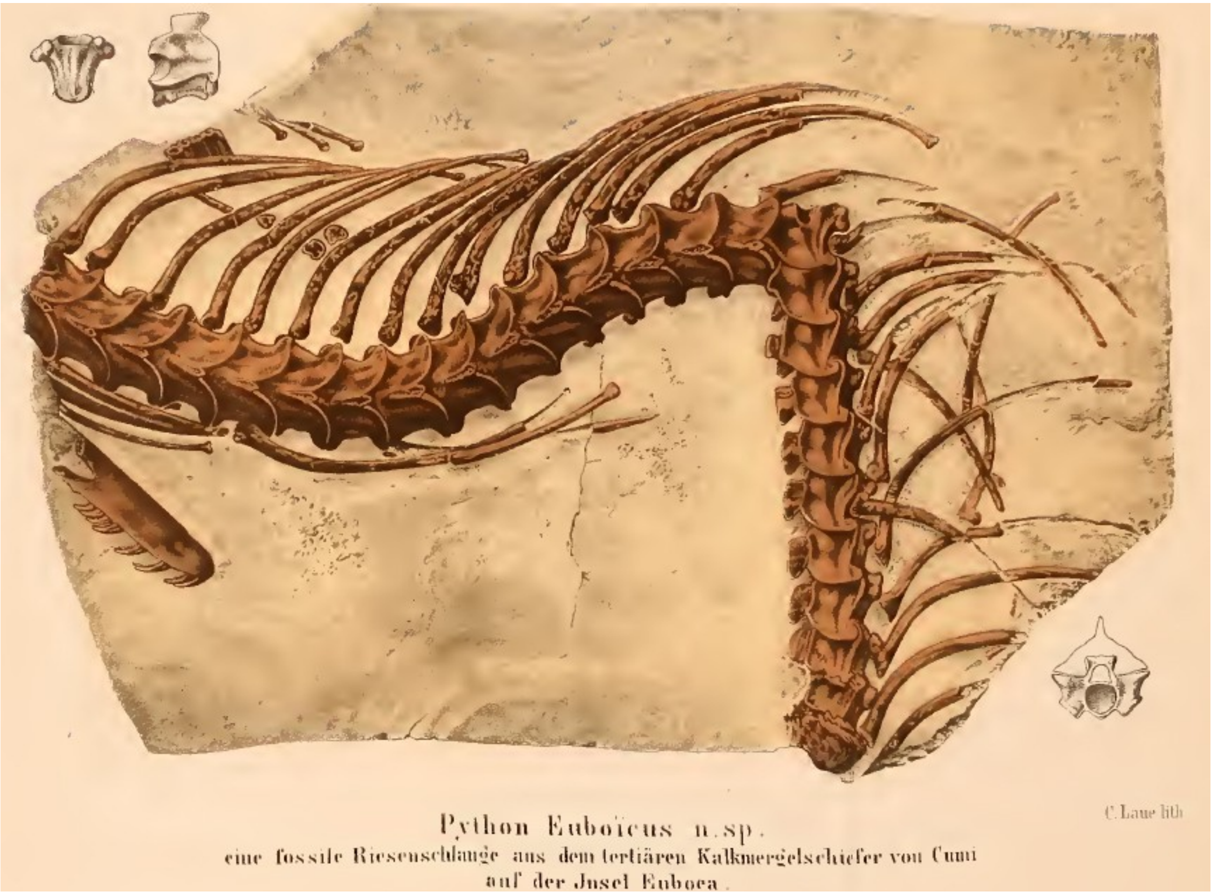

**Figure 7.** Lithograph of the holotype skeleton (currently lost) of *Python euboicus* from the early Miocene of Kymi, Euboea Island. Image adapted from Römer (1870).

*Varanus marathonensis* Weithofer, 1888.

Gaudry (1862a, 1862b, 1862–1867) was the first to describe a fossil varanid from Europe based on a specimen (a single, large trunk vertebra [MNHN.F.PIK 3715]) from the locality of Pikermi, near Athens (*Figure 8*). He estimated a 1.5 m size estimation for the Pikermi form (Gaudry 1862a, 1862b) and a few years later, he subsequently figured the sole known specimen (Gaudry 1862–1867). The author refrained from naming it but, nevertheless denoted clear varanid affinities of this material, referring to it as "Reptile du groupe des Varans" (Gaudry 1862a, 1862b, 1862–1867). A few decades later, Lydekker (1886) briefly mentioned the Pikermi varanid, emphasizing its large size, which he estimated "between four and five feet" (Lydekker 1886:236). Weithofer (1888) described new cranial remains from the same locality and established his new species, *Varanus marathonensis*, on the basis of what appear to be two syntypes (one comprising the left portion of a skull, including the maxilla, the premaxilla, and the prefrontal and another comprising a single left supraorbital), mentioning also the earlier indication of monitor lizards in Pikermi by Gaudry (1862a, 1862b, 1862–1867) (*Figure 9*). Upon establishing his new species, *Varanus hofmanni*, from the Miocene of Germany, Roger (1898, 1900) curiously ignored *V. marathonensis*, although in his former paper, he mentioned that the only known varanid from the Tertiary of Europe was *Palaeovaranus cayluxi* (currently considered to belong to another, distant lizard clade, Palaeovaranidae; Georgalis 2017 [**Appendix 3**]). Later, Nopcsa (1908) established a new species for the Pikermi large lizard, *Varanus atticus*, on the basis of Gaudry's (1862a, 1862b, 1862–1867) original vertebra. It is unclear whether Nopcsa (1908) was indeed unaware of Weithofer's (1888) work or if he deliberately ignored it, but in any case there is neither a single mention of the name "*marathonensis*," nor a reference of Weithhofer (1888) in his work. In his monumental work on fossil varanids, Fejérváry (1918) placed *V. atticus* into the synonymy of *V. marathonensis* and this synonymy has since been universally accepted (e.g.,

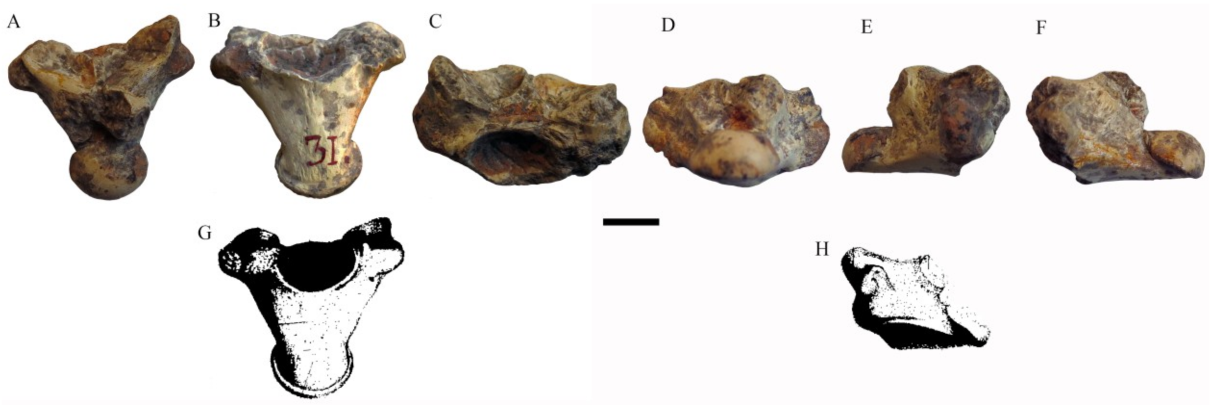

**Figure 8.** Photographs (A–F) and the original lithograph (G, H) of trunk vertebra (MNHN.F.PIK 3715) of *Varanus* sp. from the late Miocene of Pikermi, near Athens. The same vertebra later served as the holotype of *Varanus atticus* Nopcsa, 1908. Lithograph modified from Gaudry (1862–1867) and photographs by GLG (courtesy of MNHN). Note that the original lithograph of Gaudry (1862–1867) figured the specimen only in two views. Also, similarly to the figure of *T. marmorum* above, the original figures of Gaudry (1862–1867) appear to be a reverse images of the actual photographs, a case that is a common fact for 19th century's lithographs. Specimen in dorsal (A), ventral (B, G), anterior (C), posterior (D), right lateral (E, H), and left lateral (F) views. Scale bar = 1 cm.

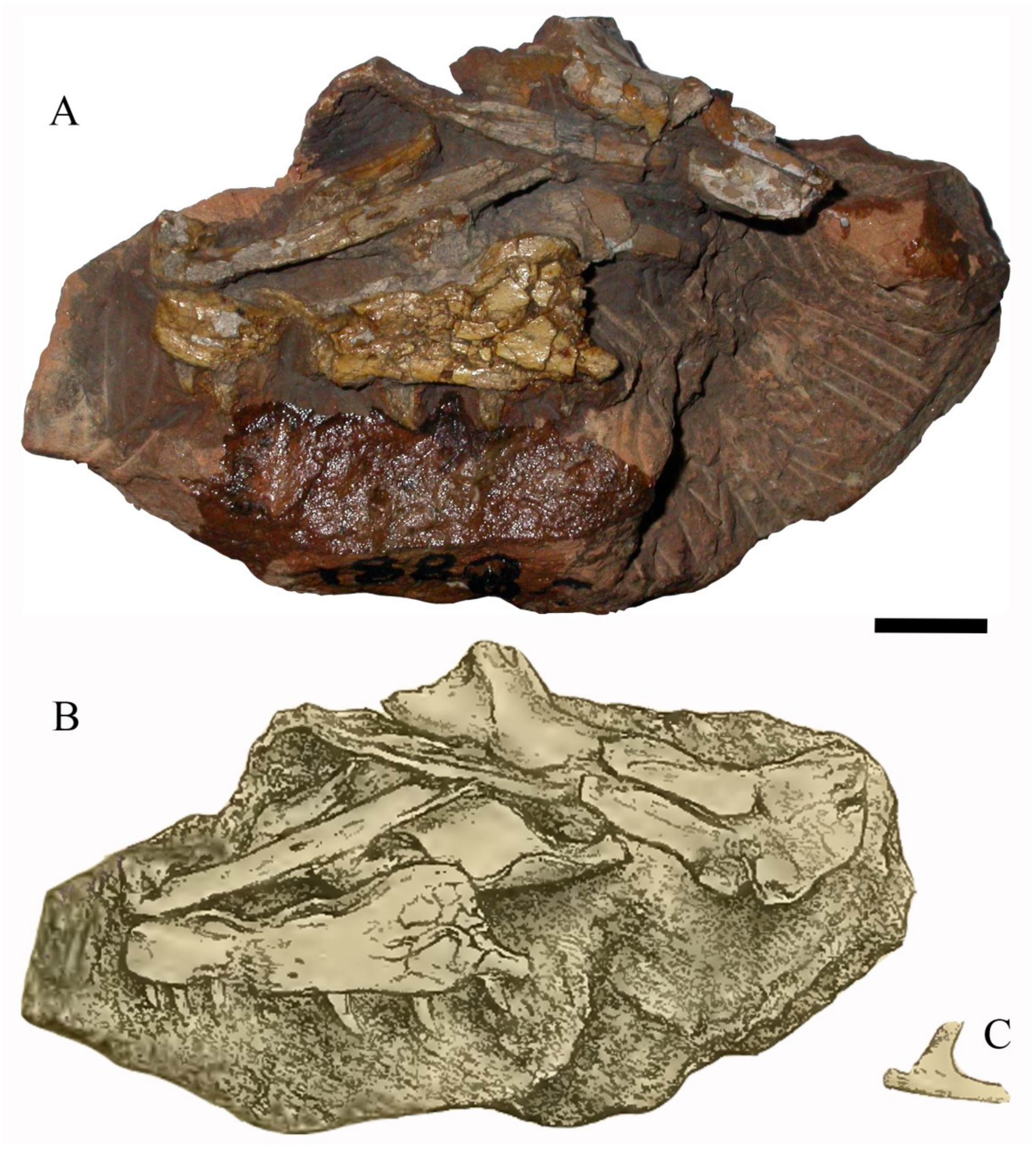

**Figure 9.** Photograph (A) and original image (B) of the first syntype (IPUW 1888-001-001; the left portion of a skull, including the maxilla, the premaxilla, and the prefrontal) and original image (C) of the second syntype (IPUW uncat.; a left supraorbital) of *Varanus marathonensis* from the the late Miocene of Pikermi, near Athens. Original images modified from Weithofer (1888) and photograph by Massimo Delfino (courtesy of IPUW). Scale bar = 1 cm.

Kuhn 1939; Rage and Sen 1976; Estes 1983; Molnar 2004). Fejérváry (1918) further described in great detail and figured again the type material of *V. marathonensis*, and assigned to the same taxon other varanid occurrences from the Miocene and Pliocene of Hungary, including part of the type series of *Varanus deserticolus* Bolkay, 1913, but also a dentary from the Pleistocene of Italy (later shown to pertain to a non-varanid lizard, probably a large lacertid [Georgalis et al. 2017b; **Appendix 8**]). Notably, the Hungarian material which Fejérváry (1918) referred to *V. marathonensis* comprised of numerous elements, including a maxilla, a dentary, a phalanx, and various vertebrae, thus enhancing our understanding of the anatomy of this animal. In his second large contribution on fossil varanids, Fejérváry (1935) mentioned again several times *Varanus marathonensis*, referring characteristically to that species as "the first well known and generically safely identifiable Varanian remains" (Fejérváry 1935:72). Dunn (1927) suggested resemblance of *V. marathonensis* with the extant *Varanus griseus* (Daudin, 1803) on the basis of the morphology of the maxilla, whereas, on the basis of vertebral size, he provided a preliminary size estimation of the Greek taxon, suggesting that it could reach two thirds the size of the extant *Varanus komodoensis* Ouwens, 1912 (about six feet [i.e., 2 m]). Rage and Sen (1976) described new varanid vertebral material from the Pliocene of Çalta, Turkey, which they referred to *V. marathonensis*. Estes (1983) provided an emended diagnosis of *V. marathonensis* but solely on the basis of vertebral characters. Conrad et al. (2012) erroneously stated that the holotype of *V. marathonensis* was Gaudry's (1862a, 1862b, 1862–1867) vertebra and not Weithofer's (1888) skull elements. Georgalis et al. (2017b [**Appendix 8**]) treated *V. marathonensis* as a valid taxon and noted resemblance of the youngest European varanid material from the Pleistocene of Tourkobounia 5 with that species on the basis of a clearly developed medial lamina on the maxilla. Molnar (2004) erroneously stated that new varanid finds have since been recovered from Pikermi and that they are attributable to *V. marathonensis*. This is, however, not the case, and apparently Molnar (2004) misread Estes (1983) who had simply anticipated more varanid finds from Pikermi. It should be noted also that similarly to the case of *Testudo marmorum*, and as was usual in older literature, the age of Pikermi, the type locality of *V. marathonensis* and *V. atticus*, is referred to as "lower Pliocene" (e.g., Lydekker 1886; Fejérváry 1935), although it is now known that its type locality pertains to the late Miocene (Georgalis and Kear 2013). I am here considering *Varanus marathonensis* to be a valid species, highlighting, nevertheless, the need of a comprehensive redescription of its syntypes. Regarding *Varanus atticus*, there is no overlap of the holotype and that of *V. marathonensis*. In addition, the taxonomic significance of the vertebrae of varanids is as yet unresolved (Delfino et al. 2013; Georgalis et al. 2018b [**Appendix 10**]). Therefore, *Varanus atticus* is herein considered to be a nomen dubium, although it must be noted that on the basis of the fact that it originates from the same locality and the overall similar size with *V. marathonensis*, the two forms could be eventually synonyms.

*Testudo sloanei* Lydekker, 1889.

The holotype and only known specimen of *Testudo sloanei* is a relatively small, 18 cm long, incomplete shell, missing the marginals and part of the plastron that was initially part of the Hans Sloane's collection until it was finally purchased by the British Museum at 1754. Lydekker (1889) established a new taxon based on this shell (NHMUK R1587) and further considered that, due to its "extremely vaulted carapace," it was allied to the extant *Stigmochelys pardalis* (Bell, 1828) and *Astrochelys radiata* (Shaw, 1802), both regarded by him as belonging to *Testudo*. However, he provided no figure of this specimen and no further geological or geographical information, besides the "Tertiary beds in Turkey" (Lydekker 1889:89). Apparently, this lack of figures explains the rare, brief, and rather sporadic mentions of this species in the chelonian literature (De Stefano 1902; Hewitt 1936; Kuhn 1964; Auffenberg 1974). In any case, affinities of *Testudo sloanei* with *S. pardalis* (Hewitt 1936) or both *S. pardalis* and *A. radiata* (De Stefano 1902; Auffenberg 1974) continued to be mentioned, with Auffenberg (1974:178) questionably recombining it into *Geochelone* Fitzinger, 1836, but also stating that "certain of its features suggest it may be close to *Testudo*", without, however, providing any evidence of these features. Staesche et al. (2007) referred to this taxon under the incorrect species epithet spelling "*sloani*", stating that it could represent a juvenile of a giant testudinid (their *Cheirogaster*), although the epiplastral lip was reportedly weakly developed. They furthermore erroneously considered that this name is a nomen nudum, simply due to the fact that the original publication did not contain illustrations

(Staesche et al. 2007). However, this taxonomic opinion is clearly erroneous and cannot be the case, as ICZN (1999: Article 12.1) only requires a description, definition or indication for publications made prior to 1931. Therefore, the name *Testudo sloanei* is certainly available for nomenclatural purposes. Furthermore, it is worth noting that illustrations in fact consist an "indication" for publications before 1931 (ICZN 1999: Article 12.2.7) (see Georgalis 2017 [**Appendix 3**] for a further discussion). The rather vague locality data provided by Lydekker (1889) are also problematic. Curiously, De Stefano (1902) considered *T. sloanei* as a Pliocene taxon and Auffenberg (1974) made it even more precise (as early Pliocene) without, however, any further justification for these age suggestions. Furthermore, the term "Turkey" at the time of Lydekker (1889) or even older at the time of Sloane's collection in the 18th century, referred in fact to a rather broad territory within the then Ottoman Empire, which variously encompassed lands far beyond the Aegean region, such as central Balkans, the Middle East, and even northeastern Africa. In my opinion, the holotype of *T. sloanei* does not probably originate from the western part of Anatolia, as 18th and 19th centuries's European scholars were mostly using the Greek names for regions and cities across that geographic area. Whatever its exact geographic and stratigraphic origin may have been, the extremely vaulted shape of the carapace appears to be an interesting feature. Without a published figure, however, it is difficult to assess the degree of this carapace vaulteness or also to state anything regarding the exact affinities of this taxon. I tentatively consider *Testudo sloanei* as a nomen dubium, probably representing a testudinid, although I acknowledge that a proper study of the material may in fact reveal diagnostic features and taxonomic distinctiveness.

*Varanus atticus* Nopcsa, 1908.
See *Varanus marathonensis* above.

*Testudo schafferi* Szalai, 1931.
Szalai (1931) established *Testudo schafferi* on the basis of an impressive, large (23.1 cm long) cranium (NHMW 2009z0103/0001) and a 35.5 cm-long femur (NHMW 1911/0005/0275) from the late Miocene (MN 12) (then considered Pliocene) locality of Mytilinii in Samos Island (*Figure 10A, B*). Szalai (1931) paid particular attention to the large size of this animal providing an estimation of its carapace length of around 150 cm, even without any shell material at hand. He further speculated that this taxon possessed an epiplastral lip in life but this was totally based on palaeoecological grounds, as he considered that this structure could enable it to properly defend against the diverse and large-sized felids of the Samos ecosystem (Szalai 1931). Later on, and as was the case with multiple European Neogene testudinid taxa, Auffenberg (1974) recombined *Testudo schafferi* into *Geochelone*, whereas he erroneously indicated the authorship date of that species as "1933" instead of "1931". Lapparent de Broin (2002) tentatively placed *Testudo schafferi* into the otherwise Eocene based genus *Cheirogaster* Bergounioux, 1935, along with several other large to giant-sized testudinids from the Paleogene and Neogene of Europe. Chkhikvadze (2010) referred to his large-sized Georgian taxon *Megalochelys natadzei* (Chkhikvadze, 1989) a large testudinid plastron specimen (AMNH 1722) from the late Miocene of Samos, without providing any further justification for such taxonomic attribution. This specimen remains hitherto undescribed, but, obviously, considering its origin and its absolute size, it is here also regarded to pertain to *Testudo schafferi*. Georgalis and Kear (2013) accepted the generic placement of the Samos testudinid into *Cheirogaster* and they further suggested that the presence of colossal tortoises in the Neogene of the Mediterranean Europe could be explained by the palaeoenvironmental reconstruction of that area at the Mio-Pliocene boundary, i.e., evolving a larger chelonian body size for metabolic purposes or for facilitating the consumption of $C_4$ vegetation in the

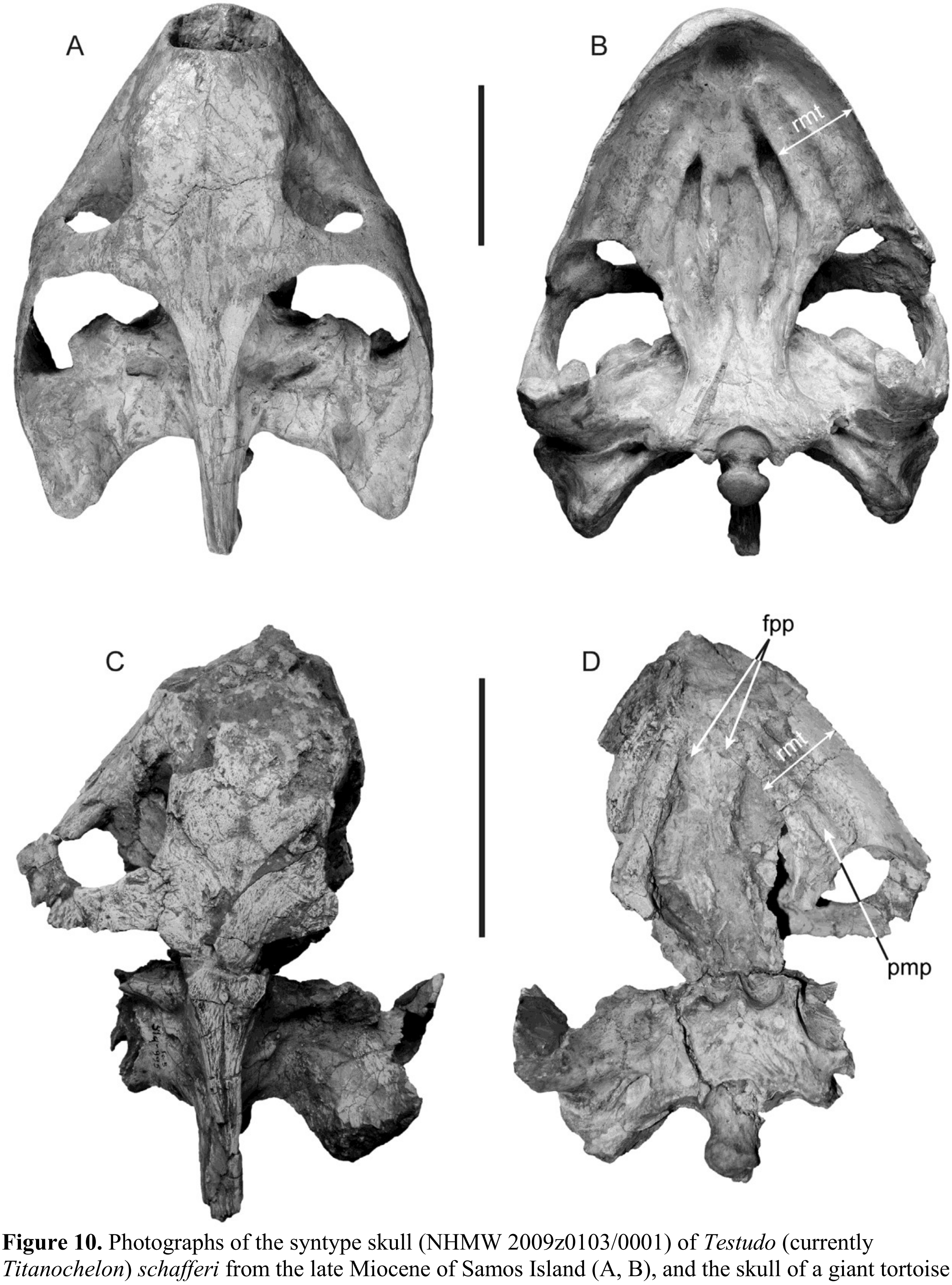

**Figure 10.** Photographs of the syntype skull (NHMW 2009z0103/0001) of *Testudo* (currently *Titanochelon*) *schafferi* from the late Miocene of Samos Island (A, B), and the skull of a giant tortoise described by Arambourg and Piveteau (1929) from the Neogene of Thessaloniki area (C, D). Image adapted from Georgalis and Kear (2013). Scale bars = 10 cm. Abbreviations: fpp, foramen praepalatinum; pmp, ‘‘posterior maxillary pit’’; rmt, ridges of the maxillary triturating surfaces.

widespread savannah grasslands. Pérez-García and Vlachos (2014) recombined *Testudo schafferi* into their new genus *Titanochelon* along with several other giant tortoises from the

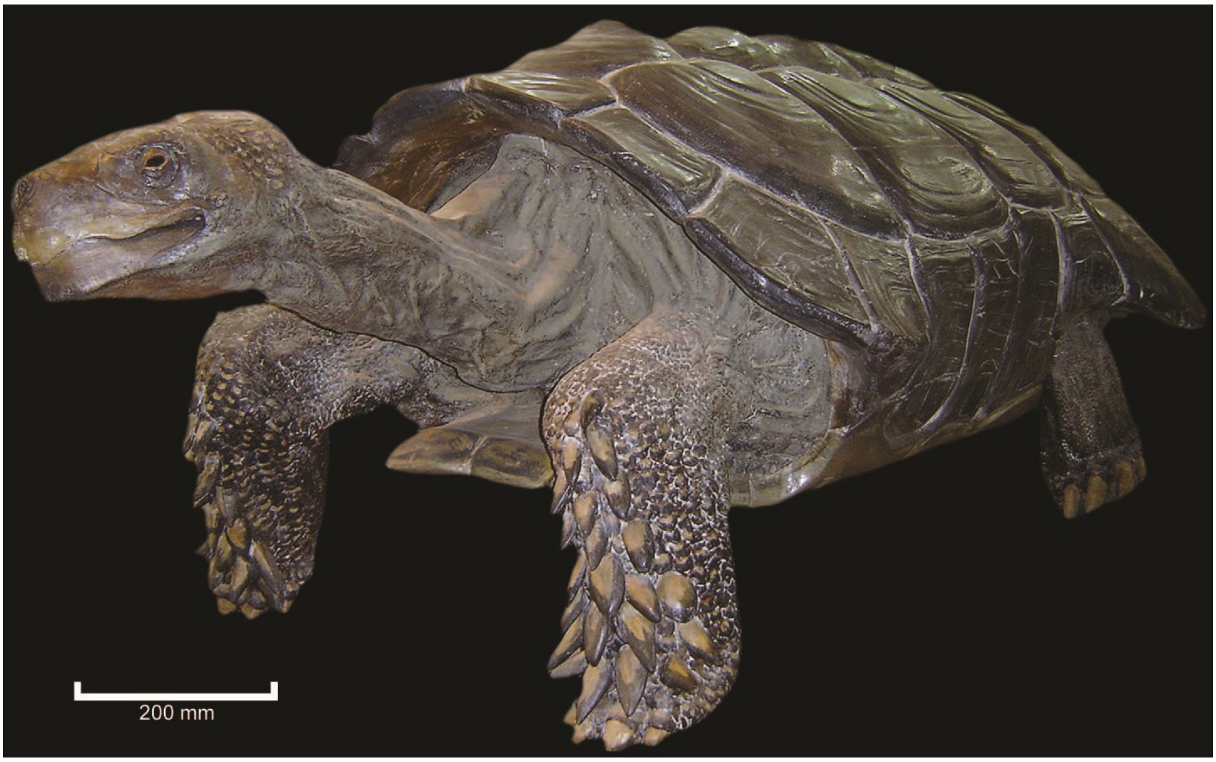

**Figure 11.** Life restoration of the giant testudinid from the early Pleistocene of Vatera, Lesvos, on display in AMPG. Photograph by Benjamin Kear.

Neogene of Europe. Regarding the distinctiveness of the syntype skull of the Samos giant tortoise, the validity of this taxon remains uncontroversial. I further agree on its generic placement in *Titanochelon* but, nevertheless, highlight the urgent need of redescription, nomenclatural clarification, and phylogenetic analysis of the Asian giant tortoises, which have been variously placed into the genera *Colossochelys* Falconer and Cautley, 1844 and *Megalochelys* Falconer and Cautley, 1837. Likewise, other Greek material that has in the past been tentatively assigned to*Titanochelon* cf. *schafferi* from the Neogene of Pikermi, Vathylakkos (*Figure 10C, D*), and Liossati and the early Quaternary of Vatera (Lesvos) (*Figure 11*) (Arambourg and Piveteau 1929; Bachmayer 1967; Bachmayer and Symeonidis 1976; Lapparent de Broin 2002) needs further reevaluation.

*Testudo marginata cretensis* Bachmayer et al., 1975.
Bachmayer et al. (1975) named *Testudo marginata cretensis* on the basis of a rather complete, large (CL = 31 cm) shell (AMPG 3/1974) of a supposedly female individual from the Late Pleistocene of Gerani Cave in Crete Island, to which they additionally referred another shell from the nearby coeval Zourida Cave (*Figure 12*). These authors differentiated their new subspecies from the nominal species *Testudo marginata* that occurs in continental Greece, mostly on the basis of the shape of neurals I and II, and the width, size, and shape of the pygals and xiphiplastra (Bachmayer et al. 1975). Two years later, Kotsakis (1977) referred to *T. marginata cretensis* additional specimens from other Pleistocene Cretan caves, namely Bate and Simonelli. Taking into consideration the total absence of testudinids from the extant herpetofauna of Crete, Georgalis and Kear (2013) speculated that *T. marginata cretensis* had been eventually driven to extinction due to post-glacial environmental and climatic change or even human arrival and interaction. Finally, on the basis of unpublished data, Rhodin et al. (2015) preliminarily regarded the Cretan tortoise as a junior synonym of the continental *T. marginata*. I here tentatively follow the latter view.

**Figure 12.** Photograph of a carapace (AMPG uncat.) referred to *Testudo marginata cretensis* from the Late Pleistocene of Zourida Cave, Crete. Specimen depicted in dorsal (A) and lateral (B) views. Photo courtesy of AMPG. Scale bars = 10 cm.

*Palaeochelys rueckerti* Schleich, 1994.

On the basis of incomplete material from the lignites of the late Oligocene or early Miocene of Küçükdoğanca Köyü, near Kesan, in the European part of Turkey, Schleich (1994) named two aquatic pan-testudinoids, *Palaeochelys ruecketi* and *Palaeochelys turcica* which he tentatively placed within *Palaeochelys* Meyer, 1847 (*Figure 13*). The former taxon was based on a partial carapace and a plastron fragment (BSPG 1980 x 233), whereas an additional partial plastron (BSPG 1980 x 232) was also rendered as the paratype of this species (Schleich 1994). *Palaeochelys rueckerti* was diagnosed and differentiated from other pan-testudinoids on the basis of its roundish and cordiform entoplastron, the projecting epiplastral lip, the hexagonal shape of neurals II, III, and IV, the shape of marginals, and its overall small size, with a carapace lenght of around 16–18 cm (Schleich 1994). *Palaeochelys turcica* was based on a more incomplete specimen, the anterior portion of a carapace and plastron (BSPG 1980 x 234), whereas an additional fragment of a plastron was referred to the same species. *Palaeochelys turcica* was differentiated from the sympatric *P. rueckerti* and other pan-testudinoids by the shape and size of its entoplastron, epiplastron, marginals, and neurals (Schleich 1994). Despite being among the only few named Oligo-Miocene pan-testudinoid taxa from southeastern Europe, *Palaeochelys rueckerti* and *P. turcica* received only minor attention and mentions in chelonian literature. Hervet (2003, 2004) diagnosed the generic placement of both Turkish taxa in *Palaeochelys*, on the basis of the absence of a small

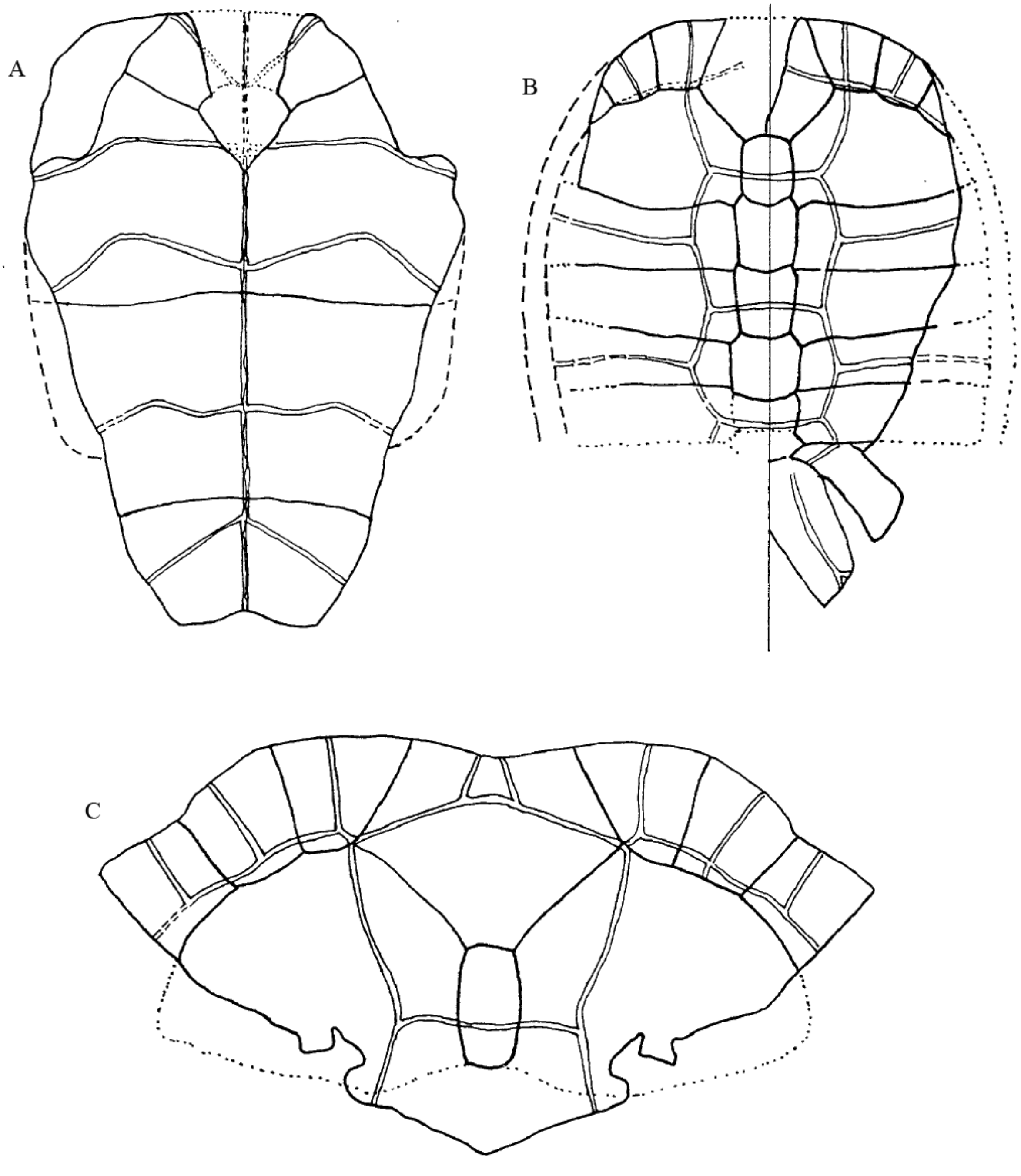

**Figure 13.** Reconstructions of the holotype shells of *Palaeochelys rueckerti* (BSPG 1980 x 233) (A, B) and *Palaeochelys turcica* (BSPG 1980 x 234) (C) from the late Oligocene or early Miocene of Küçükdoğanca Köyü, near Kesan. Both species are herein considered as synonyms and belonging to *Mauremys*. Image modified from Schleich (1994). Specimens depicted in ventral (A) and dorsal (B, C) views.

posterior concavity on vertebrals V, but nevertheless considered them as having probable affinities with *Mauremys* Gray, 1869, due to their large vertebrals. The same author further expressed preliminary thoughts that both *Palaeochelys rueckerti* and *P. turcica* could be synonyms, however, she refrained from providing any formal synonymization (Hervet 2003). Judging from the published figures of Schleich (1994), I provisionally agree with Hervet (2003, 2004) and consider both forms as belonging to *Mauremys*, rendering them as one of the oldest occurrences of that genus in Eastern Mediterranean. Furthermore, mostly on the basis of geographical and stratigraphical grounds, I consider both species as synonyms, and as first revisor, I am selecting the more complete, *Palaeochelys rueckerti*, as the senior synonym and valid taxon, which I recombine into *Mauremys*, as *Mauremys rueckerti* (Schleich, 1994).

*Palaeochelys turcica* Schleich, 1994.
See *Palaeochelys rueckerti* above.

*Varanus amnhophilis* Conrad et al., 2012.
*Varanus amnhophilis* was established by Conrad et al. (2012) on the basis of specimen AMNH FR 30630, which consists of a partial skull roof, the right side of a braincase, a partial posterior mandible, a fragment of a clavicle, and parts of six vertebrae, from the late Miocene (MN 12) of the Mytilinii Formation in Samos Island (*Figure 14*). Conrad et al. (2012) diagnosed their new varanid taxon mostly on the basis of features on the braincase and the quadrate, and they further considered that its anatomy was distinct enough to warrant the erection of a new, monotypic subgenus, *Varaneades*, in order to accommodate it. The authors conducted a phylogenetic analysis which recovered *V. amnhophilis* as belonging to the same clade with several extant Eastern Asian *Varanus* spp. (Conrad et al. 2012). The material originated from a Miocene continental environment, full of mammalian predators in terms of both diversity and quantity, and accordingly, palaeoecological implications surrounding *V. amnhophilis* were also analyzed (Conrad et al. 2012). The authors curiously misidentified the type material of the almost coeval *Varanus marathonensis* from Pikermi, stating that the holotype of this latter species was the vertebra first described by Gaudry (1862a, 1862b, 1862–1867) and not the cranial material of Weithofer (1888), which they erroneously simply regarded it as a referred one (see also above). In any case, the preserved cranial material of *V. amnhophilis* consists of elements that are rather infrequent in the fossil record of monitor lizards. As such, no direct comparison of *V. amnhophilis* with the geographically and stratigraphically proximal *V. marathonensis* or other European or Asian fossil species can be made. The only exception with partial anatomical overlap is the recently described *Varanus mokrensis* Ivanov et al., 2017, known from abundant cranial and postcranial material from the early Miocene of Czechia, which nevertheless appears to be a rather distinct form in terms of, among others, prootic, otoccipital, quadrate, and vertebral morphology. Curiously also, Ivanov et al. (2017) used in their phylogenetic analyses, except for *Varanus amnhophilis*, also

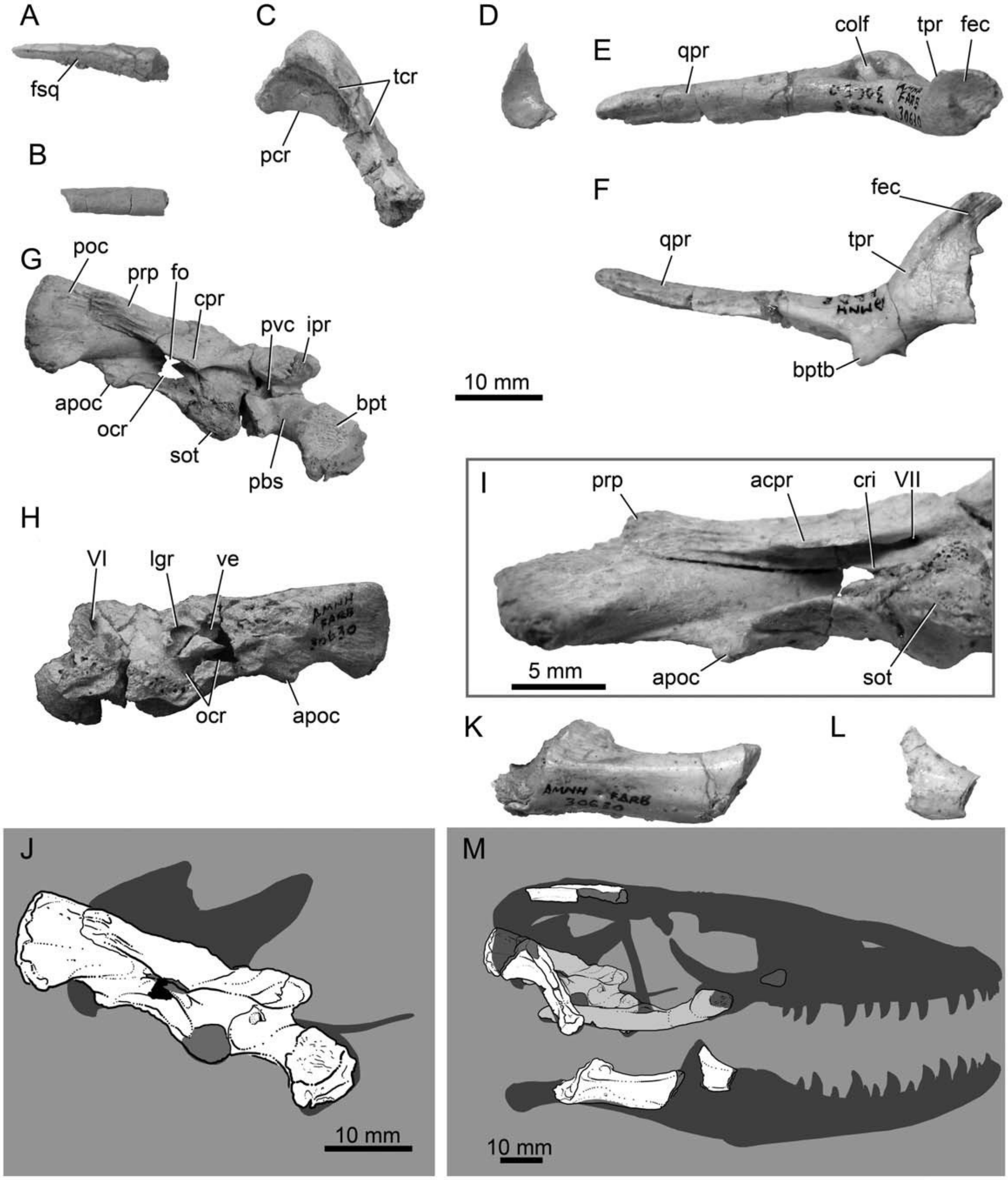

**Figure 14.** Cranial elements (A–I and K–L) of the type material (AMNH FR 30630) and reconstructions of the braincase (J) and the skull (M) of *Varanus amnhophilis* from the late Miocene of Samos. Elements include: fragmentary right postorbital (A) and squamosal (B) in lateral view, a right quadrate in lateral view (C), a fragmentary palatine in ventral view (d), a right pterygoid in lateral (E) and ventral (F) views, right side of the braincase (parabasisphenoid, prootic, basioccipital, and otooccipital) in lateral (G) and medial view (H), the otic region of the braincase in ventral view (I), a partial right surangular-prearticular/articular complex in lateral view (K), and a partial right coronoid in lateral view (L). Image adapted from Conrad et al. (2012). Abbreviations: apoc, paroccipital tuberosity; acpr, anterostapedial process of the prootic crest; bpt, basipterygoid process; bptb, basipterygoid buttress; colf, columellar fossa; cpr, prootic crest (crista prootica); cri, crista interfenestralis; fec, ectopterygoid facet; fo, fenestra ovalis; fsq, squamosal facet (on postorbital); ipr, inferior process; pbs, parabasisphenoid; pcr, posterior crest; ped, hypapophyseal pedicel; poc, otooccipital paroccipital process; prp, prootic paroccipital process; poz, postzygapophysis; pvc,

posterior opening of the vidian canal; qpr, quadrate process; sot, sphenooccipital tubercle; syn, synapophysis; tcr, tympanic crest; tpr, transverse process; I–XII, cranial nerves.

a taxon called "*Varanus mytilini*", and they recovered them at different positions in their trees. However, this is erroneous, as the latter name is simply an earlier, unpublished name (thus, a nomen nudum) of *Varanus amnhophilis*. In any case, the varanid from Samos is herein tentatively treated as a valid species.

*Nostimochelone lampra* Georgalis et al., 2012.

Georgalis et al. (2013) established *Nostimochelone lampra* on the basis of a partial carapace and plastron (NMP V1) from the early Miocene (Burdigalian) of Nostimo, in Western Macedonia (*Figure 15*). Apart from being one of the oldest fossil turtles from Greece, *N. lampra* is also one of the only two youngest records of pleurodires from Europe, the other being the now lost holotype of *Podocnemis lata* Ristori, 1895, from the Miocene of Malta, as all previously immediately older records from the continent were of Eocene age (Georgalis et al. 2013; Georgalis and Kear 2013). *Nostimochelone lampra* was referred to Podocnemidoidea (sensu Gaffney et al. 2006), however, no secure placement within the clades Bothremydidae or Podocnemididae could be made (Georgalis et al. 2013). Nevertheless, the Greek taxon is clearly distinct from all other pan-podocnemidoids by possessing six elongate and remarkably transversely-compressed neurals, and a broad nuchal embayment that extends onto the first peripherals, an anteroposteriorly elongate costal I with a concave internal axillary process scar extending to the midline of the plate and laterally crossing the juncture between peripheral II and peripheral III, an inguinal buttress contacting costals V but not extending beyond its lateral extremity, humeral scutes with a midline contact over the entoplastron, and pectoral-abdominal sulcus extending well anterior to the mesoplastron (Georgalis et al. 2013). The presence of *Nostimochelone lampra* in the early Neogene of Europe does not necessarily imply a late survival of European Paleogene pleurodires, although this could well be the case. Rather than that, Georgalis et al. (2013) and Georgalis and Kear (2013) suggested that it is more plausible that its lineage represents the product of a trans-Tethyan dispersal from Africa to Mediterranean Europe, especially taking into consideration the probably marine palaeoenvironment of the type locality of Nostimo. Note also that the authorship date of *Nostimochelone lampra* is "2012" and not "2013", as the printed version of the article postdated the first published work and the name was registered in ZooBank (ICZN 1999:21.4) (Georgalis and Kear 2013). *Nostimochelone lampra* is considered as a valid pleurodire taxon.

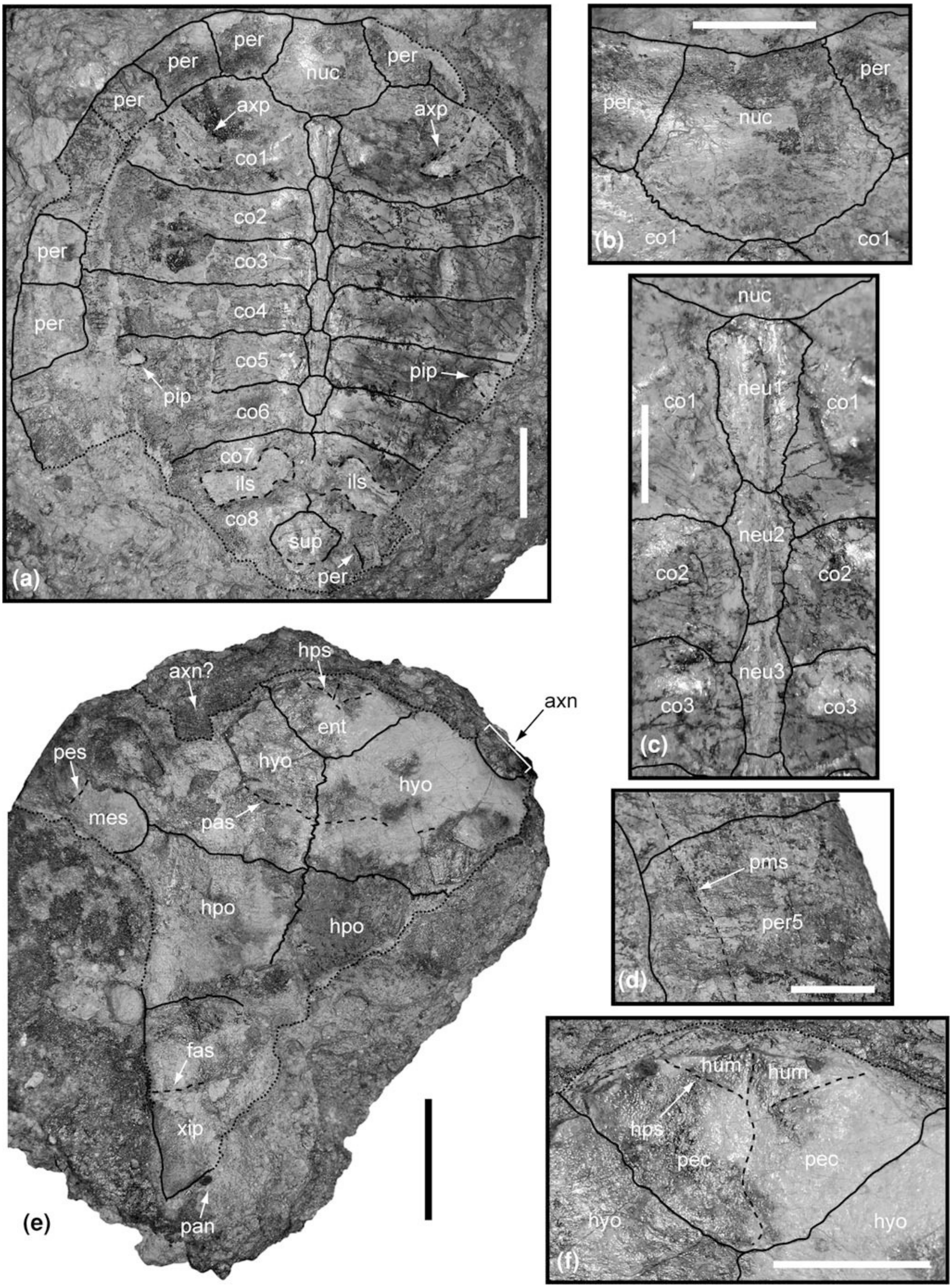

**Figure 15.** Photographs and close ups of the holotype carapace and plastron (NMP V1) of *Nostimochelone lampra* from the early Miocene of Nostimo, Western Macedonia. Image adapted from Georgalis et al. (2013). Scale bars = 50 cm for (a) and (e), 3 cm for (b) and (f), 2 cm for (c), and 1 cm for (d). Abbreviations: axp, anterior axillary process scar; axn, axillary notch; co1–co8 costals one–eight; ent, entoplastron; fas, femoral-anal sulcus; hpo, hypoplastron; hps, humeropectoral sulcus; hum, humerals; hyo, hyoplastron; ils, iliac sutural scar; mes, mesoplastron; neu1–neu3, neurals one–three;

nuc, nuchal; pan, position of anal notch; pas, pectoral-abdominal sulcus; pec, pectorals; per, peripherals; per5, peripheral five; pes, lateral peripheral suture; pip, posterior inguinal process scar; pms, pleural-marginal sulcus; sup, suprapygal; xip, xiphiplastron.

*Cheirogaster bacharidisi* Vlachos et al., 2014.

Vlachos et al. (2014) established *Cheirogaster bacharidisi* on the basis of a rather complete skeleton of a female individual, including the skull (LGPUT EPN I [100–199]) from the Pliocene of Epanomi, near Thessaloniki (Central Macedonia) (*Figure 16*) and further referred additional material from both the same and two other nearby localities. They mentioned throughout their text that a second specimen (a male; LGPUT EPN II [200–287]) from the type locality consisted a paratype, however, in their designation of the type material, they considered it simply as a referred specimen (Vlachos et al. 2014). Whatever the case, paratypes are not essential for taxonomic and nomenclatural purposes. This taxon was originally named as a species of the wastebasket genus *Cheirogaster* Bergounioux, 1935 (Vlachos et al. 2014), but soon after, a phylogenetic analysis of European giant tortoises recombined it to the genus *Titanochelon* (Pérez-García and Vlachos 2014). Based on rather complete material pertaining to different individuals, *Titanochelon bacharidisi* appears to be the most complete giant tortoise find from the Aegean region, surpassing in completeness the previously described *Titanochelon schafferi* (Szalai, 1931) from Samos. Furthermore, *Titanochelon bacharidisi* can be differentiated from all other Neogene European giant tortoises by a combination of both cranial and postcranial features, primarily in the entoplastron and the epiplastra (Vlachos et al. 2014). I herein accept the distinctiveness and validity of this taxon.

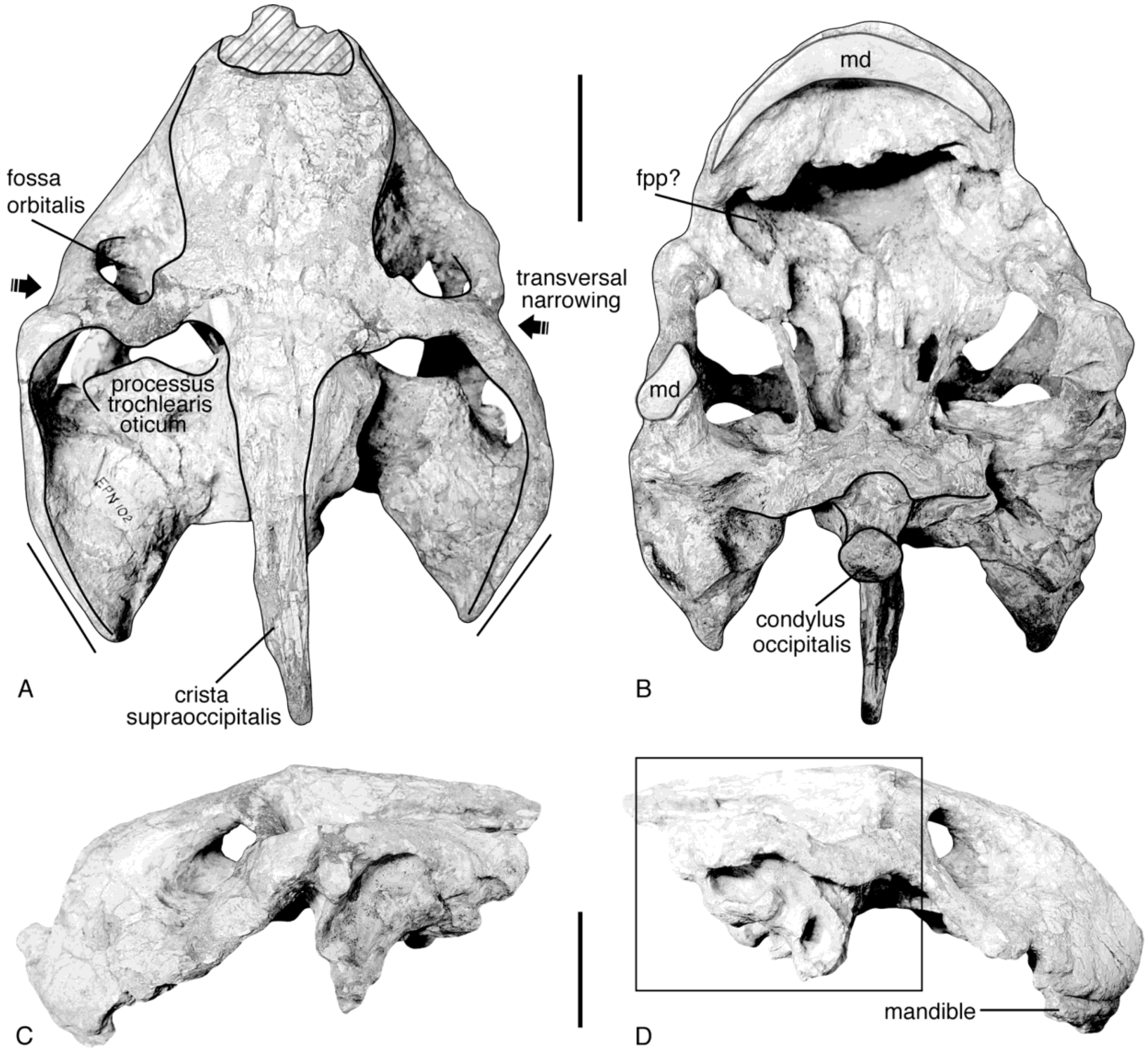

**Figure 16.** Photographs of the holotype skull of *Cheirogaster* (currently placed in *Titanochelon*) *bacharidisi* (LGPUT EPN I [100–199]) from the Pliocene of Epanomi, near Thessaloniki. Specimen depicted in dorsal (A), ventral (B), left lateral (C), and right lateral (D) views. Image adapted from Vlachos et al. (2014). Scale bar = 5 cm. Abbreviations: fpp, foramen palatinum posterius; md, mandible.

*Testudo brevitesta* Vlachos and Tsoukala, 2016.
*Testudo brevitesta* is based on a partial carapace missing its anterior and lateral margins (LGPUT MIL 495) from the early Pliocene of Milia in Western Macedonia (*Figure 17*), with additional carapacial and plastral material from the type locality being referred to the same species (Vlachos and Tsoukala 2016). This taxon was suggested to bear strong resemblance with the extant *Testudo marginata* that currently inhabits the Greek area, in possessing the characteristic posteriorly flared carapace, however, the former, extinct species can be still differentiated from the latter extant one by the posterior carapace being much taller and anteroposteriorly shorter (Vlachos and Tsoukala 2016). Such close resemblance between *Testudo brevitesta* and *T. marginata* was suggested to reflect apparent affinities among the two forms and this view was further supported by a phylogenetic analysis which constantly recovered them both as sister taxa (Vlachos and Tsoukala 2016). I herein accept the validity of this taxon and its affinities with *T. marginata*.

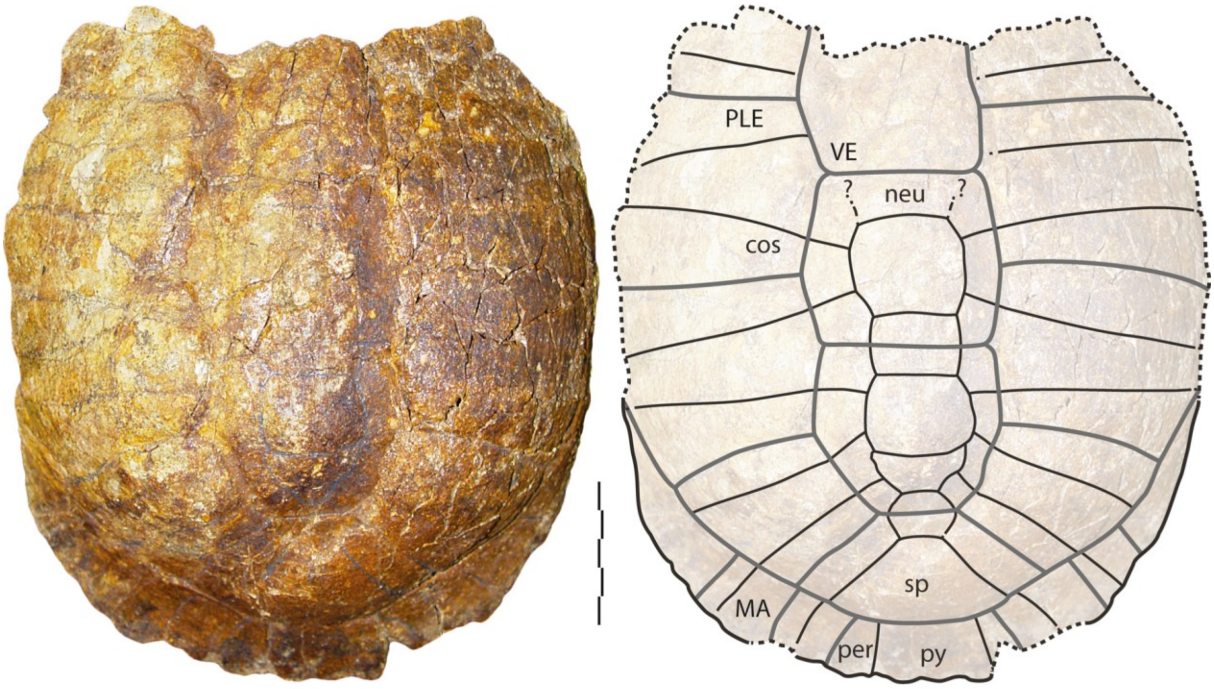

**Figure 17.** Photograph and reconstruction of the holotype carapace of *Testudo brevitesta* (LGPUT MIL 495) from the Pliocene of Milia, Western Macedonia. Image adapted from Vlachos and Tsoukala (2016). Specimen depicted in dorsal view. Abbreviations: cos, costal; MA, marginal; neu, neural; per, peripheral; PLE, pleural; py, pygal; sp, supragygal; VE, vertebral. Scale bar = 5 cm.

## Taxonomic diversity and distribution of the Aegean reptiles through time

The Aegean region currently hosts a relatively diverse extant reptile fauna, at least by European and western Asian standards (Appendix III) (Sindaco et al. 2000, 2013; Sindaco and Jeremčenko 2008; Valakos et al. 2008; Lymberakis and Poulakakis 2010). Nevertheless, the fossil record attests a rather more interesting image of the past in this region, with different extinct clades and species and wider distributions of modern forms (*Figures 18, 19, 20*). The early Cenozoic history of the Aegean reptile fauna, however, is virtually unknown, with not a single find recovered from Paleocene and Eocene sediments, whereas Oligocene records are confined to few and rather fragmentary remains from western Turkey (*Table 1*). The Eocene absence can probably be attributed to anthropogenic biases, as mammal yielding localities of that epoch do exist in Central Anatolia (Maas et al. 2001; Maaga and Beck 2017) and both the Greek and Turkish parts of Thrace (e.g., Métais and Sen 2017), whereas turtles are also known from the Eocene of southern Bulgaria (Khosatzky et al. 1983) and maybe the Former Yugoslav Republic of Macedonia (Pašić and Klinčarski 1959). The Neogene and Quaternary record of fossil reptiles in the Aegean region is more adequately preserved and, in fact, the majority of such finds originates from Miocene localities (*Table 1; Figure 2*).

| Taxon | Oligocene | Miocene | Pliocene | Pleistocene & Holocene | References |
|---|---|---|---|---|---|
| ***TESTUDINES*** | | | | | |
| *Nostimochelone lampra* | | Nostimo (Burdigalian) | | | Georgalis et al. 2013 |
| *Pan-Trionychidae* indet. | Ibribey | | | | Lebküchner 1974 |

| | | | | | |
|---|---|---|---|---|---|
| *Pan-Trionychinae* indet. | | Sofça (MN 7/8); Yeni Eskihisar (MN 7/8); Plakias (MN 9); Bayraktepe (MN 9/10); Kücükçekmece (MN 10); Silivri Maden (MN 10); Hatunsaray (MN 11) | Gefyra (MN 16) | | Malik and Nafiz 1933; Rückert-Ülkümen 1963; Tuna 1988; Staesche et al. 2007; Vlachos et al. 2015a; Georgalis et al. 2016c |
| *Chelydropsis* sp. | Küçükdoğanca Köyü (l.Olig. or e.Mioc.) | Bes Konak (e.Mioc.) | | | Paicheler et al. 1978; Schleich 1994 |
| *Emys orbicularis* | | | | Megalopolis (Late Pleist.); Francthi Cave (Late Pleist.-Holoc.) | Vlachos and Delfino 2016 |
| ?Emydidae indet. | Küçükdoğanca Köyü (l.Olig. or e. Mioc.) | | | | Schleich 1994 |
| *Clemmydopsis* sp. | | Uyurca (MN 6) | | | Staesche et al. 2007 |
| *Mauremys rueckerti* | Küçükdoğanca Köyü (l.Olig. or e. Mioc.) | | | | Schleich 1994 |
| *Mauremys rivulata* | | | | Megalopolis (Late Pleistocene); Karain (Late Pleistocene–Holocene) | Melentis 1966; Zwick and Schleich 1994; Vlachos and Delfino 2016 |
| *Mauremys* sp. | | Çandır (MN 6); Paşalar (MN 6); Sofça (MN 7/8); Karaçay (Langhian); Yaylacilar (MN 7/8); İnönü (MN 9); Plakias (MN 9); Kücükçekmece (MN 11); Amasya (MN 13); Maramena (MN 13/14); | Milia (MN 16) | | Malik and Nafiz 1933; Gad 1990; Staesche et al. 2007; Vlachos et al. 2015b; Georgalis et al. 2016c; Vlachos and Tsoukala 2016 |

| | | | | |
|---|---|---|---|---|
| | Allatini (latest Mioc. or earliest Plioc.) | | | |
| *Testudo marmorum* | Pikermi (MN 12) | | | Gaudry 1862a, 1862b, 1862–1867; Bachmayer and Symeonidis 1970; Georgalis and Kear 2013 |
| *Testudo* cf. *marmorum* | Kücükçekmece (MN 11); Nikiti 2 (MN 11) | | | Malik and Nafiz 1933; Garcia et al. 2016 |
| *Testudo brevitesta* | | Milia (MN 16) | | Vlachos and Tsoukala 2016 |
| *Testudo marginata* | | | Makriyialos (e.Pleist.); Bate Cave (L.Pleist.); Charkadio Cave (L.Pleist.); Gerani Cave (L.Pleist.); Simonelli Cave (L.Pleist.); Xerias (L.Pleist.); Zourida Cave (L.Pleist.) | Bachmayer and Symeonidis 1975; Bachmayer et al. 1975; Kotsakis 1977; Schleich 1982; Tsoukala et al. 2011 |
| *Testudo graeca* | | | Karain (L.Pleist.–e.Holoc.) | Zwick and Schleich 1994 |
| *Testudo* cf. *graeca* | Çandır (MN 6); Sofça (MN 7/8); Yaylacilar (MN 7/8); Yeni Eskihisar (MN 7/8); Termeyenice (Serravallian); Kınık (MN | Akçaköy (MN 15); Akçayır; Megalo Emvolon (MN 15) | Vatera (MN 17) | Campana 1917; Bachmayer and Symeonidis 1970; Bachmayer et al. 1980; De Vos et al. 2002; |

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|  | 12); Kavurca (MN 13); Suleymanli (MN 13); Platanias (late); Allatini (latest Mioc. or earliest Plioc.); Pylaea (latest Mioc. or earliest Plioc.) |  |  | Lapparent de Broin 2002; Staesche et al. 2007; Vlachos and Tsoukala 2014 |
| *Testudo hermanni* |  |  | Megalopolis (L.Pleist.); Francthi Cave (L.Pleist.-Holoc.) | Vlachos and Delfino 2016 |
| *Testudo* sp. | Thymiana (MN 5); Liossati (l.Mioc. or e.Plioc.) | Megalo Emvolon (MN 15) | Psychiko (e.Pleist.) | Arambourg and Piveteau 1929; Paraskevaidis 1955; Bachmayer and Symeonidis 1970, 1976 |
| *Titanochelon schafferi* | Mytilinii (MN 12) |  |  | Szalai 1931 |
| *Titanochelon* cf. *schafferi* | Pikermi (MN 12); Vathylakkos (MN 12); Liossati (late Miocene or early Pliocene) |  | Vatera (MN 17) | Arambourg and Piveteau 1929; Bachmayer 1967; Bachmayer and Symeonidis 1976; De Vos et al. 2002; Lapparent de Broin 2002 |
| *Titanochelon bacharidisi* |  | Epanomi (MN 16); Nea Kallikrateia (MN 16); Nea Michaniona (MN 16) |  | Vlachos et al. 2014 |
| *Titanochelon* sp. | Çandır (MN 6); Çatakbağyaka (MN 7/8); | Apollakia (MN 15); Megalo Emvolon |  | Campana 1917, 1919; Bachmayer et al. 1980; |

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| | | Garkin (MN 11); Pylaea (latest Mioc. or earliest Plioc.) | (MN 15); Milia (MN 16) | | Staesche et al. 2007; Mueller-Töwe et al. 2011; Vlachos and Tsoukala 2016 |
| Testudines indet. | Küçükdoğanca Köyü (l.Olig. or e. Mioc.) | Aliveri (MN 4); Karydia (MN 4) | Apollakia (MN 15) | | Schleich 1994; Mueller-Töwe et al. 2011; Georgalis et al. 2018c |
| ***CROCODYLIA*** | | | | | |
| Crocodylia indet. | Küçükdoğanca Köyü (l.Olig. or e.Mioc.) | Lapsarna (?MN 3); Aliveri (MN 4); Plakias (MN 9) | | | Schleich 1994; Georgalis et al. 2016c, 2018c; Vasileiadou et al. 2017 |
| ***SQUAMATA*** | | | | | |
| *Chamaeleo* cf. *andrusovi* | | Aliveri (MN 4) | | | Georgalis et al. 2016b |
| Chamaeleonidae indet. | | Aliveri (MN 4) | | | Georgalis et al. 2016b |
| Agamidae indet. | | Maramena (MN 13/14) | | Karain (Late Pleistocene–Holocene) | Zwick and Schleich 1994; Richter 1995 |
| cf. *Lacerta* sp. | | | Çeştepe (MN 14) | Emirkaya-2 (M.Pleist.); Karain Cave (L.Pleist.–Holoc.) | Zwick and Schleich 1994; Richter 1995; Sen et al. 2017 |
| *Podarcis* cf. *erhardii* | | | | Bate Cave (L.Pleist.) | Kotsakis 1977 |
| Lacertidae indet. | | Lapsarna (?MN 3); Aliveri (MN 4); Karydia (MN 4); Ano Metochi (MN 13); Maramena (MN 13/14) | Çalta (MN 15) | Latomi (Middle Pleistocene); Simonelli Cave | Schneider 1975; Rage and Sen 1976; Mangilli 1980; Richter 1995; Georgalis et al. 2017a, 2018c; Vasileiadou |

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|  |  |  |  |  | et al. 2017 |
| Cordylidae indet. |  | Ano Metochi (MN 13); Maramena (MN 13/14) |  |  | Richter 1995; Georgalis et al. 2017a |
| Scincomorpha indet. |  | Aliveri (MN 4); Karydia (MN 4) | Çalta (MN 15) |  | Rage and Sen 1976; Georgalis et al. 2018c |
| *Anguis* sp. |  | Bağiçi (MN 7/8); Süleymanli (MN 13) |  |  | Čerňanský et al. 2017 |
| *Ophisaurus* sp. | Kargi 2 (MP 30–MN 1) | Keseköy (MN 3); Karydia (MN 4); Çandir (MN 6); Bağiçi (MN 7/8); Ano Metochi (MN 13); Süleymanli (MN 13) |  |  | Čerňanský et al. 2017; Georgalis et al. 2017a, 2018c |
| *Pseudopus* cf. *apodus* |  |  |  | Emirkaya-2 (M.Pleist.) | Venczel and Sen 1994 |
| *Pseudopus* sp. |  |  | Çalta (MN 15) | Karain (L.Pleist.–Holoc.) | Zwick and Schleich 1994; Rage and Sen 1976 |
| Anguinae indet. | Kocayarma (MP 25); Kavakdere (MP 26/27); Kargi 2 (MP 30–MN 1) | Kargi 3 (MN 1); Kılçak 3b (MN 1); Sabuncubeli (MN 3); Keseköy (MN 3); Aliveri (MN 4); Karydia (MN 4); Çandir (MN 6); Çandir HW (MN 6); Bağiçi (MN 7/8); Ravin de la Pluie (MN 10); Ano Metochi (MN 13); Süleymanli (MN 13) | Çeştepe (MN 14) |  | Čerňanský et al. 2017; Sen et al. 2017; Georgalis et al. 2017a, 2018b, 2018c |
| *Varanus* |  | Pikermi (MN |  |  | Weithofer |

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| *marathonensis* | 12) |  |  | 1888 |
| *Varanus amnhophilis* | Mytilinii (MN 12) |  |  | Conrad et al. 2012 |
| *Varanus* sp. | Ravin de la Pluie (MN 10); Pikermi (MN 12) | Çeştepe (MN 14); Çalta (MN 15) | Tourkobounia 5 (M.Pleist.) | Gaudry 1862a, 1862b, 1862–1867; Nopcsa 1908; Rage and Sen 1976; Georgalis et al. 2017b, 2018b; Sen et al. 2017 |
| *Blanus* cf. *strauchi* | Gebeceler (MN 7/8) |  |  | Georgalis et al. 2018a |
| Amphisbaenia indet. | Plakias (MN 9) | Çalta (MN 15) |  | Rage and Sen 1976; Georgalis et al. 2016c |
| Scolecophidia indet. | Ano Metochi (MN 13) | Maritsa (MN 14); Çalta (MN 15); Tourkobounia 1 (MN 16) | Emirkaya-2 (M.Pleist.); Tourkobounia 2 (M.Pleist.); Tourkobounia 5 (M.Pleist.) | Rage and Sen 1976; Szyndlar 1991a; Venczel and Sen 1994; Georgalis et al. 2017a |
| *Python euboicus* | Kymi (MN 3/4) |  |  | Römer 1870 |
| *Eryx jaculus* |  |  | Latomi (M.Pleist.); Pili B (?L.Pleist.) | Schneider 1975; Szyndlar 1991a |
| cf. *Eryx* sp. |  | Maritsa (MN 14); Çalta (MN 15); Spilia 4 (MN 15) |  | Rage and Sen 1976; Szyndlar 1991a |
| *Dolichophis caspius* |  |  | Emirkaya-2 (M.Pleist.) | Venczel and Sen 1994 |
| cf. *Dolichophis* sp. | Ano Metochi (MN 13) |  |  | Georgalis et al. 2017a |
| *Elaphe quatuorlineata* |  |  | Tourkobounia 2 (M.Pleist.) | Szyndlar 1991a |
| *Elaphe* cf. *quatuorlineata* |  |  | Emirkaya-2 (M.Pleist.) | Venczel and Sen 1994 |
| *Hierophis* cf. *gemonensis* |  |  | Bate Cave (L.Pleist.) | Kotsakis 1977 |

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| *Hierophis* cf. *hungaricus* | Maramena (MN 13/14) |  |  | Szyndlar 1995 |
| *Malpolon* sp. |  | Tourkobounia 1 (MN 16) |  | Szyndlar 1991a |
| cf. *Telescopus* sp. |  |  | Emirkaya-2 (M.Pleist.) | Venczel and Sen 1994 |
| *Zamenis situla* |  |  | Tourkobounia 2 (M.Pleist.) | Szyndlar 1991a |
| “Colubrinae” indet. | Ravin de la Pluie (MN 10); Ano Metochi (MN 13) |  | Emirkaya-2 (M.Pleist.); Latomi (M.Pleist.); ?Karain (L.Pleist.–Holoc.) | Venczel and Sen 1994; Zwick and Schleich 1994; Schneider 1975; Georgalis et al. 2017a, 2018b |
| *Natrix* cf. *natrix* |  |  | Emirkaya-2 (M.Pleist.) | Venczel and Sen 1994 |
| *Natrix* cf. *tessellata* |  |  | Gerani (L.Pleist.) | Szyndlar 1991b |
| *Natrix* sp. | Ano Metochi (MN 13) |  |  | Georgalis et al. 2017a |
| “Natricinae” indet. | Lapsarna (?MN 3); Plakias (MN 9); Maramena (MN 13/14) | Ericek (MN 15) | Latomi (M.Pleist.) | Schneider 1975; Szyndlar 1991b, 1995; Hoek Ostende et al. 2015; Georgalis et al. 2016c; Vasileiadou et al. 2017 |
| Colubridae indet. | Aliveri (MN 4); Karydia (MN 4) |  |  | Georgalis et al. 2018c |
| *Naja* cf. *romani* | Ravin de la Pluie (MN 10) |  |  | Georgalis et al. 2018b |
| *Naja* sp. | Maramena (MN 13/14) | Çalta (MN 15); Tourkobounia 1 (MN 16) |  | Rage and Sen 1976; Szyndlar and Zerova 1990; Szyndlar 1991b, 1995 |
| *Laophis crotaloides* | Megalo Emvolon (MN 15) |  |  | Owen 1857; Georgalis et al. 2016a |
| “Oriental | Maramena | Tourkobounia | Emirkaya-2 | Schneider |

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| vipers” complex | (MN 13/14) | 1 (MN 16) | (M.Pleist.); Latomi (M.Pleist.) | 1975; Venczel and Sen 1994; Szyndlar 1991b, 1995 |
| Viperidae indet. | Aliveri (MN 4) | | | Georgalis et al. 2018c |
| Serpentes indet. | Lapsarna (?MN 3); Aliveri (MN 4); Karydia (MN 4); Ano Metochi (MN 13); Maramena (MN 13/14) | Ericek (MN 15) | | Szyndlar 1995; Hoek Ostende et al. 2015; Georgalis et al. 2017a, 2018c; Vasileiadou et al. 2017 |
| Squamata indet. | Lapsarna (?MN 3); Aliveri (MN 4); Karydia (Mn 4); Ano Metochi (MN 13) | | | Georgalis et al. 2017a, 2018c; Vasileiadou et al. 2017 |

**Table 1.** The diversity of fossil reptiles from the Aegean region. Included here are only taxa that have been formally described and/or figured in the literature. The majority of specimens in Staesche et al. (2007) was not figured or only briefly documented and therefore the respective taxonomic opinions should be regarded as tentative. *Testudo sloanei* Lydekker, 1889, is not indicated here due to its uncertainty around its stratigraphic origin and its taxonomic status. Also ommited is the indeterminate testudinid from Korydallos, described by Paraskevaidis (1961), as this was reported to originate from indifferentiated “Tertiary”.

Turtles are now represented in the Aegean region by 11 pan-trionychid, cheloniid, dermochelyid, emydid, geoemydid, and testudinid species (Sindaco et al. 2000, 2013; Sindaco and Jeremčenko 2008; Appendix III). With the notable absence of marine turtles (chelonioids), all of these clades also appear as fossils in different localities in Greece and Turkey, in addition to the now locally or totally extinct pleurodires and pan-chelydrids (*Figure 18*). Pleurodires are only represented by the holotype and only known specimen of the podocnemidoid taxon *Nostimochelone lampra* from the early Miocene (Burdigalian) of Nostimo in northwestern Greece (Georgalis et al. 2013). This is one of the stratigraphically youngest pleurodires from Europe and the sole member of that clade from the southeastern part of the continent (Georgalis and Kear 2013). The geographically most proximal Miocene pleurodires are an indeterminate form from Malta (type of *Podocnemis lata*) and several podocnemidoids from Egypt (Gaffney 2011). Considering that pleurodires had otherwise become extinct in Europe during the Paleogene, the rather sporadic occurrence of this clade in the Miocene of Mediterranean Europe probably implies a short lived marine dispersal from Northern Africa during the early Neogene, rather than a late survival of the Eocene European forms (Georgalis et al. 2013; Georgalis and Kear 2013). A single pan-trionychid taxon,

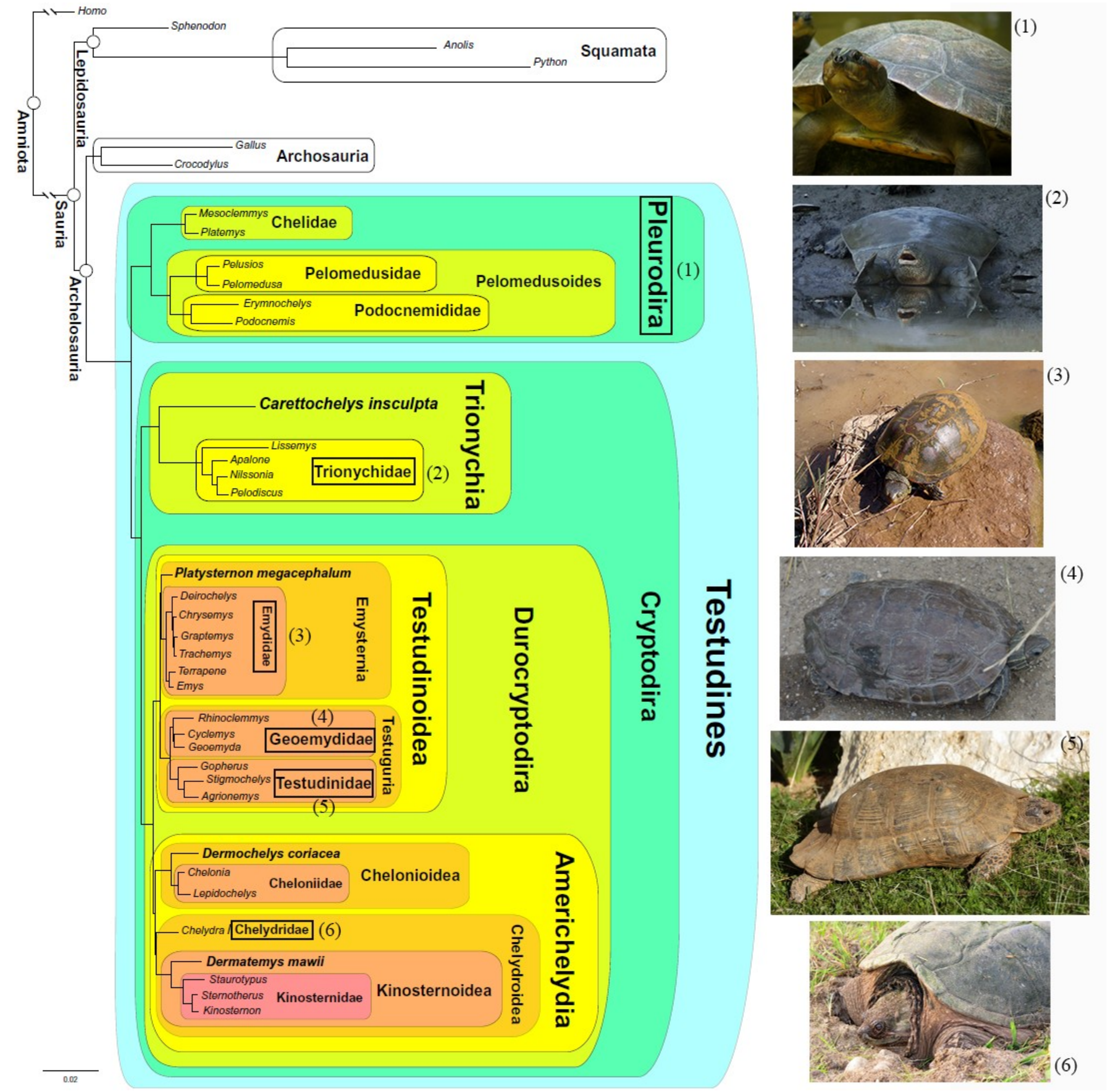

**Figure 18.** Phylogenetic relationships of turtles after Crawford et al. (2015). Rectangulars indicate the clades that have been recovered as fossils from the Aegean region. Numbers in brackets correspond to photographs of selected extant representatives from each clade. Photographs: (1), (2), (3), and (6) from Wikipedia; (5) from Ilias Strachinis archive; (4) by me.

*Trionyx triunguis* (Forskål, 1775), is known in the extant herpetofauna of the Aegean region, whereas *Rafetus euphraticus* (Daudin, 1801) currently inhabits far eastern Anatolia. Fossils of pan-trionychids have been recoved from both Greece and Turkey, spanning from the Oligocene to the Pliocene, but always consisting of rather fragmentary remains, not permitting a more precise taxonomic allocation. However, pan-trionychids seem to be already present in the broader region by much older times, as it is testified by the type of *Trionyx capellinii bulgaricus* (an indeterminate pan-trionychid according to Georgalis and Joyce (2017 [**Appendix 1**]) from the late Eocene (Priabonian) of southern Bulgaria (Khosatzky et al. 1983). In their review of Old World pan-trionychids, Georgalis and Joyce (2017

[**Appendix 1**]) treated the Paleogene material from Turkey as indeterminate pan-trionychids, taking into consideration the diversity of lineages occurring at that time in Europe, whereas for the Neogene Aegean forms, they provided a more precise designation as indeterminate pan-trionychines, regarding that pan-cyclanorbines appear to be absent from that epoch in the continent. Unfortunately, there is of yet no cranial or adequate plastral material from Greek and Turkish localities that would permit a generic attribution of these fossils to either the lineages of *Trionyx* Geoffroy Saint-Hilaire, 1809 or *Rafetus* Gray, 1864, which occurred in Europe during the Neogene (Georgalis and Joyce 2017 [**Appendix 1**]). It is probable that the Oligocene pan-trionychid specimens from western Turkey also represent pan-trionychines and that all Aegean fossils of soft shelled turtles belong indeed to a single lineage, however, this theory is speculative for the moment. In any case, judging from the few only localities that yielded their fossil remains, pan-trionychids are infrequent in the Aegean palaeoecosystems, though this could be attributed to collection biases. The youngest fossil pan-trionychids from the area are known from the late Pliocene and around then was probably marked their total and final extinction from the continental eastern Europe, as extant individuals of *Trionyx triunguis* found in the Dodecanese Islands are believed to be simply products of occasional marine dispersals from adjacent Anatolian coasts (Taskavak et al. 1999; Vlachos et al. 2015a; Georgalis and Joyce 2017 [**Appendix 1**]). Fossil pan-chelydrids were also infrequent in the Aegean herpetofauna, known by only two records from the Oligocene and Miocene of Turkey, though this scarceness of remains could be probably attributed as well to collection biases. The older record, from the Oligocene or early Miocene of Küçükdoğanca Köyü in the European part of Turkey, is rather fragmentary (Schleich 1994), but the younger one, from the early Miocene of Bes-Konak, consists of well preserved and complete material (Paicheler et al. 1978). They are both considered to be members of *Chelydropsis* Peters, 1868, the sole valid pan-chelydrid from Eurasia and also among the southern records of that clade in the Old World (Joyce 2016). Emydids have a rather poor fossil record in the Aegean region, despite the currently wide distribution and abundance of these turtles in Greece and Turkey (Sindaco et al. 2000, 2013; Sindaco and Jeremčenko 2008; Valakos et al. 2008). Apart from a single, dubious, and poorly documented occurrence in the late Oligocene or early Miocene of Küçükdoğanca Köyü (Schleich 1994), the only verified record of that clade in the Aegean is known from material attributed to the extant *Emys orbicularis* (Linnaeus, 1758) from two late Quaternary localities in Peloponnese (Vlachos and Delfino 2016). The latter authors further suggested that southern Greece acted as a kind of refugium for emydids during the glacial times, with these aquatic turtles further recovering and expanding their distribution throughout Europe at the end of the Quaternary (Vlachos and Delfino 2016). As far as it concerns the Oligo-Miocene purported emydid from Küçükdoğanca Köyü, the poor quality of the figures and the inadequate original description of Schleich (1994) casts doubts on its exact taxonomic attribution. As such, this fragmentary material may well pertain to an indeterminate geoemydid or be conspecific with *Mauremys rueckerti*, which is known from the same locality. Afterall, the name "Emydidae" was used until relaively recently to also encompass *Mauremys* (e.g., Staesche et al. 2007), so it cannot be certain exactly which turtle clade Schleich (1994) was meaning. Ptychogasterids consist an extinct clade of pan-testudinoid turtles, which probably lie near or even within geoemydids (e.g., Hervet 2003, 2004; Luján et al. 2014). In any case, in the Aegean region, ptychogasterids are known solely by a single shell fragment from the middle Miocene of central Anatolia that was referred to *Clemmydopsis* cf. *turnauensis* by Staesche et al. (2007). The same authors also attributed to the same taxon an additional fragment from eastern Anatolia (Staesche et al. 2007), which, geographically speaking, is not taken into consideration here. Nevertheless, the central Anatolian material is too fragmentary for species level determination, but an attribution to *Clemmydopsis* Boda, 1927, is tentatively accepted here. The extreme rareness of this lineage in the Aegean region, known only by a single specimen, seems to reflect a real absence from the fossil record of that area, however, the possibility that certain remains of ptychogasterids have been misidentified for geoemydids could also be the case. Geoemydids appear to be quite abundant in the fossil record of the Aegean region, being represented by the enigmatic *Mauremys rueckerti*, the extant *Mauremys rivulata* (Valenciennes, 1833), and *Mauremys caspica* (Gmelin, 1774), and several indeterminate forms of *Mauremys* (Malik and Nafiz 1933; Melentis 1966; Gad 1990; Schleich 1994; Zwick and Schleich 1994; Staesche et al. 2007; Vlachos et al. 2015b; Georgalis et al. 2016c [**Appendix 6**]; Vlachos and Delfino 2016; Vlachos and Tsoukala 2016). *Mauremys rueckerti* is a rather bizarre taxon, known only from a single locality, the late Oligocene or early Miocene Küçükdoğanca Köyü in Edirne region (Schleich 1994). If the herein proposed generic attribution of this species to *Mauremys* is correct, then it represents one of the earliest known occurrences of that genus. The extant species *Mauremys rivulata*, which is widely distributed in the Balkans and Anatolia today, is found in the fossil record of the Aegean region with confidence only in the Quaternary of two localities in Peloponnese and southern Anatolia (Melentis 1966; Zwick and Schleich 1994; Vlachos and Delfino 2016). The presence of *Mauremys caspica* in the fossil record has not been confirmed with certainty, with purported records from Greece (e.g., Melentis 1966) in fact representing the above-mentioned *M. rivulata*. Otherwise, there are plenty of fossil specimens from different localities in both Greece and Turkey, spanning between the middle Miocene and the late Pliocene, that pertain to indeterminate members of *Mauremys* (Malik and Nafiz 1933; Gad 1990; Staesche et al. 2007; Vlachos et al. 2015b; Georgalis et al. 2016c [**Appendix 6**]; Vlachos and Tsoukala 2016). Due to the incompleteness of the material, however, it is not possible to assess whether they represent multiple distinct species within *Mauremys* or are members of a single lineage. So far, no other fossil geoemydid genera have been described from the Aegean region, as is the case with other Eastern European regions, where, apart from *Mauremys*, other lineages have been described (e.g., the extant *Melanochelys* Gray, 1869, and the extinct *Sakya* Bogachev, 1960). In any case, geoemydids achieved a wide distribution in the Aegean region becoming one of the most prominent turtle clades in the area during the Neogene and Quaternary. Testudinidae consist by far the most abundant fossil turtles from the Aegean region (Georgalis and Kear 2013). This clade is also diverse in the extant herpetofauna of Greece and Turkey, especially depending the actual taxonomic content within the *Testudo graeca* species complex or the distinctive validity or not of the supposedly Peloponnese dwarf endemic taxon *Testudo weissingeri* Bour, 1995 (e.g., Bour 1995; Perälä 2002; Fritz et al. 2005; Lapparent de Broin et al. 2006a, 2006b, 2006c; Parham et al. 2006; Fritz and Havaš 2007). Aegean testudinids first appear at a relatively younger stage (middle Miocene [MN 5]) in comparison to the other previously mentioned turtle clades, but since then they have an almost continuous presence in the fossil record of the area. Two monophyletic lineages can be distinguished: small-sized forms belonging to the genus *Testudo* and large-sized ones pertaining to *Titanochelon*. The oldest confirmed occurrence of *Testudo* is documented in the middle Miocene (MN 5) of Thymiana, in Chios Island. Although the already described material has not been properly analyzed in order to evaluate its alpha taxonomy, distinct taxa have been identified or even named in the Neogene of the region. *Testudo marmorum* is the first described fossil tortoise from the region (Gaudry 1862a, 1862b, 1862–1867) and furthermore, its late Miocene (MN 12) age renders it as the stratigraphically oldest species of the *Testudo* sensu stricto lineage (Georgalis and Kear 2013; Vlachos and Rabi 2018). Rather similar or even conspecific forms have been recovered from slightly older (MN 11) sediments in Kücükçekmece, near Istanbul, and Nikiti-2, near Thessaloniki (Malik and Nafiz 1933; Garcia et al. 2016). The extant taxon *Testudo graeca* is confidently known from the Latest Pleistocene or early Holocene of the Karain Cave, Antalya (Zwick and Schleich 1994), although this lineage dates back to the latest Miocene, as is suggested by a strongly similar specimen from Platania in northern Greece (*Testudo* cf. *graeca* of Vlachos and Tsoukala 2014). Other, rather similar or even conspecific specimens are also known from the latest Miocene or earliest Pliocene of Allatini, near Thessaloniki (*Testudo amiatae* of Campana 1917; Vlachos et al. 2015b), the Pliocene of Megalo Emvolon, also near Thessaloniki (Bachmayer et al. 1980), and the early Pleistocene of Lesvos (*Testudo* sp. of De Vos et al. 2002; *Testudo* cf. *graeca ibera* of Lapparent de Broin 2002). Staesche et al. (2007) described several specimens from middle and late Miocene localities from Anatolia as *Testudo* cf. *graeca*. All of these specimens, however, are incomplete and although they provide a slight hint that the *T. graeca* lineage existed in the region already by the middle Miocene, their exact affinities cannot be reliably evaluated. A second taxon that still occurs in the area, *Testudo hermanni* Gmelin, 1789, is practically absent from the Aegean fossil record, with the exception of recently described, referred material from the late Quaternary of Peloponnese (Vlachos and Delfino 2016). Europe's largest extant testudinid taxon, *Testudo marginata*, currently distributed ony in Greece, Albania, and historically introduced to Sardinia, is also respresented in the Aegean fossil record, denoting though a much wider range during the Quaternary (Georgalis and Kear 2013). In fact, the sole known mainland occurrences of *T. marginata* are known from the early Pleistocene of Makriyialos locality in Peloponnese (Schleich 1982), well within the range of the extant populations, whereas an additional incomplete specimen from Xerias, Eastern Macedonia, originally described as indeterminate species of *Testudo* (Tsoukala et al. 2011), was eventually referred to *T. marginata* (Vlachos and Tsoukala 2016). Interestingly, however, the majority of remains and the most complete material attributed to *T. marginata* has been recovered from the islands of Crete and Tilos (Georgalis and Kear 2013). The Cretan material consists of nicely preserved specimens from a number of Late Pleistocene caves across the island that were considered to represent a supposedly endemic subspecies, *Testudo marginata cretensis* (Bachmayer et al. 1975; Kotsakis 1977). The Tilos island finds originate from Charkadio cave and appear to be of more controversial affinities, as they are solely represented by appendicular remains (Bachmayer and Symeonidis 1975), thus providing no actual diagnostic traits for species determination. Whatever the exact identity of the Tilos finds may be, it is apparent that *Testudo marginata* achieved a much wider distribution in the immediate past, managing to colonize even the distant island of Crete. It is, however, yet unclear how *T. marginata* reached Crete. One scenario suggests a marine dispersal from southern Peloponnese to Crete during the Pleistocene, as tortoises are known to have successfully colonized distant oceanic islands (Rhodin et al. 2015). Alternatively, a possible land bridge may have existed between the areas of Peloponnese and Crete at around the culmination of the Glacial events during the Pleistocene. A further scenario involves a much older dispersal during the Miocene when Peloponnese and Crete were united, however, this is incogruent with the fossil record of both continental and insular *Testudo marginata*, which are confined to the Pleistocene. A closely similar species, *Testudo brevitesta*, was recently described from the late Pliocene of Milia in Western Macedonia (Vlachos and Tsoukala 2016). Accordingly, strong affinities of *T. brevitesta* and *T. marginata* are further supported by a phylogenetic analysis, confirming a wider expansion of that lineage in the southern Balkans in the late Neogene (Vlachos and Tsoukala 2016). The large to giant-sized tortoises constitute among the most impressive fossil finds from the Aegean region (Georgalis and Kear 2013). Initially regarded as belonging to the wastebasket genus *Testudo* (Arambourg and Piveteau 1929; Szalai 1931; Bachmayer 1967; Bachmayer and Symeonidis 1976), then subsequently considered members of the wastebasket genus *Cheirogaster* (Lapperent de Broin 2002; Staesche et al. 2007; Georgalis and Kear 2013; Vlachos et al. 2014), they were subsequently referred to *Titanochelon* by Pérez-García and Vlachos (2014). At least two distinct species are known from the Aegean region, namely *Titanochelon schafferi* and *T. bacharidisi*, plus several probably related but unnamed forms (Szalai 1931; Georgalis and Kear 2013; Vlachos et al. 2014). *Titanochelon schafferi* is by far the largest and is known with confidence exclusively from its late Miocene (MN 12) type locality in Samos (Szalai 1931), whereas additional, similar forms have been provisionally referred to the same taxon from the Neogene of Attica and Central Macedonia (Arambourg and Piveteau 1929; Bachmayer 1967; Bachmayer and Symeonidis 1976). Interestingly, fragmentary remains of a huge tortoise from the early Pleistocene of Lesvos were subsequently tentatively referred to this taxon, as cf. *Cheirogaster* aff. *schafferi* by Lapparent de Broin (2002). Whether all of these Neogene and early Quaternary giant tortoises truely belong to *Titanochelon schafferi* or multiple distinct species were present in the area remains yet to be found on the light of new fossil evidence and a comprehensive analysis. *Titanochelon bacharidisi* is a large-sized tortoise, though smaller than *T. schafferi* and is based on rather complete material from the Pliocene of Central Macedonia (Vlachos et al. 2014). The Turkish material of large testudinids is, so far, less complete and understood, although specimens are known already for more than eighty years (Malik and Nafiz 1933). Staesche et al. (2007) described relatively nicely preserved carapacial, plastral, and appendicular remains of giant testudinids from the middle and late Miocene of Anatolia which they tentatively attributed to the Spanish taxon *Titanochelon* (their *Cheirogaster) bolivari*. I consider the resemblance of these Anatolian forms with *Titanochelon bolivari* (Hernández-Pacheco, 1917) to be only superficial and not to reflect taxonomic conspecificity. This Anatolian material is in need of a proper redescription under a modern phylogenetic perspective in order to clarify its exact affinities, but, nevertheless, it clearly attests the presence of giant tortoises in the Aegean region already by the middle Miocene. For the time being, I am treating the Anatolian material simply as *Titanochelon* sp. Other, indeterminate forms of *Titanochelon* are also known from Greece (Bachmayer et al. 1980; Vlachos and Tsoukala 2016), including large egg finds, which are probably attributable to that genus (Campana 1919; Mueller-Töwe et al. 2011). Lastly, the remains of indeterminate turtles from the late Oligocene/early Miocene of Küçükdoğanca Köyü (Edirne) (Schleich 1994) and the early Miocene of Karydia (Eastern Macedonia and Thrace) and Aliveri (Euboea Island) (Georgalis et al. 2018c [**Appendix 11**]) are too fragmentary to permit any further identification, but attest a wide presence of turtles in the Aegean region already by the late Paleogene and early Neogene.

Crocodylians are currently absent from the herpetofauna of the Aegean region. Their fossil record in the area is rather poor, consisting exclusively of isolated teeth from only four Oligo-Miocene localities, whereas crocodyliforms lying outside the crown crododylians have also been recently described from the Early Cretaceous of Anatolia (Jouve et al. 2017). The earliest Cenozoic record is the material described from the Oligocene or early Miocene of Küçükdoğanca Köyü in Edirne (Schleich 1994), followed by similar finds in the early Miocene of Lapsarna in Lesvos (Vasileiadou et al. 2017) and Aliveri in Euboea (Georgalis et al. 2018c [**Appendix 11**]), all confirming that crocodylians had a wide distribution in the area during the late Paleogene and early Neogene. After a long paucity of crocodylian remains, their youngest occurrence in the Aegean region is recorded from the late Miocene (MN 9) of Plakias in Crete (Georgalis et al. 2016c [**Appendix 6**]). It is yet unclear whether these last crocodylians from Crete represent relics of the same early Neogene lineage(s) or they simply managed to eventually disperse to Crete from nearby North Africa (Georgalis et al. 2016c [**Appendix 6**]), as was previously also suggested for coeval southern Italian material (Delfino et al. 2007). In any case, the final demise and extinction of crocodylians from the Aegean region during the late Miocene coincides with the similar pattern observed for that reptile clade in other parts of Mediterranean Europe (Delfino and Rook 2008; Delfino and Rossi 2013; Georgalis et al. 2016c [**Appendix 6**]).

The Aegean region is a diversity hotspot for Eurasian squamates (i.e, lizards, amphisbaenians, and snakes) with 75 different taxa present in the area (Appendix III). Lizards and amphisbaenians are abundant, being represented by gekkotans, chamaeleonids, agamids, lacertids, scincids, anguids, and blanids (Sindaco et al. 2000, 2013; Sindaco and Jeremčenko 2008) (Appendix III). Snakes are also quite diverse and are represented by scolecophidians, erycids, colubrids, and viperids (Appendix III). Fossil specimens from various Aegean localities confirm the presence of almost all (gekkotans and probably scincids excluded) of these squamate clades in the area, in addition to the now locally extinct cordylids, varanids, and pythonids (*Figure 19*). However, fossil lizard and snake remains from the Aegean region are not abundant and only relatively few localities have yielded fossil squamates (*Table 1*; Appendix II). This is likely due the often-small size of lizard and snake specimens, but also the small amount of attention that squamate palaeontology has received in this part of the Mediterranean. It is characteristic that a large number of fossil squamates have only been recently identified, despite the fact that important specimens had already been recovered by the 19th century (Owen 1857; Römer 1870; Weithofer 1888). Being widely distributed throughout the Aegean and represented by two distinct families (Gekkonidae and Phyllodactylidae), gekkotans have never been recovered in the region's fossil record. However, this certainly does not reflect a real absence of that group, as these tiny lizards are present in the Cenozoic of Western and Central Europe and are overall poorly represented in the global fossil record due to their extremelly small size and fragile skeletons that are only rarely fossilized or recovered (Daza et al. 2014). Chamaeleonids are currently distributed in the Aegean region with two species, *Chamaeleo chamaeleon* (Linnaeus, 1758) and *Chamaeleo africanus* Laurenti, 1768, with the latter probably being the product of human translocation from North Africa during the historic times (Dimaki et al. 2008). Chamaeleonids are among the rarest lizards in the Aegean fossil record, as they are exclusively known by three specimens representing cranial material from the early Miocene (MN 4) of Aliveri in Euboea Island (Central Greece) (Georgalis et al. 2016b [**Appendix 5**]). The best preserved specimen (a skull roofing bone) from Aliveri was referred to the otherwise Czech species *Chamaeleo* cf. *andrusovi* and the other two specimens (tooth bearing bones) could be only identified as indeterminate chamaeleonids, although a conspecific status with the former specimen seemed probable (Georgalis et al. 2016b [**Appendix 5**]). On the basis of this material and its probable affinities with the Czech species *Chamaeleo andrusovi* Čerňanský, 2010, Georgalis et al. (2016b) suggested possible dispersal scenaria for chamaeleonids (**Appendix 5**). According to the most probable scenario, chamaeleonids dispersed from Africa to Europe via the "*Gomphotherium* Landbridge" and used the pathway towards Anatolia and Greece before subsequently colonizing and prospering in Central Europe (Georgalis et al. 2016b [**Appendix 5**]). With the limited available material at hand, it is difficult to make inferences about the evolutionary patterns of the Aegean Neogene chamaeleonids. Nevertheless, the resemblance of the Aliveri material with the Czech form rather than with *Chamaeleo chamaeleon* probably denotes that Neogene chamaeleonids were a short living lineage in the area which eventually became extinct and that the extant lineage dispersed much later to the Aegean region. Agamids are also poorly represented in the fossil record of Greece and Turkey, being known solely by material from the latest Miocene / earliest Pliocene of Maramena (Central Macedonia) (Richter 1995) and the late Quaternary of Karain Cave (Antalya) (Zwick and Schleich 1994). It is worth noting that Delfino et al. (2008) listed additional fossil agamids from several other Miocene and Pliocene localities from Greece, however, these lacked any kind of figures or/and descriptions and as such, they are not taken into consideration here. In fact, one of these supposed occurrences (from the Ano Metochi locality) has recently turned out to pertain to fish (Georgalis et al. 2017a

[**Appendix** 7]). In any case, affinities of the Maramena and Karain fossil specimens with the extant widespread *Stellagama stellio*

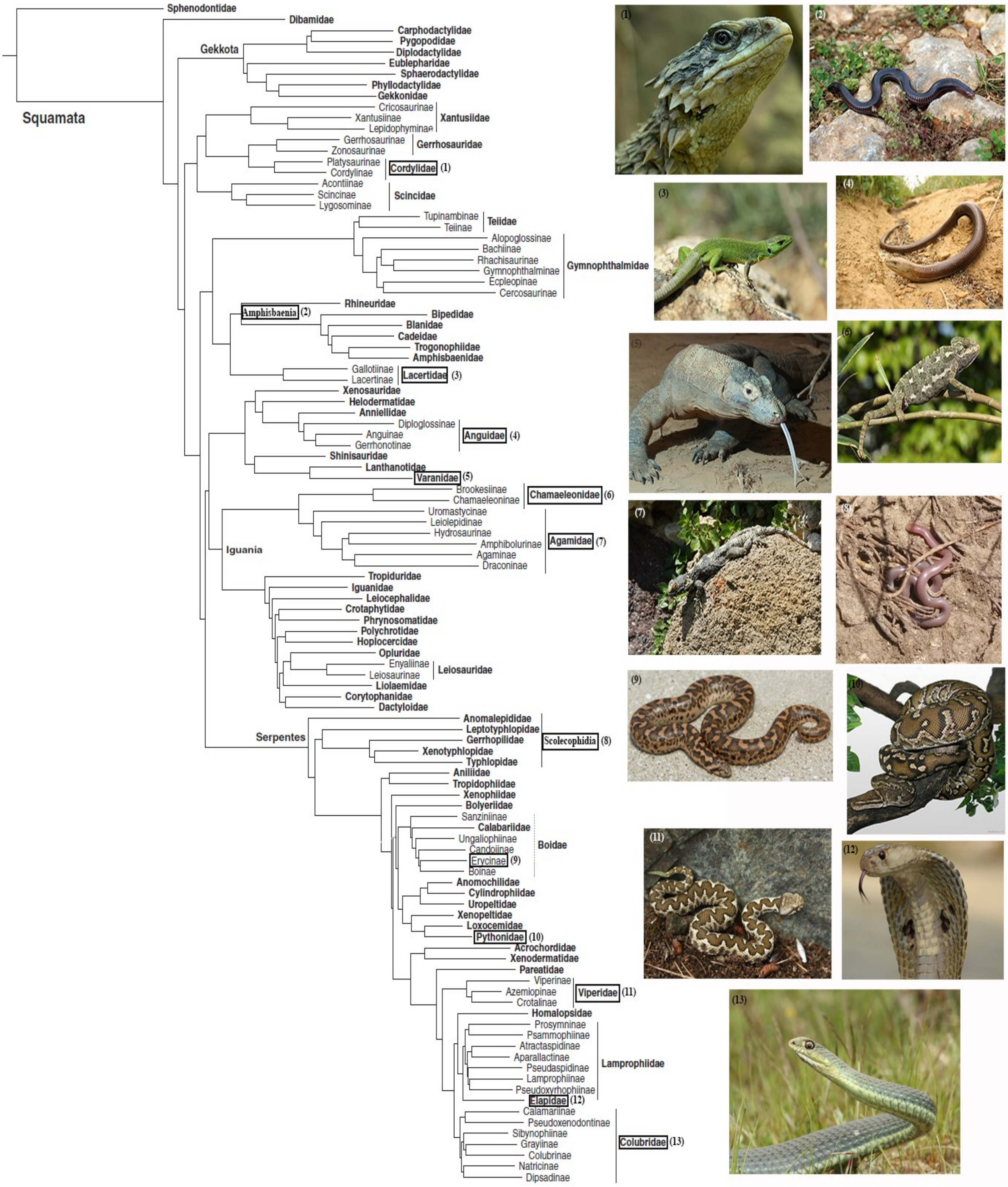

**Figure 19.** Phylogenetic relationships of squamates after Pyron et al. (2013). Rectangles indicate the clades that have been recovered as fossil from the Aegean region. Numbers in brackets correspond to photographs of selected extant representatives from each clade. Photographs: (1), (5), (10), (12) from Wikipedia; (2), (3), (4), (6), (7), (9), (11), (13) from Ilias Strachinis archive; (8) by me.

(Linnaeus, 1758) cannot be verified due to the insufficient knowledge of the skeletal anatomy of modern agamids (e.g., Delfino et al. 2008; Villa et al. 2017), although it seems probable for the latter material on the basis of a stratigraphic rationale. However, apart from *Stellagama*, certain other agamid genera (*Paralaudakia* Baig et al., 2012, *Phrynocephalus* Kaup, 1825, and *Trapelus* Cuvier, 1817) currently inhabit eastern Anatolia, so it cannot be excluded that any of these lineages had a wider range during the earlier parts of the Quaternary. Nevertheless, affinities of the Maramena and Karain Cave specimens with *Phrynocephalus* and *Trapelus* can be tentatively excluded, as the cranial anatomy of these genera is relatively well known (e.g., Ananjeva 1986, 1998; Fathinia et al. 2011), at least for agamid standards, and seem to be quite distinct. The precise taxonomic identification of the Maramena material is further complexing, as agamids were quite abundant during the Miocene of Europe (Delfino et al. 2008), and thus it could represent a distinct, now extinct lineage or also belong to some African or Asian lineages. Nevertheless, the presence of agamids in the Neogene of continental Greece is interesting, especially considering that the extant populations of *Stellagama stellio* have a rather patchy and sporadic distribution in the mainland of Greece and it is as yet unclear whether they represent relics of a wider past distribution or simply products of anthropogenic transportation during antiquity (Valakos et al. 2008). It is further worth noting that the large-sized agamid *Uromastyx* Merrem, 1820, has been purportedly reported from the Aegean region (Mangilli 1980). This record is based on a single, non-figured tibia from the Late Pleistocene of Simonelli Cave in Crete, which Mangilli (1980) referred to the extant *Uromastix* (sic) *spinipes* (Daudin, 1802), a species currently considered to be a junior synonym of the widely distributed Middle East taxon *Uromastyx aegyptia* (Forskål, 1775) (Wilms et al. 2009). With the original publication of Mangilli (1980) containing only a rather brief and generalized description and no figures, the currently unknown whereabouts of the single known tibia, and the fact that appendicular lizard remains usually offer no important taxonomic information, Georgalis et al. (2016b [**Appendix 5**]) discarded affinities of the Cretan specimen with *Uromastyx*, considering it instead as a probable large-sized lacertid. I herein follow this opinion and disregard the presence of *Uromastyx* from the Aegean fossil record. Lacertids are currently the most speciose and abundant clade of lizards in the Aegean region, being dominant in both continental and insular faunas (Sindaco et al. 2000, 2013; Sindaco and Jeremčenko 2008; Valakos et al. 2008). Their earliest record in the Aegean region is marked by probable remains from the early Miocene (?MN 3) of Lapsarna (Lesvos) (Vasileiadou et al. 2017), but they are confidently identified only from the early Miocene (MN 4) of Aliveri and Karydia (Georgalis et al. 2018c [**Appendix 11**]). Lacertids are further identified in late Miocene, Pliocene, and Quaternary sediments across the Aegean region, but all consist of indeterminate specimens. The only lacertid material that has been identified beyond the family level, are remains probably attributable to *Lacerta* Linnaeus, 1758, from both the late Neogene and the Quaternary of Turkey (Zwick and Schleich 1994; Sen et al. 2017), and a fragmentary dentary from the Late Pleistocene of Crete, tentatively referred by Kotsakis (1977) to the extant *Podarcis erhardii* (Bedriaga, 1882). An unexpected lizard clade for the late Neogene of Greece is Cordylidae, commonly known as girdled lizards. Georgalis et al. (2017a) recently described fossil cordylids from the late Miocene (MN 13) of Ano Metochi (Central Macedonia), whereas they also reidentified a previously reported indeterminate scincoid from the nearby locality of Maramena (MN 14/15) (Richter 1995) as belonging to the same clade (**Appendix 7**). Considering that the previously described youngest occurrence of cordylids in Europe was only in the middle Miocene (MN 5), the unexpected occurrences of this lizard clade in the latest Miocene / earliest Pliocene of northern Greece imply a much longer survival and a significantly later extinction (Georgalis et al. 2017a [**Appendix 7**]). Scincid fossils are practically absent from the Aegean region, despite the fact that modern representatives of that clade are common in both Greece and Turkey and are relatively diverse, being represented by five distinct lineages (*Ablepharus* Fitzinger, 1824, *Chalcides*

Laurenti, 1768, *Eumeces* Wiegmann, 1834, *Heremites* Gray, 1845, and *Ophiomorus* Duméril and Bibron, 1839) (Sindaco et al. 2000, 2013; Kumlutas et al. 2007; Sindaco and Jeremčenko 2008; Valakos et al. 2008; Karin et al. 2016). Their fossil remains have only been identified on the basis of a single humerus from the Pliocene of Çalta (Ankara) (Rage and Sen 1976), which, however, was never figured. I tentatively consider this specimen as an indeterminate scincomorph, along with other early Miocene (MN 4) cranial remains from Aliveri and Karydia (Georgalis et al. 2018c [**Appendix 11**]). The purported occurrence of *Ablepharus kitaibelii* (Bibron and Bory de Saint-Vincent, 1833) from the Late Pleistocene or Holocene of Vraona Cave made by Rauscher (1994) was not accompanied by any figure so it cannot be substantiated. Fossil anguids are abundant in the fossil record of the Aegean region and in fact, they represent the only reptile clade in the area for which a practically continuous fossil record exists from the Oligocene onwards (*Figure 20*). All their remains can be attributed to Anguinae, with not a single glyptosaurine find so far recovered from the Paleogene of the area. *Anguis* Linnaeus, 1758 and *Pseudopus* Merrem, 1820 are currently widespread in the extant herpetofauna of the Aegean region and have been identified in the fossil record of the area as well. Fossils of *Anguis* have only been recovered from two middle and late Miocene Anatolian localities, namely Bağiçi (MN 7/8) and Süleymanli (MN 13) (Čerňanský et al. 2017). Curiously, there is a paucity of *Anguis* fossil remains in the Pliocene and the Quaternary, but this absence is probably a taphonomic or a collection-bias, as this genus is currently widespread and relatively diverse in modern faunas of the area (Sindaco and Jeremčenko 2008; Gvoždík et al. 2010; Sindaco et al. 2013). The extant species *Pseudopus apodus* (Pallas, 1775) has been tentatively identified in the Middle Pleistocene of Emirkaya-2 (Venczel and Sen 1994), whereas other, indeterminate remains of *Pseudopus* have also been described from the Pliocene of Çalta (Rage and Sen 1976) and the Late Quaternary of Karain Cave (Zwick and Schleich 1994). The most common anguine, however, in the Aegean fossil record is *Ophisaurus* (sensu lato), which currently does not inhabit Europe or western Asia. Fossils of *Ophisaurus* Daudin, 1803, in the area are first described from the late Oligocene or early Miocene (MP 30–MN 1) of Kargi 2, with several other remains found across the Miocene of both Turkey and Greece (Čerňanský et al. 2017; Georgalis et al. 2017a, 2018c

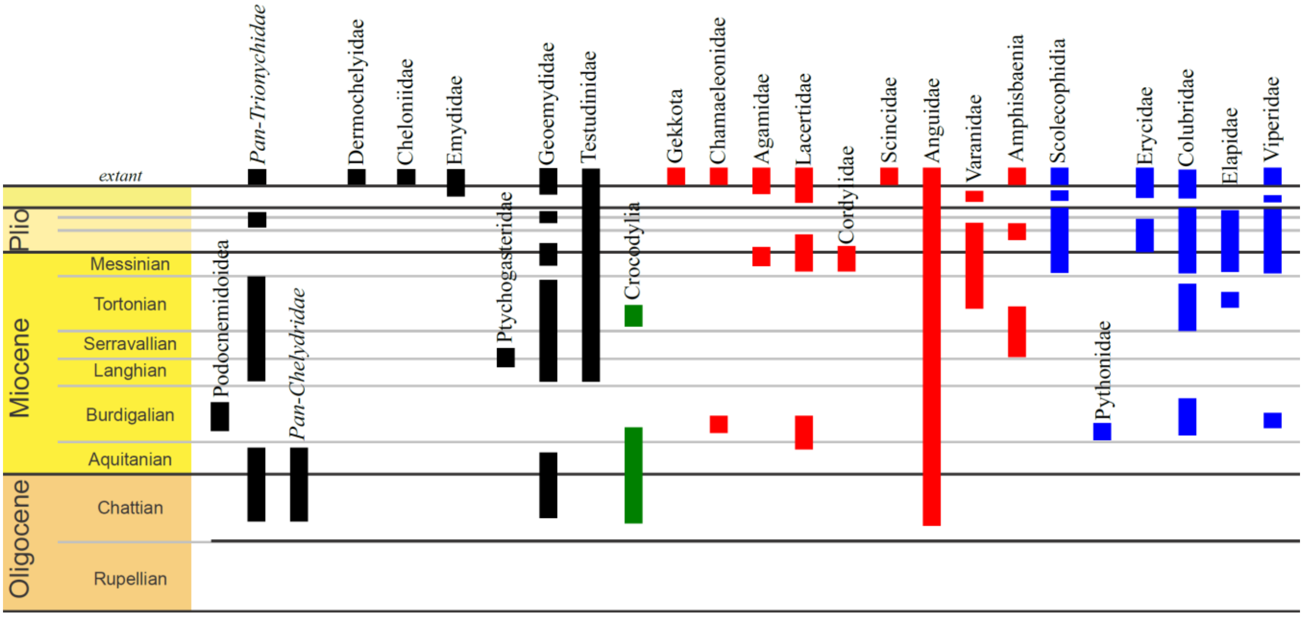

**Figure 20.** The stratigraphic and taxonomic distribution of reptiles in the Aegean region. Black colour for turtles, green for crocodylians, red for lizards and amphisbaenians, and blue for snakes. Current presence in the area of the respective clades are also indicated.

[**Appendices 7, 11**]). The last occurrence of *Ophisaurus* in the area is almost simultaneously recorded in the late Miocene (MN 13) of Ano Metochi and Süleymanli, and this is further relatively concordant with the general post-Miocene demise of that genus in Europe (Rage 2013). Besides the above identifiable genera, there are plenty of remains from the Oligocene and throughout the Neogene of Turkey and Greece that can only be attributed to indeterminate anguines (Čerňanský et al. 2017; Sen et al. 2017; Georgalis et al. 2017a, 2018b, 2018c [**Appendices 7, 10, 11**]). Most importantly, the anguines from the late Oligocene localities of Kocayarma and Kavakdere, both in the European part of Turkey, are the so far oldest lizard remains from the Aegean region (Čerňanský et al. 2017). Although represented only by isolated osteoderms, these finds from the two latter localities clearly document the presence of anguines in the late Paleogene of southeastern Europe (Čerňanský et al. 2017). Varanids are infrequent fossil components of the Neogene and Quaternary of the Aegean region and they are all assigned to the genus *Varanus* Merrem, 1820, although their exact alpha level taxonomy remains at a state of flux (Georgalis et al. 2018b [**Appendix 10**]). Varanids first appear relatively late in the Aegean fossil record in comparison with their respective early Miocene appearance in Western and Central Europe (Roger 1898, 1900; Hoffstetter 1943, 1969; Delfino et al. 2013). Characteristically, their oldest Aegean record has been only recently described from the late Miocene (MN 10) of Ravin de la Pluie (Central Macedonia) (Georgalis et al. 2018b [**Appendix 10**]). The few other records have been found only in the late Miocene (MN 12) of Pikermi and Samos (Gaudry 1862a, 1862b, 1862–1867; Weithofer 1888; Conrad et al. 2012), the Pliocene of Çeştepe (MN 14) and Çalta (MN 15) (Rage and Sen 1976; Sen et al. 2017), and the final one in the Middle Pleistocene of Tourkobounia 5, near Athens, the latter marking the youngest varanid from all over Europe (Georgalis et al. 2017b [**Appendix 8**]). In any case, most of the Aegean material consists of isolated vertebrae, which offer no further taxonomic insight (Georgalis et al. 2018b [**Appendix 10**]), whereas cranial material is only known from Pikermi, Samos, and Tourkobounia 5. As was mentioned above, the exact affinities of the Aegean varanids are clouded by a lack of a modern and comprehensive redescription of the type material of *Varanus marathonensis* from the late Miocene of Pikermi. Pending this, I cannot draw further conclusions about the species level diversity of the Aegean varanids, although it seems probable that at least two distinct taxa were present during the late Neogene. Amphisbaenians are today present in western and southern Anatolia and several adjacent Eastern Aegean Islands in the form of *Blanus strauchi* (Bedriaga, 1884) (Sindaco et al. 2014), but their fossil record denotes a much wider Neogene distribution with material from central Anatolia and Crete (Rage and Sen 1976; Georgalis et al. 2016c, 2018a [**Appendices 6, 9**]). However, their fossil material is extremely poor and up to recently consisted only of isolated vertebrae from the late Miocene (MN 9) of Plakias (Crete) and Çalta (Ankara), which are totally insufficient for species discrimination (Estes 1983; Georgalis et al. 2016c [**Appendix 6**]). As such, although on the basis of a biogeographic rationale they too could belong to the *Blanus strauchi* complex, this assignment cannot be supported by anatomical data. Only the recently described middle Miocene (MN 7/8) cranial material from Gebeceler (Afyon), which demonstrates a rather strong resemblance with the extant Anatolian amphisbaenians can be securely attributed to the *Blanus strauchi* complex (Georgalis et al. 2018a [**Appendix 9**]).

Scolecophidia, commonly known as worm snakes, are currently represented in the Aegean region by Typhlopidae (genus *Xerotyphlops* Hedges et al., 2014), whereas another typhlopid genus (*Letheobia* Cope, 1869) and another distinct scolecophidian, family, Leptotyphlopidae (genus *Myriopholis* Hedges, Adalsteinsson, and Branch in Adalsteinsson et al., 2009), are also present in Eastern Anatolia (Sindaco et al. 2000, 2013; Franzen and Wallach 2002; Sindaco and Jeremčenko 2008; Valakos et al. 2008). Due to their extremely small size, fossil scolecophidians are only rarely found and poorly represented at a global scale (Mead 2013). Furthermore, whereas the characteristic vertebral anatomy of scolecophidians, with the dorsoventrally compressed vertebrae with no neural spines and haemal keel, renders them as readily identifiable, a more precise attribution even at the family level appears to be extremely challenging (Rage 1984b; Szyndlar 1991a; Georgalis et al. 2017a [**Appendix 7**]). This is rather frustrating considering that typhlopids and leptotyphlopids are believed to have diverged from each other already during the Mesozoic (Adalsteinsson et al. 2009; Vidal et al. 2009). As such, all fossil finds from the Aegean region can only be identified as indeterminate scolecophidians and the distinguishment of any biogeographic and evolutionary pattern in typhlopids and leptotyphlopids is currently impossible. Whatever their exact affinities within either typhlopids or leptotyphlopids may be, scolecophidian fossils are found in Neogene and Quaternary localities of both Greece and Turkey, with their oldest so far record recovered from the late Miocene (MN 13) of Ano Metochi (Georgalis et al. 2017a [**Appendix 7**]). Pythonids are thermophilic reptiles that are absent in the modern Aegean fauna. Their fossil record though is comprised of a single known specimen, the holotype of *Python euboicus* from the early Miocene (MN 3/4) of Kymi (Römer 1870), which is also the largest, most complete, and most spectacular fossil snake from the whole area (see above for a discussion of this species). Pythonids of the genus *Python* were relatively frequent components of European early and middle Miocene herpetofaunas (Szyndlar and Rage 2003). It is still unclear if this single known occurrence of pythonids in Greece reflects indeed the rareness of these snakes in the area or if it is simply due to collecting or taphonomic biases. Erycids are currently widely distributed in continental and insular faunas in the Aegean region by the single species *Eryx jaculus* (Linnaeus, 1758). Fossils attributable to that taxon have been confidently recovered from the Quaternary of Chios and Kos islands respectively (Schneider 1975; Szyndlar 1991a). However, older remains pertaining to the genus *Eryx* Daudin, 1803, do exist from the Pliocene of Central Anatolia, Rhodes, and northern Greece (Rage and Sen 1976; Szyndlar 1991a) and although they cannot be attributed precisely to the species level, they all confirm the presence of erycids in the area already by the late Neogene. Colubrids are the most speciose snake clade today. Molecular and external morphological data have allowed herpetologists to identify distinct, monophyletic clades within colubrids, which are also occasionally elevated to the family level, such as Natricidae and Psammophiidae (e.g., Kelly et al. 2008; Vidal et al. 2009). On the other hand, with no reliable external morphology and molecular data, palaeoherpetologists have to usually rely only on skeletal anatomy. Therefore, in the case of colubrids, identifications and taxonomic attributions are mostly based on vertebral anatomy and, in rarer cases, on certain cranial features. According to the traditional and prevailing practice, colubrids are usually divided into "colubrines" and "natricines", an identification mostly based on the presence or absence respectively of a hypapophysis throughout the mid- and posterior trunk vertebrae (Szyndlar 1984, 1991a, 1991b). However, it is worth noting that absence of a hypapophysis throughout the trunk vertebrae occurrs occasionally also in distantly related to colubrines snake clades, and as such, it should only be dealt with extreme caution (Dowling and Duellman 1978; Pyron et al. 2013; Head et al. 2016). Indeed, the provisional distinction of fossil colubrids into "colubrines" and "natricines" should be considered as tentative, a fact that was in any case already also admitted by Szyndlar (1984, 1991a, 1991b, 2005). Accordingly, I am herein following this provisional taxonomic opinion by referring the Aegean fossil colubrid material into "colubrines" and "natricines", with quotation marks denoting the uncertainty and probable paraphyletic status of these lineages. Characteristically, a common member of Psammophiidae in the Aegean region, the genus *Malpolon* Fitzinger, 1826, known also from fossil remains, is herein lumped into "colubrines". So far, indeterminate vertebral remains attributed to that genus have been found in the late Pliocene of Tourkobounia 1 (Szyndlar 1991a), confirming the presence of this lineage in the area already by the latest Neogene. Several other of the extant genera which currently inhabit the Aegean region are also present in the fossil record of the area. One of the largest-sized taxa, *Dolichophis caspius* (Gmelin, 1789) is known from the Middle Pleistocene of Emirkaya-2 (Venczel and Sen 1994), whereas the lineage of *Dolichophis* Gistel, 1868, seems to go back to the late Miocene (MN 13), judging from vertebral material from Ano Metochi in Central Macedonia (Georgalis et al. 2017a [**Appendix 7**]). Another large-sized taxon, *Elaphe quatuorlineata* (Lacépède, 1789), has been described from the Middle Pleistocene of Tourkobounia 2 (Szyndlar 1991a), whereas a similar or even conspecific form is also known from coeval strata in Emirkaya-2 (Venczel and Sen 1994). Material resembling the extant *Hierophis gemonensis* (Laurenti, 1768) has been also recovered from the Late Pleistocene of Bate Cave in Crete (Kotsakis 1977). A related, extinct form, *Hierophis hungaricus* (Bolkay, 1913), originally described from the late Miocene of Hungary, seems to have ranged to coeval northern Greece, judging from vertebral material from the late Miocene / early Pliocene (MN 13/14) of Maramena. This material, originally described by Szyndlar (1995) as an indeterminate "colubrine" was subsequently suggested to be probably referrable to *Hierophis hungaricus* by Venczel (1998), a view that convinced Szyndlar (2005) himself. I am here referring the Maramena "colubrine" to *Hierophis* cf. *hungaricus*, thus extending to the south the geographic range of that snake species. Trunk vertebrae tentatively assigned to *Telescopus* Wagler, 1830, have only been found in the Middle Pleistocene of Emirkaya-2 (Venczel and Sen 1994), whereas *Zamenis situla* (Linnaeus, 1758) was described from the coeval Tourkobounia 2 (Szyndlar 1991a). In addition to the above-mentioned described "colubrines", there are plenty of others that were simply mentioned without any accompanying figure or description that would allow a reevaluation of that statement. Among these are material that was provisionally referred to *Zamenis longissimus* (Laurenti, 1768) and *Coronella* Laurenti, 1768, both on the basis of Middle Pleistocene material from Tourkobounia 2, near Athens (Szyndlar 1991a). Pending a comprehensive description and figuring of that material, I am here not reproducing these statements and consider both *Z. longissimus* and *Coronella* as currently absent from the Aegean fossil record, although they are both frequent components of modern faunas of the area. Indeterminate "colubrine" finds do also occur in both sides of the Aegean, spanning from the late Miocene (MN 10) to the Late Quaternary (Venczel and Sen 1994; Zwick and Schleich 1994; Schneider 1975; Georgalis et al. 2017a, 2018b [**Appendices 7, 10**]). "Natricines" are less common in comparison with "colubrines," in terms of both diversity and abundance. Both extant Aegean species, *Natrix natrix* (Linnaeus, 1758) and *Natrix tessellata* (Laurenti, 1768), have been tentatively described as fossils from Greece and Turkey, on the basis of incomplete and, admittedly, scant remains that are strictly confined between the Middle and the Late Pleistocene (Szyndlar 1991b; Venczel and Sen 1994). Nevertheless, the lineage of the genus *Natrix* Laurenti, 1768, in the Aegean region extends as far back as the late Miocene (MN 13), judging from both cranial and vertebral material from Ano Metochi in Central Macedonia (Georgalis et al. 2017a [**Appendix 7**]). Other, indeterminate occurrences of "natricines" are also known from the Neogene and Quaternary of the Aegean region (Schneider 1975; Szyndlar 1991b, 1995; Hoek Ostende et al. 2015; Georgalis et al. 2016c [**Appendix 6**]), extending probably as far back as the early Miocene (?MN 3) of Lapsarna in Lesvos (Vasileiadou et al. 2017). Beyond all these "colubrines" and "natricines," there also appears to be a unique and bizarre colubrid that cannot be confidently attributed to either of these clades. This colubrid, based on few fragmentary vertebrae from the early Miocene (MN 4) of Karydia and maybe also Aliveri, is characterized by unique features, above all, a vertebral structure, named the "paracentral ridge" that has not been observed in any other extinct or extant snake (Georgalis et al. 2018c [**Appendix 11**]). It seems thus probable that this early Miocene Greek colubrid belongs to a now extinct lineage that was geographically and stratigraphically confined, though this can be only speculative judging from the current fragmentary evidence. Elapids are not components of modern Aegean herpetofauna, though they are represented locally as fossils by large-sized cobras from few Miocene and Pliocene localities in Greece and Turkey (Rage and Sen 1976; Szyndlar and Zerova 1990; Szyndlar 1991b, 1995; Georgalis et al. 2018b [**Appendix 10**]). This elapid material consists only of incomplete vertebrae and can be assigned solely to the genus level (*Naja* sp.). The only exception is the so far oldest Aegean elapid, recovered from the late Miocene (MN 10) of Ravin de la Pluie, which was tentatively referred to the widespread European Neogene species *Naja romani* (Hoffstetter, 1939) (Georgalis et al. 2018b [**Appendix 10**]). Extant viperids are diverse across both sides of the Aegean, including also insular endemics (Sindaco and Jeremčenko 2008; Valakos et al. 2008; Sindaco et al. 2013; Georgalis et al. 2016a [**Appendix 4**]). Although morphological and molecular evidence have been applied in the past three decades in order to split modern genera into distinct monophyletic lineages (e.g., Nilson and Andrén 1986; Herrmann et al. 1992; Nilson et al. 1999; Lenk et al. 2001; Mallow et al. 2003; Wüster et al. 2008), this luxury is not provided to palaeoherpetologists who mostly have to work with isolated vertebrae. As such, fossil viperids from Europe have been usually provisionally divided into informal groups, with the smaller ones representing the "European vipers" complex (comprising the "*Vipera berus*" and "*Vipera ammodytes*" complexes) and the larger ones the "Oriental vipers" complex (comprising the extant genera *Macrovipera* Reuss, 1927, and *Montivipera* Nilson et al., 1999), with both complexes being mostly differentiated on the basis of vertebral structurar characteristics (Szyndlar 1984, 1991b; Szyndlar and Rage 1999, 2002; Georgalis et al. 2016a [**Appendix 4**]; Stümpel et al. 2016). Notable exceptions to this general informal rule are a crotaline from the late Miocene (MN 9) of Ukraine, whose cranial remains allowed a clear referral outside Viperinae (Ivanov 1999), and the gigantic *Laophis crotaloides* which cannot be confidently referred to a more precise subclade within viperids (Georgalis et al. 2016a [**Appendix 4**]). In any case, *Laophis crotaloides* (see the respective entry above for more detailed information about this species), known only from its type locality, confirms the presence of giant viperids in the Aegean region during the Neogene (Owen 1857; Georgalis et al. 2016a [**Appendix 4**]). Large viperids, belonging to the "Oriental vipers" complex, though significantly smaller than *L. crotaloides*, have been sporadically identified across the Neogene and Quaternary of Greece and Turkey (Schneider 1975; Venczel and Sen 1994; Szyndlar 1991b, 1995), confirming a wider range for these snakes in the preceding epochs. Assignement of fossil "Oriental Vipers" to the genus level is almost impossible, as distinction among the vertebrae of extant *Macrovipera* and *Montivipera*, is rather difficult due to the fact that their vertebrae are considered to be relatively similar (Szyndlar and Rage 1999). On the other hand, Codrea et al. (2017) argued that the identification of *Macrovipera* and *Montivipera* vertebrae could be feasible. However, these authors provided no characters for *Montivipera*, except the fact that its vertebrae are usually smaller than *Macrovipera*, whereas the vertebral characters they provided for *Macrovipera* are in fact rather generalized for viperids (Codrea et al. 2017). In any case, distinctive features among vertebrae of *Macrovipera* and *Montivipera* seem to do indeed exist (pers. observ.), but pending a detailed and comprehensive analysis of their vertebral anatomy, I provisionally follow previous workers and assign all European fossil occurrences of large-sized viperids to the "Oriental Vipers" complex. This taxonomic uncertainty about the alpha taxonomy of fossil "Oriental Vipers" further hinders an understanding of the biogeography and evolutionary patterns of these large snakes, especially considering that divergence dates on the basis of molecular data between *Macrovipera* and *Montivipera* suggest that the two lineages diversified already by around the middle Miocene (Langhian) (Stümpel et al. 2016). Curiously, although they constitute common elements of the extant Aegean snake faunas, no confirmed fossil material of the smaller taxa belonging to the "*Vipera ammodytes*" and the "*Vipera berus*" complexes has been described or figured from the area. It is worth noting though that their presence in the area has been preliminarily mentioned by Szyndlar (1991b), who notably also indicated the presence of the *Vipera berus* complex in the Greek islands, far outside the modern range of this group. In any case, without any figure or detailed description the latter Szyndlar's (1991b) suggestion cannot be confirmed. Even if scarce, it seems that viperids appear relatively early in the Aegean fossil record, judging from their oldest occurrence in the area, an isolated fang from the early Miocene of Aliveri (Georgalis et al. 2018c [**Appendix 11**]). Aegean viperids seem to appear significantly later in comparison with Central and Western Europe, where that clade is already known by the earliest Miocene (MN 1) (Szyndlar and Rage 1999, 2002; Kuch et al. 2006), but this could well be simply attributed to misscollection or taphonomical reasons.

## New finds, recent advances, and future perspectives

As was a general trend during the 19th century, the few early studies that dealt with fossil reptiles from the Aegean region during that time provided only minor descriptions, brief comparisons, and, sometimes, erroneous figures (Owen 1857; Gaudry 1862a, 1862b, 1862–1867; Römer 1870; Weithofer 1888). Publications with brief descriptions and preliminary comparisons, though provided with better and more accurate figuring, due to the advance of technology, continued also through most of the 20th century (e.g., Arambourg and Piveteau 1929; Szalai 1931; Malik and Nafiz 1933). A more analytical approach, along with quantitative analysis, currently offers new insights for palaeoherpetological studies. The scarceness of fossil reptile remains which have so far been recovered from the Aegean region unfortunately allows little room for extensive analytical approach. Nevertheless, the herein enclosed new studies of reptile finds [**Appendices 1–11**] offer important implications about the evolution of herpetofaunas in western Eurasia.

In order to better understand the evolution of Aegean reptiles, a comprehensive analysis and evaluation of their taxonomy and phylogenetic affinities is quintessential. This also neccessitates a more detailed anatomical study and comparisons with multiple taxa, not only from the Aegean region, but at a global scale. Species level taxonomy of certain vertebrate groups appears to be a rather puzzling and tantalizing case. The case of soft shelled turtles (*Pan-Trionychidae*) is a prominent such example, as the almost uniform anatomy of these reptiles has rendered their precise identification in the fossil record as a difficult task. A vast plethora of pan-trionychid species had been described from Europe and adjacent areas during the past two centuries, mostly defined on the basis of fragmentary material and extremely vague and widespread features, rendering as such their systematics at a state of flux (e.g., Hummel 1929, 1932; Kuhn 1964; Broin 1977; Karl 1999; Danilov 2005). By consequence, although pan-trionychids are ubiquitous elements of European Cenozoic faunas, their fossils offered so far almost no usage to biostratigraphy and evolutionary and biogeographic studies. A detailed analysis and taxonomic review of all known fossil pan-trionychid taxa, presented in **Appendix 1** (Georgalis and Joyce 2017), allows now a better reinterpetation of extinct members of this turtle clade and provides better evidence for their systematics and their distribution through time. Accordingly, this broad analysis refers to all Paleogene Aegean pan-trionychids as *Pan-Trionychidae* indet., whereas a more accurate attribution can be made for the Neogene ones, which are considered as *Pan-Trionychinae* indet. Additionally, the evolution of insular fossil pan-trionychids is aided through the study and revision of a particular taxon, *Procyclanorbis sardus* Portis, 1901b, from the late Miocene of Sardinia, which is the most complete soft shelled turtle taxon from the Mediterranean Islands, presented in **Appendix 2** (Georgalis et al. 2017c). Of course, any attempt to study the taxonomy of any animal group necessitates the comprehension and clarification of the nomenclature surrounding its inclusive taxa. A rather complexing nomenclatural and taxonomic case is presented in **Appendix 3** (Georgalis 2017), where the rules of ICZN (1999) are applied to showcase the availability or not of zoological names. Accordingly, this applies also to even some important names in palaeoherpetological literature, as is the case of the *Necrosaurus* / *Palaeovaranus* nomina presented therein and furthermore, this has additional implications about correcting the appropriate type material and emendment of names of more inclusive clades. Therefore, these new results presented in **Appendix 3** hightlight the urgent need for evaluating the nomenclature and appropriate type material before proceeding to further taxonomic or phylogenetic analysis and study.

Detailed descriptions and analyses of the herein new fossil reptiles from selected localities across the Aegean region (**Appendices 4–11**) provide clues about the evolution of herpetofaunas in the Cenozoic of Western Eurasia. New reptile clades were identified for the first time in the fossil record of the Aegean region, such as chamaeleonids, cordylids, and blanids (Georgalis et al. 2016b, 2017a, 2018a [**Appendices 5, 7, 9**]). Additionally, the geographic and stratigraphic distributions of the previously known reptile clades were now broadly expanded by the study of the new finds (Georgalis et al. 2016c, 2017a, 2017b, 2018a, 2018b, 2018c [**Appendices 6, 7, 8, 10, 11**]). Furthermore, the new descriptions of cranial and poscranial remains from the new Aegean fossil reptiles adds to the knowledge of the anatomy and clarifies the interrelationships among Cenozoic western Eurasian reptiles. Besides the taxonomic and systematic importance of these new descriptions, these studies (**Appendices 4–11**) are also essential for general biogeographic studies, biostratigraphy, and palaeoenvironmental and palaeoecological reconstructions of the Eastern Mediterranean. Faunal dispersal and extinction events which occurred during the Neogene and the Quaternary are now further supported by the new fossil reptiles from the Aegean region. Among the most important among these events, occurred during the early Miocene, when the collision of the Afro-Arabian plate with Eurasia enabled a large number of dispersals between the two continents, via the so called "*Gomphotherium* Landbridge". So far, certain reptile groups (e.g., cordylids and chamaeleonids) from the early Miocene of Europe had been suggested to have dispersed using that landbridge from Africa to Europe (Čerňanský 2010, 2012; Rage 2013), but the exact route they used was so far hindered by the absence of their finds in the Balkans and Anatolia. The recovery of several mammal groups with African affinities in the early Miocene of the Aegean provide clues about these dispersals and possible directions (Koufos et al. 2003, 2005). Now, the newly described chameleons from the early Miocene of Aliveri and the additional herpetofauna from that locality and that of Karydia provide substantial evidence that these first immigrants could probably have used Anatolia and the southern Balkans as their first steps towards Europe (Georgalis et al. 2016b, 2018c [**Appendices 5, 11**]). Extinction events of European reptiles are now better assessed through the new finds. It is characteristic that among the new Greek fossil reptiles are the youngest records of Cordylidae (late Miocene of Ano Metochi and Maramena; Georgalis et al. 2017a [**Appendix 7**]) and Varanidae (Middle Pleistocene of Tourkobounia 5; Georgalis et al. 2017b [**Appendix 8**]) from Europe. Also, the crocodylians from the late Miocene of Plakias are among the youngest occurrences of that clade from Europe as well (Georgalis et al. 2016c [**Appendix 6**]). The presence of cordylids and varanids in Greece at a much younger age than their European relatives implies a much later extinction date and that this geographic area served as a kind of a "refugium" for these reptile during different stages of the Neogene and the Quaternary. This is in further concordance with various extant reptile clades that currently persist in Greek and Anatolian herpetofaunas but are now totally absent from the rest of Europe (pan-trionychids, agamids, scolecophidians, and "Oriental vipers") or at least have now become extinct from most parts of the continent (geoemydids, chamaeleonids, scincids, large anguids of the genus *Pseudopus*, blanids, and erycids) (Georgalis et al. 2016a, 2016b, 2016c, 2017a, 2017b, 2017c, 2018a; **Appendices 3–9**). Moreover, the ectothermic nature and ecological “sensitivity” of most reptile clades, render the new finds as ideal for palaeoenvironmental and palaeoclimatic reconstructions of the Aegean localities. As such, different climates and multiple landscapes with either warm, humid, dry, forested, savannah, or wetland environments were suggested for the localities of Aliveri, Ano Metochi, Gebeceler, Karydia, Megalo Emvolon, Plakias, Ravin de la Pluie, and Tourkobounia 5 (Georgalis et al. 2016a, 2016b, 2016c, 2017a, 2017b, 2018a, 2018b, 2018c [**Appendices 4–11**]). These localities were already relatively well dated on the basis of geological data and/or associated mammal fauna and as such, the new reptile finds do not provide alternative age estimations. Nevertheless, for localities that cannot be geologically accurately dated or have not yielded mammal finds, then fossil reptile provide the only meaningful means for a precise biostatigraphic determination. Finally, the discovery of what seems to be the largest-sized viperid snake among the new finds, the referred vertebra of *Laophis crotaloides* from the Pliocene of Megalo Emvolon (Georgalis et al. 2016a [**Appendix 4**]), offers the opportunity to study patterns of gigantism among animal clades and possible correlations with climatic conditions and palaeonvironmens, as was also done for other large snakes (e.g., Head et al. 2009).

## References

Adalsteinsson, S.A., W.R. Branch, S. Trape, L.J. Vitt and S.B. Hedges. 2012. Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata). Zootaxa 2244:1–50.

Ananjeva, N.B. 1977. [The taxonomic differences in the skull structure and dentition of agamid lizards (Sauria, Agamidae) of USSR fauna]. Zoologicheskiy Zhurnal (Moscow), 56:1062 – 1070. [in Russian]

Ananjeva, N.B. 1986. [The structure of the skull and the morphometry of cranial elements of *Phrynocephalus versicolor* in Mongolia, Ekhiin-gol]. In: Herpetological Research in Mongolian People Republic. Moscow: Nauka. pp. 179–196. [in Russian]

Ananjeva, N.B. 1998. The skull structure of some arid Asian agamids of *Phrynocephalus* genus (Agamidae, Sauria). Russian Journal of Herpetology 5:29–35.

Arambourg, C. and J. Piveteau. 1929. Les vertébrés du Pontien de Salonique. Annales de Paléontologie 18:59–138.

Auffenberg, W. 1974. Checklist of fossil land tortoises (Testudinidae). Bulletin of Florida State Museum of Biological Science 18:121–251.

Augé, M. 2005. Evolution des lézards du Paléogène en Europe. Mémoires du Muséum national d’Histoire naturelle, Paris 192:1–369.

Augé, M. 2012. Amphisbaenians from the European Eocene: a biogeographical review. Palaeobiodiversity and Palaeoenvironments 92:425–443.

Augé, M. and R. Smith. 2009. An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene–Oligocene transition. Zoological Journal of the Linnean Society 155:148–170.

Bachmayer, F., 1967. Eine Riesenschildkröte aus den altpliozäne Schichten von Pikermi (Griechenland). Annales Géologiques des Pays Helléniques 19:512–526.

Bachmayer, F., J. Brinkerink and N. Symeonidis. 1975. Pleistozäne Schildkröten aus Höhlen der Insel Kreta. Annales Géologiques des Pays Helléniques 27:110–121.

Bachmayer F., M. Młynarski and N. Symeonidis. 1980. Fossile Schildkröten aus dem Pliozän von Megalo Emvolo (Karaburun) bei Saloniki (Griechenland) A. Eine fossile Maurische Landschildkröte (*Testudo* cf. *graeca* Linné). B. Fossile reste von Riesenschilkröten. Annales Géologiques des Pays Helléniques 31:267–276.

Bachmayer, F. and N. Symeonidis. 1970. Die fossilen Schildkrötenreste des Geologisch-Paläontologischen Institutes der Universität von Athen. Annales Géologiques des Pays Helléniques 22:227–246.

Bachmayer, F. and N. Symeonidis. 1975. Schildkrötenreste (*Testudo marginata* Schoepff) aus der Höhle "Charkadio", auf der Insel Tilos (Dodekanes, Griechenland). Annales Géologiques des Pays Helléniques 26:324–327.

Bachmayer, F. and N. Symeonidis. 1976. Eine neue ''Pikermi'' Fundstelle im Gebiet von Liossati (Kiourka), nördlich von Athen (Griechenland) (Beschreibung einer Riesenschildkröte). Annales Géologiques des Pays Helléniques 28:8–16.

Baig, K.J., P. Wagner, N.B. Ananjeva and W. Böhme, W. 2012. A morphology-based taxonomic revision of *Laudakia* Gray, 1845 (Squamata: Agamidae). Vertebrate Zoology 62:213–260.

Bardet, N. and C. Tunoğlu. 2002. The First Mosasaur (Squamata) from the Late Cretaceous of Turkey. Journal of Vertebrate Paleontology 22:712–715.

Bedriaga, J. von. 1881. Die Amphibien und Reptilien Griechenlands Bulletin de la Société Impériale des Naturalistes de Moscou 56:242–310.

Bedriaga, J. von. 1882. Die Amphibien und Reptilien Griechenlands. Bulletin de la Société Impériale des Naturalistes de Moscou 56:43–103.

Bedriaga, J. von. 1884. Nachträgliche Bemerkung über *Amphisbaena strauchi* v. Bedr. Zoologischer Anzeiger 7:346.

Bedriaga, J. von. 1886. Beiträge zur Kenntnis der Lacertiden-Familie (*Lacerta*, *Algiroides*, *Tropidosaura*, *Zerzumia*, *Bettaia*). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft (Frankfurt) 14:17–444.

Beerli, P., H. Hotz and T. Uzzell. 1996. Geologically dated sea barriers calibrate a protein clock for Aegean water frogs. Evolution 50:1676–1687.

Bell, T. 1828. Descriptions of three new species of land tortoises. Zoological Journal, London 3:419–421.

Bellati, A., S. Carranza, J. Garcia-Porta, M. Fasola and R. Sindaco. 2014. Cryptic diversity within the *Anatololacerta* species complex (Squamata: Lacertidae) in the Anatolian Peninsula: Evidence from a multi-locus approach. Molecular Phylogenetics and Evolution 82:219–233.

Bergounioux, F.M. 1935. Contribution à l'étude paléontologique des chéloniens: chéloniens fossiles du bassin d'Aquitaine. Mémoires de la Société Géologique de France (nouvelle série), Mémoire, no. 25. Paris: Société géologique de France. 215 pp.

Bibron, G. and J.B. Bory de Saint-Vincent. 1833. Vertébrés a sang froid. Reptiles et poissons. Reptiles. In: Geoffroy Saint-Hilaire, I. and É. Geoffroy Saint-Hilaire, eds. Expédition Scientifique de Morée, Tome III. 1re partie, Zoologie. pp. 57–76.

Blain, H.-A., J. Agustí, D. Lordkipanidze, L. Rook, and M. Delfino. 2014. Paleoclimatic and paleoenvironmental context of the Early Pleistocene hominins from Dmanisi (Georgia, Lesser Caucasus) inferred from the herpetofaunal assemblage. Quaternary Science Reviews 105:136–150.

Boda, A. 1927. *Clemmydopsis sopronensis*, n. g. n. sp. aus der unteren pannonischen Stufe von Sopron in Ungarn. Centralblatt für Mineralogie, Geologie und Paläontologie B 9:375–383.

Boettger, O. 1892. Kriechthiere der Kaukasusländer, gesammelt durch die Radde-Valentin'sche Expedition nach dem Karabagh und durch die Herren Dr. J. Valentin un P. Reibisch. Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main 1892:131–150.

Bogachev, V.V. 1960. [A new turtle from the Miocene of Crimea]. Voprosy geologii oureniya i dobychi nefti 10:88–92. [In Russian]

Böhme, M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 195:389–401.

Böhme, M. 2010. Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. Paläontologische Zeitschrift 84:3–41.

Böhme W. and U. Joger. 1984. Eine neue Art des *Vipera berus*-Komplexes aus der Turkei. Amphibia-Reptilia 4:265–271.

Bolkay, J. 1913. Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. Mittheilungen aus dem Jahrbuche der königlichen Ungarischen geologischen Reichsanstalt 21:217–230.

Boulenger, G. A. 1887. Catalogue of the Lizards in the British Museum (Nat. Hist.) III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropsidae, Dibamidae, Chamaeleontidae. London: British Museum (Natural History). 575pp.

Boulenger, G.A. 1913. On the geographical races of *Vipera ammodytes*. Annals and Magazine of Natural History, London, Series 8 11:283–287.

Bour, R. 1995. Une nouvelle espèce de tortue terrestre dans le Péloponnèse (Grèce). Dumerillia 2:23–54.

Broin, F. de.1977. Contribution à l'étude des Chéloniens: Chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum National d'Histoire Naturelle, Série C 38:1–366.

Buffetaut, E., M. Martin and O. Monod. 1988. Phytosaur remains from the Çenger Formation of the Lycian Taurus (Western Turkey): Stratigraphical implications. Geobios 21:237–243.

Calvert, F. and M. Neumayr. 1880. Die jungen Ablagerungen am Hellespont. Akademie der Wissenschaften, Vienna. Denkschriften der kaiserlichen Akademie der Wissenschaften/Mathematisch-Naturwissenschaftliche Classe 40:357–378.

Campana, D. del. 1917. Resti di *Testudo* nel Miocene superiore di Capudjlar presso Salonicco. Bollettino della Società Geologica Italiana 36:69–78.

Campana, D. del. 1919. Uova fossili di Chelonio nel Miocene superiore di Capudjlar presso Salonicco. Bollettino della Società Geologica Italiana 38:1–6.

Čerňanský, A. 2010. A revision of chamaeleonids from the Lower Miocene of the Czech Republic with description of a new species of *Chamaeleo* (Squamata, Chamaeleonidae). Geobios 43:605–613.

Čerňanský, A. 2012. The oldest known European Neogene girdled lizard fauna (Squamata, Cordylidae), with comments on Early Miocene immigration of African taxa. Geodiversitas 34:837–848.

Čerňanský, A., D. Vasilyan, G.L. Georgalis, P. Joniak, S. Mayda and J. Klembara. 2017. First record of fossil anguines (Squamata; Anguidae) from the Oligocene and Miocene of Turkey. Swiss Journal of Geosciences 110:741–751.

Chkhikvadze, V. M. 1989. [Neogene turtles from the U.S.S.R]. Academy of Sciences of the Georgian SSR, Institute Paleontology "L.S. Dabitasbili", Tbilisi, 103 pp. [in Russian]

Chkhikvadze, V.M. 2010. [An annotated catalogue of Paleogene, Neogene, and modern turtles of northern Eurasia]. Georgian National Museum. Proceedings of the Natural and Prehistoric Section 2:96–113. [in Russian]

Codrea, V., M. Venczel, L. Ursachi, and B. Răţoi. 2017. A large viper from the early Vallesian (MN 9) of Moldova (Eastern Romania) with notes on the palaeobiogeography of late Miocene "Oriental vipers". Geobios 50:401–411.

Comaschi Caria, J. 1959. Nuovi resti di Cheloni nel Miocene della Sardegna. Bollettino della Società Geologica Italiana 78:37–44.

Conrad, J.L., A.M. Balcarcel and C.M. Mehling. 2012. Earliest Example of a Giant Monitor Lizard (*Varanus*, Varanidae, Squamata). PLoS ONE 7:e41767.

Cope, E.D. 1869. Observations on reptiles of the Old World. Art. II. Proceedings of the Academy of Natural Sciences of Philadelphia 20:316–323.

Corsini, J.A., M. Böhme and W.G. Joyce. 2014. Reappraisal of *Testudo antiqua* (Testudines, Testudinidae) from the Miocene of Hohenhöwen, Germany. Journal of Paleontology 88:948–966.

Crawford, N.G., J.F. Parham, A.B. Sellas, B.C. Faircloth, T.C. Glenn, T.J. Papenfuss, J.B. Henderson, M.H. Hansen, W.B. Simison. 2015. A phylogenomic analysis of turtles. Molecular Phylogenetics and Evolution 83:250–257.

Cuvier, G. 1817. Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Tome II, contenant les reptiles, les poissons, les mollusques et les annélides. Paris: Déterville. 532 pp.

Dacqué, E. 1912. Die fossilen Schildkröten Aegyptens. Geologische und Palaeontologische Abhandlungen 14:275–337.

Danilov, I.G. 2005. Die fossilen Schildkröten Europas. In: U. Fritz, ed. Handbuch der Reptilien und Amphibien Europas, Part 3/IIIB: Schildkröten (Testudines) II. Wiebelsheim, Germany: Aula-Verlag. pp. 329–448.

Daudin, F.M. 1801. Histoire naturelle, générale et particulière des reptiles. Tome second. Paris: Imprimerie F. Dufart. 432 pp.

Daudin, F.M. 1802. Histoire naturelle, générale et particulière des reptiles. Tome quatrieme. Paris: Imprimerie F. Dufart. 397 pp.

Daudin, F.M. 1803. Histoire naturelle, générale et particulière des reptiles: ouvrage faisant suite à l'Histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini. Tome septième. Paris: Imprimerie F. Dufart. 436 pp.

Daza, J.D., A.M. Bauer and E.D. Snively. 2014. On the Fossil Record of the Gekkota. The Anatomical Record 297:433–462.

De Stefano, G. 1902. Cheloniani fossili cenozoici. Bollettino della Società Geologica Italiana 21:263–304.

De Vos, J., J. Van der Made, A. Athanassiou, G. Lyras, P. Sondaar and M.D. Dermitzakis. 2002. Preliminary note on the Late Pliocene fauna from Vatera (Lesvos, Greece). Annales Géologiques des Pays Helléniques 39:37–70.

Delfino, M., M. Böhme and L. Rook. 2007. First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy). Zoological Journal of the Linnean Society London 149:293–307.

Delfino, M., T. Kotsakis, M. Arca, C. Tuveri, G. Pitruzella and L. Rook. 2008. Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiversitas 30:641–656.

Delfino, M., J.-C. Rage, A. Bolet and D.M. Alba. 2013. Early Miocene dispersal of the lizard *Varanus* into Europe: reassessment of vertebral material from Spain. Acta Palaeontologica Polonica 58:731–735.

Delfino, M. and L. Rook. 2008. African crocodylians in the late Neogene of Europe: a revision of *Crocodylus bambolii* Ristori 1890. Journal of Paleontology 82:336–343.

Delfino, M. and M.A. Rossi. 2013. Fossil crocodylid remains from Scontrone (Tortonian Southern Italy) and the late Neogene Mediterranean biogeography of crocodylians. Geobios 46:25–31.

Delfino, M., D. Zoboli, G. Carnevale and G.L. Pillola. 2014. The rediscovered holotype of *Palaeopython sardus* Portis, 1901 from the Miocene of Sardinia belongsto a fish, not a snake. Bollettino della Società Paleontologica Italiana 53:89–92.

Depéret, C., 1885. Description géologique du bassin tertiaire du Roussillon. Description des vertébrés fossiles du terrain pliocène du Roussillon. G. Masson, Paris, 274 pp.

Dermitzakis, D.M. and D.J. Papanikolaou. 1981. Paleogeography and geodynamics of the Aegean region during the Neogene. Annales Géologique des Pays Helléniques 30:245–289.

Dimaki, M., A.K. Hundsdörfer and U. Fritz. 2008. Eastern Mediterranean chameleons (*Chamaeleo chamaeleon*, *Ch. africanus*) are distinct. Amphibia-Reptilia 29:535–540.

Dowling, H.G. and W.E. Duellman. 1978. Systematic herpetology: a synopsis of families and higher categories. New York: HISS Publications. 118 pp.

Duméril, A.M.C. and G. Bibron. 1839. Erpétologie générale ou histoire naturelle complète des reptiles. Tome cinquième. Paris: Roret. 854 pp.

Dunn, E.R. 1927. Results of the Douglas Burden expedition to the Island of Komodo. I.– Notes on *Varanus komodoensis*. American Museum Novitates 286:1–10.

Eichwald, K.E.I. 1831. Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vilnensi habendarum. Pars posterior [vol.3], specialem expositionem spondylozoorum continens. Vilnae: Josephi Zawadzki. 369 pp.

Eiselt, J. and I.Baran 1970. Ergebnisse zoologischer Sammelreisen in der Türkei: Viperidae. Annalen des Naturhistorischen Museums, Wien 74:357–369.

Eiselt, J. and F.J. Schmidtler. 1987. Der *Lacerta danfordi*-Komplex. Spixiana 9:289–328.

Estes, R. 1983. Sauria Terrestria, Amphisbaenia. In: P. Wellnhofer, ed. Encyclopedia of Paleoherpetology, part 10a. Stuttgart - New York: Gustav Fischer Verlag. 249 pp.

Eversmann, E. 1834. Lacertae Imperii Rossici variis in itineribus meis observatae. Nouveaux mémoires de la Société impériale des naturalistes de Moscou 3:339–358.

Falconer, H. and P.T. Cautley. 1837. On additional fossil species of the order Quadrumana from the Siwalik Hills. Journal of the Asiatic Society of Bengal 6:354–360.

Falconer, H. and P.T. Cautley. 1844. Communication on the *Colossochelys atlas*, a fossil tortoise of enormous size from the Tertiary strata of the Siwalk Hills in the north of India. Proceedings of the Zoological Society of London 1844:54–84.

Fathinia, B., N. Rastegar-Pouyani, A.M. Bahrami and G. Abdali. 2011. Comparative skull anatomy and dentition of *Trapelus lessonae* and *T. ruderatus* (Sauria: Agamidae) from Ilam Province, Iran. Russian Journal of Herpetology 18:83–92.

Fejérváry, de, G.J. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. Annales historico-naturales Musei nationalis hungarici 16:341–467.

Fejérváry, de, G.J. 1935. Further contributions to a monograph of the Megalanidae and Fossil Varanidae, with notes on recent varanians. Annales historico-naturales Musei nationalis hungarici, Pars Zoologica 29:1–130.

Filippi, F. de. 1865. Note di un Viaggio in Persia nel 1862. Milan: G. Daelli and C. Editori. 369 pp.

Fitzinger, L. 1824. Über den *Ablepharus pannonicus*, eine neue Eidechse aus Hungarn. Verhandlungen der Naturforschenden Gesellschaft Berlin 1:297–302.

Fitzinger, L. 1826. Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften. Nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des k. k. zoologischen Museums zu Wien. Wien (= Vienna): J. G. Huebner. 66 pp.

Fitzinger, L. 1836. Entwurf einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. Annalen des Wiener Museums der Naturgeschichte 1:104–128.

Fleischmann, F.L. 1831. Dissertatio inauguralis sistens Dalmatiae Nova Serpentum Genera quam gratiosi medicorum ordinis auctoritate in Regia Literarum Universitate Friderico–

Alexandrina pro impetrandis Doctoris Medicinae, Chirurgiae atque Artis obstetriciae Summis honoribus et privileglis eruditorum examini submittit. Erlangae (= Erlangen): Commissis C. Heyderi. 35 pp.

Forskål, P. 1775. Descriptiones Animalium. Avium, Amphibiorum, Piscium, Insectorum, Vermium. Quae in Itinere Oriental Observavit. Haunia, Denmark: Mölleri. 12 pp.

Franzen, M. and V. Wallach 2002. A new *Rhinotyphlops* from southeastern Turkey (Serpentes: Typhlopidae). Journal of Herpetology 36:176–184.

Fritz, U. and P. Havaš. 2007. Checklist of the chelonians of the world. Vertebrate Zoology 57:149–368.

Fritz, U., P. Siroki, H. Kami and M. Wink, M., 2005. Environmentally caused dwarfism or a valid species – is *Testudo weissingeri* Bour, 1996 a distinct evolutionary lineage? New evidence from mitochondrial and nuclear genomic markers. Molecular Phylogenetics and Evolution 37:389–401.

Gad, J. 1990. Nachweis einer Schildkröte des *Mauremys-Ocadia*-Komplexes aus dem Obermiozän von Nordgriechenland. Salamandra 26:311–313.

Gaffney, E.S., P.A. Meylan, R.C. Wood, E. Simons and D.A. de Campos. 2011. Evolution of the side-necked turtles: the family Podocnemididae. Bulletin of the American Museum of Natural History 350:1–238.

Garcia, G., D.S. Kostopoulos, X. Valentin and G.D. Koufos, G.D. 2016. Testudines. In: G.D. Koufos and D.S. Kostopoulos, eds.. Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Geobios 49:23–27.

Gaudry, A. 1862a. Note sur les débris d'Oiseaux et de Reptiles trouvés à Pikermi, Grèce, suivie de quelques remarques de paléontologie générale. Bulletin de la Société Géologique de France 19:629–640.

Gaudry, A. 1862b. Résultats des fouilles exécutées en Grèce sous les auspices de l'Academie. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 54:502–505.

Gaudry, A. 1862–1867. Animaux fossiles et géologie de l'Attique. Paris: Savy. 474 pp.

Geoffroy Saint-Hilaire, E.F. 1809. Mémoire sur les tortues molles, nouveau genre sous le nom de *Trionyx*, et sur la formation des carapaces. Annales du Muséum d'Histoire Naturelle 14:1–20.

Geoffroy-Saint-Hilaire, I. 1827. Description des reptiles qui se trouvent en Égypte. In: Savigny, M.J.-C.L., de, ed. Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée Française. Histoire naturelle. Tome premier. Partie premier. Paris: Imprimerie Impériale (1809–1829). pp. 121–160.

Georgalis, G.L. 2017. *Necrosaurus* or *Palaeovaranus*? Appropriate nomenclature and taxonomic content of an enigmatic fossil lizard clade (Squamata). Annales de Paléontologie 103:293–303. **[Appendix 3]**

Georgalis, G.L., K. Halaçlar, S. Mayda, T. Kaya, and D. Ayaz. 2018a. First fossil find of the *Blanus strauchi* complex (Amphisbaenia, Blanidae) from the Miocene of Anatolia. Journal of Vertebrate Paleontology e1437044. **[Appendix 9]**

Georgalis, G.L. and W.G. Joyce. 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58:115–208. **[Appendix 1]**

Georgalis, G.L., and Kear, B.P. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46:299–311.

Georgalis, G.L., J.-C. Rage, L. de Bonis and G.D. Koufos. 2018b. Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). Swiss Journal of Geosciences DOI: 10.1007/s00015-017-0291-2(0123456789. **[Appendix 10]**

Georgalis, G.L., Z. Szyndlar, B.P. Kear and M. Delfino. 2016a. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109:103–116. **[Appendix 4]**

Georgalis, G.L., A. Villa and M. Delfino. 2016b. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature 103:12. **[Appendix 5]**

Georgalis, G.L., A. Villa and M. Delfino. 2017a. Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. Historical Biology 29:730–742. **[Appendix 7]**

Georgalis, G.L., A. Villa and M. Delfino. 2017b. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. Journal of Vertebrate Paleontology 37:e1301946. **[Appendix 8]**

Georgalis, G.L., A. Villa, M. Ivanov, S. Roussiakis, P. Skandalos and M. Delfino 2018c. Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia – bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe. Historical Biology DOI: 10.1080/08912963.2017.1417404. **[Appendix 11]**

Georgalis, G.L., A. Villa, E. Vlachos and M. Delfino. 2016c. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49:433–444. **[Appendix 6]**

Georgalis, G.L., D. Zoboli, G.L. Pillola and M. Delfino. 2017c. A revision of the trionychid turtle *Procyclanorbis sardus* Portis, 1901 from the late Miocene of Sardinia (Italy). Annales de Paléontologie 103:127–134. **[Appendix 2]**

Gervais, P. 1864–1866. Du *Mesosaurus tenuidens*, reptile fossile de l'Afrique australe. Comptes Rendus de l'Academie des Sciences 60:950–955.

Gilmore, C.W. 1938. Fossil snakes of North America. Geological Society of North America, Special Papers 9:1–96.

Gistel, J.N.F.X. 1868. Die lurche Europas. Ein Beitrag zur Lehre von der geographischen Verbreitung derselben. In: Gistel, J., ed., Blicke in das Leben der Natur und des Menschen. Leipszig: Verlag von Ed. Wartig. pp. 144–167.

Gmelin, S.G. 1774. Reise durch Russland zur Untersuchung der drey Natur-Reiche. Dritter Theil. Reise durch nordliche Persien, in den Jahren 1770, 1771, bis im April 1772. St. Pétersbourg (= St. Petersburg): Kayserliche Academie der Wissenschaften. 508 pp.

Gmelin, J.F. 1789. Caroli a Linne...Systema naturae per regna tria natural, secundum classes, ordines, genera, species, cum characteribus differentilis, synonymis, locis. Tomus I, Editio decima tertia, aucta, reformata. Pars III. Amphibia et Pisces. Lipsiae (= Leipszig): Georg. Emanuel Beer. pp. 1038–1516.

Göçmen, B., Y. Kumlutas and M. Tosunoglu. 1996. A New Subspecies, *Ablepharus kitaibelii* (Bibron & Borry, 1833) *budaki* n. ssp. (Sauria: Scincidae) from the Turkish Republic of Northern Cyprus. Turkish Journal of Zoology 20:397–405.

Gray, J.E. 1849. Catalogue of the specimens of snakes in the collection of the British Museum. London: British Museum (Natural History). 125 pp.

Gray, J.E. 1845: Catalogue of the Specimens of lizards in the collection of the British museum. London: British Museum (Natural History). 289 pp.

Gray, J.E. 1864. Revision of the species of Trionychidae found in Asia and Africa, with the description of some new species. Proceedings of the Zoological Society of London 1864:76–98.

Gray, J.E. 1869. Notes on the Families and Genera of Tortoises (Testudinata), and on the Characters afforded by the Study of their Skulls. Proceedings of the Zoological Society of London 1869:165–225.

Günther A. 1876. Description of a new species of lizard from Asia Minor. Proceedings of the Zoological Society of London 1876:818.

Gvoždík, V., D. Jandzik, P. Lymberakis, D. Jablonski and J. Moravec. 2010. Slow worm, *Anguis fragilis* (Reptilia: Anguidae) as a species complex: genetic structure reveals deep divergences. Molecular Phylogenetics and Evolution 55:460–472.

Head, J.J. 2005. Snakes of the Siwalik Group (Miocene of Pakistan): Systematics and Relationship to Environmental Change. Palaeontologia Electronica 8:18A:33 pp.

Head, J.J. 2015. Fossil calibration dates for molecular phylogenetic analysis of snakes 1: Serpentes, Alethinophidia, Boidae, Pythonidae. Palaeontologia Electronica 18.1.6FC:1–17.

Head, J.J., J.I. Bloch, A.K. Hastings, J.R. Bourque, E.A. Cadena, F.A. Herrera, P.D. Polly and C.A. Jaramillo. 2009. Giant boid snake from the paleocene neotropics reveals hotter past equatorial temperatures. Nature 457:715–718.

Head, J.J., K. Mahlow and J. Müller. 2016. Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidea, Colubridae. Palaeontologia Electronica 19.2.2FC:1–21.

Hedges, S.B., A.B. Marion, K.M. Lipp, J. Marin and N. Vidal. 2014. A taxonomic framework for typhlopid snakes from the Caribbean and other regions (Reptilia, Squamata). Caribbean Herpetology 49:1–61.

Hernández-Pacheco, E. 1917. Hallazgo de tortugas gigantescas en el Mioceno de Alcalá de Henares. Boletín de la Sociedad Española de Historia Natural 17:194–202.

Herrmann, H.-W., U. Joger and G. Nilson. 1992. Phylogeny and systematics of Viperinae snakes. III: resurrection of the genus *Macrovipera* (Reuss, 1927) as suggested by biochemical evidence. Amphibia-Reptilia 13:375–392.

Hervet, S. 2003. Le groupe *Palaeochelys* sensu lato – *Mauremys* dans le contexte systématique des Testudinoidea aquatiques du Tertiaire d’Europe occidentale. Apports à la biostratigraphie et à la paléobiogéographie. Ph.D. dissertation, Muséum National d’Histoire Naturelle, Paris. 406 pp.

Hervet, S. 2004. Systématique du groupe «*Palaeochelys* sensu lato–*Mauremys*» (Chelonii, Testudinoidea) du Tertiaire d’Europe occidentale: principaux résultats. Annales de Paléontologie 90:13–78.

Hewitt, J. 1936. A note on the relationships of the Cape genera of land-tortoises. South African Journal of Science 33:788–796.

Hoek Ostende, L. W. van den, J.D. Gardner, L. van Bennekom, M.C. Alçiçek, A. Murray, F.P. Wesselingh, H. Alçiçek and A. Tesakov. 2015. Ericek, a new Pliocene vertebrate locality in the Çameli Basin (southwestern Anatolia, Turkey). Palaeobiodiversity and Palaeoenvironments 95:305–320.

Hoernes, R. 1892. Neue Schildkrötenreste aus steirischen Tertiärablagerungen. Verhandlungen der Kaiserlich-Königlichen Geologischen Bundesanstalt 1892:242–246.

Hoffstetter, R. 1939. Contribution à l'étude des Elapidae actuels et fossiles et de l'ostéologie des Ophidiens. Archives du Muséum d’Histoire Naturelle de Lyon 15:1–78.

Hoffstetter, R. 1943. Varanidae et Necrosauridae fossiles. Bulletin du Muséum national d’Histoire naturelle, Série 2 15:134–141.

Hoffstetter, R., 1955. Squamates de type moderne. In: Piveteau J., ed. Traité de Paléontologie, vol. 5. Paris: Masson.: pp. 606–662.

Hoffstetter, R. 1969. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l’histoire de la famille. Bulletin du Muséum National d’Histoire Naturelle 40:1051–1064.

Holman, A.J. 1998. Pleistocene amphibians and reptiles in Britain and Europe. Oxford Monographs on Geology and Geophysics 38. New York, Oxford: Oxford University Press. 254 pp.

Hooker, J.J., M.E. Collinson and N.P. Sille. 2004. Eocene-Oligocene mammalian faunal turnover in the Hampshire basin, UK: calibration to the global time scale and the major cooling event. Journal of the Geological Society, London 161:161–172.

Hsü, K.J. 1972. Origin of saline giants: a critical review after the discovery of the Mediterranean evaporates. Earth-Science Review 8:371–396.

Huene, F. von and I. Nikoloff. 1963. Ein pliozänes krokodil in Bulgarien. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 118:266–271.

Hummel, K. 1929. Die fossilen Weichschildkröten (Trionychia): eine morphologisch-systematische und stammesgeschichtliche Studie. Geologische und Paläontologische Abhandlungen 16:359–487.

Hummel, K. 1932. Pars 52: Trionychia fossilia. In: W. Quenstedt, ed. Fossilium Catalogus. I: Animalia. Berlin: W. Junk. 106 pp.

Hutchison, J.H. 1980. Turtle stratigraphy of the Willwood Formation, Wyoming: preliminary results. University of Michigan Papers on Paleontology 24:115–118.

[ICZN] International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. 4th ed. London: International Trust for Zoological Nomenclature. 306 pp.

Ivanov, M. 1999. The first European pit viper from the Miocene of Ukraine. Acta Palaeontologica Polonica 44:327–334.

Ivanov, M. 2001. Changes in the composition of the European snake fauna during the early Miocene and at the early/middle Miocene transition. Palaontologische Zeitschrift 74:563–573.

Ivanov, M., M. Ruta, J. Klembara and M. Böhme. 2017. A new species of *Varanus* (Anguimorpha: Varanidae) from the early Miocene of the Czech Republic, and its relationships and palaeoecology, Journal of Systematic Palaeontology

Jiménez Fuentes, E. 1981. Primeros Testudinidae (Chelonia) del Vallesiense de Los Valles de Fuentidueña (Segovia). Estudios Geológicos 37:359–368.

Jouve, S., V. Sarıgül, J.-S. Steyer and S. Sen (2017). The first crocodylomorph from the Mesozoic of Turkey (Barremian of Zonguldak) and the dispersal of the eusuchians during the Cretaceous. Journal of Systematic Palaeontology

Joyce, W.G. 2016. A review of the fossil record of turtles of the clade *Pan-Chelydridae*. Bulletin of the Peabody Museum of Natural History 57:21–56.

Joyce, W.G., J.F. Parham, T.R. Lyson, R.C.M. Warnock and P.C.J. Donoghue. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. Journal of Paleontology 87:612–634.

Khosatzky, L.I., L. Christov and D. Nankinov. 1983. An Eocene soft-shelled turtle from Bulgaria. Schriftenreihe für geologische Wissenschaften 19/20:271–280.

Kilias, A., A. Vamvaka, G. Falalakis, A. Sfeikos, E. Papadimitriou, C. Gkarlaouni and B. Karakostas. 2013. The Mesohellenic Trough and the Thrace Basin. Two Tertiary molassic basins in Hellenides: do they really correlate? Bulletin of the Geological Society of Greece 47:551–562.

Karin, B.R., M. Metallinou, J.L. Weinell, T.R. Jackman and A.M. Bauer. 2016. Resolving the higher-order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): An out-of-Asia diversification. Molecular Phylogenetics and Evolution 102:220–232.

Karl, H.-V. 1999. Die Zoogeographie der känozoischen Weichschildkröte *Trionyx triunguis* Forskål, 1775 (Testudines: Trionychidae). Joannea - Geologie und Paläontologie 1:27–60.

Kaup, J.J. 1825. Einige Bemerkungen zu Merrems Handbuch. Isis von Oken 16:589–593.

Kelly, C.M., N.P. Barker, M.H. Villet, D.G. Broadley and W.R. Branch. 2008. The snake family Psammophiidae (Reptilia: Serpentes): phylogenetics and species delimitation in the African sand snakes (*Psammophis* Boie, 1825) and allied genera. Molecular Phylogenetics and Evolution 47:1045–1060.

Koch, A. 1904. Die fossilen Fische des Boecsiner Cementmergels. A2. Beschreibung der im Beocsiner Cementmergel vorkommenden Schildkrötenreste. Annales Musei nationalis hungarici 2:56–71.

Kornilios, P., Y. Kumlutaş, P. Lymberakis and Ç. Ilgaz. 2018. Cryptic diversity and molecular systematics of the Aegean *Ophiomorus* skinks (Reptilia: Squamata), with the description of a new species. Journal of Zoological Systematics and Evolutionary Research

Kotsakis, T., 1977. I resti di anfibi e rettili pleistocenici della grotta ‘‘Bate’’ (Rethymnon, Creta). Atti della Accademia Nazionale dei Lincei 63:571–582.

Koufos, G.D., N. Zouros and O. Mourouzidou. 2003. *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from Lesvos island, Greece; the appearance of deinotheres in the Eastern Mediterranean. Geobios 36:305–315.

Koufos, G.D., D. Kostopoulos and T. Vlachou. 2005. Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belgian Journal of Zoology 135:181–190.

Krijgsman, W., F.J. Hilgen, I. Raffi, F.J. Sierro and D.S. Wilson. 1999. Chronology, causes and progression of the Messinian salinity crisis. Nature 400:652–655.

Kuch, U., J. Müller, C. Mödden and D. Mebs. 2006. Snake fangs from the Lower Miocene of Germany: evolutionary stability of perfect weapons. Naturwissenschaften 93:84–87.

Kuhn, O. 1939. Fossilium Catalogus, 1: Animalia, pars 86. Squamata: Lacertilia et Ophidia. Neubrandenburg: Verlag Gustav Feller. 89 pp.

Kuhn, O. 1963. Fossilium Catalogus, 1: Animalia, pars 103. Serpentes (Supplementum 1). The Hague: W. Junk. 45 pp.

Kuhn, O. 1964. Fossilium Catalogus, 1: Animalia, Pars 107, Testudines. The Hague: Junk. 299 pp.

Kumlutaş, Y., H. Arikan, Ç. Ilgaz and Y. Kaska. 2007. A new subspecies, *Eumeces schneiderii barani* n. ssp (Reptilia: Sauria: Scincidae) from Turkey. Zootaxa 1387:27–38.

Kuss, S.E., 1975. Die pleistozänen Hirsche der ostmediterranen Inseln Kreta, Kasos, Karpathos und Rhodos (Griechenland). Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 65:25–79.

Lacépède, B.G.E. 1789. Histoire naturelle des serpens. Tome second. Paris: Hotel de Thon. 527 pp.

Lantz, L. and C. Cyrén. 1920. Notes sur les *Lacerta viridis* du Caucase. Bulletin de la Société zoologique de France 45:33–37.

Lapparent de Broin, F. de. 2002. A giant tortoise from the Late Pliocene of Lesvos Island (Greece) and its possible relationships. Annales Géologiques des Pays Helléniques 39:99–130.

Lapparent de Broin, F. de, R. Bour, J.F. Parham and J. Perälä. 2006a. *Eurotestudo*, a new genus for the species *Testudo hermanni* Gmelin, 1789 (Chelonii, Testudinidae). Comptes Rendus Palevol 5:803–811.

Lapparent de Broin, F. de, R. Bour and J. Perälä. 2006b. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): first part. Annales de Paléontologie 92:255–304.

Lapparent de Broin, F. de, R. Bour and J. Perälä. 2006c. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): second part. Annales de Paléontologie 92:325–357.

Laurenti, J.N. 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu. Vienna: Joan. Thomae nob. De Trattnern. 217 pp.

Lebküchner, R.F. 1974. Beitrag zur Kenntnis der Geologie des Oligozäns von Mittelthrakien (Türkei). Bulletin of the Mineral Research and Exploration Institute of Turkey 83:1–30.

Lehrs, P. 1902. Zur Kenntnis der Gattung *Lacerta* und einer verkannten Form: *Lacerta ionica*. Zoologischer Anzeiger 25:225–237.

Lenk, P., S. Kalyabina, M. Wink and U. Joger. 2001. Evolutionary relationships among the true vipers (Viperinae) inferred from mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 19:94–104.

Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Stockholm: Laurentii Salvii. 824 pp.

Linnaeus, C. 1766. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio duodecima, reformata. Stockholm, Holmiae: Laurentii Salvii. 532 pp.

Longrich, N.R., B.-A.S. Bhullar and J.A. Gauthier. 2012. Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. PNAS 109:21396–21401.

Lortet, L. 1883. Etudes zoologiques sur la faune du Lac de Tiberiade. Poissons et Reptiles du lac de Tibériade de de Quelques Autres Parties de la Syrie. Archives du Muséum d'Histoire Naturelle, Lyon 3:99–194.

Luján, A., M. Delfino, I. Casanovas-Vilar and D.M. Alba. 2014. Taxonomy of subgenus *Temnoclemmys* Bergounioux, 1958 (Testudines: Geoemydidae: Ptychogasterinae) based on new material from the Vallès-Penedès Basin (NE Iberian Peninsula). Comptes Rendus Palevol 13:277–295.

Lydekker, R. 1886. Indian Tertiary & post-Tertiary Vertebrata. Siwalik Crocodilia, Lacertilia & Ophidia. Palaeontologia Indica 3:210–240.

Lydekker, R. 1888. Catalogue of Fossil Reptiles and Amphibians in the British Museum (Natural History). Part 1. The Orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria. London: British Museum (Natural History). 309 pp.

Lydekker, R. 1889. Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History): Part III. The Order Chelonia. London: British Museum (Natural History) 239 pp.

Lymberakis, P. and N. Poulakakis. 2010. Three Continents Claiming an Archipelago: The Evolution of Aegean's Herpetofaunal Diversity. Diversity 2010:233–255.

Lymberakis, P., N. Poulakakis, A. Kaliontzopoulou, E. Valakos and M. Mylonas. 2008. Two new species of *Podarcis* (Squamata; Lacertidae) from Greece. Systematics and Biodiversity 6:307–318.

Lyras, G.A. and A.A.E. Van der Geer. 2007. The Late Pliocene vertebrate fauna of Vatera (Lesvos Island, Greece). Cranium 24:11–24.

Lyson, T.R., W.G. Joyce, G.E. Knauss and D.A. Pearson. 2011. *Boremys* (Testudines, Baenidae) from the latest Cretaceous and early Paleocene of North Dakota: an 11-million-year range extension and an additional K/T survivor. Journal of Vertebrate Paleontology 31:729–737.

Maack, G.A. 1869. Diue bis jetzt bekannten fossilen Schildkröten und die im oberen Jura bei Kelheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. Palaeontographica 18:193–336.

Maas, M.C., J.G.M. Thewissen, S. Sen, N. Kazanci and J.W. Kappelman. 2001. Enigmatic new ungulates from the early middle Eocene of centralAnatolia, Turkey. Journal of Vertebrate Paleontology 21:578–590.

Maga, A.M. and R.M.D. Beck. 2017. Skeleton of an unusual, cat-sized marsupial relative (Metatheria: Marsupialiformes) from the middle Eocene (Lutetian: 44-43 million years ago) of Turkey. PLoS ONE 12:e0181712.

Malik, A. and H. Nafiz. 1933. Küçükçekmece fosil fikrali hayvanlar mecmuasi. Bulletin de la Faculté des sciences de l'Université d'Istanbul 8:1–119.

Mallow, D., D. Ludwig and G. Nilson. 2003. True Vipers: Natural History and Toxinology of Old World Vipers. Malabar, Florida: Krieger Publishing Company. 359 pp.

Mangili, G. 1980. Fossils reptiles of Simonelli cave. Accademia Nazionale dei Lincei, Problemi Attuali di Scienza e di Cultura 249:121–122.

Martin, W. 1838. Three species of Chameleon from Fernando Po. Proceedings of the Zoological Society of London 1838:63–65.

Mead, J. 2013. Scolecophidia (Serpentes) of the Late Oligocene and Early Miocene, North America, and a fossil history overview. Geobios 46:225–231.

Melentis, J.K., 1966. Studien über fossile Vertebraten Griechenlands: 10. *Clemmys caspica* aus dem Pleistozän des Beckens von Megalopolis im Peloponnes (Griechenland). Annales Géologiques des Pays Helléniques 17:169–181.

Ménétries, E. 1832. Catalogue raisonné des objets de zoologie recueillis dans un voyage au caucase et jusqu'aux frontières actuelles de la Perse. St. -Pétersbourg (St. Petersbourg): L'Académie Impériale des Sciences. 271 pp.

Merrem, B. 1820. Versuch eines systems der Amphibien, Vol. 8. Marburg: J. C. Krieger. 191 pp.

Mertens, R. 1959. Zur Kenntnis der Lacerten auf der Insel Rhodos. Senckenbergiana biologica 40:15–24.

Métais, G. and S. Sen. 2017. First occurrence of Palaeotheriidae (Perissodactyla) from the late–middle Eocene of eastern Thrace (Greece). Comptes Rendus Palevol 16:382–396.

Meulenkamp, J.E. and W. Sissingh. 2003. Tertiary palaeogeography and tectonostratigraphic evolution of the Northern and Southern Peri-Tethys platforms and the intermediate domains of the African–Eurasian convergent plate boundary zone. Palaeogeography, Palaeoclimatology, Palaeoecology 196:209–228.

Meyer, H. von. 1847. *Palaeochelys bussenensis* im älteren Süsswasserkalk. Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg 3:167–168.

Mizsei, E., D. Jablonski, S.A. Roussos, M. Dimaki, Y. Ioannidis, G. Nilson and Z.T. Nagy. 2017. Nuclear markers support the mitochondrial phylogeny of *Vipera ursinii–renardi* complex (Squamata: Viperidae) and species status for the Greek meadow viper. Zootaxa 4227:75–88.

Molnar, R.E. 2004. 2. The long and honorable history of Monitors and their kin. In: Pianka, R. E., D. King and R.A. King, eds. 2004. Varanoid Lizards of the World. Bloomington, Indiana: Indiana University Press. pp. 10–67.

Mueller-Töwe, I.J., T.A.K. Kjeldahl, J. Milàn, L. Vallon, G. Theodorou, J. Lindgren, S. Roussiakis and R.G. Bromley. 2011. First chelonian eggs and carapace fragments from the Pliocene of Rhodes, Greece. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 262/3:309–322.

Nikolsky, A. M. 1909. [New reptile species from Caucasus]. Mitteilungen Kaukasische Museum Tiflis 4:301–306. [in Russian]

Nilson, G. and C. Andrén. 1985. Systematics of the *Vipera xanthina* complex (Reptilia, Viperidae). III. Taxonomic status of the Bulgar Dagh viper in south Turkey. Journal of Herpetology 19:276–283.

Nilson, G. and C. Andrén. 1986. The mountain vipers of the Middle East - the *Vipera xanthina* complex (Reptilia, Viperidae). Bonner Zoologische Monographien 20:1–90.

Nilson, G. and C. Andrén. 1988. A new subspecies of the subalpine meadow viper, *Vipera ursinii* (Bonaparte) (Reptilia, Viperidae), from Greece. Zoologica Scripta 17:311–314.

Nilson, G., B. Tuniyev, C. Andrén, N. Orlov, U. Joger and H.-W. Herrmann. 1999. Taxonomic position of the *Vipera xanthina* complex. In: Joger, U., ed. Phylogeny and systematics of the Viperidae. Kaupia, Darmstädter Beiträge zur Naturgeschichte 8:99–102.

Nopcsa, F. 1908. Zur Kenntnis der fossilen Eidechsen. Beitrage zur Paläontologie und Geologie Osterreich-ungarns und des Orients 21:33–62.

Olivier, G.A. 1804. Voyage dans l'Empire Othoman, l'Egypte et la Perse. Vol. 2. Paris: H. Agasse. 469 pp.

Ouwens, P.A. 1912. On a large *Varanus* species from the Island of Komodo. Bulletin du Jardin botanique de Buitenzorg, series 2 1–6:1–3.

Owen, R. 1841. Description of some ophidiolites (*Palaeophis toliapicus*) from the London Clay of Sheppey, indicating an extinct species of serpent. Transaction of the Geological Society Second Series 6:209–210.

Owen, R., 1842. Report on British fossil reptiles. Part II. Report of the British Association for the Advancement of Science 1841:160–204.

Owen, R. 1850. Part III. Ophidia (*Palaeophis* &c.). In: Owen, R., ed. Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds. London: Palaeontographical Society of London. pp. 51–63.

Owen, R., 1857. On the fossil vertebræ of a Serpent (*Laophis crotaloïdes*, Ow.) discovered by Capt. Spratt, R.N., in a tertiary formation at Salonica. Quarterly Journal of the Geological Society of London 13:196–199.

Paicheler, J.-C., F. de Broin, J. Gaudant, C. Mourer-Chauvire, J.-C. Rage and C. Vergnaud-Grazzin. 1978. Le bassin lacustre Miocène de Bes-Konak (Anatolie-Turquie): géologie et introduction à la paléontologie des vertébrés. Geobios 11:43–65.

Pallas, P.S. 1775. *Lacerta apoda* descripta. Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae 19:435–454.

Pallas, P.S. 1814. Zoographia Rosso-Asiatica, sistens omnium animalium in extenso Imperio Rossico et adjacentibus maribus observatorum recensionem, domicilia, mores et descriptiones, anatomen atque icones plurimorum. Volumen tertium. Animalia monocardia seu frigidi sanguinis imperii Rosso-Asiatici. Petropoli (= St. Petersburg): Officina Caesarea Academiae Scientiarum. 428 pp.

Pantanelli, D. 1893. *Testudo amiatae* n. sp. Atti della Societa Toscana di Scienze Naturali 12:128–138.

Paraskevaidis, I. 1955. Zwei Schildkrötenreste aus dem Obermiozän von Chios. Annales Géologiques des Pays Helléniques 6:133–141.

Paraskevaidis, I. 1961. [New sediments of Tertiary vertebrates from Attica]. Annales Géologiques des Pays Helléniques 12:149–152. [in Greek]

Parham, J.F., O. Türkozan, B.L. Stuart, M. Arakelyan, S. Shafei, J.R. Macey and T.J. Papenfuss. 2006. Genetic evidence for premature taxonomic inflation in Middle Eastern tortoises. Proceedings of California Academy of Sciences 57:955–964.

Pašić, M. and V. Klinčarski. 1959. Nalazak fosilne kornjače u sedimentima gornjeg eocena okoline Štipa (Makedonija). Vesnik 27:61–73.

Perälä, J. 2002. Occurrence and taxonomic significance of thigh-spurs in *Testudo marginata* Schoepff, 1792 and *Testudo weissingeri* Bour. Herpetozoa 14:123–126.

Pérez-García, A. and E. Vlachos. 2014. New generic proposal for the European Neogene large testudinids (Cryptodira) and the first phylogenetic hypothesis for the medium and large representatives of the European Cenozoic record. Zoological Journal of the Linnean Society 172:653–719.

Peters, K.F. 1868. Zur Kenntnis der Wirbelthiere aus den Miocenschichten von Eibiswald in Steiermark. I. Die Schildkrötenreste. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe 57:72–74.

Popov, S.V., F. Rögl, A.Y. Rozanov, F.F. Steininger, I.G. Shcherba and M. Kovac. 2004. Lithologic-Paleogeographic maps of Paratethys. Courier Forschungsinstitut Senckenberg 250: 1–46.

Portis, A. 1901a. Il *Palaeopython sardus* Port. Nuovo pitonide del Miocene medio della Sardegna. Bollettino della Società Geologica Italiana 20:247–253.

Portis, A. 1901b. Il *Procyclanorbis sardus* Port., nuovo trionychide fossile della Sardegna. Bollettino della Società Geologica Italiana 20:51–79.

Poulakakis, N., P. Kapli, P. Lymberakis, A. Trichas, K. Vardinoyiannis, S. Sfenthourakis and M. Mylonas. 2015. A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions. Journal of Zoological Systematics and Evolutionary Research 53:18–32.

Poulakakis, N., P. Lymberakis, E. Valakos, P. Pafilis, E. Zouros and M. Mylonas. 2005. Phylogeography of Balkan wall lizard (*Podarcis taurica*) and its relatives inferred from mitochondrial DNA sequences. Molecular Ecology 14:2433–2443.

Pregill, G.K. and D.W. Steadman. 2004. South Pacific iguanas: human impacts and a new species. Journal of Herpetology 38:15–21.

Psonis, N., A. Antoniou, O. Kukushkin, D. Jablonski, B. Petrov, J. Crnobrnja-Isailović, K. Sotiropoulos, I. Gherghel, P. Lymberakis and N. Poulakakis. 2017. Hidden diversity in the *Podarcis tauricus* (Sauria, Lacertidae) species subgroup in the light of multilocus phylogeny and species delimitation. Molecular Phylogenetics and Evolution 106:6–17.

Pyron, R.A., F.T. Burbrink and J.J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:93.

Rage, J.-C. 1983. Les serpents aquatiques de l'Éocène européen. Définition des espèces et aspects stratigraphiques. Bulletin du Muséum National d'Histoire Naturelle, Section C, Sciences de la terre, paléontologie, géologie, minéralogie 4:213–241.

Rage, J.-C. 1984a. La "Grande Coupure" éocène / oligocène et les herpétofaunes (Amphibiens et Reptiles) : problèmes du synchronisme des événements paléobiogéographiques. Bulletin de la Société géologique de France 26:1251–1257.

Rage, J.-C. 1984b. Serpentes. In: P. Wellnhofer, ed. Encyclopedia of paleoherpetology, part 11. Stuttgart - New York: Gustav Fischer. 80 pp.

Rage, J.-C. and Z. Szyndlar. 1986. *Natrix longivertebrata* from the European Neogene, a snake with one of the longest known stratigraphic ranges. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1986:56–64.

Rage, J.-C. 2006. The lower vertebrates from the Eocene and Oligocene of the Phosphorites du Quercy (France): an overview. In: Pélissié, T. and B. Sigé, eds. 30 millions d'années de biodiversité dynamique dans le paléokarst du Quercy. Journées Bernard Gèze. Strata 13:161–173.

Rage, J.-C. 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments 93:517–534.

Rage, J.-C. and S. Sen. 1976. Les Amphibiens et les Reptiles du Pliocène supérieur de Çalta (Turquie). Géologie méditerranéenne 3:127–134.

Rage, J.-C. and Z. Szyndlar. 2005. Latest Oligocene-Early Miocene in Europe: Dark Period for booid snakes. Comptes Rendus Palevol 4:428–435.

Rauscher, K.L. 1995. Die herpetofauna der Vraona-Holhe (Attika) in Griechenland. Annales Géologiques des Pays Helléniques 36:39–41.

Reinach, A.V. 1900. Schildkrötenreste im Mainzer Tertiärbecken und in benachbarten ungefähr gleichaltrigen. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 28:1–135.

Reuss, A. 1834. Zoologische Miscellen. Reptilien, Ophidier. Abhandlungen der Senckenbergischen, Frankfurt/M. 1:129-162.

Reuss, A.F.T. 1927. Sechs europäische Giftschlangengattungen. Zoologischer Anzeiger, Leipzig 73:124–129.

Rhodin, G.J.A., S. Thomson, G.L. Georgalis, H.-V. Karl, I.G. Danilov, A. Takahashi, M.S. De La Fuente, J.S. Bourque, M. Delfino, R. Bour, J.B. Iverson, H.B. Shaffer and P.P. Van Dijk. 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. Chelonian Research Monographs 5:1–66.

Ristori, G. 1895. Di un nuovo Chelonio fossile del Miocene dell'Isola di Malta. Atti della Società Toscana di Scienze Naturali, Memoire 14:3–17.

Rögl, F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologica Carpathica 50:330–349.

Römer, F. 1870. Über *Python Euboïcus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea. Zeitschrift der Deutschen Geologischen Gesellschaft 22:582–590.

Rochebrune, A.T. de. 1880. Revision des ophidiens fossiles du Museum d'Histoire Naturelle. Nouvelles Archives du Muséum d'Histoire Naturelle, 2ème Série 3:271–296.

Roger, O. 1898. Wirbelthierreste aus dem Dinotheriensande, II. Theil. Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg in Ausburg 33:385–396.

Roger, O. 1900. Wirbelthierreste aus dem Dinotheriensande, III. Theil. Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg in Ausburg 34:53–70.

Rückert-Ülkümen, N. 1963. Tertiäre Fische aus Thrakien und Dardanellen (Türkei). Istanbul Üniversitesi Fen Fakültesi mecmuas, Series B 28:86–103.

Schleich, H.H. 1982. *Testudo marginata* Schoepff aus plio/pleistozänen Ablagerungen SE-Lakoniens (Peloponnes, Griechenland). Paläontologische Zeitschrift 56:259–264.

Schleich, H.H. 1985. Neogene Testudines of Germany. Their stratigraphic and ecological evaluation. Studia Geologica Salmanticensia, volume especial 1. Studia Palaeochelonologica 1:249–267.

Schleich, H.H. 1994. Fossil Schildkröten- und Krokodilreste aus dem Tertiär Thrakiens (W-Türkei). Courier Forschungsinstitut Senckenberg 173:137–151.

Schleip, W.D. and M. O'Shea. 2010. Annotated checklist of the recent and extinct pythons (Serpentes, Pythonidae), with notes on nomenclature, taxonomy, and distribution. ZooKeys 66:29–79.

Schmidtler, J.F. 1975. Zur Taxonomie der Riesen-Smaragdeidechsen (*Lacerta trilineata* Bedriaga) Sued-Anatoliens (Reptilia, Lacertidae). Veröffentlichungen der Zoologischen Staatssammlung München 18:45–68.

Schneider, B. 1975. Ein mittelpleistozäne Herpetofauna von der Insel Chios, Ägäis. Senckenbergiana biologica 56:191–198.

Schoepff, I.D. 1792. Historia testudinum iconibus illustrata. [part 1]. Erlangae (= Erlangen): J.J. Palm. 136 pp.

Sen, S. 2013. Dispersal of African mammals in Eurasia during the Cenozoic: Ways and whys. Geobios 46:159–172.

Sen, S., M. Delfino and N. Kazanci. 2017. Çeştepe, a new early Pliocene vertebrate locality in Central Anatolia and its stratigraphic context. Annales de Paléontologie 103:149–163.

Sfenthourakis, S. and K.A. Triantis. 2017. The Aegean archipelago: a natural laboratory of evolution, ecology and civilisations. Journal of Biological Research, Thessaloniki 24:4.

Shaw, G. 1802. General Zoology, or Systematic Natural History. Vol.3, part 2. London: G. Kearsley, Thomas Davison. pp. 313–615.

Sindaco, R. and V. Jeremčenko. 2008. The reptiles of the western Palearctic Vol 1: annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. Belvedere: Monografie della Societas Herpetologica Italica I. 579 pp.

Sindaco, R., P. Kornilios, R. Sacchi and P. Lymberakis. 2014. Taxonomic reassessment of *Blanus strauchi* (Bedriaga, 1884) (Squamata: Amphisbaenia: Blanidae), with the description of a new species from south-east Anatolia (Turkey). Zootaxa 3795:311–326.

Sindaco, R., A. Venchi, G.M. Carpaneto and M.A. Bologna. 2000. The Reptiles of Anatolia: a Checklist and Zoogeographical analysis. Biogeographia 21:441–554.

Sindaco R., A. Venchi and C. Grieco. 2013. The reptiles of the western Palearctic. 2. Annotated checklist and distributional atlas of the snakes of Europe, North Africa, Middle East and Central Asia, with an update to the Vol. 1. Belvedere: Monografie della Societas Herpetologica Italica II. 543 pp.

Smith, K. 2009. Eocene Lizards of the Clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the Early Radiation of Iguanidae (Reptilia: Squamata). Bulletin of the Peabody Museum of Natural History 50:219–306.

Staesche, K. 1975. Schildkrötenreste der Türkischen Fundstellen. In: O. Sickenberg, ed. Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten. Geologisches Jahrbuch, Series B 15:117–118.

Staesche, K., H.V. Karl and U. Staesche. 2007. Fossile Schildkröten aus der Türkei. Geologisches Jahrbuch, Series B 98:91–149.

Stehlin, H.G. 1909. Remarques sur les faunes de mammifères des couches éocènes et oligocènes du Bassin de Paris. Bulletin de la Société Géologique de France, 4e série 9:488–520.

Steindachner, F. 1870. Herpetologische Notizen (Il). Reptilien gesammelt Während einer Reise in Sengambien. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien 62:326–348.

Strauch, A. 1873. Die Schlangen des Russischen Reichs, in Systematischer und Zoogeographischer Beziehung. Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg, Series 7 21:1–287.

Stümpel, N., M. Rajabizadeh, A. Avci, W. Wüster and U. Joger. 2016. Phylogeny and diversification of mountain vipers (*Montivipera*, Nilson et al., 2001) triggered by multiple Plio–Pleistocene refugia and high-mountain topography in the Near and Middle East. Molecular Phylogenetics and Evolution 101:336–351.

Sullivan, R. 1979. Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguidae). Bulletin of the American Museum of Natural History 163:1–72.

Symeonidis, N., F. Bachmayer and H. Zapfe. 1979. Ergebnisse weiterer Grabungen in der Höhle von Vraona (Attika, Griechenland). Annales Géologiques des Pays Helléniques 30:291–299.

Szalai, T. 1931. Schildkrötenstudien. I. *Testudo Schafferi* nov. sp., eine Riesenschildkröte aus dem Pliozän von Samos. Annalen des Naturhistorischen Museums in Wien 46:153–157.

Szyndlar, Z. 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos 47:103–126.

Szyndlar, Z. 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estudios Geológicos 47:237–266.

Szyndlar, Z. 1992. "*Coluber*" *kargii* von Meyer, 1845 (Serpentes: Viperidae), from the Miocene of Öhningen (Germany). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1992:692–700.

Szyndlar, Z. 2005. Snake fauna from the Late Miocene of Rudabánya. Palaeontographia Italica 90:31–52.

Szyndlar, Z. and I. Hoşgör. 2012. Boine snake *Bavarioboa* from the Oligocene/Miocene of eastern Turkey with comments on connections between European and Asiatic snake faunas. Acta Palaeontologica Polonica 57:667–671.

Szyndlar, Z. and J.-C. Rage. 1999. Oldest fossil vipers (Serpentes: Viperidae) from the Old World. Kaupia 8:9–20.

Szyndlar, Z. and J.-C. Rage. 2002. Fossil record of the true vipers. In: Schuett, G., M. Hoggren, M. Douglas and H. Greene, eds. Biology of the Vipers. Eagle Mountain: Eagle Mountain Publishing. pp. 419–441.

Szyndlar, Z. and J.-C. Rage. 2003. Non-erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków. 111 pp.

Szyndlar, Z. and H.H. Schleich. 1993. Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern Germany. Stuttgarter Beiträge zur Naturkunde B 192:1–47.

Taskavak, E., M.J. Reimann and W.N. Polder. 1999. First record of the Nile soft-shelled Turtle, *Trionyx triunguis*, from Kos Island, Greece, with comments on its occurrence in the eastern Mediterranean. Chelonian Conservation and Biology 3:510–512.

Tranos, M.D., D.M. Mountrakis, C.B. Papazachos, E. Karagianni and D. Vamvakaris. 2010. Faulting deformation of the Mesohellenic Trough in the Kastoria-Nestorion region (Western Macedonia, Greece). Bulletin of the Geological Society of Greece, Proceedings of the 12th International Congress 43:495–505.

Tsoukala, E., D. Mol, S. Pappa, E. Vlachos, W. Longhem, M. Vaxevanopoulos and J. Reumer. 2011. *Elephas antiquus* in Greece: new finds and a reappraisal of older material (Mammalia, Proboscidea, Elephantidae). Quaternary International 245:339–349.

Tuna, V. 1988. The remains of a fossil soft-shelled Turtle (*Trionyx*) from Bayraktepe (Turkey). Zoology in the Middle East 2:63–67.

Valakos, E. D., P. Pafilis, K. Sotiropoulos, P. Lymberakis, P. Maragou and J. Foufopoulos. 2008. Amphibians and reptiles of Greece. Frankfurt: Chimaira. 463 pp.

Vandelli, D. 1761. Epistola de holothurio, et testudine coriacea ad celeberrimum Carolum Linnaeum equitem naturae curiosum Dioscoridem II. Patavii (= Padova): Conzatti. 12 pp.

Vasileiadou, K., M. Böhme, T.A. Neubauer, G.L. Georgalis, G.E. Syrides, L. Papadopoulou and N. Zouros. 2017. Early Miocene gastropod and ectothermic vertebrate remains from the Lesvos Petrified Forest (Greece). Paläontologische Zeitschrift 91:541–564.

Venczel, M. 1998. Late Miocene snakes (Reptilia: Serpentes) from Polgardi (Hungary): a second contribution. Acta Zoologica Cracoviensa 4:1–22.

Venczel, M. and S. Sen. 1994. Pleistocene amphibians and reptiles from Emirkaya-2, Turkey. Herpetological Journal 4:159–165.

Vidal, N., J.-C. Rage, A. Couloux and S.B. Hedges. 2009. Snakes (Serpentes). In: Hedges, S.B. and S. Kumar, eds. The Timetree of Life. New York: Oxford University Press. pp. 390–397.

Villa, A., E. Tschopp, G.L. Georgalis and M. Delfino. 2017. Osteology, fossil record and palaeodiversity of the European lizards. Amphibia-Reptilia 38:79–88.

Vlachos, E., I. Cerda and E. Tsoukala. 2015a. The first record of a soft-shelled turtle (Testudines: *Pan-Trionychidae*) from southern Balkans (Pliocene, Gefira, N. Greece) and new information from bone histology. Science of Nature 102:45.

Vlachos, E. and M. Delfino. 2016. Food for thought: Sub-fossil and fossil chelonian remains from Franchthi Cave and Megalopolis confirm a glacial refuge for *Emys orbicularis* in Peloponnesus (S. Greece). Quaternary Science Reviews 150:158–171.

Vlachos E., T. Kotsakis and M. Delfino. 2015b. The chelonians from the latest Miocene-earliest Pliocene locality of Allatini and Pylea (east Thessaloniki, Macedonia, Greece). Comptes Rendus Palevol 14:187–205.

Vlachos, E. and M. Rabi. 2018. Total evidence analysis and body size evolution of extant and extinct tortoises (Testudines: Cryptodira: Pan-Testudinidae). Cladistics

Vlachos E. and E. Tsoukala. 2014. *Testudo* cf. *graeca* from the new Late Miocene locality of Platania (Drama basin, N. Greece) and a reappraisal of previously published specimens. Bulletin of the Geological Society of Greece 48:27–40.

Vlachos, E. and E. Tsoukala. 2016. The diverse fossil chelonians from Milia (late Pliocene, Grevena, Greece) with a new species of *Testudo* Linnaeus, 1758 (Testudines: Testudinidae). Papers in Palaeontology 2:71–86.

Vlachos, E., E. Tsoukala and J. Corsini. 2014. *Cheirogaster bacharidisi*, sp. nov., a new species of a giant tortoise from the Pliocene of Thessaloniki (Macedonia, Greece). Journal of Vertebrate Paleontology 34:560–575.

Wagler, J.G. 1830. Natürliches System der Amphibien, mit vorangehender Classification der Saugthiere und Vogel. Ein Beitrag zur vergleichenden Zoologie. Munchen (= Munich), Stuttgart, and Tubingen: J.G. Cottaschen Buchhandlung. 354 pp.

Wallach, V., K.L. Williams and J. Boundy. 2014. Snakes of the world: a catalogue of living and extinct species. Boca Raton, London and New York: CRC Press. 1237 pp.

Wegener, A. 1912. Die Entstehung der Kontinente. Dr. A. Petermanns Mitteilungen aus Justus Perthes' Geographischer Anstalt 63:185–195.

Weithofer, A. 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. Beiträge zur Paläontologie Österreich-Ungarns 6:225–292.

Werner, F. 1894. Die Reptilien- und Batrachierfauna der jonischen Inseln. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 44:225–237.

Werner, F. 1900. Beschreibung einer bisher noch unbekannten Eidechse aus Kleinasien *Lacerta anatolica*. Anzeiger Akademie der Wissenschaften Wien 25:269–271.

Werner, F. 1902. Über Reptilien und Batrachier aus West-Asien (Anatolien und Persien). Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere 19:329–345.

Werner, F. 1930. Contribution to the knowledge of the reptiles and amphibians of Greece, especially the Aegean islands. Occasional Papers of the Museum of Zoology of the University of Michigan 211:1–46.

Werner, F. 1935. Reptilien der Ägäichen inseln. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse 144:81–117.

Wettstein, O. 1952. Dreizehn neue Reptilienrassen von den Ägäischen Inseln. Anzeiger der Mathematisch-Naturwissenschaftliche Klasse, Österreichische Akademie der Wissenschaften, Wien 89:251–256.

Wiegmann A.F.A. 1834. Herpetologia Mexicana, seu Descriptio Amphibiorum Novae Hispaniae, quae Itineribus Comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum Zoologicum Berolinense Pervenerunt. Berlin: C.G. Lüderitz. 54 pp.

Wilms, T.M., W. Böhme, P. Wagner, N. Lutzmann and A. Schmitz. 2009. On the Phylogeny and Taxonomy of the Genus *Uromastyx* Merrem, 1820 (Reptilia: Squamata: Agamidae: Uromastycinae) – Resurrection of the Genus *Saara* Gray, 1845. Bonner zoologische Beiträge 56:55–99.

Woodward, A.S., 1901. On the bone beds of Pikermi, Attica and on similar deposits in Northern Euboea. Geological Magazine 8:481–486.

Wüster, W., L. Peppin, C.E. Pook and D.E. Walker. 2008. A nesting of vipers: phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). Molecular Phylogenetics and Evolution 49:445–459.

Zagorchev, I.S. 1998. Pre-Priabonian Palaeogene formations in south-western Bulgaria and northern Greece: stratigraphy and tectonicimplications. Geological Magazine 135:101–119.

Zittel, K.A. 1887–1890. Handbuch der Paläontologie. Palaeozoologie. III. Pisces, Amphibia, Reptilia, Aves. Munchen (= Munich) and Leipsig: Druck und Verlag von R. Oldenbourg. 900 pp.

Zug, G.R., A.M. Hamilton and C.C. Austin. 2011. A new *Emoia samoensis* group lizard (Squamata: Scincidae) from the Cook Islands, Southcentral Pacific. Zootaxa 2675:47–57.

Zwick, A. and H.H. Schleich. 1994. Quartäre Reptilienfunde von der Grabungsstelle Karain (S-Türkei). (Reptilia: Testudines, Squamata). Courier Forschungsinstitut Senckenberg 173:267–281.

## List of Appendices (Enclosed Publications)

Project idea: identification of scientific problem, initiation of project
Data generation: collecting specimens, illustrating and photographing specimens, scoring characters
Data analysis: developing character/taxon matrices, analyzing matrices
Manuscript writing: actively writing manuscript or heavily editing manuscript

**APPENDIX 1.** Georgalis, G.L. and W.G. Joyce. 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58:115–208.
Project idea: 50%; Data generation: 90%; Data analysis: 50%; Manuscript writing: 80%

**APPENDIX 2.** Georgalis, G.L., Zoboli, D., Pillola, G.L. and Delfino, M. 2017. A revision of the trionychid turtle *Procyclanorbis sardus* Portis, 1901 from the late Miocene of Sardinia (Italy). Annales de Paléontologie 103:127–134.
Project idea: 50%; Data generation: 50%; Data analysis: 90%; Manuscript writing: 90%

**APPENDIX 3.** Georgalis, G.L. 2017. *Necrosaurus* or *Palaeovaranus*? Appropriate nomenclature and taxonomic content of an enigmatic fossil lizard clade (Squamata). Annales de Paléontologie 103:59–69.
Project idea: 100%; Data generation: 100%; Data analysis: 100%; Manuscript writing: 100%

**APPENDIX 4.** Georgalis, G.L., Szyndlar, Z., Kear, B.P. and Delfino, M. 2016. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109:103–116.
Project idea: 100%; Data generation: 60%; Data analysis: 80%; Manuscript writing: 90%

**APPENDIX 5.** Georgalis, G.L., Villa, A. and Delfino, M. 2016. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature 103:12.
Project idea: 100%; Data generation: 60%; Data analysis: 80%; Manuscript writing: 90%

**APPENDIX 6.** Georgalis, G.L., Villa, A., Vlachos, E. and Delfino, M. 2016. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49:433–444.
Project idea: 100%; Data generation: 60%; Data analysis: 90%; Manuscript writing: 90%

**APPENDIX 7.** Georgalis, G.L., Villa, A., and Delfino, M., 2017. Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. Historical Biology 29:730–742.
Project idea: 100%; Data generation: 60%; Data analysis: 90%; Manuscript writing: 90%

**APPENDIX 8.** Georgalis, G.L., Villa, A., and Delfino, M. 2017. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. Journal of Vertebrate Paleontology 37:e1301946.
Project idea: 100%; Data generation: 60%; Data analysis: 80%; Manuscript writing: 90%

**APPENDIX 9.** Georgalis, G.L., K. Halaçlar, S. Mayda, T. Kaya, and D. Ayaz 2018. First fossil find of the *Blanus strauchi* complex (Amphisbaenia, Blanidae) from the Miocene of Anatolia. Journal of Vertebrate Paleontology e1437044.
Project idea: 100%; Data generation: 80%; Data analysis: 100%; Manuscript writing: 90%

**APPENDIX 10.** Georgalis, G.L., Rage, J.-C., Bonis, L. de, and Koufos, G.D. 2018. Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). Swiss Journal of Geosciences
Project idea: 100%; Data generation: 70%; Data analysis: 80%; Manuscript writing: 90%

**APPENDIX 11.** Georgalis, G.L., A. Villa, M. Ivanov, S. Roussiakis, P. Skandalos, and M. Delfino 2018. Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia – bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe. Historical Biology
Project idea: 100%; Data generation: 60%; Data analysis: 70%; Manuscript writing: 90%

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Date of Birth: 04 July 1982
Place of Birth: Thessaloniki, Greece
Nationality: Greek

## Studies and Work (as of January 2018)

- 5th Lyceum of Thessaloniki (1997-2000)
- BSc. and MSc. from the Department of Chemical Engineering, Aristotle University of Thessaloniki, Greece (2000-2014).
- Socrates-Erasmus Program on Fossil Vertebrates in the Department of Zoology, Charles University in Prague, Czech Republic (by Professor Zbyněk Roček) (2005-2006).
- Socrates-Erasmus Program in the Institute of Chemical Technology (VSCHT), Prague, Czech Republic (2005-2006).
- MSc. Thesis under the supervision of Prof. Maria Liakopoulou-Kyriakides: 'DNA and protein isolation from fossils and applications in Palaeontology', (in Greek) (2014).
- PhD candidate in Palaeontology in the Department of Geosciences, University of Fribourg/Freiburg, Switzerland (under the supervision of Prof. Walter Joyce) in co-tutelle with the Dipartimento di Scienze della Terra, University of Torino, Italy (under the supervision of Prof. Massimo Delfino), with the Thesis 'Fossil Reptiles from the Aegean Region' (2014-).
- Assistant diplomé / Assistant source tierces, Department of Geosciences, University of Fribourg, Switzerland (1 January 2016 – 30 September 2016).

## Complete List of Publications

1) **Georgalis, G.L.,** Velitzelos, E., Velitzelos, D. and Kear, B.P. 2013. *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the Lower Miocene of Northern Greece. In: D. Brinkman, P. Holroyd, and J.Gardner (eds), Morphology and Evolution of Turtles: Papers in Honor of Eugene S.Gaffney. Volume 3. Pleurodires. Springer, Dordrecht, The Netherlands. pp. 277–287.
2) **Georgalis, G.L.** and Kear, B.P. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios, 46:299–311.
3) Kear, B.P, Ekrt, B., Prokop, J. and **Georgalis, G.L.** 2014. Turonian marine amniotes from the Bohemian Cretaceous Basin, Czech Republic. Geological Magazine, 151:183–198.
4) Senut, B. and **Georgalis, G.L.** 2014. *Brevirhynchocyon* gen. nov., a new name for the genus *Brachyrhynchocyon* Senut, 2008 (Mammalia, Macroscelidea) preoccupied by *Brachyrhynchocyon* Loomis, 1936 (Mammalia, Carnivora). Communications of the Geological Survey of Namibia, 15:69.
5) Rhodin, G.J.A., Thomson, S., **Georgalis, G.L.,** Karl, H.-V., Danilov, I.G., Takahashi, A., De La Fuente, M.S., Bourque, J.S., Delfino, M., Bour, R., Iverson, J.B., Shaffer, H.B. and Van Dijk, P.P. 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs, 5(8):1–66.

6) **Georgalis, G.L.,** Villa, A. and Delfino, M. 2016. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature 103:12.
7) **Georgalis, G.L.,** Szyndlar, Z., Kear, B.P. and Delfino, M. 2016. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109:103–116.
8) **Georgalis, G.L.,** Villa, A., Vlachos, E. and Delfino, M. 2016. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49:433–444.
9) Villa, A., Tschopp, E., **Georgalis, G.L.** and Delfino, M. 2017. Osteology, fossil record and palaeodiversity of the European lizards. Amphibia-Reptilia 38:79–88.
10) **Georgalis, G.L.,** Villa, A., and Delfino, M., 2017. Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. Historical Biology 29:730–742.
11) **Georgalis, G.L.** and W.G. Joyce. 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58:115–208.
12) **Georgalis, G.L.,** Zoboli, D., Pillola, G.L. and Delfino, M. 2017. A revision of the trionychid turtle *Procyclanorbis sardus* Portis, 1901 from the late Miocene of Sardinia (Italy). Annales de Paléontologie 103:127–134.
13) **Georgalis, G.L.,** Villa, A., and Delfino, M. 2017. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. Journal of Vertebrate Paleontology 37:e1301946.
14) Čerňanský, A., Vasilyan, D., **Georgalis, G.L.,** Joniak, P., Mayda, S. and Klembara, J. 2017. First record of fossil anguines (Squamata; Anguidae) from the Oligocene and Miocene of Turkey. Swiss Journal of Geosciences 110:741–751.
15) Vasileiadou, K., Böhme, M., Neubauer, T.A., **Georgalis, G.L.,** Syrides, G.E., Papadopoulou, L. and Zouros, N. 2017. Early Miocene gastropod and ectothermic vertebrate remains from the Lesvos Petrified Forest (Greece). Paläontologische Zeitschrift 91:541–564.
16) **Georgalis, G.L.** 2017. *Necrosaurus* or *Palaeovaranus*? Appropriate nomenclature and taxonomic content of an enigmatic fossil lizard clade (Squamata). Annales de Paléontologie 103:293–303.
17) **Georgalis, G.L.,** J.-C. Rage, L. de Bonis and G. Koufos. 2018. Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). Swiss Journal of Geosciences DOI: https://doi.org/10.1007/s00015-017-0291-2.
18) **Georgalis, G.L.,** A. Villa, M. Ivanov, S. Roussiakis, P. Skandalos and M. Delfino 2018. Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia – bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe. Historical Biology, DOI: 10.1080/08912963.2017.1417404.
19) **Georgalis, G.L.,** K. Halaçlar, S. Mayda, T. Kaya, and D. Ayaz 2018. First fossil find of the *Blanus strauchi* complex (Amphisbaenia, Blanidae) from the Miocene of Anatolia. Journal of Vertebrate Paleontology e1437044.

## Bibliometrics (as of January 2018)

| | |
|---|---|
| Peer reviewed papers: | **19** |
| Actual Number of Citations: | **125** |
| Google Scholar citations: | **120** |
| Google Scholar *h*-Index: | **7** |

## Published Abstracts

1) Pavelka, J. and **Georgalis, G.L.** 2007. DNA and protein isolation from the 290 million year-old amphibian *Discosauriscus austriacus* and applications of Biotechnology in Palaeontology. 10th International Congress on Amino Acids and Proteins (ICAAP), pp. 50–51.
2) Kear, B.P. and **Georgalis, G.L.** 2009. Evolution of gigantic tortoises from the Neogene of Europe. Journal of Vertebrate Paleontology, SVP Program and Abstracts Book, pp. 123–124.
3) **Georgalis, G.L.** and Kear, B.P. 2010. New Records of Fossil Turtles from Greece. Journal of Vertebrate Paleontology, SVP Program and Abstracts Book, p.95.
4) **Georgalis, G.L.,** Pavelka, J., and Liakopoulou-Kyriakides, M., 2010. Nine million year old DNA and its bearing on the understanding of extinct animals' relationships. Proceedings of the1st International Conference on Advances in Biotechnology – Industrial Microbial Biotechnology (ABIMB 2010).
5) **Georgalis, G.L.,** Kear, B.P., Campione, N.E., Szyndlar, Z., Pavia, M. and Delfino, M., 2014. New material of the enigmatic giant viperid *Laophis crotaloides* (Squamata, Serpentes) from the Pliocene of Greece, with comments on reptilian gigantism in the Neogene of Southeastern Europe. In: Delfino, M., Carnevale, G., and Pavia, M. (Eds.). Abstract Book and Field Trip Guide, XII Annual Meeting of the European Association of Vertebrate Palaeontologists. Museo Regionale di Scienze Naturali, Regione Piemonte, Torino, p. 68.
6) **Georgalis, G.L.,** Kear, B.P., Campione, N.E, Delfino, M., 2014. Rediscovery of *Laophis crotaloides* – the world's largest viper? Journal of Vertebrate Paleontology, SVP Program and Abstracts Book, p. 136.
7) **Georgalis, G.L.,** and Delfino, M., 2015. Neogene snakes from Greece: giants and dwarfs in a mammal-dominated world. Abstract Book, XIII Annual Meeting of the European Association of Vertebrate Palaeontologists, Opole, Poland. p. 93.
8) **Georgalis, G.L.,** and Delfino, M., 2015. A new diverse squamate fauna from the Late Miocene of northern Greece. Journal of Vertebrate Paleontology, SVP Program and Abstracts Book. p. 131.
9) **Georgalis, G.L.,** Villa, A., Vlachos, E. and Delfino M. 2016. A new fossil herpetofauna from the early late Miocene of Plakias (Crete, Greece). Paleodays 2016 - XVI riunione annuale SPI, Museo Civico di Scienze Naturali "Malmerendi", Faenza, Volume dei riassunti e guida all'escursione. p. 52.
10) Delfino, M., Villa, A., **Georgalis, G.L.,** and Tschopp, E., 2016. Fossil record and the origin of the Mediterranean lizard assemblages. 9th Symposium on the Lacertids of the Mediterranean Basin & 1st Symposium on Mediterranean Lizards. Limassol. Book of abstracts, p. 2.
11) **Georgalis, G.L.** and W.G. Joyce. 2017. The Biogeographic Origins of European Paleogene Trionychians. 15th Annual Meeting of the European Association of Vertebrate Palaeontologists, Munich, Germany. Zitteliana 91:37–38.
12) Vasileiadou, K., Böhme, M., Neubauer, T.A., **Georgalis, G.L.,** Syrides, G.E., Papadopoulou, L. and Zouros, N. 2017. Early Miocene small animal remains from the Lesvos Petrified Forest (Greece). Abstracts of the 15th Congress of the Regional Committee on Mediterranean Neogene Stratigraphy (RCMNS), Athens, Greece. p. 20.

## Symposia and Meetings

1) 10th International Congress on Amino Acids and Proteins (ICAAP), 20–27 August 2007, Chalkidiki, Greece.
2) 69th Annual Meeting of the Society of Vertebrate Paleontology and the 57th Symposium of Vertebrate Palaeontology and Comparative Anatomy, 23–26 September 2009, Bristol, England.

3) 1st International Conference on Advances in Biotechnology - Industrial Microbial Biotechnology (ABIMB 2010), 3–5 November 2010, Thessaloniki, Greece.
4) 12thAnnual Meeting of the European Association of Vertebrate Palaeontologists, 24–28 June 2014, Torino, Italy.
5) 74th Annual Meeting of the Society of Vertebrate Paleontology, 5–8 November 2014, Estrel Berlin, Berlin, Germany.
6) 13thAnnual Meeting of the European Association of Vertebrate Palaeontologists, 8–12 July 2015, Opole, Poland.
7) Workshop HerpeThon 2015 'Breeding and trade of amphibians and reptiles: risks and conservation opportunities', 18 September 2015, Torino, Italy.
8) 75th Annual Meeting of the Society of Vertebrate Paleontology, 14–17 October 2015, Dallas, Texas, USA.
9) 15th Annual Meeting of the European Association of Vertebrate Palaeontologists, 1–3 August 2017, Munich, Germany.

## Popular Articles

Kear, B.P, and **Georgalis, G.L.** 2010. Colossal Tortoises, Climate Change and the Evolution of Europe's Largest 'Modern' Reptiles. Deposits, 21:8–10.

## Press Releases and Media Coverage

Live Science (November 2014): *Biggest Venomous Snake Ever Revealed in New Fossils.*
http://www.livescience.com/48629-biggest-venomous-snake-fossils-found.html

USA Today (November 2014): *Five-million-year-old poison snake found.*
http://www.usatoday.com/story/news/nation/2014/11/08/dinosaur-snake-venomous-poison/18686989/

Live Science (May 2017): *Remains of Mini 'Komodo Dragon' Found in Greece.*
http://www.livescience.com/59224-fossils-of-mini-komodo-dragon-from-greece.html

Earth Archives (June 2017): *Komodo Dragon's extinct cousin from Athens.*
http://www.eartharchives.org/articles/komodo-dragon-s-extinct-cousin-from-athens/

University of Fribourg (June 2017): *The last European Monitor Lizard.*
http://www.unifr.ch/news/en/17426/the-last-european-monitor-lizard?&p=1

## Grants Awarded

- 600$ award from the Jackson School of Geosciences SVP Grant for the presentation of my work in the Society of Vertebrate Paleontology Meeting in Pittsburgh (USA), October 10-13, 2010 (not recieved due to non-possibility of attendance).
- 400$ award from the Jackson School of Geosciences SVP Grant for the presentation of my work in the Society of Vertebrate Paleontology Meeting in Berlin (Germany), November 5-8, 2014.
- 2500 CHF (Swiss Francs) Travel Grant from the University of Fribourg, May 2015.
- 5000€ Scholarship from the University of Torino, December 2015.
- SYNTHESYS ES-TAF-5910 Grant 'The Snakes of Europe: vertebral anatomy and approaches to their fossil record'. Museum of Natural Sciences, Madrid, Spain (31 January-13 February 2016).

- SYNTHESYS AT-TAF-5911 Grant ‘The Snakes of Europe: vertebral anatomy and approaches to their fossil record’. Museum of Natural History, Vienna, Austria (13-26 March 2016).
- 1300€ Travel Grant from the University of Torino, May 2016.
- SYNTHESYS HU-TAF-6145 Grant ‘The Snakes of Europe: vertebral anatomy and approaches to their fossil record’. Hungarian Natural History Museum, Budapest, Hungary (1-9 November 2016).
- SYNTHESYS GB-TAF-6591 Grant “Anatomy, taxonomy and biogeography of European fossil pan-trionychid turtles: the pan-trionychids from the Eocene of the United Kingdom”. Natural History Museum, London, United Kingdom (9-25 March 2017).
- 1200€ Travel Grant from the University of Torino, May 2017.
- 750 CHF Grant from the Swiss Geological Society 2017.

## Scientific Organizations Affiliations

- Member of the Society of Vertebrate Paleontology (SVP) for the years 2009-2015.
- Member of the European Association of Vertebrate Palaeontologists (EAVP) for the years 2014, 2015, and 2017.
- Member of the Greek Herpetological Society for the years 2014-2017.
- Member of the Swiss Geological Society for the year 2017.
- Member of the Swiss Palaeontological Society for the year 2017.

## Extra Courses and Seminars

1) Phylogeny and Taxonomy course, University of Fribourg. Fribourg, March 2016.
2) “Morphological, specimen-level phylogenetic analysis using Bayesian inference methods – theory & practice”, University of Torino. Torino, April 2016.

## Languages and Computer Knowledge

- Excellent Greek language knowledge (Native speaker)
- Excellent English language knowledge (Cambridge Proficiency).
- Degree of Italian language (Diploma Italiano).
- Basic knowledge of Czech and French languages.
- Excellent P/C knowledge.

## Appendix I.

### Number of studies dealing with fossil reptiles from the Aegean region (1857–today)

1851–1860: 1 (Owen 1857)
1861–1870: 4 (Gaudry 1862a, 1862b, 1862–1867; Römer 1870)
1871–1880: 1 (Calvert and Neumayr 1880)
1881–1890: 2 (Weithofer 1888; Lydekker 1889)
1891–1900: 0
1901–1910: 2 (Woodward 1901; Nopcsa 1908)
1911–1920: 2 (Campana 1917, 1919)
1921–1930: 1 (Arambourg and Piveteau 1929)
1931–1940: 2 (Szalai 1931; Malik and Nafiz 1933)
1941–1950: 0
1951–1960: 1 (Paraskevaidis 1955)
1961–1970: 5 (Paraskevaidis 1961; Rückert-Ülkümen 1963; Melentis 1966; Bachmayer 1967; Bachmayer and Symeonidis 1970)
1971–1980: 12 (Lebküchner 1974; Bachmayer et al. 1975; Kuss 1975; Bachmayer and Symeonidis 1975, 1976; Schneider 1975; Staesche 1975; Rage and Sen 1976; Kotsakis 1977; Paicherer et al. 1978; Bachmayer et al. 1980; Mangili 1980)
1981–1990: 4 (Schleich 1982; Tuna 1988; Gad 1990; Szyndlar and Zerova 1990)
1991–2000: 9 (Szyndlar 1991a, 1991b, 1995; Schleich 1994; Venczel and Sen 1994; Rauscher 1995; Zwick and Schleich 1994; Richter 1995; Brinkering 1996)
2001–2010: 3 (De Vos et al. 2002; Lapparent de Broin 2002; Staesche et al. 2007)
2011–today: 24 (Mueller-Töwe et al. 2011; Tsoukala et al. 2011; Conrad et al. 2012; Georgalis et al. 2013; Georgalis and Kear 2013; Vlachos and Tsoukala 2014, 2016; Vlachos et al. 2014, 2015a, 2015b; Hoek Ostende et al. 2015; Garcia et al. 2016; Georgalis et al. 2016a, 2016b, 2016c, 2017a, 2017b, 2018a, 2018b, 2018c; Vlachos and Delfino 2016; Čerňanský et al. 2017; Sen et al. 2017; Vasileiadou et al. 2017)

# Appendix II.

**Detailed Taxon / Locality data for fossil Aegean reptiles. Material which has been simply mentioned, without any figure, description, or detailed collection number, is omitted. Abbreviations: TL, Type Locality of a valid species.**

1. Kocayarma (= Kocayarmalar), Edirne (TR), late Oligocene (MP 25):
    - Anguidae Anguinae indet. (Čerňanský et al. 2017)
2. Kavakdere, Edirne (TR), late Oligocene (MP 26/27):
    - Anguidae Anguinae indet. (Čerňanský et al. 2017)
3. Ibribey, Tekirdağ (TR), Oligocene:
    - *Pan-Trionychidae* indet. (*Trionix* [sic] sp. of Lebküchner 1974)
4. Kargi 2, Çorum (TR), late Oligocene–early Miocene (MP 30–MN 1):
    - Anguidae *Ophisaurus* sp. (Čerňanský et al. 2017)
    - Anguidae Anguinae indet. (Čerňanský et al. 2017)
5. Küçükdoğanca Köyü (= Küçükdoğanaca Kökü), Edirne (TR), late Oligocene or early Miocene:
    - *Pan-Chelydridae* *Chelydropsis* sp. (Schleich 1994)
    - Geoemydidae *Mauremys rueckerti* (*Palaeochelys rueckerti* of Schleich 1994; including type of *Palaeochelys turcica* Schleich, 1994, and material referred to *Palaeochelys turcica* by Schleich 1994) (TL)
    - ?Emydidae indet. (Schleich 1994)
    - Testudines indet. (Schleich 1994)
    - Crocodylia indet. (?*Diplocynodon* sp. of Schleich 1994)
6. Kargi 3, Çorum (TR), early Miocene (MN 1):
    - Anguidae Anguinae indet. (Čerňanský et al. 2017)
7. Kılçak 3b, Ankara (TR), early Miocene (MN 1):
    - Anguidae Anguinae indet. (Čerňanský et al. 2017)
8. Sabuncubeli, Manisa (TR), early Miocene (MN 3):
    - Anguidae Anguinae indet. (Čerňanský et al. 2017)
9. Keseköy, Ankara (TR), early Miocene (MN 3):
    - Anguidae *Ophisaurus* sp. (Čerňanský et al. 2017)
    - Anguidae Anguinae indet. (Čerňanský et al. 2017)
10. Lapsarna, Lesvos (GR), early Miocene (?MN 3):
    - Crocodylia indet. (Vasileiadou et al. 2017)
    - Lacertidae indet. (Vasileiadou et al. 2017)
    - Squamata indet. (Vasileiadou et al. 2017)
    - ?Natricinae indet. (Vasileiadou et al. 2017)
    - Serpentes indet. (Vasileiadou et al. 2017)
11. Kymi (= Kumi = Koumi), Euboea (= Evia), Central Greece (GR), early Miocene (MN 3/4):
    - Pythonidae *Python euboicus* (Römer 1870) (TL)
12. Aliveri, Euboea (= Evia), Central Greece (GR), early Miocene (MN 4a):
    - Testudines indet. (Georgalis et al. 2018c)
    - Crocodylia indet. (Georgalis et al. 2018c)
    - Chamaeleonidae *Chamaeleo* cf. *andrusovi* (Georgalis et al. 2016b)
    - Chamaeleonidae indet. (Georgalis et al. 2016b)
    - Lacertidae indet. (Georgalis et al. 2018c)
    - Scincomorpha indet. (Georgalis et al. 2018c)
    - Anguidae (non-*Anguis*) Anguinae indet. (Georgalis et al. 2018c)
    - Colubridae indet. (Georgalis et al. 2018c)

Viperidae indet. (Georgalis et al. 2018c)
Serpentes indet. (Georgalis et al. 2018c)
Squamata indet. (Georgalis et al. 2018c)

13. Karydia, Eastern Macedonia and Thrace (GR), early Miocene (MN 4a):
Testudines indet. (Georgalis et al. 2018c)
Lacertidae indet. (Georgalis et al. 2018c)
Scincomorpha indet. (Georgalis et al. 2018c)
Anguidae cf. *Ophisaurus* sp. (Georgalis et al. 2018c)
Anguidae (non-*Anguis*) Anguinae indet. (Georgalis et al. 2018c)
Colubridae indet. (Georgalis et al. 2018c)
Serpentes indet. (Georgalis et al. 2018c)
Squamata indet. (Georgalis et al. 2018c)

14. Nostimo, Western Macedonia (GR), early Miocene (Burdigalian):
Podocnemidoidea *Nostimochelone lampra* (Georgalis et al. 2013) (TL)

15. Bes-Konak (= Beşkonak), Ankara (TR), early Miocene:
*Pan-Chelydridae* *Chelydropsis* sp. (Paicheler et al. 1978)

16. Thymiana, Chios (GR), middle Miocene (MN 5):
Testudinidae *Testudo* sp. (Paraskevaidis 1955; including his sp. I and sp. II)

17. Çandir, Ankara (TR), middle Miocene (MN 6):
Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)
Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
Testudinidae *Titanochelon* sp. (*Cheirogaster* cf. *bolivari* of Staesche et al. 2007)
Anguidae *Ophisaurus* sp. (Čerňanský et al. 2017)
Anguidae Anguinae indet. (Čerňanský et al. 2017)

18. Çandir HW, Ankara (TR), middle Miocene (MN 6):
Anguidae Anguinae indet. (Čerňanský et al. 2017)

19. Paşalar, Bursa (TR), middle Miocene (MN 6):
Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)

20. Uyurca, Ankara (TR), middle Miocene (MN 6):
Ptychogasteridae *Clemmydopsis* sp. (*Clemmydopsis* cf. *turnauensis* of Staesche et al. 2007)

21. Karaçay, Çorum (TR), middle Miocene (Langhian):
Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)

22. Bağiçi (= Zivra), Ankara (TR), middle Miocene (MN 7/8):
Anguidae *Anguis* sp. (Čerňanský et al. 2017)
Anguidae *Ophisaurus* sp. (Čerňanský et al. 2017)
Anguidae Anguinae indet. (Čerňanský et al. 2017)

23. Çatakbağyaka, Muğla (TR), middle Miocene (MN 7/8):
Testudinidae *Titanochelon* sp. (*Cheirogaster* cf. *bolivari* of Staesche et al. 2007)

24. Gebeceler, Afyon (TR), middle Miocene (MN 7/8):
Blanidae *Blanus* cf. *strauchi* (Georgalis et al. 2018a)

25. Sofça, Kütahya (TR), middle Miocene (MN 7/8):
*Pan-Trionychidae* *Pan-Trionychinae* indet. (*Trionyx triunguis* of Staesche et al. 2007)
Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)
Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)

25. Yaylacilar, Afyon (TR), middle Miocene (MN 7/8):

Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)
Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)

26. Yeni Eskihisar, Muğla (TR), middle Miocene (MN 7/8):
    *Pan-Trionychidae* *Pan-Trionychinae* indet. (*Trionyx triunguis* of Staesche et al. 2007)
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
27. Termeyenice, Ankara (TR), middle Miocene (Serravallian):
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
28. İnönü, Ankara (TR), late Miocene (MN 9):
    Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)
29. Plakias, Crete (GR), late Miocene (MN 9):
    *Pan-Trionychidae* *Pan-Trionychinae* indet. (Georgalis et al. 2016c)
    Geoemydidae *Mauremys* sp. (Georgalis et al. 2016c)
    Crocodylia indet. (Georgalis et al. 2016c)
    Amphisbaenia indet. (Georgalis et al. 2016c)
    ?Natricinae indet. (Georgalis et al. 2016c)
30. Bayraktepe, Çanakkale (TR), late Miocene (MN 9/10):
    *Pan-Trionychidae* *Pan-Trionychinae* indet. (*Trionyx* sp. of Tuna 1988)
31. Ravin de la Pluie, Central Macedonia (GR), late Miocene (MN 10):
    Anguidae ?Anguinae indet. (Georgalis et al. 2018b)
    Varanidae *Varanus* sp. (Georgalis et al. 2018b)
    Colubrinae indet. (Georgalis et al. 2018b)
    Elapidae *Naja* cf. *romani* (Georgalis et al. 2018b)
32. Silivri Maden, Istanbul (TR), late Miocene (MN 10:
    *Pan-Trionychidae* *Pan-Trionychinae* indet. (*Trionyx* sp. of Rückert-Ülkümen 1963)
33. Sirti, Çankırı (TR), late Miocene (MN 10):
    Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
34. Garkin, Afyon (TR), late Miocene (MN 11):
    Testudinidae *Titanochelon* sp. (*Cheirogaster* cf. *bolivari* of Staesche et al. 2007)
35. Hatunsaray, Konya (TR), late Miocene (MN 11):
    *Pan-Trionychidae* *Pan-Trionychinae* indet. (*Trionyx triunguis* of Staesche et al. 2007)
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
36. Kayadibi, Konya (TR), late Miocene (MN 11):
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
    Testudinidae *Titanochelon* sp. (*Cheirogaster* cf. *bolivari* of Staesche et al. 2007)
37. Kücükçekmece, Istanbul (TR), late Miocene (MN 11):
    *Pan-Trionychidae* *Pan-Trionychinae* indet. (*Trionyx* sp. of Malik and Nafiz 1933)
    Geoemydidae *Mauremys* sp. (*Emys* sp. of Malik and Nafiz 1933)
    Testudinidae *Testudo* cf. *marmorum* (*Testudo marmoreum* [sic] of Malik and Nafiz 1933)
    Testudinidae ?cf. *Titanochelon* sp. (*Testudo* sp. “Grand” of Malik and Nafiz 1933)
38. Nikiti 2, Central Macedonia (GR), late Miocene (MN 11):

Testudinidae *Testudo* cf. *marmorum* (Garcia et al. 2016)

39. Kınık, Afyon (TR), late Miocene (MN 12):
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
40. Mytilinii, Samos (GR), late Miocene (MN 12):
    Testudinidae *Titanochelon schafferi* (TL) (*Testudo schafferi* of Szalai 1931)
    Varanidae *Varanus amnhophilis* (Conrad et al. 2012) (TL)
41. Pikermi, Attica (GR), late Miocene (MN 12):
    Testudinidae *Testudo marmorum* (Gaudry 1862a, 1862b, 1862–1867; Bachmayer and Symeonidis 1970; Georgalis and Kear 2013) (TL)
    Testudinidae *Titanochelon* cf. *schafferi* (*Testudo* cf. *schafferi* of Bachmayer 1967)
    Varanidae *Varanus marathonensis* (Weithofer 1888) (TL)
    Varanidae *Varanus* sp. ("Reptile du groupe des Varans" of Gaudry 1862a, 1862b, 1862–1867; type of *Varanus atticus* Nopcsa, 1908)
42. Vathylakkos, Central Macedonia (GR), late Miocene (MN 12):
    Testudinidae *Titanochelon* cf. *schafferi* (*Testudo* sp. "forme de grande taille" of Arambourg and Piveteau 1929)
43. Amasya, Aydın (TR), late Miocene (MN 13):
    Geoemydidae *Mauremys* sp. (*Mauremys* cf. *caspica* of Staesche et al. 2007)
44. Ano Metochi 2, Central Macedonia (GR), late Miocene (MN 13):
    Anguidae *Ophisaurus* sp. (Georgalis et al. 2017a)
    Anguidae Anguinae indet. (Georgalis et al. 2017a)
    Cordylidae indet. (Georgalis et al. 2017a)
    Lacertidae indet. (Georgalis et al. 2017a)
    Natricinae *Natrix* sp. (Georgalis et al. 2017a)
    Serpentes indet. (Georgalis et al. 2017a)
45. Ano Metochi 3, Central Macedonia (GR), late Miocene (MN 13):
    Anguidae *Ophisaurus* sp. (Georgalis et al. 2017a)
    Anguidae Anguinae indet. (Georgalis et al. 2017a)
    Cordylidae indet. (Georgalis et al. 2017a)
    Lacertidae indet. (Georgalis et al. 2017a)
    Colubrinae cf. *Dolichophis* sp. (Georgalis et al. 2017a)
    Colubrinae indet. (Georgalis et al. 2017a)
    Natricinae *Natrix* sp. (Georgalis et al. 2017a)
    Scolecophidia indet. (Georgalis et al. 2017a)
    Serpentes indet. (Georgalis et al. 2017a)
46. Kavurca, Çankırı (TR), late Miocene (MN 13):
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
47. Süleymanli, Çankırı (TR), late Miocene (MN 13):
    Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)
    Anguidae *Anguis* sp. (Čerňanský et al. 2017)
    Anguidae *Ophisaurus* sp. (Čerňanský et al. 2017)
    Anguidae Anguinae indet. (Čerňanský et al. 2017)
48. Maramena, Central Macedonia (GR), late Miocene / early Pliocene (MN 13/14):
    Geoemydidae *Mauremys* sp. (*Mauremys caspica* of Gad 1990)
    Agamidae indet. (*Agama* sp. of Richter 1995)
    Anguidae *Ophisaurus* sp. (Richter 1995)
    Lacertidae indet. (*Lacerta* sp. of Richter 1995)
    Cordylidae indet. (Scincoidea indet. of Richter 1995)

*Hierophis* cf. *hungaricus* (Colubrinae indet. of Szyndlar 1995)
Elapidae *Naja* sp. (Szyndlar 1991b, 1995)
Natricinae indet. (Szyndlar 1991b, 1995)
Viperidae “Oriental vipers complex” sp. (Szyndlar 1995)
Serpentes indet. (Szyndlar 1995)

49. Platania, Eastern Macedonia and Thrace (GR), late Miocene:
Testudinidae *Testudo* cf. *graeca* (Vlachos and Tsoukala 2014)

50. Liossati (= Kiourka), Attica (GR), late Miocene or early Pliocene:
Testudinidae *Titanochelon* cf. *schafferi* (*Testudo* spec. ind. [nov. spec.?] of Bachmayer and Symeonidis 1976; *Cheirogaster* cf. *schafferi* of Georgalis and Kear 2013)
Testudinidae *Testudo* sp. (*Testudo* spec. ind. (nov. spec.?) of Bachmayer and Symeonidis 1976)

51. Allatini, Central Macedonia (GR), latest Miocene (or earliest Pliocene):
Geoemydidae *Mauremys* sp. (Vlachos et al. 2015)
Testudinidae *Testudo* cf. *graeca* (*Testudo amiatae* of Bachmayer and Symeonidis 1970)

52. Pylaia (= Pylea = Capudjlar), Central Macedonia (GR), latest Miocene (or earliest Pliocene):
Testudinidae *Testudo* cf. *graeca* (*Testudo amiatae* of Campana 1917)
Testudinidae ?*Titanochelon* sp. (Testudoolithidae; Campana 1917, 1919)

53. Çeştepe, Ankara (TR), early Pliocene (MN 14):
Anguidae Anguinae indet. (Sen et al. 2017)
Lacertidae cf. *Lacerta* sp. (Sen et al. 2017)
Varanidae *Varanus* sp. (Sen et al. 2017)

54. Maritsa, Rhodes (GR), early Pliocene (MN 14):
Erycidae cf. *Eryx* sp. (Szyndlar 1991a)
Scolecophidia indet. (Szyndlar 1991a)

55. Akçaköy, Afyon (TR), early Pliocene (MN 15):
Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)

56. Apollakia, Rhodes (GR), early Pliocene (MN 15):
Testudinidae *Titanochelon* sp. (ootaxon, Testudoolithidae of Mueller-Töwe et al. 2011)
Testudines indet. (Mueller-Töwe et al. 2011)

57. Çalta, Ankara (TR), early Pliocene (MN 15):
Anguidae *Pseudopus* sp. (*Ophisaurus* sp. of Rage and Sen 1976)
Lacertidae indet. (Rage and Sen 1976)
Scincomorpha indet. (Scincidae indet. of Rage and Sen 1976)
Varanidae *Varanus* sp. (*Varanus marathonensis* of Rage and Sen 1976)
Amphisbaenia indet. (Amphisbaenidae indet. of Rage and Sen 1976)
Elapidae *Naja* sp. (*Palaeonaja* sp. of Rage and Sen 1976)
Erycidae *Eryx* sp. (Rage and Sen 1976)
Scolecophidia indet. (Rage and Sen 1976)

58. Ericek, Denizli (TR), early Pliocene (MN 15):
?Natricinae (or Elapidae) indet. (Hoek Ostende et al. 2015)
Serpentes indet. (Hoek Ostende et al. 2015)

59. Megalo Emvolon (= Karabournou), Central Macedonia (GR), early Pliocene (MN 15):
Testudinidae *Testudo* cf. *graeca* (Bachmayer et al. 1980)
Testudinidae *Testudo* sp. (*Testudo* sp. “forme de taille moyene” of Arambourg and Piveteau 1929)

Testudinidae *Titanochelon* sp. ("Riesenschilkröten" of Bachmayer et al. 1980)
Viperidae *Laophis crotaloides* (Owen 1857; Georgalis et al. 2016a) (TL)

60. Epanomi, Central Macedonia (GR), late Pliocene (MN 16):
Testudinidae *Titanochelon bacharidisi* (*Cheirogaster bacharidisi* of Vlachos et al. 2014) (TL)

61. Gefyra, Central Macedonia (GR), late Pliocene (MN 16):
*Pan-Trionychidae* *Pan-Trionychinae* indet. (Vlachos et al. 2015a)

62. Milia, Western Macedonia (GR), late Pliocene (MN 16):
Geoemydidae *Mauremys* sp. (Vlachos and Tsoukala 2016)
Testudinidae *Testudo brevitesta* (Vlachos and Tsoukala 2016) (TL)
Testudinidae *Titanochelon* sp. (Vlachos and Tsoukala 2016)

63. Nea Kallikratia, Central Macedonia (GR), late Pliocene (MN 16):
Testudinidae *Titanochelon bacharidisi* (*Cheirogaster bacharidisi* of Vlachos et al. 2014)

64. Nea Michaniona, Central Macedonia (GR), late Pliocene (MN 16):
Testudinidae *Titanochelon bacharidisi* (*Cheirogaster bacharidisi* of Vlachos et al. 2014)

65. Tourkobounia 1, Attica (GR), late Pliocene (MN 16):
Elapidae *Naja* sp. (Szyndlar and Zerova 1990; Szyndlar 1991b)
Psammophiidae *Malpolon* sp. (Szyndlar 1991a)
Scolecophidia indet. (Szyndlar 1991a)
Viperidae "Oriental vipers complex" sp. (Szyndlar 1991b)

66. Akçayır, Eskişehir (TR), Pliocene:
Testudinidae *Testudo* cf. *graeca* (Staesche et al. 2007)

67. Vatera, Lesvos (GR), early Pleistocene (MN 17):
Testudinidae *Testudo* cf. *graeca ibera* (*Testudo* sp. of De Vos et al. 2002; Lapparent de Broin 2002)
Testudinidae cf. *Titanochelon* aff. *schafferi* (Chelonia indet. of De Vos et al. 2002; cf. *Cheirogaster* aff. *schafferi* of Lapparent de Broin 2002)

68. Makriyialos, Peloponnese (GR), early Pleistocene:
Testudinidae *Testudo marginata* (Schleich 1982)

69. Psychiko, Attica (GR), early Pleistocene:
Testudinidae *Testudo* sp. (Bachmayer and Symeonidis 1970)

70. Emirkaya-2, Konya (TR), Middle Pleistocene:
Anguidae *Pseudopus* cf. *apodus* (Venczel and Sen 1994)
Lacertidae *Lacerta* sp. (Venczel and Sen 1994)
Colubrinae *Dolichophis caspius* (*Coluber caspius* of Venczel and Sen 1994)
Colubrinae *Elaphe* cf. *quatuorlineata* (Venczel and Sen 1994)
Colubrinae indet. (including *Coluber* sp. of Venczel and Sen 1994)
Colubrinae cf. *Telescopus* sp. (Venczel and Sen 1994)
Natricinae *Natrix* cf. *natrix* (Venczel and Sen 1994)
Scolecophidia indet. (Venczel and Sen 1994)
Viperidae "Oriental vipers complex" sp. (Venczel and Sen 1994)

71. Latomi, Chios (GR), Middle Pleistocene:
Lacertidae indet. (Schneider 1975)
Colubrinae indet. (Schneider 1975)
Erycidae *Eryx jaculus* (*Eryx turcicus* of Schneider 1975)

Natricinae indet. (Schneider 1975; including ?*Naja* sp. of Schneider 1975)
Viperidae "Oriental vipers complex" sp. (Schneider 1975)

72. Tourkobounia 2, Attica (GR), Middle Pleistocene:
    Colubrinae *Elaphe quatuorlineata* (Szyndlar 1991a)
    Colubrinae *Zamenis situla* (Szyndlar 1991a)
    Scolecophidia indet. (Szyndlar 1991a)
73. Tourkobounia 5, Attica (GR), Middle Pleistocene:
    Varanidae *Varanus* sp. (Georgalis et al. 2017b)
    Scolecophidia indet. (Szyndlar 1991a)
74. Bate Cave, Crete (GR), Late Pleistocene:
    Testudinidae *Testudo marginata cretensis* (Kotsakis 1977)
    Lacertidae *Podarcis* cf. *erhardii* (*Lacerta* cf. *erhardi* [sic] of Kotsakis 1977)
    Colubrinae *Hierophis* cf. *gemonensis* (*Coluber* cf. *gemonensis* of Kotsakis 1977)
75. Charkadio Cave, Tilos (GR), Late Pleistocene:
    Testudinidae *Testudo marginata* (Bachmayer and Symenonidis 1975)
76. Gerani Cave, Crete (GR), Late Pleistocene:
    Testudinidae *Testudo marginata cretensis* (Bachmayer et al. 1975) (TL)
    Natricinae *Natrix* cf. *tessellata* (Szyndlar 1991b)
77. Megalopolis, Peloponnese (GR), Late Pleistocene:
    Emydidae *Emys orbicularis* (Vlachos and Delfino 2016)
    Geoemydidae *Mauremys rivulata* (*Clemmys caspica* of Melentis 1966; Vlachos and Delfino 2016)
78. Simonelli Cave, Crete (GR), Late Pleistocene:
    Testudinidae *Testudo marginata cretensis* (Kotsakis 1977)
    ?Lacertidae indet. (*Uromastix spinipes* [sic] of Mangili 1980)
79. Xerias, Eastern Macedonia and Thrace (GR), Late Pleistocene:
    Testudinidae *Testudo marginata* (*Testudo* sp. of Tsoukala et al. 2011)
80. Zourida Cave, Crete (GR), Late Pleistocene:
    Testudinidae *Testudo marginata cretensis* (Bachmayer et al. 1975)
81. Franchthi Cave, Peloponnese (GR), Late Pleistocene–Holocene:
    Emydidae *Emys orbicularis* (Vlachos and Delfino 2016)
    Testudinidae *Testudo hermanni* (Vlachos and Delfino 2016)
82. Karain Cave, Antalya (TR), Late Pleistocene–Holocene:
    Geoemydidae *Mauremys rivulata* (*Mauremys caspica* of Zwick and Schleich 1994)
    Testudinidae *Testudo graeca* (Zwick and Schleich 1994)
    Agamidae indet. (*Agama* sp. of Zwick and Schleich 1994)
    Anguidae *Pseudopus* sp. (*Ophisaurus* sp. of Zwick and Schleich 1994)
    Lacertidae indet. (*Lacerta* s.l. sp. of Zwick and Schleich 1994)
    ?Colubridae indet. (Zwick and Schleich 1994)
83. Pili B, Kos (GR), late Quaternary (probably Late Pleistocene):
    Erycidae *Eryx jaculus* (Szyndlar 1991a)
84. Korydallos, Attica (GR), "Tertiary" (unknown exact age):
    Testudinidae indet. (Paraskevaidis 1961)
85. No locality specified (TR), "Tertiary" (unknown exact age):
    Testudinidae *Testudo* sp. (type of *Testudo sloanei* Lydekker, 1889)

## Appendix III.

**List of extant reptile species from the Aegean region. Only species currently considered valid are mentioned. Numbers in brackets indicate number of species of Aegean reptiles for each clade. Taxa distributed in eastern Anatolia are omitted. Note that for convenience purposes, I am following the palaeontological perspective and include the psammophiid *Malpolon* into "Colubrinae". Data compiled from Arnold et al. (2007), Baig et al. (2012), Bellati et al. (2014), Böhme and Joger (1984), Eiselt and Baran (1970), Gvoždík et al. (2010), Karin et al. (2016), Kornilios et al. (2018), Lymberakis et al. (2008), Mallow et al. (2003), Nilson and Andrén (1985, 1986, 1988), Sindaco and Jeremčenko (2008), Sindaco et al. (2000), Lymberakis et al. (2008), Mizsei et al. (2017), Psonis et al. (2017), Sindaco et al. (2014), Stümpel et al. (2016), Valakos et al. (2008), and Wallach et al. (2014).**

***Testudines [11]***
**Cheloniidae [3]**: *Caretta caretta* (Linnaeus, 1758); *Chelonia mydas* (Linnaeus, 1758); *Eretmochelys imbricata* (Linnaeus, 1766).
**Dermochelyidae [1]**: *Dermochelys coriacea* (Vandelli, 1761).
**Trionychidae [1]**: *Trionyx triunguis* (Forskål, 1775).
**Emydidae [1]**: *Emys orbicularis* (Linnaeus, 1758).
**Geoemydidae [2]**: *Mauremys caspica* (Gmelin, 1774); *Mauremys rivulata* (Valenciennes, in Bibron and Bory de Saint-Vincent, 1833).
**Testudinidae [3]**: *Testudo graeca* Linnaeus, 1758; *Testudo hermanni* Gmelin, 1789; *Testudo marginata* Schoepff, 1792.

***Squamata [75]***
**Chamaeleonidae [2]**: *Chamaeleo chamaeleon* (Linnaeus, 1758); *Chamaeleo africanus* Laurenti, 1768.
**Agamidae [2]**: *Stellagama stellio* (Linnaeus, 1758); *Trapelus lessonae* (Filippi, 1865).
**Gekkota [3]**: *Hemidactylus turcicus* (Linnaeus, 1758); *Mediodactylus kotschyi* (Steindachner, 1870); *Tarentola mauritanica* (Linnaeus, 1758).
**Lacertidae [27]**: *Algyroides moreoticus* (Bibron and Bory de Saint-Vincent, 1833); *Algyroides nigropunctatus* (Duméril and Bibron, 1839); *Anatololacerta anatolica* (Werner, 1900); *Anatololacerta budaki* (Eiselt and Schmidtler, 1986); *Anatololacerta danfordi* (Günther, 1876); *Anatololacerta pelasgiana* (Mertens, 1959); *Apathya cappadocica* (Werner, 1902); *Darevskia praticola* (Eversmann, 1834); *Darevskia rudis* (Bedriaga, 1886); *Darevskia valentini* (Boettger, 1892); *Hellenolacerta graeca* (Bedriaga, 1886); *Lacerta agilis* Linnaus, 1758; *Lacerta media* Lantz and Cyrén, 1920; *Lacerta pamphylica* Schmidtler, 1975; *Lacerta trilineata* Bedriaga, 1886; *Lacerta viridis* Laurenti, 1768; *Ophisops elegans* Ménétries, 1832; *Parvilacerta parva* (Boulenger, 1887); *Podarcis cretensis* (Wettstein, 1952); *Podarcis erhardii* (Bedriaga, 1882); *Podarcis gaigeae* (Werner, 1930); *Podarcis ionicus* (Lehrs, 1902); *Podarcis levendis* Lymberakis, Poulakakis, Kaliontzopoulou, Valakos and Mylonas, 2008; *Podarcis milensis* (Bedriaga, 1882); *Podarcis muralis* (Laurenti, 1768); *Podarcis peloponessiacus* (Bibron and Bory de Saint-Vincent, 1833); *Podarcis tauricus* (Pallas, 1814).
**Scincidae [7]**: *Ablepharus budaki* Göcmen, Kumlutaş and Tosunoglu, 1996; *Ablepharus kitaibelii* (Bibron and Bory de Saint-Vincent, 1833); *Chalcides ocellatus* (Forskål, 1775); *Eumeces schneideri* (Daudin, 1802); *Heremites auratus* (Linnaeus, 1758); *Heremites vittatus* (Olivier, 1804); *Ophiomorus kardesi* Kornilios, Kumlutaş, Lymberakis and Ilgaz, 2018; *Ophiomorus punctatissimus* (Bibron and Bory de Saint-Vincent, 1833).
**Anguidae [4]**: *Anguis cephallonica* Werner, 1894; *Anguis fragilis* Linnaeus, 1758; *Anguis graeca* Bedriaga, 1881; *Pseudopus apodus* (Pallas, 1775).

**Blanidae [1]**: *Blanus strauchi* (Bedriaga, 1884).
**Scolecophidia [1]**: *Xerotyphlops vermicularis* (Merrem, 1820).
**Erycidae [1]**: *Eryx jaculus* (Linnaeus, 1758).
**"Colubrinae" [15]**: *Coronella austriaca* Laurenti, 1768; *Dolichophis caspius* (Gmelin, 1789); *Dolichophis jugularis* (Linnaeus, 1758); *Dolichophis schmidti* (Nikolsky, 1909); *Eirenis modestus* Martin, 1838; *Elaphe quatuorlineata* (Lacépède, 1789); *Elaphe sauromates* (Pallas, 1814); *Hemorrhois nummifer* (Reuss, 1834); *Hierophis gemonensis* (Laurenti, 1768); *Malpolon insignitus* Geoffroy Saint-Hilaire, 1827; *Platyceps najadum* (Eichwald, 1831); *Telescopus fallax* (Fleischmann, 1831); *Zamenis hohenackeri* (Strauch, 1873); *Zamenis longissimus* (Laurenti, 1768); *Zamenis situla* (Linnaeus, 1758).
**"Natricinae" [2]**: *Natrix natrix* (Linnaeus, 1758); *Natrix tessellata* (Laurenti, 1768).
**Viperidae [10]**: *Macrovipera lebetina* (Linnaeus, 1758); *Macrovipera schweizeri* (Werner, 1935); *Montivipera bulgardaghica* (Nilson and Andrén, 1985); *Montivipera xanthina* (Gray, 1849); *Vipera ammodytes* (Linnaeus, 1758); *Vipera anatolica* Eiselt and Baran, 1970; *Vipera barani* Böhme and Joger, 1984; *Vipera berus* (Linnaeus, 1758); *Vipera graeca* (Nilson and Andrén, 1988); *Vipera transcaucasiana* Boulenger, 1913.

**APPENDIX 1.** Georgalis, G.L. and W.G. Joyce. 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58:115–208.

**APPENDIX 2.** Georgalis, G.L., Zoboli, D., Pillola, G.L. and Delfino, M. 2017. A revision of the trionychid turtle *Procyclanorbis sardus* Portis, 1901 from the late Miocene of Sardinia (Italy). Annales de Paléontologie 103:127–134.

**APPENDIX 3.** Georgalis, G.L. 2017. *Necrosaurus* or *Palaeovaranus*? Appropriate nomenclature and taxonomic content of an enigmatic fossil lizard clade (Squamata). Annales de Paléontologie 103:59–69.

**APPENDIX 4.** Georgalis, G.L., Szyndlar, Z., Kear, B.P. and Delfino, M. 2016. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109:103–116.

**APPENDIX 5.** Georgalis, G.L., Villa, A. and Delfino, M. 2016. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature 103:12.

**APPENDIX 6.** Georgalis, G.L., Villa, A., Vlachos, E. and Delfino, M. 2016. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49:433–444.

**APPENDIX 7.** Georgalis, G.L., Villa, A., and Delfino, M., 2017. Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. Historical Biology 29:730–742.

**APPENDIX 8.** Georgalis, G.L., Villa, A., and Delfino, M. 2017. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. Journal of Vertebrate Paleontology 37:e1301946.

**APPENDIX 9.** Georgalis, G.L., K. Halaçlar, S. Mayda, T. Kaya, and D. Ayaz 2018. First fossil find of the *Blanus strauchi* complex (Amphisbaenia, Blanidae) from the Miocene of Anatolia. Journal of Vertebrate Paleontology

**APPENDIX 10.** Georgalis, G.L., Rage, J.-C., Bonis, L. de, and Koufos, G.D. 2018. Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). Swiss Journal of Geosciences

**APPENDIX 11.** Georgalis, G.L., A. Villa, M. Ivanov, S. Roussiakis, P. Skandalos, and M. Delfino 2018. Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia – bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe. Historical Biology

# A Review of the Fossil Record of Old World Turtles of the Clade *Pan-Trionychidae*

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## ABSTRACT

Turtles of the clade *Pan-Trionychidae* have a rich fossil record in the Old World, ranging from the Early Cretaceous (Hauterivian) to the Holocene. The clade most probably originated in Asia during the Early Cretaceous but spread from there to the Americas and Europe by the Late Cretaceous, to India and Australia by the Eocene, and to Afro-Arabia by the Neogene. The presence of a single pan-cyclanorbine in the Late Cretaceous (Maastrichtian) of Asia provides a minimum estimate for the age of the trionychid crown. As preserved, diversity was relatively high in Asia during the Late Cretaceous, but the subsequent, strong decline is likely a preservational bias, as extant faunas are relatively rich, especially throughout Asia. The range of trionychids contracted southward in Europe over the course of the Neogene, and the group is now locally extirpated. The group is now similarly absent from Arabia and Australia. A taxonomic review of the 180 named Old World taxa finds 42 nomina valida, 38 nomina invalida, 88 nomina dubia, 11 nomina nuda, and 1 nomen suppressum.

## KEYWORDS

Phylogeny, biogeography, *Pan-Trionychidae*, *Pan-Cyclanorbinae*, *Trionyx*

## Introduction

*Pan-Trionychidae* (see Vitek and Joyce [2015] for definition) is a highly distinctive clade of turtles characterized by a reduced shell that lacks peripherals, pygals, an ossified bridge, and scutes (Meylan 1987; Vitek and Joyce 2015). Extant trionychids have a relatively broad distribution across all tropical to warm temperate portions of Africa, Asia, New Guinea, and North America (Ernst and Barbour 1989). Although the group does not permanently inhabit any part of Europe, stray individuals of *Trionyx triunguis* are occasionally found in Greece, which wash in from the adjacent coasts of Asia Minor (Taskavak et al. 1999; Corsini-Foka and Masseti 2008). Because of the distinct sculpturing on the external surface of their shells, pan-trionychids are readily recognized in the fossil record. The primary goal of this contribution is to document the rich fossil record of the group in the Old World from the Early Cretaceous to the Holocene. The fossil record of the group from the New World was recently documented elsewhere (Vitek and Joyce 2015).

The first description of fossil pan-trionychids from the Old World was made by Cuvier (1812, 1821–1824, 1835–1836) on the basis of fragmentary remains found throughout France. Soon after, fossil pan-trionychids were also reported from Germany (Meyer 1832; Kaupp 1834; Fitzinger 1836) and Italy (Sismonda 1836, 1839) and later from Austria (Hörnes 1848; Peters 1855), England (Owen in Owen and Bell 1849), Spain (Ezquerra del Bayo 1850), Switzerland (Pictet and Humbert 1856), Croatia (Peters 1859), and Hungary (Peters 1859). Over the course of the second half of the 19th century and the beginning of the 20th century, almost every new find from Europe was treated as a new taxon (e.g., Laube 1900; Reinach 1900; Lörenthey 1903; Heritsch 1909; Teppner 1913, 1914c). This proliferation of names is well exemplified by the Italian record. The fossil localities

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of Monte Bolca and Monteviale in this country yielded a series of pan-trionychid specimens that were unusual for the time by being well preserved and often complete (including skulls, shells, and limb elements). However, strict application of typological species concepts prompted early workers to name a plethora of taxa, most of which occurred sympatrically in these two localities (Schauroth 1865; Negri 1892, 1893; Sacco 1894, 1895). We show here, however, that lineage-based species concepts coupled with a better understanding of intraspecific variation (Meylan 1987; Gardner and Russell 1994; Vitek and Joyce 2015) reveal that these localities only document the presence of a single lineage. Hummel (1929, 1932) provided the first complete lists of all fossil pan-trionychids named to date and a first indication that many species, especially those based on fragments, should be considered dubious, but that did not stop Bergounioux (1933, 1934b, 1935, 1936, 1938, 1953, 1954) from naming many more fossil taxa based on fragmentary remains from localities across France, Italy, and Spain. Of the taxa established by the latter author, we here recognize all as nomina dubia or junior synonyms of others.

Over the course of the second half of the 20th century, only few additional taxa were named from Europe (e.g., Hernández Sampelayo and Bataller 1944; Gramann 1956; Moody and Walker 1970; Walker and Moody 1974; Broin 1977; Rieppel 1979; Gemel 2002). Instead, most new finds were referred to already known species or recognized as not being diagnostic at the species level (Kuss 1958; Mottl 1967; Kotsakis 1977; Barbera and Leuci 1980; Böhme 1995). The fossil record of European pan-trionychids was partially or fully summarized by Kuhn (1964), Młynarski (1976), Broin (1977), Lapparent de Broin (2001), and Danilov (2005), but these workers did not try to elucidate the interrelationships or the validity of all named taxa, perhaps because of the daunting nature of this task. This contrasts with a series of papers provided by Karl (1993, 1998, 1999b), who strongly simplified the taxonomy of European pan-trionychids through explicit synonymies, often with extant taxa.

The first fossil pan-trionychids from Asia were reported by Clift (1828), followed by Falconer (1831, 1859), Cautley (1836), Falconer and Cautley (1837), Meyer (1865), Lydekker (1885, 1889b), and Pilgrim (1912), all based on abundant material from British India, now India and Pakistan. This region has since yielded additional pan-trionychid remains (Prasad 1974; West et al. 1978, 1991; Sahni et al. 1981, 1984; Corvinus and Schleich 1994; Head et al. 1999; Srivastava and Patnaik 2002), but most are fragmentary. Jaekel (1911) reported new material from Indonesia and erected new Quaternary taxa from Java. Matsumoto (1918) described the first fossil pan-trionychids from Japan, and additional finds have since been reported from this country on a regular basis (Chitani 1925; Otsuka 1969, 1970; Okazaki and Yoshida 1977; Miura and Uyama 1987; Hasegawa et al. 2007), including what may be the remains of the most basal known pan-trionychids (Hirayama et al. 2013). Gilmore (1931, 1934) reported the first fossil pan-trionychids from deposits near the Chinese-Mongolian border, and a wealth of new material has been unearthed and described ever since from these two countries (Chow and Yeh 1957, 1958; Yeh 1962, 1963, 1965, 1974; Khosatzky 1976; Shuvalov and Chkhikvadze 1979; Lei and Ye 1985; Chkhikvadze and Shuvalov 1988; Li, Joyce, and Liu 2015; Li, Tong et al. 2015). In parallel, fossiliferous localities in Kazakhstan, Kyrgyzstan, and Uzbekistan have yielded abundant pan-trionychid material that resulted also in an array of new taxa (e.g., Prinada 1927; Riabinin 1938; Khosatzky 1957; Chkhikvadze 1971, 1973, 2008a; Kuznetsov 1978; Nessov 1986, 1995b; Kuznetsov and Chkhikvadze 1987). Most named taxa from the Asian mainland lack adequate figuring and rigorous description and the systematics of these fossils therefore remains poorly understood. The situation has improved dramatically over the course of the last few years through a series of papers (Vitek and Danilov 2010, 2012, 2013, 2014, 2015; Danilov and Vitek 2012, 2013; Danilov et al. 2014; Danilov, Sukhanov et al. 2015; Danilov, Vitek et al. 2015) that revised many pan-trionychid faunas from this region and established several new taxa that are based on more complete material.

The fossil record of Afro-Arabian pan-trionychids remains obscured to date as most of the finds are only poorly documented. The stage was already set by Lydekker (1889a) who reported a large pan-trionychid specimen from the Eastern Arabian Desert but did not figure the remains. Additional finds have since been reported from Arabia and the Middle East by Bate (1934), Thomas et al. (1980), Roger et al. (1994), Lapparent de Broin and van Dijk (1999), and Beech and Hellyer (2005), but fossils remain both scarce and poorly documented. The first pan-trionychid remains from Africa per se were reported by Andrews (1902, 1906), Reinach (1903), and Dacqué (1912). Whereas relatively rich material has since been documented from Kenya that serves as the basis several pan-cyclanorbine taxa (e.g., Andrews 1914; Broin 1979; Pickford 1986; Meylan et al. 1990), most new pan-trionychid material from the remainder of that continent is relatively fragmentary (Broin 1979; Wood 1987, 2013; Hirayama 1992) or just listed as a side note (Arambourg 1947; Bishop and Pickford 1975; Pickford 1975, 1986, 2008; Vignaud et al. 2002).

Australia has a scarce pan-trionychid fossil record. As early as 1869, Clarke already reported fossil pan-trionychids from that continent, but these cannot be reevaluated, as they were not described, figured, or deposited in a collection. Verifiable pan-trionychids were otherwise reported by De Vis (1894) and more recently by Gaffney and Bartholomai (1979), White (2001), and Louys and Price (2015). It is characteristic of the scarcity of remains that only two taxa have been named from Australia (De Vis 1894; White 2001), of which we here consider only one to be valid.

Some groups of fossil vertebrates have trionychid-like sculpturing and it is therefore not surprising that several fossils were historically attributed to this group in error. Among fossil turtles, these include *Aspideretes planicostatus* Riabinin, 1930, which has since been reassigned to lindholmemydids (recombined as *Lindholmemys planicostata*; Danilov et al. 2002); *Trionyx bakewelli* Mantell, 1833, a helochelydrid (now recombined as "*Helochelydra*" *bakewelli*; Joyce 2017); *Trionyx mantelli* Gray 1831, a nomen nudum that is likely "senior synonym" of the previously listed species; *Trionyx bellunensis* Misuri, 1911, a cheloniid (junior synonym of *Trachyaspis lardyi*; Chesi et al. 2007); *Castresia munieri* De Stefano, 1902 and *T. granosa* Pomel 1847, now known to be pan-carettochelyids (the former a junior synonym of *Allaeochelys parayrei*; Joyce 2014; the other a nomen nudum); *Trionyx sansaniensis* Bergounioux, 1935, a chelydrid (junior synonym of *Chelydropsis murchisoni*; Joyce 2016); *Trionyx schlotheimii* Fitzinger, 1836, most probably an emydid (junior synonym of *Emys orbicularis*; Geinitz 1877); and *Kappachelys okurai* Hirayama et al., 2013, which was recently shown to be an indeterminate pan-trionychian that lacks unambiguous pan-trionychid characteristics (Nakajima et al. in press). We here add *Trionyx melitensis* Lydekker, 1891, to this list. This middle Miocene turtle was initially described as the best documented pan-trionychid remain from Malta and was even reassigned to the cyclanorbine lineage (Lapparent de Broin and Van Dijk 1999), but the unique sculpturing of the holotype combined with the presence of scute sulci clearly reveal that this is a marine turtle reminiscent of *Trachyaspis* spp. Of special mention here are furthermore *Trionyx impressus*, *Trionyx miliaris*, *Trionyx spinosus*, and *Trionyx sulcatus*, which were named by Kutorga (1835, 1837) based on fragmentary material from the Devonian of Estonia but have since been shown to be dermocranial fragments of psammosteid heterostracans and placoderms (Halstead Tarlo 1965; Denison 1978).

We here provide the first global overview of the taxonomy and fossil record of pan-trionychids from the Old World, which is complementary to the review of Vitek and Joyce (2015) regarding the taxonomy and fossil record of the group from the New World. The enormity of the task prompts us to be as succinct as possible. To accomplish this, we firstly keep our taxonomic justifications to a minimum, especially for the long list of taxa we conclude to be nomina nuda and nomina dubia, as lengthily discussions would be endlessly repetitive, given that we decline the validity of most taxa for the same reasons. We here openly acknowledge that many of the fossil taxa we here deem to be valid do not display unique apomorphic features and therefore cannot be justified globally, but rather only within a particular temporal and regional context. We therefore keep our diagnoses to a bare minimum by only highlighting characters that are relevant within a certain context (i.e., Paleogene pan-trionychids from Europe), instead of providing long lists of unique character combinations that overlap greatly with those of other taxa. We finally do not discuss two names that have been noted in the literature briefly, but that only exist on museum labels, in particular *Trionyx gaudini*, a name mentioned by Lawley (1876) for material housed in Siena, Italy, and *T. miocenicus*, a name mentioned by Broin (1977) for specimens housed at MHNT (see Appendix 1 for institutional abbreviations).

It is not unusual among fossil turtles that phylogenetic relationships remain poorly resolved, but pan-trionychids are notable in that it is difficult to group fossil species into genera. Therefore, according to Vitek and Joyce (2015), we place most of the valid taxa we recognize in the wastebasket genus "*Trionyx*," instead of maintaining a plethora of monotypic genera. We here only make exception for (1) fossil taxa that can be grouped into genera (e.g., *Khunnuchelys* spp.), (2) fossil taxa from the Mesozoic that most certainly will never be assigned to any extant genus, (3) a selected number of Cenozoic taxa with particularly unique morphologies (e.g., *Murgonemys braithwaitei*), and (4) fossil taxa that can be assigned clearly to extant genera (e.g., *Pelodiscus gracilia*). Although the usage of a wastebasket taxon is suboptimal, we find this approach preferable to the extensive use of monotypic genera, as these do not encode additional information.

For institutional abbreviations, see Appendix 1. Named Old World pan-trionychid genera are listed in Appendix 2.

## Skeletal Morphology of Pan-Trionychids

The bizarre nature of the shell of pan-trionychids makes them readily distinguishable from other turtles, a condition that has also rendered their monophyly as "de facto." Moreover, the highly distinctive shell sculpturing preserved in almost all fossil specimens of the group renders them easily identifiable among fossil remains even as fragments. The large amount of variation that is apparent in this sculpturing unfortunately prompted many early chelonian workers to diagnose many species on the basis of shell sculpturing pattern only, but this character has since been shown to be highly variable, although some species can be recognized regionally using their sculpturing (Vitek and Joyce 2015). For the skeletal morphology of *Pan-Trionychidae*, including descriptions of the cranium, carapace, plastron, and the postcranium, we here refer the reader to the recent summary of Vitek and Joyce (2015).

Among fossil taxa from the Old World, meaningful cranial descriptions are available for *Axestemys vittata* (Walker and Moody 1985), *Kuhnemys orlovi* (Danilov et al. 2014), *Khunnuchelys erinhotensis* (Brinkman et al. 1993), *Khunnuchelys kizylkumensis* (Brinkman et al. 1993), *Khunnuchelys lophorhothon* (Danilov, Vitek et al. 2015), *Perochelys lamadongensis* (Li, Joyce, and Liu 2015), "*Trionyx*" *gregarius* (Gilmore 1934), "*T.*" *ikoviensis* (Danilov et al. 2011), "*T.*" *messelianus* (Cadena 2016), "*T.*" *silvestris* (Walker and Moody 1974; Broin 1977), and *T. vindobonensis* (Broin 1977).

Important descriptions of the shells of fossil Old World taxa are available for *Kuhnemys breviplastra* (Danilov et al. 2014), *Kuhnemys orlovi* (Danilov et al. 2014), *Kuhnemys palaeocenica* (Danilov, Sukhanov et al. 2015), *Perochelys lamadongensis* (Li, Joyce, and Liu 2015), *Rafetus bohemicus* (Liebus 1930), "*Trionyx*" *capellinii* (Kotsakis 1977), "*T.*" *gregarius* (Gilmore 1934), "*T.*" *kansaiensis* (Vitek and Danilov 2010), "*T.*" *messelianus* (Hummel 1927; Cadena 2016), "*T.*" *ninae* (Vitek and Danilov 2015), "*T.*" *riabinini* (Vitek and Danilov 2010), and "*T.*" *shiluutulensis* (Danilov et al. 2014).

Useful descriptions pertaining to ontogenetic variation have finally been provided for *Kuhnemys* spp. (Danilov et al. 2014), "*Trionyx*" *gregarius* (Gilmore 1934), and "*T.*" *riabinini* (Vitek and Danilov 2010).

## Phylogenetic Relationships

The phylogenetic relationships of pan-trionychids were recently discussed in detail by Vitek and Joyce (2015). Under the absence of a phylogenetic analysis that includes most of the taxa listed as valid herein, we only presume that valid genera are monophyletic and that fossil taxa related with extant trionychids concur with topologies retrieved from phylogenetic analyses based on molecular data (Engstrom et al. 2002; Le et al. 2014; Figure 1).

## Paleoecology

Extant pan-trionychids occur globally today in all suitable tropical to temperate regions. Although we are unaware of studies explicitly exploring this issue, it seems that the northern distribution of the group is not necessarily limited by winter temperatures, but rather by the availability of suitable non-frozen habitat for hibernating in combination with summers of sufficient length to allow the hatchlings to emerge prior to the winter, as exemplified by pan-trionychids naturally occurring in cold continental regions of North American and Asia today (Ernst and Barbour 1989). The presence of pan-trionychids in the fossil record therefore does not reveal much about the paleoenvironment in which they occur beyond the presence of permanent bodies of water. Some Old World fossil

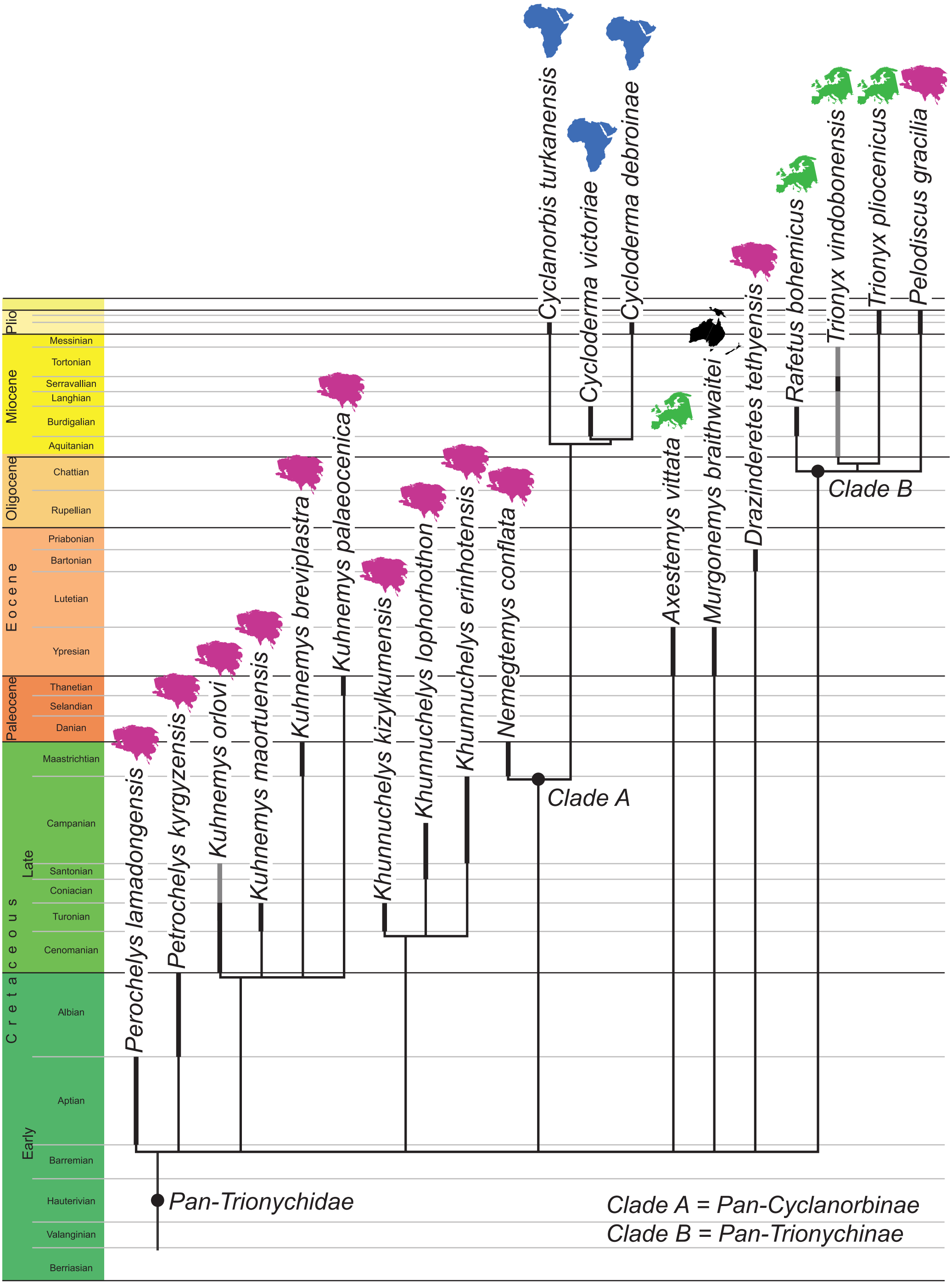

Figure 1. The phylogenetic relationships and stratigraphic and biogeographic distribution of valid pan-trionychid taxa. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material. The topology presumes that genera are monophyletic and that fossil taxa referable to extant genera follow the molecular topology of Engstrom et al. (2002) and Le et al. (2014).

trionychids have been inferred to have been marine tolerant or marine adapted, such as the Eocene *Drazinderetes tethyensis* (Head et al. 1999), but mostly because they were found in estuarine to marine sediments. Although this is a reasonable speculation given that some extant trionychids are known to venture into the marine realm, in particular *Trionyx triunguis* (Taskavak et al. 1999; Corsini-Foka and Masseti 2008) and *Pelochelys cantorii* (Fritz et al. 2014), only geochemical evidence should be able to distinguish rigorously if any fossil taxon genuinely lived in marine habitat, instead of being occasionally washed into the sea pre- or postmortem.

Gilmore (1934) suggested that the Eocene "*Trionyx*" *gregarius* was gregarious, as more than a dozens individuals were found in a single block of matrix, but it seems more likely to us that these individuals were brought together by a drought (Wings et al. 2012), as no extant turtle displays herding behavior. Taking into account their cranial anatomy, Brinkman et al. (1993) assumed that the large *Khunnuchelys* spp. from the Cretaceous of Asia may have preyed on mollusks or even dinosaur eggs. Sacco (1895) and Kotsakis (1977) speculated that the Eocene "*T.*" *capellinii* may have preyed on juvenile crocodilians and been preyed on by the adults, but under the absence of positive evidence that would support either hypothesis, such as the bite marks reported by Wood (1987) for trionychid material from the Miocene of Africa, such ideas are purely speculative.

The eggs of pan-trionychids are rigid shelled (Lawver and Jackson 2014), and fossil eggs tentatively attributed to this clade have been recovered from the Miocene of Germany (Meyer 1860, 1867) and questionably from the Cretaceous of Japan (Obata et al. 1972).

## Paleobiogeography

The oldest unequivocal pan-trionychid fossils are known from the Early Cretaceous of Asia (Nessov 1995b; Hirayama et al. 2013; Li, Joyce, and Liu 2015; Li, Tong et al. 2015), and an Asiatic origin for the group seems to be all but certain (Joyce et al. 2013). Even older pan-trionychid remains had previously been reported in the form of *Trionyx primoevus* Bergounioux, 1937 from the Late Jurassic of France and *Sinaspideretes wimani* Young and Chow, 1953 from the Late Jurassic or Early Cretaceous of China, but these have since been shown to lack trionychid characteristics (Meylan and Gaffney 1992; Tong et al. 2014). At present, the Early Cretaceous record consists of *Perochelys lamadongensis* from the Aptian of Liaoning, China, (Li, Joyce, and Liu 2015); "*T.*" *jixiensis* from the Aptian/Albian (slashes used herein connote "or") of Heilongjiang, China (Li, Tong et al. 2015); and *Petrochelys kyrgyzensis* from the Albian of Kyrgyzstan (Nessov 1995b; Danilov and Vitek 2013). Additional, indeterminate material has furthermore been reported from the Early Cretaceous of Inner Mongolia, China (Gilmore 1931), Japan (Hirayama et al. 2013; Nakajima et al. in press), Mongolia (Shuvalov and Chkhikvadze 1979; Khosatzky 1999; Suzuki and Narmandakh 2004; Scheyer et al. 2017), and Uzbekistan (Nessov 1977, 1984), revealing that the group was widely distributed across the continent early in its history, though notably absent from its southern rim. We recognize in the Late Cretaceous 15 distinct species across central Asia, in particular Kazakhstan, Mongolia, Uzbekistan, and Inner Mongolia, China, (Figures 1 and 2), with additional, fragmentary material being reported from Japan, Kazakhstan, Mongolia, Uzbekistan, and Inner Mongolia, Fujian Province, and Jilin Province, China (Figure 3; see Appendix 3 for complete summary of localities and references). Notably high levels of diversity are apparent by the end of the Late Cretaceous, as is documented by the presence of at least five distinct forms in the Maastrichtian of Mongolia (Danilov et al. 2014), a phenomenon reminiscent of the high diversity observed in the late Late Cretaceous of North America (Vitek and Joyce 2015). The phylogenetic position of many fossil pan-trionychids remains unresolved, and it is therefore unclear if most of the Cretaceous forms represent the trionychid stem or crown (Li, Joyce, and Liu 2015; Vitek and Joyce 2015), although a potential assignment to the crown is consistent with molecular dating analyses (Joyce et al. 2013).

It is unclear how well pan-trionychids survived the Cretaceous-Tertiary (K/T) extinction event in Asia, as only a single reliable fossil, the type of *Kuhnemys palaeocenica*, has been described from the Paleocene of this continent (Danilov, Sukhanov et al. 2015). Significantly richer material has been reported from the Eocene and Oligocene of the Asian main continent, but we are here only

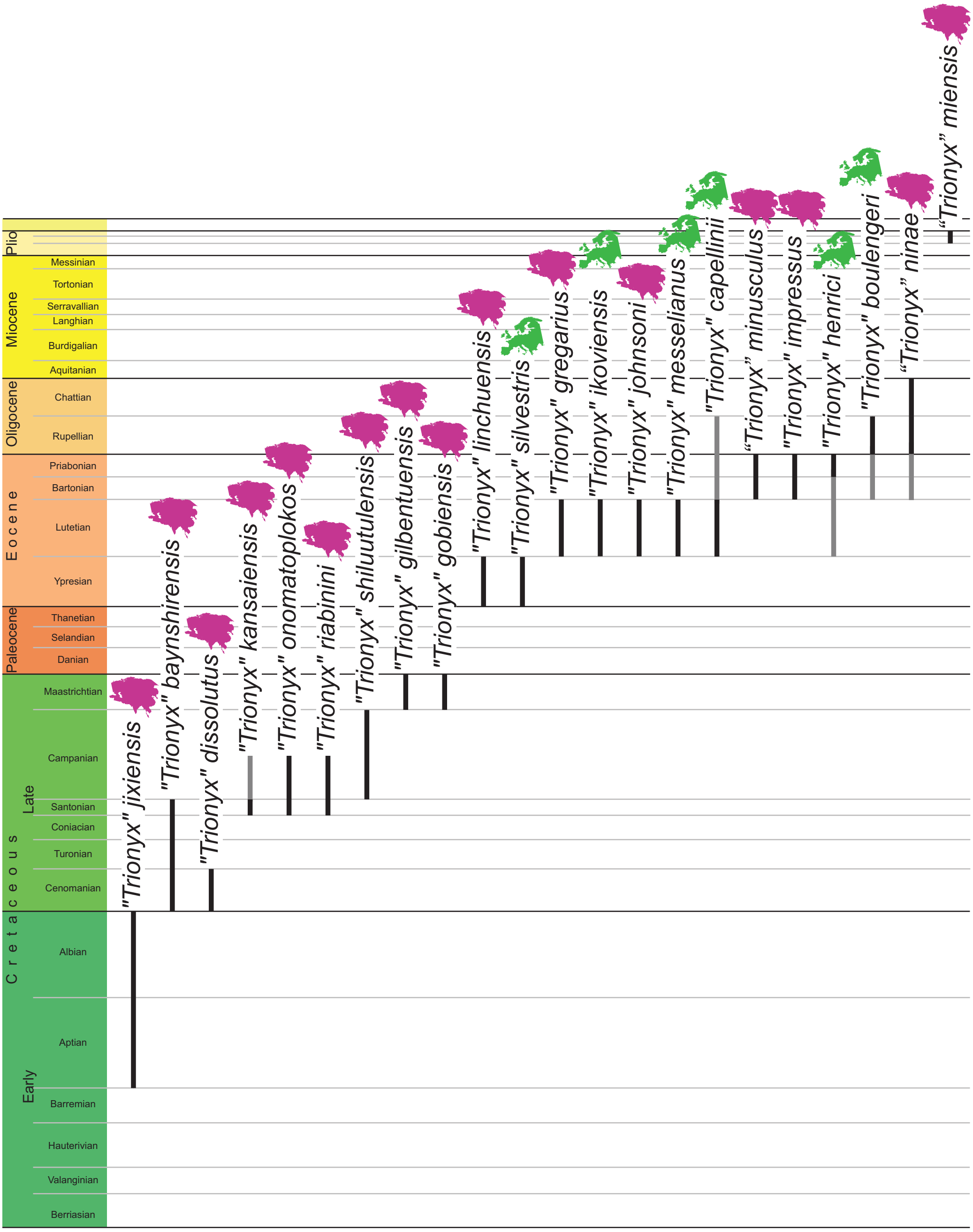

Figure 2. The stratigraphic and biogeographic distribution of valid pan-trionychid taxa herein referred to the wastebasket taxon “*Trionyx*.” Black lines indicate temporal distribution based on type material, including select extant taxa for reference. Gray lines indicate temporal distribution based on referred material.

able to recognize the validity of six, in particular “*Trionyx*” *linchuensis* from the early Eocene of Shandong Province, China (Yeh 1962); “*T.*” *gregarius* and “*T.*” *johnsoni* from the middle Eocene of Inner Mongolia, China (Gilmore 1934; Yeh 1965); “*T.*” *impressus* from the late Eocene of Guangdong Province, China (Yeh 1963); and “*T.*” *minusculus* and “*T.*” *ninae* from the late Eocene to early Oligocene of Kazakhstan (Chkhikvadze 1973; Vitek and Danilov 2015). Often rich,

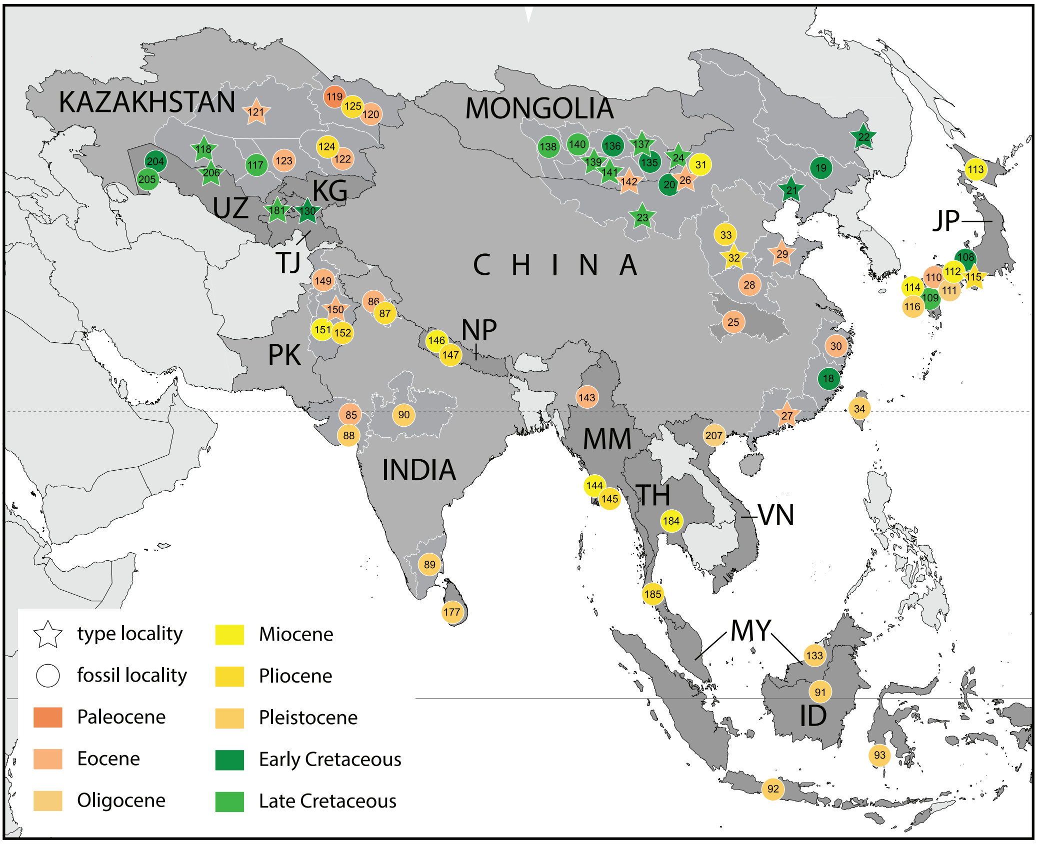

Figure 3. The geographic distribution of fossil pan-trionychids from the Cretaceous to the Neogene of the south-eastern portions of Asia. Stars mark the type localities of valid taxa. Locality numbers are cross listed in Appendix 3. *Abbreviations:* ID, Indonesia; JP, Japan; KG, Kyrgyzstan; MM, Myanmar; MY, Malaysia; NP, Nepal; PK, Pakistan; TH, Thailand; TJ, Tajikistan; UZ, Uzbekistan; VN, Vietnam.

fragmentary material has otherwise been reported from the Eocene and Oligocene of Kazakhstan (Bazhanov and Kostenko 1961; Chkhikvadze 1970, 1971, 1973, 1984, 1999b, 2007, 2008a, 2008b; Kordikova 1994b; Kordikova and Mavrin 1996; Kuznetsov and Chkhikvadze 1987); the Eocene of Inner Mongolia (Gilmore 1934; Yeh 1965) and Guangdong (Yeh 1965), Henan (Chow and Yeh 1957), Hubei (Lei and Ye 1985), Shandong (Yeh 1962), and Zhejiang Provinces (Yeh 1962), China; and the Oligocene of Japan (Hasegawa et al. 2007) and Vietnam (Böhme et al. 2011). In concert with its collision with the Asian mainland, the first trionychids also appear on the Indian subcontinent, but with the exception of *Drazinderetes tethyensis* from Pakistan (Head et al. 1999), most of the material from India (Sahni and Mishra 1975; Sahni et al. 1981, 1984; Smith et al. 2016), Myanmar (Hutchison et al. 2004), and Pakistan (Broin 1987) is fragmentary.

Although pan-trionychids are most speciose in Asia today (Ernst and Barbour 1989), only few remains have been reported from the Neogene of that continent. We here only recognize two valid species, "*Trionyx*" *miensis* from the Pliocene of Japan (Okazaki and Yoshida 1977) and *Pelodiscus gracilia* from the Pliocene of Shanxi Province, China (Yeh 1963). Fragmentary remains are otherwise documented from the Neogene of India (Tripathi 1964; Prasad 1974; Srivastava and Patnaik 2002), Indonesia (Lydekker 1889a; Jaekel 1911; Hooijer 1954), Kazakhstan (Bazhanov and Kostenko 1961; Chkhikvadze 1989), Malaysia (Pritchard et al. 2009), Myanmar (Chhibber 1934; Jaeger et al. 2011), Nepal (West et al. 1978, 1991; Corvinus and Schleich 1994), Pakistan (Lydekker

1885, 1889a, 1889b; Pilgrim 1912), Sri Lanka (Deraniyagala 1953), Thailand (Mudar and Anderson 2007; Claude et al. 2011), and Inner Mongolia, Shanxi, and Taiwan, China (Gilmore 1931; Chow and Yeh 1958; Tao 1986). For simplicity, the Georgian and Turkish record will be discussed below together with that of Europe. The Asian record of *Pan-Cyclanorbinae* is restricted to the Indian subcontinent, which mirrors its extant distribution completely.

Pan-trionychids are absent from Europe in the Mesozoic, with the exception of a recently found indeterminate form from the Late Cretaceous (Campanian) of southern Sweden (Scheyer et al. 2012). This find refutes the until recently prevailing theory that pan-trionychids dispersed to Europe no earlier than the Paleocene (e.g., Lapparent de Broin 2001), a conclusion previously supported by the notable absence of pan-trionychids in the richly sampled vertebrate faunas of France, Spain, Hungary, and Romania. Given the fragmentary nature of the Campanian material, however, it unfortunately remains unclear if the group dispersed to Europe from Asia or North America and if this early find is the precursor of later forms (Scheyer et al. 2012).

Fragmentary pan-trionychid remains have been reported from the early Paleocene of Denmark (Rosenkrantz 1923; Karl and Lindow 2012) and from the late Paleocene of Belgium (Broin 1977; Groessens van Dyck and Schleich 1988), France (Bergounioux 1932; Smith et al. 2014), and the United Kingdom (White 1931), but these are too fragmentary to allow rigorous attribution to any particular species or lineage. The situation improves dramatically in the Eocene and Oligocene. Although a long list of taxa have been named from these time periods (see Systematic Paleontology), we here only recognize seven as valid, in particular the early Eocene *Axestemys vittata* (Pomel 1847; Moody and Walker 1970; Broin 1977) and "*Trionyx*" *silvestris* (Walker and Moody 1974; Broin 1977) from Belgium, France, and the United Kingdom; the middle Eocene "*T.*" *messelianus* from Germany (Reinach 1900; Cadena 2016) and "*T.*" *ikoviensis* from Ukraine (Danilov et al. 2011); the middle Eocene to early Oligocene "*T.*" *capellinii* from Italy (Negri 1893; Sacco 1895; Bergounioux 1954; Kotsakis 1977; Barbera and Leuci 1980); the middle to late Eocene "*T.*" *henrici* from France and the United Kingdom (Owen and Bell 1849; Lydekker 1889a; Boulenger 1891; Lapparent de Broin et al. 1993); and "*T.*" *boulengeri* from the late Eocene to early Oligocene of Germany and Romania (Reinach 1900; Lörenthey 1903). Of these, the largest one, *Axestemys vittata*, is notable, as it is clearly referable to the North American taxon *Axestemys*, thereby revealing a positive faunal link between North American and Europe during the early Paleogene, similarly to the case suggested for several coeval continental squamates (Rage 2013), mammals (Rose 2006), and birds (Mayr 2009). Fragmentary remains are otherwise known from the Eocene and Oligocene of Austria, Belgium, Bulgaria, Croatia, Czechia, France, Germany, Hungary, Italy, Romania, Slovenia, Spain, Switzerland, and nearby Turkey (Figure 4; see Appendix 3 for extensive list of localities and citations). Several fragmentary finds from the Oligocene of Kaliningrad, Russia (Koken 1892; Dames 1894), were never figured or adequately described, and their pan-trionychid affinities are of dubious status.

Over the course of the Neogene, the distribution of pan-trionychids contracts southward (Karl 1999a), perhaps because of climatic cooling (Kotsakis 1980), and the clade is now extinct in Europe, with the exception of *Trionyx triunguis*, which occasionally reaches some of the Dodecanese Islands in Greece near the coast of Asia Minor (Taskavak et al. 1999; Corsini-Foka and Masseti 2008). Although an enormous number of taxa were named from this time interval, we only recognize in the Neogene two lineages that are referable to the extant *Trionyx* and *Rafetus*, much as partially proposed by Karl (1999a) and Chkhikvadze (1999b). The first lineage includes the species *T. vindobonensis* from the Miocene of Austria (e.g., Peters 1855, 1859; Hoernes 1881; Arthaber 1898; Heritsch 1909), Germany (Winkler 1869a; Reinach 1900), and France (Broin 1977) and *T. pliocenicus* from the Pliocene of Italy (Fucini 1912), whereas the other is only represented by *R. bohemicus* from the Miocene of Czechia (Liebus 1930) but may have been more widely distributed (see Systematic Paleontology). The above-mentioned contraction of the range is well documented by fragmentary remains from the Miocene of Austria, Cyprus, Czechia, France, Georgia, Greece, Hungary, Italy, Moldova, Portugal, Romania, western Russia, Slovakia, Slovenia, Spain, Switzerland, Turkey, and Ukraine, whereas

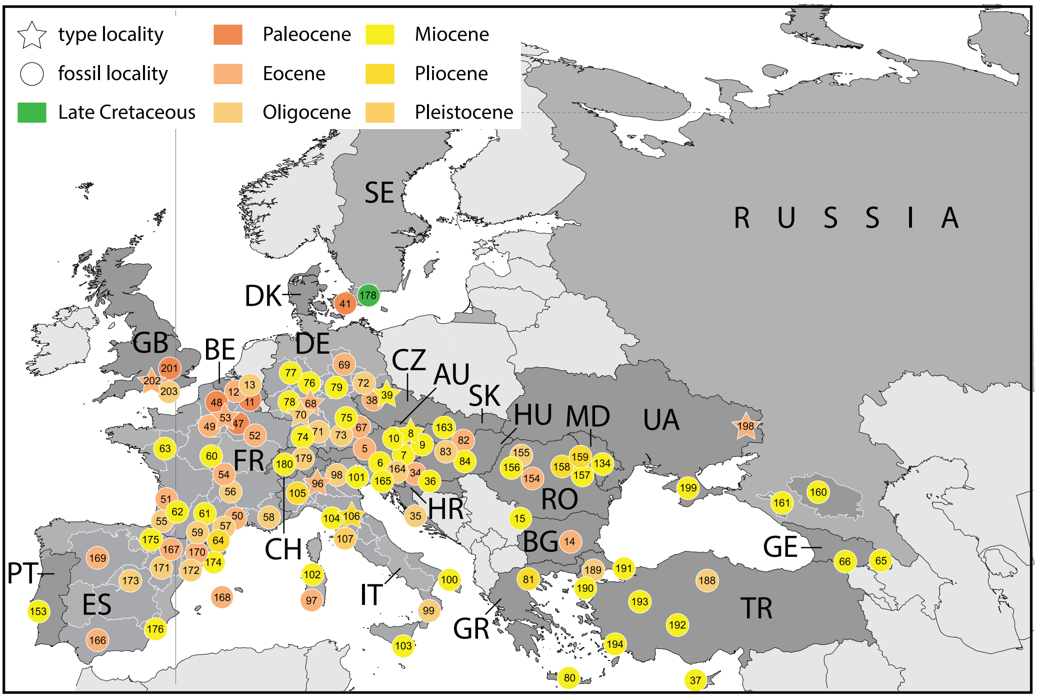

Figure 4. The geographic distribution of fossil pan-trionychids from the Cretaceous to the Neogene of Europe and adjacent portions of Asia. Stars mark the type localities of valid taxa. Locality numbers are cross listed in Appendix 3. Abbreviations: AU, Austria; BE, Belgium; BG, Bulgaria; CH, Switzerland; CZ, Czechia; DE, Germany; DK, Denmark; ES, Spain; FR, France; GB, United Kingdom; GE, Georgia; GR, Greece; HR, Croatia; HU, Hungary; IT, Italy; MD, Moldova; PT, Portugal; RO, Romania; SE, Sweden; SK, Slovakia; TR, Turkey; UA, Ukraine.

Pliocene remains are restricted to Greece, Italy, France, and Romania (Figure 4; see Appendix 3 for extensive list of localities and literature). We here ignore fossils reported from the Miocene of Malta as these either remain poorly figured or not figured at all (Gulia 1843; Cooke 1890) or do not represent pan-trionychids (contra Lydekker 1891; also Introduction). The last fossil occurrence in Europe is known from the early Pleistocene of Italy (Portis 1890; Kotsakis 1980).

The presence of pan-trionychids on the Australian continent is not well documented, mostly because of a lack of fossiliferous localities. The oldest Australian pan-trionychid is the bizarre and highly autapomorphic *Murgonemys braithwaitei* from the early Eocene of southeastern Queensland (White 2001; Figure 5) that shows no clear relationships with any other group of pan-trionychids, despite being well preserved. Although pan-trionychids are now restricted to Papua (Ernst and Barbour 1989), fragmentary finds are known from Queensland, Australia, from as recently as the Plio-Pleistocene (Gaffney and Bartholomai 1979), thereby indicating that their local extirpation occurred relatively recently. Pan-trionychids have not been recovered from neighboring Antarctica and New Zealand, although connections were available with these landmasses during the Paleogene (Scanlon 1993; Hand et al. 2015).

Fossil pan-trionychids have been reported from Neogene sediments from across Africa and Arabia (Lapparent de Broin 2000), but many of the finds have not been figured, and it is therefore difficult to rigorously assess most such claims. Fossil pan-trionychids are notably absent from the Paleogene of that continent, with the notable exception of a single carapace fragment that questionably originated from the Eocene Fayum deposits of Egypt, but more likely is Holocene (Wood 1979), an assertion supported by more than one century of intensive collecting in the Fayum that otherwise did not yield a single bona fide pan-trionychid. This lack of Paleogene

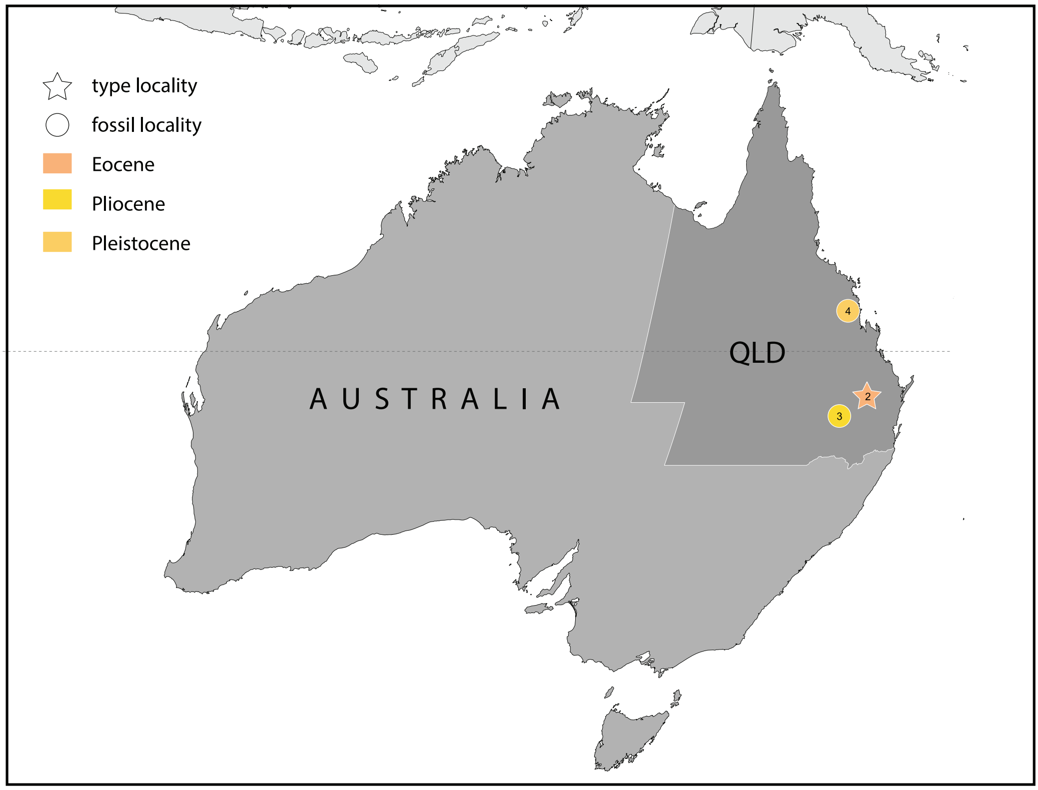

FIGURE 5. The geographic distribution of fossil pan-trionychids from the Tertiary of Australia. Stars mark the type localities of valid taxa. Locality numbers are cross listed in Appendix 3. *Abbreviation:* QLD, Queensland.

material contradicts the prediction of Le et al. (2014) that cyclanorbines should have migrated to that continent in the Eocene. Instead, we suggest that Le et al. (2014) overinterpreted their data by conflating the likely divergence date between African and Asian cyclanorbines with a possible dispersal date, but we readily admit that the Paleogene record from Africa is highly incomplete. We here recognize three valid species from Africa that are all based on well-preserved material from the Rift Valley of Kenya, in particular the early Miocene *Cycloderma victoriae* and the early Pliocene *Cyclanorbis turkanensis* and *Cycloderma debroinae* (Andrews 1914; Broin 1987; Lapparent de Broin 2000; Meylan et al. 1990). Including also the Arabian Peninsula and the Middle East, we here otherwise recognize fragmentary remains from Algeria, Chad, the Democratic Republic of Congo, Egypt, Ethiopia, Iraq, Israel, Kenya, Libya, Malawi, Oman, Saudi Arabia, Tanzania, Tunisia, Uganda, and the United Arab Emirates (Figure 6; see Appendix 3 for extensive list of localities and literature). There is no indication that pan-trionychids ever colonized nearby Madagascar.

## Systematic Paleontology

### *Valid Taxa*

See Appendix 4 for the hierarchical taxonomy of Old World *Pan-Trionychidae* used in this work.

### *Pan-Trionychidae* Joyce et al., 2004

Phylogenetic definition. In accordance with Joyce et al. (2004), the name *Pan-Trionychidae* is herein referred to the total-clade of *Trionychidae*, which, in return, is defined as the crown clade that includes all extant turtles that are more closely related to *Trionyx triunguis* (Forskål, 1775) than *Carettochelys insculpta* Ramsay, 1887.

Diagnosis. Representatives of *Pan-Trionychidae* are currently diagnosed relative to other turtles, among others, by a reduced quadratojugal that does not contact the postorbital or maxilla, exclusion of the fused premaxillae from the apertura narium externa, the presence of sculpturing that covers all metaplastic portions of the shell bones, the absence of peripherals, pygals,

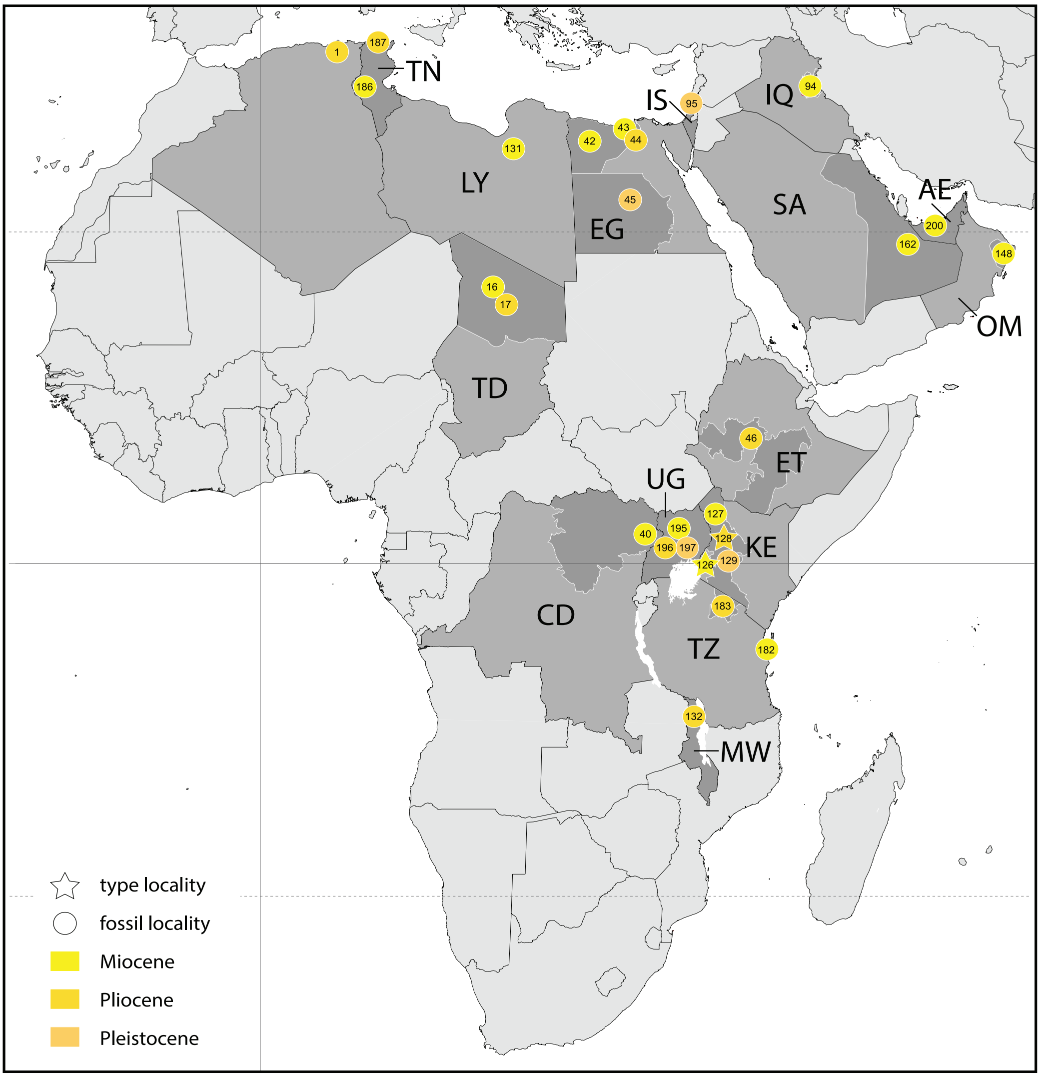

FIGURE 6. The geographic distribution of fossil pan-trionychids from the Neogene of Africa and Arabia. Stars mark the type localities of valid taxa. Locality numbers are cross listed in Appendix 3. Abbreviations: AE, United Arab Emirates; CD, Democratic Republic of the Congo; EG, Egypt; ET, Ethiopia; IQ, Iraq; IS, Israel; KE, Kenya; LY, Libya; MW, Malawi; OM, Oman; SA, Saudi Arabia; TD, Chad; TN, Tunisia; TZ, Tanzania; UG, Uganda.

suprapygals, and shell scutes, a boomerang-shaped entoplastron, a plywood-like micro-structure in the metaplastic portions of the shell, absence of central articulation between the eighth cervical and the first thoracic vertebra, hyperphalangy, and the presence of three claws in the manus and pes.

### *Axestemys* Hay, 1899

Type species. *Axestemys byssinus* (Cope, 1872).

Diagnosis. *Axestemys* can be diagnosed as a representative of *Pan-Trionychidae* by the full list of characters provided for that clade above. *Axestemys* is currently differentiated from other pan-trionychids by large size, sculpturing on the skull roof, presence of a preneural, and a single lateral hyoplastral process.

### *Axestemys vittata* (Pomel, 1847), comb. nov. (= *Eurycephalochelys fowleri* Moody and Walker, 1970)

Taxonomic history. *Trionyx vittatus* Pomel, 1847 (new species); *Palaeotrionyx vittatus* = [*T. erquelinnensis*] Broin 1977 (new combination, incorrect spelling of genus name, and senior synonym); *Eurycephalochelys vittatus* Augé et al. 1997 (new combination).

Type material. MNHN (holotype), a carapace (Gervais 1859, pl. 52), now lost (Broin 1977).

Type locality. Muirancourt, Oise, France (Pomel 1847; Figure 4); Muirancourt Lignites, Paris Basin, early Ypresian, early Eocene (Broin 1977).

Referred material and range. Early Eocene (early Ypresian), Hainaut, Belgium (material of *Trionyx erquelinnensis* Dollo 1909; referred material of Broin 1977); early Eocene (early Ypresian), Trieu de Leval, Hainaut, Belgium (material of *T. levalensis* Dollo 1909); early Eocene (early Ypresian), Île-de-France, France (referred material of Broin 1977); early Eocene (early Ypresian), Champagne-Ardenne, France (referred material of Broin 1977); early Eocene (late Ypresian), West Sussex, United Kingdom (hypodigm of *Eurycephalochelys fowleri* Walker and Moody 1985); early Eocene (late Ypresian), Prémontré, Aisne, Hauts-de-France (referred material of Augé et al. 1997).

Diagnosis. *Axestemys vittata* can be diagnosed as a member of *Pan-Trionychidae* and *Axestemys* by the full list of characters provided above for those clades. At present, biogeographic considerations most clearly differentiate the European *Axestemys vittata* from all North American representatives of this clade (see comments below).

Comments. Four names are associated with the remains of large-bodied pan-trionychids from early Eocene deposits throughout Belgium, southern England, and northern France, in particular *Trionyx vittatus* Pomel, 1847, *T. erquelinnensis* Dollo 1909, *T. levalensis* Dollo 1909, and *Eurycephalochelys fowleri* Moody and Walker, 1970. Although *T. erquelinnensis* and *T. levalensis* are based on beautifully preserved specimens, we agree with Moody and Walker (1970) and Broin (1977) that these are nomina nuda (see below), and we therefore disregard them from consideration. Broin (1977) already noted that all European material is closely related and that it shows great similarities with *Paleotrionyx quinni* Schmidt, 1945, a large-bodied pan-trionychid from the late Paleocene of North America, but she nevertheless maintained two valid species, *Axestemys* (her *Palaeotrionyx*) *vittata* and *Eurycephalochelys fowleri*. Augé et al. (1997) preferred synonymy within the available European material and therefore attributed *vittata* to *Eurycephalochelys*.

Vitek (2012) recently concluded that several large-bodied trionychids from the Late Cretaceous to Eocene of North America form a monophyletic lineage referable to *Axestemys* Hay, 1899. Earlier representatives of this lineage from the Late Cretaceous generally resemble other pan-trionychines, but the Paleocene and Eocene representatives acquire a peculiar shell that is characterized most notably by presence of a preneural, poorly developed carapacial callosities that often only cover the proximal two-thirds of the rib, carapacial ornamentation that is restricted to the proximal third of the costals, suprascapular fontanelles, plastra almost completely devoid of surficial sculpturing, and single lateral hyo- and hypoplastral processes. The skull, on the other side, is characterized by being notably short snouted and by often showing an expanded triturating surface. In all regards, the shell and skull material from Europe correspond to these derived representatives of *Axestemys* from North America, and we therefore refer all to *Axestemys* with confidence, but additional work is needed to render a meaningful diagnosis.

Broin (1977) believed that two species are apparent among the European assemblages, but we find that all described material only shows variation sufficient to warrant one species. We therefore here synonymize *vittatus* with *fowleri* but await a more detailed analysis of all material, perhaps that from Belgium. The type material of *Axestemys vittata* has been reported to be lost (Broin 1977), but we find the figures provided by Gervais (1859) to be informative, and a cast of the holotype is held at MNHN. We therefore see no need either to declare *Axestemys vittata* a nomen dubium or to designate a neotype specimen. Furthermore, the original spelling of the species epithet "*vittatus*" is herein emended to "*vittata*" in order to conform with the feminine gender of the genus name *Axestemys*.

Shell fragments of a large pan-trionychid originating from the late Paleocene (MP 6) of Rivecourt-Petit Pâtis, Oise, Hauts-de-France, Paris Basin, France (Smith et al. 2014), could eventually belong to *Axestemys vittata* as well. However, this material was not figured and was only preliminarily described. Therefore, conspecificity with *Axestemys vittata*, although possible, cannot be confirmed.

## *Drazinderetes tethyensis* Head et al., 1999

Taxonomic history. *Drazinderetes tethyensis* Head et al., 1999 (new species).

Type material. GSP UM3195 (holotype), a nearly complete carapace (Head et al. 1999, figs. 3–5).

Type locality. Bari Nadi, west of Satta Post, Punjab, Pakistan (Figure 3); Drazinda Formation, middle Bartonian, middle Eocene (Head et al. 1999).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Drazinderetes tethyensis* can be diagnosed as a member of *Pan-Trionychidae* by the absence of central articulation between the eighth cervical and first thoracic vertebra and the full list of carapacial characters provided for that clade above. *Drazinderetes tethyensis* can be differentiated from all remaining representatives of *Pan-Trionychidae* by rather large size, presence of a preneural, a single pair of costiform processes, and anteriorly oriented costals I.

Comments. *Drazinderetes tethyensis* is based on a large, nearly complete carapace from the Eocene of Pakistan, which Head et al. (1999) reconstructed as originating from an individual that may have reached a shell length of up to 150 cm. In addition to the type, Head et al. (1999) also reported from the type locality an isolated carapace fragment, an incomplete right hypoplastron, and a gigantic entoplastron with a lateral length of 57.3 cm that they estimated to have originated from an individual with a shell length of up to 220 cm, which reveals this specimen to be not only the largest known pan-trionychid, but also among the largest known turtles. These size estimates, however, must be viewed with caution as they were calculated by direct comparison to the North American *Apalone spinifera*, which is notable by having a relatively small carapace relative to a large nonossified flap. Although the presence of two sympatric giant pan-trionychids in the same sedimentary basin seems improbable, we agree that it is prudent not to refer all to one taxon pending the discovery of more complete material. Head et al. (1999) discussed possible affinities of *Drazinderetes tethyensis* with the extant *Nilssonia* (their *Aspideretes*) on the basis of geographic proximity and the presence of a preneural and several other characters, but we note that the posterior constriction of the carapace combined with the poor development of the free rib ends furthermore show similarities with pan-cyclanorbines. As it seems clear that *Drazinderetes tethyensis* is not nested within either of these clades, we here make an exception and maintain the monotypic genus to which it was referred.

The type of *Drazinderetes tethyensis* was recovered from marine sediments, and Head et al. (1999) therefore suggested that this animal may have been fully adapted to marine environments. Although it is true that some extant trionychids venture into the marine realm from nearby freshwater to brackish habitats (Taskavak et al. 1999), we note that these excursions seem to be short lived, as sightings are relatively rare. We therefore believe it to be more likely that this animal was washed into the sea from the nearby coast.

## *Khunnuchelys* Brinkman et al., 1993

Type species. *Khunnuchelys erinhotensis* Brinkman et al., 1993.

Diagnosis. *Khunnuchelys* can be diagnosed as a member of *Pan-Trionychidae* by the presence of a reduced quadratojugal that does not contact the postorbital or maxilla and exclusion of the fused premaxillae from the apertura narium externa. *Khunnuchelys* can be differentiated most notably from other pan-trionychids by having a thick skull roof, an external narial opening that is located ventral to the orbits, anteriorly oriented orbits, high maxillae, a vaulted palate, maxillae that meet at the midline of the palate to form a midventral ridge and secondary palate, a large contribution of palatines to the triturating surface, and an exclusion of the jugal from the margin of the orbit.

Comments. *Khunnuchelys* is a strange pan-trionychid taxon that has been suggested to bear affinities, among others, with the large Paleocene North American taxon "*Trionyx*" *admirabilis*, the Eocene European *Axestemys vittata*, or even *Pan-Cyclanorbinae* (Brinkman et al. 1993; Vitek and Danilov 2013; Danilov, Vitek et al. 2015), but a rigorous phylogenetic analysis is still not available that would clarify its affinities. Brinkman et al. (1993) hypothesized that the highly vaulted palate was consistent with a durophagous diet and that the rugose middorsal ridge formed by the maxillae may have served as a pressure point for crushing shells. Along those lines, hard-shelled invertebrates, such as snails, clams, or even dinosaur eggs, have been suggested as prey items for *Khunnuchelys* (Brinkman et al. 1993).

### *Khunnuchelys erinhotensis* Brinkman et al., 1993

Taxonomic history. *Khunnuchelys erinhotensis* Brinkman et al., 1993 (new species); *Kunhuchelys erinhotensis* Kordikova 2002 (incorrect spelling of genus name).

Type material. IVPP V9535 (holotype), partial skull missing ventral margin of maxilla and jugal, posterior portion of cheek region, and supraoccipital crest (Brinkman et al. 1993, figs. 1–3; Brinkman et al. 2008, fig. 79; Danilov and Vitek 2013, fig. 23.2h).

Type locality. 13 km northeast of Erinhot, Xilin Gol, Inner Mongolia, China (Figure 3); Iren Dabasu Formation (Brinkman et al. 1993), Campanian, Late Cretaceous (Xing et al. 2012).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Khunnuchelys erinhotensis* can be diagnosed as a member of *Khunnuchelys* based on the full list of characters provided for that clade above. *Khunnuchelys erinhotensis* can be differentiated most readily from other members of *Khunnuchelys* by the presence of a formed posterior jugular foramen.

Comments. *Khunnuchelys erinhotensis* is known only from a single, highly distinctive skull from the Late Cretaceous (Campanian) of China (Brinkman et al. 1993; Danilov and Vitek 2013). Similar skulls have since been described from other Late Cretaceous deposits, but these have all been diagnosed as other species (see *Khunnuchelys kizylkumensis* and *Khunnuchelys lophorhothon* below). Although the postcranial anatomy of this species remains uncertain, its taxonomic validity is uncontroversial.

### *Khunnuchelys kizylkumensis*
### Brinkman et al., 1993

Taxonomic history. *Khunnuchelys kizylkumensis* Brinkman et al., 1993 (new species).

Type material. CCMGE 8/12458 (holotype), a braincase and skull roof (Nessov 1986, pl. 1.9; Brinkman et al. 1993, figs. 4–8; Nessov 1997, pl. 13.18; Danilov and Vitek 2013, fig. 23.2i).

Type locality. Site CBI-28, Dzharakuduk (= Dzharakuduk II of Nessov 1997), 35 km southwest of Mynbulak, Navoiy Region, Uzbekistan (Brinkman et al. 1993; Figure 3); Bissekty Formation, late Turonian, Late Cretaceous (Brinkman et al. 1993; Vitek and Danilov 2013).

Referred material and range. Late Cretaceous (late Turonian) of type area, Navoiy Region, Uzbekistan (Vitek and Danilov 2013).

Diagnosis. *Khunnuchelys kizylkumensis* can be diagnosed as a member of *Khunnuchelys* on the basis of all characters listed for that taxon above. *Khunnuchelys kizylkumensis* can be differentiated from *Khunnuchelys erinhotensis* by the presence of an open foramen jugulare posterius and from *Khunnuchelys lophorhothon* by lacking a flooring of the internal nares that is formed by the palatines.

Comments. *Khunnuchelys kizylkumensis* is based on a partial skull from the Late Cretaceous (late Turonian) of Uzbekistan that was estimated to have exceeded 20 cm in length (Brinkman et al. 1993; Vitek and Danilov 2013). The type locality also yielded fragmentary shell remains of a large trionychid that may reasonably be referred to this species as well (Brinkman et al. 1993; Vitek and Danilov 2013), but an actual association is still lacking. Another distinct but indeterminate skull-based taxon has been described from the same locality (Trionychini indet. of Vitek and Danilov 2013).

## *Khunnuchelys lophorhothon* Danilov, Vitek et al., 2015

Taxonomic history. *Khunnuchelys lophorhothon* Danilov, Vitek et al., 2015 (new species); *Khunnuchelys lorhophoton* Li, Tong et al. 2015 (incorrect spelling of species epithet).

Type material. ZIN PH 5/55 (holotype), a partial skull (Danilov, Vitek et al. 2015, fig. 2; Averianov et al. 2016, fig. 4i).

Type locality. Baybishe, Kyzylorda Region, Kazakhstan (Figure 3); Bostobe Formation, Santonian or early Campanian, Late Cretaceous (Danilov, Vitek et al. 2015).

Referred material and range. Late Cretaceous (Santonian–early Campanian), Bostobe Formation, Baykhozha, Kyzylorda Region, Kazakhstan (referred material of Danilov, Vitek et al. 2015).

Diagnosis. *Khunnuchelys lophorhothon* can be diagnosed as a member of *Khunnuchelys* on the basis of the full list of characters provided for that clade above. *Khunnuchelys lophorhothon* can be differentiated from *Khunnuchelys erinhotensis* by the presence of an open foramen jugulare posterius and from *Khunnuchelys kizylkumensis* by showing a flooring of the internal nares that is formed by the palatines.

Comments. The holotype of *Khunnuchelys lophorhothon*, a partial skull from the Late Cretaceous of Kazakhstan, was initially identified as perhaps representing *Lophorhothon*, an ornithopod dinosaur otherwise known from the USA (Nessov 1995a), but actually represents the skull of a pan-trionychid (Danilov, Vitek et al. 2015). *Khunnuchelys lophorhothon* may perhaps be synonymous with the shell based taxon "*Trionyx*" *kansaiensis*, which also occurs in the Bostobe Formation (Vitek and Danilov 2010; Danilov, Vitek et al. 2015). If correct, the species name should be combined as *Khunnuchelys kansaiensis*. However, pending the discovery of associated material, "*T.*" *kansaiensis* and *Khunnuchelys lophorhothon* are herein treated as distinct, valid species.

## *Kuhnemys* Chkhikvadze, 1999b

Type species. *Aspideretes maortuensis* Yeh, 1965.

Diagnosis. *Kuhnemys* can be diagnosed as a member of *Pan-Trionychidae* by the full list of characters provided for that clade above. *Kuhnemys* can be differentiated from other Cretaceous to Paleogene pan-trionychids by the unique combination of shell characters: absence of a preneural, ratio of nuchal width to length greater than four, small or absent costals VIII, unfused hyo-hypoplastra, and two lateral hyoplastral processes.

Comments. Danilov et al. (2014) recently grouped three Late Cretaceous to Paleocene trionychids from Asia into a clade that they fittingly named *Gobiapalone*. We here confirm that the type of *Trionyx maortuensis*, as described, does not fit the diagnosis of *Gobiapalone* (Danilov et al. 2014), but personal observations of this specimen lead us to conclude that it should be placed in *Gobiapalone* as well. As described, *T. maortuensis* has a complete row of eight neurals that potentially separate the costal series completely, but our observations reveal the presence of only seven neurals and a midline contact of costals VII and VIII, as in *Gobiapalone*. *Trionyx maortuensis* furthermore resembles *Gobiapalone* by having greatly reduced costals VIII (damage to the posterior margin is only minor), open suprascapular fontanelles, and poorly developed plastral callosities. New insights into the age of *T. maortuensis* reveals that it is likely Late Cretaceous (Turonian) in age, not late Early Cretaceous (Aptian/Albian), and therefore the same age as *Gobiapalone orlovi*. These species greatly resemble one another, but we nevertheless confirm their validity herein.

*Trionyx maortuensis* is the type species of *Kuhnemys* Chkhikvadze, 1999b, which has priority over *Gobiapalone* Danilov et al., 2014. This is somewhat unfortunate, because the name *Kuhnemys* is similar to *Khunnuchelys*, the other valid genus we use herein, and because we find *Gobiapalone* to be more euphonious. We are nevertheless forced to propose new combinations for all taxa previously assigned to *Gobiapalone*.

## *Kuhnemys breviplastra* (Danilov et al., 2014), comb. nov.

Taxonomic history. *Gobiapalone breviplastra* Danilov et al., 2014 (new species).

Type material. PIN 4694-3 (holotype), a partial shell (Danilov et al. 2014, fig. 10f, g).

Type locality. Ulan Khushu (= Ulan Bulak), Ömnögovi (= Umunugovi) Aimag, Mongolia (Figure 3); Nemegt Formation, Maastrichtian, Late Cretaceous (Danilov et al. 2014).

Referred material and range. Late Cretaceous (Campanian), Barungoyot Formation, Nogon Tsav and Bugin Tsav, Bayankhongor and Ömnögovi Aimag, respectively, Mongolia (referred material of Danilov et al. 2014); Late Cretaceous (Maastrichtian), Nemegt Formation, Bugin Tsav, Ömnögovi Aimag, Mongolia (referred material of Danilov et al. 2014).

Diagnosis. *Kuhnemys breviplastra* can be diagnosed as a member of *Pan-Trionychidae* and *Kuhnemys* by the full list of characters provided for those clades above. *Kuhnemys breviplastra* can be differentiated from *Kuhnemys orlovi* and *Kuhnemys maortuensis* by having open suprascapular fontanelles in large specimens, more massive epiplastra, entoplastron, and xiphiplastra, an angle of more than 80° between the arms of the entoplastron, and a reduced count of medial hyoplastral processes. It can be differentiated from *Kuhnemys palaeocenica* by having a square neural V and shorter anterior epiplastral processes.

Comments. *Kuhnemys breviplastra* is known from several carapaces, plastra, and postcranial elements from the Late Cretaceous of Mongolia (Danilov et al. 2014). The availability of adult and juvenile individuals enables the study of intraspecific and ontogenetic variation for this taxon. Given the high quality of the available material, the validity of this species is not controversial.

## *Kuhnemys maortuensis* (Yeh, 1965) (= *Trionyx alashanensis* Yeh, 1965)

Taxonomic history. *Aspideretes maortuensis* Yeh, 1965 (new species); *Axestemys maortuensis* Kordikova 1994a (new combination); *Kuhnemys maortuensis* Chkhikvadze 1999b (new combination); *Dogania maortuensis* Karl 1999b (new combination).

Type material. IVPP V2864 (holotype), incomplete postcranium with parts of carapace, plastron, and girdles, two cervical vertebrae, and the right pes (Yeh 1965, fig. 1, pls. I–II).

Type locality. Dashukou, Maortu (= Maorty), Alxa (= Alashan), Inner Mongolia, China (Yeh 1965; Brinkman et al. 2008; Figure 3); Ulansuhai Formation, Turonian, Late Cretaceous (Brusatte et al. 2009).

Referred material and range. Late Cretaceous (Turonian) of the type locality, Inner Mongolia, China (type material of *Aspideretes alashanensis*; Yeh 1965).

Diagnosis. *Kuhnemys maortuensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters provided for that clade above and of *Kuhnemys* by absence of a preneural, small costals VIII, and unfused hyo-hypoplastra. *Kuhnemys maortuensis* can be differentiated from *Kuhnemys breviplastra* by having an angle of less than 100° between the arms of the entoplastron and from *Kuhnemys palaeocenica* and *Kuhnemys orlovi* by having additional medial hyo- and hypoplastral processes and the reversal at neural VI.

Comments. *Kuhnemys maortuensis* is based on a partial skeleton that most notably lacks the nuchal and the lateral aspects of the plastron (Yeh 1965). The same locality also yielded the type of *Trionyx alashanensis* (Yeh 1965). The age of the holotype has variously been reported as Early Cretaceous or Late Cretaceous (e.g., Yeh 1965; Brinkman et al. 2008), but without much discussion. The rich dinosaur fauna from the locality of Maortu has been reported as originating from the Ulansuhai Formation, and we here presume that the holotype of *Kuhnemys maortuensis* was collected from that formation as well. This formation was initially believed to be Early Cretaceous (Aptian/Albian) based on the dinosaur fauna it contained, but we here concur with Brusatte et al. (2009) by accepting a Late Cretaceous (Turonian) age, as established by radiometric dating of basalt flows below the formation.

Over the course of the decades, *Kuhnemys maortuensis* was variously referred to *Aspideretes*, *Axestemys*, or *Dogania* (Yeh 1965; Kordikova 1994a; Karl 1999b). The holotype of *Kuhnemys maortuensis* was initially reported as having eight neurals and perhaps lacking a midline contact of the costals, but our personal observation of the type specimen reveals that this specimen shows a more usual arrangement of seven neurals and a midline contact of costals VII and VIII. Using a stratigraphic rationale, Yeh (1965) furthermore presumed that a preneural may have been present, but we see no evidence for its former presence. A thorough redescription of the type specimen would certainly help to anchor these observations into the literature. The validity of this taxon is nevertheless uncontroversial (see *Kuhnemys* above for additional comments). We here also synonymize *Trionyx alashanensis* with *Kuhnemys maortuensis*, as the type material corresponds in all important aspects (see *T. alashanensis* below).

## *Kuhnemys orlovi* (Khosatzky, 1976), comb. nov.

Taxonomic history. *Amyda orlovi* Khosatzky in Sochava 1975 (nomen nudum); *Amyda orlovi* Khosatzky, 1976 (new species); *Gobiapalone orlovi* Danilov et al. 2014 (new combination).

Type material. PIN 557-132/1 (formerly PIN 557-1/1) (holotype), incomplete carapace (Khosatzky 1976, no figure; Sukhanov 2000, fig. 17.27; Danilov and Vitek 2013, fig. 23.2b1; Danilov et al. 2014, fig. 7f).

Type locality. Bayn Shire, Dornogovi Aimag, Mongolia (Khosatzky 1976; Figure 3); lower part of the Baynshire Formation, Cenomanian–early Turonian, Late Cretaceous (Danilov et al. 2014).

Referred material and range. Late Cretaceous (Cenomanian–Santonian), Baynshire Formation, Burkhant, Unegetu Ula, and Khongil, Dornogovi Aimag, Mongolia (referred material of Danilov et al. 2014).

Diagnosis. *Kuhnemys orlovi* can be diagnosed as a member of *Pan-Trionychidae* and *Kuhnemys* by the full list of characters provided for those clades above. *Kuhnemys orlovi* can be differentiated from *Kuhnemys breviplastra* and *Kuhnemys palaeocenica* by having closed suprascapular fontanelles in large specimens, more slender epiplastra, entoplastron, and xiphiplastra, and an angle of less than 80° between the arms of the entoplastron. It can be differentiated from *Kuhnemys maortuensis* by possessing a square sixth neural and more pectinate medial hyo- and hypoplastral processes.

Comments. The early Late Cretaceous Baynshire Formation in Mongolia has yielded rich remains of trionychids, of which most, including nearly complete skeletons that include well-preserved crania, are referable to *Kuhnemys orlovi* (Danilov et al. 2014). *Kuhnemys orlovi* is therefore well diagnosed, and the validity of this species uncontroversial.

## *Kuhnemys palaeocenica* (Danilov, Sukhanov et al., 2015), comb. nov.

Taxonomic history. *Gobiapalone palaeocenica* Danilov, Sukhanov et al., 2015 (new species).

Type material. PIN 3639/13 (holotype), an incomplete articulated skeleton of a juvenile individual, including an almost complete shell, two or three posterior cervical vertebrae, limb girdles, both humeri, hind limbs, and anterior caudal vertebrae (Danilov, Sukhanov et al. 2015, fig. 1).

Type locality. Site 3, Ömnögovi (= Umunugovi) Aimag, Mongolia ( Danilov, Sukhanov et al. 2015; Figure 3); lowermost part of the Naran Member, Naranbulak Formation, late Paleocene (Danilov, Sukhanov et al. 2015).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Kuhnemys palaeocenica* can be diagnosed as a member of *Pan-Trionychidae* and *Kuhnemys* by the full list of characters provided for those clades above. *Kuhnemys palaeocenica* can be differentiated from other members of *Kuhnemys* by a square neural IV and simplified medial hyoplastral processes.

Comments. *Kuhnemys palaeocenica* is based on a nearly complete skeleton from the Paleocene of Mongolia that Danilov, Sukhanov et al. (2015) speculated to be a juvenile, as it only has a CL of 12.5 cm and confluent suprascapular fontanelles. Although we normally discourage the use of juveniles as the basis for taxa, we make an exception here, as the specimen is well preserved. *Kuhnemys palaeocenica* constitutes the only valid and only reliable record of a pan-trionychid in the Paleocene of Asia, as all other occurrences from this epoch are based on indeterminate material. Furthermore, this taxon indicates the survivorship of the genus *Kuhnemys* across the K/T boundary ( Danilov, Sukhanov et al. 2015).

## *Murgonemys braithwaitei* White, 2001

Taxonomic history. *Murgonemys braithwaitei* White, 2001 (new species).

Type material. QM F41129 (holotype), a nearly complete carapace and a left xiphiplastron (White 2001, figs. 1, 3, 5).

Type locality. Tingamarra, Murgon, Queensland, Australia (Figure 5); Oakdale Sandstone Formation, early Eocene (White 2001).

Referred material and range. Early Eocene of the type locality, Queensland, Australia (referred material of White 2001).

Diagnosis. *Murgonemys braithwaitei* can be diagnosed as a member of *Pan-Trionychidae* by the presence of sculpturing that covers all metaplastic portions of the shell bones and the absence of peripherals, pygals, suprapygals, and shell scutes. *Murgonemys braithwaitei* can be differentiated from other pan-trionychids by the presence of an expanded trapezoidal preneural, which is more than twice as wide as the neurals, and a xiphiplastron with a six-pronged medial flange.

Comments. *Murgonemys braithwaitei* is based on a well-preserved carapace and an associated left xiphiplastron from the Eocene of Australia. This is a rather bizarre taxon whose anatomy seems to be a mosaic of different pan-trionychid clades. White (2001) originally considered pan-trionychine affinities for his new species on the basis of the anterior process of the xiphiplastron being lateral to the posterior process of the hypoplastron. We note here, however, that the presence of costals that cover most of the underlying ribs, a large, unusually shaped preneural, the absence of neural series reversal, and the posterior tapering of the carapace are reminiscent of cyclanorbines, although there is no evidence of split costiform processes, large costals VIII, or well-developed plastral callosities, thereby contradicting the association with this group at the same time (Meylan 1987; Vitek and Joyce 2015). The origins of *Murgonemys braithwaitei* are totally unclear as all other pan-trionychids recovered from Australia, including the only other named taxon, *Trionyx australiensis*, are from the Plio-Pleistocene and are too fragmentary to allow rigorous identification beyond the family level (Gaffney and Bartholomai 1979). A possible origin from South America, much like coeval meiolaniids (Sterli 2015), can be ruled out, however, as pan-trionychids are not known from the Paleogene of that continent (Vitek and Joyce 2015). The validity of *Murgonemys braithwaitei* is uncontroversial, and its morphologically, geographically, and temporally isolated nature prompts us to retain the species within its own monotypic genus.

## *Perochelys lamadongensis* Li, Joyce, and Liu, 2015

Taxonomic history. *Perochelys lamadongensis* Li, Joyce, and Liu, 2015 (new species).

Type material. IVPP V18048 (holotype), a nearly complete skeleton, comprising cranium, carapace, plastron, vertebrae, and limb elements (Li, Joyce, and Liu 2015, figs. 1–3).

Type locality. Xiaotaizi locality, Lamadong, Jianchang County, Liaoning Province, China (Li, Joyce, and Liu 2015; Figure 3); Jiufotang Formation, Aptian, Early Cretaceous (Li, Joyce, and Liu 2015).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Perochelys lamadongensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters provided for that clade above. Among Early Cretaceous pan-trionychids, *Perochelys lamadongensis* can be differentiated from "*Trionyx*" *jixiensis* and *Petrochelys kyrgyzensis* by having a poorly developed nuchal that is only lightly attached to the remaining carapacial disk, a continuous neural series that fully separates the costals from one another, and greatly reduced costals VIII.

Comments. *Perochelys lamadongensis* is based on a single, nearly complete skeleton from the Early Cretaceous (Aptian) Jehol Fauna of China (Li, Joyce, and Liu 2015). Given the complete nature of the type specimen, the validity of this species is not controversial, because it can be readily distinguished from all other named pan-trionychids. Even though *P. lamadongensis* is one of the oldest known pan-trionychids, its skeletal morphology corresponds to that of crown trionychids in all major aspects, thereby documenting the evolutionary stasis of the group. The phylogenetic placement of *Perochelys lamadongensis* within *Pan-Trionychidae* therefore remains opaque, apparently because of the high levels of homoplasy within pan-trionychids (Meylan 1987; Li, Joyce, and Liu 2015; Vitek and Joyce 2015).

## *Petrochelys kyrgyzensis* (Nessov, 1995b)

Taxonomic history. *Trionyx kyrgyzensis* Nessov, 1995b (new species); *Kuhnemys kyrgyzensis* Chkhikvadze 1999b (new combination); *Petrochelys kyrgyzensis* Vitek et al. 2017 (new combination).

Type material. CCMGE 186/12458 (holotype), an incomplete isolated xiphiplastron (Nessov 1995b, figs. 3gg; Danilov and Vitek 2013, fig. 23.3b.1).

Type locality. Left bank of Sarykungoi Spring, Kylodzhun (= Klaudzin), Osh Province, Kyrgyzstan (Nessov 1995b; Vitek and Danilov 2010; Figure 3); Alamyshik Formation, Albian, Early Cretaceous (Danilov and Vitek 2013).

Referred material and range. Early Cretaceous (Albian) of type locality, Osh Province, Kyrgyzstan (referred material of Nessov 1995).

Diagnosis. *Petrochelys kyrgyzensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters listed for that clade above. Among Early Cretaceous pan-trionychids, *Petrochelys kyrgyzensis* can be differentiated from *Perochelys lamadongensis* by exhibiting a fully formed nuchal and enlarged costals VII and VIII that have a midline contact. Among Cretaceous pan-trionychids known from cranial material, *Petrochelys kyrgyzensis* can be differentiated by the presence of a single hypoglossal foramen, a confluent foramen jugulare posterius and fenestra postotica, and the presence of a triturating surface separate from the rest of the palate. Only geographic considerations allow us to distinguish "*Trionyx*" *jixiensis* from *Petrochelys kyrgyzensis* (see below).

Comments. *Petrochelys kyrgyzensis* is based on a xiphiplastron from the Albian of Kyrgyzstan and represents one of the earliest known pan-trionychids. Additional material from the type locality, including shell and appendicular elements, vertebrae, a braincase, and a lower jaw have also been referred to this taxon (Nessov 1995b). Like many other Cretaceous Asian pan-trionychids, the affinities of this taxon remain unclear (e.g., Chkhikvadze 1999b), mostly because high levels of homoplasy make it difficult to discern phylogenetic relationships in pan-trionychids, although a recent phylogenetic analysis retrieved it well within pan-trionychines (Vitek et al. 2017). The cranium of the holotype was recently described in detail (Vitek et al. 2017) but a thorough review of the postcranium is still outstanding. We nevertheless tentatively accept the validity of this taxon.

## *Pan-Cyclanorbinae* New Clade Name

Phylogenetic definition. The name *Pan-Cyclanorbinae* is herein referred to the total clade of *Cyclanorbinae*, which in return is defined as the crown clade of all extant turtles that are more closely related with *Cyclanorbis senegalensis* (Duméril and Bibron, 1835) than *Trionyx triunguis* (Forskål, 1775).

Diagnosis. *Pan-Cyclanorbinae* can be diagnosed as a member of *Pan-Trionychidae* based on the full list of characters provided above for that clade. *Pan-Cyclanorbinae* can be differentiated from other pan-trionychids by the unique combination of the following shell characters: presence of concave posterolateral margin of the carapace, split costiform processes, costal ossifications that fully cover the ribs, large costals VIII, preneural, and seven large neurals, fusion of the hyo-hypoplastra soon after hatching, hypoplastra lateral to the xiphiplastra at the hypo-xiphiplastral suture, and the presence of extensive epiplastral, entoplastral, and xiphiplastral callosities.

Comments. The fossil record of pan-cyclanorbines is rather poor and was restricted until recently to the Neogene of Africa and India (Lydekker 1885; Meylan et al. 1990) in an area that roughly approximates their current distribution in Africa and the Indian subcontinent (Ernst and Barbour 1989). The recent reinterpretation of North American plastomenids as potential stem cyclanorbines (Joyce and Lyson 2010a) combined with the identification of an unambiguous Late Cretaceous pan-cyclanorbine from Mongolia (Danilov et al. 2014) radically changed our understanding of the evolution of these turtles, implying a rather large ghost lineage and a formerly more extensive distribution. Given that pan-cyclanorbines are mostly known from shell material, we here only diagnose this taxon using shell characters. A more extensive list of characters is available in Meylan (1987).

## *Cyclanorbis* Gray, 1854

Type species. *Cyclanorbis petersii* Gray, 1854 (= *Cryptopus senegalensis* Duméril and Bibron, 1835).

Diagnosis. *Cyclanorbis* can be diagnosed as a member of *Pan-Trionychidae* and *Pan-Cyclanorbinae* based on the full list of characters provided for those clades above. *Cyclanorbis* can be differentiated from other cyclanorbines by lacking split costiform processes and a variable tendency of the costals to divide the neural series by meeting along the midline.

Comments. Dacqué (1912) reported a large shell fragment from the Miocene of Egypt that he attributed to *Cyclanorbis*, but this fragment has since been shown to be a carettochelyid (Lapparent de Broin 2000; Joyce 2014). Meylan et al. (1990), Lapparent de Broin and Gmira (1994), and Karl (2012) reported rich remains from the Mio-Pleistocene of Kenya, Uganda, and Malawi, respectively, that they variously attributed to *Cyclanorbis* or the extant species *Cyclanorbis elegans* and *Cyclanorbis senegalensis*, but given that most remains are not figured and that detailed stratigraphic data are not reported for most localities, we are only able to partially confirm these identifications (Appendix 3). Lapparent de Broin (2000) listed several *Cyclanorbis* occurrences throughout Africa, but none of the relevant material seems to be figured, and we therefore dismiss these occurrences herein. We here once again restrict our diagnosis to characters that pertain to the shell, as only this region is relevant for the available fossil material.

## *Cyclanorbis turkanensis* Meylan et al., 1990

Taxonomic history. *Cyclanorbis turkanensis* Meylan et al., 1990 (new species).

Type material. NMK KP17196 (holotype), a carapace, missing costals VIII and the lateral portions of all left costals (Meylan et al. 1990, fig. 2).

Type locality. Kanapoi, Rift Valley Province, Kenya (Figure 6); Bed E, Zanclean, early Pliocene (Meylan et al. 1990).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Cyclanorbis turkanensis* can be diagnosed as a member of *Pan-Trionychidae*, *Pan-Cyclanorbinae*, and *Cyclanorbis* by the full list of carapacial characters provided for those clades above. *Cyclanorbis turkanensis* can be differentiated from other *Cyclanorbis* species by large size (CL of about 62 cm) and hypertrophied and distinctly V-shaped dorsal centra.

Comments. *Cyclanorbis turkanensis* is based on a partial shell from the early Pliocene of Kenya that can be easily diagnosed as a representative of *Cyclanorbis* by lacking subdivided costiform processes. This species convincingly documents the former distribution of the *Cyclanorbis* lineage outside its current range along the Ivory Coast of the African continent. The validity of this species is not controversial.

## *Cycloderma* Peters, 1854

Type species. *Cycloderma frenatum* Peters, 1854

Diagnosis. *Cycloderma* can be diagnosed as a member of *Pan-Trionychidae* and *Pan-Cyclanorbinae* based on the full list of characters provided above for those clades. *Cycloderma* can be differentiated from other pan-cyclanorbines by the presence of I-shaped epiplastra, combined with the symplesiomorphic retention of split costiform processes and a continuous neural series.

Comments. Similarly to *Cyclanorbis*, several fossil specimens from the Pliocene until the Holocene of Africa have been attributed to *Cycloderma* (Lapparent de Broin 2000). Only a thorough redescription of these remains, along with a reevaluation of the taxonomic characters of cyclanorbines, will clarify whether these taxonomic assignments are valid. Among the most important finds that were figured and described, and can be therefore confidently assigned to *Cycloderma*, are the extinct taxa *Cycloderma victoriae* and *Cycloderma debroinae* from the Miocene and Pliocene, respectively, of Kenya (Meylan et al. 1990), a carapace from the Pleistocene of Uganda (Arambourg 1947), and material from the Plio-Pleistocene of Kenya and Malawi (Wood 1979; Meylan et al. 1990; Karl 2012).

## *Cycloderma debroinae* Meylan et al., 1990

Taxonomic history. *Cycloderma debroinae* Meylan et al., 1990 (new species); *Cycloderma debrionae* Wood 2013 (incorrect spelling of species epithet).

Type material. NMK LT17200 (holotype), nearly complete skeleton including most of the carapace and plastron, complete girdles, significant portions of all four limbs, portions of the cervical and caudal vertebral columns, and fragments of the skull and hyoid (Meylan et al. 1990, figs. 9–10).

Type locality. Lothagam Hill, Turkana District, Rift Valley Province, Kenya (Figure 6); Pliocene (Meylan et al. 1990).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Cycloderma debroinae* can be diagnosed as a member of *Pan-Trionychidae*, *Pan-Cyclanorbinae*, and *Cycloderma* by the full list of shell characters provided for those clades above. *Cycloderma debroinae* can be differentiated from *Cycloderma aubryi*, by lacking well-developed entoplastral callosities, and from *Cycloderma frenatum* by having a deep nuchal notch and expanded distal margin of costals II. *Cycloderma debroinae* can currently only be distinguished from *Cycloderma victoriae* using temporal considerations.

Comments. *Cycloderma debroinae* is based on a well-preserved, nearly complete skeleton from the early Pliocene of Kenya (Meylan et al. 1990), whereas *Cycloderma victoriae* is based on a relatively complete carapace from the early Miocene of the same country (Andrews 1914). Phylogenetic analysis places *Cycloderma debroinae* and *Cycloderma victoriae* as sisters to the extant *Cycloderma aubryi*, which occurs in the same region today, though with a notably different morphology (Meylan et al. 1990). We can only distinguish *Cycloderma victoriae* from *Cycloderma debroinae* using stratigraphic arguments, as the carapaces of both taxa only show a minimal amount of variation. Given that *Cycloderma debroinae* differs substantially from the extant *Cycloderma aubryi* in the development of its plastron, however, we speculate that future finds may also reveal a unique morphology for the Miocene taxon as well, and we therefore retain both taxa for the moment.

## *Cycloderma victoriae* Andrews, 1914

Taxonomic history. *Cycloderma victoriae* Andrews, 1914 (new species).

Type material. BMNH R4105 (holotype), almost complete carapace (Andrews 1914, pl. 27.1–3; Meylan et al. 1990, fig. 8).

Type locality. Bed 21 at Kachuku, adjacent to the eastern shore of Lake Victoria, Nyanza Province, Kenya (Andrews 1914; Meylan et al. 1990; Figure 6); Burdigalian, early Miocene (Drake et al. 1988; Joyce et al. 2013).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Cycloderma victoriae* can be diagnosed as a representative of *Pan-Trionychidae*, *Pan-Cyclanorbinae*, and *Cycloderma* by the full list of carapacial characters provided for those clades above. *Cycloderma victoriae* can be differentiated from *Cycloderma frenatum* by having a deep nuchal notch and expanded distal margin of costals II. *Cycloderma victoriae* can currently only be distinguished from *Cycloderma debroinae* using temporal considerations.

Comments. For a brief discussion on fossil *Cycloderma* species, see *Cycloderma debroinae* above.

## *Nemegtemys conflata* Danilov et al., 2014

Taxonomic history. *Nemegtemys conflata* Danilov et al., 2014 (new species).

Type material. ZIN PH 1/157 (holotype), lateral fragment of left hyo-hypoplastra (Danilov et al. 2014, figs. 3, 17f).

Type locality. Nemegt, Ömnögovi (= Umunugovi) Aimag, Mongolia (Figure 3); Nemegt Formation, Maastrichtian, Late Cretaceous (Danilov et al. 2014).

Referred material and range. Late Cretaceous (Maastrichtian), Nemegt Formation, Bugin Tsav, Ömnögovi (= Umunugovi) Aimag, Mongolia (referred material of Danilov et al. 2014).

Diagnosis. *Nemegtemys conflata* can be diagnosed as a member of *Pan-Trionychidae* and *Pan-Cyclanorbinae* by all characters listed above for those clades that pertain to the hyo-hypoplastron. *Nemegtemys conflata* can be differentiated from other pan-cyclanorbines by its small size and the presence of a small hyoplastral lappet.

Comments. *Nemegtemys conflata* is based on a partial hyo-hypoplastron that represents the oldest unambiguous pan-cyclanorbine in the Old World. The remaining fossil record of the group in the Old World is restricted to the Neogene of Africa and the Indian subcontinent, implying a significant ghost lineage and dispersal outside the original ancestral area in central Asia (Danilov et al. 2014). The validity of this taxon is not controversial.

## *Pan-Trionychinae* New Clade Name

Phylogenetic definition. The name *Pan-Trionychinae* is herein referred to the total clade of Trionychinae, which in return is defined as the crown clade arising from the common ancestor of all extant turtles more closely related to *Trionyx triunguis* (Forskål, 1775) than *Cyclanorbis senegalensis* (Duméril and Bibron, 1835).

Diagnosis. *Pan-Trionychinae* can be diagnosed as a member of *Pan-Trionychidae* based on the full list of characters provided above for that clade. Among extant trionychids, representatives of *Pan-Trionychinae* can be easily differentiated from representatives of *Pan-Cyclanorbinae* by an extensive list of characters, but it remains unclear which of these characters are derived, as opposed to plesiomorphies.

Comments. Extant trionychids form two monophyletic clades, Cyclanorbinae and Trionychinae, that are easily distinguished from one another by an extensive list of characters (Meylan 1987). If the characters that diagnose the extant groups are applied to the fossil record literally, one must conclude that nearly all known Cretaceous and Paleogene must be representatives of the trionychine lineage (with the notable exception of *Nemegtemys conflata* and *Murgonemys braithwaitei*) and that no trionychid stem lineage is apparent. Although this may be the true signal, it seems plausible that the trionychine morphotype may be ancestral to the crown (Joyce and Lyson 2010a). We herein therefore only refer those fossils to *Pan-Trionychinae* that are attributable to extant trionychine genera. This section therefore is mostly restricted to the Neogene.

## *Pelodiscus* Fitzinger, 1836

Type species. *Trionyx sinensis* Wiegmann, 1835.

Diagnosis. *Pelodiscus* can be diagnosed as a member of *Pan-Trionychidae* by the presence of all characters listed for that clade above. *Pelodiscus* can be differentiated from all other pan-trionychids by small size, absence of a preneural, suprascapular fontanelles that only close in mature adults, extremely elongate anterior epiplastral processes, seven callosities, and xiphiplastra that are broader than long.

## *Pelodiscus gracilia* (Yeh, 1963), comb. nov.

Taxonomic history. *Amyda gracilia* Yeh, 1963 (new species); *Trionyx sinensis* = *T. gracilis* Młynarski 1976 (new combination, junior synonym, incorrect spelling of species epithet).

Type material. IVPP V1038 (holotype), a carapace, with left costals I–IV, right costals I and VII, and the last two neurals damaged, seven cervical vertebrae, complete left pectoral girdle, right coracoid, complete left and right pelvic girdles, left xiphiplastron and additional fragments of the plastron (Yeh 1963, figs. 33, 34, pl. 21.1–7; Ye 1994, fig. 76).

Type locality. Yushe County, Shanxi (= Shansi) Province, China (Figure 3); Pliocene (Yeh 1963).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Pelodiscus gracilia* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters provided for that clade above and *Pelodiscus* by small size, absence of a preneural, suprascapular fontanelles that only close in mature adults, and xiphiplastra that are broader than long. *Pelodiscus gracilia* can be differentiated from *Pelodiscus sinensis* by larger costals VIII.

Comments. *Pelodiscus gracilia* is based on a partial skeleton from the Pliocene of Yushe County, China (Yeh 1963), within the current range of the extant *Pelodiscus sinensis* (TTWG 2014). Yeh (1963) already noted strong resemblance with *Pelodiscus sinensis* but nevertheless referred this species to *Amyda*. Młynarski (1976), on the other side, confirmed close resemblance with *Pelodiscus sinensis* but suggested synonymy with it instead. We herein agree that both *Pelodiscus gracilia* and *Pelodiscus sinensis* are extremely similar by being small sized, having a broad nuchal, possessing open suprascapular fontanelles, and having broad xiphiplastra, but we note that the type of *Pelodiscus gracilia* possesses much larger costals VIII than the extant *Pelodiscus sinensis*. We therefore confirm the validity of this species. A second species with clear affinities with the *Pelodiscus* lineage, *Trionyx sinuosus* Chow and Yeh, 1958, was named from this region that could have priority over *Pelodiscus gracilia*, but we here disregard this taxon, as it is based on fragmentary material (see below).

## *Rafetus* Gray, 1864

Type species. *Testudo euphratica* Daudin, 1801.

Diagnosis. *Rafetus* can be diagnosed as a representative of *Pan-Trionychidae* by the full list of characters provided for that clade above. Using shell characters, *Rafetus* is most readily differentiated from other pan-trionychids by the combined absence of a preneural, presence of seven neurals of which neural V or VI is square, highly reduced costals VIII, a reduced count of medial hyo- and hypoplastral processes, and poorly developed callosities that are restricted to the hyo-hypoplastron.

## *Rafetus bohemicus* (Liebus, 1930), comb. nov.

Taxonomic history. *Trionyx bohemicus* Liebus, 1930 (new species); *T. triunguis* = [*Aspidonectes gergensi*] = *T. aspidiformis* = *T. bohemicus* = *T. brunhuberi* = *T. croaticus* = *T. elongatus* = *T. hilberi* = *T. hoernesi* = [*T. oweni*] = [*T. partschii*] = *T. peneckei* = *T. petersi* = *T. petersi trifailensis* = [*T. pliocenicus*] = *T. pontanus* = *T. preschenensis* = *T. pseudovindobonensis* = *T. senckenbergianus* = *T. septemcostatus* = *T. siegeri* = *T. sophiae* = *T. stadleri* = *T. stiriacus* = *T. teyleri* = *T. vindobonensis* Karl 1998 (junior synonym); *Rafetus pontanus* = *T. aspidiformis* = *T. bohemicus* = *T. elongatus* = *T. preschenensis* Chkhikvadze 1999b (junior synonym).

Type material. The syntype series consists of the following specimens: MMUL 633/2a/G 12908 and MMUL 633/2b/G 12941, a complete carapace with its imprint (Liebus 1930, pl. 1.1); NMP 1485, a carapace (Liebus 1930, pl. 2.1); MMUL 1444/G 12927, an entoplastron (Liebus 1930, pl. 2.2); MMUL 1447/G 12931, an epiplastron (Liebus 1930, pl. 2.3); NMP P9640, an epiplastron (Liebus 1930, pl. 2.4); MMUL 1486/G 12939, a hyoplastron (Liebus 1930, pl. 2.5); MMUL 1035/G 12915, a right hypoplastron (Liebus 1930, pl. 2.6); MMUL 1038/G 12918, a xiphiplastron (Liebus 1930, pl. 3.1); MMUL 1036/G 12916 and MMUL 1041/G 12921, a partial pelvic girdle and its imprint (Liebus 1930, pl. 3.2); MMUL 1442/G 10193, a complete skull (Liebus 1930, pl. 3.3); MMUL 631/G 12912, a partial pectoral girdle (Liebus 1930, pl. 3.4); MMUL 1451/G 12933, a cervical vertebra (Liebus 1930, pl. 3.5); MMUL 1461/G 12937, a partial epiplastron; MMUL 1037/G 12917, a xiphiplastron; MMUL 1443/G 12926, a skull; MMUL 1048/G 10194, a skull; MMUL 1037/G 12917 and MMUL 1042, a skull and xiphiplastron and their imprints; MMUL 1043/G 12923, a skull; MMUL 1045/G 12925, a mandible; MMUL 1450/G 12932, a radius and an ulna; MMUL 1453/G 12935, a fibula; MMUL 1446/G 12929 and MMUL 1445/G 12930, a tibia with and epiplastron fragment and its imprint; MMUL 1462/G 12938, a left femur.

Type locality. Břestány (= Preschen), near Bilina, Ústí nad Labem, Czechia (Liebus 1930; Figure 4); Most Formation, MN 3, Burdigalian, early Miocene (Aguilar et al. 1997).

Referred material and range. No specimens are referred herein.

Diagnosis. *Rafetus bohemicus* can be diagnosed as a member of *Pan-Trionychidae* and *Rafetus* by the full list of shell characters listed for those clades. *Rafetus bohemicus* is differentiated from *Rafetus swinhoei* by being significantly smaller and from *Rafetus euphraticus* by having a more pronounced constriction to the xiphiplastra.

Comments. Liebus (1930) established *Rafetus bohemicus* on the basis of abundant skeletal material from the early Miocene of Břestány, Czechia. Like most fossil trionychids, the phylogenetic affinities and taxonomic validity of this taxon were mostly ignored over the course of the subsequent decades, but Karl (1998) more recently proposed that this species is synonymous with *Trionyx triunguis*, whereas Chkhikvadze (1999b) suggested junior synonymy with the coeval *T. pontanus*, which he referred to *Rafetus*.

We here conclude that the described pan-trionychid remains from the Miocene of Europe can be grouped into two morphotypes that broadly agree with the extant *Trionyx triunguis* and *Rafetus euphraticus*, but also that representatives of these two lineages can only be differentiated rigorously using plastral remains. Whereas many Miocene pan-trionychids can be attributed to the *T. triunguis* lineage, only a single find, the type material of *bohemicus*, can be attributed to the *Rafetus euphraticus* lineage with confidence based on the absence of plastral callosities on the xiphiplastra. We therefore agree with Chkhikvadze (1999b) that the *Rafetus* lineage was present during the Miocene in Europe but consider *bohemicus* to be valid, not *pontanus*, as the latter taxon is not represented by plastral material. The *T. triunguis* and *Rafetus euphraticus* lineages can furthermore be distinguished by the relative size of the costals VIII, but this character shows much variation and should therefore be used with caution, the primary reason why we herein disregard all Miocene taxa that are based on carapacial material alone. Along those lines, we note that the types of *T. moldaviensis*, *T. pontanus*, and *T. rostratus* show the reduced costals VIII more typical of the *Rafetus euphraticus*, thereby hinting at the possibility that this lineage may have been more widespread in the Miocene than is alluded to by the isolated type of *Rafetus bohemicus*. The relative scarcity of plastral material that would more rigorously document the presence of this lineage, however, may be caused by various taxonomic filters that disfavor bones with poorly developed callosities. Several skulls have been collected from the type locality of *Rafetus bohemicus* (Liebus 1930) that might be able to test our assertion that this taxon is referable to the *Rafetus* lineage, but they are poorly preserved and seem to be uninformative. We here note that three other pan-trionychid species have been established from the type locality of *Rafetus bohemicus*: *Trionyx aspidiformis* and *T. preschenensis* by Laube (1900) and *T. elongatus* by Liebus (1930). Although the former two taxa were described well before *Rafetus bohemicus*, we consider all of these names to be nomina dubia, as they are based on nondiagnostic material. For a more extensive discussion, see *T. vindobonensis* (below).

*Rafetus bohemicus* has otherwise been reported from the middle Miocene (Serravallian) of Viehhausen (*Trionyx bohemicus jaegeri* of Fuchs 1939) and Sandelzhausen (*T.* aff. *bohemicus* of Schleich 1981), Bavaria, Germany, but this material lacks plastral material and is therefore herein identified as an indeterminate pan-trionychine.

## *Trionyx* Geoffroy Saint-Hilaire, 1809

Type species. *Testudo triunguis* Forskål, 1775.

Diagnosis. *Trionyx* can be diagnosed as a representative of *Pan-Trionychidae* by the full list of characters provided for that clade above. Using shell characters, *Trionyx* is most readily differentiated from other pan-trionychids by the combined absence of a preneural, presence of seven neurals of which neural V or VI is square, a broadly developed medial fan of hypoplastral processes, and four pairs of well-developed plastral callosities.

Comments. We herein refer many fossil pan-trionychids to "*Trionyx*" as this genus has historically served as a wastebasket for fossil taxa with uncertain affiliation. However, we herein also refer two species to *Trionyx* as we believe that these are fossil relatives of the extant *Trionyx triunguis*. We highlight the two different meanings through the usage of quotation marks.

## *Trionyx pliocenicus* Fucini, 1912

Taxonomic history. *Trionyx pliocenica* Lawley 1876 (nomen nudum); *T. pliocenicus* Fucini, 1912 (new species); *T. hilberi* = *T. pliocenicus* Teppner 1914b (junior synonym); *T. pliopedemontanus* = *T. blayaci* = *T. pliocenicus* = *T. pompignanensis* = *T. rotundiformis* Broin 1977 (junior synonym); *T. triunguis* = [*T. pliocenicus*] = 24 others Karl 1998 (junior synonym, nomen dubium, see *Rafetus bohemicus* for complete synonym); *T. pliocaenicus* Karl 1998 (incorrect spelling of species epithet).

Type material. A relatively complete skeleton, including most of skull, carapace, plastron, vertebrae, and appendicular elements (holotype) (Fucini 1912, pls. 1–5), unknown whereabouts (G. Bianucci and C. Sorbini, pers. comm., 2016).

Type locality. Mapesi (= Malpessi) near Poggio Alle Monache, Tuscany, Italy (Lawley 1876; Fucini 1912; Figure 4); Pliocene (Kotsakis 1985).

Referred material and range. No specimens are referred herein.

Diagnosis. *Trionyx pliocenicus* can be diagnosed as a representative of *Pan-Trionychidae* and *Trionyx* by the full list of characters provided for those clades above. *Trionyx pliocenicus* can be differentiated from *T. triunguis* and *T. vindobonensis* by having more extensive plastral callosities, a hypo-xiphiplastral suture outlined by callosities, and a midline contact of the xiphiplastral callosities.

Comments. Lawley (1876) provided the name *Trionyx pliocenicus* for beautifully preserved material from the Pliocene of Italy, but this contribution was not accompanied by a description or a definition, and Lawley's name must therefore be considered a nomen nudum (Kotsakis 1985). The specimen was much later described by Fucini (1912) and the name thereby made available. Teppner (1914b) soon after hypothesized that *T. pliocenicus* is conspecific with *T. hilberi*, but Broin (1977) and Kotsakis (1980, 1985) more recently argued for synonymy with the spatially and temporally close *T. pliopedemontana*. We herein regard both *T. hilberi* and *T. pliopedemontana* to be nomina dubia, as they are solely known by carapacial material.

The holotype of *Trionyx pliocenicus* is the only known partial trionychid skeleton from the northern shores of the Mediterranean Sea and therefore of particular relevance to the taxonomy and evolutionary history of Neogene trionychids. The postcranium, in particular the shell, is fully consistent with the morphology of the extant *T. triunguis* and notably distinct from the geographically close *Rafetus euphraticus*, in particular in regard to the size of the nuchal, number and arrangement of neurals, the number of lateral processes, and the number and dimensions of the plastral callosities (Meylan 1987). This specimen therefore firmly establishes the presence of the *T. triunguis* lineage in the Neogene of southern Europe. Given that all other known material from the same region is highly fragmentary, it is unclear to us if *T. pliocenicus* shared its habitat with other trionychids. The lack of quality material therefore precludes us from assuming that it is the only trionychid in the region (contra Karl 1999a). The type and only known specimen was originally deposited in the private collection of R. Lawley (Fucini 1912), a collection that was partly destroyed during WWII and now is scattered accross Italy (G. Bianucci and C. Sorbini, pers. comm., 2016). We were not able to locate the holotype of *T. pliocenicus* and therefore consider this specimen to be lost.

## *Trionyx vindobonensis* Peters, 1855 (= *T. brunhuberi* Ammon, 1911 = *T. gergensi* Reinach, 1900 = *T. hoernesi* Heritsch, 1909 = *T. peneckei* Heritsch, 1909 = *T. petersi* Hoernes, 1881 = *T. rostratus* Arthaber, 1898 = *T. septemcostatus* Hoernes, 1881 = *T. teiritzbergensis* Gemel, 2002 = *T. teyleri* Winkler, 1869a)

Taxonomic history. *Trionyx vindobonensis* Peters, 1855 (new species); *T. vindibonensis* Lawley 1876 (incorrect spelling of species epithet); *Tryonix vindobonensis* Portis 1879 (incorrect spelling of genus name); *T. vindobonensis* = *T. partschi* (*sic*) Glaessner 1933 (senior synonym); *T. triunguis* = *T. vindobonensis* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. NHMW 1853/0016/0003 (holotype), partial skeleton, including fragments of the carapace, plastron, and limbs (Peters 1855, pls. 1.1, 2.1, 3.1–3; Peters 1859, pl. 1).

Type locality. Hernals, Vienna, Austria (Peters 1855; Figure 4); MN 7+8, Serravallian, middle Miocene (Aguilar et al. 1997).

Referred material and range. Early Miocene (Aquitanian), Rhineland-Palatinate, Germany (type material of *Trionyx gergensi*; Reinach 1900); early Miocene (Burdigalian), Lower Austria, Austria (type material of *T. teiritzbergensis*; Gemel 2002); early Miocene (Burdigalian), Centre-Val de Loire, France (material previously referred to *T. stiriacus* by Broin 1977); middle Miocene (Langhian), Styria, Austria (type material of *T. septemcostatus*, *T. hoernesi, T. petersi, and T. peneckei*; Hoernes 1881; Heritsch 1909); middle Miocene (Langhian), Bavaria, Germany (type material of *T. brunhuberi*; Ammon 1911; referred material of Fuchs 1939); middle Miocene (Serravallian), Vienna, Austria (referred material of Peters 1859); middle Miocene (Serravallian), Baden-Württemberg, Germany (type material of *T. teyleri*; Winkler 1869a); late Miocene (Tortonian), Burgenland, Austria (type material of *T. rostratus*; Arthaber 1898); late Miocene (Tortonian), Lower Austria, Austria (referred material of Papp et al. 1953).

Diagnosis. *Trionyx vindobonensis* can be diagnosed as a representative of *Pan-Trionychidae* and *Trionyx* by the full list of characters provided for those clades above. *Trionyx vindobonensis* can be differentiated from *T. triunguis* and *T. pliocenicus* by having plastral callosities that are more extensive than *T. triunguis*, but less extensive than *T. pliocenicus*.

Comments. For reasons beyond our comprehension, a total of 29 trionychid names were provided for specimens recovered from Miocene sediments exposed in Europe north of the Alpide belt, in particular *Trionyx hilberi* Hoernes, 1892, *T. hoernesi* Heritsch, 1909, *T. partschii* Peters, 1855, *T. peneckei* Heritsch, 1909, *T. petersi* Hoernes, 1881, *T. rostratus* Arthaber, 1898, *T. septemcostatus* Hoernes, 1881, *T. siegeri* Heritsch, 1909, *T. sophiae* Heritsch, 1909, *T. stiriacus* Peters, 1855, *T. teiritzbergensis* Gemel, 2002, and *T. vindobonensis* Peters, 1855 from Austria; *T. aspidiformis* Laube, 1900, *T. bohemicus* Liebus, 1930, *T. elongatus* Liebus, 1930, *T. pontanus* Laube, 1895, and *T. preschenensis* Laube, 1900 from Czechia; *T. aquitanicus* Delfortrie, 1869 and *T. lockardi* Gray 1831 from France; *T. bohemicus jaegeri* Fuchs, 1939, *T. brunhuberi* Ammon, 1911, *T. gergensi* Reinach, 1900, *T. münzenbergensis* Hummel 1927, *T. oweni* Reinach, 1900, and *T. teyleri* Winkler, 1869a from Germany; *T. pseudovindobonensis* Szalai, 1934 from Hungary; *T. moldaviensis* Khosatzky, 1986 from Moldova; *T. nopcsai* Szalai, 1934 from Romania; and *T. reticulatus* Rieppel, 1979 from Switzerland. Five additional taxa are based on poorly dated late Oligocene to early Miocene sediments exposed in France, in particular *T. acutiformis* Bergounioux, 1935, *T. chaubeti* Bergounioux, 1935, *T. ciryi* Bergounioux, 1935, *T. manouri* Gray, 1831, and *T. mourieri* Bergounioux, 1935, and will be discussed here for simplicity as well.

We conclude after reviewing all available shell material from Miocene localities north of the Alps that only two morphotypes are apparent that can be attributed to the stem lineages of *Rafetus euphraticus* and *Trionyx triunguis*. Extant representatives of these two species can readily be distinguished by their plastral morphology, as *T. triunguis* possesses four well-developed callosities that cover the hyo-hypoplastra and xiphiplastra, whereas *R. euphraticus* only possesses two poorly developed callosities that cover just the hyo-hypoplastra (Meylan 1987). The carapaces of both taxa resemble one another greatly by being well ossified, by having a surface texture that varies from netted to pitted, by lacking a preneural, and by typically possessing seven neurals, of which the fifth is squared and that allow for medial contact of costals VII and VIII. The primary carapacial difference between the two is that *Rafetus euphraticus* possesses smaller costals VIII than *T. triunguis*, but extensive variation makes it impractical to use this character to rigorously distinguish the two lineages.

Of the 34 taxa listed above, we immediately are able to disregard 8 from consideration, because they represent either nomina nuda or unambiguous nomina dubia. These include *Trionyx aquitanicus* (a nomen dubium based on two costal fragments that may well be referable to a marine turtle), *T. lockardi* (a nomen nudum), *T. manouri* (a nomen dubium based on fragmentary, now lost material), *T. münzenbergensis* (a nomen nudum), *T. nopcsai* (a nomen dubium based on a partial dentary and carapace fragment), *T. oweni* (a nomen dubium based on unfigured costal fragments), *T. pseudovindobonensis* (a nomen dubium based on a femur), and *T. partschii* (a nomen dubium based on two costal fragments). We similarly disregard 4 additional taxa a priori, as they are based on juvenile specimens (e.g., *T. aspidiformis*, *T. elongatus*, *T. preschenensis*, and *T. sophiae*). As we find no evidence of cyclanorbines in the Neogene north of the Alps, despite previous claims to the contrary (Portis 1901), we refer all indeterminate material from this region to *Pan-Trionychinae* indet.

We can confirm based on the available material that the two morphotypes we recognize cannot be distinguished rigorously using carapacial material alone, much as their recent relatives *Rafetus euphraticus* and *Trionyx triunguis*. We therefore disregard 11 further taxa from nomenclatural considerations that are based on carapacial material alone. These include *T. acutiformis*, *T. chaubeti*, *T. ciryi*, *T. moldaviensis*, *T. mourieri*, *T. siegeri*, and *T. stiriacus*, which are based on partial carapaces, and *T. bohemicus jaegeri*, *T. hilberi*, *T. pontanus*, and *T. reticulatus*, which are based on complete carapaces.

Of the 11 remaining taxa, 10 can be attributed to the *Trionyx triunguis* lineage based on the presence of four well-developed plastral callosities that broadly cover the hyo-hypoplastra and xiphiplastra. These are *T. brunhuberi*, *T. gergensi*, *T. hoernesi*, *T. peneckei*, *T. petersi*, *T. rostratus*, *T. septemcostatus*, *T. teiritzbergensis*, *T. teyleri*, and *T. vindobonensis*. Of these, *T. vindobonensis* was named first and therefore serves as the senior synonym. The sole remaining taxon, *T. bohemicus*, possesses a highly reduced plastron that lacks xiphiplastral callosities, and we therefore partially agree with Chkhikvadze (1999b) that this taxon is referable to the *Rafetus* lineage, but as a valid species and not a junior synonym of *T. pontanus* (a nomen dubium, as it is based solely on carapace material) (see *Rafetus bohemicus* above).

Apart from the aforementioned type specimens, we here refer material from the Miocene of Carinthia, Austria, which had previously been attributed to *Trionyx petersi siegeri* (Mottl 1967) to *T. vindobonensis* based on the presence of four well-developed plastral callosities. To the contrary, Miocene specimens that are known solely by carapacial material and have in the past been variously assigned to *T. petersi* and *T. stiriacus* are herein considered to be indeterminate pan-trionychines as they lack plastral remains. These include carapacial material from the middle Miocene of Carinthia (*T. petersi* of Wank 1977 and *T. petersi siegeri* of Mottl 1967), Styria (*T. hilberi* of Teppner 1914a; *T. petersi* of Heritsch 1910), and Slovakia (*T. rostratus* of Holec and Schlögl 2000).

The holotype of *Trionyx vindobonensis* does not include cranial material, but many specimens that are referred based on their plastral anatomy do. The most notable remains are a complete skull and mandible from the late Miocene of Austria (part of the type of *T. rostratus*, Arthaber 1898) and the anterior half of a skull from the middle Miocene of Austria (the lectotype of *T. petersi*, Hoernes 1881), which already show much variation, as the complete skull has a narrow palate, whereas the partial skull shows a broad palate with incipient secondary palate. Although the early Miocene locality of Artenay, France, only yielded disassociated material (*T. stiriacus* of Broin 1977), we find it prudent to refer all to *T. vindobonensis*, as the plastral material is diagnostic of this taxon. The beautifully preserved skulls known from Artenay (Broin 1977) once again display an extremely broad palate, much like the partial skull from Austria. On the other hand, we do not attribute the nicely preserved skull from the early Pliocene of Leobersdorf, Austria (*Trionyx* sp. aff. *rostratus* of Glaessner 1933), to *T. vindobonensis*, as it is not associated with diagnostic plastral material and because its morphology is insufficiently described to allow referral by comparison with the other skulls. Although the narrow and extremely broad skull morphotypes apparent in the available material could be used to justify the presence of two closely related taxa in the Miocene of Europe, we note that the narrow skull originates from a subadult individual, at least as inferred from its postcranium, whereas the broad skulls originate from larger individuals. We here therefore attribute the apparent differences to ontogenetic variation, as has otherwise been extensively documented for some extant and extinct trionychids (Dalrymple 1977; Joyce et al. 2016). A meaningful comparison with skulls likely referable to the coeval *Rafetus bohemicus* is not possible, as these are poorly preserved (see *Rafetus bohemicus* above).

The idea that most of the fossil pan-trionychids from Europe form a single lineage attributable to the extant *Trionyx triunguis* is not novel. Reinach (1900) was the first to propose that most Tertiary pan-trionychids from Europe form a single lineage with many concurrent species that he named the "*Trionyx protriunguis* succession" (die Reihe des *Trionyx protriunguis* in German). Teppner (1914c) went further by providing a dendrogram depicting ancestor-descendant relationships among all named taxa and by suggesting that all are representatives of a single species. However, as Hummel (1927, 1929) already noted, Teppner (1914c) apparently did not heed his own conclusions, as he did not formally propose any synonymies and even named yet another taxon. Hummel (1927, 1929) also agreed with the conclusions of Reinach (1900) as he too saw great similarities between all named pan-trionychids from the Tertiary of Europe and the extant *T. triunguis*, but he nevertheless felt that all named morphotypes represent true species and that the lineage is not necessary restricted to Europe and therefore does not lead only to the extant *T. triunguis*. According to the classification scheme of Hay (1908), he assigned all relevant taxa, including the extant *T. triunguis*, to the subgenus *Amyda*. In a series of papers, Karl (1998) partially revived Reinach's (1900) "*Trionyx protriunguis* succession" by explicitly synonymizing most of the Miocene to Pleistocene soft-shelled turtles from central Europe with the extant *T. triunguis*. Karl (1999a) soon united all known fossil pan-trionychids from the Tertiary of Europe into *T. triunguis*, but an explicit synonym list is lacking. Although we here arrive at the conclusion that at least two lineages are apparent in the Neogene of Europe, we agree that the *T. triunguis* lineage is only represented by a single morphotype at any given time interval. If one were to employ a lineage species concept, Karl (1998) would certainly be right to synonymize so many fossil taxa with *T. triunguis*. However, given that a rigorous phylogenetic analysis is still outstanding and that the apparent *T. triunguis* lineage shows evidence of anagenesis, we here conform to the paleontological convention of establishing chronospecies, while explicitly acknowledging that these are paraphyletic.

## *Pan-Trionychidae* Incertae Sedis

Comments. We consider the following list of fossil pan-trionychid taxa to be valid, but given that their relationships with extant trionychids and with other fossil trionychids are unclear, we refer them to the wastebasket taxon "*Trionyx*." The polyphyletic nature of "*Trionyx*" is highlighted with the use of quotation marks, in contrast to *Trionyx* without quotation marks, which refers to the monophyletic group associated with the extant *T. triunguis*.

### "*Trionyx*" *baynshirensis* Danilov et al., 2014

Taxonomic history. "*Trionyx*" *baynshirensis* Danilov et al., 2014 (new species).

Type material. PIN 557-134 (formerly PIN 557-130) (holotype), medial fragment of right hyo-hypoplastra (Danilov et al. 2014, fig. 13a, b).

Type locality. Bayn Shire, Dornogovi Aimag, Mongolia (Figure 3); Baynshire Formation, Cenomanian/Santonian, Late Cretaceous (Danilov et al. 2014).

Referred material and range. No specimens have been referred to date.

Diagnosis. "*Trionyx*" *baynshirensis* can be diagnosed as a member of *Pan-Trionychidae* by the presence of sculpturing that covers all metaplastic portions of the shell bones and the absence of shell scutes. "*Trionyx*" *baynshirensis* can be differentiated from all other early Late Cretaceous pan-trionychids by having a hyo-hypoplastral callosity with an expanded, blunt medial edge that fully covers the medial processes.

Comments. The early Late Cretaceous Baynshire Formation has yielded rich trionychid material. Danilov et al. (2014) noted that most of the specimens can be assigned to *Kuhnemys orlovi* (see above), but that a second, less prominent taxon is available as well that can be diagnosed easily based on a single plastral fragment that shows many similarities with the Santonian "*Trionyx*" *kansaiensis* in terms of overall shape of the hyo-hypoplastra and sculpturing pattern (Danilov et al. 2014). We provisionally accept the validity of this species herein.

### "*Trionyx*" *boulengeri* Reinach, 1900
### (= *T. clavatomarginatus* Lörenthey, 1903)

Taxonomic history. *Trionyx boulengeri* Reinach, 1900 (new species); *Amyda boulengeri* = *T. borkenensis* Karl 1993 (new combination, senior synonym); *T. triunguis* = *T. boulengeri* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. BMNH 36765 (holotype), a complete carapace (Lydekker 1889a, unnumbered figure; Reinach 1900, pl. 38; Karl 2007, pl. 2).

Type locality. Alzey, Rhineland-Palatinate, Germany (Reinach 1900; Figure 4); Rupelian, early Oligocene (Karl 1999a).

Referred material and range. Late Eocene or Oligocene, Cluj, Romania (lectotype of *Trionyx clavatomarginatus*; Lörenthey 1903).

Diagnosis. "*Trionyx*" *boulengeri* can be diagnosed as a member of *Pan-Trionychidae* by the full list of carapacial characters provided for that clade above. Among Paleogene pan-trionychids from Europe, "*T.*" *boulengeri* can be differentiated from *Axestemys vittata* by size, more extensive development of the carapacial callosities, and the absence of a preneural, and from all others by having reduced costals VIII and sinuous carapacial margins.

Comments. "*Trionyx*" *boulengeri* is based on a nearly complete carapace from the Oligocene of Alzey, Germany, that had originally been referred to *T. gergensi* (Lydekker 1889a) but was later used for the basis of a new species (Reinach 1900). The type is notable among Oligocene pan-trionychids from north of the Alps, as it is relatively complete and therefore displays at least some traits that can be considered diagnostic. However, given that "*T.*" *boulengeri* lacks plastral material (see *T. vindobonensis* above for more extensive discussion), it is difficult to diagnose this taxon rigorously once temporal and biogeographic concerns are omitted. We here nevertheless recognize two valid taxa in the Oligocene of Europe, "*T.*" *boulengeri* north of the Alps and "*T.*" *capellinii* south of the Alps, which can be differentiated using relative nuanced characters apparent in the carapace. However, whereas "*T.*" *capellinii* seems to be restricted to the Eocene to Oligocene of Italy, we here attribute the lectotype of *T. clavatomarginatus* from the late Eocene of Romania to "*T.*" *boulengeri*, as this specimens also shows reduced costals VIII and sinuous carapacial margins. The future finding of more completely material, especially associated plastral remains, will allow more rigorously diagnosing the taxon "*T.*" *boulengeri* relative to other pan-trionychids from Europe.

Karl (1993, 1996) attributed fragmentary remains from the early Eocene of Salzburg, Austria, and the Eocene and Oligocene of Germany, respectively, to *Amyda* cf. *boulengeri*, but we believe that these specimens are too fragmentary to allow identification at the species level. On the other side, we here reluctantly refer the well-preserved lectotype of *T. clavatomarginatus* to "*T.*" *boulengeri* as it displays the sinuous carapacial margin that is diagnostic for this taxon.

### "*Trionyx*" *capellinii* Negri, 1892 (= *T. affinis* Negri, 1892 = *T. capellinii conjugens* Sacco, 1894 = *T. capellinii gracilina* Sacco, 1895 = *T. capellinii perexpansa* Sacco, 1895 = *T. gemmellaroi* Negri, 1892 = *T. intermedius* Bergounioux, 1954 = *T. insolitus* Bergounioux, 1954 = *T. capellinii montevialensis* Negri, 1892 = *T. schaurothianus* Negri, 1893)

Taxonomic history. *Trionyx capellinii* Negri, 1892 (new species); *T. capellinii* = *T. schaurothianus* Sacco 1895 (senior synonym); *T. capellini* Teppner 1913 (incorrect spelling of species epithet); *T. c. capellinii* = *T. c. affinis* = *T. c. conjugens* Kotsakis 1977 (senior synonym); *T. c. capellinii* = *T. c. affinis* = *T. c. conjugens* = *T. gemmellaroi* = *T. intermedius* Broin 1977 (senior synonym).

Type material. MGP-PD 12883 (syntype), a partial skeleton consisting of parts of the cranium, the complete carapace, a hyohypoplastron, a humerus, and a femur (Negri 1892, pl. 2; Bergounioux 1954, fig. 9, pl. 1.7; Kotsakis 1977, fig. 3c); MGP-PD 12882 (syntype), a carapace (Negri 1892, pl. 3).

Type locality. Monte Bolca (= Purga di Bolca), Veneto, Italy (Negri 1892; Figure 4); Prati Valeno Horizon, Lutetian, middle Eocene (Giusberti et al. 2014).

Referred material and range. Middle Eocene (probably Lutetian) of the type locality, Veneto, Italy (type material of *Trionyx affinis*, *T. capellinii conjugens*, *T. gemmellaroi*, *T. intermedius*; Negri 1892; Sacco 1894; Bergounioux 1954; and referred material of Kotsakis 1977); early Oligocene (early Rupelian), Veneto, Italy (type material of *T. capellinii gracilina*, *T. capellinii montevialensis*, *T. capellinii perexpansa*, *T. insolitus*, and *T. schaurothianus*; Negri 1893; Sacco 1895; Bergounioux 1954; material referred to *T. capellinii montevialensis* and *T. c. schaurothianus* by Barbera and Leuci 1980).

Diagnosis. "*Trionyx*" *capellinii* can be diagnosed as a member of *Pan-Trionychidae* by the full list of characters listed for that clade above. Among pan-trionychids from the Paleogene of Europe, "*T.*" *capellinii* can be differentiated readily from *Axestemys vittata* by smaller size, more extensive development of all callosities, and the absence of a preneural, and from "*T.*" *boulengeri*, "*T.*" *henrici*, and "*T.*" *messelianus* by having larger costals VIII. A rigorous diagnosis is not possible relative to "*T.*" *silvestris* and "*T.*" *ikoviensis*, as these are mostly based on cranial material.

Comments. The middle Eocene (Lutetian) locality of Monte Bolca and the nearby early Oligocene (early Rupelian) locality of Monteviale in the Region of Veneto, Italy, have yielded a rich pan-trionychid fauna that serves as the basis of 11 taxa. For Monte Bolca, these names are *Trionyx affinis* Negri, 1892, *T. capellinii* Negri, 1892, *T. capellinii conjugens* Sacco, 1894, *T. intermedius* Bergounioux, 1954, and *T. gemmellaroi* Negri, 1892, and for Monteviale, *T. capellinii gracilina* Sacco, 1895, *T. italicus* Schauroth, 1865, *T. capellinii montevialensis* Negri, 1892, *T. capellinii perexpansa* Sacco, 1895, *T. insolitus* Bergounioux, 1954, and *T. schaurothianus* Negri, 1893. In contrast to similar accumulations of names from other regions in Europe, most of these names are based on partial skeletons, although crushing prohibits studying the nonshell anatomy in detail. The proliferation of names is nevertheless baffling, as there always was universal agreement that all named taxa are closely related. Indeed, four species were already named as subspecies or varieties of *T. capellinii* (i.e., *conjugens*, *gracilina*, *montevialensis*, and *perexpansa*), whereas two others were secondarily denoted to subspecies of *T. capellinii* (i.e., *affinis* and *schaurothianus*). In his review of this material, Kotsakis (1977) concluded that all material from both localities represent a single species, *T. capellinii*, although he retained the validity of two subspecies, one for each locality. Broin (1977), on the other hand, preferred recognizing two separate species, although she did not provide a justification for this preference. Barbera and Leuci (1980) soon after provided morphometric evidence to support the presence of one subspecies in each locality, but this study cannot be considered statistically significant, as only four specimens were used. Kotsakis (1985) nevertheless used this study to change his previous taxonomic opinion and conclude that each locality is characterized by its own species, *T. capellinii* for the Eocene of Monte Bolca and *T. italicus* for the early Oligocene of Monteviale. We were initially inclined to recognize the validity of two species as well because of stratigraphic concerns, but after our firsthand observation of all type specimens (except for the now lost holotype of *Trionyx capellinii perexpansa*) and several referred specimens from both Monte Bolca and Monteviale, we ultimately concluded that the differences between the two populations are so minor, while variation remains so great, that a rigorous diagnosis is impossible. We therefore only see evidence for a single taxon in this region with uncertain generic affinities. Given that we disregard *T. italicus* from consideration (see below), we conclude that "*T.*" *capellinii* is the valid name for this Italian pan-trionychid.

### “*Trionyx*” *dissolutus* Vitek and Danilov, 2014

Taxonomic history. “*Trionyx*” *dissolutus* Vitek and Danilov, 2014 (new species).

Type material. ZIN PH 51/86 (holotype), external and visceral impressions of posterior part of carapace of one individual (Nessov 1984, figs. 6, 7, 9; Nessov 1997, pls. 34.17, 35.7; Vitek and Danilov 2014, fig. 5).

Type locality. Itemir locality, Central Kizylkum Desert, Navoiy Region, Uzbekistan (Figure 3); Khodzhakul Formation, Cenomanian, Late Cretaceous (Vitek and Danilov 2014).

Referred material and range. Late Cretaceous (early Cenomanian), Khodzhakul Formation, Kizylkum Desert area, Karakalpakstan, Uzbekistan (referred material of Vitek and Danilov 2014).

Diagnosis. “*Trionyx*” *dissolutus* can be diagnosed as a member of *Pan-Trionychidae* by the presence of sculpturing that covers all metaplastic portions of the shell bones and the absence of shell scutes. Among early Late Cretaceous pan-trionychids, “*T.*” *dissolutus* can be differentiated from all by the presence of an epiplastral notch on the hyoplastron and an extensive medial contact between the hyo- and hypoplastra.

Comments. Vitek and Danilov (2014) recently described the pan-trionychid fauna from the Cenomanian Khodzhakul Formation of Uzbekistan. Although this fauna is mostly known from fragments, Vitek and Danilov (2014) were able to document the presence of two morphotypes, of which one displays a less ossified shell that resembles the slightly younger *Petrochelys kyrgyzensis*, whereas the other is better ossified that resembles the younger “*T.*” *kansaiensis* and North American plastomenids. Vitek and Danilov (2014) provided the name “*T.*” *dissolutus* for the latter morphotype and designated a partial shell as the holotype.

We generally agree that “*Trionyx*” *dissolutus* is a valid species, but we disagree on the exact interpretation of the holotype. In all trionychids that we are aware of that are known from complete shells, costals IV are the widest elements and situated at the midpoint of the specimen. As interpreted by Vitek and Danilov (2014), costals IV of the holotype of “*T.*” *dissolutus* are clearly positioned at the posterior half of the shell, and the more posterior elements are unusually crowded toward the back. We are able to confirm the presence of most sutures in this specimen in high-quality photographs we were able to obtain, but we are not fully convinced that the last pair of minute costals is actually present. We therefore favor that this specimen consists of more usually proportioned costals V–VIII and that costals VIII are rather large, conclusions that are more in line with a plastomenid-like morphotype. Our assertions will hopefully be tested in the near future by additional finds.

### “*Trionyx*” *gilbentuensis* Danilov et al., 2014

Taxonomic history. “*Trionyx*” *gilbentuensis* Danilov et al., 2014 (new species).

Type material. ZIN PH T/M46-2 (holotype), incomplete left hyo-hypoplastra (Danilov et al. 2014, fig. 13c, d).

Type locality. Gilbentu, Ömnögovi (= Umunugovi) Aimag, Mongolia (Figure 3); Nemegt Formation, Maastrichtian, Late Cretaceous (Danilov et al. 2014).

Referred material and range. No specimens haven been referred to date.

Diagnosis. “*Trionyx*” *gilbentuensis* can be diagnosed as a member of *Pan-Trionychidae* by the presence of sculpturing that covers all metaplastic portions of the shell bones. Among late Late Cretaceous pan-trionychids from Asia, “*T.*” *gilbentuensis* can most readily be differentiated by its large size, with an estimated CL of about 50 cm.

Comments. “*Trionyx*” *gilbentuensis* is based on a partial hyo-hypoplastron. Although we herein generally do not support the validity of a pan-trionychid species based on a single plastral element, we feel that this species is well justified, as the rich pan-trionychid fauna of the Nemegt Formation is well described (Danilov et al. 2014) and thereby highlights the uniqueness of this taxon within this assemblage. We nevertheless hope that additional finds will soon confirm the validity of this taxon and clarify its phylogenetic relationships.

### “*Trionyx*” *gobiensis* Danilov et al., 2014

Taxonomic history. “*Trionyx*” *gobiensis* Danilov et al., 2014 (new species).

Type material. PIN 4064-2 (holotype), an incomplete carapace (Danilov et al. 2014, fig. 14).

Type locality. Bamba Khuduk (= Eastern Sayr), Ömnögovi (= Umunugovi) Aimag, Mongolia (Figure 3); Nemegt Formation, Maastrichtian, Late Cretaceous (Danilov et al. 2014).

Referred material and range. Late Cretaceous (Maastrichtian), Nemegt Formation, Tsagan Khushu and Altan Ula III, Ömnögovi Aimag, Mongolia (referred material of Danilov et al. 2014).

Diagnosis. “*Trionyx*” *gobiensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of carapacial characters provided for that clade above. Among late Late Cretaceous pan-trionychids, “*T.*” *gobiensis* can be differentiated from *Kuhnemys breviplastra* by having well-developed costals VIII, from “*T.*” *gilbentuensis* by being much smaller, and from “*T.*” *shiluutulensis* by lacking a preneural. “*Trionyx*” *gobiensis* cannot be distinguished rigorously from *Nemegtemys conflata*, as these taxa are not known from overlapping material.

Comments. “*Trionyx*” *gobiensis* is a rather small pan-trionychid (estimated CL only 13 cm), known from several carapaces that readily distinguish this species from its contemporaries, with exception of the pan-cyclanorbine *Nemegtemys conflata*, which is only known from plastral material. The validity of this species is otherwise not controversial.

## “*Trionyx*” *gregarius* (Gilmore, 1934) (= *Rafetus gilmorei* Chkhikvadze, 1999b)

Taxonomic history. *Amyda gregaria* Gilmore, 1934 (new species); *Trionyx gregaria* Kuhn 1964 (new combination); *T. gregarius* Karl 1998 (emended spelling); *Amyda gregaria* = *Rafetus gilmorei* Vitek and Danilov 2015 (senior synonym).

Type material. AMNH 6734 (holotype), carapace, plastron, and much of skeleton lacking the skull (Gilmore 1934, figs. 1, 3, 7); AMNH 6735 (paratype), skull, lower jaws, portions of carapace, plastron, and postcranial skeleton (Gilmore 1934, figs. 5–7); AMNH 6736 (paratype), a nearly complete skeleton of a juvenile individual (Gilmore 1934, figs. 2, 3, 7).

Type locality. Camp Margetts, 25 miles southwest of Iren Dabasu, Inner Mongolia, China (Gilmore 1934; Figure 3); Irdin Manha Formation, middle Eocene (Meng et al. 2007).

Referred material and range. Middle Eocene of type locality, Inner Mongolia, China (referred material of Gilmore 1934, including type material of *Rafetus gilmorei*; Chkhikvadze 1999b).

Diagnosis. “*Trionyx*” *gregarius* can be diagnosed as a member of *Pan-Trionychidae* by the full list of characters provided for that clade above. Among Paleogene pan-trionychids from Asia, “*T.*” *gregarius* can be most readily differentiated by small size, lacking a preneural, a midline contact of the posterior costals, broad costals VIII, a finely crenulated sculpturing, and well-formed plastral callosities.

Comments. “*Trionyx*” *gregarius* is based on a large block of matrix containing an assemblage of 14 individuals in various ontogenetic stages. However, given that many mechanisms are available to concentrate turtles in a single fossil locality (Wings et al. 2012), we see no reason to infer gregarious behavior for this taxon. The type locality was initially believed to be located within the Oligocene Houldjin Formation (Gilmore 1934) but was recently reassigned to the middle Eocene Irdin Manha Formation (Meng et al. 2007). The holotype of “*T.*” *gregarius* lacks cranial material, but Gilmore (1934) designated two rather complete skeletons that include skulls as the paratypes of his new species. The original attribution of this species to the genus *Amyda* seems to have been based on the absence of a preneural (Gilmore 1934), but this attribution is probably based on the classification scheme of Hay (1908) and does not imply that Gilmore (1934) believed this taxon to be closely related to the extant southeast Asian *Amyda cartilaginea*. Chkhikvadze (1999b) established a new species, *Rafetus gilmorei*, on the basis of two specimens that are preserved in the fossil slab of the type of “*T.*” *gregarius* and that were initially considered to be juveniles by Gilmore (1934). The new species was said to differ from all other pan-trionychids by the presence of suprascapular fontanelles, reduced costals VII or VIII, more elongated medial processes, and weakly sculpted hyo-hypoplastron (Chkhikvadze 1999b), but Vitek and Danilov (2015) recently affirmed that these characters are consistent with ontogenetic variation. We agree with this assessment. Given the large amount of quality material documenting the entire skeleton, the validity of this species is uncontroversial.

## “*Trionyx*” *henrici* Owen in Owen and Bell, 1849 (= *T. barbarae* Owen in Owen and Bell, 1849 = *T. circumsulcatus* Owen in Owen and Bell, 1849 = *T. incrassatus* Owen in Owen and Bell, 1849 = *T. marginatus* Owen in Owen and Bell, 1849 = *T. planus* Owen in Owen and Bell, 1849 = *T. rivosus* Owen in Owen and Bell, 1849)

Taxonomic history. *Trionyx henrici* Owen in Owen and Bell, 1849 (new species); *T. henrici* = *T. marginatus* Lydekker 1889a (senior synonym); *Rafetoides henrici* = *T. barbarae* = *T. circumsulcatus* = *T. incrassatus* = *T. marginatus* = *T. planus* = *T. pustulatus* = *T. rivosus* = *T. silvestris* Karl 1998 (new combination and senior synonym).

Type material. BMNH R30407 (holotype), a complete carapace, missing the nuchal (Owen and Bell 1849, pl. 16; Owen 1849–1884, pl. 6; Benton and Spencer 1995, fig. 9.7).

Type locality. Hordle (= Hordwell) Cliff, Hampshire, United Kingdom (Owen and Bell 1849; Figure 4); Totland Bay Member, Headon Hill Formation, Priabonian, late Eocene (Benton and Spencer 1995).

Referred material and range. Middle Eocene (late Lutetian), Guitrancourt, Yvelines, Île-de-France, France (*Trionyx* sp. of Lapparent de Broin et al. 1993); late Eocene (Priabonian) of type locality, Hampshire, United Kingdom (type material of *T. barbarae*, *T. circumsulcatus*, *T. marginatus*, *T. planus*, and *T. rivosus*; Owen and Bell 1849; referred material to *T. barbarae*, *T. henrici*, *T. planus*, and *T. rivosus* of Lydekker 1889a; referred material to *T. planus* of Boulenger 1891); late Eocene (Priabonian), Isle of Wight (type material of *T. incrassatus*; Owen and Bell 1849).

Diagnosis. “*Trionyx*” *henrici* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters listed for that clade above. Among Paleogene pan-trionychids from Europe, “*T.*” *henrici* can be differentiated from others by intermediate size (CL about 30 cm), a rounded shell margin, thick callosities, absence of a preneural, and short but broad costals VIII.

Comments. Owen (in Owen and Bell 1849) named a total of seven pan-trionychids based on rich material, including many complete carapaces, from the late Eocene of southern England, in particular *Trionyx barbarae*, *T. circumsulcatus*, *T. henrici*, *T. incrassatus*, *T. marginatus*, *T. planus*, and *T. rivosus*. Most of the type specimens were originally kept in the Museum of the Marchioness of Hastings (Owen and Bell 1849) but had since been transferred to BMNH (Lydekker 1889a). All species were originally diagnosed using characteristics, such as shell sculpturing and the size and orientation of the neurals, that are now known to be highly variable. Owen (in Owen and Bell 1849), Lydekker (1889a), and Boulenger (1891) variously referred additional material to various named taxa, including additional shell remains, two mandibles, and a partial skull, but it is difficult to reproduce their assignments, as most material was found in isolation and does not overlap anatomically. Along those lines, Lydekker (1889a) assigned the two mandibles to "*T.*" *henrici* and *T. planus* even though these are not associated with any shell remains. Although some of the late Eocene English species were already synonymized by Lydekker (1889a), most were maintained as valid (e.g., Hummel 1932; Kuhn 1964), until Karl (1998) united all named English pan-trionychids, including the early Eocene skull taxon *T. silvestris*, into a single taxon, for which he, as the first reviser, designated *T. henrici* as the senior synonym and the type species of his new genus *Rafetoides*. Although we broadly agree with the conclusion of Karl (1998) that most of the Eocene trionychids from Europe represent a single lineage for which *Rafetoides* is available as a name, a rigorous phylogenetic analysis is needed to establish their monophyly relative to later taxa.

Lapparent de Broin et al. (1993) described and figured a pan-trionychid from the middle Eocene of Guitrancourt, France. Judging from the figure, we herein assign this material to "*Trionyx*" *henrici*, as the two forms share a rather enlarged nuchal, an elongated neural I, similar size, and overall a strong resemblance in terms of carapace shape and sculpturing pattern. The number of eight neurals (contra seven in the English forms) suggested for the French form in Lapparent de Broin et al. (1993) cannot be verified with certainty. If our identification of the Guitrancourt pan-trionychid as conspecific with "*T.*" *henrici* is correct, then it represents not only a significant geographic range extension for this species, but also a stratigraphic range extension.

Karl and Lindow (2012) referred fragmentary remains from the Paleocene (Danian) of Denmark to *Rafetoides* cf. *henrici*, but we here consider these fragments to be too fragmentary to allow identification at the species level.

## "*Trionyx*" *ikoviensis* Danilov et al., 2011

Taxonomic history. *Trionyx ikoviensis* Danilov et al., 2011 (new species).

Type material. ZIN PH 37/145 (holotype), a partial skull (Danilov et al. 2011, figs. 2–4).

Type locality. Ikovo, Luhansk Province, Ukraine (Figure 4); early Lutetian, middle Eocene (Danilov et al. 2011).

Referred material and range. Middle Eocene (early Lutetian) of type locality, Ukraine (referred material of Danilov et al. 2011).

Diagnosis. "*Trionyx*" *ikoviensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of characters provided for that clade above. Among Paleogene turtles from Europe, "*T.*" *ikoviensis* can be differentiated by intermediate size, a broad skull with narrow contribution of the parietals to the skull roof, and short but wide costals VIII.

Comments. "*Trionyx*" *ikoviensis* was only recently described based on a large skull and associated shell elements from the middle Eocene locality of Ikovo, Ukraine (Danilov et al. 2011). Although a great resemblance is apparent with the skulls of the early Eocene "*T.*" *silvestris* (including the skull of *T. michauxi*), the middle Eocene "*T.*" *messelianus*, and other poorly documented cranial remains of "*T.*" *henrici* (skull referred to *T. planus* by Boulenger [1891]), we agree with Danilov et al. (2011) that the morphology of "*T.*" *ikoviensis* supports the recognition of a distinct, though closely related species of pan-trionychids, although we agree that biogeographic rationales most strongly support this notion, not morphological differences.

## "*Trionyx*" *impressus* (Yeh, 1963)

Taxonomic history. *Aspideretes impressus* Yeh, 1963 (new species); *Trionyx impressus* Danilov et al. 2013 (new combination).

Type material. IVPP V1036 (holotype), a negative cast of a nearly complete carapace (Yeh 1963, fig. 32, pls. 19.3, 20.1, 1a).

Type locality. Maoming, Guangdong (= Kwantung) Province, China (Yeh 1963; Figure 3); Youkanwo (= Youganwo) Formation, late Eocene (Tong et al. 2010).

Referred material and range. No specimens have been referred to date.

Diagnosis. "*Trionyx*" *impressus* can be diagnosed as a member of *Pan-Trionychidae* by the full list of carapacial characters that diagnose that clade. Among Paleogene pan-trionychids from East Asia, "*T.*" *impressus* is provisionally differentiated by the presence of a preneural, broad costals VIII, and many longitudinal ridges that decorate the carapace.

Comments. "*Trionyx*" *impressus* is based on the external imprint of a carapace from the late Eocene of Maoming, China. Yeh (1963) initially referred this species to *Nilssonia* (his *Aspideretes*) based on the purported presence of a preneural. Judging from the published figures, we were initially skeptical that a preneural is present indeed, but low resolution photographs available to us seem to confirm the presence of a preneural that differs from the shape documented by Yeh (1963) but that resembles that of extant *Nilssonia* in size and shape. Given that the validity of this taxon pivots on the presence of this structure, we herein only conditionally accept the validity "*T.*" *impressus*, await the redescription of the type, and retain the species in the neutral "*Trionyx*." It is an amusing factoid that a taxon already exists that was named *T. impressus* (Kutorga 1835) at one point, but this fossil is now known to be a basal vertebrate from the Paleozoic and therefore has no nomenclatural significance for turtle paleontology.

## "*Trionyx*" *jixiensis* Li, Tong et al., 2015

Taxonomic history. "*Trionyx*" *jixiensis* Li, Tong et al., 2015 (new species).

Type material. GMH H2008JI20 (holotype), an almost complete carapace and the impression of its external surface (Li, Tong et al. 2015, fig. 2).

Type locality. Yufeng village, Jixi, Heilongjiang Province, China (Figure 3); Chengzihe Formation, Aptian/Albian, Early Cretaceous (Li, Tong et al. 2015).

Referred material and range. No specimens have been referred to date.

Diagnosis. “*Trionyx*” *jixiensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of carapacial characters provided for that clade above. Among Early Cretaceous pan-trionychids, “*T.*” *jixiensis* can be differentiated from *Perochelys lamadongensis* by showing a fully formed nuchal and enlarged costals VII and VIII that have a midline contact. Only geographic considerations allow us to distinguish “*T.*” *jixiensis* from *Petrochelys kyrgyzensis*.

Comments. “*Trionyx*” *jixiensis* is based on a well-preserved, partial carapace from the Early Cretaceous of Heilongjiang Province, China (Li, Tong et al. 2015). Much like other Early Cretaceous pan-trionychids that are known from more complete material (see *Perochelys lamadongensis* above), this species is striking once again by greatly resembling extant pan-trionychines. However, given that the trionychine morphotype may reasonably be ancestral for Trionychidae, we are wary about attribution of this species to Trionychinae, as done by Li, Tong et al. 2015), and anticipate a more formal phylogenetic analysis. We are not able to rigorously distinguish “*T.*” *jixiensis* from the roughly coeval *Petrochelys kyrgyzensis* from nearby Kyrgyzstan, because the carapacial reconstruction of Nessov (1995b) must be viewed with caution, as it is based on many isolated fragments and therefore does not necessarily faithfully depict the morphology of this taxon. We therefore provisionally accept both taxa but anticipate the discovery of articulated shells of *Petrochelys kyrgyzensis* or plastral remains of “*T.*” *jixiensis* that will allow more rigorous comparison.

## “*Trionyx*” *johnsoni* Gilmore, 1931 (= *Amyda neimenguensis* Yeh, 1965)

Taxonomic history. *Amyda johnsoni* Gilmore, 1931 (new species); *Trionyx johnsoni* Kuhn 1964 (new combination).

Type material. AMNH 6357 (holotype), the posterior portion of a carapace (Gilmore 1931, fig. 29, pl. 11).

Type locality. Telegraph Line Camp, Irdin Manha, Inner Mongolia, China (Gilmore 1931; Figure 3); Irdin Manha Horizon, middle Eocene (Danilov, Sukhanov et al. 2015).

Referred material and range. Middle Eocene of type locality, Inner Mongolia, China (referred material of Gilmore 1931); middle Eocene, Ulan Shireh, Inner Mongolia, China (type material of *Amyda neimenguensis*; Yeh 1965).

Diagnosis. “*Trionyx*” *johnsoni* can be diagnosed as a member of *Pan-Trionychidae* by the full list of carapacial characters provided for that clade above. Among Paleogene pan-trionychids from Asia, “*T.*” *johnsoni* can be differentiated by large size, greatly expanded distal margins of costals VII, reduced costals VIII, and a coarse sculpturing pattern.

Comments. “*Trionyx*” *johnsoni* is based on the partial carapace of a relatively large pan-trionychid. The type locality of “*T.*” *johnsoni* was initially believed to be late Eocene (Gilmore 1931) but was more recently reallocated to the middle Eocene ( Danilov, Sukhanov et al. 2015). Gilmore (1931) was reluctant to determine the generic affinities of his new species, as the nuchal and the anterior part of the first neural were entirely missing from the holotype. Nevertheless, he provisionally assigned the species to *Amyda* on the basis of overall resemblance, a view that was also subsequently adhered to by Yeh (1963). In our assessment, the presence of reduced costals VIII makes a relationship with the *Amyda cartilaginea* lineage unlikely, and we therefore assign this species to the neutral “*Trionyx*.” The unusually broadly developed distal margins of costals VI nevertheless prompt us to recognize the validity of this species.

## “*Trionyx*” *kansaiensis* Vitek and Danilov, 2010

Taxonomic history. “*Trionyx*” *kansaiensis* Vitek and Danilov, 2010 (new species).

Type material. ZIN PH 630/64 (holotype), a partial nuchal (Vitek and Danilov 2010, fig. 6a, b; Danilov and Vitek 2013, fig. 23.3a1).

Type locality. Kansai, Khodzhent Province, Tajikistan (Figure 3); Yalovach Formation, early Santonian, Late Cretaceous (Vitek and Danilov 2010).

Referred material and range. Late Cretaceous (Santonian–early Campanian), Bostobe Formation, Kyzylorda Region, Kazakhstan; Late Cretaceous (Santonian–Campanian), Syuk-Syuk Formation and probably the lower part of the Darbaza Formation, Kyrkkuduk well (= Sary-Agach = Kyrkkuduk I), South Kazakhstan Region, Kazakhstan (referred material of Vitek and Danilov 2012).

Diagnosis. “*Trionyx*” *kansaiensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters provided for that clade above. Among middle Late Cretaceous pan-trionychids, “*T.*” *kansaiensis* can be differentiated by large size (CL up to 75 cm), a deep nuchal notch, unreduced costals VIII, and well-developed hyo-hypoplastral callosities that cover most of the medial and lateral processes.

Comments. “*Trionyx*” *kansaiensis* is based on an assemblage of shell pieces that clearly document that it is distinct from all other roughly coeval forms (Vitek and Danilov 2010; Li, Joyce, and Liu 2015), but comparison with skull-based taxa is not possible. Danilov, Vitek et al. (2015) recently suggested that “*T.*” *kansaiensis* may belong to the skull-based *Khunnuchelys lophorhothon*, because both taxa co-occur in the Bostobe Formation and are known from similarly large specimens. This conclusion is supported by the recent report of a rather similar or even conspecific form from the late Turonian of Dzharakuduk, Uzbekistan, which also happens to be the type locality of *Khunnuchelys kizylkumensis* (Danilov and Vitek 2013). A similar argument can be made for the type of *T. zakhidovi*, a nomen dubium that is based on an enormous femur from coeval sediments. Pending the discovery of associated material, we nevertheless maintain “*T.*” *kansaiensis* as a valid species.

### "*Trionyx*" *linchuensis* (Yeh, 1962)

Taxonomic history. *Amyda linchuensis* Yeh, 1962 (new species); *Trionyx linchuensis* Kuhn 1964 (new combination).

Type material. IVPP V1050 (holotype), a partial carapace, the right coracoid, and a partial skull (Yeh 1962, pl. 1.1).

Type locality. Niushan, Linqu (= Linchu) County, Shandong (= Shantung) Province, China (Yeh 1962; Figure 3); early Eocene (Ye 1994).

Referred material and range. No specimens have been referred to date.

Diagnosis. "*Trionyx*" *linchuensis* can be diagnosed as a member of *Pan-Trionychidae* by the full list of carapacial characters provided for that clade above. Among Paleogene pan-trionychids from Asia, "*T.*" *linchuensis* can be differentiated from all the others by small size and a complete neural column that fully separates the costals from one another.

Comments. "*Trionyx*" *linchuensis* is based on a carapace and an unfigured skull from Shandong, China, that was originally reported to be late Eocene to Oligocene (Yeh 1962), but more recently corrected to be early Eocene in age (Ye 1994). As was typical prior to the work of Meylan (1987), Yeh (1962) attempted to classify this small species (CL of 17 cm) using the simplified classification key developed by Hay (1908) for fossil trionychids from North America. On the one side, Yeh (1962) reasoned that "*T.*" *linchuensis* is not a representative of *Nilssonia* (his *Aspideretes*) as it lacks preneurals. However, he was uncertain in regard to the number of costals and therefore was not able to rigorously distinguish between *Amyda* (eight costals) and *Apalone* (his *Platypeltis*, seven costals). This statement is baffling, however, as the type figures clearly display a trionychid with eight pairs of costals. Yeh (1962) tentatively placed his new taxon into *Amyda* and further noted that it was similar overall to the late Eocene "*T.*" *johnsoni* from nearby Inner Mongolia, especially in terms of carapace sculpturing. We herein note that costals VIII do not seem to contact each other along the carapace midline, and the specimen therefore seems to bear a complete neural column, a feature that has otherwise only been observed in a small handful of species (e.g., the early Cretaceous *Perochelys lamadongensis* and the extant *Dogania subplana*). Although we believe that the type specimen likely represents a juvenile, we nevertheless feel confident in diagnosing a valid species using this rare characteristic.

### "*Trionyx*" *messelianus* Reinach, 1900 (= *T. messelianus lepsiusi* Hummel, 1927 = *T. messelianus kochi* Hummel, 1927)

Taxonomic history. *Trionyx messelianus* Reinach, 1900 (new species); *Rafetoides austriacus* = *T. messelianus* = *T. messelianus kochi* = *T. messelianus lepsiusi* Karl 1998 (junior synonym); *Palaeoamyda messeliana* Cadena 2016 (new combination and emended spelling of species epithet).

Type material. SMF R106 (holotype), an almost complete carapace and a hyoplastron fragment (Reinach 1900, pls. 41, 42; Hummel 1927, pl. 6.24; Karl 1998, pl. 8.5).

Type locality. Messel pit fossil site, Hesse, Germany (Reinach 1900; Figure 4); MP 11, early Lutetian, middle Eocene (Joyce et al. 2012).

Referred material and range. Middle Eocene (MP 11, Lutetian) of type locality, Germany (referred material of Harrassowitz 1919; Hummel 1927; Karl 1998; Cadena 2016); middle Eocene (Lutetian), Geiseltal, Saxony-Anhalt, Germany (referred material of Cadena 2016).

Diagnosis. "*Trionyx*" *messelianus* can be diagnosed as a member of *Pan-Trionychidae* by the full list of characters listed for that clade above. Among Paleogene pan-trionychids from Europe, "*T.*" *messelianus* can be differentiated from the others by being medium-sized and having thinner callosities, a nuchal that is only partially covered by metaplastic bone, no preneural, and relatively small, equidimensional costals VIII.

Comments. "*Trionyx*" *messelianus* is known from rich material from the middle Eocene localities of Messel and Geiseltal, Germany (Reinach 1900; Harrassowitz 1919; Hummel 1927; Karl 1998; Cadena 2016), including many articulated skeletons. Three subspecies were named based on material from the type locality (e.g., *T. messelianus messelianus*, *T. messelianus kochi*, and *T. messelianus lepsiusi*), but we herein universally disregard varieties and subspecies and refer all material to the specific level alone. Karl (1998) suggested "*T.*" *messelianus* to be a junior synonym of the late Eocene *T. austriacus*, but we disregard that assessment, as *T. austriacus* is based on a partial, now lost carapace (see below) that lacks diagnostic features.

Cadena (2016) recently provided an updated description of some specimens from Messel and Geiseltal, concluded that "*Trionyx*" *messelianus* is the sister to the extant *Amyda cartilaginea* from Southeast Asia, and therefore assigned this taxon to a new genus, *Palaeoamyda*. This conclusion contradicts other recent arguments that "*T.*" *messelianus* is an early representative of the *T. triunguis* lineage (e.g., Broin 1977; Karl 1999a). Although a reanalysis of this taxon is outside of the scope of this contribution, we here note that "*T.*" *messelianus* was incorrectly coded for the length of the epiplastra processes (long, not short) and that many apparent differences of "*T.*" *messelianus* with the *Amyda* lineage have not yet been encoded, in particular different developments of costal rib VIII and costal VIII, varying lengths of the intermaxillary suture, and different developments of the pterygoid muscle scar. For these reasons, we here retain *messelianus* in *Trionyx* for the moment but highlight phylogenetic ambiguity through the use of quotation marks.

### "*Trionyx*" *miensis* Okazaki and Yoshida, 1977

Taxonomic history. *Trionyx miensis* Okazaki and Yoshida, 1977 (new species).

Type material. Aichi University (holotype), a partial cranium (Okazaki and Yoshida 1977, figs. 2, 3, pl. 1.1–4).

Type locality. Kitakoyama, Mie Prefecture, Japan (Okazaki and Yoshida 1977; Figure 3); Kameyama Formation, late Pliocene (Hirayama 2007).

Referred material and range. No specimens have been referred to date.

Diagnosis. "*Trionyx*" *miensis* can be diagnosed as a member of *Pan-Trionychidae* by a quadratojugal that does not contact the postorbital or maxilla. Among Neogene to Recent pan-trionychids from Asia, "*T.*" *miensis* can be differentiated by the development of broad triturating surfaces and an incipient secondary palate.

Comments. "*Trionyx*" *miensis* is based on a well-preserved, partial skull from the Pliocene of Japan. Okazaki and Yoshida (1977) noticed similarity of their new taxon with the extant *Pelodiscus sinensis* and differentiated their new species on the basis of skull proportions and maxillae shape, but we fully disagree, as the skull in *Pelodiscus sinensis* is notably slender and lacks expanded triturating surfaces or an incipient secondary palate. To our knowledge, incipient or fully formed secondary palates otherwise only occur among pan-trionychids in Late Cretaceous *Khunnuchelys* spp. (e.g., Brinkman et al. 1993), Late Cretaceous to Paleocene plastomenids (Joyce and Lyson 2011; Joyce et al. 2016), the Eocene "*T.*" *henrici* and "*T.*" *ikoviensis* (Walker and Moody 1974; Danilov et al. 2011), and the Miocene "*T.*" *vindobonensis* (Broin 1977). Given that spatial and temporal arguments render close relationships with these forms unlikely, we feel confident in supporting the validity of "*T.*" *miensis* using this character complex.

## "*Trionyx*" *minusculus* (Chkhikvadze, 1973), comb. nov.

Taxonomic history. *Plastomenus minusculus* Chkhikvadze, 1973 (new species); *Paraplastomenus minusculus* Kordikova 1994a (new combination); *Francedebroinella minuscula* Chkhikvadze 1999a (new combination, emended spelling of species epithet).

Type material. IPGAS Z-13-1 (holotype), a partial hyo-hypoplastron (Chkhikvadze 1973, pl. 4.2; Chkhikvadze 2008b, fig. 5 [bottom]).

Type locality. Konur-Kura (= Djeman-Gora = Djuva-Kara = Djeman-Kara), 12 km south of Karabulak, Zaysan Depression, East Kazakhstan Region, Kazakhstan (Chkhikvadze 2007, 2008a, 2010; Figure 3); lower Aksyir suite, late Eocene (Kordikova 1994b; Chkhikvadze 2008a).

Referred material and range. No specimens are referred herein.

Diagnosis. "*Trionyx*" *minusculus* can be diagnosed as a member of *Pan-Trionychidae* by the full list of plastral characters provided for that clade above. Among Paleogene pan-trionychids from Asia, "*T.*" *minusculus* can be differentiated from the others by being notably small and having well-developed, thick hyo-hypoplastral callosities that form a relatively narrow bridge, but fully cover the lateral plastral processes.

Comments. "*Trionyx*" *minusculus* is yet another Asian pan-trionychid taxon that is based on a partial hyo-hypoplastron and that has purported plastomenid affinities (Chkhikvadze 1973). The thick shell bones, which originally hinted at relationships with this North American clade, are now believed to be a widespread feature among Paleogene Asian pan-trionychids (Vitek and Danilov 2014), and their relationships with the North American clade remain unclear. Chkhikvadze (1999a) established his new monotypic genus *Francedebroinella* to accommodate for the unique morphology of this taxon and diagnosed it by the hyperossification of the shell. Our decision to not accept the validity of most named pan-trionychids that are based on fragmentary material is rooted on our conclusion that most of the isolated trionychid finds are not that unusual by themselves and therefore cannot diagnose a valid species. The type of "*T.*" *minusculus* is the exception to the rule, as we are not aware of any other pan-trionychid globally to possess such a massive ossified hyo-hypoplastron, while maintaining a narrow bridge, and small size. We therefore here recognize the validity of this species but once again await the description of the remainders of the skeleton.

## "*Trionyx*" *ninae* Chkhikvadze, 1971 (= *T. turgaicus* Kuznetsov and Chkhikvadze, 1977 = *T. zaisanensis* Chkhikvadze, 1973)

Taxonomic history. *Trionyx ninae* Chkhikvadze, 1971 (new species); *Palaeotrionyx ninae* Broin 1977 (new combination and incorrect spelling of genus name); *Rafetus ninae* Chkhikvadze 1989 (new combination); *Ulutrionyx ninae* Kordikova 1994a (new combination); *Yuen ninae* Chkhikvadze 2007 (new combination); *Oscaria ninae* Chkhikvadze 2008b (new combination); *Ulutrionyx ninae* = *T. turgaicus* = *T. zaisanensis* Vitek and Danilov 2015 (senior synonym).

Type material. IPGAS KK-19 (holotype), a left hypoplastron (Chkhikvadze 1971, fig. 2; Chkhikvadze 2008b, fig. 1).

Type locality. Kyzyl-Kak, 60 km southwest of Zhezqazghan (= Jezkazgan = Dzhezgazgan), Karagandy Region, Kazakhstan (Chkhikvadze 1971; Vitek and Danilov 2015; Figure 3); Betpakdalinskaya suite (Betpakdala Formation), Oligocene (Vitek and Danilov 2015).

Referred material and range. Late Eocene–Oligocene, Chelkarnurinskaya (= Chiliktinskaya suite) and Betpakdalinskaya suite, Turgai Depression, Karagandy Region, Kazakhstan (type material of *Trionyx turgaicus* and referred material of Vitek and Danilov 2015); late Eocene–Oligocene, Kustovskaya suite, Zaysan Depression, East Kazakhstan Region, Kazakhstan (type material of *T. zaisanensis*; Chkhikvadze 1973).

Diagnosis. "*Trionyx*" *ninae* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters listed for that clade above. Among Paleogene pan-trionychids from Asia, "*T.*" *ninae* can be differentiated from all taxa (except for *Kuhnemys palaeocenica*) by having reduced costals VIII, and from *K. palaeocenica* by being larger and having two lateral hyoplastral processes.

Comments. Over the course of four decades, Chkhikvadze (1970, 1971, 1973, 1984, 1989, 1999b, 2008a, 2008b) and Kuznetsov and Chkhikvadze (1977) published a series of papers in which they named a total of 13 pan-trionychid taxa based on isolated fragments collected in Eocene to Miocene sediments exposed in Kazakhstan. These are, in temporal order, *Plastomenus mlynarskii* Chkhikvadze, 1970; *Trionyx ninae* Chkhikvadze, 1971; *T. zaisanensis* and *Plastomenus minusculus* Chkhikvadze, 1973; *T. turgaicus* Kuznetsov and Chkhikvadze, 1977; *Plastomenus gabunii* Chkhikvadze, 1984; *T. jakhimovitchae* Chkhikvadze, 1989; *Zaisanonyx jimenezfuentesi* Chkhikvadze, 2008b; *Rafetus yexiangkuii* Chkhikvadze, 1999b; *Altaytrionyx burtschaki*, *Altaytrionyx devjatkini*, and *Altaytrionyx phiruzae* Chkhikvadze, 2008a; and *Rafetus karkhualexandri* Chkhikvadze 2000b. The description of turtles based on isolated fragments was commonplace during the 19th century (see Vitek and Joyce [2015] for North American pan-trionychids), but this practice is now generally frowned on, because most modern taxonomists recognize that turtles show substantial and overlapping interspecific and intraspecific variation and that a single fragment is therefore rarely representative for a single species. The validity of fragment taxa can sometimes be "saved," if a particular stratigraphic unit yields a rich fauna that allows attribution of a type using morphology assisted by a stratigraphic rationale (e.g., Gardner et al. [1995] for pan-trionychid remains found in the Campanian of Alberta, Canada). Conversely, it is acceptable to typify a new species based on a single fragment, if the description is accompanied by a comprehensive description of the associated fauna. The extensive literature produced by Chkhikvadze unfortunately does not provide outsiders with any insights regarding the pan-trionychid fauna of Kazakhstan, and, despite many attempts, we are unaware of any taxonomist having been granted access to collections held at IPGAS. We are therefore inclined to fully disregard this assortment of names. We nevertheless make exception for "*Trionyx*" *ninae*, *T. turgaicus*, and *T. zaisanensis*, which were exonerated as each other's synonyms by the more recent work of Vitek and Danilov (2015), and "*Trionyx*" *minusculus*, which indeed reveals a highly unusually morphology diagnostic for a valid species (see above).

"*Trionyx*" *ninae*, *T. turgaicus*, and *T. zaisanensis* are based on fragmentary remains from the Oligocene Turgai and Zaisan Depressions of Kazakhstan (Chkhikvadze 1971, 1973; Kuznetsov and Chkhikvadze 1977). *Trionyx turgaicus* was initially differentiated from "*T.*" *ninae* by lacking a suture between the nuchal and costal I, but Vitek and Danilov (2015) more recently attributed this difference to ontogenetic variation, as this suture often closes up during ontogeny. *Trionyx zaisanensis* was similarly differentiated from "*T.*" *ninae* by having a more massive shell and longer posteromedial process of the hypoplastron, but Vitek and Danilov (2015) recently cast doubt on the veracity or usefulness of these characters. We here agree with these assessments.

We find that none of the available type material is particularly diagnostic for a valid species of pan-trionychids, but Vitek and Danilov (2015) recently described new material from the Oligocene from Kazakhstan that is consistent in its morphology with the type of these three taxa but also documents much of the remainder of the shell. We therefore agree that it is prudent to support the validity of a single species of pan-trionychid in the Oligocene of Kazakhstan, with "*T.*" *ninae* as the valid senior synonym.

## "*Trionyx*" *onomatoplokos*, new name

Taxonomic history. *Palaeotrionyx riabinini* Kuznetsov and Chkhikvadze, 1987 (new species and incorrect spelling of genus name); "*Paleotrionyx*" *riabinini* Kordikova 1992 (emended genus spelling); *Axestemys riabinini* Kordikova 1994a (new combination); *Khunnuchelys riabinini* Chkhikvadze 2000b (new combination); *Eurycephalochelys riabinini* Chkhikvadze 2007 (new combination).

Etymology. The new specific epithet *onomatoplokos* is derived from the Greek όνομα (i.e., onoma) meaning "name" and the verb πλέκω (i.e., pleko) meaning "to enfold or twist," alluding to the taxonomic confusion caused by the original specific epithet *riabinini* being applied to two distinct species from the same locality in the same publication.

Type material. IZK R-3920 (holotype), a nearly complete nuchal (Vitek and Danilov 2010, fig. 8; Danilov and Vitek 2013, fig. 23.2j).

Type locality. Shakh-Shakh, Kyzylorda Region, Kazakhstan (Kuznetsov and Chkhikvadze 1987; Vitek and Danilov 2010; Figure 3); Bostobe Formation, Santonian–early Campanian, Late Cretaceous (Vitek and Danilov 2010).

Referred material and range. No specimens haven been referred to date.

Diagnosis. "*Trionyx*" *onomatoplokos* can be diagnosed as a member of *Pan-Trionychidae* by the presence of sculpturing that covers all metaplastic portions of the shell bones and the absence of scutes. Among middle Late Cretaceous pan-trionychids, "*T.*" *onomatoplokos* can be differentiated from "*T.*" *kansaiensis* by lacking a broad nuchal notch and from "*T.*" *riabinini* by being larger and having a nuchal that is only partially covered by metaplastic bone.

Comments. "*Trionyx*" *onomatoplokos* is based on a single, large (15 cm wide) nuchal from the Late Cretaceous (Santonian or early Campanian) portions of the Bostobe Formation of Kazakhstan. We herein usually conclude that taxa based on single fragments should be considered dubious, but we here make an exception, as the pan-trionychid faunas of the Bostobe Formation are now well documented (Vitek and Danilov 2010), making it clear that the morphology being displayed by the type specimen is different from that displayed in the remainders of the fauna. We therefore here maintain this species as valid, while anticipating the discovery and description of more meaningful material.

In their review of fragmentary turtle material from the Bostobe Formation of Kazakhstan, Kuznetsov and Chkhikvadze (1987) named two new pan-trionychid species within the genera *Trionyx* and *Paleotrionyx*, but for reasons beyond our comprehension, they used the same species epithet twice, *riabinini*. From a taxonomic and nomenclatural perspective, this action is permissible, but highly confusing and impractical, because both species share the same authorship and publication date, because their generic affiliation remains under flux, and because both species were likely sympatric. As both taxa have unclear generic affiliations, we here assign both to "*Trionyx*," resulting in two homonymous species of pan-trionychids within the Bostobe Formation. We here provide the new name "*T.*" *onomatoplokos* for the species originally published as *Pal*[*a*]*eotrionyx riabinini*. This name may be short lived, as future work may support the referral of both species to two genera once again, but could be maintained permanently, if a petition is submitted to the International Commission on Zoological Nomenclature (ICZN).

## "*Trionyx*" *riabinini* Kuznetsov and Chkhikvadze, 1987

Taxonomic history. *Trionyx riabinini* Kuznetsov and Chkhikvadze, 1987 (new species); *Plastomenus riabinini* Chkhikvadze and Shuvalov 1988 (new combination); *Paraplastomenus riabinini* Kordikova 1994a (new combination); *Crassithecachelys riabinini* Chkhikvadze 2000b (new combination); *Aspideretoides riabinini* Vitek and Danilov 2010 (new combination).

Type material. IZK R-3919, (holotype), a partial nuchal (Vitek and Danilov 2010, fig. 5b, c; Danilov and Vitek 2013, fig. 23.2d).

Type locality. Shakh-Shakh, Kyzylorda Region, Kazakhstan (Kuznetsov and Chkhikvadze 1987; Vitek and Danilov 2010; Figure 3); Bostobe Formation, Santonian–early Campanian, Late Cretaceous (Vitek and Danilov 2010).

Referred material and range. Late Cretaceous (Santonian) Yalovach Formation, Fergana Depression, Kansai, Khodzhent Province, Tajikistan (referred material of Vitek and Danilov 2010).

Diagnosis. "*Trionyx*" *riabinini* can be diagnosed as a member of *Pan-Trionychidae* by the full list of shell characters listed above for that species. Among middle Late Cretaceous pan-trionychids, "*T.*" *riabinini* can be differentiated from "*T.*" *kansaiensis* by being smaller and lacking a broad nuchal notch, and from "*T.*" *onomatoplokos* by being smaller and having a nuchal that is fully covered by metaplastic bone.

Comments. "*Trionyx*" *riabinini* is based on a partial nuchal from the Late Cretaceous (Santonian or early Campanian) of Kazakhstan, but its validity is mostly supported by a rich collection of fragmentary material that was referred by Vitek and Danilov (2010) from roughly coeval sediments exposed in Tajikistan. Vitek and Danilov (2010) considered it highly probable that "*T.*" *riabinini* possesses a preneural, but this cannot be affirmed with certainty based on the available material. The rich Tajik material nevertheless allows reconstructing anatomical changes during ontogeny (Vitek and Danilov 2010). Over the course of the decades, "*T.*" *riabinini* has variously been referred to *Plastomenus* (Chkhikvadze and Shuvalov 1988), *Paraplastomenus* (Kordikova 1994a), *Crassithecachelys* (Chkhikvadze 2000b), and, most recently, *Aspideretoides* (Vitek and Danilov 2010). However, given new insights into the phylogenetic relationships of the type species of the latter genus (Vitek and Joyce 2015; Joyce et al. 2016), we find it prudent to reassign this species to the neutral "*Trionyx*." See also "*T.*" *onomatoplokos* above for the case of homonymy with *Pal*[*a*]*eotrionyx riabinini*.

## "*Trionyx*" *shiluutulensis* Danilov et al., 2014

Taxonomic history. "*Trionyx*" *shiluutulensis* Danilov et al., 2014 (new species).

Type material. MPC 25/166 (holotype), a carapace (Danilov et al. 2014, fig. 15).

Type locality. Shiluut Ula, Ömnögovi (= Umunugovi) Aimag, Mongolia (Figure 3); unknown formation, Campanian, Late Cretaceous (Danilov et al. 2014).

Referred material and range. No specimens haven been referred to date.

Diagnosis. "*Trionyx*" *shiluutulensis* can be diagnosed as a member of *Pan-Trionychidae* by the complete list of carapacial characters provided for that clade above. Among late Late Cretaceous pan-trionychids from Asia, "*T.*" *shiluutulensis* can most readily be differentiated from others by the presence of a preneural and eight neurals.

Comments. "*Trionyx*" *shiluutulensis* is based on a well-preserved, small (CL about 20 cm) carapace from the Late Cretaceous (Campanian) of Mongolia (Danilov et al. 2014) that can easily be distinguished from other Late Cretaceous taxa from Asia by the presence of a preneural. This bone is otherwise known from coeval plastomenids preserved in North America (Vitek and Joyce 2015; Joyce et al. 2016), but all known representatives of this lineage only possess seven neurals and significantly larger costals VIII. Additional material will be needed to clarify the phylogenetic placement of "*T.*" *shiluutulensis*, but its validity seems uncontroversial.

## "*Trionyx*" *silvestris* Walker and Moody, 1974 (= *T. michauxi* Broin, 1977)

Taxonomic history. *Trionyx silvestris* Walker and Moody, 1974 (new species); *T. sylvestris* Broin 1977 (incorrect spelling of species epithet); *Rafetoides henrici* = *T. silvestris* = 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. BMNH R 8567 (holotype), an almost complete cranium (Walker and Moody 1974, pl. 118.1–3; Karl 1998, pl. 6.1).

Type locality. Abbey Wood, Kent, United Kingdom (Figure 4); Blackheath Beds, early Ypresian, early Eocene (Walker and Moody 1974).

Referred material and range. Early Eocene (Ypresian), Sables à Unios et Térédines, Marne, France (type material of *Trionyx michauxi*; Broin 1977).

Diagnosis. "*Trionyx*" *silvestris* can be diagnosed as a member of *Pan-Trionychidae* by the full list of cranial characters provided for that clade above. Among Paleogene pan-trionychids from Europe known from cranial material, "*T.*" *silvestris* can only be differentiated by a broader contribution of the parietals to the skull roof.

Comments. "*Trionyx*" *silvestris* is based on a skull from the early Eocene of England (Walker and Moody 1974), which can be easily distinguished from the coeval giant pan-trionychid *Axestemys vittata* (see above) by its size and the development of broad anterior triturating surfaces. Early Eocene sediments in Belgium, France, and Great Britain have yielded many fragmentary remains that might be attributable to this taxon (e.g., Broin 1977), including the types of *T. bowerbanki* and *T. pustulatus* (see below), but clear associations are still lacking, and we are therefore reluctant to synonymize these taxa. Karl (1998) synonymized all medium-sized pan-trionychids from the early and late Eocene of Great Britain into "*T.*" *henrici*, which is typified by late Eocene material. We generally sympathize with this idea, as we too find strong resemblance among most Eocene pan-trionychid material, but we here do not support Karl's (1998) proposed synonymy, as the only preserved late Eocene skull (Boulenger 1891) is too poorly preserved to allow meaningful comparison. We find a close relationship with "*T.*" *messelianus* from the middle Eocene of Germany plausible as well, but the palate of this taxon remains undescribed, and we therefore cannot assess if meaningful similarities are apparent with the distinctive triturating surfaces of "*T.*" *silvestris*. By contrast, we see overwhelming similarities between the skull of "*T.*" *silvestris* and that of the coeval skull-based taxon *T. michauxi* from nearby France, in that both possess expanded triturating surfaces that are formed by a broad midline contact of the maxillae. Differences are apparent to the width of the triturating surfaces, the palate of *T. michauxi* being wider, but this is easily referable to interspecific variation, as previously documented for other extant and fossil pan-trionychids (Dalrymple 1977; Joyce et al. 2016). We therefore here synonymize these two species with confidence, though without certain generic affiliations. We are only able to differentiate "*T.*" *silvestris* from the roughly coeval "*T.*" *ikoviensis* from Ukraine by nuanced differences to the development of the parietal and biogeographic concerns.

## *Invalid and Problematic Taxa*

### *Altaytrionyx burtschaki* Chkhikvadze, 2008a nomen dubium

Taxonomic history. *Altaytrionyx burtschaki* Chkhikvadze 2008b (nomen nudum); *Altaytrionyx burtschaki* Chkhikvadze, 2008a (new species).

Type material. IPGAS 7-1-58 (holotype), medial part of a left hypoplastron (Chkhikvadze 2008b, fig. 11; Chkhikvadze 2008a, fig. 2); IPGAS 7-1-66 (paratype), medial part of a left hypoplastron (Chkhikvadze 2008a, fig. 3).

Type locality. Treugol'nik Locality, Kalmakpay River, Zaysan Depression, East Kazakhstan Region, Kazakhstan; lower part of Obaylinskoy suite (Chkhikvadze 2008a), middle Eocene (Danilov, Sukhanov et al. 2015).

Comments. Chkhikvadze (2008b) initially introduced this name along with a figure of what would later become the holotype, but he did not provide a description, and this contribution therefore does not qualify for nomenclatural purposes (ICZN 1999). In the same year, Chkhikvadze (2008a) formally described *Altaytrionyx burtschaki* and referred a partial hypoplastron to this taxon, which serves as a paratype. Chkhikvadze (2008a) considered this turtle to be the largest species of his newly established genus *Altaytrionyx* and diagnosed it relative to its congeners by the thickness of the shell, which is about 12 mm in the thickest part of the holotype, and by its sculpturing. Judging from the published figures, however, the available material bears no diagnostic characters and should rather be interpreted as an indeterminate pan-trionychid. For additional discussion, see "*Trionyx*" *ninae* (above).

### *Altaytrionyx devjatkini* Chkhikvadze, 2008a nomen dubium

Taxonomic history. *Altaytrionyx devjatkini* Chkhikvadze, 2008a (new species).

Type material. IPGAS (holotype), a right hypoplastron (Chkhikvadze 2008a, fig. 4); IPGAS (paratype), fragment of the right hyoplastron of a juvenile individual (Chkhikvadze 2008a, fig. 5); IPGAS (paratype), a left hyoplastron (Chkhikvadze 2008a, fig. 6); IPGAS (paratype), fragment of the medial part of the right hypoplastron of an old individual (Chkhikvadze 2008a, fig. 7).

Type locality. Sem'kamney Locality, Kalmakpay River, Zaysan Depression, East Kazakhstan Region, Kazakhstan; basal part of the Chakpaktasskoy suite (Chkhikvadze 2008a), early Eocene (Danilov, Sukhanov et al. 2015).

Comments. *Altaytrionyx devjatkini* is based on fragmentary plastral material that was originally reported to be Paleocene (Chkhikvadze 2008a), but more recently corrected to be early Eocene (Danilov, Sukhanov et al. 2015). Chkhikvadze (2008a) differentiated *Altaytrionyx devjatkini* from the other species of his *Altaytrionyx* by the absence of an epiplastral notch on the hyoplastron, presence of two axillary and inguinal processes on the hyo- and hypoplastra, and prominent sculpturing of the hyo- and hypoplastra, but these characters are now considered to be too general. For a discussion on the validity of pan-trionychid taxa from the Tertiary of Kazakhstan, see "*Trionyx*" *ninae* (above).

### *Altaytrionyx phiruzae* Chkhikvadze, 2008a nomen dubium

Taxonomic history. *Crassithecachelys phirusae* Chkhikvadze 1995 (nomen nudum); *Altaytrionyx phirusae* Chkhikvadze 2008b (nomen nudum); *Altaytrionyx phiruzae* Chkhikvadze, 2008a (new species, with alternative spelling of species epithet).

Type material. IPGAS 7-8-1 (holotype), medial part of a right hypoplastron (Chkhikvadze 2008b, fig. 10; Chkhikvadze 2008a, fig. 1).

Type locality. Chkhikvadze Locality, Aksyir River, Zaysan Depression, East Kazakhstan Region, Kazakhstan; the lower part of Obaylinskoy or Chakpaktasskoy suites (Chkhikvadze 2008a), early–middle Eocene (Danilov, Sukhanov et al. 2015).

Comments. Chkhikvadze (1995) initially introduced the name *Crassithecachelys phirusae*, but this action was not accompanied by a description, and this name therefore does not qualify for nomenclatural purposes (ICZN 1999). A few years later, Chkhikvadze (2008b) published the name *Altaytrionyx phirusae* together with a figure of the only known specimen, but a description was still lacking, and this name too cannot be considered for nomenclatural purposes (ICZN 1999). The name *Altaytrionyx phiruzae* finally became available when Chkhikvadze (2008a) published the name in concert with a brief description, although, frustratingly, two spellings were introduced, *Altaytrionyx phirusae* and *Altaytrionyx phiruzae*. We here select *Altaytrionyx phiruzae* as the valid spelling, as it appeared earlier in the text than the other spelling. Chkhikvadze (2008a) considered the age of *Altaytrionyx phiruzae* to be Paleocene, but it is now believed to be Eocene (Danilov, Sukhanov et al. 2015). *Altaytrionyx phiruzae* purportedly differs from the other species attributed to the same genus in terms of size, shell thickness, and the proportions of the hypoplastra (Chkhikvadze 2008a). However, judging from the published figures of the only known specimen, a hypoplastron, these differences seem to be minute and not sufficient to justify a valid trionychid taxon. For a discussion on the validity of pan-trionychid taxa from the Tertiary of Kazakhstan, see "*Trionyx*" *ninae* (above).

### *Amyda menneri* Chkhikvadze, 1988
### nomen dubium

Taxonomic history. *Amyda menneri* Chkhikvadze in Chkhikvadze and Shuvalov, 1988 (new species); *Amyda menenri* Sukhanov 2000 (incorrect spelling of species epithet); [*Amyda menneri*] Danilov et al. 2014 (nomen dubium).

Type material. IPGAS 11-5-1 (holotype), incomplete postcranium of a single individual, including a nuchal, the proximal part of costal I, a fragment of the right hyo-hypoplastron, a fragment of a xiphiplastron, and assorted nonshell bones (Chkhikvadze and Shuvalov 1988, fig. 1a); IPGAS 11-5-2 (paratype), nuchal fragment; IPGAS 11-5-3 (paratype), anterior part of a carapace; IPGAS 11-5-4 (paratype), distal part of right hyoplastron; IPGAS 11-5-5 (paratype), right costal VII; IPGAS 11-5-6 (paratype), right hyoplastron (Chkhikvadze and Shuvalov 1988, fig. 1c); IPGAS 11-13-11 (paratype), medial part of right hyoplastron; IPGAS 11-14-2 (paratype), left posterior part of carapace; IPGAS 11-14-3 (paratype), medial part of left hypoplastron (Chkhikvadze and Shuvalov 1988, fig. 1d); IPGAS 11-14-4 (paratype), posterior part of carapace (Chkhikvadze and Shuvalov 1988, fig. 1e); IPGAS 11-17-1 (paratype), left half of carapace.

Type locality. Gurilin Tsav, Ömnögovi (= Umunugovi) Aimag, Mongolia (Chkhikvadze in Chkhikvadze and Shuvalov 1988; Danilov et al. 2014); Nemegt Formation, Maastrichtian, Late Cretaceous (Danilov et al. 2014).

Comments. *Amyda menneri* was established on the basis of isolated shell fragments from several localities within the Nemegt Formation of south central Mongolia (Chkhikvadze and Shuvalov 1988). Danilov et al. (2014) concluded that the material may represent a chimera, that the holotype is not diagnostic, and that *Amyda menneri* is a nomen dubium (Danilov et al. 2014). We fully agree with this assessment.

### *Amyda neimenguensis* Yeh, 1965
### nomen invalidum
### (junior synonym of "*Trionyx*" *johnsoni* [Gilmore, 1931])

Taxonomic history. *Amyda neimenguensis* Yeh, 1965 (new species).

Type material. IVPP V 2870 (holotype), posterior portions of a carapace (Yeh 1965, fig. 4, pl. 7).

Type locality. Ulan Shireh, Inner Mongolia, China (Yeh 1965); middle Eocene (Danilov, Sukhanov et al. 2015).

Comments. *Amyda neimenguensis* is based on a large carapace (CL about 50 cm) from the middle Eocene of Inner Mongolia. The holotype was initially believed to be late Eocene in age (Yeh 1965), but was more recently reassigned to the middle Eocene. Yeh (1965) noted similarities with "*Trionyx*" *johnsoni* but nevertheless justified the recognition of a new species based on differences in carapace shape and size, shape and size of neural VI, and carapace sculpturing. Given that both *Amyda neimenguensis* and "*T.*" *johnsoni* are now known to originate from roughly coeval sediments in the same geographic area and that both are characterized by small costals VIII combined with unusually enlarged distal margins of costals VI, we here synonymize these taxa with confidence.

### *Aspideretes alashanensis* Yeh, 1965
### nomen invalidum
### (junior synonym of *Kuhnemys maortuensis* [Yeh, 1965])

Taxonomic history. *Aspideretes alashanensis* Yeh, 1965 (new species); *Paraplastomenus alashanensis* Kordikova 1994a (new combination).

Type material. IVPP V2865 (holotype), a damaged carapace (Yeh 1965, fig. 2, pl. 3; Danilov and Vitek 2013, fig. 23.2c).

Type locality. Dashukou, Maortu (= Maorty), Alxa (= Alashan), Inner Mongolia, China (Yeh 1965); Ulansuhai Formation, Turonian, Late Cretaceous (Brusatte et al. 2009).

Comments. *Aspideretes alashanensis* is based on a partial carapace from Inner Mongolia, China, that was recovered from the same locality as the holotype of *Kuhnemys maortuensis* (Yeh 1965). These specimens were long believed to be poorly dated at either late Early Cretaceous or early Late Cretaceous (Brinkman et al. 2008), but we here show that they most likely originate from the Ulansuhai Formation, which is currently dated as Late Cretaceous (Turonian). The type of *Aspideretes alashanensis* corresponds in all important details with that of the better-preserved type of *Kuhnemys maortuensis*, especially by showing highly reduced costals VIII, and we therefore synonymize the two. As both names were formed in the same publication, and as no rules exist that should be given preference, such as page priority, we, as primary revisers, here chose *maortuensis* as the senior synonym (see *Kuhnemys maortuensis* above for additional comments).

### *Aspideretes jaxarticus* Riabinin 1938
### nomen nudum

Material. None discussed or designated.

Locality. Kyrkkuduk well (= Sary-Agach = Kyrkkuduk I), South Kazakhstan Region, Kazakhstan (Riabinin 1938; Kordikova 1994b); Syuk-Syuk Formation or lower part of Darbaza Formation, Santonian or Campanian, Late Cretaceous (Kordikova 1994b; Danilov and Vitek 2013).

Comments. Riabinin (1938) briefly mentioned pan-trionychid remains from the Sary-Agach (now Kyrkkuduk well) locality as representing two new species of pan-trionychid turtles: *Plastomenus jaxarticus* (see below) and *Aspideretes jaxarticus*. It is mystifying that he assigned the same species epithet to both taxa, as this creates much confusion, even if both taxa are not available or valid (see discussion in "*Trionyx*" *onomatoplokos* about *Trionyx riabinini* Kuznetsov and Chkhikvadze, 1987, and *Paleotrionyx riabinini* Kuznetsov and Chkhikvadze, 1987, for a similar example). Riabinin (1938) did not provide descriptions, diagnoses, figures, or holotypes for either taxon, and these names can therefore be interpreted as nomina nuda (Vitek and Danilov 2012), thereby sparing the fossil turtle community additional taxonomic aggravation.

### *Aspideretes muyuensis* Lei and Ye, 1985
### nomen dubium

Taxonomic history. *Aspideretes muyuensis* Lei and Ye, 1985 (new species); *Paleotrionyx muyuensis* Chkhikvadze 1990 (new combination); *Eurycephalochelys muyuensis* Chkhikvadze 2007 (new combination).

Type material. YIGM V 25517 (holotype), a rather complete carapace, plastron, and parts of the pelvis (Lei and Ye 1985, figs. 2, 3; Ye 1994, fig. 69).

Type locality. Muyu, Nanzhang County, Hubei Province, China; Yangxi Formation, early Eocene (Lei and Ye 1985).

Comments. *Aspideretes muyuensis* is based on a relatively small, poorly documented shell from the Eocene of China (Lei and Ye 1985). The size of the holotype is unclear, as two different scale bars and the table imply different sizes, but is seems that the carapace is relatively small, likely less than 15 cm. Lei and Ye (1985) considered this taxon to be a probable member of *Nilssonia* (his *Aspideretes*) on the basis of the presence of a preneural, but we question the veracity of this observation, as the relevant portion of the shell is not well preserved. Chkhikvadze (1990, 2007) saw similarities with the giant pan-trionychids of North America, but this is perhaps a misunderstanding caused by the confusing use of conflicting scale bars. Until the holotype has been redescribed in greater detail, we find this taxon to be dubious, as we cannot find characters that allow us to rigorously diagnose a valid taxon. Chkhikvadze (1990) described fragments from the middle Eocene of Kazakhstan under the name *Paleotrionyx* cf. *muyuensis* (Chkhikvadze 1990), which now serve as the holotype of *Zaisanonyx jimenezfuentesi* (see below). We confirm that these have no apparent similarities with the taxon from China.

### *Aspilus cortesii* Portis, 1885
### nomen dubium

Taxonomic history. *Aspilus cortesii* Portis, 1885 (new species); [*Trionyx cortesii*] Hummel 1929 (new combination, nomen dubium); *Trionyx cortisii* Bergounioux 1935 (incorrect spelling of species epithet).

Type material. MPP (holotype), a partial cranium with mandible (Portis 1885, pl. 11.2–3).

Type locality. Exact locality unknown (Portis 1885; Kotsakis 1985), probably Montezago, Emilia-Romagna, Italy (Broin 1977; Chesi 2009); late Miocene or Pliocene (Portis 1885; Kotsakis 1985).

Comments. *Aspilus cortesii* is based on a 13 cm long skull with uncertain provenience. Portis (1885) suggested that this specimen shows close relationship with the extant *Amyda cartilaginea* (his *Aspilus cariniferus*), thereby establishing the purported presence of this Asian group in Europe, but Hummel (1929) believed it to be an indeterminate trionychid.

The skull of *Aspilus cortesii* is elongated and has relatively large orbits, but it was only figured in dorsal and lateral view and shows extensive damage. As such, although this is one of the few European taxa based on cranial material, no characters are available that would rigorously diagnose this as a valid taxon. We here therefore consider *Aspilus cortesii* to be nomen dubium but join Kotsakis (1985) in calling for a systematic revision of the available material.

### *Chitra minor* Jaekel, 1911
### nomen dubium

Taxonomic history. *Chitra minor* Jaekel, 1911 (new species); [*Chitra minor*] Hummel 1929 (nomen dubium); *Chitra indica* = *Chitra minor* Karl 1987 (junior synonym); *Pelochelys cantorii* = *Chitra minor* Rhodin et al. 2015 (junior synonym).

Type material. MB R2496.1-2 (syntypes), a right xiphiplastron and a left hypoplastron (Jaekel 1911, pl. 15.3, 4).

Type locality. Trinil, Java, Indonesia (Jaekel 1911); Trinil Formation, Pleistocene (McCord and Pritchard 2002).

Comments. *Chitra minor* is based on two plastral fragments from the Pleistocene of Java, Indonesia (Jaekel 1911). Karl (1987) considered this taxon to be a junior synonym of the extant *Chitra indica* as he believed their morphology, at least as present, to correspond fully. McCord and Pritchard (2002), on the other had, suggested that the features presented in the available material were not sufficient to diagnose a valid species. However, given the current distribution of giant soft-shelled turtles, they suggested that these fragments are not referable to *Chitra*, but rather *Pelochelys*, and that *Chitra minor* is probably a junior synonym of *Pelochelys cantorii*, which occurs in the extant fauna of Java. The type and only known material is fragmentary, and, judging from the original figures of Jaekel (1911), we find it insufficient to allow attribution to either *Chitra* or *Pelochelys*. We therefore suggest that *Chitra minor* is a nomen dubium.

## *Chitra selenkae* Jaekel, 1911
## nomen suppressum
## (suppressed senior synonym of *Chitra chitra* Nutaphand, 1986)

Taxonomic history. *Chitra selenkae* Jaekel, 1911 (new species); *Chitra indica* = *Chitra selenkae* Karl 1987 (junior synonym); *Chitra chitra* = *Chitra selenkae* ICZN 2005 (suppressed senior synonym).

Type material. MB R2495.1-3 (syntypes), a scapula, a right xiphiplastron, and a clavicle (Jaekel 1911, pl. 15.1, 2, 11; Karl 1987, pl. 14.2).

Type locality. Trinil, Java, Indonesia (Jaekel 1911); Trinil Formation, Pleistocene (McCord and Pritchard 2002, 2003; Rhodin et al. 2015).

Comments. This species is based, among others, on a large carapace with a midline length of 64 cm (McCord and Pritchard 2002). Karl (1987) considered this to be a junior synonym of *Chitra indica* based on overall correspondence in morphology. A few years later, McCord and Pritchard (2002) noted several features that establish a close vicinity of *Chitra selenkae* with extant *Chitra chitra*, but they were reluctant to formally propose a synonymy, as such a synonymy would partially depend on the species concept being chosen and because the extinct *Chitra selenkae* Jaekel, 1911, would have priority over the extant *Chitra chitra* Nutaphand, 1986. The same authors therefore soon after made a formal petition to the ICZN (McCord and Pritchard 2003) requesting that *Chitra chitra* should receive priority over *Chitra selenkae* whenever the two are considered synonyms, a petition that was accepted by the ICZN (Opinion 2119, ICZN 2005). Rhodin et al. (2015) recently listed *Chitra selenkae* as a junior synonym of *Chitra chitra*. Although cryptic diversity in extant *Chitra* has been documented (Engstrom et al. 2002), the resemblance of *Chitra selenkae* with the extant *Chitra chitra* is remarkable. We agree that *Chitra selenkae* is the suppressed senior synonym of *Chitra chitra*.

## *Emyda lineata* Lydekker, 1885
## nomen dubium, designation of lectotype

Taxonomic history. *Emyda lineata* Lydekker, 1885 (new species); [*Emyda lineata*] Hummel 1929 (nomen dubium); *Lissemys lineata* Kuhn 1964 (new combination).

Type material. IMC E210 (lectotype), a fragmentary peripheral (Lydekker 1885, pl. 26.6); IMC E132 (paralectotype), a partial nuchal (Lydekker 1885, pl. 26.3).

Type locality. Siwaliks, Punjab, Pakistan (see comments below); Pliocene (Lydekker 1885).

Comments. Lydekker (1885) established three new pan-trionychid taxa from the Pliocene of British India on the basis of rather fragmentary material: *Emyda lineata*, *Emyda palaeindica*, and *Emyda sivalensis*. For all three taxa, he did not specify an explicit type locality, but rather only mentioned that the specimens originated from "the Indus Valley of Punjab," an area that more or less matches the entire Punjab, if the Indus Valley is interpreted as the Indus Valley drainage basin. After the dissolution of British India, the Punjab was divided by the newly established countries of India and Pakistan into two provinces holding this name. Given that the Punjabi portion of the Siwalik hills is almost entirely located within the Pakistani side and that most of the fossils with good provenience were collected on this side as well (e.g., Joyce and Lyson 2010b), it seems reasonable to infer that the fossils described by Lydekker (1885) were collected within the boundary of modern-day Pakistan.

Lydekker (1885) erected *Emyda lineata*, *Emyda palaeindica*, and *Emyda sivalensis* on the basis of three syntype series that each consist of at least one peripheral and one nuchal, and he differentiated these three taxa relative to the extant *Lissemys punctata* by their sculpturing pattern (Lydekker 1885). As it remains unclear if the syntypes of these taxa originate from the same locality, we here designate a peripheral for each taxon as its lectotype. Hummel (1929) thought all three taxa to be dubious, but Delfino et al. (2010) more recently suggested that they may eventually be shown to be junior synonyms of the extant *Lissemys punctata*. Taking into consideration the Pliocene age of Lydekker's (1885) specimens, the cryptic diversity observed among extant *Lissemys* (Praschag et al. 2011), and legitimate criticism regarding the identification of fragmentary fossils based on the currently existing herpetofauna (Bell et al. 2010), we here defy the synonymization of the Punjabi taxa with the extant *Lissemys punctata*, although assignment to the *Lissemys* lineage seems certain based on the presence of peripherals (Meylan 1987).

In addition to the fragmentary syntypes of *Emyda lineata*, *Emyda palaeindica*, and *Emyda sivalensis*, Lydekker (1885) also described a relatively complete shell from the same region that he identified as the extant *Lissemys punctata* (his *Emyda vittata*). Although we find no evidence that would contradict that conclusion, we refer this specimen to *Lissemys* sp. and await further preparation, description, and analysis of that specimen.

## *Emyda palaeindica* Lydekker, 1885
## nomen dubium, designation of lectotype

Taxonomic history. *Emyda palaeindica* Lydekker, 1885 (new species); [*Emyda palaeindica*] Hummel 1929 (nomen dubium); *Lissemys palaeindica* Kuhn 1964 (new combination).

Type material. IMC E134a (lectotype), one complete peripheral (Lydekker 1885, pl. 14.5, 5a); IMC E132a (paralectotype), one nuchal fragment (Lydekker 1885, pl. 14.10).

Type locality. Siwaliks, Punjab, Pakistan (see *Emyda lineata* above); Pliocene (Lydekker 1885).

Comments. See *Emyda lineata* above for comments.

### *Emyda sivalensis* Lydekker, 1885 nomen dubium, designation of lectotype

Taxonomic history. *Emyda sivalensis* Lydekker, 1885 (new species); [*Emyda sivalensis*] Hummel 1929 (nomen dubium); *Lissemys sivalensis* Kuhn 1964 (new combination).

Type material. IMC E134 (lectotype), fragment of a peripheral (Lydekker 1885, pl. 26.9); IMC E133 (paralectotype), right half of a nuchal (Lydekker 1885, pl. 26.2); IMC E135 (paralectotype), a partial peripheral (Lydekker 1885, pl. 26.7).

Type locality. Siwaliks, Punjab, Pakistan (see *Emyda lineata* above); Pliocene (Lydekker 1885).

Comments. *Emyda sivalensis* Lydekker, 1885 should not be confused with *Trionyx hurum sivalensis* Lydekker, 1889a, a probable junior synonym of the extant *Nilssonia hurum* (see below). See *Emyda lineata* above for additional comments.

### *Eurycephalochelys fowleri* Moody and Walker, 1970 nomen invalidum (junior synonym of *Axestemys vittata* [Pomel, 1847])

Taxonomic history. *Eurycephalochelys fowleri* Moody and Walker, 1970 (new species); *Erycephalochelys fowleri* Benton and Spencer 1995 (incorrect spelling of genus name).

Type material. BMNH R8445 (holotype), an almost complete skull, without the lower jaw (Moody and Walker 1970, figs. 1–5, pl. 102).

Type locality. East Wittering, West Sussex, United Kingdom; Wittering Formation, Bracklesham Series, late Ypresian, early Eocene (Moody and Walker 1970; Walker and Moody 1985).

Comments. *Eurycephalochelys fowleri* is based on a large skull with a total length of 21.5 cm (Moody and Walker 1970), but a much larger and better-preserved specimen was more recently described from the same formation with a 23.4 cm length from the premaxilla to occipital condyle only (Walker and Moody 1985). Moody and Walker (1970) and Walker and Moody (1985) repeatedly ascertained the distinctness of their taxon relative to material from the European mainland, but we here synonymize it with *Axestemys vittata* (see above).

Early Eocene sediments exposed at Bracklesham, England, also yielded the type specimen of *Trionyx bowerbanki* Lydekker, 1889a, but we here agree that these two are not synonymous, as the holotype of *T. bowerbanki*, an isolated nuchal, is too small and too well ossified for a representative of the *Axestemys* lineage. On the other side, unpublished specimens held in the collections of the BMNH indicate the presence of plastral elements that correspond to those of *Axestemys vittata* by being large and by having extremely reduced callosities. We are therefore certain that *T. bowerbanki* is not closely related with *Axestemys vittata*.

### *Lissemys piramensis* Prasad, 1974 nomen dubium

Taxonomic history. *Lyssemys piramensis* Prasad, 1974 (new species and incorrect spelling of genus name).

Type material. GSI 18134 (holotype), an incomplete peripheral (Prasad 1974, pl. 2.8).

Type locality. Piram (= Perim) Island, Gujarat, India; Piram Conglomerate, Pliocene (Prasad 1974).

Comments. Prasad (1974) established *Lissemys piramensis* on the basis of an incomplete peripheral from the Pliocene of Piram Island, India, that he differentiated relative to fossil (Lydekker 1885) and extant species of *Lissemys* on the basis of sculpturing pattern. Curiously, Prasad (1974) did not mention the beautiful *Lissemys* skull that had been described by Lydekker (1889b) from Perim Island. In any case, the type material of *Lissemys piramensis* is not adequate for diagnosing a specimen to the species level, and we herein therefore consider *Lissemys piramensis* to be a nomen dubium.

### *Lissemys punctata sinhaleyus* Deraniyagala, 1953 nomen dubium

Taxonomic history. *Lissemys punctata sinhaleyus* Deraniyagala, 1953 (new subspecies).

Type material. NMC F283 (holotype), a left hypoplastron (Deraniyagala 1953, not figured).

Type locality. Sabaragamuwa Province, Sri Lanka (Deraniyagala 1953); Ratnapura Beds, Late Pleistocene (Rhodin et al. 2015).

Comments. This taxon was described on the basis of a single hypoplastron that was purported to be rather similar to the extant Sri Lankan endemic *Lissemys ceylonensis*, but the type was never figured (Deraniyagala 1953) making it impossible to reproduce this claim. Rhodin et al. (2015) somewhat inconsistently stated that this species is a nomen dubium but nevertheless referred it to *Lissemys ceylonensis* pending further analysis. Considering that the holotype was never figured, we here refrain from synonymizing this taxon with the extant form and rather consider it to be a nomen dubium.

### *Pelochelys taihuensis* Zhang, 1984 nomen invalidum, designation of lectotype (junior synonym of *Rafetus swinhoei* [Gray, 1873])

Taxonomic history. *Pelochelys taihuensis* Zhang, 1984 (new species); *Rafetus swinhoei* = *Pelochelys taihuensis* = *Trionyx liupani* Farkas 1992 (junior synonym); *Rafetus swinhoei* = *Pelochelys taihuensis* Chkhikvadze 1999b (junior synonym).

Type material. ZPM TNO9.5 (lectotype), a fossil skull (Zhang 1984, figs. 1.2, 3.4), probably lost (Farkas and Fritz 1998); ZPM TNO9.9 (paralectotype), a fossil left costal IV (Zhang 1984, fig.

3.5); ZPM (paralectotypes), two extant individuals, skeletonized and stuffed (Zhang 1984, figs. 1.1, 3.1, 2,6).

Type locality. Tongxiang County, Zhejiang Province, China (Zhang 1984); Neolithic, Holocene (Farkas and Fritz 1998). The extant specimens are from Zhejiang Province, China.

Comments. *Pelochelys taihuensis* is based on a mixture of subfossil and extant material from Zhejiang Province, China (Zhang 1984). For the sake of taxonomic clarity, we herein designate the most complete fossil specimen, a subfossil skull, as the lectotype of this taxon. The lectotype cannot be located now (Farkas and Fritz 1998), and the available illustrations only document a skull that must have exceeded 20 cm in total length when it was complete in dorsal view. Farkas (1992) and Farkas and Fritz (1998) stated that this subfossil skull can be safely attributed to the extant taxon *Rafetus swinhoei*, which used to occur in the same region, and that both taxa are therefore synonymous. Although no quality characters evidence is available, we nevertheless support this conclusion as geographic and temporal concerns combined with the large size of the lectotype make this attribution highly likely.

## *Plastomenus gabunii* Chkhikvadze, 1984 nomen dubium

Taxonomic history. *Plastomenus gabunii* Chkhikvadze, 1984 (new species); *Paraplastomenus gabunii* Kordikova 1994a (new combination); *Amyda gabunii* Chkhikvadze 1999a (new combination); *Altaytrionyx gabunii* Chkhikvadze 2008b (new combination).

Type material. IPGAS (holotype), a hypoplastron (Chkhikvadze 1984, pl. 11.4; Chkhikvadze 2008b, fig. 9a, b).

Type locality. Chyornyy Trioniks, Aksyir River, Zaysan Depression, East Kazakhstan Region, Kazakhstan; upper Obaylinskoy suits, middle Eocene (Chkhikvadze 1984, 2008a, 2008b).

Comments. *Plastomenus gabunii* has had a complex taxonomic history by being referred to multiple genera, incidentally by the same person who established the species in the first place (Chkhikvadze 1984, 1990, 2007, 2008b). In its latest combination, *Plastomenus gabunii* was rendered as the type species of *Altaytrionyx*, a poorly defined genus diagnosed by its hypoplastral morphology (Chkhikvadze 2008b). In addition to having thick shell bones, a feature first thought to link this species with the North American clade *Plastomenidae*, *Plastomenus gabunii* is also characterized by the absence of a midline contact of the hyohypoplastra, a small xiphiplastral fontanelle, thickened inguinal notch, and an estimated CL of 25 to 35 cm. These characters are extremely general among pan-trionychids and therefore not adequate to diagnose a taxon, even in their combination. For a discussion on the validity of pan-trionychid taxa from the Tertiary of Kazakhstan, see "*Trionyx*" *ninae* (above).

Kordikova (1994b) referred several specimens from the middle Eocene of Chinzhaly, Balkhash Lake region, Kazakhstan, to this taxon, but given that we conclude that *Plastomenus gabunii* is a nomen dubium, we reidentify Kordikova's (1994b) material as belonging to an indeterminate pan-trionychid.

## *Plastomenus jaxarticus* Riabinin 1938 nomen nudum

Material. None discussed or designated.

Locality. Kyrkkuduk well (= Sary-Agach = Kyrkkuduk I), South Kazakhstan Region, Kazakhstan (Riabinin 1938; Kordikova 1994b); Syuk-Syuk Formation or lower part of Darbaza Formation, Santonian or Campanian, Late Cretaceous (Kordikova 1994b; Vitek and Danilov 2012).

Comments. For a discussion on material from the Kyrkkuduk well locality, see *Aspideretes jaxarticus* (above).

## *Plastomenus mlynarskii* Chkhikvadze, 1970 nomen dubium

Taxonomic history. *Plastomenus mlynarskii* Chkhikvadze, 1970 (new species); *Paraplastomenus mlynarskii* Kordikova 1994a (new combination); *Crassithecachelys mlynarskii* Chkhikvadze 2000a (new combination); *Plastomenus mlnarskii* Broin 1977 (incorrect spelling of species epithet).

Type material. IPGAS Z-1-64 (holotype), a right hypoplastron (Chkhikvadze 1970; Chkhikvadze 1973, fig. 3, pl. 3.1).

Type locality. "Trugol'nik," Kalmakpay River, East Kazakhstan Region, Kazakhstan; middle Eocene (Chkhikvadze 1970, 2000a).

Comments. Chkhikvadze (1970) established *Plastomenus mlynarskii* based on a hypoplastron from the middle Eocene of Kazakhstan, for which he initially only provided a plastral restoration. Three years later, the same author provided photographs of the holotype and of a referred hyoplastron and a xiphiplastron, apparently the ones he used to originally diagnose this species (Chkhikvadze 1973). Kordikova, (1994a) felt that this species is highly unusual and therefore referred it to a new genus, *Paraplastomenus*. Chkhikvadze (2000a) later accused Kordikova (1994a) of plagiarism, invalidated *Paraplastomenus*, and established a new genus, *Crassithecachelys*, as a replacement. However, even if the cause of Chkhikvadze (2000a) was just, it is clear according to the rules of the ICZN (1999) that *Paraplastomenus* has priority over *Crassithecachelys*. For a discussion on the validity of pan-trionychid taxa from the Tertiary of Kazakhstan, see "*Trionyx*" *ninae* (above).

Kordikova (1994b) referred fragmentary material from the early to middle Eocene of East Kazakhstan Region to this taxon. However, none of this material was figured, and we therefore refer it all to *Pan-Trionychidae* indet.

## *Platypeltis subcircularis* Chow and Yeh, 1957 nomen dubium

Taxonomic history. *Platypeltis subcircularis* Chow and Yeh, 1957 (new species); *Trionyx subcircularis* Kuhn 1964 (new combination); *Platypeltis subcircularus* Chkhikvadze 1973 (incorrect spelling of species epithet).

Type material. IVPP V914 (holotype), anterior two-thirds of the right part of a carapace (Chow and Yeh 1957, pl. 1.1–3).

Type locality. Lushi (= Lushih) County, Henan (= Honan) Province, China; late Eocene (Chow and Yeh 1957).

Comments. *Platypeltis subcircularis* is a relatively small pan-trionychid known from a single, fragmentary specimen representing the anterior right part of the carapace. Chow and Yeh (1957) assigned this taxon to the otherwise American *Apalone* (their *Platypeltis*), highlighting affinities especially with *Platypeltis serialis* (= *Plastomenus serialis*) and *Platypeltis trepida*, which are both now considered nomina dubia (Vitek and Joyce 2015). *Platypeltis subcircularis* was differentiated based on the presence of six neurals only, but this character by itself is not particularly diagnostic. Given that this species is based on what is best interpreted as a juvenile specimen, we here consider this taxon to be a nomen dubium.

## *Procyclanorbis sardus* Portis, 1901
## nomen dubium

Taxonomic history. *Procyclanorbis sardus* Portis, 1901 (new species); *Trionyx sardus* Hummel 1929 (new combination); *Amyda sardus* Comaschi Caria 1959 (new combination); *Amyda sarda* Comaschi Caria 1986 (emended spelling of species epithet).

Type material. MDLCA 14007 (holotype), a carapace and its mold (Portis 1901, pl. 1.1; Zoboli and Pillola 2016, fig. 2a, c, d).

Type locality. Is Mirrionis, Cagliari, Sardinia, Italy (Portis 1901); Calcari di Cagliari Formation, late Tortonian–Messinian, late Miocene (Kotsakis 1985).

Comments. *Procyclanorbis sardus* is based on a carapace from the late Miocene of Sardinia, Italy, that was described in concert with plastral material and a skull from the same locality (Portis 1901). The same author further referred an internal mold of a carapace from a different Sardinian locality (Sassari) to the same species (Portis 1901). As the name readily suggests, Portis (1901) considered his new species to have close affinities with pan-cyclanorbines. Hummel (1932), however, soon after defied this identification and assigned this species to *Trionyx*. Other specimens from Sardinia have been referred to the same species using geographic considerations (Comaschi Caria 1959; Kotsakis 1985), but none of these display diagnostic characteristics beyond *Pan-Trionychinae* indet.

It is unclear to us if Portis (1901) would have considered the plastron and skull to be part of the syntype series, but even a cursory glance reveals that these are not trionychid in nature. Broin (1977) already noted that the skull, which was destroyed during World War II (Kotsakis 1985), pertains to a cheloniid turtle, instead of a pan-trionychid, a view subsequently adopted by Kotsakis (1985) and also supported by us based on the published figure. Previous authors seem to have ignored the plastral material, but we find that this is also referable to a marine turtle. At best, *Procyclanorbis sardus* is therefore a poorly diagnosed trionychid, and, at worst, a chimera that includes trionychid and cheloniid material.

Our study of photographs available to us confirms that *Procyclanorbis sardus* is not a cyclanorbine, because a preneural is missing and because the nuchal, which is preserved in internal view, clearly lacks split costiform processes (Meylan 1987). Although the specimen is once again consistent with the morphology of the *Trionyx triunguis* lineage (Karl 1999a), it can only be diagnosed as *Pan-Trionychinae* indet. We therefore herein consider *Procyclanorbis sardus* to be a nomen dubium. Bergounioux (1935) reported the presence of *Procyclanorbis* (his *Amyda*) *sardus* from the Miocene of Switzerland, but this appears to be an error (Esu and Kotsakis 1983).

## *Rafetus gilmorei* Chkhikvadze, 1999b
## nomen invalidum
## (junior synonym of "*Trionyx*" *gregarius* [Gilmore, 1934])

Taxonomic history. *Rafetus gilmorei* Chkhikvadze, 1999b (new species); *Oskaria gilmorei* Chkhikvadze 2008b (new combination and incorrect spelling of genus name); *Amyda gregaria* = *Rafetus gilmorei* Vitek and Danilov 2015 (junior synonym).

Type material. AMNH 6736 and AMNH 6737 (syntypes), two complete skeletons (Gilmore 1934, figs. 2, 4; Chkhikvadze 2008b, fig. 4a–c).

Type locality. Camp Margetts, 25 miles southwest of Iren Dabasu, Inner Mongolia, China (Gilmore 1934); Irdin Manha Formation, middle Eocene (Vitek and Danilov 2015).

Comments. For a discussion on the validity of *Rafetus gilmorei*, see "*Trionyx*" *gregarius* above.

## *Rafetus karkhualexandri* Chkhikvadze 2000b
## nomen nudum

Material. None discussed or designated.

Locality. Bulkair, Zaysan Depression, East Kazakhstan Region, Kazakhstan (Chkhikvadze 2007); Nizhnesvirsky subsuite, probably Eocene or Oligocene (Chkhikvadze 2007).

Comments. This name was only mentioned in passing by Chkhikvadze (2000b, 2007) in regard to a taxon that might be named in the future, but no specimens are either referred, listed, or described. This is therefore herein considered to be a nomen nudum.

## *Rafetus yexiangkuii* Chkhikvadze, 1999b
## nomen dubium

Taxonomic history. *Rafetus yexaiangkui* Chkhikvadze 1999a (nomen nudum); *Rafetus yexiangkuii* Chkhikvadze, 1999b (new species); *Yuen yexiangkuii* Chkhikvadze 2007 (new combination); *Oskaria yexiangkuii* Chkhikvadze 2010 (new combination).

Type material. IPGAS 7-370-1 (holotype), a left hypoplastron (Chkhikvadze 1999b, not figured).

Type locality. Mailibai, East Kazakhstan Region, Kazakhstan; Buranskaya suite, Buran Formation, early Oligocene (Chkhikvadze 1999b, 2007; Vitek and Danilov 2015).

Comments. The type description of *Rafetus yexiangkuii* does not include any figures, but a description and diagnosis are present (Chkhikvadze 1999b), and this name therefore fulfills the minimum requirements of the ICZN (1999) for the availability of names published prior to 2000. The holotype unfortunately remains unfigured to date making it particularly taxing to evaluate the validity of this taxon. Chkhikvadze (1999b) differentiated *Rafetus yexiangkuii* from all other extinct pan-trionychids by several characters that pertain to the nuchal, even though no such element was ever referred to this taxon (Chkhikvadze 1999b). We therefore here consider this taxon to be a nomen dubium (also see "*Trionyx*" *ninae* above for more extensive discussion).

## *Trionyx acutiformis* Bergounioux, 1935
## nomen dubium

Taxonomic history. *Trionyx acutiformis* Bergounioux, 1935 (new species).

Type material. LG-FSM (holotype), a carapace fragment (Bergounioux 1935, fig. 28, pl. 11.2), probably lost (Broin 1977).

Type locality. Armissan, Aude, France (Bergounioux 1935); Chattian or Aquitanian, late Oligocene or early Miocene (Hervet 2004).

Comments. Bergounioux (1935) named a total of four trionychid taxa, *Trionyx acutiformis*, *T. chaubeti*, *T. ciryi*, and *T. mourieri* based on fragmentary material recovered from the late Oligocene or early Miocene of Armissan, France. Broin (1977) reported the presence of carapace fragments in the collections of MNHN that bear the label "*Trionyx armissansis* Gervais," which apparently pertain to the pan-trionychid from Armissan described and figured by Gervais (1867–1869), but this name only appears in a museum label and does not meet the standards of ICZN (1999) for availability. Broin (1977) in additional considered all Armissan species to be probable synonyms but ultimately concluded that the material is not diagnostic. We here conclude all named specimens from Armissan to be nomina dubia, as they do not display diagnostic characters (see *T. vindobonensis* for more extensive discussion).

## *Trionyx affinis* Negri, 1892
## nomen invalidum
## (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx affinis* Negri, 1892 (new species); *T. capellinii affinis* Sacco 1894 (new combination); *T. c. capellinii* = *T. c. affinis* = *T. c. conjugens* Kotsakis 1977 (junior synonym); *T. capellinii* = *T. c. affinis* = *T. c. conjugens* = *T. gemmellaroi* = *T. intermedius* Kotsakis 1985 (junior synonym).

Type material. MGP-PD 12806 (holotype), a nearly complete carapace (Negri 1892, pl. 5.1; Bergounioux 1954, fig. 10, pl. 2; Kotsakis 1977, fig. 3e).

Type locality. Monte Bolca (= Purga di Bolca), Veneto, Italy (Negri 1892); Prati Valeno Horizon, Lutetian, middle Eocene (Giusberti et al. 2014).

Comments. For a discussion on pan-trionychid material from the middle Eocene locality of Monte Bolca, Italy, see "*Trionyx*" *capellinii* above.

## *Trionyx amansii* Gray, 1831
## nomen dubium

Taxonomic history. *Trionyx amansii* Gray, 1831 (new species); [*T. amansii*] Hummel 1929 (nomen dubium); *Trionyx amansi* Karl 1999a (incorrect spelling of species epithet).

Type material. MNHN (holotype), a skull fragment (Gray 1831, not figured).

Type locality. Hautesvignes, Lot-et-Garonne, France (Cuvier 1821–1824); Rupelian, early Oligocene (Broin 1977).

Comments. *Trionyx amansii* was erected on the basis of a cranial fragment that was originally described by Cuvier (1821–1824), but not named or figured. Gray (1831) provided a name and an indication to the description of Cuvier (1821–1824) and thus formally made this name available (ICZN 1999). Hummel (1929, 1932) considered this taxon to be of dubious validity, and this view was also adopted by Broin (1977). Given that the type was never figured and that the characters discussed by Cuvier (1821–1824) have no diagnostic value, we herein agree with these opinions and also regard *T. amansii* to be a nomen dubium.

## *Trionyx anthracotheriorum* Portis, 1883
## nomen dubium

Taxonomic history. *Trionyx anthracotheriorum* Portis, 1883 (new species); *T. antracotheriorum* Portis 1883 (incorrect spelling of species epithet); [*T. anthracotheriorum*] Hummel 1929 (nomen dubium); *T. anthracotherium* Broin 1977 (incorrect spelling of species epithet); *T. anthracoteriorum* Chesi 2009 (incorrect spelling of species epithet).

Type material. MGPT-PU17275 (holotype), a partial cranium, carapace, and plastron (Portis 1883, pls. 1.4, 2.3).

Type locality. Nucetto (= Nuceto), Piedmont, Italy (Portis 1883); Chattian or Aquitanian, late Oligocene or early Miocene (Chesi 2009).

Comments. *Trionyx anthracotheriorum* is based on a shell and associated partial cranium (Portis 1883), but the skull is badly crushed and only displays little anatomical detail. Portis (1883) originally differentiated *T. anthracotheriorum* from the roughly coeval Piedmontese taxon *T. pedemontana* on the basis of carapace size and shape and the size of costals VII and VIII, but he noted similarities with the Croatian taxon *T. austriacus* (Peters 1859). Kotsakis (1985) concluded that the original diagnosis of Portis (1883) was not adequate, but he provisionally regarded

*T. anthracotheriorum* to be a valid species, mostly on the basis of geographic considerations. Our firsthand investigation of the holotype of this taxon revealed distinct sculpturing consisting of well-developed tubercles and ridges but additionally confirmed the bad preservation of the cranial and carapacial material. Although we acknowledge the possibility that this species could be a junior synonym of the slightly older "*T.*" *capellinii*, which is also from Italy, the fragmentary nature of the available material prompts us to consider it to be an indeterminate pan-trionychid. *Trionyx anthracotheriorum* is here regarded a nomen dubium.

*Trionyx anthracotheriorum* has been featured in the literature under an array of incorrect spellings. Indeed, Portis (1883) himself introduced two spellings in the type description: *antracotheriorum* and *anthracotheriorum*. Although the first spelling has page priority over the latter, a criterion not explicitly demanded by the ICZN (1999), we here give preference to the latter, because it is grammatically correct, appeared in the etymology section, and is also more widespread in the literature (e.g., Sacco 1889; Hummel 1929, 1932).

## *Trionyx aquitanicus* Delfortrie, 1869 nomen dubium

Taxonomic history. *Trionyx aquitanicus* Delfortrie, 1869 (new species); *T. girundica* Lawley 1876 (incorrect spelling of species epithet); [*T. aquitanicus*] Hummel 1929 (nomen dubium).

Type material. MHNB (holotype), neurals, costals, and a detached nuchal (Delfortrie 1869, pl. 28.20–23).

Type locality. Léognan, Gironde, France (Delfortrie 1869); Burdigalian, early Miocene (Broin 1977).

Comments. *Trionyx aquitanicus* is based on the fragmentary remains of a relatively large-sized pan-trionychid (Delfortrie 1869), to which Lydekker (1889a) subsequently referred an isolated costal collected within close vicinity. Lawley (1876) explicitly referenced Delfortrie (1869) but, for inexplicable reasons, applied the name *T. girundica*. This is, of course, one of many strange name applications that occurred prior to the establishment of internationally recognized priority rules many decades later. *Trionyx girundica* could be interpreted as yet another available name, but it would be the objective junior synonym of *T. aquitanicus* as it is based on the same type material. As an alternative, *T. girundica* could be interpreted as a terrible misspelling, in which case this name can be disregarded. In any case, given the fragmentary nature of the type material, we here consider *T. aquitanicus* to be a nomen dubium (also see *T. vindobonensis* above).

## *Trionyx aspidiformis* Laube, 1900 nomen dubium

Taxonomic history. *Trionyx aspidiformis* Laube, 1900 (new species); *Tryonyx aspidiformis* Laube 1900 (incorrect spelling of genus name); *T. triunguis* = *T. aspidiformis* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym); *Rafetus pontanus* = *T. aspidiformis* = *T. bohemicus* = *T. elongatus* = *T. preschenensis* Chkhikvadze 1999b (junior synonym).

Type material. NMP 36675 (holotype), external imprint of a carapace, missing the posterior left side (Laube 1900, pl. 2.2; Liebus 1930, pl. 4.1, 2).

Type locality. Břestány (= Preschen), near Bilina, Ústí nad Labem, Czechia (Liebus 1930); Most Formation, MN 3, Burdigalian, early Miocene (Aguilar et al. 1997).

Comments. *Trionyx aspidiformis* is based on a partial carapace from the early Miocene of Břestány, Czechia, that was initially housed at the Geological Institute of the German University, Prague, but has since been transferred to NMP. We here consider this taxon to be a nomen dubium, as it is based on a juvenile specimen that lacks diagnostic characters (see *T. vindobonensis* above for more extensive discussion).

## *Trionyx australiensis* De Vis, 1894 nomen dubium

Taxonomic history. *Trionyx australiensis* De Vis, 1894 (new species); *T. australiensis* Gaffney and Bartholomai 1979 (lectotype designation); *Pelochelys australiensis* Rhodin et al. 2015 (new combination).

Type material. QM F1101A (lectotype), a left costal VIII (De Vis 1894, fig. f; Gaffney and Bartholomai 1979, pl. 1.1–2); QM F1101B–G (paralectotypes), carapace elements, consisting of a neural and costal fragments (De Vis 1894, pl. 1a–e, g; Hill et al. 1970, pl. 7.8; Gaffney and Bartholomai 1979, pl. 1).

Type locality. Tara Creek, Mackay Region, Queensland, Australia (De Vis 1894); late Pliocene or Pleistocene (Gaffney and Bartholomai 1979).

Comments. *Trionyx australiensis* is based on rather fragmentary carapace material. The exact locality of *T. australiensis* is a matter of debate. It was originally suggested to originate from Darling Downs (De Vis 1894), but on the basis of preservation, it was later shown to have come from Tara Creek (Gaffney and Bartholomai 1979). Gaffney and Bartholomai (1979) designated a lectotype from the syntype series, compared the taxon to *Pelochelys* from New Guinea, the only Pleistocene or Holocene trionychid genus recorded from the region, but found that it differed significantly. We here agree with Gaffney and Bartholomai (1979) that the available material is insufficient to diagnose a valid taxon.

## *Trionyx austriacus* Peters, 1859 nomen dubium

Taxonomic history. *Trionyx austriacus* Peters, 1859 (new species); *Rafetoides austriacus* = *T. messelianus* = *T. messelianus kochi* = *T. messelianus lepsiusi* Karl 1998 (new combination, senior synonym); *Rafetoides austriacus* = *T. borkenensis* Karl and Müller 2008 (senior synonym).

Type material. GBAW (holotype), an incomplete carapace (Peters 1859, pl. 3.1), now lost (E. Cadena, pers. comm., 2016).

Type locality. Promina Mountain (= Siverich), Šibenik-Knin County, Croatia (Peters 1859; Hummel 1929); Priabonian, late Eocene (Karl 1998).

Comments. *Trionyx austriacus* was established on the basis of a large partial carapace from the late Eocene of Croatia (Peters 1859). In addition to the holotype, Peters (1859) referred a second specimen from the late Eocene of Kis-Győr (= Hisgyőr), Hungary, to this species, but this find was never figured apart from a cross section in the original description depicting the thickness of the carapace (Peters 1859, pl. 3.2). The whereabouts of the type and referred material are currently unknown, and it is therefore impossible to evaluate potential affinities. The date of publication is often provided as 1858 (Szalai 1934; Kuhn 1964; Karl 1998, 1999a), but, in fact, it is 1859. Karl (1998) suggested that *T. austriacus* is the senior synonym of the German "*T.*" *messelianus*, but Karl and Müller (2008) more recently proposed that it is also the senior synonym of *T. borkenensis*. In both cases, no sufficient justification was provided to allow reproducing these claims. Given that the holotype is fragmentary and now lost, we find it best to consider *T. austriacus* a nomen dubium.

## *Trionyx bambolii* Ristori, 1891b nomen dubium

Taxonomic history. *Trionyx bambolii* Ristori, 1891b (new species); *T. bambolis* Reinach 1900 (incorrect spelling of species epithet); *T. bamboli* Teppner 1913 (incorrect spelling of species epithet).

Type material. MUSNAF (syntype), a partial carapace and associated thoracic vertebrae (Ristori 1895, pl. 1.1, 2; Guasparri 1992, fig. 30.2); MUSNAF (syntype), a carapace fragment, one cervical vertebra, and a partial epiplastron (Ristori 1895, pl. 1.3); MSNP (syntype), a carapace fragment, consisting of right costals and neurals I and II (Ristori 1895, pl. 1.4); IGF 999V (syntype), fragment of a hyoplastron and coracoid (Ristori 1895, pl. 2.9); MUSNAF (syntype), a carapace fragment of a juvenile individual (Ristori 1895, not figured).

Type locality. Montebamboli, Tuscany, Italy (Ristori 1891b); MN 12, Tortonian, late Miocene (Chesi 2009).

Comments. The late Miocene localities of Montebamboli, Casteani, Ribolla, and Casino in Tuscany, Italy, have produced a wealth of pan-trionychid fossils (Kotsakis 1985). Ristori (1891a, 1891b) recognized four new species from these localities that he named *Trionyx bambolii*, *T. portisi*, *T. senensis*, and *T. propinquus*. Although the associated descriptions are extremely brief, they fulfill the minimum requirements of the ICZN (1999) for the creation of an available name. Later authors (e.g., Hummel 1932; Kuhn 1964; Kotsakis 1985) were therefore in error by attributing authorship to Ristori (1895), where the relevant material was described in much greater detail and figured.

Ristori (1891a, 1891b, 1895) already noted that all specimens greatly overlapped in the morphology of their shells, but he nevertheless justified the creation of four species based on differences in the shape of the neurals and carapace sculpturing. Using modern standards, such minute differences in neural patterning or sculpturing cannot warrant specific distinction, as these characteristics are known to be highly variable (Meylan 1987; Vitek and Joyce 2015). Kotsakis (1985) tentatively considered these taxa to be conspecific but concluded that a second taxon may be present. We find that all material is once again consistent with an attribution to the *Trionyx triunguis* lineage (Karl 1999a), but modern standards only allow attribution of these fossils to *Pan-Trionychinae* indet. based on the presence of relatively short costals VIII. We therefore here interpret all four taxa as nomina dubia.

## *Trionyx barbarae* Owen in Owen and Bell, 1849 nomen invalidum (junior synonym of "*Trionyx*" *henrici* Owen in Owen and Bell, 1849)

Taxonomic history. *Trionyx barbarae* Owen in Owen and Bell, 1849 (new species); *Rafetoides henrici* = *T. barbarae* = 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. BMNH R30409 (holotype), a carapace (Owen and Bell 1849, pl. 16a; Owen 1849–1884, pl. 5).

Type locality. Hordle (= Hordwell) Cliff, Hampshire, United Kingdom (Owen and Bell 1849); Totland Bay Member, Headon Hill Formation, Priabonian, late Eocene (Benton and Spencer 1995).

Comments. For a discussion regarding pan-trionychid material from the late Eocene of England, see "*Trionyx*" *henrici* above.

## *Trionyx blayaci* Bergounioux, 1933 nomen dubium

Taxonomic history. *Trionyx blayaci* Bergounioux, 1933 (new species); *T. pliopedemontanus* = *T. blayaci* = *T. pliocenicus* = *T. pompignanensis* = *T. rotundiformis* Broin 1977 (junior synonym).

Type material. LG-FSM (holotype), anterior portion of a carapace (Bergounioux 1933, fig. 1, pl. 1.1).

Type locality. La Pompignane, Montpellier, Hérault, France (Bergounioux 1933); Pliocene (Broin 1977).

Comments. Bergounioux (1933) established three species of trionychids, *Trionyx blayaci*, *T. pompignanensis*, and *T. rotundiformis*, on the basis of carapacial fragments from the Pliocene of Montpellier, France, that he differentiated from the coeval *T. pliopedemontana* by nuanced variations in nuchal morphology and carapace sculpturing. More recently, Broin (1977) considered all three forms to be junior synonyms of *T. pliopedemontana*. Strictly speaking, the type of *T. pompignanensis* can only be identified as *Pan-Trionychidae* indet. as it only consists of a partial costal, whereas the more complete types of *T. blayaci* and *T. rotundiformis*, which only represent the anterior portions of the carapace, can only be identified as *Pan-Trionychinae* based on the absence of a preneural. We therefore conclude that Bergounioux's (1933) three species are nomina dubia.

## *Trionyx bohemicus jaegeri* Fuchs, 1939
## nomen dubium

Taxonomic history. *Trionyx bohemicus jaegeri* Fuchs, 1939 (new subspecies).

Type material. BSPG NMR 326 (holotype), a carapace (Fuchs 1939, fig. 11, pls. 2.3, 4; Młynarski 1976, fig. 74.5).

Type locality. Viehhausen, Sinzing, Bavaria, Germany (Fuchs 1939); MN 5, Langhian, middle Miocene (Aguilar et al. 1997).

Comments. Fuchs (1939) attributed several specimens from the locality of Viehhausen to the Czech taxon *Rafetus* (her *Trionyx*) *bohemicus*, but she diagnosed one carapace as a new subspecies, *T. bohemicus jaegeri*, on the basis of the presence and shape of an eighth neural. As we do not find carapaces by themselves to be diagnostic, even if they have an unusual neural count, we here consider this taxon to be a nomen dubium (see *Rafetus bohemicus* and *T. vindobonensis* above for a more extensive discussion).

## *Trionyx borkenensis* Gramann, 1956
## nomen dubium

Taxonomic history. *Trionyx borkenensis* Gramann, 1956 (new species); *T. borkensis* Kuhn 1964 (incorrect spelling of species epithet); *Amyda boulengeri* = *T. borkenensis* Karl 1993 (junior synonym); *Rafetoides austriacus* = *T. borkenensis* Karl and Müller 2008 (junior synonym).

Type material. UVF 6100 (holotype), a partial carapace (Gramann 1956, pl. 3.1,2).

Type locality. Gombeth, Borken, Hesse, Germany; lower "Melanian Clay" (= Melanienton), Rupelian, early Oligocene (Gramann 1956).

Comments. *Trionyx borkenensis* is based on a partial carapace that was originally diagnosed as a new species on the basis of an anterior convexity (Gramann 1956), a character that is now believed to be highly variable with pan-trionychids (Gardner and Russell 1994). A partial carapace from the same locality was more recently attributed to *T.* cf. *borkenensis* (Schleich 1986), likely based on biogeographic considerations. Karl (1993) synonymized *T. borkenensis* with "*T.*" *boulengeri*, also from the Oligocene, whereas Karl and Müller (2008) synonymized it with the late Eocene *T. austriacus* and assigned to the same taxon further fragmentary material from the locality. As the type material does not display any diagnostic characters, we here consider *T. borkenensis* to be a nomen dubium.

## *Trionyx bowerbanki* Lydekker, 1889a
## nomen dubium

Taxonomic history. *Trionyx bowerbanki* Lydekker, 1889a (new species); [*T. bowerbanki*] Hummel 1929 (nomen dubium); *T. boweroanki* Bergounioux 1954 (incorrect spelling of species epithet).

Type material. BMNH R38960 (holotype), an incomplete nuchal (Lydekker 1889a, fig. 4).

Type locality. Bracklesham, West Sussex, United Kingdom (Lydekker 1889a); Bracklesham Beds, late Ypresian, early Eocene (Moody and Walker 1970).

Comments. Lydekker (1889a) established *Trionyx bowerbanki* on the basis of an isolated nuchal to which he referred a right hypoplastron from the type locality. The only other pan-trionychid that has been recovered from Bracklesham, West Sussex, is *Axestemys vittata* (Moody and Walker 1970; Walker and Moody 1985), which is known to have a significantly different postcranial anatomy (see *Axestemys vittata* and *Eurycephalochelys fowleri* above). Some superficial similarities are apparent with slightly younger material from Germany (see "*T.*" *messelianus* above), but the fragmentary nature of the available material precludes any confident assessment. We therefore agree with Hummel (1929) that *T. bowerbanki* should be considered a nomen dubium.

## *Trionyx brunhuberi* Ammon, 1911
## nomen invalidum
## (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Trionyx brunhuberi* Ammon, 1911 (new species); *T. triunguis* = *T. brunhuberi* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. BSPG 1911 I 23 (holotype), a complete carapace and right hyo-, hypo-, and xiphiplastron (Ammon 1911, pls. 2, 3.6–7, 4).

Type locality. Dechbetten, Regensburg, Bavaria, Germany (Ammon 1911); Langhian, middle Miocene (Mottl 1967).

Comments. *Trionyx brunhuberi* is known from relatively well-preserved shell material from the middle Miocene of Regensburg (Ammon 1911). The species was originally differentiated from coeval European forms by the shape of its carapace, shape and size of the neurals and costals, and details to the sculpturing of the hyo-hypoplastra, but these characteristics are now known to be highly variable (Meylan 1987; Gardner and Russell 1994). We note that the plastral material indicates the presence of four callosities, and we therefore synonymize this taxon with *T. vindobonensis*. We attribute apparent differences to the extent of the callosities to ontogenetic variation, with the material from Regensburg representing a more adult morphotype (see *T. vindobonensis* for more extensive discussion).

## *Trionyx bruxelliensis* Winkler, 1869a
## nomen dubium

Taxonomic history. *Trionyx bruxelliensis* Winkler, 1869a (new species); *T. bruxellensis* Vincent 1875 (incorrect spelling of species epithet); [*T. bruxelliensis*] Hummel 1929 (nomen dubium).

Type material. IRSNB 1659 (holotype), a partial carapace, along with fragments of limb elements and vertebrae (Winkler 1869a, pls. 29.73, 30.74–91; Broin 1977, pl. 9.1).

Type locality. Brussels Capital Region, Belgium (Winkler 1869a); early Lutetian, middle Eocene (Broin 1977).

Comments. *Trionyx bruxelliensis* was established on the basis of a partial carapace and several isolated postcranial remains (Winkler 1869a). Winkler (1869a) briefly mentioned that he initially intended to name this taxon *T. duponti*, but he ended up choosing the name *T. bruxelliensis*. The surface of the holotype shows much damage, as the surface sculpturing is only preserved in some portions of the shell, although superficial similarities are apparent with the coeval "*T.*" *messelianus* from Germany. We here therefore consider the holotype to represent an indeterminate pan-trionychid and *T. bruxelliensis* to be a nomen dubium, as already proposed by Hummel (1929).

*Trionyx michauxi* from the early Eocene of Marne, France, was initially identified as *T. bruxelliensis* as well (Michaux 1973) but later considered a separate, valid taxon (Broin 1977). Taking the fragmentary nature of the holotype of *T. bruxelliensis* into consideration, no further comparison with the French taxon can be made.

### *Trionyx burdigalensis* Bergounioux, 1935
### nomen dubium

Taxonomic history. *Trionyx burdigalensis* Bergounioux, 1935 (new species); *Amyda burdigalensis* Comaschi Caria 1959 (new combination).

Type material. MHNB (holotype), anterior part of a carapace (Bergounioux 1935, fig. 26, pl. 10.2).

Type locality. Saint-Vivien-de-Monségur, Gironde, France (Bergounioux 1935); Rupelian, early Oligocene (Broin 1977).

Comments. Bergounioux (1935) established *Trionyx burdigalensis* on the basis of the anterior portion of a rather large carapace. He originally diagnosed this taxon by the presence of a highly reduced nuchal, a widely distributed feature among pan-trionychids, and the W-shaped posterior part of neural I (Bergounioux 1935). The W-like shape in the posterior part of neural I is apparent in the drawing published by Bergounioux (1935), but not clear in the associated photograph, and it seems likely that this feature is attributable to breakage. Along those lines, Broin (1977) already considered the available material to represent an indeterminate pan-trionychid. We agree with this assessment and here consider *T. burdigalensis* to be a nomen dubium.

Comaschi Caria (1959) referred fragments of a pan-trionychid from the Miocene of Cagliari, Sardinia, to *Trionyx burdigalensis*. Kotsakis (1985) suggested that this material is too fragmentary to allow identification at the species level but also noted that it seemed probable that it originated from *Procyclanorbis sardus*. However, Zoboli and Pilolla (2016) more recently showed that this material pertains to a cheloniid. We agree with this conclusion.

### *Trionyx capellinii bulgaricus*
### Khosatzky et al., 1983
### nomen dubium

Taxonomic history. *Trionyx capellinii bulgaricus* Khosatzky et al., 1983 (new subspecies).

Type material. IZ-BAS 1/1959 (holotype), an incomplete carapace (Khosatzky et al. 1983, figs. 1–3).

Type locality. Nikolaevo, Stara Zagora, Bulgaria (Khosatzky et al. 1983); Priabonian, late Eocene (Stojanov 2009).

Comments. *Trionyx capellinii bulgaricus* was described as a new Bulgarian subspecies of the Italian "*T.*" *capellinii* (Khosatzky et al. 1983). Most of the specimen is missing, however, and much of the anatomy of the carapace can only be gleaned by observing the remaining imprint. Given that the internal morphology of turtle shells does not faithfully reflect the external arrangement of the bones, we consider this taxon to be a nomen dubium, although we do agree that the internal imprint indeed shows similarities with "*T.*" *capellinii*.

### *Trionyx capellinii conjugens* Sacco, 1894
### nomen invalidum
### (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx capellinii conjugens* Sacco, 1894 (new subspecies); *T. c. conjungens* Reinach 1900 (incorrect spelling of subspecies name); *T. c. capellinii* = *T. c. conjugens* Bergounioux 1954 (junior synonym); *T. conjugens* Kuhn 1964 (elevation to species); *T. c. capellinii* = *T. c. affinis* = *T. c. conjugens* Kotsakis 1977 (junior synonym); *T. c. capellinii* = *T. c. affinis* = *T. c. conjugens* = *T. gemmellaroi* = *T. intermedius* Kotsakis 1985 (junior synonym).

Type material. MGPT-PU 17281 (syntype), a complete carapace embedded in a slab (Sacco 1894, fig. 1; Bergounioux 1954, fig. 8; Kotsakis 1977, fig. 3d); MGPT-PU 17282 (syntype), a partial carapace (Sacco 1894, fig. 2); MGPT-PU 17283 (syntype), carapace fragments (Sacco 1894, figs. 3–5).

Type locality. Monte Bolca (= Purga di Bolca), Veneto, Italy (Sacco 1894); Prati Valeno Horizon, probably Lutetian, middle Eocene (Giusberti et al. 2014).

Comments. For a discussion on pan-trionychid material from the middle Eocene locality of Monte Bolca, Italy, see "*T.*" *capellinii* above.

### *Trionyx capellinii gracilina* Sacco, 1895
### nomen invalidum
### (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx capellinii gracilina* Sacco, 1895 (new subspecies); *T. c. gracillima* Reinach 1900 (incorrect spelling of subspecies epithet); *T. capellini gracilina* Bergounioux 1933 (incorrect spelling of species epithet); *T. c. montevialensis* = *T. c. gracilina* = *T. c. perexpansa* = *T. c. schaurothianus* = *T. insolitus* = [*T. italicus*] Kotsakis 1977 (junior synonym); *T. italicus* = *T. c. montevialensis* = *T. c. schaurothianus* = *T. c. gracilina* = *T. c. perexpansa* = *T. insolitus* Kotsakis 1985 (junior synonym).

Type material. MGPT-PU 17285 (holotype), an almost complete carapace (Sacco 1895, fig. 2; Bergounioux 1954, fig. 25; Kotsakis 1977, fig. 3j).

Type locality. Monteviale, Veneto, Italy (Sacco 1895); MP 21, early Rupelian, early Oligocene (Pandolfi et al. 2017).

Comments. For a discussion on pan-trionychid material from the early Oligocene locality of Monteviale, Italy, see "*T.*" *capellinii* above.

### *Trionyx capellinii montevialensis* Negri, 1892 nomen invalidum (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx capellinii montevialensis* Negri, 1892 (new subspecies); *T. capellini montevialensis* Teppner 1913 (incorrect spelling of species epithet); *T. c. monsvialensis* Fabiani 1915 (incorrect spelling of subspecies epithet); *T. c. monsvialensis* Bergounioux 1954 (incorrect spelling of subspecies epithet); *T. c. monsilvalensis* Młynarski 1976 (incorrect spelling of subspecies epithet); *T. c. montevidensis* Kotsakis 1977 (incorrect spelling of subspecies epithet); *T. c. montevialensis* = *T. c. gracilina* = *T. c. perexpansa* = *T. c. schaurothianus* = *T. insolitus* = [*T. italicus*] Kotsakis 1977 (senior synonym); *T. italicus* = *T. c. montevialensis* = *T. c. schaurothianus* = *T. c. gracilina* = *T. c. perexpansa* = *T. insolitus* Kotsakis 1985 (junior synonym).

Type material. MGP-PD 9273 (syntype), a rather complete carapace with associated limb elements and plastral fragments (Negri 1892, pl. 4; Bergounioux 1954, fig. 19, pl. 7; Kotsakis 1977, fig. 3g–h; Kotsakis et al. 2005, fig. 11; Pandolfi et al. 2017, fig. 7a); MGP-PD 27636 (syntype), a complete carapace in visceral view, along with plastral elements (Bergounioux 1954, pl. 11); MGP-PD 27637 (syntype), a partial carapace, two complete limb elements, and fragments of the plastron (Bergounioux 1954, figs. 20, 21, pls. 8, 9).

Type locality. Monteviale, Veneto, Italy (Negri 1892); MP 21, early Rupelian, early Oligocene (Pandolfi et al. 2017).

Comments. The type series of *Trionyx capellinii montevialensis* includes some of the most complete fossil pan-trionychids known to date. For a discussion on pan-trionychid material from the early Oligocene locality of Monteviale, Italy, see "*T.*" *capellinii* above.

### *Trionyx capellinii perexpansa* Sacco, 1895 nomen invalidum (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx capellinii perexpansa* Sacco, 1895 (new subspecies); *T. c. montevialensis* = *T. c. gracilina* = *T. c. perexpansa* = *T. c. schaurothianus* = *T. insolitus* = [*T. italicus*] Kotsakis 1977 (junior synonym); *T. italicus* = *T. c. montevialensis* = *T. c. schaurothianus* = *T. c. gracilina* = *T. c. perexpansa* = *T. insolitus* Kotsakis 1985 (junior synonym).

Type material. A complete carapace with fragmentary imprints of the skull (holotype) (Sacco 1895, fig. 1; Bergounioux 1954, fig. 26; Kotsakis 1977, fig. 3k), now lost (Bergounioux 1954).

Type locality. Monteviale, Veneto, Italy (Sacco 1895); MP21, early Rupelian, early Oligocene (Pandolfi et al. 2017).

Comments. *Trionyx capellinii perexpansa* is one of many pan-trionychid taxa named from Monteviale, Italy (Kotsakis 1977, 1985). Its type and only known specimen is among the largest pan-trionychids (CL of 31 cm) from that locality, and it was differentiated from other purportedly sympatric taxa by larger size, size and shape of neurals, and, most notably, the distal expansion of costals I and II, features that are now attributed to individual variation (Gardner and Russell 1994). For a discussion on pan-trionychid material from this locality, see "*T.*" *capellinii* above.

### *Trionyx chaubeti* Bergounioux, 1935 nomen dubium

Taxonomic history. *Trionyx chaubeti* Bergounioux, 1935 (new species); *T. chauberti* Kuhn 1964 (incorrect spelling of species epithet).

Type material. LG-FSM (holotype), left part of a carapace (Gervais 1867–1869, pl. 40.2; Bergounioux 1935, fig. 30, pl. 12.1).

Type locality. Armissan, Aude, France (Bergounioux 1935); Chattian or Aquitanian, late Oligocene or early Miocene (Hervet 2004).

Comments. Bergounioux (1935) diagnosed his new species *Trionyx chaubeti* on the basis of its small size (CL of 18 cm), reduced size of nuchal, shape of neurals, and shape of the anterior portion of the carapace. For a discussion on Bergounioux's (1935) material from Armissan, France, see *T. acutiformis* and *T. vindobonensis* above.

### *Trionyx circumsulcatus* Owen in Owen and Bell, 1849 nomen invalidum (junior synonym of "*T.*" *henrici* Owen in Owen and Bell, 1849)

Taxonomic history. *Trionyx circumsulcatus* Owen in Owen and Bell, 1849 (new species); *Aulacochelys circumsulcata* Lydekker 1889a (new combination); [*T. circumsulcatus*] Hummel 1929 (nomen dubium); *Rafetoides henrici* = *T. circumsulcatus* = 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. BMNH R30404 (holotype), a costal III (Owen and Bell 1849, pl. 19b.1–3; Owen 1849–1884, pl. 31.1–3).

Type locality. Hordle (= Hordwell) Cliff, Hampshire, United Kingdom (Owen and Bell 1849); Totland Bay Member, Headon Hill Formation, Priabonian, late Eocene (Benton and Spencer 1995).

Comments. *Trionyx circumsulcatus* is based on a single costal that was diagnosed based on the presence of a deep groove along its distal margin (Owen and Bell 1849:59). Lydekker (1889a) later tentatively assigned a right hypoplastral fragment from the same locality to this species and placed it in a new, monotypic genus, *Aulacochelys*, as he felt its morphology to be so distinct. A deep groove traversing the thickened distal margin of the costals is now known to be highly variable among pan-trionychids (Gardner and Russell 1994), but is nevertheless diagnostic for North American plastomenids (Vitek and Joyce 2015). Given the apparent lack of plastomenids in the European fossil record, we here attribute *T. circumsulcatus* to the coeval "*T.*" *henrici* and attribute apparent differences to ontogenetic variation. For more detail regarding pan-trionychid material from the late Eocene of England, see "*T.*" *henrici* above.

## *Trionyx ciryi* Bergounioux, 1935
## nomen dubium

Taxonomic history. *Trionyx ciryi* Bergounioux, 1935 (new species).

Type material. LGB-UD (syntype), a carapace fragment (Bergounioux 1935, not figured), now lost (Broin 1977); LBG-UD (syntype), a partial carapace (Bergounioux 1935, fig. 27, pl. 11.1).

Type locality. Armissan, Aude, France (Bergounioux 1935); Chattian or Aquitanian, late Oligocene or early Miocene (Hervet 2004).

Comments. Bergounioux originally diagnosed his new species *Trionyx ciryi* on the basis of the shape and size of neurals, characters that are now known to be variable with trionychids (Meylan 1987). For a discussion on Bergounioux's (1935) material from Armissan, France, see *T. acutiformis* and *T. vindobonensis* above.

## *Trionyx clavatomarginatus* Lörenthey, 1903
## nomen invalidum, designation of lectotype (junior synonym of "*T.*" *boulengeri* Reinach, 1900)

Taxonomic history. *Trionyx clavatomarginatus* Lörenthey, 1903 (new species).

Type material. MTB 15982H (not MTB 15983, as stated in Farkas [1995]) (lectotype), a complete carapace (Lörenthey 1903, pl. 6.1–3); MTB 15983 (paralectotype), posterior carapace fragment (Farkas 1995, fig. 4); MTB 15984 (paralectotype), a partial carapace of a juvenile individual (Lörenthey 1903, pl. 5.1).

Type locality. Cluj-Mănăştur (= Kolozsmonostor), near Cluj-Napoja (= Kolozsvár), Cluj County, Romania (Lörenthey 1903; Młynarski 1966; Farkas 1995); Priabonian, late Eocene (Vremir 2004). The paralectotypes originate from late Eocene to early Oligocene quarries in the broader vicinity of Cluj-Napoja, Romania (Młynarski 1966; Farkas 1995; Vremir et al. 1997).

Comments. The original type material of *Trionyx clavatomarginatus* includes the remains of several individuals found in three different sites within the broader vicinity of Cluj-Napoja, Romania. Given that these cites are not synchronous, it is not surprising that the age of this taxon has variously been reported as being late Eocene (Lörenthey 1903; Vremir et al. 1997) or early Oligocene (Młynarski 1966). As it is highly undesirable to have a taxon being based on nonsynchronous material, we here render the best-preserved specimen as the lectotype of this species, which, to the best of our knowledge, was collected in late Eocene sediments (Vremir et al. 1997).

We consider the paralectotypes to be identifiable only to the level of *Pan-Trionychidae* indet., as they are too fragmentary to allow identification at the species level. However, we agree with Farkas (1995) that the lectotype of *Trionyx clavatomarginatus* greatly resembles "*T.*" *boulengeri* in having greatly reduced costals VIII, and we further note the sinuous lateral margins of the carapace. We therefore formally synonymize these two taxa herein, thereby temporally and geographically extending the range of "*T.*" *boulengeri* (also see above).

## *Trionyx cliftii* Fitzinger 1836
## nomen nudum

Type material. None discussed or designated.

Locality. None specified.

Comments. Fitzinger (1836) did not describe or figure this species, but rather just mentioned a name in his classic work. Fitzinger (1836) furthermore did not mention a locality where this taxon was collected or the probable age or the available material. It is therefore apparent that *Trionyx cliftii* does not fulfill the minimum requirements of the ICZN (1999) for names published prior to 1931, and it must therefore be considered a nomen nudum.

## *Trionyx croaticus* Koch, 1915
## nomen dubium

Taxonomic history. *Trionyx croaticus* Koch, 1915 (new species); *T. stadleri croaticus* Paunović 1986 (referral to subspecies level); *T. triunguis* = *T. croaticus* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. CNHM 25.1-1-(1.485) and CNHM 25.1-2-(1486) (holotype), an almost complete carapace and its mold, with traces of the nuchal, costals, and neurals (Koch 1915, pls. 1.1, 1.2, 1.3; Paunović 1986, fig. 1).

Type locality. Voča, Varaždin County, Croatia (Koch 1915; Paunović 1986); Langhian, middle Miocene (Paunović 1986; Vremir et al. 1997).

Comments. This species is known from a single, at least 37 cm long, well-preserved carapace (Koch 1915) from the Miocene of Croatia. At the time of its discovery, most pan-trionychids from the neighboring regions in Austria and Slovenia had been treated as distinct taxa (Peters 1855; Hoernes 1881; Heritsch 1909; Teppner 1913, 1914c). Accordingly, Koch (1915) established the new species *Trionyx croaticus* and differentiated it from other coeval pan-trionychids on the basis of carapace size, shape and size of costals, and sculpturing pattern. Paunović (1986) regarded this taxon simply as a variety of the geographically proximal but older taxon *T. stadleri* from the late Oligocene of Slovenia. Much like most of the coeval pan-trionychids from north of the Alps, we here conclude that the available material is too fragmentary to allow rigorously attributing it to any of the lineages apparent in Europe at that time (see *T. vindobonensis* for more extensive discussion above). We therefore regard this taxon as a nomen dubium.

### *Trionyx danovi* Chkhikvadze, 1989
### nomen dubium

Taxonomic history. *Trionyx danovi* Chkhikvadze, 1989 (new species); *Rafetus danovi* Chkhikvadze 2010 (new combination).

Type material. IPGAS 3-10-1 (holotype), a nuchal (Chkhikvadze 1989, fig. 6); IPGAS (paratypes), three costal fragments (Chkhikvadze 1989, not figured).

Type locality. Belomechetskaya (= Bjelometscheska), Stavropol Territory, Russia; Langhian, middle Miocene (Chkhikvadze 1989, 2010).

Comments. This species is based on a nuchal and three costals. Chkhikvadze (1989) differentiated his taxon by carapace size, nuchal morphology, and costals shape. He originally noted affinities of his new taxon with *Trionyx stiriacus* (Chkhikvadze 1989) but later reallocated it to *Rafetus* (Chkhikvadze 2010). The sole figure of the holotype nuchal is of poor quality (Chkhikvadze 1989), and the paratypes were never figured. We therefore identify this material as an indeterminate pan-trionychid and declare *T. danovi* to be a nomen dubium. This species has sometimes been reported as having been named in 1988 (Chkhikvadze 2007, 2010), but in fact was named in 1989.

### *Trionyx desmostyli* Matsumoto, 1918
### nomen dubium

Taxonomic history. *Trionyx desmostyli* Matsumoto, 1918 (new species).

Type material. TU (holotype), a partial carapace (Matsumoto 1918, pl. 21).

Type locality. Teshio, Hokkaido, Japan (Matsumoto 1918); Kawabata series, early Miocene (Otsuka 1970).

Comments. *Trionyx desmostyli* is based on a partial carapace from the Miocene of Hokkaido, Japan. Matsumoto (1918) noted in the type description that this taxon shares many similarities with the extant *Pelodiscus sinensis* and even hinted at the possibility that the former could be the ancestor of the latter, but these statements were likely made without access to much comparative material from the recent and past. Judging from the presence of at least one reversal in the neural series, the type specimen can be diagnosed as a pan-trionychine, but this specimen otherwise lacks diagnostic traits. We therefore regard *T. desmostyli* to be a nomen dubium.

Otsuka (1970) more recently referred the posterior margin of a carapace from the middle Miocene of Sasebo, Nagasaki, Japan, to *Trionyx* sp. aff. *desmostyli*, based on the presence of a pair of rather prolonged costals VIII and a straight posterior carapacial border, but these features occur broadly across *Pan-Trionychidae*. We therefore believe this fragment to be an indeterminate pan-trionychid.

### *Trionyx dieupentalensis* Bergounioux, 1935
### nomen dubium

Taxonomic history. *Trionyx dieupentalensis* Bergounioux, 1935 (new species); *T. deupentalensis* Karl 1999a (incorrect spelling of species epithet).

Type material. MHNT PAL2010.0.137 (holotype), an incomplete carapace, preserving mostly its anterior and right side (Bergounioux 1935, fig. 25, pl. 10.1).

Type locality. Dieupentale, Tarn-et-Garonne, France (Bergounioux 1935); Chattian, late Oligocene (Broin 1977).

Comments. *Trionyx dieupentalensis* is based on a single, incomplete carapace, but only the anterior portions are well preserved, and most of the neurals are damaged (Bergounioux 1935). Bergounioux (1935) diagnosed his new taxon on the basis of nuances in the shape of the nuchal and neurals. Given the highly fragmentary nature of the type specimen and its poor preservation, however, we judge this specimen to be an indeterminate pan-trionychine. *Trionyx dieupentalensis* is therefore herein considered to be a nomen dubium.

### *Trionyx dodunii* Gray 1831
### nomen nudum

Material. MNHN 8330, a costal fragment (not figured); MNHN 8373, an indeterminate fragment (not figured) (Broin 1977).

Locality. Castelnaudary, Aude, France (Gray 1831); late Lutetian, middle Eocene (Broin 1977).

Comments. Cuvier (1821–1824) briefly mentioned the presence of a pan-trionychid at Castelnaudary, France, but he did not describe or figure this material but rather simply mentioned that it could be identified as pan-trionychid costal fragments on the basis of its sculpturing. Gray (1831) suggested the name *Trionyx dodunii* for the material described by Cuvier (1821–1824). However, given that Gray (1831) provided neither a description nor a definition nor an indication (i.e., a reference to a description or definition), *Trionyx dodunii* must be considered to be a nomen nudum (ICZN 1999). According to Broin (1977), the material from Castelnaudary includes not only an indeterminate pan-trionychid but possibly also fragments of a pan-carettochelyid. Auffenberg (1974) listed the species *Testudo doduni* (*sic*) Gray, 1831 as a representative of *Testudinidae*, but this seems to be an error.

### *Trionyx elongatus* Liebus, 1930
### nomen dubium

Taxonomic history. *Trionyx elongatus* Liebus, 1930 (new species); *T. triunguis* = *T. elongatus* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym); *Rafetus pontanus* = *T. aspidiformis* = *T. bohemicus* = *T. elongatus* = *T. preschenensis* Chkhikvadze 1999b (junior synonym).

Type material. NMP 1488 (syntype), a carapace (Liebus 1930, pl. 3.6; Nečas et al. 1997, fig. p.17); MMUL 129/G12911 (syntype), a nuchal (Liebus 1930, pl. 3.7).

Type locality. Břestány (= Preschen), near Bilina, Ústí nad Labem, Czechia (Liebus 1930); Most Formation, MN 3, Burdigalian, early Miocene (Aguilar et al. 1997).

Comments. *Trionyx elongatus* is known from a rather small and elongated carapace of a juvenile individual and an isolated nuchal (Liebus 1930) that was initially characterized by a reduced number of neurals (Liebus 1930), thus prompting Hummel (1932) to tentatively include it in the North American *Apalone* (his *Platypeltis*). It is now known that the number of neurals is a variable character within pan-trionychids (Meylan 1987). Given that *T. elongatus* is based on a juvenile specimen (CL of 11 cm), we herein consider it to be a nomen dubium (see *T. vindobonensis* and *Rafetus bohemicus* for more extensive discussions).

## *Trionyx erquelinnensis* Dollo 1909
## nomen nudum

Material. IRSNB 3908, a carapace (Broin 1977, pl. 9.2).

Locality. Erquelinnes, Hainaut, Belgium (Dollo 1909); Tienen Formation, MP 7, early Ypresian, early Eocene (Delfino and Smith 2009).

Comments. Similarly to *Trionyx levalensis*, the other Belgian pan-trionychid named by Dollo (1909), the name *T. erquelinnensis* was simply provided in a list of taxa and was not accompanied by a description of material, a diagnosis, or reference to a prior published description or definition. Dollo (1909) therefore did not make this name available. Broin (1977) much later described and figured the original material of Dollo (1909) under the name *T. erquelinnensis*, but nevertheless concluded that the name is not available, because it would be the junior synonym of *Axestemys* (her *Palaeotrionyx* [*sic*]) *vittata* even if it were available. We here concur with this assessment and consider *T. erquelinnensis* to be a nomen nudum, but on the basis of Broin's (1977) description and figures, we refer all material to *Axestemys vittata* (see above).

## *Trionyx fuchienensis* (Yeh, 1974)
## nomen dubium

Taxonomic history. *Trionyx fuchienensis* Yeh, 1974 (new species); *Aspideretes fuchienensis* Ye 1994 (new combination); *Sinamyda fuchienensis* Chkhikvadze 2000a (new combination); *Aspideretes fuchiensis* Brinkman et al. 2008 (incorrect spelling of species epithet); *Synamyda fuchienensis* Li, Tong et al. 2015 (incorrect spelling of genus name).

Type material. IVPP V4708 (holotype), an incomplete carapace (Yeh 1974, pl. 1).

Type locality. Hekou, Ninghua County, Fujian (= Fuchien) Province, China (Yeh 1974; Brinkman et al. 2008; Figure 4); unknown Formation, Cretaceous (epoch and age unclear) (Brinkman et al. 2008; Danilov and Vitek 2013).

Comments. *Trionyx fuchienensis* is based on a complete, but poorly preserved carapace with vague stratigraphic provenience that documents the purported presence of a trionychid with a carapace that is more than twice as long as wide, an unusual morphology otherwise not seen in any other pan-trionychid. According to personal observations by one of us (W.G.J.), we conclude that the holotype shows extensive repair, is heavily crushed, and displays an unusual surface texture that is not necessarily reminiscent of a trionychid. Given that the provenience of the type is uncertain, that the morphology of the type is so highly unusual, and that the authenticity of the morphology captured in the type is doubtful, we here regard this taxon as a nomen dubium.

## *Trionyx gemmellaroi* Negri, 1892
## nomen invalidum
## (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx gemmellaroi* Negri, 1892 (new species); *T. gemellarioi* Sacco 1894 (incorrect spelling of species epithet); *T. gemellarii* Reinach 1900 (incorrect spelling of species epithet); *T. gemellaroi* Hummel 1932 (incorrect spelling); *T. gemmelarvoi* Bergounioux 1953 (incorrect spelling of species epithet); *T. capellinii* = *T. c. affinis* = *T. c. conjugens* = *T. gemmellaroi* = *T. intermedius* Kotsakis 1985 (junior synonym).

Type material. MGP-PD 5157 (holotype), almost complete skeleton, including the plastron and carapace, all limb elements, and partial skull and mandible (Negri 1892, pls. 1, 5.2–5; Bergounioux 1954, figs. 11, 12, pl. 3; Giusberti et al. 2014, fig. 4a–b).

Type locality. Monte Bolca (= Purga di Bolca), Veneto, Italy (Negri 1892); Prati Valeno Horizon, probably Lutetian, middle Eocene (Giusberti et al. 2014).

Comments. *Trionyx gemmellaroi* is based on a beautifully preserved specimen that is almost identical to the syntypes of "*T.*" *capellinii*. Given that *T. gemmellaroi* and "*T.*" *capellinii* were named in the same publication (Negri 1892), we here concur with Kotsakis (1985), the first revisor, by acknowledging "*T.*" *capellinii* as the senior synonym. For a discussion on pan-trionychid material from the middle Eocene locality of Monte Bolca, Italy, see "*T.*" *capellinii* above.

## *Trionyx gergensi* Reinach, 1900
## nomen invalidum
## (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Aspidonectes gergensii* Meyer 1844 (nomen nudum); *Aspidonectes gergensi* Meyer 1860 (nomen nudum);

*Trionyx gergensi* Reinach, 1900 (new species), *Procyclanorbis gergensi* Portis 1901 (new combination); *T. gergensis* Harrassowitz 1919 (incorrect spelling of species epithet); [*T. gergensi*] Hummel 1929 (nomen dubium); *Aspideretes gergensi* Karl 1993 (new combination); *T. triunguis* = [*Aspidonectes gergensi*] = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. NMM (holotype), a fragmentary specimen consisting of partial nuchal right costal I, left hyo-hypoplastron, right xiphiplastron, and limb bones (Reinach 1900, pl. 40.1–5, 8–10).

Type locality. Hechtsheim, Mainz, Rhineland-Palatinate, Germany (Meyer 1844); Aquitanian, early Miocene (Karl 1999a).

Comments. *Trionyx gergensi* has a tortured nomenclatural history. Meyer (1844) reported fragments from the Miocene of Mainz, Germany, under the name *Aspidonectes gergensii*, but this was not accompanied by any characters, a definition, or an indication, and he therefore did not make the name available. In a later contribution (Meyer 1860, 1867), he mentioned the name again with a slightly different spelling, but once again did not make it available. Maack (1869) listed this taxon as valid but also did not make it available, by not including any characters, a definition, or an indication. Lydekker (1889a) referred an additional specimen from Mainz to this name, but we do not believe that he made the taxon available, as he explicitly refers to the type specimen, for which he lacked character evidence. Reinach (1900) figured the original material of Meyer (1844), provided a description, and only then finally made the name available, though under the combination *T. gergensi*. Reinach (1900) attributed additional fragments from Weisenau near Mainz to *T. gergensi* but designated Lydekker's (1889a) shell as the type of another taxon, *T. boulengeri* (see above). Portis (1901) believed this taxon to be a cyclanorbine, and he further considered this to represent the northernmost occurrence of this group known to that date, but we cannot reproduce his rationale.

We here conclude that all of Reinach's (1900) specimens reveal the presence of well-developed plastral callosities and we therefore synonymize *Trionyx gergensi* with *T. vindobonensis*. The greater extent of the callosities in the material from Mainz is attributable to ontogenetic variation, as *T. vindobonensis* is typified by a relatively immature specimen (see *T. vindobonensis* above for more extensive discussion).

Meyer (1860, 1867) described and figured fossil eggs from the Miocene of Mainz that he attributed tentatively to *Trionyx gergensi* (his *Aspidonectes gergensii*), a conclusion subsequently adopted by Hummel (1929), but challenged by Gergens (1860), who instead considered these eggs to be of cheloniid origin. If the attribution to a trionychid is correct, this find would represent the only confirmed record of pan-trionychid eggs in the fossil record (Lawver and Jackson 2014).

## *Trionyx harmati* Szalai, 1934
nomen dubium

Taxonomic history. *Trionyx harmati* Szalai, 1934 (new species).

Type material. A left humerus (holotype) (Szalai 1934, pl. 4.21); now considered lost (Farkas 1995).

Type locality. Budapest, Central Hungary, Hungary; Rupelian, early Oligocene (Szalai 1934).

Comments. Szalai (1934) named *Trionyx harmati* on the basis of a single humerus. Pan-trionychid humeri do not bear diagnostic features at the species level, and the type specimen of *T. harmati* can therefore at best be identified as an indeterminate pan-trionychine, a conclusion previously drawn by Młynarski (1966) and Farkas (1995). *Trionyx harmati* is therefore herein considered to be a nomen dubium.

## *Trionyx hilberi* Hoernes, 1892
nomen dubium

Taxonomic history. *Trionyx hilberi* Hoernes, 1892 (new species); *T. hilberti* Kuhn 1964 (incorrect spelling of species epithet); *T. petersi* = *T. hilberi* Mottl 1967 (junior synonym); *T. hilbari* Młynarski 1976 (incorrect spelling of species epithet); *T. triunguis* = *T. hilberi* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 200692 (holotype), a complete carapace (Heritsch 1909, pl. 9.1; Gross 2002, pl. 10.3).

Type locality. Wies, Styria, Austria (Heritsch 1909); Eibiswald Formation, MN 5, early Langhian, middle Miocene (Aguilar et al. 1997).

Comments. *Trionyx hilberi* is based on a well-preserved, rounded carapace (CL of 26.8 cm) from the middle Miocene of Austria (Hoernes 1892). We herein nevertheless find this taxon to be a nomen dubium because we disregard taxa from that time period that are based on carapacial material alone, as this part of the body is not sufficient to diagnose a valid taxon (see *T. vindobonensis* above for extensive discussion).

## *Trionyx hoernesi* Heritsch, 1909
nomen invalidum, designation of lectotype
(junior synonym of *T. vindobonensis*
Peters, 1855)

Taxonomic history. *Trionyx hoernesi* Heritsch, 1909 (new species); *T. triunguis* = *T. hoernesi* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 200694 (lectotype), a partial left and right hyo-hypoplastron, and a partial skull and mandible (Heritsch 1909, fig. 2; Karl 1998, pl. 5; Gross 2002, pl. 11.1); UMJGP 200708 (paralectotype), bone fragments (Gross 2002, pl. 11.2); UMJGP 200709 (paralectotype), carapace fragments (Gross 2002, pl. 11.3); UMJGP 200703 (paralectotype), a partial carapace (Heritsch 1909, pl. 9.3; Gross 2002, pl. 11. 4); UMJGP 201158 (paralectotype), a carapace (Heritsch 1909, pl. 9.4; Gross 2005, fig. 1). Some of these specimens also serve as the types for *Trionyx petersi* (see below).

Type locality. Großradl (= Grossradl), Styria, Austria (Heritsch 1909); Eibiswald Formation, MN 5, early Langhian, middle Miocene (Aguilar et al. 1997).

Comments. The Miocene locality of Großradl, Austria, yielded several pan-trionychid remains in the 19th century (Hoernes 1881; Heritsch 1909). On the basis of this material, Hoernes (1881) established the species *Trionyx petersi*, but Heritsch (1909) later described *T. hoernesi* on partially overlapping specimens from the same locality. As a result, part of the type material of *T. hoernesi* (UMJGP 200694, UMJGP 200709, and UMJGP 201158) also serves as the type material of *T. petersi*. To clarify this taxonomic puzzle, we designate the same specimen for both taxa as the lectotype, thereby rending both objective synonyms. The lectotype most notably includes partial right and left hyo-hypoplastra that clearly document the presence of well-developed plastral callosities. We therefore confidently synonymize both *T. hoernesi* and *T. petersi* with *T. vindobonensis*. The notable differences to the extent of the ossification of the plastra are once again attributable to ontogenetic variation, as the lectotypes of *T. hoernesi* and *T. petersi* represent a skeletally mature individual, in contrast to the type of *T. vindobonensis* (also see *T. vindobonensis* for extended discussion, including a discussion regarding variation in cranial morphology).

### *Trionyx hurum sivalensis* Lydekker, 1889a nomen invalidum (junior synonym of *Nilssonia hurum* [Gray, 1830])

Taxonomic history. *Trionyx hurum sivalensis* Lydekker, 1889a (new subspecies); *Nilssonia hurum* = *T. hurum sivalensis* Rhodin et al. 2015 (junior synonym).

Type material. IMC E163 (holotype), a plastron and carapace fragment (Lydekker 1885, pl. 27.3, 3a; Lydekker 1889a, no figure).

Type locality. Siwaliks, Punjab (Lydekker 1889a), Pakistan (see *Emyda lineata*); late Pliocene–early Pleistocene (Rhodin et al. 2015).

Comments. Lydekker (1885) initially described the type material of *Trionyx hurum sivalensis* as an unnamed, indeterminate species of *Trionyx*. Four years later, Lydekker (1889a) designated the same material as a new variety of *Nilssonia* (his *Trionyx*) *hurum*, which he characterized by a median and two lateral ridges on the carapace (Lydekker 1889a) while noting that the new taxon is almost identical to the extant form. We here fully agree with Rhodin et al. (2015) by considering *T. hurum sivalensis* to be a junior synonym of *Nilssonia hurum*. However, as was explicitly stated by Bell et al. (2010), synonymization of Pleistocene taxa with extant representatives should only be done cautiously, as cryptic diversity and conservative skeletal morphology is widespread among extant forms.

### *Trionyx incrassatus* Owen in Owen and Bell, 1849 nomen invalidum (junior synonym of "*Trionyx*" *henrici* Owen in Owen and Bell, 1849)

Taxonomic history. *Trionyx incrassatus* Owen in Owen and Bell, 1849 (new species); *T. incrassus* Peters 1855 (incorrect spelling); *T. incrassatum* Bergounioux 1933 (incorrect spelling of species epithet); *Rafetoides henrici* = *T. incrassatus* = 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. BMNH R1433 (syntype), a carapace (Owen and Bell 1849, pl. 17; Owen 1849–1884, pl. 26); BMNH R30403 (syntype), anterior part of a carapace (Owen and Bell 1849, pl. 18; Owen 1849–1884, pl. 27); BMNH R30508 (syntype), elements of the plastron, vertebrae, and the appendicular skeleton (Owen and Bell 1849, pl. 19; Owen 1849–1884, pl. 28).

Type locality. Isle of Wight, United Kingdom (Owen and Bell 1849); upper Headon Hill Formation, late Eocene (Benton and Spencer 1995).

Comments. *Trionyx incrassatus* was initially distinguished from the type of "*T.*" *henrici* by the presence of a more depressed carapace, differences in nuchal and costal shape, a coarser sculpturing pattern, and slight differences in the shapes of the dorsal vertebrae (Owen and Bell 1849; Lydekker 1889a), but these differences are now attributed to individual variation (Meylan 1987). Additional material from Hordle, Hampshire, assigned to *T. incrassatus* (Lydekker 1889a) is here referred to "*T.*" *henrici* as well. The postcranial material attributed to *T. incrassatus* enhances our understanding of the appendicular skeletal anatomy of "*T.*" *henrici*. For a discussion regarding pan-trionychid material from the late Eocene of England, see "*T.*" *henrici* above.

### *Trionyx insolitus* Bergounioux, 1954 nomen invalidum (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx insolitus* Bergounioux 1953 (nomen nudum); *T. insolitus* Bergounioux, 1954 (new species); *T. capellinii montevialensis* = *T. c. gracilina* = *T. c. perexpansa* = *T. c. schaurothianus* = *T. insolitus* = [*T. italicus*] Kotsakis 1977 (junior synonym); *T. italicus* = *T. c. montevialensis* = *T. c. schaurothianus* = *T. c. gracilina* = *T. c. perexpansa* = *T. insolitus* Kotsakis 1985 (junior synonym).

Type material. MGP-PD 26560 (holotype), a complete carapace in dorsal view (Bergounioux 1954, fig. 27, pl. 13; Kotsakis 1977, fig. 31; Pandolfi et al. 2017, fig. 7c).

Type locality. Monteviale, Veneto, Italy (Bergounioux 1954); MP 21, early Rupelian, early Oligocene (Pandolfi et al. 2017).

Comments. *Trionyx insolitus* is based on a large specimen from the Oligocene of Monteviale, Italy, that Bergounioux (1954) claimed to have a preneural, a feature that would readily differentiate it from most other pan-trionychids from the Paleogene of Europe. Whereas Kotsakis (1977) interpreted this as an anomaly or pathology, we reject the presence of a preneural based on personal observations of the type specimen. For a discussion on pan-trionychid material from the early Oligocene locality of Monteviale, Italy, see "*T.*" *capellinii* above.

### *Trionyx intermedius* Bergounioux, 1954 nomen invalidum (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx intermedius* Bergounioux 1953 (nomen nudum); *T. intermedius* Bergounioux, 1954 (new species); *T. capellinii capellinii* = *T. c. affinis* = *T. c. conjugens* = *T. gemmellaroi* = *T. intermedius* Kotsakis 1985 (junior synonym).

Type material. MGP-PD 12814 (holotype), a complete carapace (Bergounioux 1954, fig. 13, pl. 4; Kotsakis 1977, fig. 3f; Giusberti et al. 2014, fig. 4d).

Type locality. Monte Bolca (= Purga di Bolca), Veneto, Italy (Bergounioux 1954); Prati Valeno Horizon, probably Lutetian, middle Eocene (Giusberti et al. 2014).

Comments. Bergounioux (1954) differentiated *Trionyx intermedius* from the sympatric "*T.*" *capellinii* by carapace shape, shape and size of neurals, and carapacial sculpturing. Kotsakis (1977) thought that *T. intermedius* is probably distinct from "*T.*" *capellinii*, as the former taxon lacks a posterior carapacial truncation, but Broin (1977) and Kotsakis (1985) attributed this difference to interspecific variation, an opinion soon after adopted by Kotsakis (1985) as well. For a discussion on pan-trionychid material from the middle Eocene locality of Monte Bolca, Italy, see "*T.*" *capellinii* above.

### *Trionyx irregularis* Bergounioux, 1954 nomen dubium

Taxonomic history. *Trionyx irregularis* Bergounioux 1953 (nomen nudum); *T. irregularis* Bergounioux, 1954 (new species).

Type material. MGP-PD 26561 (holotype), a fragmentary carapace (Bergounioux 1954, fig. 28, pl. 14).

Type locality. Ignago-Zovo (= Ignago), Veneto, Italy (Bergounioux 1954; Chesi 2009); Oligocene (Kotsakis 1985).

Comments. *Trionyx irregularis* is based on a rather fragmentary carapace from Ignago-Zovo, Italy, not Spain, as erroneously reported by Karl (1999a), that was originally diagnosed by reference to its carapacial sculpturing pattern and, more notably, irregularly shaped neurals (Bergounioux 1954; Kotsakis 1985). However, based on our personal observations of the holotype, we regard an assignment beyond *Pan-Trionychinae* implausible because this specimen is too fragmentary to allow identification at the species level. *Trionyx irregularis* is therefore here considered to be a nomen dubium.

### *Trionyx ishiharaensis* Miura and Uyama, 1987 nomen dubium

Taxonomic history. *Trionyx ishiharaensis* Miura and Uyama, 1987 (new species); *T. ishiharensis* Hasegawa et al. 2007 (incorrect spelling of species epithet).

Type material. HNSM (holotype), a partial carapace (Miura and Uyama 1987, pl. 5.a, b).

Type locality. Bihoku-sôgun Kimita-son, Hiroshima, Japan (Miura and Uyama 1987; Figure 3); Bihoku Group, late Burdigalian, early Miocene (Hirayama 2007).

Comments. *Trionyx ishiharaensis* is based on a notably large, nearly complete carapace (CL ca. 78 cm) from the Miocene of Japan. Although the type specimen is unusually complete, the type description is extremely short and the associated figures and line drawing difficult to interpret. Indeed, based on the available evidence, we cannot estimate if the type specimen is attributable to any lineage of extant giant trionychids (e.g., the *Amyda*, *Chitra*, or *Pelochelys* lineages) or represents a separate, evolutionary lineage. Although more detailed reanalysis may confirm its validity, we here consider this taxon to be a nomen dubium.

### *Trionyx italicus* Schauroth, 1865 nomen dubium

Taxonomic history. *Trionyx italicus* Schauroth, 1865 (new species); *Trionix italicus* De Gregorio 1892 (incorrect spelling of genus name); *T. capellinii montevialensis* = *T. c. gracilina* = *T. c. perexpansa* = *T. c. schaurothianus* = *T. insolitus* = [*T. italicus*] Kotsakis 1977 (nomen oblitum, junior synonym); *T. italicus* = *T. capellinii gracilina* = *T. capellinii montevialensis* = *T. capellinii perexpansa* = *T. capellinii schaurothianus* = *T. insolitus* Kotsakis 1985 (senior synonym).

Type material. NMCL 3897 (holotype), an incomplete carapace (Schauroth 1865, pl. 29.1), now lost (E. Mönnig, pers. comm., 2016).

Type locality. Monteviale, Veneto, Italy (Schauroth 1865; Kotsakis 1977; Figure 5); MP 21, early Rupelian, early Oligocene (Pandolfi et al. 2017).

Comments. The Oligocene locality of Monteviale, Italy has yielded several pan-trionychid specimens that serve as the basis for six named taxa. Given that all material seems to represent a single species, Kotsakis (1977) concluded that *Trionyx italicus* should serve as the senior synonym, as it was named first, but he also concluded that the name had been in disuse for an extended amount of time and that it actually represents a nomen oblitum. A few years later, however, Kotsakis (1985) changed his opinion and resurrected *T. italicus* as the senior synonym of all taxa named from Monteviale. Kotsakis's (1977) initial conclusion that *T. italicus* is a nomen oblitum does not fulfill the requirements of the ICZN (1999), as the name *T. italicus* was used as a valid nomen multiple times over the course of the 20th century (e.g., Heritsch 1909; Teppner 1913; Hummel 1929, 1932; Kuhn 1964). However, we nevertheless agree with the conclusion that *T. italicus* is not an appropriate senior synonym for material from Monteviale, as the holotype only consists of undiagnostic shell fragments and now seems to be lost (E. Mönnig, pers. comm., 2016). We therefore consider this name to be a nomen dubium.

## *Trionyx jakhimovitchae* Chkhikvadze, 1989
## nomen dubium

Taxonomic history. *Trionyx jakhimovitchae* Chkhikvadze, 1989 (new species); *Pelodiscus jakhimovitchae* Kordikova 1994a (new combination).

Type material. IPGAS 7-63-21 (holotype), left costal I (Chkhikvadze 1989, fig. 7); IPGAS 7-63-22 (paratype), fragment of left hypoplastron (Chkhikvadze 1989, not figured); IPGAS 7-64-I (paratypes), fragment of a hypoplastron (Chkhikvadze 1989, not figured); IPGAS (paratypes), costal fragments, a frontal and an ungual phalanx (Chkhikvadze 1989, not figured).

Type locality. Sarybulak, East Kazakhstan Region, Kazakhstan (Chkhikvadze 1989, 2010); Sarybulak suite, middle Miocene (Chkhikvadze 2010).

Comments. The holotype of *Trionyx jakhimovitchae* is a fragmentary costal that cannot be identified beyond *Pan-Trionychidae* indet. The paratypes listed in the type description (Chkhikvadze 1989) were never figured, and referral can therefore not be reproduced. *Trionyx jakhimovitchae* is here considered a nomen dubium. Kordikova (1994b) referred additional material to this species from four additional localities across the Zaysan Basin, East Kazakhstan Region, but this referred material was neither described nor figured. As the identification of pan-trionychid remains is straightforward, we here refer these fragments to *Pan-Trionychidae* indet. For a more extensive discussion, see "*T.*" *ninae* above.

## *Trionyx kazusensis* Otsuka, 1969
## nomen dubium

Taxonomic history. *Trionyx kazusensis* Otsuka, 1969 (new species).

Type material. KUL GK.M.1180–1183 (holotype), fragments of a carapace (Otsuka 1969).

Type locality. Shimabara Peninsula, Nagasaki, Japan; Kuchinotsu Group, Oya Formation, early Pleistocene (Otsuka 1969, 1970).

Comments. *Trionyx kazusensis* is a small trionychid taxon (CL ca. 24 cm) that was established on the basis of fragmentary shell material, a scapula, and an incomplete ilium from the Pleistocene of Japan. Otsuka (1969, 1970) distinguished it from the extant *Pelodiscus sinensis* by its larger size and thicker shell with deep and wide pits and variations to the shape of neural I and the quadrate. However, as stated in Hirayama (2007), the material bears no diagnostic features and should therefore be regarded as an indeterminate pan-trionychid. We concur with this view here and consider *T. kazusensis* to be a nomen dubium.

## *Trionyx khosatzkyi* Chkhikvadze, 1983
## nomen dubium

Taxonomic history. *Trionyx khosatzkyi* Chkhikvadze, 1983 (new species); *Rafetus khosatzkyi* Chkhikvadze 2007 (new combination).

Type material. IPGAS 3-101-3 (holotype), a cervical vertebra VI (Chkhikvadze 1983, fig. 17; Chkhikvadze and Lungu 1984, fig. 6).

Type locality. Maykop, Adygea Republic, Russia (Chkhikvadze 1983); Serravallian, middle Miocene (Kordikova 1994b).

Comments. *Trionyx khosatzkyi* was established on the basis of a cervical vertebra (Chkhikvadze 1983). Two scapulae, a distal fragment of a costal, and a medial fragment of a hypoplastron from the same locality were also referred to this taxon, but these were never figured (Chkhikvadze 1983). On the basis of this material, this taxon was diagnosed by its large size (estimated CL of around 60–70 cm) and a sculpturing pattern described as finely rippled ridges (Chkhikvadze 1983). However, the cervical vertebrae of pan-trionychids are not diagnostic at the species level, and the taxonomic status of the referred material cannot be verified, as it was never figured or described. We therefore consider this material to represent an indeterminate pan-trionychid and *T. khosatzkyi* a nomen dubium.

Shebzukhova and Tarasenko (2007) more recently referred isolated carapace fragments from the type locality of *Trionyx khosatzkyi* to that species, but these are here also classified as indeterminate pan-trionychids.

## *Trionyx laurillardii* Gray, 1831
## nomen dubium

Taxonomic history. *Trionyx laurillardii* Gray, 1831 (new species); [*T. laurillardi*] Hummel 1929 (nomen dubium and incorrect spelling of species epithet).

Type material. MNHN (holotype), a nuchal (Cuvier 1821–1824, pl. 15.3; Broin 1977).

Type locality. Ambarès-et-Lagrave (= La Grave), Gironde, France (Cuvier 1821–1824); Priabonian, late Eocene (Broin 1977).

Comments. Cuvier (1821–1824) figured and briefly described pan-trionychid fragments from the region surrounding Bordeaux, to which Gray (1831) soon after applied the name *Trionyx laurillardii*. As Gray (1831) provided an indication to a previous description, his action complies with the rules of ICZN (1999) for the availability of a new name established prior to 1931. The validity of *T. laurillardii* was nevertheless challenged by Hummel (1929, 1932) and Broin (1977) as the holotype, a nuchal, bears no diagnostic characters. We agree with this opinion and therefore consider *T. laurillardii* to be a nomen dubium.

## *Trionyx levalensis* Dollo 1909
## nomen nudum

Material. IRSNB 1720, a partial carapace and plastron with associated skull fragments (Broin 1977).

Locality. Trieu de Leval, Hainaut, Belgium (Dollo 1909; Moody and Walker 1970); Tienen Formation, MP 7, early Ypresian, early Eocene (Delfino and Smith 2009).

Comments. Dollo (1909) reported on the presence of some of the oldest known pan-trionychid material from Europe under the name *Trionyx levalensis*, but he did not provide a description, definition, or indication, and this name must therefore be considered a nomen nudum, as already noted by Moody and Walker (1970) and Broin (1977). The specimen to which Dollo (1909) was referring has since been identified as consisting of a shell, postcranial elements, and skull fragments (Moody and Walker 1970) as it is labeled under this name in the collections of the IRSNB. We agree with these authors that *T. levalensis* must be considered a nomen nudum but conclude that the relevant specimens are referable to *Axestemys vittata* (see above).

## *Trionyx liupani* Tao, 1986 nomen invalidum (junior synonym of *Rafetus swinhoei* [Gray, 1873])

Taxonomic history. *Trionyx liupani* Tao, 1986 (new species); *Rafetus swinhoei* = *Pelochelys taihuensis* = *T. liupani* Farkas 1992 (junior synonym).

Type material. Private collection in Tainan, Taiwan (syntype), a nearly complete cranium (Tao 1986, text figs. 1, 3, 5, 7 and figs. 2, 4, 6, 9); private collection in Chia-Yi, Taiwan (syntype), a hyo-hypoplastron (Tao 1986, text fig. 9 and figs. 8, 10–12).

Type locality. Penghu (Pescadores) Channel, Taiwan (Tao 1986); Late Pleistocene (Farkas 1992).

Comments. *Trionyx liupani* is based on a skull and a hyo-hypoplastron found by fishers in the Penghu Channel, off the coast of Taiwan, at a depth of more than 150 m. The type material is housed in two different private collections, but plaster models are kept in the Museum of Zoology in the National Taiwan University under the repository numbers NTUM 002 and NTUM 003, respectively. In the type description, this species was only compared to *Pelodiscus sinensis*, but nevertheless assigned to *Trionyx* (Tao 1986). Farkas (1992) soon after noted great similarities with *Rafetus swinhoei* and therefore considered *T. liupani* to be its junior synonym. This synonymy has since been accepted by Le and Pritchard (2009) and Rhodin et al. (2015), and we concur with this assessment herein as well.

## *Trionyx lockardi* Gray 1831 nomen nudum

Material. MNHN 8369, a plastron fragment (Gray 1831, not figured; Broin 1977).

Type locality. Avaray, Loire, France (Gray 1831; Fitzinger 1836); Burdigalian, early Miocene (Broin 1977).

Comments. Cuvier (1821–1824) mentioned the presence of pan-trionychid remains from the Miocene of Avaray, France, but he did not provide a description of this material or the definition of a new taxon. Gray (1831) soon after provided the name *Trionyx lockardi* for this material, but he did not provide a description or definition as well. The name *T. lockardi* therefore does not fulfill the minimum requirements of ICZN (1999), and the name is not available (see *T. dodunii*), much as Gervais (1859), Hummel (1929, 1932), and Broin (1977) noted before.

## *Trionyx lorioli* Portis, 1882 nomen dubium

Taxonomic history. *Trionyx lorioli* Portis, 1882 (new species).

Type material. MGL 8889 (syntype), posterior part of a carapace (Portis 1882, pl. 6.2); MGL 8907 (syntype), anterior part of a carapace (Portis 1882, pl. 21); MGL 8902 (syntype), posterior part of a carapace, along with parts of the hyo-hypoplastron (Portis 1882, pls. 22, 23).

Type locality. La Rocchette (= Rochette) Locality, Belmont, Vaud, Switzerland (Portis 1882); MP 29, Chattian, late Oligocene (Berger 1998).

Comments. *Trionyx lorioli* is based on several fragmentary specimens from the late Oligocene of La Rocchette, Switzerland, one of which had already been described and figured by Pictet and Hubert (1856) as an indeterminate species of *Trionyx*. We herein consider this taxon to be a nomen dubium, as the type material is not sufficient to diagnose a valid species (see *T. valdensis* for more extensive discussions).

Souza Torres (1947) attributed a carapace fragment from the late Miocene of Portugal to *Trionyx lorioli* on the basis of sculpturing pattern, but we here consider this fossil to be an indeterminate pan-trionychine.

## *Trionyx manouri* Gray, 1831 nomen dubium

Taxonomic history. *Trionyx maunoir* Cuvier 1821–1824 (nomen nudum); *T. manouri* Gray, 1831 (new species); *T. maunoiri* Fitzinger 1836 (incorrect spelling of species epithet); *T. maunori* Ezquerra del Bayo 1850 (incorrect spelling of species epithet); *T. monoiri* Reinach 1900 (incorrect spelling of species epithet); *T. monoiiri* Heritsch 1909 (incorrect spelling of species epithet).

Type material. A partial carapace and fragments of a plastron (Cuvier 1821–1824, pl. 15.1, 2; Cuvier 1835–1836, pl. 243.1, 2), now lost (Broin 1977).

Type locality. Aix-en-Provence, Bouches-du-Rhône, France (Gray 1831); Rupelian or early Aquitanian, early Oligocene or early Miocene (Broin 1977).

Comments. This taxon was first described under the name *Trionyx maunoir* by Cuvier (1821–1824), who attributed the name to an unpublished abstract by Boulet, but as he was uncertain if the material represents a valid taxon, he did not make that name available for nomenclatural purposes. Gray (1831) soon after used a slightly different spelling of that name, *T. manouri*, as valid and referred to the work of Cuvier (1821–1824) and thereby made that name available (ICZN 1999). For this reason, we herein attribute authorship of *T. manouri* to Gray (1831) and not to Boulet, as has been previously suggested (Hummel 1932; Kuhn 1964). The available material is highly fragmentary and now lost. We therefore consider *T. manouri* to be a nomen dubium (also see *T. vindobonensis* above).

Ezquerra del Bayo (1850) referred material from Spain to this taxon, but this attribution seems questionable (Hummel 1929). This Spanish specimen is unfortunately lost, and no further comparisons can be made (Jiménez Fuentes and Alonso Andres 1994). We therefore do not list this material in our geographic summary.

## *Trionyx marginatus* Owen in Owen and Bell, 1849 nomen invalidum (junior synonym of "*T.*" *henrici* Owen in Owen and Bell, 1849)

Taxonomic history. *Trionyx marginatus* Owen in Owen and Bell, 1849 (new species); *T. henrici* = *T. marginatus* Lydekker 1889a (junior synonym); *T. marginatus* Kuhn 1964 (nomen validum); *Rafetoides henrici* = *T. marginatus* = 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. BMNH R30406 (holotype), a complete carapace (Owen and Bell 1849, pl. 19; Owen 1849–1884, pl. 30).

Type locality. Hordle (= Hordwell) Cliff, Hampshire, United Kingdom (Owen and Bell 1849); Totland Bay Member, Headon Hill Formation, Priabonian, late Eocene (Benton and Spencer 1995).

Comments. *Trionyx marginatus* was established on the basis of a rather complete carapace that was solely differentiated from the other late Eocene English taxa by sculpturing pattern (Owen and Bell 1849). For a discussion regarding pan-trionychid material from the late Eocene of England, see "*T.*" *henrici* above. Zigno (1889) attributed a fossil from the Eocene of Monte Zuello, Veneto, Italy, to *T.* cf. *marginatus*, but Kotsakis (1977) believed this to be closer to "*T.*" *capellinii*. We find this specimen to be rather fragmentary for identification and consider it to be an indeterminate pan-trionychid.

## *Trionyx marini* Hernández Sampelayo and Bataller, 1944 nomen dubium

Taxonomic history. *Trionyx marini* Hernández Sampelayo and Bataller, 1944 (new species); *T. marini* Jiménez Fuentes and Martín de Jesús 1991 (lectotype designation).

Type material. MG-IGME 1560N (not MG-IGME 1.101N as stated by Jiménez Fuentes and Alonso Andres [1991]) (lectotype), a nearly complete carapace (Hernández Sampelayo and Bataller 1944, figs. 1, 2; Bergounioux 1958, pl. 25.4); MMB (paralectotype), a partial epiplastron (Jiménez Fuentes and Martín de Jesús 1991).

Type locality. Lignite mines of Almatret, Lerida, Catalonia, Spain (Hernández Sampelayo and Bataller 1944; Jiménez Fuentes and Alonso Andres 1994); Rupelian, early Oligocene (Jiménez Fuentes and Martín de Jesús 1991).

Comments. *Trionyx marini* is based on a partial epiplastron and a small (CL of 18 cm), nearly complete shell from the early Oligocene of Spain (Hernández Sampelayo and Bataller 1944), of which the latter was later designated as the lectotype (Jiménez Fuentes and Martín de Jesús 1991). Bergounioux (1958) stated that the lectotype originated from Zaragoza, Aragon, but this seems to be an error (Jiménez Fuentes and Alonso Andres 1994). Jiménez Fuentes and Martín de Jesús (1991) concluded that little could be said about the affinities of this species and that its validity was based mostly on the age and provenience of the specimen. Our firsthand observation of the material reveals that although the holotype is beautifully preserved, rib ends are mostly lacking, and the posterior carapacial margin is damaged. We therefore conclude that this taxon is a nomen dubium.

## *Trionyx messelianus kochi* Hummel, 1927 nomen invalidum (junior synonym of "*T.*" *messelianus* Reinach, 1900)

Taxonomic history. *Trionyx messelianus kochi* Hummel, 1927 (new subspecies); *Amyda messeliana kochi* Karl 1993 (new combination, emended spelling of species epithet); *Rafetoides austriacus* = *T. messelianus* = *T. messelianus kochi* = *T. messelianus lepsiusi* Karl 1998 (junior synonym).

Type material. HLMD Me4194a,b (holotype), the anterior portions of a skeleton (Hummel 1927, pl. 10).

Type locality. Messel pit fossil site, Hesse, Germany (Reinach 1900); MP 11, early Lutetian, middle Eocene (Joyce et al. 2012).

Comments. Hummel (1927) described *Trionyx messelianus kochi* on the basis of two specimens from Messel pit, which were supposed to represent a distinct variety relative to the nominal form "*T.*" *messelianus* from the same locality. We find that varieties based on material from the same locality have no relationship to modern species concepts and therefore disregard *T. messelianus kochi* from consideration completely.

## *Trionyx messelianus lepsiusi* Hummel, 1927 nomen invalidum (junior synonym of "*T.*" *messelianus* Reinach, 1900)

Taxonomic history. *Trionyx lepsii* Harrassowitz 1919 (nomen nudum); *T. lepsiusii* Harrassowitz 1922 (nomen nudum); *T. messelianus lepsiusi* Hummel, 1927 (new subspecies); *Rafetoides austriacus* = *T. messelianus* = *T. messelianus kochi* = *T. messelianus lepsiusi* Karl 1998 (junior synonym).

Type material. HLMD Me1460 (holotype), a well-preserved carapace and plastron (Hummel 1927, pl. 3).

Type locality. Messel pit fossil site, Hesse, Germany (Harrassowitz 1919; Hummel 1927); MP 11, early Lutetian, middle Eocene (Joyce et al. 2012).

Comments. Harrassowitz (1919, 1922) introduced the names *Trionyx lepsii* and *T. lepsiusii*, but he did not provide a description, definition, or indication and therefore did not make either spelling available for nomenclatural considerations. The taxon was therefore only formally established by Hummel (1927), who provided a detailed description and figured several specimens. *Trionyx messelianus lepsiusi* was principally differentiated by its sculpturing pattern, nuchal morphology, shape of costals I, and reversal of the neural series orientation at neural VI, but we do not find this to be relevant, as we do not see any value in recognizing subspecies within material from the same locality. We therefore disregard this taxon completely.

### *Trionyx michauxi* Broin, 1977 nomen invalidum (junior synonym of "*T.*" *silvestris* Walker and Moody, 1974)

Taxonomic history. *Trionyx michauxi* Broin, 1977 (new species); *T. michausi* Broin 1977 (incorrect spelling).

Type material. LG-FSM 3488 (MCY 1) (holotype), a skull (Michaux 1973, fig. 1; Broin 1977, fig. 72, pl. 11.1–3).

Type locality. Mancy, Marne, France; Sables à Unios et Térédines, MP 9, late Ypresian, early Eocene (Broin 1977).

Comments. *Trionyx michauxi* is based on a skull and nonassociated shell fragments that were initially believed to have strong affinities with *T. bruxelliensis* (Michaux 1973). Broin (1977) erected *T. michauxi* on the basis of that skull, described its anatomy, and suggested affinities with the coeval, English form "*T.*" *silvestris*. Despite apparent similarities, Broin (1977) differentiated both forms on the basis of skull thickness, snout, orbit, and palatine shape. Several studies have since shown that fossil and extant trionychids can show considerable ontogenetic, geographic, or sexual variation comparable to that observed between "*T.*" *silvestris* and *T. michauxi* (Dalrymple 1977; Joyce et al. 2016). We therefore synonymize these coeval taxa with confidence (see "*T.*" *silvestris* above). Broin (1977) listed several shell elements (costal and plastral fragments and a xiphiplastron) from coeval sediments as "presumed paratypes." As this does not seem to represent the formal designation of paratype material, we do not list these specimens herein.

Jiménez Fuentes and Alonso Andres (1994) referred two hypoplastra of presumably immature specimens from the middle Eocene (Lutetian) of Castile and León, Spain, to *Trionyx* cf. *michauxi*, based on supposed similarities to the sinuous morphology of the anterior margin of the hypoplastra, a referral we cannot reproduce, as Broin (1977) did not describe the plastral material for her French taxon. Kotsakis (1985) similarly discussed similarities with material from the middle Eocene of Sardinia. In both cases, we find the available material to be too fragmentary to allow identification beyond *Pan-Trionychidae* indet.

### *Trionyx moldaviensis* Khosatzky, 1986 nomen dubium

Taxonomic history. *Trionyx moldaviensis* Khosatzky, 1986 (new species).

Type material. NMENHM 3491 (holotype), a complete carapace (Chkhikvadze 1983, fig. 19; Chkhikvadze and Lungu 1984, fig. 5; Khosatzky 1986, pls. 1.1, 2.1–4; Khosatsky and Redkozubov 1989, figs. 7, 8).

Type locality. Mileştii Mici (= Malye Mileshty), Ialoveni, Moldova (Khosatzky 1986); Serravallian, middle Miocene (Vremir et al 1997).

Comments. The type specimen of *Trionyx moldaviensis* is a relatively complete, large carapace from the middle Miocene of Moldova. The type was initially referred to *T. brunhuberi* by Chkhikvadze (1983) but was later described as a new species by Khosatzky (1986). According to the rationale we outline herein, we here consider this taxon to be a nomen dubium, as a carapace by itself is not diagnostic (see *T. vindobonensis* above for more extensive discussion).

### *Trionyx mourieri* Bergounioux, 1935 nomen dubium

Taxonomic history. *Trionyx mourieri* Bergounioux, 1935 (new species).

Type material. MHNT PAL2011.0.82 (holotype), the imprint of a shell (Bergounioux 1935, fig. 29, pl. 12.1).

Type locality. Armissan, Aude, France (Bergounioux 1935); Chattian or Aquitanian, late Oligocene or early Miocene (Hervet 2004).

Comments. *Trionyx mourieri* is based on several shell imprints from Armissan, Aude, France, of which one serves as the holotype (Bergounioux 1935). Bergounioux (1935) suggested that the neural column of the type specimen continues to the posterior margin of the carapace, but we cannot reproduce this conclusion based on high resolution photographs we obtained. For additional discussion regarding trionychid material from Armissan, France, see *T. acutiformis* and *T. vindobonensis* above.

### *Trionyx münzenbergensis* Hummel 1927 nomen nudum

Material. SMF R260 (holotype), a carapace (Hummel 1927, pl. 11.39).

Locality. Münzenberg, Hesse, Germany (Hummel 1927); Aquitanian, early Miocene (Hummel 1927).

Comments. Hummel (1927) provided *Trionyx münzenbergensis* as a provisional name for a nearly complete carapace from the Miocene of Germany, but as he did not intend the name to be valid, it cannot be considered for nomenclatural purposes (Karl 1993). We therefore disregard this name as a nomen nudum. The name conversely does not need to be Latinized through the removal of the German umlaut, as required by the ICZN (1999) for available names.

### *Trionyx nopcsai* Szalai, 1934 nomen dubium, designation of lectotype

Taxonomic history. *Trionyx nopcsai* Szalai, 1934 (new species); *Chelydropsis nopcsai* Chkhikvadze 1989 (new combination).

Type material. MFGI Ob.3980 (lectotype), a dentary (Szalai 1934, pl. 4.22; Młynarski 1966, fig. 15; Farkas 1995, fig. 1); MFGI 3136 (paralectotype), a carapace fragment (not figured), now considered lost (Farkas 1995).

Type locality. Brusturi (= Tataros), Bihor, Romania (Szalai 1934); Serravallian–Tortonian, middle–late Miocene (Farkas 1995).

Comments. *Trionyx nopcsai* is based on a carapace fragment and a partial lower jaw from the Miocene of Romania (Szalai 1934). Młynarski (1966) challenged the taxonomic status of the lower jaw, which he tentatively identified as belonging to a chelydrid. This view was later adopted by Farkas (1995), Karl (1999a), and Rhodin et al. (2015), and *T. nopcsai* was considered to be a chimera of chelydrid and trionychid fossils. More recently, Joyce (2016) reaffirmed the original identification of the mandible as being pan-trionychid in nature, as members of this group usually have delicate, slopping mandibles, quite in contrast to the more vertically oriented mandibles of chelydrids. Our firsthand observation of this material at MFGI confirms that the dentary indeed belongs to a pan-trionychid. Given that the carapace fragment now seems to be lost (Farkas 1995), we herein designate the dentary as the lectotype of the species. However, given that it is unclear to us if it is possible to firmly identify a pan-trionychid using the dentary alone, we consider *T. nopcsai* to be a nomen dubium (also see *T. vindobonensis* above).

## *Trionyx oligocenica* Negri 1892
## nomen nudum

Material. MGPT-PU, carapacial and plastral fragments (Portis 1885, not figured).

Locality. Agnana Calabria, Calabria, Italy (Portis 1885); Chattian, late Oligocene (Kotsakis 1985).

Comments. This name is not available, as Portis (1885:889) only used the phrase "*Trionyx oligocenica di Agnana*" as a heading to accompany the description of trionychid specimens from the Oligocene of Agnana, Italy, but did not include any indication that he intended to create a new scientific name. The name *T. oligocenica* appeared in the taxonomic lists of Negri (1892), Hummel (1929), Bergounioux (1934b), and Kuhn (1964), who universally considered it to be an available name, but Esu and Kotsakis (1983) and Kotsakis (1985) later clarified that the name is not available in the first place. We here concur with this assessment and consider *T. oligocenica* to be a nomen nudum, especially considering that neither Negri (1892) nor Hummel (1929), Bergounioux (1934b), or Kuhn (1964) made the name available according to the rules of the ICZN (1999). Given that the relevant specimen remains poorly described, we consider it only to document an indeterminate pan-trionychid in the late Oligocene of Calabria.

## *Trionyx oweni* Reinach, 1900
## nomen dubium

Taxonomic history. *Trionyx oweni* Reinach, 1900 (new species); [*T. oweni*] Hummel 1929 (nomen dubium); *T. triunguis* = [*T. oweni*] = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. PUM (holotype), fragments of a carapace and plastron (Reinach 1900, not figured).

Type locality. Eppelsheim, Rhineland-Palatinate, Germany (Kaup 1834; Karl 1999a); Messinian, late Miocene (Karl 1999a).

Comments. The name *Trionyx oweni* first appeared in Reinach (1900), who described a pan-trionychid from Eppelsheim and attributed authorship to Kaup (1834). However, even though Kaup (1834) indeed reported trionychid material from this locality, he never used this name. As was suggested by Hummel (1929, 1932), it seems that Reinach (1900) falsely attributed authorship to Kaup on the basis of a specimen from the University of Marburg that bears the label with this species name. We nevertheless refer authorship to Reinach (1900) according to the rules of the ICZN (1999). Given the fragmentary nature of the type material, we consider this taxon to be a nomen dubium (also see *T. vindobonensis* above).

## *Trionyx parisiensis* Gray, 1831
## nomen dubium

Taxonomic history. *Trionyx parisiensis* Gray, 1831(new species); [*T. parisiensis*] Hummel 1929 (nomen dubium).

Type material. MNHN (holotype), a costal (Cuvier 1821–1824, pl. 76.12, 77; Gray 1831, not figured; Cuvier 1835–1836, pl. 157).

Type locality. Montmarte, Paris, France (Cuvier 1821–1824; Gray 1831); MP 19, Priabonian, late Eocene (Broin 1977).

Comments. Fossil pan-trionychids from the Paris Basin were already described and figured at the beginning of the 19th century (Cuvier 1812), and these are, in fact, the earliest descriptions and figures of fossil pan-trionychids in the chelonian literature. *Trionyx parisiensis* is based on a single costal that was described and discussed by Cuvier (1821–1824). This taxon, however, was only formally named a few years later by Gray (1831), who provided an indication to the previous description of Cuvier (1821–1824). We therefore attribute authorship to Gray (1831), contrary to Lydekker (1889a), Reinach (1900), Hummel (1929), Kuhn (1964), and Broin (1977), who attributed authorship to Meyer (1832). We nevertheless here concur with Hummel (1929, 1932) and Broin (1977) by regarding *T. parisiensis* as a nomen dubium, as we do not find a single costal fragment to be sufficient to diagnose a valid taxon.

## *Trionyx partschii* Peters, 1855
## nomen dubium

Taxonomic history. *Trionyx partschii* Fitzinger 1836 (nomen nudum); *T. partschii* Peters, 1855 (new species); *T. partschi* Laube 1896 (incorrect spelling of species epithet); [*T. partschii*] Hummel 1929 (nomen dubium); *T. vindobonensis* = *T. partschi* (*sic*) Glaessner 1933 (incorrect spelling of species epithet and junior synonym); *T. triunguis* = [*T. partschii*] = 24 others Karl

1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. Two costal fragments (syntypes) with uncertain whereabouts (Peters 1855, pl. 4.4, 5).

Type locality. Loretto (= Loreto), Burgenland, Austria (Peters 1855); Tortonian, late Miocene (Karl 1999a).

Comments. *Trionyx partschii* was first mentioned by Fitzinger (1836), but this action was not accompanied by a description, definition, or indication and therefore does not fulfill the standards of ICZN (1999) for availability of taxonomic names. The species was only later described and figured by Peters (1855), and we consequently attribute authorship to him. Given the fragmentary nature of the type material, we here consider this taxon to be a nomen dubium (also see *T. vindobonensis* above).

### *Trionyx pedemontana* Portis, 1879
### nomen dubium

Taxonomic history. *Tryonix pedemontana* Portis, 1879 (new species and incorrect genus spelling); *Trionyx pedemontana* Portis 1883 (emended genus spelling); *T. pedemontanus* Teppner 1913 (emended spelling of species epithet); *T. pedemontensis* Teppner 1914c (incorrect spelling of species epithet).

Type material. An almost complete carapace, with remains of the left hyo-hypoplastron (holotype) (Portis 1879, pl. 4), unknown whereabouts.

Type locality. Ceva, Mondovi, Piedmont, Italy (Portis 1879); Chattian or Aquitanian, late Oligocene or early Miocene (Kotsakis 1985).

Comments. *Trionyx pedemontana* was established on the basis of a well-preserved carapace and associated plastral elements from Ceva, Italy, that Portis (1879) originally reported to be early Miocene, but Rieppel (1979) thought to be late Oligocene based on anthracotheriids found nearby. Portis (1879) referred to his new species a complete carapace from the Pliocene of nearby San Stefano Roero, which had previously been described and figured by Sismonda (1836, 1839) as a turtle similar to the extant *T. triunguis* (his *T. aegyptiacus*), and which subsequently became the holotype of *T. pliopedemontana* (Sacco 1889) (see also *T. pliopedemontana* below). *Trionyx pedemontana* was originally differentiated by the shape and size of neural I (Portis 1879), but this character has only limited diagnostic value. Moreover, as it was already noted by Portis (1879), the type specimen pertained to a young individual. Given that the whereabouts of the type are furthermore unknown, we here conclude that this taxon should be viewed as a nomen dubium.

### *Trionyx peneckei* Heritsch, 1909
### nomen invalidum
### (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Trionyx peneckei* Heritsch, 1909 (new species); [*T. peneckei*] Hummel 1929 (nomen dubium); *T. triunguis* = *T. peneckei* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 200693 (holotype), a partial carapace and hypoplastron (Heritsch 1909, pl. 10.1–2; Gross 2002, pl. 12.1).

Type locality. Pölfing-Brunn, Styria, Austria (Heritsch 1909; Gross 2002); Eibiswald Formation, MN 5, early Langhian, middle Miocene (Aguilar et al. 1997).

Comments. *Trionyx peneckei* is based on a disarticulated, partial shell that fully corresponds in its morphology with *T. vindobonensis*, as it also represents a less skeletally mature individual. We therefore find the synonymy of these two taxa from equally dated sediments in Austria unproblematic (for a more extensive discussion, see *T. vindobonensis*).

### *Trionyx petersi* Hoernes, 1881
### nomen invalidum, lectotype designation
### (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Trionyx petersi* Hoernes, 1881 (new species); *T. petersi* = *T. hilberi* Mottl 1967 (senior synonym); *T. triunguis* = *T. petersi* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 200694 (lectotype), partial hyo-hypoplastra and partial skull (Gross 2002, pl. 11.1); UMJGP 200708 (paralectotype), bone fragments (Gross 2002, pl. 11.2); UMJGP 200709 (paralectotype), carapace fragments (Gross 2002, pl. 11.3); UMJGP 201158 (paralectotype), a carapace (Heritsch 1909, pl. 9.4; Gross 2005, fig. 1).

Type locality. Feisternitz, Großradl, Styria, Austria (Hoernes 1881; Gross 2002); Eibiswald Formation, early Langhian (MN 5), middle Miocene (Aguilar et al. 1997).

Comments. For a discussion on material from Großradl, Austria, see *Trionyx hoernesi* and *T. vindobonensis* (above). A juvenile shell from the middle Miocene of Pölfing-Brunn (= Schönegg bei Wies), Styria, Austria, that was attributed by Heritsch (1910) to *T. petersi* is herein considered to pertain to an indeterminate pan-trionychid. The same is true for the partial carapace described as *T. petersi*, also from the middle Miocene of Carinthia, by Wank (1977).

### *Trionyx petersi trifailensis* Teppner, 1914c
### nomen dubium

Taxonomic history. *Trionyx petersi trifailensis* Teppner, 1914c (new subspecies); *T. triunguis* = *T. petersi trifailensis* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. GIML (holotype), a carapace (Teppner 1914c).

Type locality. Trbovlje (= Trifail), Slovenia; Langhian, middle Miocene (Teppner 1914c).

Comments. *Trionyx petersi trifailensis* was established on the basis of a carapace from the middle Miocene of Trbovlje, Slovenia (Teppner 1914c), but the type material was never figured. We therefore here consider this taxon to be a nomen dubium.

## *Trionyx planus* Owen in Owen and Bell, 1849 nomen invalidum (junior synonym of "*T.*" *henrici* Owen in Owen and Bell, 1849)

Taxonomic history. *Trionyx planus* Owen in Owen and Bell, 1849 (new species); *T. plana* Hummel 1927 (incorrect spelling of species epithet); *Rafetoides henrici = T. planus =* 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. BMNH R30410x (holotype), posterior half of a carapace (Owen and Bell 1849, pl. 19c; Owen 1849–1884, pl. 32).

Type locality. Hordle (= Hordwell) Cliff, Hampshire, United Kingdom (Owen and Bell 1849); Totland Bay Member, Headon Hill Formation, Priabonian, late Eocene (Benton and Spencer 1995).

Comments. *Trionyx planus* Owen in Owen and Bell, 1849, should not be confused with its junior homonym *Aspideretes planus* Parks, 1933 (recombined as *T. planus* by Russell [1934]) from the Late Cretaceous of Canada, which is a junior synonym of *Axestemys splendidus* (Hay, 1908) according to Gardner et al. (1995).

*Trionyx planus* is known from the posterior half of a carapace from the late Eocene of Hordle, United Kingdom (Owen and Bell 1849). Lydekker (1889a) diagnosed this taxon by its rather coarse sculpturing, the narrowness of neurals V and VI, and the presence of expanded costals VIII, but we find that these characters fall within the expected range of variability displayed by other material found at Hordle. As such, we herein treat *T. planus* as a junior synonym of "*T.*" *henrici*. Owen (in Owen and Bell 1849), Lydekker (1889a), and Boulenger (1891) referred a plastral fragment, a mandible, and a cranium, respectively, from the type locality to *T. planus* as well, using size concerns or similarities in shell sculpturing, but we here assign all of these to "*T.*" *henrici* as well, mostly based on a geographic rationale (see "*T.*" *henrici* above for more extensive discussion).

## *Trionyx pliocaenicus* Reinach, 1903 nomen dubium

Taxonomic history. *Trionyx pliocaenicus* Reinach, 1903 (new species); [*T. pliocaenicus*] Dacqué 1912 (nomen dubium).

Type material. SMF R 4144 (holotype), carapacial and plastral fragments (Reinach 1903, pl. 17.1, 3, 4, 7).

Type locality. Wadi El Natrun, Beheira, Egypt; Pliocene (Reinach 1903).

Comments. *Trionyx pliocaenicus* Reinach, 1903, should not be confused with *T. pliocenicus* Fucini, 1912. Reinach (1903) mostly differentiated his new taxon, which is based on a collection of shell fragments, on the basis of the shape of the costals and carapace sculpturing pattern. The validity of *T. pliocaenicus* was challenged by Dacqué (1912) and Wood (1979), and we agree that the listed characters are insufficient to support a valid species. The type material thus can only be identified as an indeterminate pan-trionychid, and *T. pliocaenicus* is herein therefore considered to be a nomen dubium.

## *Trionyx pliopedemontana* Sacco, 1889 nomen dubium

Taxonomic history. *Trionyx pliopedemontana* Sacco, 1889 (new species); *Trionyx pliopedemontanus* Hummel 1929 (emended spelling of species epithet); *Testudo pliopedemontana* Kuhn 1964 (new combination); *T. pliopedemontanus = T. blayaci = T. pliocenicus = T. pompignanensis = T. rotundiformis* Broin 1977 (senior synonym).

Type material. MGPT-PU 17276 and MGPT-PU 17276/2 (holotype), internal and external imprint of a complete carapace (Sismonda 1836, pl. 1; Sismonda 1839, pl. 2).

Type locality. San Stefano Roero, Piedmont, Italy (Sismonda 1836, 1839; Portis 1879); Piacenzian, late Pliocene (Kotsakis 1985).

Comments. Sismonda (1836, 1839) described and figured the first known fossil trionychid from Italy, a specimen (the internal and external imprints of a nearly complete carapace) from the late Pliocene of San Stefano Roero, Piedmont, that he tentatively assigned to the extant *Trionyx triunguis* (his *T. aegyptiacus*). Four decades later, Portis (1879) referred this specimen to his newly erected taxon *T pedemontana*, which he typified by material from the late Oligocene or early Miocene also from Piedmont (see above). Sacco (1889) finally used the same specimen to establish *T. pliopedemontana*, which he differentiated from the older *T. pedemontana* on the basis of much larger size, shape of neurals, size and shape of neurals V–VII, and the shape of costals I. Whereas Hummel (1929, 1932) and Kotsakis (1980, 1985) considered this species to be a member of the *Amyda* lineage, Karl (1999a) considered it to be synonymous with *T. triunguis.*

Our firsthand investigation of the type specimen reveals that sutures are clear, but that the margins of the carapacial disk are universally lacking. The available material is consistent with being referable to the *Trionyx triunguis* lineage but can only be diagnosed as *Pan-Trionychinae* indet. We therefore conclude that *T. pliopedemontana* is best considered a nomen dubium, contrary to more than 100 years of nomenclatural practice. Instead, we here consider *T. pliocenicus* to be valid, a taxon historically synonymized with *T. pliopedemontana*, as this is based on a nearly complete skeleton (see above). All specimens from the Neogene of Italy (Portis 1890; Kotsakis 1980, 1985; Girotti et al. 2003), France (Depéret and Donnezan 1890–1897; Bergounioux 1933; Broin 1977), and Romania (Macarovici and Motas 1965) that were historically affiliated with *T. pliopedemontana*, mostly using temporal and spatial considerations, are herein referred to *Pan-Trionychinae* indet., given that pan-cyclanorbines seem to be missing in the Neogene of Europe. The same is true also for what seems to be the last European fossil pan-trionychid, a costal fragment and a fragmentary tibia from the early Pleistocene of Valdarno, Tuscany, Italy, which was originally described by Portis (1890) and later further described and attributed to *Trionyx* cf. *pliopedemontana* by Kotsakis (1980).

Kuhn (1964) listed *pliopedemontana* under *Testudo*, but we agree with Auffenberg (1974) that this is likely an error.

## *Trionyx pompignanensis* Bergounioux, 1933 nomen dubium

Taxonomic history. *Trionyx pompignanensis* Bergounioux, 1933 (new species); *T. pliopedemontanus* = *T. blayaci* = *T. pliocenicus* = *T. pompignanensis* = *T. rotundiformis* Broin 1977 (junior synonym).

Type material. LG-FSM (holotype), a fragment of a costal (Bergounioux 1933, pl. 1.2).

Type locality. La Pompignane, Montpellier, Hérault, France (Bergounioux 1933); Pliocene (Broin 1977).

Comments. For a discussion on Bergounioux's (1933) material from Montpellier, France, see *Trionyx blayaci* above.

## *Trionyx pontanus* Laube, 1895 nomen dubium

Taxonomic history. *Trionyx pontanus* Laube, 1895 (new species); *Amyda pontanus* Comaschi Caria 1959 (new combination); *T. triunguis* = *T. pontanus* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. OMM Gpa77 (syntype), a rather complete carapace and its imprint (Laube 1896, pls. 1, 2); unknown collection (syntype), a complete carapace (Laube 1896, pls. 3, 4).

Type locality. Most (= Brüx), Ústí nad Labem, Czechia (Laube 1895); Most Formation, Burdigalian, early Miocene (Aguilar et al. 1997).

Comments. *Trionyx pontanus* is based on two well-preserved, large (CL almost equal to 40 cm) carapaces from the Miocene of Czechia that Laube (1895) only introduced briefly but soon after extensively described and figured (Laube 1896). *Trionyx pontanus* was originally diagnosed based on sculpturing pattern and the shape of last neurals and costals (Laube 1895, 1896). Karl (1998, 1999a) considered *T. pontanus* to be a junior synonym of the extant *T. triunguis*, but Chkhikvadze (1999b) considered *T. pontanus* to be the sole European member of *Rafetus* and the senior synonym of all early Miocene Czech taxa (*T. aspidiformis*, *T. bohemicus*, *T. elongatus*, and *T. preschenensis*). Given that this taxon is based on carapacial material alone, affinities with *Rafetus bohemicus* cannot be concluded with certainty, and we herein consider *T. pontanus* to be a nomen dubium (see *T. vindobonensis* and *Rafetus bohemicus* for more extensive discussions).

Bergounioux (1935) reported the presence of *Trionyx pontanus* from the late Miocene of Sardinia, but we believe this is be a typographic error, as it seems more likely that he intended to mean *Trionyx* (= *Procyclanorbis*) *sardus* (Esu and Kotsakis 1983).

## *Trionyx portisi* Ristori, 1891b nomen dubium

Taxonomic history. *Trionyx portisi* Ristori, 1891b (new species).

Type material. Probably IGF (syntype), a rather complete carapace, missing only the nuchal, and parts of neural I and costals I (Ristori 1895, pl. 2.8); probably IGF (syntype), a carapace fragment (Ristori 1895, pl. 2.12); probably IGF (syntype), a carapace fragment (Ristori 1895, pl. 2.13).

Type locality. Montebamboli, Tuscany, Italy (Ristori 1891b); MN 12, Tortonian, late Miocene (Chesi 2009).

Comments. For a discussion on material named by Ristori (1891a, 1891b), from the late Miocene of Tuscany, Italy, see *Trionyx bambolii* above.

## *Trionyx preschenensis* Laube, 1900 nomen dubium

Taxonomic history. *Trionyx preschenensis* Laube 1898 (nomen nudum); *T. preschenensis* Laube, 1900 (new species); *Tryonyx preschensis* Laube 1900 (incorrect spelling); *T. preschensis* Reinach 1900 (incorrect spelling of species epithet); *Procyclanorbis preschenensis* Portis 1901 (new combination); *T. preschnensis* Rieppel 1979 (incorrect spelling of species epithet); *T. triunguis* = *T. preschenensis* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. NMP 20205 (holotype), negative and positive imprints of an almost complete carapace, along with remains of the hyo-hypoplastron (Laube 1900, pls. 1, 2.1).

Type locality. Břestány (= Preschen), near Bilina, Ústí nad Labem, Czechia (Liebus 1930); Most Formation, MN 3, Burdigalian, early Miocene (Aguilar et al. 1997).

Comments. Laube (1898) first introduced the name *Trionyx preschenensis* without description or definition, but soon after formally made the name available (Laube 1900). Portis (1901) regarded this taxon as a pan-cyclanorbine and included it into his new genus *Procyclanorbis.* Chkhikvadze (1999b), on the other hand, more recently argued that this is a junior synonym of *T.* (his *Rafetus*) *pontanus*, the only European representative of the *Rafetus* lineage. We herein regard *T. preschenensis* to be a nomen dubium, as it is based on a juvenile specimen (see *T. vindobonensis* and *Rafetus bohemicus* for more extensive discussions).

## *Trionyx propinquus* Ristori, 1891a nomen dubium

Taxonomic history. *Trionyx propinquus* Ristori, 1891a (new species); *T. propinquens* Bergounioux 1935 (incorrect spelling of species epithet).

Type material. Probably MSNP (syntype), fragments of a carapace (Ristori 1895, pl. 2.11); MUSNAF (syntype), a partial carapace (Ristori 1895, pl. 5.27).

Type locality. Near Sienna, Tuscany, Italy (Ristori 1891a, 1895); Casino Clays, Messinian, late Miocene (Abbazzi et al. 2008).

Comments. For a discussion on material named by Ristori (1891a, 1891b), from the late Miocene of Tuscany, Italy, see *Trionyx bambolii* above.

### *Trionyx pseudovindobonensis* Szalai, 1934 nomen dubium

Taxonomic history. *Trionyx pseudovindobonensis* Szalai, 1934 (new species); *Testudo pseudovindobonensis* Kuhn 1964 (new combination); [*Trionyx pseudovindobonensis*] Farkas 1995 (nomen dubium); *Trionyx triunguis* = *Trionyx pseudovindobonensis* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. MFGI Ob.3145 (holotype), a left femur fragment (Szalai 1934, pl. 5, fig. 23; Młynarski 1966, fig. 13; Farkas 1995, fig. 2).

Type locality. Rákos, Budapest, Hungary (Szalai 1934; Młynarski 1966); Serravallian, middle Miocene (Farkas 1995).

Comments. Szalai (1934) erected *Trionyx pseudovindobonensis* on the basis of a purported humerus from the middle Miocene of Hungary that he differentiated from that of *T. vindobonensis* from the late Miocene of Austria on the basis of the humeral morphology. The diagnosis of a species based on a humerus was heavily criticized by Glaessner (1935), but Młynarski (1966) was nevertheless reluctant to reject the validity of this taxon. More recently, Farkas (1995) challenged the original identification of the holotype as a right humerus and instead showed that it is in fact a partial left femur, which still is insufficient to diagnose a valid taxon. After our personal investigation of the holotype at MFGI, we agree with Farkas (1995) in considering *T. pseudovindobonensis* to be a nomen dubium (also see *T. vindobonensis* above).

Kuhn (1964) listed the name *Testudo pseudovindobonensis* in his compendium, but it is unclear to us if this is an error or if he truly believe this taxon to be a tortoise (*Testudinidae*).

### *Trionyx pustulatus* Owen in Owen and Bell, 1849 nomen dubium

Taxonomic history. *Trionyx pustulatus* Owen in Owen and Bell, 1849 (new species); [*T. pustulatus*] Hummel 1929 (nomen dubium); *Rafetoides henrici* = *T. pustulatus* = 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. A costal fragment (holotype) (Owen and Bell 1849, pl. 19b.7–9), whereabouts unknown.

Type locality. A costal fragment (holotype) (Owen and Bell 1849, pl. 19b.7–9; Owen 1849–1884, pl. 31.7–9), whereabouts unknown.

Comments. *Trionyx pustulatus* is based on a costal fragment that was characterized by its distinct, reticulate sculpturing (Owen and Bell 1849). The holotype was originally held in the collections of the Marchioness of Hasting, but unlike the remainders of that collection, this fragment was not transferred to the BMNH, and we are therefore uncertain as to its whereabouts. The reticulate sculpturing mentioned by Owen and Bell (1849) is now considered to be highly variable among pan-trionychids (Gardner and Russell 1994). Given the highly fragmentary nature of the lost type specimen, we agree with Hummel (1929) that this taxon should be regarded as a nomen dubium.

### *Trionyx ragusensis* De Gregorio, 1883 nomen dubium

Taxonomic history. *Trionix ragusensis* De Gregorio, 1883 (new species and incorrect spelling of genus name); [*Trionyx ragusensis*] Kotsakis 1985 (nomen nudum).

Type material. ITCAM (holotype), a carapace (De Gregorio 1883, not figured), probably lost (Kotsakis 1985).

Type locality. Ragusa, Sicily, Italy (De Gregorio 1883, 1892); Langhian, middle Miocene (Kotsakis 1985).

Comments. De Gregorio (1883) introduced the name *Trionix ragusensis* (note the incorrect spelling of the genus name) on the basis of a carapace that was kept at the Cabinetto di Scienze naturali dell'Istituto tecnico di Modica, in Modica, Sicily, Italy. The specimen was never figured and is now believed to be lost (Kotsakis 1985). In a subsequent publication, De Gregorio (1892) considered his taxon to share affinities with *Trionyx melitensis* (herein considered to be a marine turtle) from nearby Malta, "*T. capellinii*" (his *T. italicus*) from Italy, and "*T.*" *henrici* from England, but he did not provide any rationale for these affinities and he only mentioned that he would describe *Trionix ragusensis* in detail at a later stage. This unfortunately never happened. *Trionix ragusensis* was strangely ignored by Hummel (1929, 1932) and (Kuhn 1964), but Kotsakis (1985) more recently suggested that it was never formally described and should therefore be considered to be a nomen nudum. In our opinion, De Gregorio (1883) fulfilled the minimum requirements of ICZN (1999) by listing a single character, which is the size of the holotype specimen (CL of 25 cm). Given that the description of De Gregorio (1883) is not informative and that the type is now lost, it is clear that *T. ragusensis* must be considered a nomen dubium.

### *Trionyx reticulatus* Rieppel, 1979 nomen dubium

Taxonomic history. *Trionyx reticulatus* Rieppel, 1979 (new species).

Type material. PIMUZ A/111 502 (holotype), a well-preserved carapace, with vertebrae and parts of the shoulder girdle (Rieppel 1979, figs. 1, 2).

Type locality. Oerlikon, Zurich, Switzerland (Rieppel 1979); Upper Freshwater Molasse (Rieppel 1979), Langhian/Serravallian, middle Miocene.

Comments. *Trionyx reticulatus* is based on a heavily cracked carapace from the Molasse Basin of Switzerland. Rieppel (1979) reported the specimen to be from the late Miocene, but the updated geological map of Switzerland provides a middle Miocene age of sediments exposed in the town of Oerlikon. This species is partially diagnosed based on the presence of an extremely elongate neural I, but we do not believe this to be factual, but rather an artifact resulting from the preparation and restoration of the type specimen. According to the rationale we developed herein, we disregard this taxon from nomenclatural consideration, as we conclude that isolated carapaces from Europe are not sufficient to diagnose a valid taxon (see *T. vindobonensis* above for a more extensive discussion).

## *Trionyx rivosus* Owen in Owen and Bell, 1849 nomen invalidum (junior synonym of "*Trionyx*" *henrici* Owen in Owen and Bell, 1849)

Taxonomic history. *Trionyx rivosus* Owen in Owen and Bell, 1849 (new species); *Rafetoides henrici* = *T. rivosus* = 7 others Karl 1998 (junior synonym, see "*T.*" *henrici* for complete synonym).

Type material. BMNH R30405 (holotype), posterior part of a carapace of a juvenile individual (Owen and Bell 1849, pl. 18a; Owen 1849–1884, pl. 29).

Type locality. Hordle (= Hordwell) Cliff, Hampshire, United Kingdom (Owen and Bell 1849); Totland Bay Member, Headon Hill Formation, Priabonian, late Eocene (Benton and Spencer 1995).

Comments. *Trionyx rivosus* is known from a single, fragmentary carapace that was originally diagnosed on the basis of its distinctive carapacial sculpturing (Owen and Bell 1849). Lydekker (1889a) suggested that *T. rivosus* could be a junior synonym of the sympatric *T. planus* (herein considered a junior synonym of "*T.*" *henrici*) and attributed differences to ontogeny, with the former representing a younger individual of the latter. For a more extensive discussion regarding pan-trionychid material from the late Eocene of England, see "*T.*" *henrici* above.

## *Trionyx rocchettiana* Portis, 1882 nomen dubium

Taxonomic history. *Trionyx rocchettiana* Portis, 1882 (new species); *T. rochettianus* Harrassowitz 1919 (incorrect spelling of species epithet); *T. rocchettianus* Hummel 1932 (emended spelling of species epithet); *T. rochettiana* Rieppel 1979 (incorrect spelling of species epithet).

Type material. MGL 8895 (syntype), anterior part of a carapace (Portis 1882, pl. 24); MGL 8894 (syntype), central portion of a carapace (Portis 1882, pl. 25).

Type locality. La Rocchette (= Rochette) Locality, Belmont, Vaud, Switzerland (Portis 1882); MP 29, Chattian, late Oligocene (Berger 1998).

Comments. Portis (1882) formally named three pan-trionychid taxa based on abundant fossil material from La Rocchette, Switzerland. Of these, *Trionyx rocchettiana* is based on the most fragmentary material. We herein consider this taxon to be a nomen dubium, as the type material is fully insufficient to diagnose a valid species (see *T. valdensis* for more extensive discussion).

## *Trionyx roncensis* Harrassowitz, 1919 nomen dubium

Taxonomic history. *Trionyx roncensis* Harrassowitz, 1919 (new species); [*T. roncensis*] Hummel 1929 (nomen dubium); *Amyda roncensis* Bergounioux 1934b (new combination).

Type material. MGPT-PU (holotype), a carapace fragment (Portis 1885, pl. 11.1; Harrassowitz 1919), probably lost.

Type locality. Roncà, Veneto, Italy (Harrassowitz 1919); Bartonian, middle Eocene (Kotsakis 1977, 1985).

Comments. Harrassowitz (1919) established *Trionyx roncensis* on the basis of a rather fragmentary specimen, which was originally figured by Portis (1885) but now seems to be lost, as we were not able to find this specimen during a recent visit to MGPT-PU. The new taxon was differentiated from other pan-trionychids solely by its sculpturing pattern, despite the fact that Harrassowitz (1919) himself pointed out the dubious nature of this feature. Hummel (1929) considered this taxon to bear strong resemblance to the German "*T.*" *messelianus*. Kotsakis (1977, 1985) considered the status of this species as uncertain and doubtful, noting that the remains could not be identified beyond the genus level of *Trionyx*. Differences with "*T.*" *capellinii* in carapace sculpturing , however, lead Kotsakis (1985) to believe that *T. roncensis* could represent a distinct species. Such differences in sculpturing are now considered to be a character that is highly variable within species (Vitek and Joyce 2015). Given the fragmentary nature of the type specimen, we therefore regard *T. roncensis* to be a nomen dubium.

## *Trionyx rostratus* Arthaber, 1898 nomen invalidum (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Trionyx rostratus* Arthaber, 1898 (new species); *Amyda cartilaginea* = *T. rostratus* = *T. trinilensis* Karl 1998 (junior synonym).

Type material. IPUW 1897 IV (holotype), a skeleton, including most of the skull, mandible, and carapace, a fragment of an epiplastron, the hyoids, vertebrae, and several limb elements (Arthaber 1898, pls. 25–28; Hummel 1927, pl. 2.6; Karl 1998, pls. 1.2, 2, 3, 4.3, 4.4).

Type locality. Au am Leithaberge (= Au am Leithagebirge), Lower Austria, Austria (Arthaber 1898); early Tortonian, late Miocene (Karl 1999a).

Comments. Among Miocene trionychids from central Europe, the holotype of *Trionyx rostratus* stands out by consisting of a relatively complete skeleton that includes a skull and mandible. Given the complete nature of the type specimen, the validity of this species remained unchallenged historically. However, Karl (1998) recently highlighted that the name *T. rostratus* could be considered preoccupied by *Testudo rostrata* Thunberg, 1787, as this is a suppressed junior synonym of the extant trionychid *Pelodiscus sinensis* Wiegmann, 1835. We here, however, consider this name to be available, as Thunberg's (1787) taxon is now associated with *Pelodiscus*, not *Trionyx*, its historical generic placement. Karl (1998, 1999a) furthermore referred the type specimen of *T. rostratus* to the extant southeast Asian taxon *Amyda cartilaginea*. We here nevertheless synonymize this species with *T. vindobonensis* (see above).

## *Trionyx rotundiformis* Bergounioux, 1933
## nomen dubium

Taxonomic history. *Trionyx rotundiformis* Bergounioux, 1933 (new species); *T. rotondiformis* Bergounioux 1958 (incorrect spelling of species epithet); *T. pliopedemontanus* = *T. blayaci* = *T. pliocenicus* = *T. pompignanensis* = *T. rotundiformis* Broin 1977 (junior synonym).

Type material. CPS-UL 92864 (holotype), an incomplete carapace (Bergounioux 1933, fig. 2, pl. 2.2).

Type locality. Montpellier, Hérault, France (Bergounioux 1933); MN 14, Zanclean, early Pliocene (Hervet 2004).

Comments. Bergounioux (1933) established *Trionyx rotundiformis* on the basis of a single, incomplete carapace from the Pliocene of Montpellier, France, that he diagnosed relative to other trionychids by minor differences in the shape of the costals, neurals, and sculpturing pattern. For a discussion on trionychid material from Montpellier, France, described by Bergounioux (1933), see *T. blayaci* above.

## *Trionyx schaurothianus* Negri, 1893
## nomen invalidum
## (junior synonym of "*T.*" *capellinii* Negri, 1892)

Taxonomic history. *Trionyx schaurothianus* Negri, 1893 (new species); *T. capellinii schaurothiames* Bergounioux 1934b (incorrect spelling of subspecies epithet); *T. capellinii schaurotianus* Bergounioux 1958 (incorrect spelling of subspecies epithet); *T. capellinii schaurothiana* Kuhn 1964 (emended spelling of subspecies epithet); *T. c. montevialensis* = *T. c. gracilina* = *T. c. perexpansa* = *T. c. schaurothianus* = *T. insolitus* = [*T. italicus*] Kotsakis 1977 (junior synonym); *T. italicus* = *T. c. montevialensis* = *T. c. schaurothianus* = *T. c. gracilina* = *T. c. perexpansa* = *T. insolitus* Kotsakis 1985 (junior synonym).

Type material. MGP-PD 10818Z (holotype), a complete skeleton in dorsal view, including the skull, carapace, a hyo-hypoplastron, limb elements, and caudal vertebrae (Negri 1893, pl. 2; Bergounioux 1954, fig. 24, pl. 12; Kotsakis 1977, fig. 3i; Pandolfi et al. 2017, fig. 7b).

Type locality. Monteviale, Veneto, Italy (Negri 1893); MP 21, early Rupelian, early Oligocene (Pandolfi et al. 2017).

Comments. Negri (1893) established *Trionyx schaurothianus* on the basis of an unusually well-preserved fossil pan-trionychid from the early Oligocene of Monteviale, Italy. For a discussion on pan-trionychid material from this locality, see "*T.*" *capellinii* above.

## *Trionyx sculptus* Gilmore, 1931
## nomen dubium

Taxonomic history. *Trionyx sculptus* Gilmore, 1931 (new species); *Aspideretes sculptus* Yeh 1963 (new combination).

Type material. AMNH 6700 (holotype), a carapace, lacking the nuchal and the distal ends of many of the costals (Gilmore 1931, pl. 10).

Type locality. Tairum Nor, Inner Mongolia, China (Gilmore 1931); Tunggur Formation, Serravallian, middle Miocene (Wang et al. 2003).

Comments. *Trionyx sculptus* is based on a partial carapace from Inner Mongolia, China, that was originally believed to be Pliocene (Gilmore 1931), but more recently clarified to be middle Miocene in age (Wang et al. 2003). Although the anterior portion of the carapace is missing, Gilmore (1931) believed this specimen to once have possessed a preneural, a view later adopted by Yeh (1963), who reassigned this taxon to *Nilssonia* (his *Aspideretes*). Judging from photographs of the holotype, we cannot refute nor confirm the presence of a preneural. In addition, given that the remainder of the carapace does not display a sufficient amount of character evidence to support its validity, we here consider this taxon to be a nomen dubium.

## *Trionyx senckenbergianus* Reinach, 1903
## nomen dubium

Taxonomic history. *Trionyx senckenbergianus* Reinach, 1903 (new species); [*T. senckenbergianus*] Dacqué 1912 (nomen dubium); *T. triunguis* = *T. senckenbergianus* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. SMF R430 (syntype), a fragment of a right hyoplastron (Reinach 1903, pl. 17.6); SMF (syntype), a costal fragment (Reinach 1903, pl. 17.5); SMF (syntype), a costal fragment (Reinach 1903, pl. 17.2).

Type locality. Wadi Moghra (= Moghara), Matruh Governorate, Egypt (Reinach 1903); Burdigalian, early Miocene (Lapparent de Broin 2000).

Comments. It is notable that most of the pan-trionychid fossils from Africa either have not been identified beyond the family level or have been assigned to extant taxa, even though most of them are not subfossils (e.g., Lapparent de Broin 2000). *Trionyx senckenbergianus* is one of few named fossil pan-trionychid taxa from Africa. Reinach (1903) mostly differentiated his new species on the basis of shell sculpturing and the shape of the costals, but these characters are now understood to be highly variable (Meylan 1987; Gardner and Russell 1994). Indeed, soon after the original description of *T. senckenbergianus*, Dacqué (1912), Hummel (1929), and Wood (1979) doubted its validity, likely as it is based on an assortment of fragments. We fully agree with this opinion and therefore regard this taxon to be a nomen dubium.

### *Trionyx senensis* Ristori, 1891b
### nomen dubium

Taxonomic history. *Trionyx senensis* Ristori, 1891b (new species).

Type material. IGF (syntype), an almost complete carapace (Ristori 1895, pl. 2.7); probably IGF (syntype), a carapace fragment, containing the last neurals (Ristori 1895, pls. 1.5, 2.10); probably IGF (syntype), a carapace fragment in visceral view, along with parts of vertebrae and pectoral girdle (Ristori 1895, pl. 1.6).

Type locality. Montebamboli, Tuscany, Italy (Ristori 1895; Kotsakis 1985); Tortonian, late Miocene (Chesi 2009).

Comments. For a discussion on material from the late Miocene of Tuscany named by Ristori (1891a, 1891b), see *Trionyx bambolii* above.

### *Trionyx septemcostatus* Hoernes, 1881
### nomen invalidum
### (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Trionyx septemcostatus* Hoernes, 1881 (new species); *T. septemradiatus* Portis 1901 (incorrect spelling of species epithet); *T. septemcostata* Liebus 1930 (incorrect spelling of species epithet); *T. triunguis* = *T. septemcostatus* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 200698 (holotype), a partial shell (Hoernes 1881, fig. 3; Heritsch 1909, fig. 1, pl. 9.2; Gross 2002, pl. 14.4).

Type locality. Eibiswald, Styria, Austria (Hoernes 1881); Eibiswald Formation, MN 5, early Langhian, middle Miocene (Aguilar et al. 1997).

Comments. *Trionyx septemcostatus* was established on the basis of a small (CL of 23 cm), partial shell (Hoernes 1881) from the Miocene locality of Eibiswald, Austria. The same locality also produced the type series of *T. petersi* (herein considered a junior synonym of *T. vindobonensis*), which is almost identical to *T. septemcostatus* with exception of the presence of eight costals, instead of the seven apparent in *T. septemcostatus*. The presence of seven costals was considered to be unique among European pan-trionychids and prompted early workers to speculate affinities with the North American *Platypeltis* (= *Apalone*) (Hummel 1932), which is characterized, among others, by regularly possessing only seven costals (Hay 1908). It is now known, however, that the number of costals is variable among some extant trionychids and that a reduced number by itself is not diagnostic. Indeed, the most posterior pair of costals is rather large in the type specimen, and we therefore also see the possibility that the posterior two pairs of costals fused with one another. According to the rationale we outlined above, we here consider *T. septemcostatus* to be a junior synonym of *T. vindobonensis*. For a more extensive discussion, please refer to the latter taxon above.

### *Trionyx siegeri* Heritsch, 1909
### nomen dubium, designation of lectotype

Taxonomic history. *Trionyx siegeri* Heritsch, 1909 (new species); *T. petersi siegeri* Mottl 1967 (referral to subspecies level); *T. triunguis* = *T. siegeri* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 200710 (lectotype), a partial carapace (Heritsch 1909, pl. 11.4; Gross 2002, pl. 15.1); UMJGP 200707 (paralectotype), carapace fragments, likely a chimera (Gross 2002, pl. 15.2).

Type locality. Vordersdorf, Wies, Styria, Austria (Heritsch 1909); Eibiswald Formation, MN 5, early Langhian, middle Miocene (Aguilar et al. 1997).

Comments. *Trionyx siegeri* is only known from an incomplete carapace from the Miocene of Styria, Austria (Heritsch 1909). Mottl (1967) believed *T. siegeri* to be a subspecies of *T. petersi*, whereas Karl (1998) synonymized it with the extant *T. triunguis*. Gross (2002) noted that one of the two syntypes represents a chimera consisting of a pan-trionychid and a chelydrid. We therefore render the other specimen as the lectotype for the sake of nomenclatural clarity. We nevertheless consider *T. siegeri* to be a nomen dubium, as it is only based on carapacial material (see *T. vindobonensis* above for more extensive justification).

Mottl (1967) attributed several fossils from the middle Miocene of Carinthia, Austria, to *Trionyx petersi siegeri*. Of these, we refer all specimens that include plastral elements diagnostic for the *T. triunguis* lineage to *T. vindobonensis* but consider all specimens lacking plastral material as indeterminate pan-trionychines.

### *Trionyx sinuosus* Chow and Yeh, 1958
### nomen dubium

Taxonomic history. *Trionyx sinuosus* Chow and Yeh, 1958 (new species); *Aspideretes sinuosus* Yeh 1963 (new combination).

Type material. IVPP V 944 (holotype), anterior two-thirds of carapace (Chow and Yeh 1958, figs. 1, 2).

Type locality. Kengsiu (= Gensiu), Yushe County, Shanxi Province, China (Chow and Yeh 1958; Ye 1994); late Pliocene or early Pleistocene (Rhodin et al. 2015).

Comments. *Trionyx sinuosus* is based on a partial shell from the Plio-Pleistocene of Shanxi, China (Chow and Yeh 1958), a province within the current range of the extant *Pelodiscus sinensis* (TTWG 2014). Chow and Yeh (1958) noted a resemblance with *Nilssonia* (their *Aspideretes*) but also stated that the preneural, which is the most diagnostic character for this clade, cannot be clearly distinguished in this specimen. Judging from the figures, we cannot confirm the presence of a preneural either but instead note that the specimen is consistent with the morphology of the *Pelodiscus* lineage by being relatively small and by showing open suprascapular fontanelles (Meylan 1987). However, the specimen is too fragmentary to allow rigorously distinguishing it from the extant *Pelodiscus sinensis* and the Pliocene *Pelodiscus gracilia* (see above). We therefore consider the type to be an indeterminate representative of the *Pelodiscus* lineage and the taxon to be a nomen dubium.

## *Trionyx sophiae* Heritsch, 1909
## nomen dubium

Taxonomic history. *Trionyx sophiae* Heritsch, 1909 (new species); *T. triunguis* = *T. sophiae* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 200700 (holotype), the carapace of a juvenile and associated plastral fragments (Heritsch 1909, pl. 11.3; Gross 2002, pl. 15.3).

Type locality. Eibiswald, Styria, Austria (Heritsch 1909); Eibiswald Formation, MN 5, early Langhian, middle Miocene (Aguilar et al. 1997).

Comments. *Trionyx sophiae* is known from a single, oval-shaped carapace, which is only 14.3 cm long and 11.5 cm wide (Heritsch 1909), that Mottl (1967) suggested to be a juvenile form of *T. petersi*, which is herein considered to be a junior synonym of *T. vindobonensis.* We conclude here, however, that *T. sophiae* is a nomen dubium, as it is both a juvenile and consists only of carapacial material (see *T. vindobonensis* for a more extensive discussion).

## *Trionyx stadleri* Teppner, 1913
## nomen dubium

Taxonomic history. *Trionyx stadleri* Teppner, 1913 (new species); *T. triunguis* = *T. stadleri* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 11831 (holotype), a nearly complete carapace (Teppner 1913, fig. 1; Jurkovšek and Kolar-Jurkovšek 1994, pl. 1.1; Ramovš 1974, fig. 417; Paunović 1986, fig. 1; Gross 2002, pl. 16.1; Karl 2007, pl. 3.1).

Type locality. Trbovlje (formerly known as Trifail), Central Sava, Slovenia (Hoernes 1882; Teppner 1913); Trbovlje Formation, late Chattian, late Oligocene (Gross 2002).

Comments. *Trionyx stadleri* is based on a carapace from the late Oligocene of Slovenia (Teppner 1913) that was initially diagnosed based on characters now known to be highly variable within extant trionychids, such as the shape of the nuchal, neurals, and costals and the sculpturing of the shell. Given that the posterior margin of the shells seems to be damaged, we here conclude that this specimen can be identified as an indeterminate pan-trionychine at best. We therefore consider this taxon to be a nomen dubium.

## *Trionyx stiriacus* Peters, 1855
## nomen dubium, designation of lectotype

Taxonomic history. *Trionyx stiriacus* Peters, 1855 (new species); *Tryonix stiriacus* Portis 1879 (incorrect spelling of genus name); *T. styriacus* Hoernes 1881, Peters 1881 (incorrect spelling of species epithet); *T. stiriaca* Toula 1882 (incorrect spelling of species epithet); *T. triunguis* = *T. stiriacus* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. UMJGP 5847 (lectotype), a partial carapace (Peters 1855, pl. 4.1, 3; Gross 2002, pl. 16.2); UMJGP 1776 (paralectotype), carapace and plastral fragments, counterpart of UMJGP 1777 (Peters 1855, pl. 6.2, 4, 6; Gemel 2002, pl. 2.d; Gross 2002, pl. 16.3); UMJGP 1777 (paralectotype), carapace and plastral fragments, counterpart of UMJGP 1776 (Peters 1855, pl. 6.1, 3, 5; Gross 2002, pl. 16.4).

Type locality. Schönegg, Pölfing-Brunn, Styria, Austria (Peters 1855; Gross 2002); Eibiswald Formation, MN 5, early Langhian, middle Miocene (Aguilar et al. 1997).

Comments. *Trionyx stiriacus* is one of the first named trionychids from the Miocene of central Europe. It has therefore been extensively discussed in the literature, though often using the wrong spelling "*styriacus*" (Peters 1881; Hoernes 1881, 1882; Depéret and Donnezan 1890–1897; Negri 1892; Laube 1895; Ristori 1895; Arthaber 1898; Reinach 1900; Heritsch 1909; Ammon 1911; Liebus 1930; Bergounioux 1935; Kuhn 1964; Tuna 1988; Lapparent de Broin 2001; Danilov et al. 2011), probably because Peters (1855) himself used the spelling "*styriacus*" in the plate accompanying the original publication. Given the central importance of *T. stiriacus* to the taxonomy of Miocene trionychids, we here designate one of the three syntypes as the lectotype, because the syntype material consists of dissociated specimens that well may represent a chimera. As a result, however, *T. stiriacus* is rendered a nomen dubium, because we conclude the lectotype is insufficient to diagnose a taxon, as it is only a partial carapace. The lectotype and both paralectotypes are herein identified as indeterminate pan-trionychines. For a more extensive discussion regarding our rationale, see *T. vindobonensis* above.

## *Trionyx stormsi* Delheid, 1899
## nomen dubium

Taxonomic history. *Trionyx stormsi* Delheid, 1899 (new species); [*T. stormsi*] Hummel 1929 (nomen dubium).

Type material. IRSNB R 354a–c (holotype), four costal fragments (Delheid 1899, not figured).

Type locality. Boom clay, Boom or Terhaegen, Antwerp, Belgium (Delheid 1899); Boom Formation, Rupelian, early Oligocene (Mayr and Smith 2012).

Comments. *Trionyx stormsi* is based on four costal fragments that were never figured, but briefly described (Delheid 1899), and this action therefore fulfills the minimum requirements of the ICZN (1999) for the availability of names published prior to 1931. There was no indication about where the material was housed, but we were able to locate carapace fragments from Boom in the collections of IRSNB that are labeled *T. stormsi* and that correspond to the brief description of Delheid (1899), although repair to the specimens resulted in a different count of bones (T. Smith and A. Folie, pers. comm., 2016). We consider this material to be the holotype of *T. stormsi*. Although the material without doubt pertains to an indeterminate pan-trionychid, we here consider *T. stormsi* to be a nomen dubium.

### *Trionyx subangularis* Bergounioux, 1954 nomen dubium

Taxonomic history. *Trionyx subangularis* Bergounioux 1953 (nomen nudum); *T. subangularis* Bergounioux, 1954 (new species).

Type material. MGP-PD 26565 (holotype), a partial carapace and its imprint (Bergounioux 1954, figs. 35, 36, pls. 18, 19).

Type locality. Bolzano Bellunense, Veneto, Italy (Bergounioux 1954); Burdigalian, early Miocene (Kotsakis 1985).

Comments. *Trionyx subangularis* is based on a moderately sized specimen (CL of 29 cm) that was initially diagnosed as a new taxon by the shape of its carapace and the number, shape, and size of the neurals and costals (Bergounioux 1954). Kotsakis (1985) tentatively considered this taxon to be valid and distinguished it from other pan-trionychids on the basis of shell ornamentation and the number and morphology of the neurals. However, these characters have since been shown to be highly variable within many extant trionychid species (Meylan 1987; Vitek and Joyce 2015). Our firsthand observation of the holotype reveals that it lacks characters that would allow identifying it beyond *Pan-Trionychinae* indet. We therefore here consider *T. subangularis* to be a nomen dubium.

### *Trionyx teiritzbergensis* Gemel, 2002 nomen invalidum (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Trionyx teiritzbergensis* Gemel, 2002 (new species).

Type material. NOLM F/4972 (holotype), an almost complete hypoplastron (Gemel 2002, pls. 1.2, 2.a, 3.1).

Type locality. Teiritzberg, Lower Austria, Austria; Burdigalian, early Miocene (Gemel 2002).

Comments. *Trionyx teiritzbergensis* was only recently established on the basis of a single hypoplastron from the early Miocene of Austria that was thought to show an unusually low angle between the processus lateralis and the longitudinal axis of the hypoplastron (Gemel 2002). We do not find this characteristic to be either particularly apparent or of any systematic value and therefore attribute this material to *T. vindobonensis*, which is typified on slightly younger material from the same basin. For a more extensive discussion, see *T. vindobonensis* above.

### *Trionyx teyleri* Winkler, 1869a nomen invalidum (junior synonym of *T. vindobonensis* Peters, 1855)

Taxonomic history. *Trionyx teyleri* Winkler, 1869a (new species); *Tryonix teyleri* Portis 1879 (incorrect spelling of genus name); *T. tayleri* Laube 1896 (incorrect spelling of species epithet); *T. triunguis* = *T. teyleri* = 24 others Karl 1998 (junior synonym, see *Rafetus bohemicus* for complete synonym).

Type material. TM 8446 (holotype), fragments of a skull, mandible, hyoids, plastron, limbs, and cervical vertebrae (Winkler 1869a, pl. 15.51, 51a).

Type locality. Öhningen (= Oeningen or Oehningen), Baden-Württemberg, Germany (Winkler 1869a); MN 7+8, Serravallian, middle Miocene (Aguilar et al. 1997).

Comments. *Trionyx teyleri* is based on a single, incomplete skeleton that was characterized by its prominent plastral sculpturing, hyo-hypoplastron morphology, a pointed, triangular skull, and long cervical vertebrae (Winkler 1869a). However, the listed shell characters are now known to be highly variable (Meylan 1987; Gardner and Russell 1994), whereas the skull is badly crushed and therefore not informative. *Trionyx teyleri* is notable in that it possesses a single lateral hyoplastral process, at least judging from the figures (Winkler 1869a), which is typical for North American pan-trionychids (Vitek and Joyce 2015) but has never been described in European forms. However, inaccuracies credited to the fantasy of 19th-century lithographers have been documented repeatedly for turtles (e.g., Anquetin and Joyce 2014) and snakes (e.g., Georgalis et al. 2016a), among others, and we therefore are skeptical about the accuracy of this observation. We therefore attribute this material to *T. vindobonensis* (also see *T. vindobonensis* above).

### *Trionyx trinilensis* Jaekel, 1911 nomen invalidum (junior synonym of *Amyda cartilaginea* [Boddaert, 1770])

Taxonomic history. *Trionyx trinilensis* Jaekel, 1911 (new species); [*T. trinilensis*] Hummel 1929 (nomen dubium); *T. cartilagineus* = *T. trinilensis* Karl 1987 (junior synonym); *Amyda cartilaginea* = *T. rostratus* = *T. trinilensis* Karl 1998 (junior synonym).

Type material. MB R.2754.1-2 (holotype), an epiplastron and entoplastron (Jaekel 1911, pl. 15.12, 13).

Type locality. Trinil, Java, Indonesia (Jaekel 1911); *Pithecanthropus* Trinil Beds, Pleistocene (Rhodin et al. 2015).

Comments. Jaekel (1911) based *Trionyx trinilensis* on an epiplastron and entoplastron but furthermore referred cervical vertebrae, two scapulae, and tibial fragments to this species. All elements show strong resemblance with the extant *Amyda cartilaginea*, and the nuanced characters that were used by Jaekel

(1911) to distinguish this taxon can be attributed to intraspecific variation. As such, *T. trinilensis* is herein considered a junior synonym of the extant *Amyda cartilaginea,* as was initially proposed by Karl (1987) and more recently confirmed by Rhodin et al. (2015). It is worth noting that the extant populations of *Amyda* were recently shown to be genetically diverse. As a result, the type species *Amyda cartilaginea* is now confined to the islands of Indonesia, whereas the name *Amyda ornata* was resurrected from synonymy for the populations on the Asian mainland (Fritz et al. 2014). In light of these new insights, we here still support the synonymy of *T. trinilensis* with *Amyda cartilaginea* but note that this decision is based on geographic concerns.

## *Trionyx tshelkarensis* Chkhikvadze 1973
## nomen nudum

Material. None discussed or designated.

Locality. Chelkar-Teniz Lake (= Tshelkar), Karagandy Region, Kazakhstan (Chkhikvadze 1973); Chelkarnurinskaya suite, late Eocene to Oligocene (Vitek and Danilov 2015).

Comments. *Trionyx tshelkarensis* was simply mentioned by Chkhikvadze (1973) in a taxonomic list of Asian trionychids citing his unpublished thesis of 1972. The name has otherwise not appeared again in the chelonian literature and therefore must be considered a nomen nudum.

## *Trionyx turgaicus* Kuznetsov and Chkhikvadze, 1977
## nomen invalidum
## (junior synonym of "*T.*" *ninae* [Chkhikvadze, 1971])

Taxonomic history. *Trionyx turgaicus* Kuznetsov and Chkhikvadze, 1977 (new species); *T. turgaica* Kuznetsov 1978 (unjustified emendation of spelling of species epithet); *Palaeotrionyx turgaicus* Chkhikvadze and Shuvalov 1988 (new combination and incorrect spelling of genus name); *Rafetus turgaicus* Chkhikvadze 1989 (new combination); *Ulutrionyx turgaicus* Kordikova 1994a (new combination); *Yuen turgaicus* Chkhikvadze 2007 (new combination); *Oscaria turgaicus* Chkhikvadze 2010 (new combination); *Ulutrionyx ninae* = *T. turgaicus* = *T. zaisanensis* Vitek and Danilov 2015 (junior synonym).

Type material. IPGAS C-5-3 (holotype), an almost complete shell, skull fragments, and limb elements of one individual (Kuznetsov and Chkhikvadze 1977, pls. 1.1–10, 2.1–5; Kuznetsov 1978, pl. 4.1, 2, 4, 6–10).

Type locality. Donguz Tau, Karagandy Region, Kazakhstan (Kuznetsov and Chkhikvadze 1977; Vitek and Danilov 2015); Chelkarnurinskaya suite, late Eocene to Oligocene (Vitek and Danilov 2015).

Comments. *Trionyx turgaicus* is based on a partial skeleton from the Paleogene of Kazakhstan. This is yet another Asian taxon with a complicated nomenclatural history, as it was initially referred to *Trionyx* (Kuznetsov and Chkhikvadze 1977) but later variously referred to *Paleotrionyx* (*Palaeotrionyx* of Chkhikvadze and Shuvalov 1988), *Rafetus* (Chkhikvadze 1989), *Ulutrionyx* (Kordikova 1994a), *Yuen* (Chkhikvadze 2007), and *Oscaria* (Chkhikvadze 2010).

*Trionyx turgaicus* is overall similar to the temporally and spatially close "*T.*" *ninae* but notably lacks a suture between the nuchal and costals. Vitek and Danilov (2015) more recently noted that this is an ontogenetic feature typical of juvenile individuals. Moreover, given that the type of *T. turgaicus* belongs to a small individual, Vitek and Danilov (2015) concluded that this taxon is an ontogenetic variant of "*T.*" *ninae* and therefore its junior synonym (also see "*T.*" *ninae* above). We here agree with that assessment.

## *Trionyx ubeensis* Chitani, 1925
## nomen dubium

Taxonomic history. *Trionyx ubeensis* Chitani, 1925 (new species).

Type material. GSJ (holotype), a partial carapace (Chitani 1925, unnumbered figure), destroyed by fire (Hirayama 2007).

Type locality. Ube coal mine, Yamaguchi, Japan (Chitani 1925); Ube Group, Priabonian, late Eocene (Hirayama 2007).

Comments. *Trionyx ubeensis* is known from a fragmentary carapace (CL approximately 40 cm), consisting of the nuchal, neurals I and II, right costals I–III and VI–VIII, and fragments of the left side of the shell (Chitani 1925). According to the type description, this taxon can be differentiated from *T. desmostyli* from the Miocene of Japan and *T. hilberi* from the Miocene of Europe, both of which are herein considered to be nomina dubia, by having an anteriorly convex shell and variations to the shape and contacts of the neurals and costals. All of these characters are now considered to be highly variable within pan-trionychids (Meylan 1987; Gardner and Russell 1994). Moreover, the type and only known specimen is now destroyed (Hirayama 2007). All of these factors prompt us to regard this as an indeterminate pan-trionychid and *T. ubeensis* as a nomen dubium.

## *Trionyx valdensis* Portis, 1882
## nomen dubium

Taxonomic history. *Trionyx valdensis* Portis, 1882 (new species).

Type material. MGL 8898 (holotype), a carapace (Portis 1882, pl. 26).

Type locality. La Rocchette (= Rochette) Locality, Belmont, Vaud, Switzerland (Portis 1882); MP 29, Chattian, late Oligocene (Berger 1998).

Comments. A significant number of pan-trionychid fossils have been unearthed from the late Oligocene locality of La Rocchette, Switzerland (Portis 1882). Among these, Portis (1882) described three supposedly distinct species, namely *Trionyx lorioli*, *T. rocchettiana*, and *T. valdensis*, which he differentiated from one another by the shape of the nuchal, the shape of neural I, the number of costals, and carapacial sculpturing. In our assessment, the posterior region of the type of *T. valdensis* is damaged, and we therefore doubt that this specimen shows a reduced costal count, whereas all other listed differences are now known to be variable within extant pan-trionychid species (Meylan 1987; Gardner and Russell 1994). We therefore treat the La Rocchette pan-trionychid fauna as a monospecific assemblage. We nevertheless consider all material from Rochette to be undiagnostic at the species level, because all specimens lack plastral elements or the posterior margin of the carapace. We therefore refer all to *Pan-Trionychidae* indet. and declare all three taxa to be nomina dubia.

### *Trionyx zaisanensis* Chkhikvadze, 1973 nomen invalidum (junior synonym of "*T.*" *ninae* [Chkhikvadze, 1971])

Taxonomic history. *Trionyx zaisanensis* Chkhikvadze, 1973 (new species); *Palaeotrionyx zaisanensis* Chkhikvadze and Shuvalov 1988 (new combination and incorrect spelling of genus name); *Rafetus zaisanensis* Chkhikvadze 1989 (new combination); *Eurycephalochelys zaisanensis* Kordikova and Chkhikvadze 1990 (new combination); *Ulutrionyx zaisanensis* Kordikova 1994a (new combination); *Yuen zaisanensis* Chkhikvadze 2007 (new combination); *Oskaria zaisanensis* Chkhikvadze 2008b (new combination and incorrect spelling of genus name); *Ulutrionyx ninae* = *T. turgaicus* = *T. zaisanensis* Vitek and Danilov 2015 (junior synonym).

Type material. IPGAS Z-34-6 (holotype), a medial half of a hypoplastron (Chkhikvadze 1973, fig. 4, pl. 5; Kuznetsov 1978, pl. 14.5; Kordikova 1994a, fig. 2; Chkhikvadze 2008a, figs. 2, 3).

Type locality. Kiin-Kerish, East Kazakhstan Region, Kazakhstan (Chkhikvadze 1973; Vitek and Danilov 2015); Kustovskaya suite, Kusto Formation, late Eocene–Oligocene (Vitek and Danilov 2015).

Comments. *Trionyx zaisanensis* is based on the medial half of a hypoplastron from the Paleogene of Kazakhstan (Chkhikvadze 1973). According to its type description, *T. zaisanensis* differs from the temporally and spatially close "*T.*" *ninae* by having a more massive shell and longer posteromedial processes of the hypoplastron (Chkhikvadze 1973). Vitek and Danilov (2015) more recently casted doubt on the usefulness of these characters, noting that it was in fact "*T.*" *ninae* that possesses the larger carapace, but they nevertheless considered the apparent difference to be of dubious utility and both taxa to be synonyms. We acknowledge that the available material of *T. zaisanensis* is fragmentary, but the close resemblance and the stratigraphic and geographic proximity with the type of *Ulutrionyx ninae* prompt us to concur with the assessment of Vitek and Danilov (2015; see *Ulutrionyx ninae* above). We therefore agree that *T. zaisanensis* is a junior synonym of "*T.*" *ninae*.

### *Trionyx zakhidovi* Khosatzky, 1966 nomen dubium

Taxonomic history. *Trionyx zakhidovi* Khosatzky, 1966 (new species); *Paleotrionyx riabinini* = *T. zakhidovi* Chkhikvadze 2007 (junior synonym); [*T. zakhidovi*] Vitek and Danilov 2010 (nomen dubium).

Type material. CCMGE 411/1341 (holotype), a right femur (Khosatzky 1966, fig. 2; Danilov and Vitek 2013, fig. 23.3i).

Type locality. Kyrkkuduk well (= Sary-Agach = Kyrkkuduk I), South Kazakhstan Region, Kazakhstan (Khosatzky 1966; Vitek and Danilov 2010); Syuk-Syuk Formation or lower part of the Darbaza Formation, Santonian or Campanian, Late Cretaceous (Vitek and Danilov 2010).

Comments. *Trionyx zakhidovi* is based on a large, isolated femur about 20 cm in length from the Late Cretaceous (Santonian or Campanian) of Kazakhstan (Khosatzky 1966). Kordikova (1994a) and Chkhikvadze (2007) considered *T. zakhidovi* to be a possible synonym of one of the two other contemporaneous taxa from Kazakhstan ("*T.*" *onomatoplokos* [their *Palaeotrionyx riabinini*] or "*T.*" *riabinini*) or simply an indeterminate pan-trionychid. However, given that isolated pan-trionychid limb bones are undiagnostic below the family level, we agree with Vitek and Danilov (2010) that this taxon is a nomen dubium.

Khosatzky (1966) referred the caudal part of a large pan-trionychid carapace with an estimated shell length of about 70 cm from the type locality to *Trionyx zakhidovi*, probably using a geographic rationale. Given that *T. zakhidovi* must be considered a nomen dubium, we agree with Vitek and Danilov (2010) and Danilov and Vitek (2012) that it is best to refer this specimen to the roughly coeval "*T.*" *kansaiensis* using the diagnostic characters it displays.

### *Zaisanonyx jimenezfuentesi* Chkhikvadze, 2008b nomen dubium

Taxonomic history. *Paleotrionyx jimenezfuentesi* Chkhikvadze 1995 (nomen nudum); *Eurycephalochelys jimenezfuentesi* Chkhikvadze 2007 (nomen nudum); *Zaisanonyx jimenezfuentesi* Chkhikvadze, 2008b (new species).

Type material. IPGAS 7-1-137 (holotype), a partial nuchal (Chkhikvadze 2008b, fig. 8a, b).

Type locality. Treugol'nik Locality, Kalmakpay River, Zaysan Depression, East Kazakhstan Region, Kazakhstan; Obayla suite, middle Eocene (Chkhikvadze 2008b, 2010).

Comments. *Zaisanonyx jimenezfuentesi* was established on the basis of a partial nuchal, which was initially tentatively referred to *Paleotrionyx muyuensis* (Chkhikvadze 1990). The full nuchal can be inferred to have been about 20 cm wide. Chkhikvadze (2007) discussed possible affinities of this fragment with the European giant form *Axestemys vittata*, assigning it to *Eurycephalochelys*, but finally used it for the basis of a new species (Chkhikvadze 2008b). We find the type material to be too fragmentary to diagnose a valid taxon and therefore consider *Zaisanonyx jimenezfuentesi* to be a nomen dubium.

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## Appendix 1
## Institutional Abbreviations

| | |
|---|---|
| AMNH | American Museum of Natural History, New York, New York, USA |
| BMNH | Natural History Museum, London, United Kingdom |
| BSPG | Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany |
| CCMGE | Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia |
| CNHM | Croatian Natural History Museum, Zagreb, Croatia |
| CPS-UL | Centre de paléontologie stratigraphique et paléoécologie, Université de Lyon 1, Villeurbanne, France |
| GBAW | Geologische Bundesanstalt Wien, Vienna, Austria |
| GIML | Department für angewandte Geowissenschaften und Geophysik, Montanuniversität Leoben, Leoben, Austria |
| GMH | Geological Museum of Heilongjiang, Harbin, China |
| GSI | Geological Society of India, Bengaluru, India |
| GSJ | Geological Survey of Japan, Tsukuba, Japan |
| GSP | Geological Survey of Pakistan, Islamabad, Pakistan |
| HLMD | Hessisches Landesmuseum Darmstadt, Darmstadt, Germany |
| HNSM | Hiwa Natural Sciences Museum, Hiwa, Japan |
| IGF | Museo di Storia Naturale, Università degli Studi di Firenze, Florence, Italy |
| IMC | Indian Museum of Kolkata, Kolkata, India |
| IPGAS | Institute of Paleobiology, Georgian Academy of Sciences, Tbilisi, Georgia |
| IPUW | Institut für Paläontologie, University of Vienna, Austria |
| IRSNB | Institut royal des Sciences naturelles de Belgique, Brussels, Belgium |
| ITCAM | Istituto Tecnico Commerciale Archimede, Modica, Italy |
| IVPP | Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China |
| IZ-BAS | Institute of Zoology, Bulgarian Academy of Sciences, Sofia, Bulgaria |
| IZK | Institute of Zoology, Academy of Sciences of Kazakhstan, Almaty, Kazakhstan |
| KUL | Kyushu University Library, Kyushu, Japan |
| LBG-UD | Laboratoire Biogéosciences, Université de Bourgogne, Dijon, France |
| LG-FSM | Laboratoire de Geologie, Université de Montpellier, Montpellier, France |
| MB | Museum für Naturkunde Berlin, Berlin, Germany |
| MDLCA | Museo Sardo di Geologia e Paleontologia "Domenico Lovisato," Cagliari, Italy |

| | |
|---|---|
| MFGI | Magyar Földtani és Geofizikai Intézet, Budapest, Hungary |
| MFM | Mizunami Fossil Museum, Mizunami, Japan |
| MG-IGME | Museo Geominero, Instituto Geológico y Minero de España, Madrid, Spain |
| MGL | Musée cantonal de Géologie, Lausanne, Switzerland |
| MGP-PD | Museo di Geologia e Paleontologia dell'Università di Padova, Padua, Italy |
| MGPT-PU | Museo di Geologia e Paleontologia, Università degli Studi di Torino, Turin, Italy |
| MHNB | Museum d'histoire naturelle de Bordeaux, Bordeaux, France |
| MHNF | Musée d'histoire naturelle Fribourg, Switzerland |
| MHNT | Museum d'histoire naturelle de Toulouse, Toulouse, France |
| MMB | Museo Municipal de Barcelona, Barcelona, Spain |
| MMUL | Municipal Museum of Ústí nad Labem, Ústí, Czechia |
| MNHN | Muséum national d'Histoire naturelle, Paris, France |
| MPC | Mongolian Palaeontological Centre, Ulaanbaatar, Mongolia |
| MPP | Museo Paleontologico Parmense, Parma, Italy |
| MSNP | Museo di Storia Naturale di Pisa, Pisa, Italy |
| MTB | Museum of the Transylvanian Basin, University of Cluj, Cluj-Napoca, Romania |
| MUSNAF | Museo di Storia Naturale dell'Accademia dei Fisiocritici, Siena, Italy |
| NHMW | Naturhistorisches Museum Wien, Vienna, Austria |
| NMC | National Museum of Colombo, Colombo, Sri Lanka |
| NMCL | Naturkundemuseum Coburg, Coburg, Germany |
| NMENHM | National Museum of Ethnography and Natural History of Moldova, Chișinau, Moldova |
| NMK | National Museum of Kenya, Nairobi, Kenya |
| NMM | Naturhistorisches Museum Mainz, Mainz, Germany |
| NMP | Národní Muzeum Praha, Prague, Czechia |
| NMR | Naturkundemuseum Ostbayern, Regensburg, Germany |
| NOLM | Landesmuseum Niederösterreich, St. Pölten, Austria |
| NTUM | National Taiwan University, Taipei, China |
| OMM | Oblastní muzeum v Mostě, Most, Czechia |
| PIMUZ | Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland |
| PIN | Paleontological Institute, Russian Academy of Sciences, Moscow, Russia |
| PUM | Philipps-Universität Marburg, Marburg, Germany |
| QM | Queensland Museum, Brisbane, Australia |
| SMF | Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany |
| TM | Teylers Museum, Haarlem, The Netherlands |
| TU | Tohoku University, Tohoku, Japan |
| UMJGP | Universalmuseum Joanneum, Geologie und Paläontologie, Graz, Austria |
| UVF | Ur- und Vorgeschichtsmuseum Fritzlar, Fritzlar, Germany |
| YIGM | Yichang Institute of Geology and Mineral Resources, Wuhan, China |
| ZIN PH | Paleoherpetological Collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia |
| ZPM | Zhejiang Provincial Museum, Hangzhou, China |

## Appendix 2
## Named Old World Fossil Pan-Trionychid Genera

*Altaytrionyx* Chkhikvadze, 2008b (type species: *Plastomenus gabunii* Chkhikvadze, 1984)

*Aulacochelys* Lydekker, 1889a (type species *Trionyx circumsulcatus* Owen in Owen and Bell, 1849)

*Crassithecachelys* Chkhikvadze, 2000a (type species: *Plastomenus mlynarskii* Chkhikvadze, 1970)

*Drazinderetes* Head et al., 1999 (type species: *Drazinderetes tethyensis* Head et al., 1999)

*Eurycephalochelys* Moody and Walker, 1970 (type species: *Eurycephalochelys fowleri* Moody and Walker, 1970)

*Francedebroinella* Chkhikvadze, 1999a (type species: *Plastomenus minusculus* Chkhikvadze, 1973)

*Gobiapalone* Danilov et al., 2014 (type species: *Amyda orlovi* Khosatzky, 1976)

*Khunnuchelys* Brinkman et al., 1993 (type species: *Khunnuchelys erinhotensis* Brinkman et al., 1993)

*Kuhnemys* Chkhikvadze, 1999b (type species *Aspideretes maortuensis* Yeh, 1965)

*Murgonemys* White, 2001 (type species: *Murgonemys braithwaitei* White, 2001)

*Nemegtemys* Danilov et al., 2014 (type species: *Nemegtemys conflata* Danilov et al., 2014)

*Palaeoamyda* Cadena, 2016 (type species: *Trionyx messelianus* Reinach, 1900)

*Paraplastomenus* Kordikova, 1994a (type species: *Plastomenus mlynarskii* Chkhikvadze, 1970)

*Perochelys* Li, Joyce, and Liu, 2015 (type species: *Perochelys lamadongensis* Li, Joyce, and Liu 2015)

*Petrochelys* Vitek et al., 2017 (type species: *Trionyx kyrgyzensis* Nessov, 1995b)

*Procyclanorbis* Portis, 1901 (type species: *Procyclanorbis sardus* Portis, 1901)

*Rafetoides* Karl, 1998 (type species: *Trionyx henrici* Owen in Owen and Bell, 1849)

*Sinamyda* Chkhikvadze, 2000a (type species: *Trionyx fuchienensis* Yeh, 1974)

*Ulutrionyx* Kordikova, 1994a (type species: *Trionyx ninae* Chkhikvadze, 1971)

*Zaisanonyx* Chkhikvadze, 2008b (type species: *Zaisanonyx jimenezfuentesi* Chkhikvadze, 2008b)

## Appendix 3
## Biogeographical Summary of Old World Pan-Trionychid Turtles

Numbers in brackets reference Figures 3 to 6. Literature lacking catalogued or described or figured specimens is omitted, as also all fossil Holocene records. *Abbreviations*: *T.*, *Trionyx*; TL, type locality.

### Algeria

[1] Pliocene, Zanclean–early Piacenzian; Constantine Province; *Pan-Trionychidae* indet. (Arambourg 1956)

### Australia

[2] Early Eocene; Murgon, Queensland; *Murgonemys braithwaitei* (TL) (White 2001; *Trionychidae* indet. of Gaffney and Bartholomai 1979)

[3] Pliocene; Darling Downs, Queensland; *Pan-Trionychidae* indet. (Louys and Price 2015)

[4] Pleistocene; Queensland; *Pan-Trionychidae* indet. (*T. australiensis* of De Vis 1894; *Trionychidae* indet. of Gaffney and Bartholomai 1979)

### Austria

[5] Early Eocene, late Ypresian; Salzburg; *Pan-Trionychidae* indet. (*Trionyx* sp. of Schleich 1988; *Amyda* cf. *boulengeri* of Karl 1996)

[6] Middle Miocene; Carinthia; *T. vindobonensis* (*T. petersi siegeri* of Mottl 1967), *Pan-Trionychinae* indet. (*T. petersi siegeri* of Mottl 1967; *T. petersi* of Wank 1977)

[7] Miocene; Styria; middle Miocene, Langhian: *T. vindobonensis* (Peters 1855, 1859; *T. petersi* and *T. septemcostatus* of Hoernes 1881; *T. hoernesi*, *T. peneckei*, and *T. siegeri* of Heritsch 1909), *Pan-Trionychinae* indet. (*T. stiriacus* of Peters 1855, 1859, 1869; *T. sophiae* of Heritsch 1909; *T. petersi* of Heritsch 1910; *T. hilberi* of Teppner 1914a); middle Miocene, Langhian–Serravallian: *Pan-Trionychinae* indet. (*T. hilberi* of Hoernes 1892); late Miocene: *Pan-Trionychinae* indet. (*Trionyx* sp. of Toula 1882)

[8] Miocene; Vienna; middle Miocene, Serravallian: *T. vindobonensis* (TL) (Peters 1855, 1859); late Miocene, Tortonian: *Pan-Trionychidae* indet. (*Trionyx* sp. of Bachmayer 1966)

[9] Late Miocene, Tortonian; Burgenland; *T. vindobonensis* (*T. rostratus* of Arthaber 1898), *Pan-Trionychinae* indet. (*T. partschii* of Peters 1855)

[10] Mio/Pliocene; Lower Austria; early Miocene, Burdigalian: *T. vindobonensis* (*T. teiritzbergensis* of Gemel 2002), *Pan-Trionychinae* indet. (*Trionychidae* indet. of Depéret 1895); late Miocene, Tortonian: *T. vindobonensis* (Papp et al. 1953), *Pan-Trionychidae* indet. (*Trionyx* sp. of Delfino and Göhlich 2009); Early Pliocene; *Pan-Trionychinae* indet. (*Trionyx* sp. aff. *rostratus* of Glaessner 1933)

### Belgium

[11] Late Paleocene, Thanetian; Walloon Brabant; *Pan-Trionychidae* indet. (Broin 1977; Groessens van Dyck and Schleich 1988)

[12] Eocene; early Eocene, Ypresian, Flemish Brabant: *Pan-Trionychidae* indet. (*Trionyx* sp. of Groessens van Dyck and Schleich 1988); early Eocene, Ypresian, Hainaut: *Axestemys vittata* (*T. erquelinnensis* and *T. levalensis* of Dollo 1909; Broin 1977); middle Eocene, Lutetian, Brussels Capital Region: *Pan-Trionychidae* indet. (*T. bruxelliensis* of Winkler 1869a, 1869b); middle Eocene, Lutetian, East Flanders: *Pan-Trionychidae* indet. (Groessens van Dyck and Schleich 1988); middle Eocene, Lutetian, Flemish Brabant: *Pan-Trionychidae* indet. (Groessens van Dyck and Schleich 1988); middle Eocene, Lutetian, Walloon Brabant: *Pan-Trionychidae* indet. (*Trionyx* sp. of Groessens van Dyck and Schleich 1988)

[13] Early Oligocene, Rupelian; Antwerp; *Pan-Trionychidae* indet. (*T. stormsi* of Delheid 1899)

### Bulgaria

[14] Late Eocene, Priabonian; Stara Zagora; *Trionychidae* indet. (*T. capellinii bulgaricus* of Khosatzky et al. 1983)

[15] Miocene; Vidin; *Pan-Trionychinae* indet. (*Trionyx* sp. of Pamouktchiev et al. 1998)

### Chad

[16] Late Miocene, Tortonian; Borkou; *Pan-Trionychidae* indet. (*Trionychidae* indet. of Vignaud et al. 2002)

[17] Late Pliocene, Piacenzian; Borkou; *Pan-Trionychidae* indet. (*Trionyx* sp. of Priem 1914)

### China

[18] Cretaceous, state uncertain; Fujian Province; *Pan-Trionychidae* indet. (*Sinamyda fuchienensis* of Yeh 1974)

[19] Cretaceous, stage uncertain; Jilin (= Chilin) Province; *Pan-Trionychidae* indet. (Yeh 1963)

[20] Early Cretaceous, stage uncertain; Inner Mongolia; *Pan-Trionychidae* indet. (Gilmore 1931)

[21] Early Cretaceous, Aptian; Liaoning Province; *Perochelys lamadongensis* (TL) (Li, Joyce, and Liu 2015)

[22] Early Cretaceous, Aptian/Albian; Heilongjiang Province; "*T.*" *jixiensis* (TL) (Li, Tong et al. 2015)

[23] Late Cretaceous, Turonian; Alxa (= Alashan), Inner Mongolia; *Kuhnemys maortuensis* (TL) (including *T. alashanensis* of Yeh 1965)

[24] Late Cretaceous, Campanian; Xilin Gol, Inner Mongolia; *Khunnuchelys erinhotensis* (TL) (Brinkman et al. 1993)

[25] Early Eocene; Hubei Province; *Pan-Trionychidae* indet. (*Aspideretes muyuensis* of Lei and Ye 1985)

[26] Eocene; Inner Mongolia; early Eocene: *Pan-Trionychidae* indet. (Gilmore 1934); middle Eocene: "*T.*" *gregarius* (TL) (Gilmore 1934; including *Rafetus gilmorei* of Chkhikvadze 1999b), "*T.*" *johnsoni* (TL) (Gilmore 1931, 1934; including "*T.*" *neimenguensis* of Yeh 1965)

[27] Late Eocene; Guangdong Province; "*T.*" *impressus* (TL) (Yeh 1965)

[28] Late Eocene; Henan Province; *Pan-Trionychidae* indet. (*Platypeltis subcircularis* of Chow and Yeh 1957)

[29] Early Eocene; Shandong Province; "*T.*" *linchuensis* (TL) (Yeh 1962)

[30] Late Eocene–early Oligocene; Zhejiang Province; *Pan-Trionychidae* indet. (= *Amyda* sp. of Yeh 1962)

[31] Middle Miocene, Serravallian; Inner Mongolia; *Pan-Trionychidae* indet. (*T. sculptus* of Gilmore 1931)

[32] Pliocene; Shanxi Province; *Pelodiscus gracilia* (TL), *Pan-Trionychidae* indet. (including *Pelodiscus* cf. *sinensis* of Yeh 1963)

[33] Late Pliocene or early Pleistocene; Shanxi Province; *Pelodiscus* indet. (*T. sinuosus* of Chow and Yeh 1958)

[34] Late Pleistocene; Taiwan Island; *Rafetus swinhoei* (*T. liupani* of Tao 1986)

**Croatia**

[35] Late Eocene–early Oligocene, Priabonian–Rupelian; Šibenik-Knin; *Pan-Trionychidae* indet. (*T. austriacus* of Peters 1859; *T.* cf. *capellinii* of Paunović 1984)

[36] Middle Miocene, Langhian; Varaždin; *Pan-Trionychinae* indet. (*T. croaticus* of Koch 1915)

**Cyprus**

[37] Miocene; *Pan-Trionychidae* indet. (Reed 1932; Hadjisterkotis et al. 2000)

**Czechia**

[38] Late Eocene; Ústí nad Labem (= Ústecký); *Pan-Trionychidae* indet. (*Trionyx* sp. of Laube 1882 and Kvaček 2002)

[39] Early Miocene, Burdigalian; Ústí nad Labem (= Ústecký); *Rafetus bohemicus* (TL) (Liebus 1930), *Pan-Trionychinae* indet. (*Trionyx* sp. of Stur 1874; *T. pontanus* of Laube 1895, 1896; *T. aspidiformis* and *T. preschenensis* of Laube 1898, 1900; *T. elongatus* of Liebus 1930)

**Democratic Republic of Congo**

[40] Late Miocene–early Pliocene; Orientale Province; *Pan-Trionychidae* indet. (Hirayama 1992)

**Denmark**

[41] Early Paleocene, Danian; Capital Region of Denmark; *Pan-Trionychidae* indet. (*Trionyx* sp. of Rosenkrantz 1923; *Rafetoides* cf. *henrici* of Karl and Lindow 2012)

**Egypt**

[42] Early Miocene, Burdigalian; Matruh Governorate; *Pan-Trionychidae* indet. (*T. senckenbergianus* of Reinach 1903; *Trionyx* sp. of Dacqué 1912)

[43] Late Miocene, Messinian; Beheira Governorate; *Pan-Trionychidae* indet. (Dacqué 1912).

[44] Pliocene; Beheira Governorate; *Pan-Trionychidae* indet. (Andrews 1902; *T. pliocaenicus* of Reinach 1903)

[45] Middle Pleistocene; New Valley Governorate; *Pan-Trionychidae* indet. (Churcher et al. 1999)

**Ethiopia**

[46] Pliocene–Pleistocene; Oromia Region; *Pan-Trionychidae* indet. (Broin 1979)

**France**

[47] Late Paleocene, late Thanetian; Grand Est; *Pan-Trionychidae* indet. (*Trionyx* sp. of Bergounioux 1932)

[48] Late Paleocene, late Thanetian; Hauts-de-France; *Pan-Trionychidae* indet. (*Palaeotrionyx* [*sic*] sp. and *Trionychidae* indet. of Smith et al. 2014)

[49] Eocene; Île-de-France; early Eocene, early Ypresian: *Axestemys vittata* (*Palaeotrionyx* [*sic*] *vittatus* of Broin 1977); middle Eocene, late Lutetian: "*T.*" *henrici* (*Trionyx* sp. of Lapparent de Broin et al. 1993); late Eocene, Priabonian: *Pan-Trionychidae* indet. (*Trionyx* sp. of Cuvier 1821–1824; *T. parisiensis* of Gray 1831, Meyer 1832, and Lydekker 1889a)

[50] Eocene; Occitanie; early Eocene, Ypresian: *Pan-Trionychidae* indet. (Broin 1977; *Trionyx* sp. of Laurent et al. 2010); middle Eocene, Lutetian: *Pan-Trionychidae* indet. (*Trionyx* sp. of Cuvier 1821–1824; *T. dodunii* of Gray 1831; Fitzinger 1836)

[51] Eocene; Nouvelle-Aquitaine; middle Eocene, Bartonian: *Pan-Trionychidae* indet. (Broin 1977); late Eocene, Priabonian: *Pan-Trionychidae* indet. (*Trionyx* sp. Cuvier 1821–1824; *T. laurillardii* of Gray 1831; Bergounioux 1935)

[52] Early Eocene, Ypresian; Grand-Est; "*T.*" *silvestris* (*T. michauxi* of Broin 1977), *Axestemys vittata*, *Pan-Trionychidae* indet. (*Palaeotrionyx* [*sic*] *vittatus* of Broin 1977)

[53] Early Eocene, Ypresian; Hauts-de-France; *Axestemys vittata* (TL) (*T. vittatus* of Pomel 1847; *Palaeotrionyx* [*sic*] *vittatus* of Broin 1977; *Eurycephalochelys* aff. *vittatus* of Augé et al. 1997), *Pan-Trionychidae* indet. (*Trionyx* sp. of Augé et al. 1997)

[54] Late Eocene; Auvergne-Rhône-Alpes; *Pan-Trionychidae* indet. (*Trionyx* sp. of Bergounioux 1936)

[55] Early Oligocene, Rupelian; Nouvelle-Aquitaine; *Pan-Trionychidae* indet. (*T. burdigalensis* of Bergounioux 1935; *Trionyx* sp. of Broin 1977)

[56] Early Oligocene, Rupelian; Auvergne-Rhône-Alpes; *Pan-Trionychidae* indet. (*Tryonix* [*sic*] sp. of Pomel 1846)

[57] Oligocene; Occitanie; early Oligocene, Rupelian: *Pan-Trionychidae* indet. (Broin 1977); late Oligocene, Chattian: *Pan-Trionychidae* indet. (*Trionyx* sp. of Cuvier 1821–1824; *T. amansii* of Gray 1831; *T. dieupentalensis* of Bergounioux 1935; *Trionyx* sp. of Broin 1977)

[58] Early Oligocene or early Miocene, Rupelian or Aquitanian; Provence-Alpes-Côte d'Azur; *Pan-Trionychidae* indet. (*T. manouri* of Cuvier 1821–1824 and Gray 1831)

[59] Late Oligocene or early Miocene, Chattian or Aquitanian; Occitanie; *Pan-Trionychidae* indet. (*Trionyx* sp. of Gervais 1867–1869; *T. acutiformis*, *T. chaubeti*, *T. ciryi*, and *T. mourieri* of Bergounioux 1935; *Trionyx* sp. of Broin 1977)

[60] Miocene; Centre-Val de Loire; early Miocene, Burdigalian: *T. vindobonensis* (*T. stiriacus* of Broin 1977), *Pan-Trionychinae* indet. (*Trionyx* sp. of Cuvier 1821–1824; *T. lockardi* of Gray 1831); middle Miocene, Langhian: *Pan-Trionychinae* indet. (Broin 1977; Gobé et al. 1980; *Trionyx* sp. of Augé et al. 2002; *Trionyx* sp. of Gagnaison et al. 2012)

[61] Miocene; Occitanie; early Miocene, Burdigalian: *Pan-Trionychidae* indet. (Broin 1977); middle Miocene, Langhian: *Pan-Trionychidae* indet. (Broin 1977); late Miocene, Tortonian: *Pan-Trionychidae* indet. (Broin 1977)

[62] Early Miocene; Nouvelle-Aquitaine; Aquitanian: *Pan-Trionychidae* indet. (Broin 1977); Burdigalian: *Pan-Trionychinae* indet. (*T. aquitanicus* of Delfortrie 1869 and Lydekker 1889a)

[63] Middle Miocene, Langhian; Pays de la Loire; *Pan-Trionychinae* indet. (Broin 1977)

[64] Pliocene; Occitanie; Trionychinae indet. (*Trionyx* sp. of Gervais 1867–1869; *Trionyx pliopedemontana* of Depéret and Donnezan 1890–1897; *T. blayaci*, *T. pliopedemontana*, *T. pompignanensis*, *T. rotundiformis*, and *Trionyx* sp. of Bergounioux 1933, 1935; *T. pliopedemontanus* of Broin 1977)

**Georgia**

[65] Middle Miocene, Serravallian; Kakheti Region; *Pan-Trionychidae* indet. (Bakradze and Chkhikvadze 1988)

[66] Middle Miocene, Serravallian; Kvemo Kartli Region; *Pan-Trionychidae* indet. (Bakradze and Chkhikvadze 1988)

**Germany**

[67] Middle Eocene, Lutetian; Bavaria; *Pan-Trionychidae* indet. (*Rafetoides* cf. *austriacus* of Karl 2002)

[68] Middle Eocene; Upper Rhine Basin (Hesse and Rhineland-Palatinate); "*T.*" *messelianus* (TL) (Reinach 1900; Harrassowitz 1919; Hummel 1927; *Palaeoamyda messeliana* of Cadena 2016), *Pan-Trionychidae* indet. (Schleich 1994; Gröning and Brauckmann 1996)

[69] Middle Eocene, Lutetian; Saxony-Anhalt; "*T.*" *messelianus* (*Palaeoamyda messeliana* of Cadena 2016), *Pan-Trionychidae* indet. (*Trionyx* sp. of Barnes 1927; *Trionyx* sp. of Hummel 1935; Krumbiegel 1963; *Amyda boulengeri* of Karl 1993)

[70] Oligocene; Upper Rhine Basin; early Oligocene, Rupelian, Hesse: *Pan-Trionychidae* indet. (*T. borkenensis* of Gramann 1956; *T.* aff. *borkenensis* of Schleich 1986; Schleich 1994; *Rafetoides austriacus* of Karl and Müller 2008); early Oligocene, Rupelian, Rhineland-Palatinate: "*T.*" *boulengeri* (TL) (*T. gergensi* of Lydekker 1889a; Reinach 1900); late Oligocene, Chattian, Rhineland-Palatinate: *Pan-Trionychidae* indet. (Mörs 1998)

[71] Early Oligocene, Rupelian; Baden-Württemberg; *Pan-Trionychidae* indet. (Trionychidae indet. of Maxwell et al. 2016)

[72] Early Oligocene, Rupelian; Saxony; *Pan-Trionychidae* indet. (Karl 1993; *T. triunguis* of Karl 2007)

[73] Late Oligocene, Chattian; Bavaria; *Pan-Trionychidae* indet. (Schleich 1985; *Trionyx* sp. of Darga et al. 1999; *Trionyx* sp. of Böhme 2008; *Trionyx* cf. *triunguis* of Karl et al. 2011)

[74] Miocene; Baden-Württemberg; early Miocene, Aquitanian: *Pan-Trionychinae* indet. (Schleich 1985); early Miocene, Burdigalian: *Pan-Trionychinae* indet. (Schleich 1985); early to middle Miocene, Burdigalian–Langhian: *Pan-Trionychinae* indet. (*T. triunguis* of Karl 2013); middle Miocene, Serravallian: *T. vindobonensis* (*T. teyleri* of Winkler 1869a, 1869b); middle–late Miocene, Serravallian–Tortonian: *Pan-Trionychinae* indet. (*T. triunguis* of Karl 2013); late Miocene, Tortonian: *Pan-Trionychinae* indet. (Schleich 1985)

[75] Miocene; Bavaria; early Miocene, Aquitanian: *Pan-Trionychinae* indet. (*Trionyx* sp. of Kuss 1958); early Miocene, Burdigalian: *Pan-Trionychinae* indet. (Schleich 1985); middle Miocene, Langhian: *T. vindobonensis* (*T. brunhuberi* of Ammon 1911 and Fuchs 1939); *Trionychinae* indet. (*T. bohemicus*, *T. bohemicus jaegeri*, and *Trionyx* sp. of Fuchs 1939), *Pan-Trionychidae* indet. (*Trionyx* aff. *bohemicus* of Schleich 1981, 1985; Groessens-van Dyck and Schleich 1985); middle Miocene, Serravallian: *Pan-Trionychidae* indet. (Schleich 1985; Karl 1993); late Miocene, Tortonian: *Pan-Trionychinae* indet. (Schleich 1985)

[76] Miocene; Hesse; early Miocene, Aquitanian: *Pan-Trionychinae* indet. (*T. münzenbergensis* of Hummel 1927); late Miocene (Tortonian): *Pan-Trionychidae* indet. (Trionychidae of Eikamp 1978)

[77] Miocene; North Rhine-Westphalia; early Miocene, Burdigalian: *Pan-Trionychinae* indet. (Schleich 1985); middle Miocene: *Pan-Trionychinae* indet. (*Trionyx* sp. of Klein and Mörs 2003)

[78] Miocene; Rhineland-Palatinate; early Miocene, Aquitanian: *T. vindobonensis* (*Aspidonectes/T. gergensi* of Meyer 1844, Lydekker 1889a, and Reinach 1900); late Miocene, Messinian: *Pan-Trionychinae* indet. (*T. oweni* of Reinach 1900)

[79] Miocene; Thuringia; early Miocene, Burdigalian: *Pan-Trionychinae* indet. (Böhme 1995); early to middle Miocene, Burdigalian–Langhian: *Pan-Trionychinae* indet. (Karl 1993)

**Greece**

[80] Late Miocene, Tortonian; Crete; *Pan-Trionychidae* indet. (Georgalis et al. 2016b)

[81] Late Pliocene, Piacenzian; Central Macedonia; *Pan-Trionychidae* indet. (Vlachos et al. 2015)

**Hungary**

[82] Eocene; Northern Hungary: *Pan-Trionychidae* indet. (*T. austriacus* of Peters 1859); middle Eocene, Central Transdanubia: *Pan-Trionychidae* indet. (Ősi 2001); late Eocene, Central Hungary: *Pan-Trionychidae* indet. (Młynarski 1966)

[83] Oligocene; Early Oligocene, Rupelian, Central Hungary: *Pan-Trionychidae* indet. (Szalai 1934; Młynarski 1966); Oligocene, Central Transdanubia: *Pan-Trionychidae* indet. (Młynarski 1966; Rabi and Botfalvai 2008)

[84] Miocene; early Miocene, Burdigalian, Central Hungary: *Pan-Trionychinae* indet. (Szalai 1934; Młynarski 1966); middle Miocene, Serravallian, Central Hungary: *Pan-Trionychinae* indet. (*T. pseudovindobonensis* of Szalai 1934); late Miocene, early Messinian, Central Hungary: *Pan-Trionychinae* indet. (Szalai 1934; Młynarski 1966); late Miocene, Northern Hungary: *Pan-Trionychinae* indet. (Młynarski 1966); late Miocene, Tortonian, Southern Transdanubia: *Pan-Trionychinae* indet. (Młynarski 1966)

**India**

[85] Eocene Gujarat; early Eocene, Ypresian: *Pan-Trionychidae* indet. (Trionychidae indet. of Smith et al. 2016); middle Eocene: *Pan-Trionychidae* indet. (*Trionyx* sp. of Sahni and Mishra 1975)

[86] Middle Eocene; Himachal Pradesh; *Pan-Trionychidae* indet. (*Trionyx* sp. of Sahni et al. 1981, 1984)

[87] Late Pliocene; Himachal Pradesh; *Chitra* indet., *Nilssonia* indet. (*Aspideretes* cf. *gangeticus* and *Chitra* cf. *indica* of Srivastava and Patnaik 2002)

[88] Pliocene; Piram (= Perim) Island, Gujarat; *Lissemys* indet. (*Emyda* cf. *vittata* of Lydekker 1889a; *Emyda* cf. *granosa* of Lydekker 1889b; *Lyssemys* [*sic*] *piramensis* of Prasad 1974)

[89] Pleistocene; Tamil Nadu; *Lissemys* indet. (*Lissemys punctata* of Tripathi 1964)

[90] Pleistocene; Madhya Pradesh; *Nilssonia gangetica*, *Pan-Trionychidae* indet. (*T. gangeticus* and *Trionyx* sp. of Lydekker 1889b)

**Indonesia**

[91] Late Pleistocene; Borneo; *Pan-Trionychidae* indet. (*T. phayrei* of Lydekker 1889a)

[92] Pleistocene; Java; *Amyda cartilaginea* (*T. trinilensis* of Jaekel 1911; *T. cartilagineus* of Karl 1987), *Chitra chitra* (*Chitra selenkae* of Jaekel 1911; *Chitra indica* of Karl 1987), *Pelochelys cantorii*, *Pan-Trionychinae* indet. (*Chitra minor* of Jaekel 1911)

[93] Pleistocene; Sulawesi (= Celebes); *Pan-Trionychidae* indet. (Hooijer 1954)

**Iraq**

[94] Late Miocene, Tortonian; Diyala Governorate; *Pan-Trionychidae* indet. (*Trionyx* sp. of Thomas et al. 1980)

**Israel**

[95] Pleistocene; Haifa; *Pan-Trionychidae* indet. (*Trionyx* sp. of Bate 1934)

**Italy**

[96] Eocene; Prealpine Basin; middle Eocene, Piedmont: *Pan-Trionychidae* indet. (Sacco 1889); middle Eocene, Lutetian, Veneto: "*T.*" *capellinii* (TL) (including *T. affinis* and *T. gemmellaroi* of Negri 1892, *T. c. conjugens* of Sacco 1894, *T. intermedius* of Bergounioux 1954, and *T. c. capellinii* of Kotsakis 1977), *Pan-Trionychidae* indet. (*T. marginatus* of Zigno 1889); middle Eocene, Bartonian, Veneto: *Pan-Trionychinae* indet. (Portis 1885; *T. roncensis* of Harrassowitz 1919)

[97] Middle Eocene, early Lutetian; Sardinia; *Pan-Trionychidae* indet. (*Trionyx* sp. of Kotsakis 1985)

[98] Oligocene; Prealpine Basin; late Oligocene, Chattian, Liguria: *Pan-Trionychidae* indet. (Issel 1892); Oligocene, Piedmont: *Pan-Trionychidae* indet. (*T. pedemontana* of Portis 1879); late Oligocene or early Miocene, Piedmont: *Pan-Trionychidae* indet. (*T. pedemontana* of Portis 1879; *T. anthracotheriorum* of Portis 1883; *Trionyx* sp. of Chesi 2009); early Oligocene, early Rupelian, Veneto: "*T.*" *capellinii* (*T. italicus* of Schauroth 1865; *T. c. montevialensis* of Negri 1892 and Fabiani 1915; *T. schaurothianus* of Negri 1893; *T. c. gracilina* and *T. c. perexpansa* of Sacco 1895; *T. insolitus* of Bergounioux 1954; *T. c. montevialensis* and *T. c. schaurothianus* of Barbera and Leuci 1980); Oligocene, Veneto: *Pan-Trionychinae* indet. (*T irregularis* of Bergounioux 1954)

[99] Late Oligocene, Chattian; Calabria; *Pan-Trionychinae* indet. (*Tryonix* [*sic*] sp. of Gastaldi 1863; *T. oligocenica* of Portis 1885)

[100] Early to middle Miocene, Burdigalian–Langhian; Apulia; *Pan-Trionychidae* indet. (Chesi 2009); Miocene; Apulia; *Pan-Trionychidae* indet. (Capellini 1878)

[101] Miocene; Prealpine Basin; late Miocene, Messinian, Emilia-Romagna: *Pan-Trionychidae* indet. (*Trionyx* sp. of Kotsakis 1989); late Miocene or Pliocene, Emilia-Romagna: *Pan-Trionychinae* indet. (*Aspilus cortesii* of Portis 1885); middle Miocene, Serravallian, Friuli-Venezia Giulia: *Pan-Trionychidae* indet. (Dalla Vecchia 2007); early Miocene, Piedmont: *Pan-Trionychidae* indet. (Negri 1892); early Miocene, Burdigalian, Veneto: *Pan-Trionychinae* indet. (*T. subangularis* of Bergounioux 1954)

[102] Miocene; Sardinia; early Miocene: *Pan-Trionychidae* indet. (*Trionyx* sp. of Chesi 2009; Zoboli and Pillola 2017); late Miocene, Tortonian–Messinian; *Pan-Trionychinae* indet. (*Procyclanorbis sardus* of Portis 1901; *Amyda sardus* of Comaschi Caria 1959)

[103] Middle Miocene (Langhian); Sicily; *Pan-Trionychidae* indet. (*Trionix ragusensis* of De Gregorio 1883)

[104] Late Miocene, Tortonian; Tuscany; *Pan-Trionychinae* indet. (*T. bambolii*, *T. portisi*, *T. senensis*, *T. propinquus*, and *Trionyx* sp. of Ristori 1891a, 1891b, 1895; *Trionyx* sp. of Merciai 1907)

[105] Pliocene; Piedmont; *Pan-Trionychidae* indet. (*T. aegypticus* of Sismonda 1836, 1839; *T. pedemontana* of Portis 1879; *T. pliopedemontana* of Sacco 1889; Delfino 2002; Chesi 2009)

[106] Pliocene; early Pliocene, Zanclean, Tuscany: *Pan-Trionychinae* indet. (*T. propinquus* of Ristori 1891a, 1895); Pliocene, indeterminate stage, Tuscany: *T. pliocenicus* (TL) (Lawley 1876; Fucini 1912); late Pliocene–early Pleistocene, late Zanclean–Piacenzian, Tuscany: *Pan-Trionychinae* indet. (*Trionyx* sp. of Portis 1890; *T.* cf. *pliopedemontanus* of Kotsakis 1980); late Pliocene–early Pleistocene, Zanclean–Piacenzian, Umbria: *Pan-Trionychidae* indet. (*Trionyx* sp. of Girotti et al. 2003)

[107] Early Pleistocene (Gelasian); Tuscany; *Pan-Trionychinae* indet. (*Trionyx* sp. of Portis 1890; *T.* cf. *pliopedemontanus* of Kotsakis 1980)

**Japan**

[108] Early Cretaceous, Barremian/Aptian; Fukui; *Pan-Trionychidae* indet. (Hirayama 1998; Hirayama et al. 2013; Nakajima et al. in press)

[109] Late Cretaceous, Coniacian/Santonian; Kumamoto; *Pan-Trionychidae* indet. (Hirayama 1998)

[110] Late Eocene, Priabonian; Yamaguchi; *Pan-Trionychidae* indet. (*T. ubeensis* of Chitani 1925)

[111] Late Oligocene; Yamaguchi; *Pan-Trionychidae* indet. (Trionychinae gen. et sp. indet. of Hasegawa et al. 2007)

[112] Early Miocene, Burdigalian; Hiroshima; *Pan-Trionychidae* indet. (*T. ishiharaensis* of Miura and Uyama 1987)

[113] Middle Miocene; Hokkaidō; *Pan-Trionychidae* indet. (*T. desmostyli* of Matsumoto 1918)

[114] Middle Miocene; Nagasaki; *Pan-Trionychidae* indet. (*Trionyx* sp. aff. *desmostyli* of Otsuka 1970)

[115] Late Pliocene; Mie; "*T.*" *miensis* (TL) (Okazaki and Yoshida 1977)

[116] Early Pleistocene; Nagasaki; *Pan-Trionychidae* indet. (*T. kazusensis* of Otsuka 1969)

**Kazakhstan**

[117] Late Cretaceous, Santonian/early Campanian; South Kazakhstan Region; "*T.*" *kansaiensis* (Vitek and Danilov 2012), *Pan-Trionychidae* indet. (Prinada 1927; including *Aspideretes jaxarticus* and *Plastomenus jaxarticus* of Riabinin 1938 and *T. zakhidovi* of Khosatzky 1966)

[118] Late Cretaceous, Santonian/early Campanian; Kyzylorda Region; *Khunnuchelys lophorhothon* (TL), "*T.*" *kansaiensis*, "*T.*" *onomatoplokos* (TL), "*T.*" *riabinini* (TL), *Pan-Trionychidae* indet. (Khosatzky 1957; Kuznetsov 1976; Kuznetsov and Shilin 1983; Nessov 1984; Kuznetsov and Chkhikvadze 1987; Vitek and Danilov 2010; Danilov, Vitek et al. 2015)

[119] Eocene; East Kazakhstan Region; early Eocene: *Pan-Trionychidae* indet. (Chkhikvadze 1970; Kordikova 1994b; *Altaytrionyx devjatkini* and *Altaytrionyx phiruzae* of Chkhikvadze 2008a; *Plastomenus mlynarskii* of Chkhikvadze 1970); middle Eocene: *Pan-Trionychidae* indet. (Chkhikvadze 1973; *Plastomenus gabunii* of Chkhikvadze 1984; *Zaisanonyx jimenezfuentesi* of Chkhikvadze 2008b; *Altaytrionyx burtschaki* of Chkhikvadze 2008a; *Trionychidae* indet. of Scheyer et al. 2017); late Eocene: "*T.*" *ninae* (*T. zaisanensis* of Chkhikvadze 1973; Vitek and Danilov 2015), "*T.*" *minusculus* (TL) (*Plastomenus minusculus* of Chkhikvadze 1973; *Paraplastomenus minusculus* of Kordikova 1994b)

[120] Early Oligocene; East Kazakhstan Region; *Pan-Trionychidae* indet. (*Rafetus yexiangkuii* of Chkhikvadze 1999b, 2007)

[121] Oligocene; Karagandy Region; "*T.*" *ninae* (TL) (Chkhikvadze 1971; *T. turgaicus* of Kuznetsov and Chkhikvadze 1987; Vitek and Danilov 2015)

[122] Oligocene; Almaty Region; early Oligocene: *Pan-Trionychidae* indet. (Bazhanov and Kostenko 1961; Kordikova and Mavrin 1996); late Oligocene: *Pan-Trionychidae* indet. (Bazhanov and Kostenko 1961)

[123] Oligocene; Jambyl Region; *Pan-Trionychidae* indet. (Chkhikvadze 1971; Kordikova 1994b)

[124] Early to middle Miocene, late Burdigalian–early Langhian; Almaty Region; *Pan-Trionychidae* indet. (Bazhanov and Kostenko 1961)

[125] middle Miocene; East Kazakhstan Region; *Pan-Trionychidae* indet. (*T. jakhimovitchae* of Chkhikvadze 1989)

**Kenya**

[126] Early Miocene, Burdigalian; Nyanza; *Cycloderma victoriae* (TL), *Pan-Cyclanorbinae* indet. (Andrews 1914; Broin 1979; Pickford 1986)

[127] Miocene; Rift Valley; middle Miocene, Serravallian: *Pan-Cyclanorbinae* indet. (Bishop and Pickford 1975); late Miocene: *Pan-Trionychidae* indet. (Pickford 1975; Wood 2013)

[128] Pliocene; Rift Valley; early Pliocene: *Cycloderma debroinae* (TL), *Cyclanorbis turkanensis* (TL), *Pan-Cyclanorbinae* indet. (Meylan et al. 1990); Pliocene (indeterminate stage): *Pan-Cyclanorbinae* indet., *Pan-Trionychidae* indet. (Pickford 1986; Meylan et al. 1990); Plio/Pleistocene: *Cyclanorbis elegans* (Meylan et al. 1990)

[129] Pleistocene; Rift Valley; early Pleistocene: *Trionyx* sp. (*T.* cf. *triunguis* of Wood 1979); Middle Pleistocene, Calabrian; Rift Valley; *Pan-Cyclanorbinae* indet. (Bishop, Pickford, and Hill 1975)

**Kyrgyzstan**

[130] Early Cretaceous, Albian; Osh Province; *Petrochelys kyrgyzensis* (TL) (Vitek et al. 2017; "*T.*" *kyrgyzensis* of Nessov 1995b; Danilov and Vitek 2013)

**Libya**

[131] Late Miocene, late Messinian; Benghazi Governorate; *Pan-Trionychidae* indet. (*Trionyx* sp. of D' Erasmo 1933; *T.* cf. *triunguis* of Wood 1987)

**Malawi**

[132] Pliocene; Northern Region; Pliocene, indeterminate stage: *Cycloderma* sp. (Wood 1979; Meylan et al. 1990); late Pliocene–early Pleistocene: *Cyclanorbis* sp., *Cycloderma* sp. (including *Cycloderma senegalensis* of Karl 2012)

**Malaysia**

[133] Late Pleistocene; Sarawak, Borneo Island; *Amyda cartilaginea*, *Dogania subplana* (Pritchard et al. 2009)

**Moldova**

[134] Miocene; middle Miocene, Serravallian, Anenii Noi: *Pan-Trionychidae* indet. (Khosatzky and Tofan 1970; Chkhikvadze 1983); middle Miocene, Serravallian, Ialoveni: *Trionyx* sp. (Khosatzky and Tofan 1970; Chkhikvadze 1983; *T. moldaviensis* of Khosatzky 1986); middle Miocene, Chişinau: *Pan-Trionychidae* indet. (Khosatzky and Tofan 1970)

**Mongolia**

[135] Early Cretaceous; Dornogovi Aimag; *Pan-Trionychidae* indet. (Suzuki and Narmandakh 2004)

[136] Early Cretaceous, Aptian–Albian; Dundgovi Aimag; *Pan-Trionychidae* indet. (*Trionychidae* indet. of Scheyer et al. 2017)

[137] Late Cretaceous, Cenomanian–early Turonian; Dornogovi Aimag; *Kuhnemys orlovi* (TL), "*T.*" *baynshirensis* (TL) (Khosatzky 1976; Danilov et al. 2014)

[138] Late Cretaceous, Campanian; Bayankhongor Aimag; *Kuhnemys breviplastra* (Danilov et al. 2014)

[139] Late Cretaceous, Campanian; Ömnögovi Aimag; *Kuhnemys breviplastra*, "*T.*" *shiluutulensis* (TL), *Pan-Trionychidae* indet. (Khosatzky 1999; Danilov et al. 2014)

[140] Late Cretaceous, Campanian; Övörkhangai Aimag; *Pan-Trionychidae* indet. (Danilov et al. 2014)

[141] Late Cretaceous, Maastrichtian; Ömnögovi Aimag; *Kuhnemys breviplastra* (TL), *Nemegtemys conflata* (TL), "*T.*" *gilbentuensis* (TL), "*T.*" *gobiensis* (TL), *Pan-Trionychidae* indet. (Khosatzky and Młynarski 1971; *Trionyx* sp. of Młynarski and Narmandach 1972; Shuvalov and Chkhikvadze 1975, 1979; Merkulova 1978; Chkhikvadze and Shuvalov 1988; Danilov et al. 2014; including *Amyda menneri* of Chkhikvadze in Chkhikvadze and Shuvalov 1988)

[142] Late Paleocene; Ömnögovi Aimag; *Kuhnemys palaeocenica* (TL) (Danilov, Sukhanov et al. 2015)

**Myanmar**

[143] Late middle Eocene; Sagaing Region; *Pan-Trionychidae* indet. (Trionychinae indet. of Hutchison et al. 2004)

[144] Late Miocene; Ayeyarwady Region; *Pan-Trionychidae* indet. (*Trionyx* sp. of Jaeger et al. 2011)

[145] Pliocene–Pleistocene; Ayeyarwady Region; *Pan-Trionychidae* indet. (Chhibber 1934)

**Nepal**

[146] Late Miocene; Province 5; *Pan-Cyclanorbinae* indet. (*Lissemys punctata* of West et al. 1991), *Pan-Trionychinae* indet. (West et al. 1978; *Chitra* cf. *C. indica* and Trionychinae indet. of West et al. 1991)

[147] Pliocene–early Pleistocene; Province 5; *Lissemys* sp. (*Lissemys* cf. *punctata* of Corvinus and Schleich 1994), *Pan-Trionychinae* indet. (*Aspideretes* sp. vel *Chitra* sp. of Corvinus and Schleich 1994)

**Oman**

[148] Early Miocene; Ash Sharqiyah; *Pan-Trionychidae* indet. (aff. *Cycloderma* sp. of Roger et al. 1994)

**Pakistan**

[149] Early to middle Eocene; Khyber Pakhtunkhwa; *Pan-Trionychidae* indet. (Broin 1987)

[150] Middle Eocene, middle Bartonian; Punjab; *Drazinderetes tethyensis* (TL), *Pan-Trionychidae* indet. (Head et al. 1999)

[151] Early Miocene; Punjab; *Pan-Trionychidae* indet. (Pilgrim 1912)

[152] Pliocene–Pleistocene; Punjab; *Nilssonia hurum* (*T. hurum sivalensis* of Lydekker 1889a), *Chitra* sp., *Pan-Cyclanorbinae* indet. (*Emyda lineata*, *Emyda palaeindica*, *Emyda sivalensis*, and *Emyda vittata* of Lydekker 1885), *Pan-Trionychidae* indet. (Lydekker 1885, 1889a, 1889b)

**Portugal**

[153] Miocene; Lisbon; Early Miocene, Burdigalian: *Pan-Trionychidae* indet. (Zbyszewsky 1949); late Miocene, Tortonian: *Pan-Trionychidae* indet. (*T. lorioli* of Souza Torres 1947)

**Romania**

[154] Eocene; Early Eocene, Ypresian, Argeş County: *Pan-Trionychidae* indet. (Vremir 2013); middle Eocene, Sibiu County: *Pan-Trionychidae* indet. (*Trionyx* sp. of Peters 1855); late Eocene, Cluj County: *Pan-Trionychidae* indet. (*Trionyx* sp. of Koch 1894); late Eocene (Priabonian) or Oligocene, Cluj County: "*T.*" *boulengeri* (*T. clavatomarginatus* of Lörenthey 1903)

[155] Oligocene; early Oligocene (Rupelian), Cluj County: *Pan-Trionychidae* indet. (Vang-Lauridsen 1998); late Oligocene (Chattian); Hunedoara County: *Pan-Trionychinae* indet. (*Trionyx* sp. of Poporogu 1972)

[156] Miocene; Early Miocene, Cluj County: *Pan-Trionychinae* indet. (*Trionyx* sp. of Fuchs 1962; *Trionyx* sp. of Vremir and Codrea 1997); middle Miocene, Serravallian, Arad County: *Pan-Trionychinae* indet. (*T. stiriacus* of Vremir et al. 1997); middle–late Miocene, Serravallian–Tortonian, Bihor County: *Pan-Trionychinae* indet. (*T. harmati* and *T. nopcsai* of Szalai 1934)

[157] Late Miocene, Tortonian; Vrancea County; *Pan-Trionychidae* indet. (*T.* cf. *pliopedemontana* of Macarovici and Motas 1965)

[158] Pliocene; Harghita County; *Pan-Trionychidae* indet. (*Trionyx* sp. of Młynarski 1966)

[159] Pliocene; Vaslui County; *Pan-Trionychidae* indet. (*Trionyx* sp. of Simionescu 1930)

**Russia**

[160] Middle Miocene, Langhian; Stavropol Territory; *Pan-Trionychidae* indet. (*T. danovi* of Chkhikvadze 1989)

[161] Middle Miocene, Serravallian; Adygea Republic; *Pan-Trionychidae* indet. (*T. khosatzkyi* of Chkhikvadze 1983, 1989, and Shebzukhova and Tarasenko 2007)

**Saudi Arabia**

[162] Early Miocene, Burdigalian; Eastern Province; *Pan-Cyclanorbinae* indet. (aff. *Cycloderma* sp. of Thomas et al. 1982)

**Slovakia**

[163] Miocene; early Miocene, middle Burdigalian, Banská Bystrica: *Pan-Trionychinae* indet. (?Trionychidae indet. of Čerňanský et al. 2012); middle Miocene, late Langhian, Bratislava: *Pan-Trionychinae* indet. (*T. rostratus* of Holec and Schlögl 2000), *Pan-Trionychidae* indet. (*Trionyx* sp. of Hörnes 1848; *Trionyx* sp. of Młynarski 1966; *Trionyx* sp. of Holec 2006; *Trionyx* sp. of Danilov et al. 2012); late Miocene, Tortonian, Trnava: *Pan-Trionychinae* indet. (Trionychidae indet. of Danilov et al. 2012)

**Slovenia**

[164] Late Oligocene, Chattian; Central Sava; *Pan-Trionychinae* indet. (*T. stadleri* of Teppner 1913; *T. styriacus* [*sic*] of Bergounioux 1934a)

[165] Miocene; Central Sava; early Miocene, Aquitanian: *Pan-Trionychidae* indet. (Jurkovšek and Kolar-Jurkovšek 1994); middle Miocene, Langhian: *Pan-Trionychidae* indet. (*T. petersi trifailensis* of Teppner 1914c)

**Spain**

[166] Middle Eocene, Lutetian; Andalusia; *Pan-Trionychidae* indet. (Jiménez Fuentes and Alonso Andres 1994)

[167] Middle Eocene, Lutetian; Aragon; *Pan-Trionychidae* indet. (*Trionyx* sp. of Pérez-García et al. 2013)

[168] Middle Eocene, ?Bartonian; Balearic Islands; *Pan-Trionychidae* indet. (Jiménez Fuentes et al. 1990)

[169] Eocene; Castile and León; middle Eocene, Lutetian: *Pan-Trionychidae* indet. (*T.* cf. *michauxi* of Jiménez Fuentes and Alonso Andres 1994; Jiménez Fuentes 2003); middle Eocene, Bartonian: *Pan-Trionychidae* indet. (Jiménez Fuentes and Alonso Andres 1994); late Eocene, Priabonian: *Pan-Trionychidae* indet. (Jiménez Fuentes and Alonso Andres 1994)

[170] Middle Eocene, Lutetian; Catalonia; *Pan-Trionychidae* indet. (Crusafont and Villalta 1954; Bergounioux 1958)

[171] Early Oligocene; Aragon; *Pan-Trionychidae* indet. (Jiménez Fuentes and Alonso Andres 1994)

[172] Early Oligocene; Catalonia; *Pan-Trionychidae* indet. (Vidal and Depéret 1906; *T. marini* of Hernández Sampelayo and Bataller 1944, Crusafont and Villalta 1954, Bataller 1956, and Bergounioux 1958)

[173] Oligocene; Guadalajara, Castile-La Mancha; early Oligocene, Rupelian: *Pan-Trionychidae* indet. (Crusafont et al. 1960); Oligocene (undetermined stage): *Pan-Trionychidae* indet. (*Trionyx* sp. of Jiménez Fuentes 2003)

[174] Early Miocene, Burdigalian; Catalonia; *Pan-Trionychidae* indet. (Pérez García et al. 2011)

[175] Early Miocene, Aquitanian; Navarre; *Pan-Trionychidae* indet. (*Trionyx* cf. *maunori* [*sic*] of Ezquerra del Bayo 1850; Trionychinae indet. of Murelaga et al. 2002)

[176] Late Miocene, Messinian; Murcia; *Pan-Trionychidae* indet. (Pérez García et al. 2011)

**Sri Lanka**

[177] Late Pleistocene; Sabaragamuwa Province; *Pan-Trionychidae* indet. (*Lissemys punctata sinhaleyus* of Deraniyagala 1953)

**Sweden**

[178] Late Cretaceous, Campanian; Skåne; *Pan-Trionychidae* indet. (Trionychidae indet. of Scheyer et al. 2012)

**Switzerland**

[179] Oligocene; early Oligocene, Rupelian, Fribourg: *Pan-Trionychinae* indet. (MHNF); late Oligocene, Chattian; Vaud; *Pan-Trionychinae* indet. (*T. lorioli*, *T. rocchettiana*, and *T. valdensis* of Portis 1882)

[180] Miocene; early Miocene, Aquitanian, Aargau: *Pan-Trionychidae* indet. (Meyer 1839); early Miocene, Aquitanian, Vaud: *Pan-Trionychidae* indet. (Pictet and Humbert 1856); middle Miocene, Serravallian, Neuchâtel: *Pan-Trionychidae* indet. (Jaccard 1888); late Miocene, Zurich: *Pan-Trionychinae* indet. (*T. reticulatus* and *T.* cf. *stiriacus* of Rieppel 1979)

**Tajikistan**

[181] Late Cretaceous, early Santonian; Khodzhent Province; "*T.*" *kansaiensis* (TL), "*T.*" *riabinini*, *Pan-Trionychidae* indet. (Khosatzky and Nessov 1979; Nessov 1984; Kordikova 1994b; Vitek and Danilov 2010)

**Tanzania**

[182] Middle Miocene; Zanzibar; *Pan-Trionychidae* indet. (Trionychidae indet. of Pickford 2008)

[183] Pleistocene; Arusha Region; *Trionyx* sp. (Leakey 1965)

**Thailand**

[184] Middle Miocene–Pleistocene; Nakhon Ratchasima Province; *Pan-Trionychidae* indet. (*Amyda* sp., *Chitra* sp. of Claude et al. 2011)

[185] Late Pleistocene; Krabi Province; *Pan-Trionychidae* indet. (Mudar and Anderson 2007)

**Tunisia**

[186] Late Miocene, Tortonian; Gafsa Governorate; *Pan-Trionychidae* indet. (*Trionyx* sp. of Robinson and Black 1974)

[187] Late Pliocene, Piacenzian; Bizerte Governorate; *Pan-Trionychidae* indet. (Arambourg 1979)

**Turkey**

[188] ?Oligocene; Çorum; *Pan-Trionychidae* indet. (Staesche 1975)

[189] Oligocene; Tekirdağ; *Pan-Trionychidae* indet. (*Trionix* [sic] sp. of Lebküchner 1974; Staesche 1975)

[190] Miocene; Çanakkale; middle Miocene, Serravallian: *Pan-Trionychidae* indet. (*Trionyx* sp. of Calvert and Neumayr 1880); late Miocene: *Pan-Trionychidae* indet. (*Trionyx* sp. of Tuna 1988)

[191] Late Miocene; İstanbul; *Pan-Trionychidae* indet. (*Trionyx* sp. of Malik and Nafiz 1933; *Trionyx* sp. of Rückert-Ülkümen 1963; Staesche 1975)

[192] Late Miocene, middle Tortonian; Konya; *Pan-Trionychinae* indet. (*T. triunguis* of Staesche et al. 2007)

[193] Late middle–early late Miocene, Serravallian–early Tortonian; Kütahya; *Pan-Trionychinae* indet. (*T. triunguis* of Staesche et al. 2007)

[194] Middle Miocene, Serravallian; Mugla; *Pan-Trionychinae* indet. (Staesche et al. 2007)

**Uganda**

[195] Late Miocene, Messinian; Central Region; *Pan-Cyclanorbinae* indet. (*Cyclanorbis* sp. of Lapparent de Broin and Gmira 1994)

[196] Pliocene; Central Region; early Pliocene, Zanclean: *Cyclanorbis* indet. (Lapparent de Broin and Gmira 1994); late Pliocene, Piacenzian: *Cyclanorbis* indet. (Lapparent de Broin and Gmira 1994)

[197] Early Pleistocene, Gelasian; Central Region; *Cycloderma* sp. (*Cycloderma frenatum* of Arambourg 1947), *Pan-Cyclanorbinae* indet. (Swinton 1926; Lapparent de Broin and Gmira 1994)

**Ukraine**

[198] Middle Eocene, early Lutetian; Luhansk Province; "*T.*" *ikoviensis* (TL) (Danilov et al. 2011)

[199] Middle Miocene, Serravallian; Crimea Province (currently administered by Russia); *Pan-Trionychidae* indet. (*Trionyx* sp. of Khosatzky 1948; Chkhikvadze 1989)

**United Arab Emirates**

[200] late Miocene, Tortonian; Abu Dhabi; *Pan-Trionychinae* indet. (*Trionyx* sp. of Lapparent de Broin and van Dijk 1999; Beech and Hellyer 2005)

**United Kingdom**

[201] Late Paleocene, ?Thanetian; London; *Pan-Trionychidae* indet. (White 1931)

[202] Eocene; middle Eocene, Bartonian, Dorset: *Pan-Trionychidae* indet. (Burton 1933); middle Eocene, Lutetian, Hampshire: *Pan-Trionychidae* indet. (Benton and Spencer 1995); late Eocene, Priabonian, Hampshire: "*T.*" *henrici* (TL) (including *T. barbarae*, *T.* [or *Aulacochelys*] *circumsulcatus*, *T. marginatus*, *T. planus*, and *T. rivosus* of Owen in Owen and Bell 1849, Lydekker 1889a, and Boulenger 1891); late

Eocene, Isle of Wight: “*T.*” *henrici* (*T. incrassatus* of Owen in Owen and Bell 1849); early Eocene, Ypresian, Kent: “*T.*” *silvestris* (TL) (Walker and Moody 1974), *Pan-Trionychinae* indet. (*T. pustulatus* of Owen in Owen and Bell 1849); early Eocene, late Ypresian, West Sussex: *Axestemys vittata* (*Eurycephalochelys fowleri* of Moody and Walker 1970 and Walker and Moody 1985), *Pan-Trionychinae* indet. (*Trionyx* sp. of Owen in Owen and Bell 1849; *T. bowerbanki* of Lydekker 1889a)

[203] Oligocene; Isle of Wight; early Oligocene, Rupelian: *Pan-Trionychidae* indet. (Hooker and Ward 1980); late Oligocene–early Miocene: *Pan-Trionychidae* indet. (Lydekker 1889a)

**Uzbekistan**

[204] Early Cretaceous, early Albian; Karakalpakstan; *Pan-Trionychidae* indet. (Nessov 1977, 1984)

[205] Late Cretaceous; Karakalpakstan; early Cenomanian: “*T.*” *dissolutus*, *Pan-Trionychidae* indet. (“*T.*” cf. *kyrgyzensis* of Vitek and Danilov 2014); late Turonian: *Pan-Trionychidae* indet. (Nessov 1984, 1987)

[206] Late Cretaceous; Navoiy Region; Cenomanian: “*T.*” *dissolutus* (TL), *Pan-Trionychidae* indet. (“*T.*” cf. *kyrgyzensis* of Vitek and Danilov 2014); late Turonian: *Khunnuchelys kizylkumensis* (TL) (Brinkman et al. 1993; Vitek and Danilov 2013), *Pan-Trionychidae* indet. (Nessov 1984, 1987, 1997; Brinkman et al. 1993; *Aspideretoides* cf. *riabinini* and “*T.*” cf. *kansaiensis* of Danilov and Vitek 2013)

**Vietnam**

[207] Oligocene; Lạng Son Province; *Pan-Trionychidae* indet. (Böhme et al. 2011)

## Appendix 4
## Hierarchical Taxonomy of Old World *Pan-Trionychidae*

- *Pan-Trionychidae* Joyce et al., 2004
  - *Axestemys vittata* (Pomel, 1847), comb. nov.
  - *Drazinderetes tethyensis* Head et al., 1999
  - *Khunnuchelys* Brinkman et al., 1993
      - *Khunnuchelys erinhotensis* Brinkman et al., 1993
      - *Khunnuchelys kizylkumensis* Brinkman et al., 1993
      - *Khunnuchelys lophorhothon* Danilov, Vitek et al., 2015
- *Kuhnemys* Chkhikvadze, 1999b
      - *Kuhnemys breviplastra* (Danilov et al., 2014), comb. nov.
      - *Kuhnemys maortuensis* (Yeh, 1965)
      - *Kuhnemys orlovi* (Khosatzky, 1976), comb. nov.
      - *Kuhnemys palaeocenica* (Danilov, Sukhanov et al., 2015), comb. nov.
- *Murgonemys braithwaitei* White, 2001
- *Perochelys lamadongensis* Li, Joyce, and Liu, 2015
- *Petrochelys kyrgyzensis* (Nessov, 1995b)
- *Pan-Cyclanorbinae* New Clade Name
      - *Cyclanorbis turkanensis* Meylan et al., 1990
      - *Cycloderma* Peters, 1854
          - *Cycloderma debroinae* Meylan et al., 1990
          - *Cycloderma victoriae* Andrews, 1914
      - *Nemegtemys conflata* Danilov et al., 2014
- *Pan-Trionychinae* New Clade Name
      - *Pelodiscus gracilia* (Yeh, 1963), comb. nov.
      - *Rafetus bohemicus* (Liebus, 1930), comb. nov.
      - *Trionyx* Geoffroy Saint-Hilaire, 1809
          - *Trionyx pliocenicus* Fucini, 1912
          - *Trionyx vindobonensis* Peters, 1855
- *Pan-Trionychidae* Incertae Sedis
  - *Trionyx* Geoffroy Saint-Hilaire, 1809
          - “*Trionyx*” *baynshirensis* Danilov et al., 2014
          - “*Trionyx*” *boulengeri* Reinach, 1900
          - “*Trionyx*” *capellinii* Negri, 1892
          - “*Trionyx*” *dissolutus* Vitek and Danilov, 2014
          - “*Trionyx*” *gilbentuensis* Danilov et al., 2014
          - “*Trionyx*” *gobiensis* Danilov et al., 2014
          - “*Trionyx*” *gregarius* (Gilmore, 1934)
          - “*Trionyx*” *henrici* Owen in Owen and Bell, 1849
          - “*Trionyx*” *impressus* (Yeh, 1963)
          - “*Trionyx*” *ikoviensis* Danilov et al., 2011
          - “*Trionyx*” *jixiensis* Li, Tong et al., 2015
          - “*Trionyx*” *johnsoni* Gilmore, 1931
          - “*Trionyx*” *kansaiensis* Vitek and Danilov, 2010
          - “*Trionyx*” *linchuensis* (Yeh, 1962)
          - “*Trionyx*” *messelianus* Reinach, 1900
          - “*Trionyx*” *miensis* Okazaki and Yoshida, 1977
          - “*Trionyx*” *minusculus* (Chkhikvadze, 1973), comb. nov.
          - “*Trionyx*” *ninae* Chkhikvadze, 1971
          - “*Trionyx*” *onomatoplokos*, new name
          - “*Trionyx*” *riabinini* Kuznetsov and Chkhikvadze, 1987
          - “*Trionyx*” *shiluutulensis* Danilov et al., 2014
          - “*Trionyx*” *silvestris* Walker and Moody, 1974

## Literature Cited

Abbazzi, L., M. Benvenuti, M.E. Ceci, D. Esu, C. Faranda, L. Rook and F. Tangocci. 2008. The end of the Lago-Mare time in the SE Valdelsa Basin (Central Italy): interference between local tectonism and regional sea-level rise. Geodiversitas 30:611–639.

Aguilar, J.-P., S. Legendre and J. Mechaux, eds. 1997. Actes du Congrès BiochroM'97, Montpellier, 14–17 avril: biochronologie mammalienne du cénozoïque en Europe et domaines reliés. Mémoires et travaux de l'Institut de Montpellier, no. 21. Montpellier, France: Ecole pratique des hautes études, Institut de Montpellier. 817 pp.

Ammon, L. von. 1911. Schildkröten aus dem Regensburger Braunkohlenton. Jahresbericht des Naturwissenschaftlichen Vereins zu Regensburg 12:1–35.

Andrews, C.W. 1902. I.—Note on a Pliocene vertebrate fauna from the Wadi-Natrun, Egypt. Geological Magazine 9:433–439.

—1906. Order Chelonia. In: C.W. Andrews, ed. A Descriptive Catalogue of the Tertiary Vertebrata of the Fayum, Egypt. London: Trustees of the British Museum Editions. pp. 275–306.

—1914. Appendix II. On the Lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. Quarterly Journal of the Geological Society of London 70:163–186.

Anquetin, J. and W.G. Joyce. 2014. A reassessment of the Late Jurassic turtle *Eurysternum wagleri* (Eucryptodira, Eurysternidae). Journal of Vertebrate Paleontology 34:1317–1328.

Arambourg, C. 1947. Contribution à l'étude géologique et paléontologique du bassin du Lac Rodolphe et de la basse vallée de l'Omo. In: C. Arambourg, ed. Mission scientifique de l'Omo 1932–1933. Tome I. Géologie-Anthropologie. Fascicule III, 2ème partie, Paléontologie. Paris: Museum national d'Histoire naturelle. pp. 231–562.

—1956. Nouvelles recherches dans le gisement de l'Ain Hanech. In: G.A. Blanc, ed. Actes du IV Congrès International du Quaternaire; 1953 Aug–Sep; Rome-Pise, Italy. Rome: Istituto Italiano di Paleontologia Umana. p. 4.

—1979. Vertébrés villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux). Paris: Fondation Singer-Polignac. 141 pp.

Arthaber, G. von. 1898. Über *Trionyx rostratus* n. sp. von Au am Leithagebirge. Beiträge zur Palaeontologie und Geologie Oesterreich-Ungarns und des Orients 21:179–198.

Auffenberg, W. 1974. Checklist of fossil land tortoises (Testudinidae). Bulletin of the Florida State Museum, Biological Sciences Series 18:121–251.

Augé, M., S. Duffaud, F. de Lapparent de Broin, J.-C. Rage and D. Vasse. 1997. Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin parisien): une herpétofaune de référence pour l'Eocène inférieur. Géologie de la France 1:23–33.

Augé, M., L. Ginsburg, F. de Lapparent de Broin, M. Makinsky, C. Mourer, D. Pouit and S. Sen. 2002. Les vertébrés du Miocène moyen de Contres (Loir-et-Cher, France). Revue de Paléobiologie, Genève 21:819–852.

Averianov, A.O., I.G. Danilov, P.P. Skutschas, I.T. Kuzmin, H.-D. Sues and G. Dyke. 2016. The Late Cretaceous vertebrate assemblages of western Kazakhstan. New Mexico Museum of Natural History and Science Bulletin 71:5–18.

Bachmayer, F. 1966. Ein bemerkenswerter Schildkrötenfund aus dem Ober-Pannon der Schottergrube "Heidfeld" beim Flughafen Schwechat (Wien). Annalen des Naturhistorischen Museums in Wien 69:101–103.

Bakradze, M.A. and V.M. Chkhikvadze. 1988. [Materials on the Tertiary history of the herpetofauna of the Caucasus and adjoining regions]. Vestnik Gosudarstvennogo Muzeya Gruzii 34:176–193. [in Russian]

Barbera, C. and G. Leuci. 1980. I trionicidi di Monteviale presenti presso il Museo di Paleontologia dell' Universita di Napoli. Atti dell'Accademia Pontaniana 29:37–52.

Barnes, B. 1927. Eine eozäne Wirbeltierfauna aus der Braunkohle des Geiseltals. Jahrbuch des Halleschen Verbandes für die Erforschung der mitteldeutschen Bodenschätze 6:5–24.

Bataller, J.R. 1956. Contribución al conocimiento de los Vertebrados terciarios de España. Cursillos y conferencias del Instituto Lucas Mallada del Consejo Superior de Investigaciones Científicas 3:11–28.

Bate, D.M.A. 1934. Two additions to the Pleistocene cave-fauna of Palestine (*Trionyx* and *Crocodilus*). Annals and Magazine of Natural History 14:474–478.

Bazhanov, V.S. and N.N. Kostenko. 1961. [Geological section of Dzhungarian Alatau and its paleontological basis]. Materialy po istorii fauny i flory Kazakhstana 3:47–52. [in Russian]

Beech, M. and P. Hellyer. 2005. Abu Dhabi—8 Million Years Ago: Late Miocene Fossils from the Western Region. Abu Dhabi, United Arab Emirates: Abu Dhabi Islands Archaeological Survey. 92 pp.

Bell, C.J., J.A. Gauthier and G.S. Bever. 2010. Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary herpetofaunal stability hypothesis. Quaternary International 217:30–36.

Benton, M.J. and P.S. Spencer. 1995. Fossil Reptiles of Great Britain, Geological Conservation Review Series 10. London: Chapman and Hall. 386 pp.

Berger, J.-P. 1998. 'Rochette' (Upper Oligocene, Swiss Molasse): a strange example of a fossil assemblage. Review of Palaeobotany and Palynology 101:95–110.

Bergounioux, F.-M. 1932. Chéloniens fossiles conservés au Museum d'Histoire Naturelle de Munich. Bulletin de la Société d'histoire naturelle de Toulouse 64:523–544.

—1933. Monographie paléontologique de la faune de vertébrés des sables de Montpellier. 2. Chéloniens fossiles des sables Pliocènes astiens de Montpellier. Travaux du Laboratoire de Géologie de la Faculté des sciences de Lyon 23:1–32.

—1934a. Catalogue des chéloniens fossiles conservés à Vienne (Autriche). Bulletin de la Société d'Histoire Naturelle de Toulouse 66:369–376.

—1934b. Sur quelques Chéloniens fossiles du Nord de l'Italie. Bulletin de la Société d'Histoire Naturelle de Toulouse 66:271–280.

—1935. Contribution à l'étude paléontologique des chéloniens: chéloniens fossiles du bassin d'Aquitaine. Mémoires de la Société Géologique de France (nouvelle série) 25:1–215.

—1936. Chéloniens fossiles conservés au laboratoire de géologie de la faculté des sciences de Clermont-Ferrand. Bulletin de la Société d'Histoire Naturelle de Toulouse 69:50–58.

—1937. Chéloniens fossiles du Kimméridgien du Cap de la Hève. Bulletin de la Société d'Histoire Naturelle de Toulouse 71:180–191.

—1938. Chéloniens fossiles d'Espagne. Bulletin de la Société d'Histoire Naturelle de Toulouse 72:257–288.

—1953. Chéloniens fossiles des terrains tertiaires de la Vénétie. Comptes rendus hebdomadaires des séances de l'Académie des sciences de Paris 236:222–224.

—1954. Les chéloniens fossiles des terrains tertiaires de la Vénétie. Memorie degli Istituti di geologia e mineralogia dell'Università di Padova 18:1–115.

—1958. Les reptiles fossiles du Tertiaire de la Catalogne. Estudios Geológicos 14:129–219.

Bishop, W.W. and M.H.L. Pickford. 1975. Geology, fauna and palaeoenvironments of the Ngorora Formation, Kenya Rift Valley. Nature 254:185–192.

Bishop, W.W., M. Pickford and A. Hill. 1975. New evidence regarding the Quaternary geology, archaeology and hominids of Chesowanja, Kenya. Nature 258:204–208.

Boddaert, P. 1770. Brief van de kraakbeenige schildpad. Epistola de testudine cartilaginea. Amsterdam: Kornelis van Tongerlo. 39 pp.

Böhme, M. 1995. Eine Weichschildkröte (Trionychidae) aus dem Untermiozän vom Dietrichsberg bei Vacha (Rhön). Mauritania (Altenburg) 15:357–366.

—2008. Ectothermic vertebrates (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) from the Upper Oligocene of Oberleichtersbach (Northern Bavaria, Germany). Courier Forschungsinstitut Senckenberg 260:161–183.

Böhme, M., J. Prieto, S. Schneider, N.V. Hung, D.D. Quang and D.N. Tran. 2011. The Cenozoic on-shore basins of northern Vietnam: biostratigraphy, vertebrate and invertebrate faunas. Journal of Asian Earth Sciences 40: 672–687.

Boulenger, G.A. 1891. On some chelonian remains preserved in the Museum of the Royal College of Surgeons. Proceedings of the Zoological Society of London 1891:4–8.

Brinkman, D.B., J. Li and X. Ye. 2008. Order Testudines. In: J. Li, X. Wu and F. Zhang, eds. The Chinese Fossil Reptiles and Their Kin. Beijing: Science Press. pp. 35–102.

Brinkman, D.B., L.A. Nessov and J.-H. Peng. 1993. *Khunnuchelys* gen. nov., a new trionychid (Testudines: Trionychidae) from the Late Cretaceous of Inner Mongolia and Uzbekistan. Canadian Journal of Earth Sciences 30:2214–2223.

Broin, F. de. 1977. Contribution à l'étude des Chéloniens: Chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum National d'Histoire Naturelle, Série C 38:1–366.

—1979. Chéloniens du Miocène et du Plio-Pléistocène d'Afrique orientale. Bulletin de la Société Géologique de France 21:323–327.

—1987. Lower vertebrates from the early-Middle Eocene Kuldana Formation of Kohat (Pakistan): Chelonia. Contribution from the Museum of Paleontology, the University of Michigan 27:169–185.

Brusatte, S.L., R.B.J. Benson, D.J. Chure, X. Xu, C. Sullivan and D.W.E. Hone. 2009. The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. Naturwissenschaften 96:1051–1058.

Burton, E.S.J. 1933. Faunal horizons in the Barton Beds in Hampshire. Proceedings of the Geologists' Association 44:131–167.

Cadena, E. 2016. *Palaeoamyda messeliana* nov. comb. (Testudines, Pan-Trionychidae) from the Eocene Messel Pit and Geiseltal localities, Germany, taxonomic and phylogenetic insights. PeerJ 4:e2647. doi: 10.7717/peerj.2647

Calvert, F. and M. Neumayr. 1880. Die jungen Ablagerungen am Hellespont. Akademie der Wissenschaften, Vienna. Denkschriften der kaiserlichen Akademie der Wissenschaften/Mathematisch-Naturwissenschaftliche Classe 40:357–378.

Capellini, G. 1878. Della Pietra Leccese e di alcuni suoi fossili. Memorie dell'Accademia delle Scienze dell'Istituto di Bologna 9:225–258.

Cautley, P.T. 1836. On the structure of the Siwalik Hills, and the organic remains found in them. Transactions of the Geological Society of London 5:267–278.

Čerňanský, A., T. Csaba and J. Šurka. 2012. Crocodylian and turtle finds from the Early Miocene of the Baňa Dolina Mine in Veľkrý Krtíš (Slovakia). Acta Geologica Slovaca 4:113–123.

Chesi, F. 2009. Il registro fossile italiano dei cheloni [dissertation]. Florence, Italy: Università di Firenze. 178 pp.

Chesi, F., M. Delfino, A. Varola and L. Rook. 2007. Fossil sea turtles (Chelonii, Dermochelyidae and Cheloniidae) from the Miocene of Pietra Leccese (late Burdigalian-early Messinian), southern Italy. Geodiversitas 29:321–333.

Chhibber, H.L. 1934. Geology of Burma. London: Macmillan. 538 pp.

Chitani, Y. 1925. On a new fossil *Trionyx* from the Yamaguchi Prefecture. Journal of the Geological Society of Japan 32(387):28–33.

Chkhikvadze, V.M. 1970. [The oldest Cenozoic turtles of the U.S.S.R.]. Soobshcheniya Akademii Nauk Gruzinskoi SSR 60:749–752. [in Russian]

—1971. [New turtles from the Oligocene of Kazakhstan and the systematic position of some species in Mongolia]. Soobshcheniya Akademii Nauk Gruzinskoi SSR 62:489–492. [in Russian]

—1973. [Tertiary Turtles of the Zaisan Depression]. Tbilisi, Georgia: Metsniereba. 100 pp. [in Russian]

—1983. [Fossil Turtles of the Caucasus and the northern Black Sea region]. Tbilisi, Georgia: Metsniereba. 149 pp. [in Russian]

—1984. [Early Paleogene Turtles from Zaisan]. In: [Flora and fauna of the Zaisan Depression]. Tbilisi, Georgia: Metsniereba. pp. 128–139. [in Russian]

—1988. [New data on turtles of the Miocene and Pliocene of Cis-Caucasus]. In: [Animal World of Ciscaucasia and Adjacent Territories]. Stavropol, Russia: Stavropol' State Pedagogical Institute. pp. 128–139. [in Russian]

—1989. [Neogene Turtles of the USSR]. Tbilisi, Georgia: Metsniereba. 102 pp. [in Russian]

—1990. [Paleogene Turtles of the USSR]. Tbilisi, Georgia: Metsniereba. 96 pp. [in Russian]

—1995. [New data on Paleogene turtles of Zaisan]. In: Nauchnaya sessiya Instituta paleobiologii Gruzii. Tbilisi, Georgia: Metsniereba. p. 21 [in Russian]

—1999a. [The history of the development of the Paleogene herpetofauna of the CIS]. Problems of Paleobiology, Tbilisi 1:259–279. [in Russian]

—1999b. [Some fossil soft-shelled turtles of Asia (Rafetini trib. nov.)]. Trudy Tbilisskogo Gosudarstvennogo Pedagogicheskogo Universiteta 5:215–225. [in Russian]

—2000a. [About the systematic positions of some extinct soft-shelled turtles of North America and Asia]. Trudy Tbilisskogo Gosudarstvennogo Pedagogicheskogo Universiteta 7:199–213. [in Russian]

—2000b. Fossil trionychid turtles from the territory of the former Soviet Union. In: Fourth Asian Herpetological Conference; 2000 Jul 16–20; Chengdu, China. Chengdu: Chengdu Institute of Biology. p. 56.

—2007. [A short catalogue of fossil turtles of northern Eurasia]. Problems of Paleobiology, Tbilisi 2:126–137. [in Russian with English summary]

—2008a. [New trionychids and current problems of biostratigraphy of the Early Paleogene of Zaysan depression]. In: [Paleontological Monuments of Nature—Natural Heritage: Studying, Research Prospect and Conservation Problems]; Pavlodar, Kazakhstan: Pavlodarian State University. pp. 117–122. [in Russian]

—2008b. [Soft-shell turtles (Trionychidae) of Asia and North America: Morphology, phylogeny, systematics, terminology of elements of carapace]. Problems of Paleobiology, Tbilisi 3:85–95. [in Russian]

—2010. [An annotated catalogue of Paleogene, Neogene, and modern turtles of northern Eurasia]. Georgian National Museum. Proceedings of the Natural and Prehistoric Section 2:96–113. [in Russian]

Chkhikvadze, V.M. and A.N. Lungu. 1984. [New data on the Miocene herpetofauna of Moldavia and the Caucasus.]. In: A.N. Lungu, ed. [Palaeobiological research on the Mesozoic and Caenozoic of the Dnestr and Transnistria-Prut interfluve]. Kishinev: Ştiinţsa. pp. 72–86. [in Russian]

Chkhikvadze, V.M. and V.F. Shuvalov. 1988. [A new species of a trionychid from the Upper Cretaceous deposits of Mongolia]. Izvestiya Akademii Nauk Gruzinskoi SSR 14:198–204. [in Russian]

Chow, M.M. and S.K. Yeh. 1957. A new Eocene *Platypeltis* from Lushih, Honan. Vertebrata Palasiatica 1:261–262.

—1958. A new species of *Trionyx* from Yushe, Shansi. Vertebrata Palasiatica 2:55–56.

Churcher, C.S., M.R. Kleindienst and H.P. Schwarcz. 1999. Faunal remains from a Middle Pleistocene lacustrine marl in Dakhleh Oasis, Egypt: palaeoenvironmental reconstructions. Palaeogeography, Palaeoclimatology, Palaeoecology 154:301–312.

Clarke, W.B. 1869. *Dinornis* an Australian genus. Geological Magazine 6:383–384.

Claude, J., W. Naksri, N. Boonchai, E. Buffetaut, J. Duangkrayom, C. Laojumpon, P. Jintasakul, K. Lauprasert, J. Martin, V. Suteethorn and H. Tong. 2011. Neogene reptiles of northeastern Thailand and their paleogeographical significance. Annales de Paléontologie 97:113–131.

Clift, W. 1828. On the fossil remains of two new species of *Mastodon* and of other vertebrate animals, found on the left bank of the Irawaddi. Transactions of the Geological Society of London 2:369–374.

Comaschi Caria, J. 1959. Nuovi resti di cheloni nel Miocene della Sardegna. Bollettino della Società Geologica Italiana 78:37–44.

—1986. Animali e piante fossili della Sardegna. Cagliari, Italy: Edizioni della Torre. 107 pp.

Cooke, J.H. 1890. Notes on the fossil reptiles of Malta. Il Naturalista Maltese 1:18–20.

Cope, E.D. 1872. Descriptions of some new Vertebrata from the Bridger Group of the Eocene. Palaeontological Bulletin 1:1–6.

Corsini-Foka, M. and M. Masseti. 2008. On the oldest record of the Nile soft-shelled turtle, *Trionyx triunguis* (Forskål, 1775), in the Eastern Aegean islands (Greece). Zoology in the Middle East 43:108–110.

Corvinus, G. and H.H. Schleich. 1994. An Upper Siwalik reptile fauna from Nepal. Courier Forschungsinstitut Senckenberg 173:239–259.

Crusafont, M., B. Meléndez and J. Truyols Santonja. 1960. El yacimiento de Huérmeces del Cerro y su significado cronoestratigráfico. Estudios Geológicos 16:243–254.

Crusafont, M. and J.F. Villalta. 1954. "Almogáver", un nuevo primate del Eoceno pirenaico. Estudios Geológicos 22:165–176.

Cuvier, G. 1812. Recherches sur les ossements fossiles de quadrupèdes, où l'on rétablit les caractères de plusieurs espèces d'animaux que les révolutions du globe paraissent avoir détruites. Paris: Déterville.

—1821–1824. Recherches sur les ossements fossiles, où l'on rétablit les caractères de plusieurs animaux, dont les révolutions du globe ont détruits les espèces. Nouvelle édition. Paris: Dufour and D'Ocagne.

—1835–1836. Recherches sur les ossements fossiles, où l'on rétablit les caractères de plusieurs animaux, dont les révolutions du globe ont détruits les espèces. Quatrième édition. Paris: Dufour and D'Ocagne.

Dacqué, E. 1912. Die fossilen Schildkröten Aegyptens. Geologische und Paläontologische Abhandlungen 14:275–337.

Dalla Vecchia, F.M. 2007. 300 milioni di anni di evoluzione. In: Salvaguardia dell'Erpetofauna nel Territorio di Alpe-Adria. Un contributo della Regione Friuli Venezia Giulia a favore della Biodiversità. Udine, Italy: Regione Friuli Venezia Giulia. pp. 11–25.

Dalrymple, G.H. 1977. Intraspecific variation in the cranial feeding mechanism of turtles of the genus *Trionyx* (Reptilia, Testudines, Trionychidae). Journal of Herpetology 11:255–285.

Dames, W. 1894. Die Chelonier der norddeutschen Tertiärformation. Palaeontologische Abhandlungen 6:197–220.

Danilov, I.G. 2005. Die fossilen Schildkröten Europas. In: U. Fritz, ed. Handbuch der Reptilien und Amphibien Europas, Part 3/IIIB: Schildkröten (Testudines) II. Wiebelsheim, Germany: Aula-Verlag. pp. 329–448.

Danilov, I.G., Y. Bolotsky, A.O. Averianov and I.V. Donchenko. 2002. A new genus of lindholmemydid turtle (Testudines: Testudinoidea) from the Late Cretaceous of the Amur River Region, Russia. Russian Journal of Herpetology 9:155–168.

Danilov, I.G., A. Čerňanský, E.V. Syromyatnikova and P. Joniak. 2012. Fossil turtles of Slovakia: new material and a review of the previous record. Amphibia-Reptilia 33:423–442.

Danilov, I.G., R. Hirayama, V.B. Sukhanov, S. Suzuki, M. Watabe and N.S. Vitek. 2014. Cretaceous soft-shelled turtles (Trionychidae) of Mongolia: new diversity, records and a revision. Journal of Systematic Paleontology 12:799–832.

Danilov, I.G., V.B. Sukhanov, E.M. Obratzova and N.S. Vitek. 2015. The first reliable record of trionychid turtles in the Paleocene of Asia. Paleontological Journal 49:407–412.

Danilov, I.G., E.V. Syromyatnikova, P.P. Skutschas, T.M. Kodrul and J. Jin. 2013. The first 'true' *Adocus* (Testudines, Adocidae) from the Paleogene of Asia. Journal of Vertebrate Paleontology 33:1071–1080.

Danilov, I.G. and N.S. Vitek. 2012. Soft-shelled turtles (Trionychidae) from the Bissekty Formation (Late Cretaceous: late Turonian) of Uzbekistan: Shell-based taxa. Cretaceous Research 41:55–64.

—2013. Cretaceous trionychids of Asia: an expanded review of their record and biogeography. In: D.B. Brinkman, P.A. Holroyd and J.D. Gardner, eds. Morphology and Evolution of Turtles. Dordrecht, The Netherlands: Springer. pp. 419–438.

Danilov, I.G., N.S. Vitek, A.O. Averianov and V.N. Glinskiy. 2015. A new softshelled trionychid turtle of the genus *Khunnuchelys* from the Upper Cretaceous Bostobe Formation of Kazakhstan. Acta Palaeontologica Polonica 60: 155–161.

Danilov, I.G., E.A. Zvonok, E.V. Syromyatnikova and N.I. Udovichenko. 2011. A new species of soft-shelled turtle (Trionychidae) from the middle Eocene of Ukraine. Proceedings of the Zoological Institute of the Russian Academy of Sciences 315:399–411.

Darga, R., M. Böhme, U. Göhlich and G. Rössner. 1999. Reste höherer Wirbeltiere aus dem Alttertiär des Alpenvorlandes bei Siegsdorf/Oberbayern. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 39:91–114.

Daudin, F.M. 1801. Histoire naturelle, générale et particulière des reptiles. Tome second. Paris: Imprimerie F. Dufart. 432 pp.

De Gregorio, A. 1883. Nuovi fossili terziari (vertebrati e invertebrati). Palermo, Italy. 4 pp.

—1892. Sulla *Trionix ragusensis*, De Greg. e la *Tr. Melitensis* Lyd. Il Naturalista Siciliano 11:182–183.

Delfino, M. 2002. Erpetofaune italiane del Neogene e del Quaternario [dissertation]. Modena and Reggio Emilia, Italy: University of Modena and Reggio Emilia. 382 pp.

Delfino, M. and U.B. Göhlich. 2009. The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria). 4. Testudines. Annalen des Naturhistorischen Museums in Wien 111A:499–508.

Delfino, M., T.M. Scheyer, U. Fritz and M.R. Sánchez-Villagra. 2010. An integrative approach to examining a homology question: shell structures in soft-shell turtles. Biological Journal of the Linnean Society 99:462–476.

Delfino, M. and T. Smith. 2009. A reassessment of the morphology and taxonomic status of '*Crocodylus*' *depressifrons* Blainville, 1855 (Crocodylia, Crocodyloidea) based on the early Eocene remains from Belgium. Zoological Journal of the Linnean Society 156:140–167.

Delfortrie, E. 1869. Les chéloniens du Miocène supérieur de la Gironde. Actes de la Société linnéenne de Bordeaux 27:399–440.

Delheid, E. 1899. Un *Trionyx* de l'argile de Boom (Oligocène moyen). Annales de la Société Zoologique de Belgique 33:76–77.

Denison, R. 1978. Handbook of Paleoichthyology, Volume 2: Placodermi. Stuttgart, Germany: Gustav Fischer Verlag. 71 pp.

Depéret, C. 1895. Über die Fauna von miocänen Wirbelthieren aus der ersten Mediterranstufe von Eggenburg. Sitzungsberichte der Akademie der Wissenschaften in Wien 104:395–416.

Depéret, C. and A. Donnezan. 1890–1897. Classe des reptiles. In: C. Depéret, ed. Les animaux Pliocènes du Roussillon. Mémoires de la Société Géologique de France, Paléontologie 3:140–194.

Deraniyagala, P.E.P. 1953. A Colored Atlas of Some Vertebrates from Ceylon, Volume 2: Tetrapod Reptilia. Colombo, Sri Lanka: Ceylon Natural History Museum. 101 pp.

D'Erasmo, G. 1933. Sui resti di vertebrati terziari raccolti nella Sirtica dalla missione della Reale Accademia d'Italia (1931). Atti Reale Accademia Nazionale dei Lincei. Rendiconti Classe di Scienze Fisiche, Matematiche e Naturali 17:656–658.

De Stefano, G. 1902. Un nuovo Chelonide della Famiglia Trionychidae appartenente all'Eocene francese. Bollettino della Società Geologica Italiana e del Servizio Geologico d'Italia 21:389–397.

De Vis, C.W. 1894. The lesser chelonians of the Nototherian drifts. Proceedings of the Royal Society of Queensland 10:123–127.

Dollo, L. 1909. The fossil vertebrates of Belgium. Annals of the New York Academy of Sciences 19:99–119.

Drake, R.E., J.A. Van Couvering, M.H. Pickford, G.H. Curtis and J.A. Harris. 1988. New chronology for the Early Miocene mammalian faunas of Kisingiri, western Kenya. Journal of the Geological Society 145:479–491.

Duméril, A.M.C. and G. Bibron. 1835. Erpétologie générale ou histoire naturelle complète des reptiles, Tome 2. Paris: Roret. 680 pp.

Eikamp, H. 1978. Zur obermiozänen Kieselgurlagerstätte von Beuern (Kreis Giessen) und ihrer ehemaligen Flora und Fauna. Jahresberichte der Wetterauischen Gesellschaft für die Gesamte Naturkunde zu Hanau 129–130:91–103.

Engstrom, T.N., H.B. Shaffer and W.P. McCord. 2002. Phylogenetic diversity of endangered and critically endangered Southeast Asian softshell turtles (Trionychidae: *Chitra*). Biological Conservation 104:173–179.

Ernst, C.H. and R.W. Barbour. 1989. Turtles of the World. Washington, DC: Smithsonian Institution Press. 313 pp.

Esu, D. and T. Kotsakis. 1983. Les vertébrés et les mollusques continentaux du Tertiaire de la Sardaigne: paléobiogéographie et biostratigraphie. Geologia Romana 22:177–206.

Ezquerra del Bayo, J. 1850. Ensayo de una descripción general de la estructura geológica del terreno de España en la Península. Memorias de la Real Academia de Ciencias l:35–65.

Fabiani, R. 1915. Il Paleogene del Veneto. Memorie dell'Istituto di Geologia dell'Università di Padova 3:1–336.

Falconer, H. 1831. Note on certain specimens of animal remains from Ava. Gleanings in Science 3:167–170.

—1859. Descriptive Catalogue of the Fossil Remains of Vertebrata from the Sewalik Hills, the Nerbudda, Perim Island, &c. in the Museum of the Asiatic Society of Bengal. Calcutta, India: Asiatic Society of Bengal. 261 pp.

Falconer, H. and P.T. Cautley. 1837. Notice on the remains of a fossil monkey from the Tertiary strata of the Siwalik Hills in the north of Hindustan. Transactions of the Geological Society of London 5:499–504.

Farkas, B.L. 1992. Wiederentdeckung eines Exemplars von *Rafetus swinhoei* (Gray, 1873) im Naturhistorischen Museum Wien. Salamandra 28:145–152.

—1995. Fossil trionychid turtle types in Hungarian collections—a preliminary review (Reptilia, Testudines). Annales Historico-Naturales Musei Nationalis Hungarici 87:57–62.

Farkas, B. and U. Fritz. 1998. On the identity of *Rafetus swinhoei* (Gray, 1873) and *Pelochelys maculatus* (Heude, 1880). Zoologische Abhandlungen des Museums für Tierkunde, Dresden 50:59–75.

Fitzinger, L. 1836. Entwurf einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. Annalen des Wiener Museums der Naturgeschichte 1:104–128.

Forskål, P. 1775. Descriptiones Animalium. Avium, Amphibiorum, Piscium, Insectorum, Vermium. Quae in Itinere Oriental Observavit. Haunia, Denmark: Mölleri. 12 pp.

Fritz, U., R. Gemel, C. Kehlmaier, M. Vamberger and P. Praschag. 2014. Phylogeography of the Asian softshell turtle *Amyda cartilaginea* (Boddaert, 1770): evidence for a species complex. Vertebrate Zoology 64:229–243.

Fuchs, E. 1939. Die Schildkrötenreste aus dem Oberpfälzer Braunkohlentertiär. Palaeontographica Abteilung A 89:57–104.

Fuchs, H. 1962. Adatok a kóródi rétegek ősállatvilágának fontosabb ismeretéhez. Földtani Közlöny 91:448–449.

Fucini, A. 1912. *Trionyx pliocenicus* Law. Paleontographia Italica 18:1–28.

Gaffney, E.S. and A. Bartholomai. 1979. Fossil trionychids of Australia. Journal of Paleontology 53:1354–1360.

Gagnaison, C., B. Guevel, S. Xerri, J.-L. Sicot, J.-M. Villeneuve and B. Cossard. 2012. La falunière du Tourrelet (Thenay, Loir-et-Cher, France): nouvelles données sur les vertébrés des sables continentaux du Miocène moyen (Orléanien supérieur: MN5). Revue de Paléobiologie, Genève 31:219–234.

Gardner, J.D. and A.P. Russell. 1994. Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 193:209–244.

Gardner, J.D., A.P. Russell and D.B. Brinkman. 1995. Systematics and taxonomy of soft-shelled turtles (Family Trionychidae) from the Judith River Group (mid-Campanian) of North America. Canadian Journal of Earth Sciences 32:631–643.

Gastaldi, E. 1863. Antracoterio di Agnana, balenottera di Cà Lunga presso S. Damiano e mastodonte di Mongrosso. Atti della Società Italiana di Scienze Naturali 5:88–91.

Geinitz, E. 1877. Die angebliche *Trionyx schlotheimii* im diluvialen Kalktuff von Burgtonna ist eine *Cistudo europaea*. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, Stuttgart 1877:278–279.

Gemel, R. 2002. Weichschildkrötenreste aus dem Karpatium des Korneuburger Beckens (Untermiozän; Niederösterreich). Beiträge zur Paläontologie 27:355–371.

Geoffroy Saint-Hilaire, E.F. 1809. Mémoire sur les tortues molles, nouveau genre sous le nom de *Trionyx*, et sur la formation des carapaces. Annales du Muséum d'Histoire Naturelle 14:1–20.

Georgalis, G.L., Z. Szyndlar, B.P. Kear and M. Delfino. 2016a. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109:103–116.

Georgalis, G.L., A. Villa, E. Vlachos and M. Delfino. 2016b. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49:433–444.

Gergens, F. 1860. Mitteilung an Geheimrat v. Leonhard gerichtet. Jahrbuch fur Mineralogie, Geologie und Palaeontologie 1860:554–555.

Gervais, P. 1859. Zoologie et paléontologie française. 2nd ed. Paris: Arthus Bertrand. 544 pp.

—1867–1869. Zoologie et paléontologie générales (animaux vertébrés): ou nouvelles recherches sur les animaux vivants et fossiles. Paris: Arthus Bertrand. 263 pp.

Gilmore, C.W. 1931. Fossil turtles of Mongolia. Bulletin of the American Museum of Natural History 59:1–14.

—1934. Fossil turtles of Mongolia: second contribution. American Museum of Natural History Novitates 689:1–14.

Girotti, O., L. Capasso Barbato, D. Esu, E. Gliozzi, T. Kotsakis, E. Martinetto, C. Petronio, R. Sardella and E. Squazzini. 2003. The section of Torre di Picchio (Terni, Umbria, Central Italy): a Villafranchian site rich in vertebrates, molluscs, ostracods and plants. Rivista Italiana di Paleontologia e Stratigrafia 109:77–98.

Giusberti, L., L. Del Favero and G. Roghi. 2014. The Purga di Bolca-Vegroni sites. Rendiconti della Società Paleontologica Italiana 4:95–103.

Glaessner, M.F. 1933. Die Tertiärschildkröten Niederösterreichs. Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie, Abteilung B 69:353–387.

—1935. Bemerkungen zur tertiären Schildkrötenfauna Ungarns. Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B 1:124–127.

Gobé, J.-F., J. Mornand and D. Pouit. 1980. Les restes des reptiles des faluns de l'Anjou-Touraine (et supplément Poissons). Mémoires de la Société d'Etudes scientifiques de l'Anjou, Angers 5:1–40.

Gramann, F. 1956. Schildkröten aus dem Malnienton von Borken (Niederhessische Senke) (*Trionyx*, *Anosteira*). Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden 84:16–20.

Gray, J.E. 1830. A synopsis of the species of the class Reptilia. In: E. Griffith and E. Pidgeon, eds. The Class Reptilia arranged by the Baron Cuvier, with specific descriptions. In: E. Griffith, ed. The Animal Kingdom arranged in conformity with its organization, by the Baron Cuvier, with additional descriptions of all the species hitherto named, and of many not before noticed, Volume 9: Reptilia. Supplement. London: Whittaker, Treacher, and Co. pp. 75–76.

—1831. Synopsis Reptilium. Part I. Cataphracta. Tortoises, Crocodiles, Enaliosauria. London: G.B. Sowerby. 85 pp.

—1854. Description of a new genus and some new species of tortoises. Proceedings of the Zoological Society of London 1852:133–135.

—1864. Revision of the species of Trionychidae found in Asia and Africa, with the description of some new species. Proceedings of the Zoological Society of London 1864:76–98.

—1873. Notes on the tortoises of the 'Zoology of Mexico' of MM. A. Duméril and Bocourt. Annals and Magazine of Natural History, Series 4 12:109–114.

Groessens-van Dyck, M.-C. and H.H. Schleich. 1985. New reptile material from the German Tertiary. 5. Fossil turtle remains (*Chelydropsis*, *Trionyx*) from the Miocene fissure filling of Appertshofen/N-Ingolstadt. Bulletin de la Société Belge de Géologie 94:101–112.

Groessens van Dyck, M.-C. and H.H. Schleich. 1988. Zur Verbreitung tertiärer und quartärer Reptilien und Amphibien Europas. Belgien, Dänemark, Niederlande, Schweden. Studia Geologica Salmanticensia, Volume Especial 3:113–147.

Gröning, E. and C. Brauckmann. 1996. Schildkröten-Reste (Testudines) aus dem Mittel-Eozän des Eckfelder Maares (SW-Eifel, Deutschland). Mainzer Naturwissenschaftliches Archiv 34:45–53.

Gross, M. 2002. Aus der paläontologischen Sammlung des Landesmuseums Joanneum – Die fossilen Schildkröten (Testudines). Joannea Geologie und Paläontologie 4:5–68.

—2005. Nachtrag zum Katalog der fossilen Schildkröten am Landesmuseums Joanneum. Joannea Geologie und Paläontologie 6:61–64.

Guasparri, G. 1992. L'Accademia dei Fisiocritici di Siena: Guida ai Musei. San Quirico d'Orcia, Italy: Editoriale Donchisciotte. 166 pp.

Gulia, G. 1843. Guscio di testuggine fossile trovato a Malta. Repertorio di Conoscenze Utile, Zoologia Fossile 27: 77–78.

Hadjisterkotis, E., I. Kassapis and N. Klerides. 2000. Paleontological evidence for the presence of *Trionyx* sp. on Cyprus, with new information on living and alien species of terrapins. Newsletter, Hellenic Zoological Society 33:8–10.

Halstead Tarlo, L.B. 1965. Psammosteiformes (Agnatha)—a review with descriptions of new material from the Lower Devonian of Poland, II: Systematic part. Palaeontologia Polonica 15:1–167.

Hand, S.J., D.E. Lee, T.H. Worthy, M. Archer, J.P. Worthy, A.J.D. Tennyson, S.W. Salisbury, R.R. Scofield, D.C. Mildenhall, E.M. Kennedy and J.K. Lindqvist. 2015. Miocene fossils reveal ancient roots for New Zealand's endemic *Mystacina* (Chiroptera) and its rainforest habitat. PLoS ONE 10:e0128871. doi: 10.1371/journal.pone.0128871

Harrassowitz, H.L.F. 1919. Eocäne Schildkröten von Messel bei Darmstadt. Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B 9/10:147–154.

—1922. Die Schildkrötengattung *Anosteira* von Messel bei Darmstadt und ihre stammesgeschichtliche Bedeutung. Abhandlungen der Hessische Geologische Landesanstalt 6:137–238.

Hasegawa, Y., Y. Suyama and A. Kameyama. 2007. Fossil turtle from the Upper Oligocene, Taoyama Formation, Hioki Group, in Tobou-cho, Shimonoseki, Yamaguchi, Japan. Bulletin of the Gunma Museum of Natural History 11:29–36.

Hay, O.P. 1899. Notes on the nomenclature of some North American fossil vertebrates. Science 10:253–254.

—1908. The fossil turtles of North America. Carnegie Institute of Washington Publication 75:1–568.

Head, J.J., S.M. Raza and P.D. Gingerich. 1999. *Drazinderetes tethyensis*, a new large trionychid (Reptilia: Testudines) from the marine Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology of the University of Michigan 30:199–214.

Heritsch, F. 1909. Jungtertiäre Trionyxreste aus Mittelsteiermark. Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt 59:333–382.

—1910. Ein Jugendexemplar von *Trionyx Petersi* R. Hoernes aus Schönegg bei Wies. Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark 46:348–355.

Hernández Sampelayo, P.H. and J.R. Bataller. 1944. *Trionyx marini*, tortuga nueva del Oligoceno leridano. Notas y Comunicaciones del Instituto Geológico y Minero de España 13:9–19.

Hervet, S. 2004. Systématique du groupe <<*Palaeochelys* sensu lato—*Mauremys*>> (Chelonii, Testudinoidea) du Tertiaire d'Europe occidentale: principaux résultats. Annales de Paléontologie 90:13–78.

Hill, D., G. Playford and J.T. Woods. 1970. Cainozoic Fossils of Queensland. Brisbane, Australia: Queensland Palaeontographical Society. 36 pp.

Hirayama, R. 1992. Fossil Turtles from the Neogene strata in the Sinda Basin, eastern Zaire. African Study Monographs 17:49–65.

—1998. Fossil turtles from the Mifune Group (Late Cretaceous) of Kumamoto Prefecture, western Japan. In: Dinosaurs from the Mifune Group, Kumamoto Prefecture, Japan. Mifune, Japan: Mifune Town Education Board. pp. 85–99. [in Japanese with English abstract]

—2007. Revision of the systematics of the fossil turtles from Japan. In: N. Inuzuka, ed. Jubilee Publication in Commemoration of Professor Kamei Tadao's 80th Birthday. pp. 145–153.

Hirayama, R., S. Isaji and T. Hibino. 2013. *Kappachelys okurai* gen. et sp. nov., a new stem soft-shelled turtle from the Early Cretaceous of Japan. In: D.B. Brinkman, P.A. Holroyd and J.D. Gardner, eds. Morphology and Evolution of Turtles. Dordrecht, The Netherlands: Springer. pp. 179–185.

Hoernes, R. 1881. Zur Kenntnis der mittelmiozänen Trionyxformen. Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt 31:479–482.

—1882. *Trionyx*-Reste des Klagenfurter Museums von Trifail in Steiermark. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt 1882:39–40.

—1892. Neue Schildkrötenreste aus steirischen Tertiärablagerungen. Verhandlungen der Kaiserlich-Königlichen Geologischen Bundesanstalt 1892:242–246.

Holec, P. 2006. Remnants of the turtles genus *Trionyx* sp. from Miocene sediments of Devinska Kobyla hill near Bratislava. Mineralia Slovaca 38:67–70. [in Slovakian, with English abstract]

Holec, P. and J. Schlögl. 2000. Find of *Trionyx rostratus* Arth. in the upper Badenian deposits of the Malé Karpaty Mts., western Carpathians. Slovak Geological Magazine 6:106–109.

Hooijer, D.A. 1954. Pleistocene vertebrates from Celebes. X Testudinata. Proceedings of the Koninklijke Nederlandsche Akademie van Wetenschappen, Series B 57:486–489.

Hooker, J.J. and D.J. Ward. 1980. List of localities. Tertiary Research 3:3–12.

Hörnes, M. 1848. Verzeichnis der Fossil-Reste aus 135 Fundorten des Tertiär-Beckens von Wien. In: J. Czjzek, ed. Erläuterungen zur geognostischen Karte der Umgebung Wiens. Vienna: Braumüller. pp. 1–43.

Hummel, K. 1927. Die Schildkrötengattung *Trionyx* im Eozän von Messel bei Darmstadt und im aquitanischen Bättersandstein vom Münzenberg in der Wetterau. Abhandlungen der Hessische Geologische Landesanstalt 8:5–96.

—1929. Die fossilen Weichschildkröten (Trionychia): eine morphologisch-systematische und stammesgeschichtliche Studie. Geologische und Paläontologische Abhandlungen 16:359–487.

—1932. Pars 52: Trionychia fossilia. In: W. Quenstedt, ed. Fossilium Catalogus. I: Animalia. Berlin: W. Junk. 106 pp.

—1935. Schildkröten aus der mitteleozänen Braunkohle des Geiseltales. Nova Acta Leopoldina 2:457–483.

Hutchison, J.H., P.A. Holroyd and R.L. Ciochon. 2004. A preliminary report on Southeast Asia's oldest Cenozoic turtle fauna from the late Middle Eocene Pondaung Formation, Myanmar. Asiatic Herpetological Research 10:38–52.

[ICZN] International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. 4th ed. London: International Trust for Zoological Nomenclature. 306 pp.

—2005. Opinion 2119 (case 3277). *Chitra chitra* Nutaphand, 1986 (Reptilia, Testudines): specific name given precedence over *Chitra selenkae* Jaekel, 1911. Bulletin of Zoological Nomenclature 62:118–119.

Issel, A. 1892. Liguria geologica e preistorica, Volume 1. Genoa, Italy: Donath Editore. 440 pp.

Jaccard, A. 1888. Sur les animaux vertébrés fossiles de l'étage Oeningen du Loche. Bulletin de la Société des Sciences Naturelles de Neuchâtel 16:52–57.

Jaeger, J.-J., A.N. Soe, O. Chavasseau, P. Coster, E.-G. Emonet, F. Guy, R. Lebrun, et al. 2011. First hominoid from the Late Miocene of the Irrawaddy Formation (Myanmar). PLoS ONE 6:e17065. doi: 10.1371/journal.pone.0017065.

Jaekel, O. 1911. Die fossilen Schildkröten von Trinil. In: M.L. Selenka and M. Blanckenhorn, eds. Die *Pithecanthropus*-Schichten auf Java. Geologische und Paläontologische Ergebnisse der Trinil-Expedition (1907 und 1908). Leipzig, Germany: Engelmann. pp. 75–81.

Jiménez Fuentes, E. 2003. Quelonios fósiles de la Cuenca del Duero. In: E. Jiménez Fuentes and J. Civis Llovera, eds. Los vertebrados fósiles en la historia de la vida. Excavación, estudio y patrimonio. Salamanca, Spain: Universidad de Salamanca. pp. 177–195.

Jiménez Fuentes, E. and L. Alonso Andres. 1994. Nuevos hallazgos de Trionychidae (Chelonii) en el Eoceno de Salamanca y Zamora. Studia Geologica Salmanticensia 29:95–113.

Jiménez Fuentes, E. and S. Martín de Jesús. 1991. Ejemplares-tipo de quelonios fósiles españoles. Revista Española de Paleontología 6:98–106.

Jiménez Fuentes, E., E. Ramos Guerrero, S. Martín De Jesús, E. Pérez Ramos and E. Mulas Alonso. 1990. Quelonios del Eoceno medio de Mallorca. Paleontologia i Evolució 23:153–156.

Joyce, W.G. 2014. A review of the fossil record of turtles of the clade *Pan-Carettochelys*. Bulletin of the Peabody Museum of Natural History 55:3–33.

—2016. A review of the fossil record of turtles of the clade *Pan-Chelydridae*. Bulletin of the Peabody Museum of Natural History 57:21–56.

—2017. A review of the fossil record of basal Mesozoic turtles. Bulletin of the Peabody Museum of Natural History 58(1):65–113.

Joyce, W.G. and T.R. Lyson. 2010a. A neglected lineage of North American turtles fills a major gap in the fossil record. Palaeontology 53:241–248.

—2010b. *Pangshura tatrotia*, a new species of pond turtle (Testudinoidea) from the Pliocene Siwaliks of Pakistan. Journal of Systematic Palaeontology 8:449–458.

—2011. New material of *Gilmoremys lancensis* nov. comb. (Testudines: Trionychidae) from the Hell Creek Formation and the diagnosis of plastomenid turtles. Journal of Paleontology 85:442–459.

Joyce, W.G., T.R. Lyson and S. Williams. 2016. New cranial material of *Gilmoremys lancensis* (Testudines, Trionychidae) from the Hell Creek Formation of southeastern Montana, U.S.A. Journal of Vertebrate Paleontology 36:e1225748. doi: 10.1080/02724634.2016.1225748

Joyce, W.G., N. Micklich, S.F.K. Schaal and T.M. Scheyer. 2012. Caught in the act: the first record of copulating fossil vertebrates. Biology Letters 8:846–848.

Joyce, W.G., J.F. Parham and J.A. Gauthier. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology 78:989–1013.

Joyce, W.G., J.F. Parham, T.R. Lyson, R.C.M. Warnock and P.C.J. Donoghue. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. Journal of Paleontology 87:612–634.

Jurkovšek, B. and T. Kolar-Jurkovšek. 1994. Fossil turtles in Slovenia. Geologija 36:75–93.

Karl, H.-V. 1987. Revision der fossilen Schildkröten (Reptilia, Testudines) von Jawa. Gothaer Museumsheft 14:37–44.

—1993. Revision der känozoischen Weichschildkröten (Testudines, Trionychidae) Mitteldeutschlands. Mauritiana 14:115–134.

—1996. Some remarks on the fossil turtles (Reptilia, Testudines) from the federal country of Salzburg, Austria. Mitteilungen der Gesellschaft für Salzburger Landeskunde 136:389–426.

—1998. Zur Taxonomie der känozoischen Weichschildkröten Österreichs und Deutschlands (Trionychidae: Trionychinae). Mitteilungen zur Geologie und Paläontologie, Landesmuseum Joanneum 56:273–328.

—1999a. Die Zoogeographie der känozoischen Weichschildkröte *Trionyx triunguis* Forskål, 1775 (Testudines: Trionychidae). Joannea - Geologie und Paläontologie 1:27–60.

—1999b. Paleogeography and systematics of the genus *Dogania* Gray, 1844 (Testudines: Trionychidae). Studia Geologica Salmanticensia 35:3–8.

—2002. Über Reptilienreste aus dem Alttertiär des nördlichen Alpenvorlandes bei Siegsdorf/Oberbayern. Joannea - Geologie und Paläontologie 4:69–81.

—2007. The fossil reptiles (Reptilia: Chelonii, Crocodylia) from the marine Early Oligocene of the Weisselster Basin (Central Germany: Saxonia). Studia Geologica Salmanticensia 43:25–66.

—2012. Human consumption of turtles of the *Homo rudolfensis* site Uraha (Malawi, East Africa). Archaeofauna 21:253–264.

—2013. Die fossilen Schildkröten aus der Molasse von Oberschwaben mit taxonomischen Notizen zu "*Promalacoclemmys* Reinach, 1900" und *Testudo antiqua* Bronn, 1831 (Testudines: Cryptodira). Mainzer Naturwissenschaftliches Archiv 50:121–146.

Karl, H.-V., E. Gröning and C. Brauckmann. 2011. New Oligocene turtle remains of the Oberleichtersbach doline filling (Lower Franconia, Germany) and revision of the genus *Palaeomauremys* (Testudines: Geoemydidae). Studia Geologica Salmanticensia 47:175–194.

Karl, H.-V. and B.E.K. Lindow. 2012. Revision of the Palaeocene turtles (Reptilia: Testudines) of Denmark. Studia Palaeocheloniologica 4:175–192.

Karl, H.-V. and A. Müller. 2008. New fossil reptil [*sic*] material (Reptilia: Chelonii, Crocodylia) from the lower Oligocene of Borken (central Germany: Hesse). Studia Geologica Salmanticensia 44:41–58.

Kaup, J.J. 1834. *Pisoodon Coleanus*, ein neues Genus der Saurier aus dem tertiären Sande bey Eppelsheim. Isis 5:533–536.

Khosatzky, L.I. 1948. [About remains of turtles from the Sarmatian of the Crimea]. Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, Otdel geologii 23:17–22. [in Russian]

—1957. [On the history of trionychids in Kazakhstan]. Izvestiya Akademii Nauk Kazakh SSR, Seriya Biologicheskaya 2:15–30. [in Russian]

—1966. [About a gigantic Mesozoic representative of trionychids and several features of the shell of these turtles]. In: Pozvonochnye zhivotnye Sredney Azii. Tashkent, Uzbekistan: Fan. pp. 150–157. [in Russian]

—1976. [A new representative of trionychids from the Late Cretaceous of Mongolia]. In: Gerpetologiya, Kubanskiy Gosudarstvennyy Universitet. Nauchnye Trudy 218:3–19. [in Russian]

—1986. [A large trionychid from the Sarmatian of Moldavia]. Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva 29:158–170. [in Russian]

—1999. [Turtles—trionychids of the Cretaceous of Mongolia]. Voprosy Paleontologii 11:141–149. [in Russian]

Khosatzky, L.I., L. Christov and D. Nankinov. 1983. An Eocene soft-shelled turtle from Bulgaria. Schriftenreihe für geologische Wissenschaften 19/20:271–280.

Khosatzky, L.I. and M. Młynarski. 1971. Chelonians from the Upper Cretaceous of the Gobi Desert, Mongolia. Palaeontologia Polonica 25:131–144.

Khosatzky, L.I. and L.A. Nessov. 1979. [Big turtles of the Late Cretaceous of Middle Asia]. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 89:98–108.

Khosatsky, L.I. and O.I. Redkozubov. 1989. [The Neogene turtles of Moldova]. Chişinau, Moldova: Shtiinca. 94 pp. [in Russian]

Khosatzky, L.I. and V.I. Tofan. 1970. [Past and present state of the herpetofauna of Moldavia]. Uchenye Zapiski Tiraspol'skogo Gosudarstvennogo Pedagogicheskogo Instituta 20:157–181. [in Russian]

Klein, N. and T. Mörs. 2003. Die Schildkröten (Reptilia: Testudines) aus dem Mittel-Miozän von Hambach (Niederrheinische Bucht, NW-Deutschland). Palaeontographica Abteilung A 268:1–48.

Koch, A., 1894. Az erdélyrészi medencze harmadkori képző̋dményei. 1. Paleogén csoport. Magyar Királyi Földtani Intézet Évkönyve 10:161–356.

Koch, F. 1915. Über *Trionyx croaticus* n. sp. aus dem Mittelmiozän von Voca in Kroatien. Glasnik Hrvatskoga prirodoslovnoga društva 27:203–211.

Koken, 1892. Über Wirbeltierreste der samländischen Unteroligocäns. Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg 33:42–43.

Kordikova, E.G. 1992. [Review of fossil trionychid turtles of the USSR]. Izvestiya Akademii Nauk Gruzii, Seriya Biologicheskaya 18:131–141. [in Russian]

—1994a. About systematics of fossil trionychids in Kazakhstan. Selevinia 2:3–8.

—1994b. Review of fossil trionychid localities in the Soviet Union. Courier Forschungs-Institut Senckenberg 173:341–358.

—2002. Heterochrony in the evolution of the shell of Chelonia. Part 1: Terminology, Cheloniidae, Dermochelyidae, Trionychidae, Cyclanorbidae and Carettochelyidae. Neues Jahrbuch für Geologie und Paläontologie 226:343–417.

Kordikova, E.G. and V.M. Chkhikvadze. 1990. [Stratigraphic significance of fossil trionychids of Kazakhstan]. Materialy po istorii fauny i flory Kazakhstana 11:135–139. [in Russian]

Kordikova, E.G. and A.V. Mavrin. 1996. Stratigraphy and Oligocene–Miocene mammalian biochronology of the Aktau Mountains, Dzhungarian Alatau Range, Kazakhstan. Palaeovertebrata 25:141–174.

Kotsakis, T. 1977. Due nuovi *Trionyx capellinii* Negri (Testudinata, Trionychidae) dell'Eocene di Monte Bolca (Verona, Italia). Bollettino della Società Paleontologica Italiana 16:203–228.

—1980. Révision des tortues (Emydidae, Testudinidae, Trionychidae) du Plio–Pléistocène de Valdarno supérieur (Toscane, Italie). Quaternaria 22:11–37.

—1985. Les Trionychidae (Testudinata, Reptilia) fossiles de l'Italie. Bollettino della Società Paleontologica Italiana 24:161–168.

—1989. Late Turolian amphibians and reptiles from Brisighella (northern Italy): preliminary report. Bollettino della Società Paleontologica Italiana 28:277–280.

Kotsakis, T., P. Argenti, G. Barisone, M. Delfino, M.R. Palombo, M. Pavia and P. Piras. 2005. I vertebrati continentali. Memorie del Museo Civico di Storia Naturale di Verona, Scienze della Terra 6:11–139.

Krumbiegel, G. 1963. Trionychidenfunde (Flussschildkröten) der Gattung *Trionyx* Geoffroy 1809 aus der eozänen Braunkohle des Geiseltales. Geologie 12:196–223.

Kuhn, O. 1964. Fossilium Catalogus, Volume I: Animalia, Part 107, Testudines. The Hague, The Neatherlands: Junk. 299 pp.

Kuss, S.E. 1958. Schildkrötenreste (*Ptychogaster buechelbergense* n. sp., *Ocadia malthaneri* n. sp., *Trionyx* sp.) aus dem aquitanen Tonlager von Bichelberg in der Pfalz. Notizblatt des Hessischen Landesamtes für Bodenforschung 86:50–76.

Kutorga, S.S. 1835. Beitrag zur Geognosie und Paläontologie Dorpats und seiner nächsten Umgebungen. St. Petersburg: Mineralogische Gesellschaft. 45 pp.

—1837. Beitrag zur Geognosie und Paläontologie Dorpat's und seiner nächsten Umgebungen. St. Petersburg: Mineralogische Gesellschaft. 51 pp.

Kuznetsov, V.V. 1976. [A freshwater turtle from the Senonian deposits of the northeastern Cis-Aralia region]. Paleontologicheskii Zhurnal 4:125–127. [in Russian]

—1978. [Materials on fossil turtles of Kazakhstan]. Moscow: VINITI. 119 pp. [in Russian]

Kuznetsov, V.V. and V.M. Chkhikvadze. 1977. [Fossil soft-shelled turtles from the middle Oligocene of the Turgai Depression]. Materialy po istorii fauny i flory Kazakhstana 7:10–14. [in Russian]

—1987. [The Late Cretaceous trionychids from Shakh-Shakh locality in Kazakhstan]. Materialy po istorii fauny i flory Kazakhstana 9:33–39. [in Russian]

Kuznetsov, V.V. and P.V. Shilin. 1983. [Late Cretaceous turtle from Baybishe northeastern Aral Sea region]. Izvestiya

Akademii Nauk Kazakh SSR, Seriya Biologicheskaya 6:41–44. [in Russian]

Kvaček, Z. 2002. Late Eocene landscape, ecosystems and climate in northern Bohemia with particular reference to the locality of Kuclín near Bílina. Bulletin of Geosciences 77:217–236.

Lapparent de Broin, F. de. 2000. African chelonians from the Jurassic to the present: phases of development and preliminary catalogue of the fossil record. Paleontologia Africana 36:43–82.

—2001. The European turtle fauna from the Triassic to the Present. Dumerilia 4:155–217.

Lapparent de Broin, F. de and S. Gmira. 1994. Les chéloniens dulçaquicoles du Rift occidental, Ouganda. In: M. Pickford, B. Senut and D. Hadoto, eds. Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. II: Palaeobiology. Paris: Fondation CIFEG. pp. 157–186.

Lapparent de Broin, F. de, D. Merle, M. Fontana, L. Ginsburg, P. Hervat, Y. Le Calvez and J. Riveline. 1993. Une faune continentale à vertébrés dans le Lutétien supérieur de Guitrancourt (Yvelines) et son environnement. Bulletin d'information des géologues du Bassin de Paris 30:3–16.

Lapparent de Broin, F. de and P.P. Van Dijk. 1999. Chelonia from the Late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates: palaeogeographical implications. In: P.J. Whybrow and A. Hill, eds. Fossil Vertebrates of Arabia. New Haven, CT: Yale University Press. pp. 136–162.

Laube, G.C. 1882. Notiz über das Vorkommen von *Trionyx* resten im Diatomeenschiefer von Kutschlin bei Bilin. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt 1882:107–108.

—1895. Vorläufiger Bericht über Schildkrötenreste aus der böhmischen Braunkohlenformation. Verhandlungen der Geologischen Bundesanstalt 1895:391–392.

—1896. Schildkrötenreste aus der böhmischen Braunkohlenformation. Abhandlungen des Deutschen Naturwissenschaftlich-Medizinischen Vereins für Böhmen "Lotos" 1:1–19.

—1898. Bericht über einen neuen *Trionyx* aus den aquitanischen (plastischen) Thonen von Preschen bei Bilin in Böhmen. Verhandlungen der Geologischen Bundesanstalt 1898:232–233.

—1900. Neue Schildkröten und Fische aus der böhmischen Braunkohlenformation. Abhandlungen des Deutschen Naturwissenschaftlich-Medizinischen Vereins für Böhmen "Lotos" 2:37–56.

Laurent, Y., S. Adnet, E. Bourdon, D. Corbalan, L. Danilo, S. Duffaud, G. Fleury, et al. 2010. La Borie (Saint-Papoul, Aude): un gisement exceptionnel dans l'Éocène basal du Sud de la France. Bulletin de la Société d'Histoire Naturelle de Toulouse 146:89–103.

Lawley, R. 1876. Nuovi studi sopra ai pesci ed altri vertebrati fossili delle Colline Toscane. Florence, Italy: Tipografia dell'Arte Della Stampa. 122 pp.

Lawver, D.R. and F.D. Jackson. 2014. A review of the fossil record of turtle reproduction: eggs, embryos, nests and copulating pairs. Bulletin of the Peabody Museum of Natural History 55:215–236.

Le, M., H.T. Duong, L.D. Dinh, T.Q. Nguyen, P.C.H. Pritchard and T. McCormack. 2014. A phylogeny of softshell turtles (Testudines: Trionychidae) with reference to the taxonomic status of the critically endangered, giant softshell turtle, *Rafetus swinhoei*. Organisms, Diversity and Evolution 14:279–293.

Le, M.D. and P. Pritchard. 2009. Genetic variability of the critically endangered softshell turtle, *Rafetus swinhoei*: a preliminary report. In: D.C. Ngo, H.T. Ta, N.N. Le, X.Q. Hoang, V.P. Vo, V.S. Nguyen, V.T. Nguyen, T.T. Le and Q.D. Tran, eds. Proceedings of the First Vietnamese National Symposium on Reptiles and Amphibians. Hue, Vietnam: Hue University Press. pp. 84–92.

Leakey, L.S.B. 1965. Olduvai Gorge, 1951–1961. A Preliminary Report on the Geology and the Fauna. Cambridge: Cambridge University Press. 109 pp.

Lebküchner, R.F. 1974. Beitrag zur Kenntnis der Geologie des Oligozäns von Mittelthrakien (Türkei). Bulletin of the Mineral Research and Exploration Institute of Turkey 83:1–30.

Lei, Y. and X. Ye. 1985. An early Eocene trionychid from Nanzhang, Hubei. Vertebrata Palasiatica 23:19–26.

Li, L., W.G. Joyce and J. Liu. 2015. The first soft-shelled turtle from the Jehol Biota of China. Journal of Vertebrate Paleontology 35:e909450. doi: 10.1080/02724634.2014.909450

Li, L., H. Tong, W. Gu and J. Liu. 2015. A new trionychid turtle from the Early Cretaceous of Heilongjiang Province, northeastern China. Cretaceous Research 56:155–160.

Liebus, A. 1930. Neue Schildkröten aus den Tertiären Süsswassertonen von Preschen bei Bilin in Böhmen. Rozpravy Státního geologického ústavu Ceskoslovenské Republiky 4:1–57.

Lörenthey, E. 1903. Zwei neue Schildkrötenarten aus dem Eocän von Kolozsvár. Földtani Közlöny 33:249–266.

Louys, J. and G.J. Price. 2015. The Chinchilla local fauna: an exceptionally rich and well-preserved Pliocene vertebrate assemblage from fluviatile deposits of south-eastern Queensland, Australia. Acta Palaeontologica Polonica 60:551–572.

Lydekker, R. 1885. Indian Tertiary and post-Tertiary Vertebrata. Siwalik and Nerbada Chelonia. Memoirs of the Geological Survey of India 21:155–208.

—1889a. Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History), Part III: The Order Chelonia. London: British Museum (Natural History). 239 pp.

—1889b. Notes on Siwalik and Narbada Chelonia. Records of the Geological Survey of India 22:56–58.

—1891. On a new species of *Trionyx* from the Miocene of Malta and a chelonian scapula from the London Clay. Quarterly Journal of the Geological Society of London 47:37–40.

Maack, G.A. 1869. Die bis jetzt bekannten fossilen Schildkröten und die im oberen Jura bei Kelheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. Palaeontographica 18:193–336.

Macarovici, N. and I. Motas. 1965. Asupra unui *Trionyx* sp. găsit în Kersonianul din Munţii Vrancei. Analele ştiinţifice ale Universităţii "Alexandru Ioan Cuza" din Iaşi 11:93–96.

Malik, A. and H. Nafiz. 1933. Küçükçekmece fosil fikrali hayvanlar mecmuası. Bulletin de la Faculté des sciences de l'Université d'Istanbul 8:1–119.

Mantell, G.A. 1833. The Geology of the South East of England. London: Longman. 415 pp.

Matsumoto, H. 1918. On a new fossil *Trionyx* from Hokkaidō. Science Reports of the Tohoku Imperial University, Geology 3:57–60.

Maxwell, E.E., S. Alexander, G. Bechly, K. Eck, E. Frey, K. Grimm, J. Kovar-Eder, et al. 2016. The Rauenberg fossil Lagerstätte (Baden-Württemberg, Germany): a window into early Oligocene marine and coastal ecosystems of Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 463:238–260.

Mayr, G. 2009. Paleogene Fossil Birds. Berlin: Springer-Verlag. 262 pp.

Mayr, G. and T. Smith. 2012. Phylogenetic affinities and taxonomy of the Oligocene Diomedeoididae, and the basal divergences amongst extant procellariiform birds. Zoological Journal of the Linnean Society 166:854–875.

McCord, W.P. and P.C.H. Pritchard. 2002. A review of the softshell turtles of the genus *Chitra*, with the description of new taxa from Myanmar and Indonesia (Java). Hamadryad 27:11–56.

—2003. Case 3277. *Chitra chitra* Nutaphand, 1986 (Reptilia, Testudines): Proposed precedence of the specific name over that of *Chitra selenkae* Jaekel, 1911. Bulletin of Zoological Nomenclature 60:208–210.

Meng, J., Y. Wang, X. Ni, K.C. Beard, C. Sun, Q. Li, X. Jin and B. Bai. 2007. New stratigraphic data from the Erlian Basin: implications for the division, correlation, and definition of Paleogene lithological units in Nei Mongol (Inner Mongolia). American Museum Novitates 3570:1–31.

Merciai, G. 1907. Sopra alcuni resti di vertebrati miocenici delle ligniti di Ribolla. Atti della Società Toscana di Scienze Naturali, Memoire 23:79–87.

Merkulova, N.N. 1978. [A new *Trionyx* from the Nemegt (MPR)]. Byulleten Moskovskogo Obshchestva Ispytateley Prirody. Otdel Geologicheskiy 53:156. [in Russian]

Meyer, H. von. 1832. Paläologica zur Geschichte der Erde und ihrer Geschöpfe. Frankfurt am Main: Siegmund Schmerber. 560 pp.

—1839. Die Säugetiere, Reptilien und Vögel aus den Molasse-Gebilden der Schweiz. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1839:1–9.

—1844. Mitteilung an Prof. Bronn gerichtet. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1844:564–567.

—1860. *Trionyx* Eier im Mainzer Becken. Jahrbuch fur Mineralogie, Geologie und Palaeontologie 1860:556–560.

—1865. Ueber die fossilen Reste von Wirbelthieren, welche die Herren von Schlagintweit von ihren Reisen in Indien und Hoch-Asien mitgebracht haben. Palaeontographica 15:1–40.

—1867. Ueber fossile Eier und Federn. Palaeontographica 15:223–252.

Meylan, P.A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186:1–101.

Meylan, P.A. and E.S. Gaffney. 1992. *Sinaspideretes* is not the oldest trionychoid turtle. Journal of Vertebrate Paleontology 12:257–259.

Meylan, P.A., B.S. Weig and R.C. Wood. 1990. Fossil soft-shelled turtles (Family Trionychidae) of the Lake Turkana Basin, Africa. Copeia 1990:508–528.

Michaux, J. 1973. Description d'un crâne de *Trionyx* cf. *bruxelliensis* Winckler, 1869 (Reptilia, Chelonia) du Cuisien d'Epernay (Marne). Compte rendu sommaire des séances de la Société géologique de France 3:92–94.

Misuri, A. 1911. Sopra un nuovo trionichide dell'arenaria miocenica del Bellunese (*Trionyx bellunensis* Dal Piaz in sch.). Perugia, Italy: Bartelli. 11 pp.

Miura, M. and Y. Uyama. 1987. A new species of the fossil soft-shelled turtle Trionychidae Testudinata from the Miocene Bihoku-sogun Kimita-son, Hiroshima Prefecture. Miscellaneous Reports of the Hiwa Museum for Natural History 25:11–14.

Młynarski, M. 1966. Die fossilen Schildkröten in den ungarischen Sammlungen. Acta Zoologica Cracoviensa 11:223–288.

—1976. Encyclopedia of Paleoherpetology. Part 7, Testudines. Stuttgart, Germany: Gustav Fischer Verlag. 129 pp.

Młynarski, M. and P. Narmandach. 1972. New turtle remains from the Upper Cretaceous of the Gobi Desert, Mongolia. Palaeontologia Polonica 27:95–102.

Moody, R.T.J. and C.A. Walker. 1970. A new trionychid turtle from the British lower Eocene. Palaeontology 13:503–510.

Mörs, T., 1998. Über das Vorkommen von *Trionyx* s. l. (Testudines: Trionychidae) im Oberoligozän von Rott (Rheinland). Bonner Zoologische Beiträge 48:31–34.

Mottl, M., 1967. Neue Schildkrötenreste aus dem Mittelmiozän SW-Österreichs. Carinthia 77:169–182.

Mudar, K. and D. Anderson. 2007. New evidence for Southeast Asian Pleistocene foraging economies: faunal remains from the early levels of Lang Rongrien Rockshelter, Krabi, Thailand. Asian Perspectives 46:298–334.

Murelaga, X., X.P. Suberbiola, F. de Lapparent de Broin, J.-C. Rage, S. Duffaud, H. Astibia and A. Badiola. 2002. Amphibians and reptiles from the Early Miocene of the Bardenas Reales of Navarre (Ebro Basin, Iberian Peninsula). Geobios 35:347–365.

Nakajima, Y., I.G. Danilov, R. Hirayama, T. Sonoda and T. Scheyer. Morphological and histological evidence for the oldest known softshell turtles from Japan. Journal of Vertebrate Paleontology. In Press.

Nečas, P., D. Modry and V. Zavadil. 1997. Czech Recent and Fossil Amphibians and Reptiles: An Atlas and Field Guide. Frankfurt am Main, Germany: Edition Chimaira. 94 pp.

Negri, A. 1892. Trionici eocenici ed oligocenici del Veneto. Memorie della Società Italiana di Scienze 8:1–53.

—1893. Nuove osservazioni sopra i trionici delle ligniti di Monteviale. Padua, Italy: Prosperini. 13 pp.

Nessov, L.A. 1977. [Turtles and some other reptiles from the Cretaceous of Karakalpakia]. In: Voprosy gerpetologii. Avtoreferaty dokladov IV Vsesoyuznoi gerpetologicheskoi konferentsii. Leningrad: Nauka. pp. 155–156. [in Russian]

—1984. [Preservation of remains of organisms and conditions of their burial in Kulbike Member of Itemir]. In: V.G. Ochev, ed. Tafonomiya i Voprosy Paleogeografii. Saratov, Russia: Saratov University. pp. 62–76. [in Russian]

—1986. Some late Mesozoic and Paleocene turtles of Soviet Middle Asia. Studia Palaeocheloniologica 2:7–22.

—1987. On some Mesozoic turtles of Soviet Union, Mongolia and China, with comments on systematics. Studia Palaeocheloniologica 2:87–102.

—1995a. [Dinosaurs of northern Eurasia: new data about assemblages, ecology, and paleobiogeography]. St. Petersburg: Izdatel'stvo Sankt-Peterburgskogo Universiteta. [in Russian]

—1995b. On some Mesozoic turtles of the Fergana Depression (Kyrgyzstan) and Dzhungar Alatau Ridge (Kazakhstan). Russian Journal of Herpetology 2:134–141.

—1997. [Cretaceous Non-marine Vertebrates of Northern Eurasia]. St. Petersburg: Saint Petersburg State University, Institute of Earth Crust. 218 pp. [in Russian]

Nutaphand, W. 1986. [Manlai. The world's biggest softshell turtle]. Thai Zoological Magazine 1:64–70. [in Thai]

Obata, I., H. Yoshikazu and O. Hiroyuki. 1972. Preliminary report on the Cretaceous reptile fossils from Hokkaidō. Memoirs of the National Science Museum 5:213–222.

Okazaki, Y. and S. Yoshida. 1977. On a new fossil *Trionyx* from the Pliocene age group, Mie Prefecture, west Japan. Bulletin of the Mizunami Fossil Museum 4:87–95.

Ősi, A. 2001. Középső-eocén teknősleletek Nyires-pusztáról (Déli-Bakony). Földtani Közlöny 131:353–360.

Otsuka, H. 1969. Pleistocene vertebrate fauna from the Kuchinotsu Group of west Kyushu (part III–V). Reports of the Faculty of Science, Kagoshima University 2:53–84.

—1970. Tertiary Chelonia from northwestern Kyushu. Reports of the Faculty of Science, Kagoshima University 3:23–28.

Owen, R. 1849–1884. A History of British Fossil Reptiles. London: Cassell and Company. 657 pp.

Owen, R. and T. Bell. 1849. Part I: Chelonia. In: R. Owen and T. Bell, eds. Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds. London: Palaeontographical Society of London. pp. 1–76.

Pamouktchiev, A., F. de Lapparent de Broin and A. Anguelov. 1998. Nouvelle trouvaille de tortue fossile en Bulgarie. Annuaire de l'Université de Sofia "St. Kliment Ohridski" Faculté de Géologie et Géographie, Livre 1 Geologie 90:5–8.

Pandolfi, L., G. Carnevale, L. Costeur, L. del Favero, M. Fornasiero, E. Ghezzo, L. Maiorino, et al. 2017. Reassessing the earliest Oligocene vertebrate assemblage of Monteviale (Vicenza, Italy). Journal of Systematic Palaeontology 15:83–127.

Papp, V.A., E. Thenius, W. Berger and E. Weinfurter. 1953. Vösendorf—ein Lebensbild aus dem Pannon des Wiener Beckens: ein Beitrag zur Geologie und Paläontologie der unterpliozänen Congerienschichten des südlichen Wiener Beckens. Mitteilungen der Geologischen Gesellschaft in Wien 46:1–109.

Parks, W.A. 1933. New species of dinosaurs and turtles from the Upper Cretaceous formations of Alberta. University of Toronto Studies, Geological Series 34:1–33.

Paunović, M. 1984. Süsswasserschildkrötenrest aus den Promina-Schichten bei Varoš (Siverić, Kroatien). Rod jugoslavenske Akademije Znanosti i Umjetnosti 411:7–16.

—1986. Revision of the Species *Trionyx croaticus* Koch, 1915. In: Z. Roček, ed. Studies in Herpetology. Prague: Charles University of Prague. pp. 183–186.

Pérez-García, A., X. Murelaga, J. Cadiel Lalueza, A. Badiola and E. Díaz-Berenguer. 2013. Presence of several clades of continental turtles in the Lutetian (Middle Eocene) of the Sobrarbe Formation (Ainsa Basin, south-central Pyrenees, northeast Spain). Geologica Belgica 16:311–319.

Pérez García, A., X. Murelaga, M.A. Mancheño and I. Fierro. 2011. Nuevos datos sobre las tortugas del Puerto de la Cadena (Mioceno superior de Murcia). Geogaceta 50:185–188.

Peters, K.F. 1855. Schildkrötenreste aus den österreichischen Tertiär-Ablagerungen. Denkschriften der Kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe 9:1–22.

—1859. Beiträge zur Kenntniss der Schildkrötenreste aus den österreichischen Tertiärablagerungen. Beiträge zur Palaeontographie von Österreich 1:59–64.

—1869. Zur Kenntniss der Wirbelthiere aus den Miocänschichten von Eibiswald in Steiermark. 1. Die Schildkrötenreste. Denkschriften der Kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe 29:111–124.

—1881. Der Schädel von *Trionyx Styriacus*. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt 1881: 221–222.

Peters, W.C.H. 1854. Übersicht der auf seiner Reise nach Mossambique beobachteten Schildkröten. Monatsberichte der Akademie der Wissenschaften zu Berlin 1854:215–216.

Pickford, M. 1975. Late Miocene sediments and fossils from the northern Kenya Rift Valley. Nature 256:279–284.

—1986. Cainozoic paleontological sites of western Kenya. Münchner Geowissenschaftliche Abhandlungen A 8:1–151.

—2008. Middle Miocene vertebrate fauna from Pemba Island, Tanzania. South African Journal of Science 104:231–237.

Pictet, F.-J. and A. Humbert. 1856. Monographie des chéloniens de la Molasse Suisse. Matériaux pour la paléontologie suisse 1:1–71.

Pilgrim, G.E. 1912. The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. Memoirs of the Geological Survey of India, New Series 4:1–83.

Pomel, A. 1846. Mémoire pour servir à la géologie paléontologique des terrains tertiaires du département de l'Allier. Bulletin de la Société géologique de France 3:353–373.

—1847. Note sur les mammifères et reptiles fossiles des terrains éocènes de Paris, inférieurs au dépôt gypseux. Archives des Sciences Physiques et Naturelles de Genève 4:326–330.

Poporogu, E. 1972. Prezenţa unui chelonian fosil—*Trionyx* sp. în sedimentele orizontului 2 din bazinul Petroşani în câmpul minier Lupeni. Acta Musei Devensis, Sargetia, Series Scienta Naturae 9:211–212.

Portis, A. 1879. Di alcuni fossili terziarii del Piemonte e della Liguria appartenenti all'ordine dei chelonii. Memorie della Reale Accademia delle Scienze di Torino, serie 2 32: 113–134.

—1882. Les chéloniens de la molasse Vaudoise conservés dans le musée géologique de Lausanne. Mémoires de la Société Paléontologique Suisse 9:1–78.

—1883. Nuovi chelonii fossili del Piemonte. Memorie della Reale Accademia delle Scienze di Torino 35:369–378.

—1885. Resti di chelonii terziarii italiani. Atti della Reale Accademia delle Scienze di Torino 20:881–896.

—1890. I rettili pliocenici del Valdarno superiore e di alcune altre località plioceniche di Toscana. Florence, Italy: Le Monnier. 32 pp.

—1901. Il *Procyclanorbis sardus* Port., nuovo trionychide fossile della Sardegna. Bollettino della Società Geologica Italiana 20:51–79.

Prasad, K.N. 1974. The vertebrate fauna from Piram Island, Gujarat, India. Memoirs of the Geological Survey of India 41:1–23.

Praschag, P., H. Stuckas, M. Päckert, J. Maran and U. Fritz. 2011. Mitochondrial DNA sequences suggest a revised taxonomy of Asian flapshell turtles (*Lissemys* Smith, 1931) and the validity of previously unrecognized taxa (Testudines: Trionychidae). Vertebrate Zoology 61:147–160.

Priem, F. 1914. Sur des poissons fossiles et en particulier des siludires du Tertiaire supérieur et des couches récentes d'Afrique (Egypte et région du Tchad). Mémoires de la Société Géologique de France. Paléontologie 49:5–13.

Prinada, V.D. 1927. [Report on excavation of sites, where dinosaur bones were discovered]. Izvestiya Geologicheskogo komiteta 45:453–454. [in Russian]

Pritchard, P.C.H., R.J. Rabett and P.J. Piper. 2009. Distinguishing species of geoemydid and trionychid turtles from shell fragments: evidence from the Pleistocene at Niah Caves, Sarawak. International Journal of Osteoarchaeology 19:531–550.

Rabi, M. and G. Botfalvai. 2008. A preliminary report on the Late Oligocene vertebrate fauna from Máriahalom, Hungary. Hantkeniana 6:177–185.

Rage, J.-C. 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments 93:517–534.

Ramovš, A. 1974. Paleontologija. Ljubljana, Slovenia: Fakulteta za naravoslovje in tehnologijo, Univerza v Ljubljani. 304 pp.

Ramsay, E.P. 1887. On a new genus and species of fresh water tortoise from the Fly River, New Guinea. Proceedings of the Linnean Society of New South Wales (Second Series) 1:158–162.

Reed, F.R.C. 1932. New Miocene faunas from Cyprus. Geological Magazine 69:511–517.

Reinach, A. von. 1900. Schildkrötenreste im Mainzer Tertiärbecken und in benachbarten ungefähr gleichaltrigen Ablagerungen. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 28:1–135.

—1903. Schildkrötenreste aus dem ägyptischen Tertiär. Abhandlungen Herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft 29:1–64.

Rhodin, G.J.A., S. Thomson, G.L. Georgalis, H.-V. Karl, I.G. Danilov, A. Takahashi, M.S. de la Fuente, et al. 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. Chelonian Research Monographs 5:1–66.

Riabinin, A.N. 1930. On the fauna and age of the dinosaur beds in Amur River. Zapiski Rossiiskogo mineralogicheskogo obshchestva 59:41–51. [in Russian with English summary]

—1938. [Some results of the study of the Upper Cretaceous dinosaurian fauna from the vicinity of the station Sary-Agach, South Kazakhstan]. Problemy Palaeontologii 4:130–136. [in Russian, with English summary]

Rieppel, O. 1979. Eine neue *Trionyx* (Reptilia, Chelonia) aus der oberen Süsswassermolasse von Oerlikon, Kanton Zürich. Vierteljahrsschrift der Naturforschende Gesellschaft in Zürich 124:141–155.

Ristori, G. 1891a. I cheloniani delle ligniti del Casino (Siena). Atti della Società Toscana di Scienze Naturali, Processi Verbali 7:308.

—1891b. I cheloniani fossili di Montebamboli e Casteani (Maremma, Toscana). Atti della Società Toscana di Scienze Naturali, Processi Verbali 7:304–307.

—1895. Cheloniani fossili di Montebamboli e Casteani. Memoria paleontologica del prof. Giuseppe Ristori. Con appendice sui Cheloniani fossili del Casino (Siena). Pubblicazioni del Reale Istituto di Studi superiori in Firenze, lezione di scienze fisiche e naturale 21:1–104.

Robinson, P. and C.C. Black. 1974. Vertebrate faunas from the Neogene of Tunisia. Annals of the Geological Survey of Egypt 4:319–332.

Roger, J., M. Pickford, H. Thomas, F. de Lapparent de Broin, P. Tassy, W. Van Neer, C. Bourdillon-de-Grissac and S. Al-Busaldi. 1994. Découverte de vertébrés fossiles dans le Miocène de la région du Huqf au Sultanat d'Oman. Annales de Paléontologie 80:253–273.

Rose, K.D. 2006. The Beginning of the Age of Mammals. Baltimore, MD: Johns Hopkins University Press. 428 pp.

Rosenkrantz, A. 1923. En *Trionyx* fra Crania-Kalkblokke. Meddelelser fra Dansk geologisk Forening 6:3–14.

Rückert-Ülkümen, N. 1963. Tertiäre Fische aus Thrakien und Dardanellen (Türkei). İstanbul Üniversitesi Fen Fakültesi mecmuası, Series B 28:86–103.

Russell, L.S. 1934. Fossil turtles from Saskatchewan and Alberta. Transactions of the Royal Society of Canada 28:101–110.

Sacco, F. 1889. I Cheloni astiani del Piemonte. Memorie della Reale Accademia delle Scienze di Torino 39:427–461.

—1894. Trionici di Monte Bolca. Atti della Reale Accademia delle Scienze di Torino 29:3–12.

—1895. Trionici di Monteviale. Atti della Reale Accademia delle Scienze di Torino 30:3–8.

Sahni, A., R.S. Batra and S.B. Bhatia. 1984. Vertebrate assemblage from the Upper Subathu (middle Eocene) of the Bilaspur area, Himachal Pradesh, India. Proceedings of the Indian Colloquium on Micropalaeontology and Stratigraphy 10:357–368.

Sahni, A., S.B. Bhatia, J.-L. Hartenberger, J.-J. Jaeger, K. Kumar, J. Sudre and M. Vianey-Liaud. 1981. Vertebrates from the Subathu formation and comments on the biogeography of Indian subcontinent during the early Paleogene. Bulletin de la Société Géologique de France 23:684–695.

Sahni, A. and V.P. Mishra. 1975. Lower Tertiary vertebrates from western India. Monographs of the Paleontological Society of India 3:1–48.

Scanlon, J.D. 1993. Madtsoiid snakes from the Eocene Tingamarra Fauna of eastern Queensland. Kaupia, Darmstädter Beiträge zur Naturgeschichte 3:3–8.

Schauroth, C.V. 1865. Verzeichnis der Versteinerungen im Herzoglichen Naturalienkabinett zu Coburg No. 1-4328. Coburg, Germany: Dietzsche Hofdruckerei. 265 pp.

Scheyer, T.M., T. Mörs and E. Einarsson. 2012. First record of soft-shelled turtles (Cryptodira, Trionychidae) from the Late Cretaceous of Europe. Journal of Vertebrate Paleontology 32:1027–1032.

Scheyer, T.M., E.V. Syromyatnikova and I.G. Danilov. 2017. Turtle shell bone and osteoderm histology of Mesozoic and Cenozoic stem-trionychian Adocidae and Nanhsiungchelyidae (Cryptodira: Adocusia) from Central Asia, Mongolia, and North America. Fossil Record 20:69–85.

Schleich, H.-H. 1981. Jungtertiäre Schildkröten Süddeutschlands unter besonderer Berücksichtigung der Fundstelle Sandelzhausen. Courier Forschungsinstitut Senckenberg 48:1–372.

—1985. Zur Verbreitung tertiärer und quartärer Reptilien und Amphibien. I. Süddeutschland. Münchner Geowissenschaftliche Abhandlungen, Series A: Geologie und Paläontologie 4:67–149.

—1986. Neue Reptilienfunde im Tertiär Deutschlands: 6. Schildkröten- und Krokodilreste aus dem Braunkohlentagebau Gombeth bei Borken (Hessen). Lippischen Mitteilungen aus Geschichte und Landeskunde 55:281–288.

—1988. Eozäne Schildkrötenreste (Reptilia, Testudines) von St. Pankraz am Haunsberg (Österreich). Studia Geologica Salmanticensia, Volume Especial 3:165–184.

—1994. Neue Reptilienfunde aus dem Tertiär Deutschlands. 13. Schildkröten- und Krokodilreste aus der eozänen Braunkohle des Untertagebaues Stolzenbach bei Borken (Hessen). Courier Forschungsinstitut Senckenberg 173:79–101.

Schmidt, K.P. 1945. A new turtle from the Paleocene of Colorado. Fieldiana Geology 10:1–4.

Shebzukhova, E.A. and K.K. Tarasenko. 2007. [New findings of *Trionyx khosatzkyi* from the Middle Sarmatian sediments in the Belaya River]. Bulletin of Adyghe State University, Natural-Mathematical and Technical Sciences Series 2007:1–2. [in Russian]

Shuvalov, V.F. and V.M. Chkhikvadze. 1975. [New data on the Late Cretaceous turtles of south Mongolia]. Trudy Sovmestnoy Sovetsko-Mongolskoy Paleontologicheskoy Ekspeditsii 2:214–229. [in Russian]

—1979. [On the stratigraphic and systematic position of some freshwater turtles from new Cretaceous localities in Mongolia]. Trudy Sovmestnoy Sovetsko-Mongolskoy Paleontologicheskoy Ekspeditsii 8:58–76. [in Russian]

Simionescu, I. 1930. Vertebratele Pliocene de la Măluşteni (Covurlui). Publicaţiunile Fondului Vasile Adamachi 9:83–151.

Sismonda, A. 1836. Découverte d'une *Trionix* et d'un crustacé aux collines de Saint-Etienne Poevo, Province d'Alva. Bulletin de la Société Géologique de France 7:207.

—1839. Notizie intorno a due fossili trovati nei colli di San Stefano Roero. Memorie della Reale Accademia delle Scienze di Torino 1:85–90.

Smith, T., K. Kumar, R.S. Rana, A. Folie, F. Solé, C. Noiret, T. Steeman, A. Sahni and K.D. Rose. 2016. New early Eocene vertebrate assemblage from western India reveals a mixed fauna of European and Gondwana affinities. Geoscience Frontiers 7:969–1001.

Smith, T., F. Quesnel, G. de Plöeg, D. De Franceschi, G. Métais, E. De Bast, F. Solé, et al. 2014. First Clarkforkian equivalent Land Mammal Age in the latest Paleocene basal Sparnacian facies of Europe: fauna, flora, paleoenvironment and (bio)stratigraphy. PLoS ONE 9:e86229. doi: 10.1371/journal.pone.0086229.

Sochava, A.V. 1975. [Stratigraphy and lithology of the Upper Cretaceous deposits of southern Mongolia]. Trudy Sovmestnoy Sovetsko-Mongolskoy Nauchno-Issledovatelskoy Geologicheskoy Ekspeditsii 13:113–182. [in Russian]

Souza Torres, A. 1947. Um *Trionyx* do Tortoniano portugués. Las Ciencias 12:535–537.

Srivastava, R. and R. Patnaik. 2002. Large soft-shelled turtles from the Upper Pliocene rocks of Saketi (district, Sirmaur), Himachal Pradesh, India. Journal of the Palaeontological Society of India 47:65–76.

Staesche, K. 1975. Die Schildkrötenreste der türkischen Fundstellen. Geologisches Jahrbuch, Series B 15:117–118.

Staesche, K., H.-V. Karl and U. Staesche. 2007. Fossile Schildkröten aus der Türkei. Geologisches Jahrbuch, Series B 98:91–149.

Sterli, J. 2015. A review of the fossil record of Gondwanan turtles of the clade *Meiolaniformes*. Bulletin of the Peabody Museum of Natural History 56:21–45.

Stojanov, A. 2009. Erster Nachweis einer Riesenlandschildkröte (*Geochelone* s.l. Gray, 1872) aus Bulgarien. Revue de Paléobiologie 28:457–470.

Stur, D. 1874. *Trionyx* und andere Petrefakten aus der Braunkohle von Klösterle. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt 1874:225–226.

Sukhanov, V.B. 2000. Mesozoic turtles of Middle and Central Asia. In: M.J. Benton, M.A. Shishkin, D.M. Unwin and E.N. Kurochkin, eds. The Age of Dinosaurs in Russia and Mongolia. Cambridge: Cambridge University Press. pp. 309–367.

Suzuki, S. and P. Narmandakh. 2004. Change of the Cretaceous turtle faunas in Mongolia. Hayashibara Museum of Natural Sciences Research Bulletin 2:7–14.

Swinton, W.E. 1926. Fossil Reptilia. Geological Survey of Uganda Occasional Papers 2:37–44.

Szalai, T. 1934. Die fossilen Schildkröten Ungarns. Folia Zoologica et Hydrobiologica 6:97–142.

Tao, H. 1986. Report of a new fossil soft-shelled turtle, *Trionyx liupani* from Taiwan, with comparative study to the living species, *Trionyx sinensis* (Wiegmann). Journal of the Taiwan Museum 39:21–41.

Taskavak, E., M.J. Reimann and W.N. Polder. 1999. First record of the Nile soft-shelled Turtle, *Trionyx triunguis*, from Kos Island, Greece, with comments on its occurrence in the eastern Mediterranean. Chelonian Conservation and Biology 3:510–512.

Teppner, W. 1913. Südsteirische *Trionyx*-Reste im Kärntner Landesmuseum in Klagenfurt. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt 1913:322–332.

—1914a. Fossile Schildkrötenreste von Göriach in Steiermark. Mitteilungen des naturwissenschaftlichen Vereins für Steiermark 50:95–98.

—1914b. *Trionyx pliocenicus* Lawley = *Trionyx Hilberi* R. Hoernes. Centralblatt für Mineralogie, Geologie und Paläontologie 1914:29–31.

—1914c. Zur phylogenetischen Entwicklung der 'protriunguiden Trionychiden' des Tertiärs und *Trionyx petersi* var. *trifailensis* nov. var. aus dem Miozän von Trifail in Steiermark. Centralblatt für Mineralogie, Geologie und Paläontologie 1914:628–638.

Thomas, H., S. Sen, M. Khan, B. Battail and G. Ligabue. 1982. The lower Miocene of As Sarrar (Eastern Province, Saudi Arabia). Atlal 5:109–136.

Thomas, H., S. Sen and G. Ligabue. 1980. La faune miocène de la Formation Agha Jari du Jebel Hamrin (Irak). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 83:269–287.

Thunberg, C.P. 1787. Beskrifning på Trenne Sköld-paddor. Kongliga Vetenskaps Academiens Nya Handlingar, Stockholm 8:178–180. [in Swedish]

Tong, H., L. Li and H. Ouyang. 2014. A revision of *Sinaspideretes wimani* Young & Chow, 1953 (Testudines: Cryptodira: Trionychoidae) from the Jurassic of the Sichuan Basin, China. Geological Magazine 151:600–610.

Tong, H., J. Zhang and J. Li. 2010. *Anosteira maomingensis* (Testudines: Carettochelyidae) from the Late Eocene of Maoming, Guangdong, southern China: new material and re-description. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 256:279–290.

Toula, F. 1882. Einige neue Wirbelthierreste aus der Braunkohle von Göriach bei Turnau in Steiermark. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt 1882:274–279.

Tripathi, C. 1964. A note on the geology and vertebrate fossils of Sayamalai area, Tirunelveli district, Madras. Records of the Geological Survey of India 93:257–262.

Tuna, V. 1988. The remains of a fossil soft-shelled Turtle (*Trionyx*) from Bayraktepe (Turkey). Zoology in the Middle East 2:63–67.

[TTWG] Turtle Taxonomy Working Group. 2014. Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. Chelonian Research Monographs 5:329–479.

Vang-Lauridsen, H. 1998: Tertiary Trionychidae (Reptilia; Testudines) from the Carpathian Basin [dissertation]. Copenhagen, Denmark: University of Copenhagen, 130 pp.

Vidal, L.M. and C. Depéret. 1906. Contribución al estudio del Oligoceno en Cataluña. Memorias de la Real Academia de Ciencias y Artes de Barcelona 19:1–19.

Vignaud, P., P. Duringer, H.T. Mackaye, A. Likius, C. Blondel, J.-R. Boisserie, L. de Bonis, et al. 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. Nature 418:152–155.

Vincent, G. 1875. Note sur la faune Bruxelliense des environs de Bruxelles. Annales de la Société malacologique de Belgique 10:23–32.

Vitek, N.S. 2012. Giant fossil soft-shelled turtles of North America. Palaeontologia Electronica 15:1–43.

Vitek, N.S. and I.G. Danilov. 2010. New material and a reassessment of soft-shelled turtles (Trionychidae) from the Late Cretaceous of Middle Asia and Kazakhstan. Journal of Vertebrate Paleontology 30:383–393.

—2012. New data on the soft-shelled turtles from the Upper Cretaceous Kyrkkuduk I locality of southern Kazakhstan. Proceedings of the Zoological Institute of the Russian Academy of Sciences 316:50–56.

—2013. Soft-shelled turtles (Trionychidae) from the Bissekty Formation (Upper Cretaceous: Turonian) of Uzbekistan: Skull-based taxa and probable skull-shell associations. Cretaceous Research 43:48–58.

—2014. Soft-shelled turtles (Trionychidae) from the Cenomanian of Uzbekistan. Cretaceous Research 49:1–12.

—2015. New material of *Ulutrionyx ninae* from the Oligocene of Kazakhstan, with a review of Oligocene trionychids of Asia. Journal of Vertebrate Paleontology 35:e973570. doi: 10.1080/02724634.2015.973570.

Vitek, N., I.G. Danilov, Y. Nakajima and R. Hirayama. 2017. Redescription of the skull of '*Trionyx*' *kyrgyzensis* and improved phylogenetic taxon sampling of Cretaceous and Palaeogene soft-shelled turtles (Trionychidae) of Asia, including the oldest crown trionychids. Journal of Systematic Palaeontology. doi: 10.1080/14772019.2017.1283365.

Vitek, N.S. and W.G. Joyce. 2015. A review of the fossil record of New World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 56:185–244.

Vlachos, E., I. Cerda and E. Tsoukala. 2015. The first record of a soft-shelled turtle (Testudines: Pan-Trionychidae) from southern Balkans (Pliocene, Gefira, N. Greece) and new information from bone histology. Science of Nature 102:45. doi: 10.1007/s00114-015-1295-2

Vremir, M. 2004. Fossil turtle found in Romania—overview. A Magyar Állami Földtani Intézet Évi Jelentése 2002:143–152.

—2013. An early Eocene freshwater turtle assemblage from the şimleu Basin (NW Romania): paleobiogeographic significance. Acta Musei Sabesiensis 5:597–625.

Vremir, M. and V. Codrea. 1997. A soft-shelled turtle (Testudines, Trionychidae) in the Eggenburgian of Coasta Mare (Cluj). Nymphaea, Folia Naturae Bihariae 23–25:69–76.

Vremir, M., V. Codrea and B. Farkas. 1997. *Trionyx stiriacus* Peters, 1855 (Reptilia, Testudines) from the Sarmatian (Middle Miocene) of Minişu de Sus (Romania). Annales Historico-Naturales Musei Nationalis Hungarici 89:43–52.

Walker, C.A. and R.T.J. Moody. 1974. A new trionychid turtle from the Lower Eocene of Kent. Palaeontology 17:901–907.

—1985. Redescription of *Eurycephalochelys*, a trionychid turtle from the lower Eocene of England. Bulletin of the British Museum, Geology 38:373–380.

Wang, X., Z. Qiu and N.D. Opdyke. 2003. Litho-, bio-, and magnetostratigraphy and paleoenvironment of Tunggur Formation (Middle Miocene) in central Inner Mongolia, China. American Museum Novitates 3411:1–31.

Wank, M. 1977. Fischotter- und Schildkrötenfunde im Mittelmiozän von Schönweg (Lavanttal, Kärnten). Carinthia II 167:153–156.

West, R.M., J.H. Hutchison and J. Munthe. 1991. Miocene vertebrates from the Siwalik Group, western Nepal. Journal of Vertebrate Paleontology 11:108–129.

West, R.M., J.R. Lukacs, J. Munthe Jr. and S.T. Hussain. 1978. Vertebrate fauna from Neogene Siwalik Group, Dang Valley, western Nepal. Journal of Paleontology 52: 1015–1022.

White, A.W. 2001. A new Eocene soft-shelled turtle (Trionychidae) from Murgon, south-eastern Queensland. Memoirs of the Association of Australasian Palaeontologists 25:37–43.

White, E.I. 1931. The Vertebrate Faunas of the English Eocene, Volume 1. London: British Museum (Natural History). 123 pp.

Wiegmann, A.F.A. 1835. Beiträge zur Zoologie gesammelt auf einer Reise um die Erde von Dr. F.J.F. Meyen. Siebente Abhandlung. Amphibien. Nova Acta Physico-Medica Academia Caesarea Leopoldino-Carolina 17:185–268.

Wings, O., M. Rabi, J.W. Schneider, L. Schwermann, G. Sun, C. Zhou and W.G. Joyce. 2012. An enormous Jurassic turtle bone bed from the Turpan Basin of Xinjiang, China. Naturwissenschaften 99:925–935.

Winkler, T.C. 1869a. Des tortues fossiles conservées dans le Musée Teyler et dans quelques autres Musées. Haarlem, The Netherlands: Héritiers Loosjes. 151 pp.

—1869b. Deux nouvelles tortues fossiles. Archives néerlandaises des sciences exactes et naturelles 4:342–358.

Wood, R.C. 1979. First record of a fossil trionychid skull from Africa. Herpetologica 35:360–364.

—1987. Fossil turtles from the Sahabi Formation. In: N.T. Boaz, A. El-Amauti, A.W. Gaziry, J. de Heinzelin and D. Dechant Boaz, eds. Neogene Palaeontology and Geology of Sahabi. New York: Alan R. Liss. pp. 107–112.

—2013. Fossil turtles from Lothagam. In: M.G. Leakey and J.M. Harris. Lothagam: The Dawn of Humanity in Eastern Africa. New York: Columbia University Press. pp. 115–136.

Xing, H., Y. He, L. Li and D. Xi. 2012. A review on the study of the stratigraphy, sedimentology, and paleontology of the Iren Dabasu Formation, Inner Mongolia. In: W. Dong, ed. Proceedings of the Thirteenth Annual Meeting of the Chinese Society of Vertebrate Paleontology. Beijing: China Ocean Press. pp. 1-44.

Ye, X. 1994. Fossil and Recent Turtles of China. Beijing: Science Press. 112 pp.

Yeh, H.-K. 1962. Note on two fossil trionychid turtles from Shantung and Chekiang. Vertebrata Palasiatica 6:384–389.

—1963. Fossil turtles of China. Palaeontologia Sinica, New Series C 150:1–113.

—1965. New materials of fossil turtles of Inner Mongolia. Vertebrata Palasiatica 9:47–69.

—1974. [A new fossil *Trionyx* from Fuchien]. Vertebrata Palasiatica 12:190–192. [in Chinese with English abstract]

Young, C.-C. and M.-C. Chow. 1953. [New Mesozoic reptiles from Szechuan]. Palaeontologia Sinica 1:87–110. [in Chinese with English abstract]

Zbyszewsky, G. 1949. Les vertébrés du Burdigalien supérieur de Lisbonne. Lisbon, Portugal: Services ge¥ologiques du Portugal. 77 pp.

Zhang, M. 1984. A new species of *Pelochelys* from Zhejiang, with subfossil description. Acta Herpetologica Sinica 3:71–76. [in Chinese with English summary]

Zigno, A. de. 1889. Chelonii scoperti nei terreni Cenozoici delle Prealpi Venete: Memoria. Memorie del Regio Istituto Veneto di Scienze Lettere Arti 23:119–130.

Zoboli, D. and G.L. Pillola. 2016. I rettili miocenici conservati nel Museo Sardo di Geologia e Paleontologia Domenico Lovisato (Cagliari, Italia). Museologia Scientifica 10:81–87.

—2017. Early Miocene insular vertebrates from Laerru (Sardinia, Italy): preliminary note. Rivista Italiana di Paleontologia e Stratigrafia 123:149–158.

*Editor's note:* This article is intended to be included with others in a forthcoming book being coordinated by Walter G. Joyce to elucidate the fossil record of turtles. The individual articles that will form the components of this book are being published separately in the next several volumes of the *Bulletin of the Peabody Museum of Natural History.*

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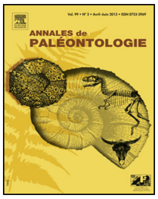

Original article

# A revision of the trionychid turtle *Procyclanorbis sardus* Portis, 1901 from the late Miocene of Sardinia (Italy)

## *Une révision de la tortue trionychidé* Procyclanorbis sardus *Portis, 1901 du Miocène supérieur de Sardaigne (Italie)*

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ABSTRACT

*Procyclanorbis sardus* Portis, 1901 is the first fossil trionychid turtle described from Sardinia. This late Miocene taxon was originally considered to have affinities with the African and southern Asian cyclanorbines. We here redescribe in detail the holotype specimen of this species, which has suffered severe degradation since its original publication. A comparison between the original state of the fossil and its current state of preservation is provided. On the basis of its anatomy, affinities of *Procyclanorbis sardus* with cyclanorbines are discarded and this taxon is demonstrated to be an indeterminate pan-trionychine. The distribution of fossil trionychids in the Mediterranean Islands is also discussed.

*Mots clés :*
*Procyclanorbis*
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Insularité

RÉSUMÉ

*Procyclanorbis sardus* Portis, 1901 est la première tortue trionychidé fossile décrite en Sardaigne. Ce taxon du Miocène supérieur a été initialement considéré comme ayant des affinités avec les cyclanorbines d'Afrique et d'Asie du Sud. Nous décrivons ici en détail et figurons l'holotype de cette espèce, qui a subi une importante dégradation depuis sa publication originale. Une comparaison entre l'état originel du fossile et son état de conservation actuel est fournie. Sur la base de son anatomie, les affinités de *Procyclanorbis sardus* avec les cyclanorbinés sont rejetées car ce taxon s'avère être un pantrionychiné indéterminé. La distribution des trionychidés fossiles dans les îles de la Méditerranée est également discutée.

## 1. Introduction

*Procyclanorbis sardus* Portis, 1901 is the first named fossil soft-shelled turtle from the island of Sardinia, Italy (Portis, 1901a). This taxon has had a problematic taxonomic history, being originally described as a European member of pan-cyclanorbines (Portis, 1901a), later considered as a member of *Amyda* (Hummel, 1929; Comaschi Caria, 1959) and subsequently treated as an indeterminate pan-trionychine (Georgalis and Joyce, 2017). We restudied in detail the holotype carapace that still exists, severely damaged, in the collections of the Museo Sardo di Geologia e Paleontologia "Domenico Lovisato", Cagliari, Italy (MDLCA), and we herein redescribe and attempt to revise this historical taxon reevaluating its taxonomic status for the first time on the basis of first hand observation and with a modern approach.

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Institutional Abbreviations: MDLCA: Museo Sardo di Geologia e Paleontologia "Domenico Lovisato", Cagliari, Italy.

## 2. Material and methods

The holotype carapace of *Procyclanorbis sardus* is curated, along with its natural mold, at MDLCA under the collection number MDLCA 14007. Other specimens (another carapace, a skull, and additional plastral elements) that were also originally referred to *P. sardus* by Portis (1901a) could not be located and we agree with Kotsakis (1985) that they were probably destroyed during World War II. The partial carapace of a trionychid, also from the type area, that was subsequently referred to *P. sardus* by Comaschi Caria (1959) is also housed in the collections of MDLCA under the number MDLCA 14008.

## 3. Geological setting

The Calcari di Cagliari Formation (Gandolfi and Porcu, 1967; Cherchi, 1974) carbonate succession is represented by three main lithofacies which are, from the bottom to top: "PietraCantone", "Tramezzario" and "Pietra Forte". Note that the names, informally adopted in the most recent official geological map (Barca et al., 2005), are derived from the names used by quarrymen.

The "Pietra Cantone" is composed of a stratified yellow marly-arenaceous limestone with common intense bioturbation. The intermediate lithofacies ("Tramezzario") is represented by whitish calcarenites, is locally marly and bears abundant bioclastic components, and shows widespread phenomena of synsedimentary breccias, slumpings, erosional surfaces and faulting. The "Pietra Forte" represents mainly the top of the succession and consists of massive coarse bioclastic (mainly rodalgal-mollusc) biostromallimestones [for further details on lithology and facies distribution see Barca et al. (2005)].

The Calcari di Cagliari Formation is considered to be late Miocene in age (Kotsakis, 1985; Zoboli and Pillola, 2016). The Tortonian/Messinian boundary is tentatively placed within the upper part of the "Pietra Cantone" (Cherchi A., personal communication, 2016).

The holotype carapace with its internal mold, as also the referred skull and plastral elements described by Portis (1901a) and now lost, as also the referred carapace imprint described by Comaschi Caria (1959), were all found in the Is Mirrionis area in Cagliari. The associated reptile fauna from Is Mirrionis consists only of the type material of the crocodylian *Tomistoma calaritanum* Capellini, 1890.

The entire area of Is Mirrionis and the adjacent Tuvixeddu and Tuvumannu hills and Sant'Avendrace, currently inhabited but with several outcrops and sections still cropping-out, was intensively quarried for building materials since historical times. The studied material originates, in most likelihood, from the lower "Tramezzario" facies; therefore, we tentatively assign a Messinian age to these remains.

## 4. Historical background

Portis (1901a) originally established the new species *Procyclanorbis sardus* on the basis of an incomplete carapace and its mold from the late Miocene of Is Mirrionis, Cagliari and Sardinia. The same author additionally referred to the same species a rather complete but crushed skull and two plastral fragments from the same locality, as also another, partial carapace from the late Miocene of Sassari, near Nulvi, northern Sardinia (Portis, 1901a). On the basis of all this material, and mostly the morphology of the nuchal and the costals, Portis (1901a) considered *Procyclanorbis sardus* to be the first European member of *Pan-Cyclanorbinae*, a clade that has extant representatives only in Africa and southern Asia, and, at that time, a poor fossil record confined to few finds in the Indian subcontinent (Lydekker, 1885, 1889). Portis (1901a) also envisaged similarities of his new Sardinian pan-trionychid with certain Central European finds, more specifically with *Trionyx gergensi* Reinach von, 1900 from the early Miocene of Germany and *Trionyx preschenensis* Laube, 1900 from the early Miocene of the Czech Republic. He furthermore considered this resemblance as adequate enough to suggest congeneric affinities between the Sardinian, German and Czech specimens, therefore recombining both *T. gergensi* and *T. preschenensis* into his new genus *Procyclanorbis*, and thereby treating them as the northernmost occurrences of pan-cyclanorbines known to that date (Portis, 1901a).

Since then, only few mentions of *Procyclanorbis sardus* have occurred in the chelonian literature. Furthermore, besides sporadic simple mentions of just the name (e.g. Bergounioux, 1954; Kotsakis and Palombo, 1979; Comaschi Caria, 1986; Kotsakis, 1989; Karl, 1999), only few authors have dealt with the taxonomic affinities of the Sardinian taxon. Fucini (1912) was the first to express doubts on the validity of the genus *Procyclanorbis* and stated that *P. sardus* could only be differentiated from *Trionyx pliocenicus* Fucini, 1912 from the Pliocene of Tuscany, Italy, on the basis of minor morphological characters. Few years later, Hummel (1929, 1932) defied Portis's (1901a) original identification of the Sardinian material as a cyclanorbine and he rather included it into *Amyda*, recombining it as *Trionyx* (*Amyda*) *sardus*. Such subgeneric assignment was a common practice for most European fossil trionychids according to Hummel (1929), who erroneously also referred *Trionyx triunguis* to *Amyda*. Bergounioux (1935) mentioned the presence of the otherwise Czech taxon *Trionyx pontanus* Laube, 1895, in the Miocene of Sardinia without providing any other information, but it is now believed that this is rather an error, and that this author intended to mean instead *Trionyx sardus* (Georgalis and Joyce, 2017). In the same paper, Bergounioux (1935) mentioned that *P. sardus* was also known from Switzerland, again most probably an error. Comaschi Caria (1959) later described new trionychid remains from the Miocene of Sardinia. The new finds originated from the Miocene localities of Is Mirrionis (type locality of *P. sardus*) and Sant'Avendrace, with the author assigning them to *P. sardus* and the Oligocene French taxon *Trionyx burdigalensis* Bergounioux, 1935, respectively, but treating both species as members of *Amyda* (Comaschi Caria, 1959). Few years later, in his compendium, Kuhn (1964) continued to treat *P. sardus* as a pan-trionychine and a member of *Trionyx*. Broin (1977) made a brief mention of *P. sardus* stating that the referred skull that was originally described by Portis (1901a) belonged in fact to a cheloniid marine turtle. In his review of the Italian trionychids, Kotsakis (1985) followed the opinion of Broin (1977) that the referred skull does not belong to trionychids, further mentioning that this specimen was probably lost (destroyed during the World War II), and he tentatively treated all Miocene finds from Sardinia as pertaining to one species, *P. sardus*, which he considered as a member of *Trionyx*. Delfino (2002) followed Kotsakis (1985) and reported *P. sardus* as a tentative valid species of *Trionyx*. Chesi (2009) also considered *P. sardus* as a member of *Trionyx* but noted that the validity of this taxon should be tested using a modern systematic approach. He further described new Sardinian finds from the early Miocene locality of Noragugume, which he treated as an indeterminate pan-trionychid (Chesi, 2009). In their review of the Miocene reptiles housed at the MDLCA, Zoboli and Pillola (2016) mentioned *P. sardus* and provided a new figure of the actual preservation state of the holotype specimen. They additionally showed that the carapace referred to *T. burdigalensis* by Comaschi Caria (1959) is in fact a cheloniid, and this specimen is not located in a museum, but is a walled part of a fountain in Sant'Avendrace (Cagliari). In their overview of all Old World fossil pan-trionychids, Georgalis and Joyce (2017) briefly discussed the status of *P. sardus* on the basis of its published descriptions. They considered that the referred skull and plastral elements belong in fact to cheloniids, whereas the holotype carapace and the other two referred carapaces of Portis (1901a) and Comaschi Caria (1959) represent indeterminate pan-trionychines. As such, *Procyclanorbis sardus* was considered to be a nomen dubium (Georgalis and Joyce, 2017).

## 5. Systematic paleontology

Class: Reptilia Laurenti, 1768
Order: Testudines Batsch, 1788
Family: Trionychidae Gray, 1825
Sub-Family: Pan-Trionychinae Georgalis and Joyce, 2017

**Pan-Trionychinae indet.** (Figs. 1–3)
Synonymy:
1901a *Procyclanorbis sardus* Portis: Plate 1 Plate 1.
1912 *Procyclanorbis sardus* Portis: Fucini, 1912, p. 3.
1929 *Trionyx sardus* Portis: Hummel, 1929, p. 25.
1954 *Procyclanorbis sardus* Portis: Bergounioux, 1954, p. 191.
1959 *Amyda sardus* Portis: Comaschi Caria, 1959, p. 38.
1977 *Procyclanorbis sardus* Portis: Broin 1977, p. 191.
1979 *Procyclanorbis sardus* Portis: Kotsakis and Palombo, 1979, p. 624.
1983 *Trionyx sardus* Portis: Esu and Kotsakis, 1983, p. 198.
1986 *Amyda sarda* Portis: Comaschi Caria, 1986, p. 29.

**Description of the holotype:**

Portis (1901a) described both the carapace and its internal mold, but figured only the former specimen. Judging from the published figure (Fig. 1) and the current preservation state of this specimen (Fig. 2), it seems that it has suffered a lot of damage since its original description. Indeed, the carapace is much better preserved in Plate 1.1 of Portis (1901a), while currently the posterior half of the specimen is almost totally missing. Such damage was probably caused during the World War II, although Portis (1901a) already mentioned that the whole turtle material from Is Mirrionis had suffered damage during the transport from Cagliari to Turin, where the author was based at that time.

Judging from the published figure and the original description, where the specimen appears more complete (Fig. 1a), it seems that the holotype pertains to a medium-sized trionychid, with a carapace length of about 45 cm. The margins of the carapace, however, are universally not preserved. Especially, the latter margin is severely deformed, rendering the size of last costals ambiguous. There is no preneural. The nuchal is rather enlarged and sits anterior to the disc formed by the costals. There are seven neurals. The first two neurals are large and elongated, especially neural I which is also relatively wide. It is not possible to determine whether there is a reversal in the neural orientation, as is the typical condition

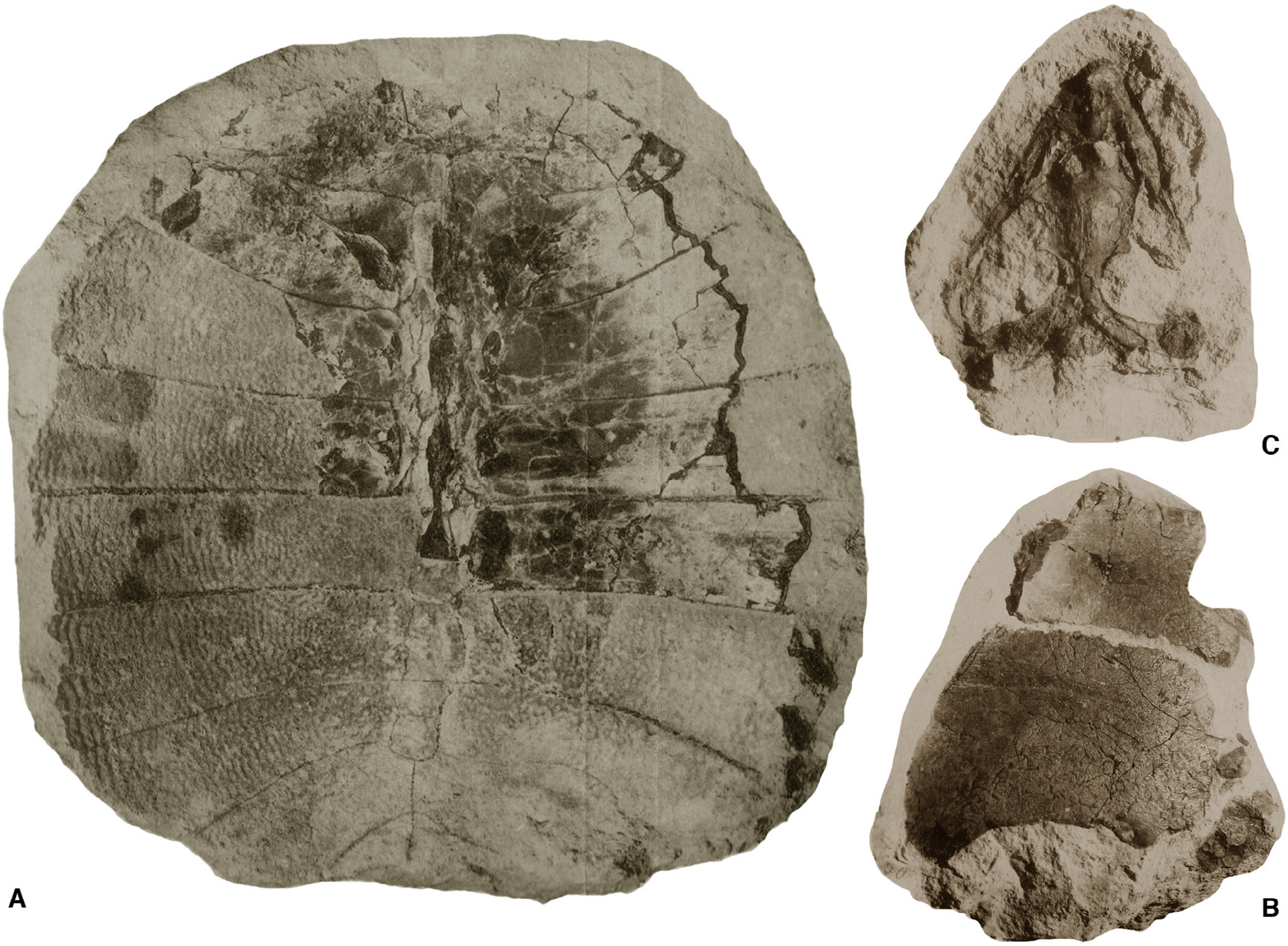

**Fig. 1.** The original plate of Portis (1901a) with the holotype carapace of *Procyclanorbis sardus* and the referred plastral and cranial material. **A**. The holotype carapace. **B**. The now lost partial left hyo-hypoplastron (now identified as a probable cheloniid). **C**. The now lost skull (now identified as a probable cheloniid).
*Planche originale de Portis (1901a) avec l'holotype de Procyclanorbis sardus (Carapace) et le matériel référé (plastron et crâne). **A**. Carapace, holotype. **B**. Hyo-hypoplastron gauche aujourd'hui perdu (maintenant identifié comme un chéloniidé probable). **C**. Crâne aujourd'hui perdu (maintenant identifié comme un chéloniidé probable).*

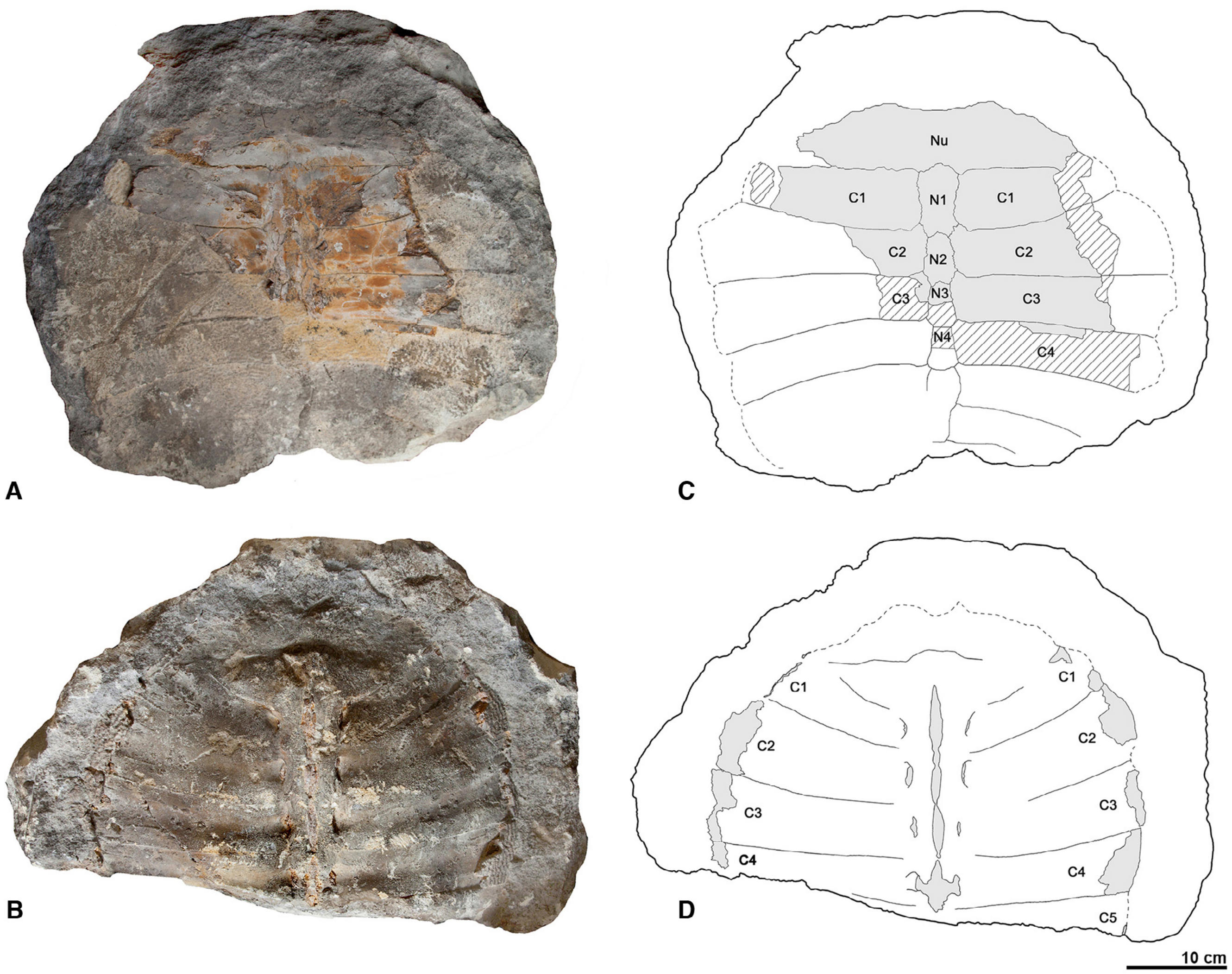

**Fig. 2.** The current state of preservation of the holotype partial carapace (MDLCA 14007) of *Procyclanorbis sardus* (**A**, **C**) and its imprint (**B**, **D**). Abbreviations: Nu–nuchal, N1–N4–neurals I–IV, C1–C5–costals I–V.

*État de conservation actuel de l'holotype (carapace partielle) (MDLCA 14007) de Procyclanorbis sardus* (***A, C***) *et son empreinte* (***B, D***)*. Abréviations : Nu - nucale, N1–N4 - neurales I–IV, C1–C5 - costales I–V.*

for pan-trionychines (Meylan, 1987). The last neural meets at the midline costals VI and the anteriormost part of costals VII. There are eight pairs of costals. Costals are relatively large, with costals II being distally expanded, whereas costals VIII seem to be reduced and short and fully meet at the midline of the carapace. However, the reduced size of costals VIII should be taken with caution, due to the breakage at the posterior margin of the carapace. The sculpturing pattern consists of a network of ridges at the lateral margins of the carapace, whereas it slightly fades towards the center of the shell, consisting mostly of small tubercles at the neural region. The sculpturing in the nuchal region has been totally faded out and it is impossible to state the nature of that pattern at this region of the shell.

In the current and severely damaged form, only the anterior part of the carapace is preserved (Fig. 2). As such, only the nuchal, the first four neurals, the first four right and first three left costals can be observed, whereas in its natural mold, remnants of the nuchal and the first five left and four right costals are preserved (Fig. 2). Of course, the visible preserved features in the imprint should not be taken into full consideration, as they do not reliably reflect the external arrangement of the bones (Georgalis and Joyce, 2017). Indeed the size, shape and inclination of all preserved costals are radically different from those observed in the actual carapace. The sculpturing pattern is currently not well preserved, and it appears that it has severely faded out (Fig. 3).

## 6. Discussion

### 6.1. *Taxonomic identification and status of* Procyclanorbis sardus

A vast number of trionychid taxa have been named from the European Miocene, in particular from the central and southern parts of the continent (Georgalis and Joyce, 2017). The validity of the majority of these species has been recently rejected by Georgalis and Joyce (2017), who demonstrated the presence of two different pan-trionychid lineages in the European Miocene, belonging to the extant pan-trionychine genera *Rafetus* and *Trionyx*. According to these authors, only differences in the number and extent of sculpturing callosities on the plastron is a reliable character for discriminating fossils of these two lineages based on shell material, and minor carapacial characters among *Rafetus* and *Trionyx*, such as differences in the size of the last costals, should be better considered tentative and variable. Furthermore, the presence of pan-cyclanorbines in the European fossil record was recently discarded, as the European purported member of this clade, *Trionyx*

**Fig. 3.** A close up of the sculpturing pattern of MDLCA 14007 (holotype of *Procyclanorbis sardus*).
*Vue rapprochée sur l'ornementation de la carapace MDLCA 14007 (holotype de* Procyclanorbis sardus*).*

*melitensis* Lydekker, 1891, from the Miocene of Malta, was shown to be in fact a cheloniid (Georgalis and Joyce, 2017; see below). Therefore, only material containing plastral elements could be adequately assigned to either *Rafetus* or *Trionyx*. The identification of the now lost partial hyo-hypoplastron referred to *P. sardus* by Portis (1901a) as a probable cheloniid (see below), leaves the Sardinian form as a carapace based only taxon. For this reason, in addition with the incomplete nature of the holotype, *P. sardus* has to be considered to be a nomen dubium, pertaining an indeterminate pan-trionychine.

Portis (1901a) envisaged his new species *Procyclanorbis sardus* as pertaining to cyclanorbines. He noted strong resemblance with the extant African cyclanorbine genera *Cyclanorbis* and *Cycloderma*, whereas among extinct taxa, *Procyclanorbis sardus* was most similar with *Trionyx gergensi* and *T. preschenensis*, for which he formally suggested congeneric affinities with his new Sardinian form (Portis, 1901a). However, all such affinities were proposed on the basis of highly variable characters, such as the sculpturing pattern and the shape and size of costals and neurals (Meylan, 1987; Vitek and Joyce, 2015). Furthermore, the type carapace of *P. sardus* can be readily excluded from *Pan-Cyclanorbinae* by the absence of a preneural and the lack of split costiform processes on the nuchal (Meylan, 1987). Additionally, the carapacial sculpturing of *P. sardus* is not so prominent as that of extant cyclanorbines. Furthermore, the suggestion of Hummel (1929, 1932) and Comaschi Caria (1959) that the Sardinian taxon belongs to *Amyda*, is also attributed to highly homoplastic and variable characters and the latter genus should be confined only to Asian forms. In particular, judging from the carapace morphology, it seems most probable that *P. sardus* belongs to the same lineage with trionychines, although the absence of plastral material prevents any definite conclusion. Exact affinities with the three valid pan-trionychid taxa from the Neogene of Europe, *Rafetus bohemicus* (Liebus, 1930), from the Miocene of the Czech Republic, *Trionyx vindobonensis* Peters, 1855, from the Miocene of central and western Europe, and *Trionyx pliocenicus* Fucini, 1912, from the Pliocene of Italy, cannot be made with certainty due to the absence of plastral material for the Sardinian taxon. As was stated above, the holotype carapace of *P. sardus* seems to bear rather small costals VIII, a common feature of the *Rafetus* lineage. However, the damaging of the posterior margins of the carapace hinders the exact shape and size of these elements, and we are therefore reluctant to make any generic assignment of the Sardinian form. As such, the fact that there is no reliable plastral material, in addition with the incomplete nature of the holotype and its unfortunate subsequent severe damaging, prompt us to consider *Procyclanorbis sardus* to be a nomen dubium.

Regarding the skull that was originally referred to *Procyclanorbis sardus* by Portis (1901a), this specimen is now lost, but it was at least figured. Broin (1977) and subsequently Esu and Kotsakis (1983) and Kotsakis (1985) considered that this specimen does not belong to pan-trionychids, but instead it has cheloniid affinities. Indeed, judging from the published image of this specimen (Fig. 1c), it seems that the skull did not belong to pan-trionychids: its basicranium appears to be extremely slender (and not broad as in most pan-trionychids) and possibly also, prepalatine foramina are present (which are totally absent in pan-trionychids).

The plastral fragments that were originally referred by Portis (1901a) to *Procyclanorbis sardus* correspond to a partial left hyo-hypoplastron. This material is also lost, probably during the World War II. In any case, judging from the published figure of the original publication (Fig. 1b), and the shape and the size of the hyo-hypoplastron, it seems that these elements also pertain to a marine turtle. Indeed, even in the original description, Portis (1901a) admitted that at first glance this plastral material seemed to pertain to a cheloniid, but after his subsequent study he denoted strong resemblance with the plastron of the extant African cyclanorbines *Cyclanorbis* and *Cycloderma*. Pan-cyclanorbine hyo-hypoplastra are characterized by their fusion soon after hatchling (Meylan, 1987). Portis (1901a) also stated the presence of sculpturing on the hyo-hypoplastron, though this character could not be evaluated in the accompanying image of the specimen. On the basis of the only existing and poor quality figure, the plastral elements referred to *P. sardus* seem to have stronger resemblance to cheloniids rather than that of any pan-trionychid.

As for the putative, now lost, carapace from Sassari, Portis (1901a) only briefly described this specimen, without figuring it, stating that this specimen was smaller than the holotype and apparently pertained to a younger individual. Fortunately, however, the partial carapace imprint from the type locality described by Comaschi Caria (1959) as referable to *P. sardus* is still located in the collections of MDLCA under the accession number 14008. However, this specimen also has suffered severe degradation since its original description (Fig. 4). Although it was initially an almost complete imprint of a carapace, missing only its upper right and lower margins of the shell, in its current state of preservation, large parts of the carapace imprint are missing and the edges of most costals have faded. We consider this specimen as well to be an indeterminate pan-trionychine, on the basis of the absence of peripherals and shell scutes.

### 6.2. Trionychids *from the Mediterranean Islands*

As evidenced by the fossil record, soft-shelled turtles variously occurred in the Mediterranean islands (Georgalis and Joyce, 2017). This clade has no extant representatives in the Mediterranean islands, although living individuals of *Trionyx triunguis* have been repeatedly reported from the Dodecanese Islands in Greece,

**Fig. 4.** The current state of preservation of the trionychid referred to *Procyclanorbis sardus* by Comaschi Caria (1959) (MDLCA 14008).
*État de conservation actuel du trionychidé rapporté à* Procyclanorbis sardus *par* Comaschi Caria (1959) *(MDLCA 14008).*

specifically Kos, Symi, Leros, Kalymnos and Rhodes, some kilometers away from the southwestern coast of Asia Minor (Corsini-Foka and Masseti, 2008). However, these sightings of living individuals of *T. triunguis* should be better considered as random cases of marine dispersals across narrow straights of the Aegean Sea, as this species has been well documented to swim at certain marine distances from the coast (Taskavak et al., 1999). Nevertheless, most fossil finds from this region are rather fragmentary, hindering the exact taxonomic affinities of the Mediterranean Islands pan-trionychids. Such remains have been found in the Eocene of the Balearic Islands (Mallorca; Jiménez Fuentes et al., 1990) and Sardinia (Kotsakis, 1985), and the Miocene of Cyprus (Reed, 1932; Hadjisterkotis et al., 2000), Crete (Georgalis et al., 2016), Sicily (De Gregorio, 1883), and of course Sardinia. Among these, only the Miocene Sardinian and Sicilian material has been identified at the species level, with the two supposedly endemic taxa *Procyclanorbis sardus* and *Trionyx ragusensis* De Gregorio, 1883, respectively. The latter occurrence is rather problematic, as the only known specimen is lost and has never been figured, and therefore, *T. ragusensis* should better be considered a nomen dubium (Georgalis and Joyce, 2017). Curiously, pan-trionychids are totally absent from the well-known Miocene faunas of the Aegean Islands (Georgalis and Kear, 2013), with the exception of Crete, from where they were only recently described (Georgalis et al., 2016). Additionally, their total absence from Corsica seems bizarre, as pan-trionychids are abundant in the late Paleogene and Neogene of southern France and northwestern and central western Italy (e.g. Portis, 1879, 1883; Ristori, 1895; Bergounioux, 1933). The case of Malta is intriguing, as from that island, Lydekker (1891) established *Trionyx melitensis*, a purported trionychid that was either assigned to cyclanorbines (Lapparent de Broin and Van Dijk, 1999), *Trionyx* sensu lato (Kotsakis, 1985), or the Asian *Nilssonia* lineage (Hummel, 1929). However, Georgalis and Joyce (2017) recently showed that the holotype and only known specimen of *T. melitensis* pertains to a cheloniid, and more specifically to *Trachyaspis* or a *Trachyaspis*-like genus, a marine turtle that is characterized by a distinctive sculpturing pattern. Other purported occurrences of fossil trionychids from Malta (Gulia, 1843; Cooke, 1890) most probably pertain to the same individual, the holotype of *T. melitensis* (Zammit-Maempel, 1979). Accordingly, the holotype of *P. sardus* remains the most complete fossil pan-trionychid specimen from the Mediterranean Islands.

Of course the paleogeography of the Mediterranean Islands was totally different during the Paleogene and the Neogene, with certain islands either connected with the European and African mainland or emerging only more recently (Esu and Kotsakis, 1983; Rögl, 1999). This fact inevitably hinders our understanding of the Mediterranean Islands trionychids, and it cannot be known with certainty if they represent indeed insular forms or are simply representatives of continental taxa. The scarceness of fossil trionychids from North Africa (Georgalis and Joyce, 2017) also hampers this situation, although few complete finds clearly denote the presence of the *Trionyx triunguis* lineage already in that region (Wood, 1987). In the case of Sardinia and *Procyclanorbis sardus*, during the Tortonian–Messinian the Sardo-Corsican Massif and the Tuscany area formed an archipelago of islands, isolated from continental Europe (Casanovas-Vilar et al., 2011). This insular paleobioprovince comprised a highly unique island vertebrate fauna, as it is testified by fossils recovered from the Fiume Santo locality (Portotorres, northwestern Sardinia), which include the primate *Oreopithecus* and several peculiar bovids and rodents (Abbazzi et al., 2008b). Consequently, we suggest that *P. sardus* was an insular taxon. Subsequently, the Sardinia-Corsica area was isolated from Tuscany by the mid–late Messinian due to the opening of the Tyrrhenian Sea (Palombo, 2009).

## 7. Conclusions

The holotype shell of *Procyclanorbis sardus* Portis, 1901a, is described herein and the taxonomic status of this species is reevaluated. New and detailed figures of the holotype (including interpretative drawings), which has suffered severe damaging since its original description, are provided. Affinities of *P. sardus* with cyclanorbines are discarded on the basis of its shell anatomy, and the Sardinian taxon clearly belongs to trionychines. However, a referral to either *Rafetus* or *Trionyx*, the trionychine lineages that are present in the Miocene of Europe, is currently not possible. The skull and the hyo-hypoplastron that were originally referred to *P. sardus* by Portis (1901a), belong in fact to cheloniid turtles. *Procyclanorbis sardus* is considered to be an indeterminate pan-trionychine and the name is considered a nomen dubium. However, even if it does not bear distinctive diagnostic features, the holotype specimen of *P. sardus* represents the best-preserved trionychid fossil from the Mediterranean Islands.

Despite a conspicuous fossil record (Delfino, 2002; Chesi et al., 2007; Chesi, 2009), the only valid turtle species from Sardinia is therefore *Testudo pecorinii* Delfino, 2008 that was described on the basis of a complete shell from the Early Pleistocene of the D4 local fauna of Capo Mannu (Abbazzi et al., 2008a). The status of nomen dubium for the trionychid turtle *Procyclanorbis sardus* Portis, 1901a follows that of *Palaeopython sardus* Portis, 1901, whose holotype was originally referred to a pythonid snake (Portis, 1901b), but that is in fact an indeterminate acanthomorphan fish (Delfino et al., 2014). Similarly, we planned the revision of *Tomistoma calaritanum* Capellini, 1890, because is not clear if this species, originally described in two papers published in the same year (Capellini, 1890a, b) is valid or not (see Kotsakis et al., 2004, and Piras et al., 2007, and literature therein) and the type was severely damaged during the World War II, and therefore few morphological characters are left for its revision. The revision of type materials and the retrieval of new remains from the type or neighboring localities [not always possible but very useful; see Zoboli et al. (2016) for a recent example concerning a Sardinian monkey] is mandatory to reassess the validity of taxa that were erected in the late nineteenth or early twentieth century by enthusiastic paleontologists that knew very well the literature, but had little direct familiarity with the morphology and variation of extant and extinct reptiles (Delfino et al., 2014).

## Disclosure of interest

The authors declare that they have no competing interest.

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## References

Abbazzi, L., Carboni, S., Delfino, M., Gallai, G., Lecca, L., Rook, L., 2008a. Fossil vertebrates (Mammalia and Reptilia) from Capo Mannu (Late Pliocene, Western Sardinia, Italy) with description of a new *Testudo* (Chelonii Testudinidae) species. Rivista Italiana di Paleontologia e Stratigrafia 114, 119–132.

Abbazzi, A., Delfino, M., Gallai, G., Trebini, L., Rook, L., 2008b. New data on the vertebrate assemblage of Fiume Santo (North-West Sardinia Italy) and overview on the Late Miocene Tusco-Sardinian palaeobioprovince. Palaeontology 52, 251–425.

Barca, S., Melis, E., Annino, E., Cincotti, F., Ulzega, A., Orrù, P., Pintus, C., 2005. Note Illustrative della Carta Geologica d'Italia alla scala 1:50.000. In: Foglio 557 "Cagliari". Servizio Geologico d'Italia, Regione Autonoma della Sardegna, S.EL.CA, Firenze.

Bergounioux, F.M., 1933. Monographie paléontologique de la faune de vertébrés des sables de Montpellier 2. Chéloniens fossiles des sables Pliocènes astiens de Montpellier. Travaux du Laboratoire de Géologie de la Faculté des sciences de Lyon 23, 1–32.

Bergounioux, F.M., 1935. Contribution à l'étude paléontologique des chéloniens: chéloniens fossiles du bassin d'Aquitaine. Mémoires de la Société Géologique de France 25, 1–215.

Bergounioux, F.M., 1954. Les chéloniens fossiles des terrains tertiaires de la Vénétie. Memorie degli Istituti di geologia e mineralogia del l'Università di Padova 18, 1–115.

Broin, F. de, 1977. Contribution à l'étude des Chéloniens : Chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum National d'Histoire Naturelle, Série C, 38., pp. 1–366.

Capellini, G., 1890a. Sul coccodrilliano garialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel 1868. Rendiconti della Reale Accademia dei Lincei, serie 4 6, 149–151.

Capellini, G., 1890b. Sul coccodrilliano garialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel MDCCCLXVIII. Atti della Reale Accademia Lincei, Memorie della Classe di Scienze Fisiche. Matematiche e Naturali, serie 4 6, 507–533.

Casanovas-Vilar, I., Dam, J.A., van, Trebini, L., Rook, L., 2011. The rodents from the Late Miocene *Oreopithecus*-bearing site of Fiume Santo (Sardinia, Italy). Geobios 44, 173–187.

Cherchi, A., 1974. Appunti biostratigrafici sul Miocene della Sardegna (Italia) , Actes V Congrès du Néogene Méditerranée Lyon 1971. Mémoire du Bureau de Recherches Géologiques et Minières 78, pp. 433–445.

Chesi, F., (PhD dissertation) 2009. Il registro fossile italiano dei cheloni. Università di Firenze, Florence (Unpublished).

Chesi, F., Delfino, M., Abbazzi, L., Carboni, S., Lecca, L., Rook, L., 2007. New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia Testudines) in the Central Mediterranean. Rivista Italiana di Paleontologia e Stratigrafia 113, 287–297.

Comaschi Caria, J., 1959. Nuovi resti di cheloni nel Miocene della Sardegna. Bollettino della Società Geologica Italiana 78, 37–44.

Comaschi Caria, I., 1986. Animali e piante fossili della Sardegna. (Terza edizione ampliata e con un guida breve allo studio della Paleontologia). Edizioni della Torre, Cagliari.

Cooke, J.H., 1890. Notes on the fossil reptiles of Malta. Il Naturalista Maltese 1, 18–20.

Corsini-Foka, M., Masseti, M., 2008. On the oldest record of the Nile soft-shelled turtle, *Trionyx triunguis* (Forskal, 1775), in the Eastern Aegean islands (Greece). Zoology in the Middle East 43, 108–110.

De Gregorio, A., 1883. Nuovi fossili terziari (vertebrati e invertebrati). Palermo.

Delfino, M., (PhD dissertation) 2002. Erpetofaune italiane del Neogene e del Quaternario. University of Modena and Reggio Emilia, Modena and Reggio Emilia (Unpublished).

Delfino, M., Zoboli, D., Carnevale, G., Pillola, G.L., 2014. The rediscovered holotype of *Palaeopython sardus* Portis, 1901 from the Miocene of Sardinia belongs to a fish, not a snake. Bollettino della Società Paleontologica Italiana 53, 89–92.

Esu, D., Kotsakis, T., 1983. Les vertébrés et les mollusques continentaux du Tertiaire de la Sardaigne : paléobiogéographie et biostratigraphie. Geologia Romana 22, 177–206.

Fucini, A., 1912. *Trionyx pliocenicus* Law. Paleontographia Italica 18, 1–28.

Gandolfi, R., Porcu, A., 1967. Contributo alla conoscenza delle microfacies mioceniche delle colline di Cagliari (Sardegna). Rivista Italiana di Paleontologia e Stratigrafia 73, 313–348.

Georgalis, G.L., Joyce, W.G., 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58, 115–208.

Georgalis, G.L., Kear, B.P., 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46, 299–311.

Georgalis, G.L., Villa, A., Vlachos, E., Delfino, M., 2016. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49, 433–444.

Gray, J.E., 1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. Annals of Philosophy 10, 193–217.

Gulia, G., 1843. Guscio di testuggine fossile trovato a Malta. Repertorio di Conoscenze Utile Zoologia Fossile 27, 77–78.

Hadjisterkotis, E., Kassapis, I., Klerides, N., 2000. Paleontological evidence for the presence of *Trionyx* sp. on Cyprus, with new information on living and alien species of terrapins. Newsletter, Hellenic Zoological Society 33, 8–10.

Hummel, K., 1929. Die fossilen Weichschildkröten (Trionychia): eine morphologisch-systematische und stammesgeschichtliche Studie. Geologische und Paläontologische Abhandlungen 16, 359–487.

Hummel, K., 1932. Pars 52: Trionychia fossilia. In: Quenstedt, W. (Ed.), Fossilium Catalogus. I: Animalia. W. Junk, Berlin.

Jiménez Fuentes, E., Ramos Guerrero, E., Martín De Jesús, S., Pérez Ramos, E., Mulas Alonso, E., 1990. Quelonios del Eoceno medio de Mallorca. Paleontologia i Evolució 23, 153–156.

Karl, H.V., 1999. Die Zoogeographie der känozoischen Weichschildkröte *Trionyx triunguis* Forskål, 1775 (Testudines: Trionychidae). Joannea – Geologie und Paläontologie 1, 27–60.

Kotsakis, T., 1985. Les Trionychidae (Testudinata Reptilia) fossiles de l'Italie. Bollettino della Società Paleontologica Italiana 24, 161–168.

Kotsakis, T., 1989. Late Turolian amphibians and reptiles from Brisighella (northern Italy): preliminary report. Bollettino della Societa Palaeontologica Italiana 28, 277–280.

Kotsakis, A., Delfino, M., Piras, P., 2004. Italian Cenozoic crocodilians: taxa, timing and palaeobiogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 210, 67–87.

Kotsakis, T., Palombo, M.R., 1979. Vertebrati continentali e paleogeografia della Sardegna durante il Neogene. Annales Géologiques des Pays Helléniques. Tome Hors Série 2, 621–630.

Kuhn, O., 1964. Part 107, Testudines. In: Kuhn, O. (Ed.), Fossilium Catalogus, Volume I: Animalia. W. Junk, The Hague.

Lapparent de Broin, F., Van Dijk, P.P., 1999. Chelonia from the Late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates: palaeogeographical implications. In: Whybrow, P.J., Hill, A. (Eds.), Fossil Vertebrates of Arabia. Yale University Press Yale, pp. 136–162.

Laube, G.C., 1895. Vorläufiger Bericht über Schildkrötenreste aus der böhmischen Braunkohlenformation. Verhandlungen der Geologischen Bundesanstalt 1895, 391–392.

Laube, G.C., 1900. Neue Schildkröten und Fische aus der böhmischen Braunkohlenformation. Lotos 2, 37–56.

Liebus, A., 1930. Neue Schildkröten aus den Tertiären Süsswassertonen von Preschen bei Bilin in Böhmen. Rozpravy Státního geologického ústavu Československé Republiky 4, 1–57.

Lydekker, R., 1885. Indian Tertiary and post-Tertiary Vertebrata. Siwalik and Nerbada Chelonia. Memoirs of the Geological Survey of India, 21., pp. 155–208.

Lydekker, R., 1889. Notes on Siwalik and Narbada Chelonia. Records of the Geological Survey of India 22, 56–58.

Lydekker, R., 1891. On a new species of *Trionyx* from the Miocene of Malta and a chelonian scapula from the London Clay. The Quarterly Journal of the Geological Society of London 47, 37–40.

Meylan, P.A., 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186, 1–101.

Palombo, M.R., 2009. Biochronology, paleobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. Integrative Zoology 4, 367–386.

Peters, K.F., 1855. Schildkrötenreste aus den österreichischen Tertiärablagerungen. Denkschriften der Kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe 9, 1–22.

Piras, P., Delfino, M., Del Favero, L., Kotsakis, T., 2007. Phylogenetic position of the crocodylian *Megadontosuchus arduini* (de Zigno, 1880) and tomistomine palaeobiogeography. Acta Palaeontologica Polonica 52, 315–328.

Portis, A., 1879. Di alcuni fossili terziarii del Piemonte e della Liguria appartenenti all'ordine dei chelonii. Memorie della Reale Accademia delle Scienze di Torino, serie 2, 2., pp. 113–134.

Portis, A., 1883. Nuovi chelonii fossili del Piemonte. Memorie della Reale Accademia delle Scienze di Torino, serie 2, 35., pp. 369–378.

Portis, A., 1901a. Il *Procyclanorbis sardus* Port., nuovo trionychide fossile della Sardegna. Bollettino della Società Geologica Italiana 20, 51–79.

Portis, A., 1901b. Il *Palaeopython sardus* Port. Nuovo pitonide del Miocene medio della Sardegna. Bollettino della Società Geologica Italiana 20, 247–253.

Reed, F.R.C., 1932. New Miocene faunas from Cyprus. Geological Magazine 69, 511–517.

Reinach von, A., 1900. Schildkrötenreste im Mainzer Tertiärbecken und in benachbarten ungefähr gleichaltrigen. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 28, 1–135.

Ristori, G., 1895. Cheloniani fossili di Montebamboli e Casteani. Memoria paleontologica del prof. Giuseppe Ristori. Con appendice sui Cheloniani fossili del Casino (Siena), 21. Pubblicazioni del Reale Istituto di Studi superiori in Firenze, lezione di scienze fisiche e naturale, pp. 1–104.

Rögl, F., 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologica Carpathica 50, 330–349.

Taskavak, E., Reimann, M.J., Polder, W.N., 1999. First record of the Nile soft-shelled Turtle, *Trionyx triunguis*, from Kos Island, Greece, with comments on its occurrence in the eastern Mediterranean. Chelonian Conservation and Biology 3, 510–512.

Vitek, N.S., Joyce, W.G., 2015. A review of the fossil record of New World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 56, 185–244.

Wood, R.C., 1987. Fossil turtles from the Sahabi Formation. In: Boaz, T., El-Amauti, A., Gaziry, A.W., de Heinzelin, J., Dechant Boaz, D. (Eds.), Neogene Palaeontology and Geology of Sahabi. Alan R. Liss, New York, pp. 107–112.

Zammit-Maempel, G., 1979. The Indo-Pacific affinity of some Maltese Tertiary fossils. The Central Mediterranean Naturalist 1, 1–12.

Zoboli, D., Pillola, G.L., 2016. I rettili miocenici conservati nel Museo Sardo di Geologia e Paleontologia Domenico Lovisato (Cagliari, Italia). Museologia Scientifica nuova serie 10, 81–87.

Zoboli, D., Pillola, G.L., Rook, L., 2016. New remains of *Macaca majori* Azzaroli, 1946 (Primates, Cercopithecidae) from Is Oreris (Fluminimaggiore, southwestern Sardinia). Bollettino della Società Paleontologica Italiana 55, 227–230.

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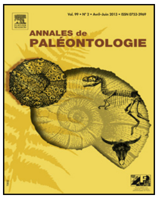

Original article

# *Necrosaurus* or *Palaeovaranus*? Appropriate nomenclature and taxonomic content of an enigmatic fossil lizard clade (Squamata)

## Necrosaurus *ou* Palaeovaranus *? Nomenclature appropriée et contenu systématique d'un clade énigmatique de lézards fossiles (Squamata)*

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ABSTRACT

*Necrosaurus cayluxi* is an enigmatic lizard from the Paleogene of the Phosphorites of Quercy, France that was first mentioned in the 19th century. Although it is generally believed that Filhol was the author who established this taxon, I am herein demonstrating that authorship should in fact be attributed to Zittel, a fact that also influences not only its generic nomenclature, but also its appropriate type material. As such, the valid name for this taxon should be *Palaeovaranus cayluxi* and its holotype is a left maxilla. Additionally, *Ophisauriscus eucarinatus* from the middle Eocene of Geiseltal, Germany, another taxon that was previously assigned to *Necrosaurus*, is herein shown to be a *nomen dubium*, whereas *Melanosauroides giganteus* from the same locality, is considered a valid species and is recombined as *Palaeovaranus giganteus* comb. nov. The suggested changes in nomenclature also affect "Necrosauridae", a poorly defined clade of lizards from the Cretaceous–Paleogene of Europe, North America, and Asia. In order to maintain nomenclatural stability and define a monophyletic lineage, I am here establishing the new family Palaeovaranidae fam. nov., which includes solely the genus *Palaeovaranus*. The known occurrences of *Palaeovaranus* across the Paleogene of Western Europe are discussed.

RÉSUMÉ

*Mots clés :*
Squamata
Paléogène
*Palaeovaranus*
*Necrosaurus*
Taxonomie

*Necrosaurus cayluxi* est un lézard énigmatique du Paléogène des Phosphorites du Quercy, France, qui a été mentionné pour la première fois au 19e siècle. Bien qu'il soit généralement admis que Filhol est l'auteur qui a établi ce taxon, je démontre ici que la paternité devrait en fait en être attribuée à Zittel, ce qui influence également non seulement la nomenclature générique, mais aussi le matériel type approprié. En tant que tel, le nom valide pour ce taxon devrait être *Palaeovaranus cayluxi* et son holotype est un maxillaire gauche. En outre, *Ophisauriscus eucarinatus* de l'Éocène Moyen de Geiseltal, Allemagne, autre taxon précédemment assigné à *Necrosaurus*, est considéré comme étant un *nomen dubium*, tandis que *Melanosauroides giganteus* de la même localité est considéré comme une espèce valable et est recombinée comme *Palaeovaranus giganteus* comb. nov. Les changements suggérés dans la nomenclature affectent également les « Necrosauridae », un clade mal défini de lézards du Crétacé–Paléogène d'Europe, d'Amérique du Nord et d'Asie. Afin de maintenir la stabilité de la nomenclature et de définir une lignée monophylétique, j'établis ici la nouvelle famille Palaeovaranidae fam. nov., qui comprend uniquement le genre *Palaeovaranus*. Les exemples connus de *Palaeovaranus* à travers le Paléogène d'Europe occidentale sont discutés.

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## 1. Introduction

The Phosphorites of Quercy ("Phosphorites du Quercy") in southern France have been known since the 19th century and have yielded a large array of fossil vertebrate finds that span stratigraphically from the early Eocene (MP 8+9) until the early Miocene (MN 3), though the majority of the respective fossiliferous localities ranges between the late middle Eocene (MP 16) and the late Oligocene (MP 28) (Rage, 2006; Rage and Augé, 2015). Among this bulk of material, the French palaeontologist Henri Filhol mentioned in a series of papers the presence of a large lizard and noted strong resemblance with modern monitor lizards (Varanidae) (Filhol, 1873, 1876, 1877a,b,c). Curiously, Filhol used a single specific epithet but three different generic names for this animal in an array of subsequent papers: *Palaeosaurus cayluxi*, *Necrosaurus cayluxi*, and *Palaeovaranus cayluxi* (Filhol, 1873, 1876, 1877a,b,c)! The genus name *Necrosaurus* is the most widely accepted one in modern literature and it is currently considered that it is not a varanid but rather represents a more distantly related form (Estes, 1983; Augé, 2005). This taxonomic view is also complemented by additional finds from the Paleogene of Europe and even a new family, Necrosauridae, was established in order to encompass them and denote their distinctiveness (Hoffstetter, 1943; Estes, 1983; Augé, 2005). However, by studying the primary literature and the 19th century papers mentioning this enigmatic reptile from Quercy, I am here demonstrating that the current nomenclature surrounding *Necrosaurus* is erroneous and that this affects also the identification of the type material and the taxonomic content of this genus.

*Institutional Abbreviations*: AMNH, American Museum of Natural History, New York, USA; BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; GMH, Geiseltalmuseum of Martin-Luther Universität Halle-Wittenberg, now referred to as the Geiseltalsammlung, housed as part of the Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle, Germany; HNHM, Hungarian Natural History Museum, Budapest, Hungary; MFGI, Magyar Földtani és Geofizikai Intézet, Budapest, Hungary; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, United Kingdom.

## 2. *Necrosaurus cayluxi* or *Palaeovaranus cayluxi*?

The first mention of a "necrosaurid" lizard was originally made by Filhol (1873) who introduced the name *Palaeosaurus cayluxi* for fossil remains from the Phosphorites of Quercy, France. In that short contribution, Filhol (1873:89) only mentioned that this animal was of large size ("un Lézard égalant l'Iguane") and that its skeletal remains resembled those of extant varanids ("une analogie remarquable avec l'ancien genre Monitor de Cuvier"), without, however, mentioning any character denoting this resemblance. In any case, the original generic name *Palaeosaurus* was already preoccupied by the, now considered indeterminate archosaur, *Palaeosaurus* Riley and Stutchbury, 1836. Three years later, Filhol (1876) provided another name, *Necrosaurus cayluxi*, for this taxon, referring also to this a fragment of a dentary ("une portion de maxillaire inférieur"), and stated again the resemblance of this taxon with extant varanids ("qui me paraissait avoir de grandes affinités, d'après les os des membres que j'avais pu étudier, avec le genre *Monitor*") (Filhol, 1876:27). The following year, in three almost identical papers, Filhol (1877a,b,c) again provided a new name, *Palaeovaranus cayluxi*, and figured the respective material (a partial dentary and a femur) for the first time (Fig. 1A). However, he still did not describe the material and only considered this lizard as having close affinities with extant varanids ("Sauriens très-voisins des Varans et des *Monitor*"), whereas at the same time he also speculated close and probable conspecific affinities with another Quercy lizard, "*Varanus*? *margaritiferus*" (an incorrect spelling of *Varanus margariticeps* Gervais, 1876, now considered an indeterminate glyptosaurine anguid [Augé, 2005]) (Filhol, 1877a,b,c).

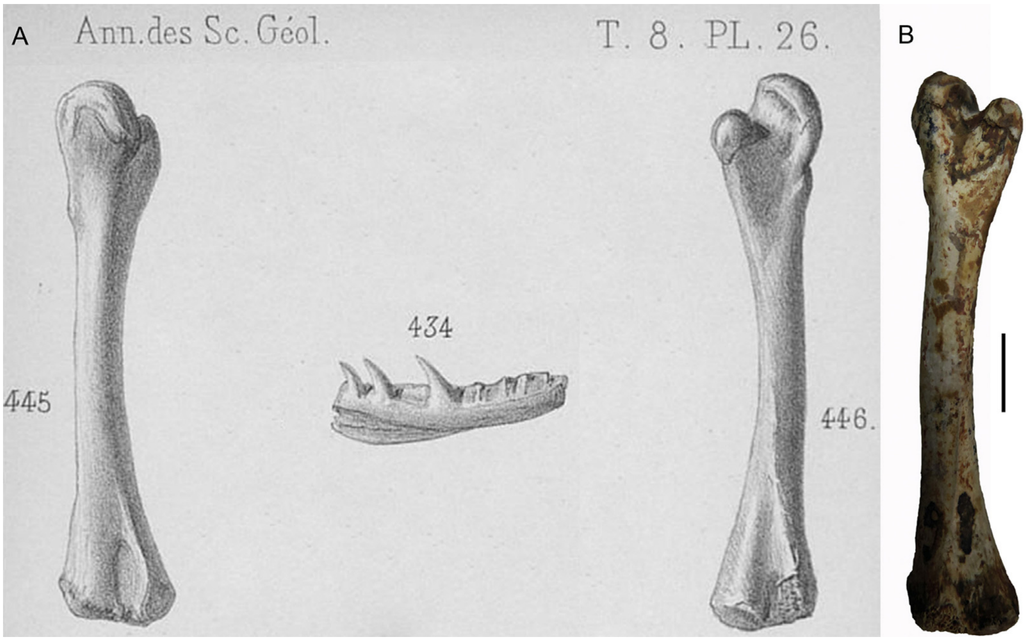

**Fig. 1.** The originally figured dentary and femur of "*Palaeovaranus cayluxi*" taken from Filhol's (1877a: plate 26) lithograph, herein referred to *Palaeovaranus* sp. (A). The same exactly lithograph was also featured in Filhol (1877b,c). Femur MNHN.F.QU17626, most probably representing the same specimen as the femur in Filhol's (1877a, b, c) lithograph (B). Scale bar = 1 cm. Photograph by G. Georgalis, courtesy of MNHN.

*Figures du dentaire et du fémur de «* Palaeovaranus cayluxi *» extraites de la planche lithographique de Filhol (1877a : planche 26), rapportés ici à* Palaeovaranus *sp. (A). La même planche lithographique a également été publiée dans Filhol (1877b,c). Fémur MNHN.F.QU17626, représentant probablement le même spécimen que le fémur dans la lithographie de Filhol (1877a,b,c) (B). Barre d'échelle = 1 cm. Photographie par G. Georgalis, autorisation de MNHN.*

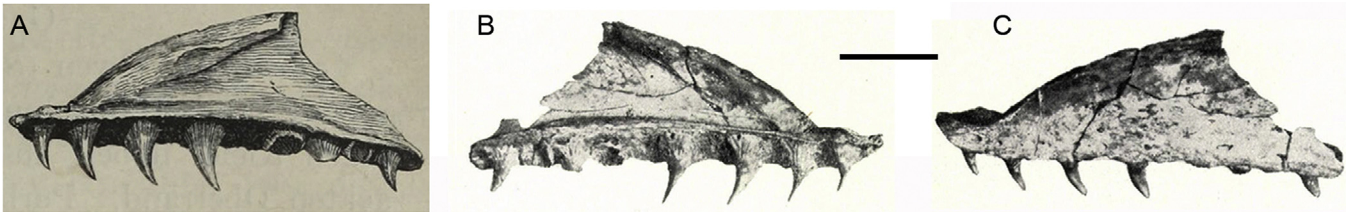

**Fig. 2.** The holotype of *Palaeovaranus cayluxi* (originally kept in BSPG, now probably lost) as being figured in the original lithograph of Zittel (1887–1890) (A) and the photograph of Fejérváry (1935) (B), (C). Note that the specimen in (A) seems like a right (and not left) maxilla, but it is in fact the reverse image, as is the common practice in lithography. (A), (B) represent the lingual view and (C) represents the labial view. Scale bar = 1 cm, adapted according to Fejérváry's (1935) measurements.

*L'holotype de* Palaeovaranus cayluxi *(initialement conservé au BSPG, probablement perdu maintenant), tel qu'il est figuré dans la lithographie originale de Zittel (1887–1890) (A) et la photographie de Fejérváry (1935) (B), (C). Noter que le spécimen en (A) semble être un maxillaire droit (et non gauche), mais c'est en fait une image inversée, pratique courante en lithographie. (A), (B) représentent la vue linguale et (C) représente la vue labiale. Barre d'échelle = 1 cm, adaptée selon les mesures de Fejérváry (1935).*

It is thus obvious, that in his first two papers, Filhol (1873, 1876) failed to provide any kind of even a brief description, definition, or indication to a previously published description, which are the minimum requirements for availability of zoological names in publications before 1931 (ICZN, 1999:Article 12.1). Indeed, the identification of a single specimen as a dentary (Filhol, 1876) or a general comment about the large size of a lizard (Filhol, 1873) cannot be considered descriptions, neither also the fact that the author constantly noted resemblance of his taxon with modern varanids. Regarding Filhol's (1877a,b,c) papers, which were the only that provided figures of the material, they still contained no description or definition. According to ICZN (1999:Article 12.2.7) though, an illustration of the material consists indeed of an indication for publications prior to 1931, and as such this could fulfill the minimum requirements of ICZN (1999) for availability of the name *Palaeovaranus cayluxi* that he suggested. However, by expressing his assumption that his taxon could probably be conspecific with *Varanus margaritiferus* (sic) and not a distinct form, Filhol (1877a, b, c) still failed also to render *Palaeovaranus cayluxi* available, as the author was uncertain about its validity, a criterion that is obligatory for ICZN (1999:Article 11.5), which clearly states that "[t]o be available, a name must be used as valid for a taxon when proposed, unless it was first published as a junior synonym and subsequently made available under the provisions of Article 11.6.1". Note also that Article 11.6.1 about availability of names originally introduced as junior synonyms, cannot apply in this case, as Filhol (1877a,b,c) did not formally render his *Palaeovaranus cayluxi* as a synonym of *Varanus margaritiferus* (sic). Therefore, all the three names created by Filhol for this animal do not fulfill the minimum requirements of ICZN (1999:Article 12.1) for availability of zoological names established prior to 1931. Accordingly, *Palaeosaurus* Filhol 1873, *Necrosaurus* Filhol 1876, *Palaeovaranus* Filhol 1877a,b,c, *Palaeosaurus cayluxi* Filhol, 1873, *Necrosaurus cayluxi* Filhol 1876, and *Palaeovaranus cayluxi* Filhol 1877a,b,c, are all nomina nuda and no attribution of these genera or the species epithet "*cayluxi*" to Filhol can be made.

Richard Lydekker further complicated the taxonomic status of this lizard, as he initially briefly mentioned that Filhol had described an imperfect mandibular ramus from the late Eocene of Quercy under the name *Palaeovaranus cayluxi* (Lydekker, 1886), whereas soon after, and during a single year, he proposed two different taxonomic opinions regarding its affinities and validity: one suggesting that *Palaeovaranus cayluxi* is a valid taxon with clear varanid affinities (Lydekker, 1888b) and one considering the former as synonymous with *Varanus* (his *Placosaurus*) *margariticeps* (Lydekker, 1888a). In his both contributions though, he rejected varanid affinities for the Filhol's (1877a,b,c) originally figured femur (Lydekker, 1888a, b). Interestingly also, Lydekker (1888a:279) described and figured additional vertebrae from Quercy housed at NHMUK, which he referred to *Placosaurus margariticeps*, but which have since been referred indeed to *Palaeovaranus cayluxi* (as *Necrosaurus cayluxi*) (Hoffstetter, 1943; Augé, 2005). Accordingly, although Lydekker (1888a) provided description of these vertebrae, authorship of *Palaeovaranus cayluxi* cannot be attributed to him, as he considered the name invalid (junior synonym of *Placosaurus margariticeps*) (ICZN, 1999:Article 11.5). In a similar way, his other same year's publication (Lydekker, 1888b) failed also to comply with the rules of ICZN (1999) for availability of names prior to 1931, as this provided no description, definition or indication. This applies also to the first mention of *Palaeovaranus cayluxi* by this author (Lydekker, 1886), as his mention that Filhol had described this taxon cannot be an indication according to ICZN (1999), due to the fact that the French author had never in fact described it. It is worth noting that at the same year with Lydekker's (1888a, b) publications, a brief mention about *Palaeovaranus cayluxi* was also made by Weithofer (1888), but this still also lacked any kind of description, definition or indication.

The first formal description that treated this species as valid was only provided by Zittel (1887–1890), who briefly described and figured a maxilla (in lingual view) from "Labenque" (an erroneous spelling for the village of Lalbenque) under the name *Palaeovaranus cayluxi* (his fig. 540; this paper, Fig. 2A). Zittel (1887–1890:609) noted again resemblance with *Varanus* and only briefly described the shape of teeth of the maxilla as strong, sharply pointed and slightly curved ("welche sich durch kräftige, scharf zugespitzte und etwas gekrümmte, an der Basis gestreifte Zähne auszeichnet"). Nevertheless, this rather brief description complies with the minimum requirements of ICZN (1999:Article 12.1) for availability of zoological names established prior to 1931 for nomenclatural purposes. Therefore, Zittel (1887–1890) was the first to make the name available for this fossil lizard from France. The same author also tentatively referred to the same taxon an axis and an anterior caudal vertebra (Zittel, 1887–1890).

The fact that Zittel was the author who made the name available remained largely unnoticed by most subsequent workers who attributed authorship to Filhol but nevertheless, until the early 1940's, they utilized the name *Palaeovaranus cayluxi* (Roger, 1898; Eastman, 1902; De Stefano, 1903, 1905; Nopcsa, 1908; Broili, 1911; Boulenger, 1918; Gilmore, 1928; Fejérváry, 1935; Kuhn, 1939a, b, 1940b; Romer, 1945), with only few exceptions (Fejérváry, 1918; Dunn, 1927). Roger (1898) made a brief mention on *Palaeovaranus cayluxi* and continued to refer the taxon to varanids. In the English translation of Zittel's great compendium, Eastman (1902) reproduced the lithograph of Zittel's (1887–1890) maxilla of *Palaeovaranus cayluxi* and mentioned it among the other then known fossil lizards from Quercy. De Stefano (1903) used the generic name *Palaeovaranus* for "*cayluxi*", and he further established another taxon of this genus, *Palaeovaranus filholi*, on the basis of abundant cranial, vertebral and appendicular material, also from Quercy. The same author continued to use the name *Palaeovaranus* on his palaeoherpetofaunal lists of Quercy in his subsequent article two years later (De Stefano, 1905). Nopcsa (1908) also used the generic name *Palaeovaranus* but challenged the specific distinction of *P. filholi* from *P. cayluxi*, although he did not formally synonymize them. Broili (1911) also used the name *Palaeovaranus cayluxi*, reproduced the original lithograph of Zittel's (1887–1890) figured maxilla, and mentioned that this taxon is the oldest member of Varanidae. A brief mention on *Palaeovaranus cayluxi* was also made by Boulenger (1918), with comments on its affinities with *Varanus margariticeps*. In his first important monograph on varanoid lizards, Fejérváry (1918) considered *P. cayluxi* as belonging to *Varanus* and he further reinstated the status of the original right femur as belonging to a varanid. He also provided a new drawing of Zittel's (1887–1890) maxilla whereas he additionally, significantly expanded the stratigraphic distribution of this taxon by tentatively referring to it material from the middle Miocene of La Grive, France (Fejérváry, 1918), which was, however, subsequently shown to pertain to a true varanid (*Varanus* cf. *hofmanni* of Hoffstetter, 1969). It seems that, for some reason, Fejérváry (1918) considered that Filhol had indeed described this taxon and that is why he attributed authorship to the French author, although in the same manuscript he admitted that Filhol made "a study of very superficial nature, not even containing a real, particular description of the fossils" [Fejérváry, 1918:350]. Following the view of Fejérváry (1918), the generic attribution of "*cayluxi*" to *Varanus* was also followed by Dunn (1927). Nevertheless, Fejérváry reassessed his initial taxonomic opinion, and in his subsequent, posthumous, large treatise on monitor lizards, he used the binomen *Palaeovaranus cayluxi* for this lizard from Quercy (Fejérváry, 1935). He described this taxon in extensive detail, provided an approximate size estimation (average total length around 1.2 m) and even a life reconstruction of the animal, and among the new material he referred to it, which comprised several dentaries, maxillae, ribs and appendicular elements, he distinguished also the original maxilla of Zittel, for which he provided the first photographs (Fejérváry, 1935) (his figs. 1, 2 on plate 10; this paper, Fig. 2B, C). He furthermore provided more detailed locality data for the respective material, mentioning that it originates from "Escamps near Lalbenque, (Dep. Lot), Quercy, Caylux (Dep. Tarn-et-Garonne), France" (Fejérváry, 1935:57), a locality that is now known to pertain to the late Eocene (MP 19) (Augé, 2005). Fejérváry (1935) also mentioned that this material of *Palaeovaranus cayluxi* that he described was labeled into the collections of BSPG under the binomen "*Palaeovaranus cadurcensis*", which is of course not an available name (ICZN, 1999:Article 12.3), and as such, should not be further taken into consideration. Gilmore (1928) briefly referred to *Palaeovaranus cayluxi* by noting the strong resemblance in tooth morphology between the Quercy taxon and his new Cretaceous North American species *Parasaniwa wyomingensis*. The same author also mentioned *Palaeovaranus* (using no species epithet) few years layer and compared the curvature of its teeth with that of his new taxon *Provaranosaurus acutus* Gilmore, 1942, from the Paleocene of Wyoming (Gilmore, 1942). Weigelt (1929) tentatively referred nineteen vertebrae from the Eocene of Geiseltal (Quarry "Cecilie I [MP 13/?14]), Germany, to *Palaeovaranus* (mentioning no species epithet), but this material was later realized by Kuhn (1939a) to belong to a booid snake (after my personal observation of this material [GMH CeI-5837-1926] I fully concur with its snake affinities). Kuhn (1939a,b, 1940b) and Romer (1945) were the last authors who treated *Palaeovaranus* as the valid generic name for this lizard, but nevertheless, they later both changed their opinion and used *Necrosaurus* as well (Romer, 1956; Kuhn, 1963), apparently influenced from the work of Hoffstetter (1943) (see below). Interestingly, Kuhn (1939a) considered that the vertebrae of *Palaeovaranus* share a rather similar morphology to those of the booid snake *Paleryx* and corrected the above-mentioned initial identification of Weigelt (1929) for the vertebrae from Geiseltal. Kuhn (1940b) also figured two additional specimens (a maxillary fragment and a partial dentary) from Quercy (his plates 9.12 and 10.5) that he referred to *Palaeovaranus cayluxi*, although he stated the possibility that they could pertain to the North American genus *Parasaniwa* Gilmore, 1928.

Judging from the above, *Palaeovaranus* was treated as the valid genus name for this taxon for the first four decades of the 20th century. However, on a rather vague statement and a misconception that Filhol's works included descriptions, the prominent squamate researcher Robert Hoffstetter suggested that the appropriate generic name for this lizard should be *Necrosaurus* and not *Palaeovaranus*. In fact, the only nomenclatural comment that Hoffstetter (1943) provided was that the initial proposed Filhol's genus name, *Palaeosaurus*, was preoccupied, and as such, the second chronologically provided Filhol's name, *Necrosaurus*, should have immediate priority. Nevertheless, Hoffstetter (1943) was the first to recognize the high distinctiveness between *Necrosaurus cayluxi* and *Varanus* spp. and he established a new family, Necrosauridae, to accommodate the former taxon. He summarized all the up to then known occurrences of "necrosaurids", and he further assigned the vertebrae figured by Lydekker (1888a) as *Placosaurus margariticeps* and a caudal vertebra previously referred to *Iguana europaea* by De Stefano (1903) to *Necrosaurus*. However, due to this nomenclatural misconception, the name *Palaeovaranus* was never again treated as valid ever since, and *Necrosaurus* was chosen as the appropriate generic name by all subsequent workers (e.g. Hoffstetter, 1954, 1955, 1962a,b, 1969; McDowell and Bogert, 1954; Romer, 1956; Hecht and Hoffstetter, 1962; Kuhn, 1963; Haubold, 1977; Meszoely et al., 1978; Rage, 1978, 1984a, b, 1988, 2013; Rage and Ford, 1980; Rieppel, 1980; Estes, 1983; Borsuk-Białynicka, 1984; Carroll, 1988; Augé, 1990a, b, 1993, 2003, 2005; Alifanov, 1993; Rage and Augé, 1993; Cifelli and Nydam, 1995; Norell and Gao, 1997; Gao and Norell, 1998; Cifelli et al., 1999; Nydam, 2000; Rieppel et al., 2007; Conrad, 2008; Conrad et al., 2008, 2011, 2014; Augé and Smith, 2009; Klembara and Green, 2010; Laurent et al., 2010; Rage and Augé, 2010, 2015; Hong-Yu and Norell, 2013; Smith and Gauthier, 2013; Smith, 2017).

Considering that the name *Necrosaurus cayluxi* was the prevailing one that has been applied to this taxon over the last seven decades, one would regard that a petition to ICZN in order to maintain that name would be the appropriate way to deal with this nomenclatural problem. However, besides the fact that the genus name *Necrosaurus* is in fact unavailable, it should be noted that among the number of papers that have mentioned the name *Necrosaurus cayluxi*, only few have in fact dealt with this taxon and included new material of it and/or descriptions or designation of differentiating characters (Hoffstetter, 1969; Rage, 1978; Estes, 1983; Augé, 2005; Augé and Smith, 2009). Furthermore, one of the most complete descriptions of this lizard remains still that of Fejérváry (1935) who used the binomen *Palaeovaranus cayluxi* and also provided detailed figures and photographs of the material. Also, the left maxilla figured by Zittel (1887–1890) and photographed also in Fejérváry (1935) provides more important taxonomic characters than Filhol's (1877a,b,c) dentary (see below). Additionally, as Zittel (1887–1890) and especially Fejérváry (1935) were more precise with giving locality data for this specimen, it seems that it most probably originates from the well-dated Escamps locality which pertains to the late Eocene MP 19 Mammal Zone, although it cannot be excluded that it well originates from some other locality in the vicinity of the village of Escamps (e.g. Rosières 2 and 3 that are also MP 19, but Rosières 5 is MP 17) (J.-C. Rage, personal communication, July 2017). It is worth noting that Zittel (1887–1890) provided also Escamps as the locality of another tetrapod from Quercy, his new salamander taxon *Megalotriton filholi* Zittel, 1887–1890, and this precise geographic provenance is also followed in modern literature (Rage and Augé, 2015). In any case, Zittel's (1887–1890) figured maxilla of *Palaeovaranus cayluxi* seems to be much more precisely geographically and stratigraphically defined in comparison with the vague origins of Filhol's (1873, 1876, 1877a,b,c) material.

For all the above-mentioned reasons, I here consider that a petition to ICZN for maintaining the name *Necrosaurus cayluxi* is not needed and in fact, would only further cause taxonomic problems with the diagnosis of the taxon and even its validity. I instead attribute authorship of both the genus *Palaeovaranus* and the specific epithet "*cayluxi*" to Zittel (1887–1890). As such, the proper name for the genus should be *Palaeovaranus* Zittel, 1887–1890 and for the species *Palaeovaranus cayluxi* Zittel, 1887–1890. As a consequence, *Palaeovaranus cayluxi* is the type species of the genus *Palaeovaranus*.

The herein suggested attribution of the genus and species name *Palaeovaranus cayluxi* to Zittel (1887–1890) inevitably affects also the type material of this taxon. Contrary to the prevailing aspect that Filhol's figured dentary and femur (Fig. 1A) represent the type material of this taxon, the "true" holotype is Zittel's (1887–1890) figured left maxilla (Fig. 2). An additional axis and an anterior caudal vertebra that were figured in the same publication by Zittel (1887–1890:603) were only tentatively referred by him to this taxon, as ?*Palaeovaranus cayluxi*, so, due to his uncertainty, they should not therefore be considered as belonging to the type series of the species. The holotype left maxilla was further figured again by Eastman (1902), Broili (1911), Fejérváry (1918, 1935), and Estes (1983). Furthermore, Fejérváry (1935) was the first to provide photographs of the holotype maxilla and depicted also the labial view of the specimen, noting also inaccuracies in the original lithograph of Zittel (1887–1890). Such inaccuracies in the original lithographs are not rare in palaeontological papers from the 19th century, as has also been demonstrated for various fossil vertebrate clades, among others, fossil snakes (Georgalis et al., 2016) and turtles (Anquetin and Joyce, 2014; Georgalis and Joyce, 2017). Fejérváry (1935) also provided for the first time detailed measurements for this specimen, whose preserved total length was 38.58 mm. Unfortunately, the holotype maxilla cannot be located currently in the collections of BSPG where it was originally housed, so it is possible that the material was destroyed during the WW II (Oliver Rauhut, personal communication, July 2017). Alternatively, this specimen could still be in Hungary, as Fejérváry (1935) noted that he had taken it with him on loan from Munich on 1923. However, unfortunately it could not be located in the collections of neither HNHM, MFGI, nor the University of Pécs (Hungarian institutions that Fejérváry was affiliated) (Zoltán Szentesi, László Makádi, and Krisztina Sebe, personal communication, August 2017). Despite the fact that this specimen seems to be currently lost, I do not consider that the selection of a new one as the neotype is necessary, as the holotype was rather adequately figured and described, especially in the works of Fejérváry (1918, 1935). On the other hand, Filhol's (1877a,b,c) figured partial dentary and right femur (Fig. 1A), the previously supposed syntypes of *Palaeovaranus cayluxi*, are part of the old, not well-dated, Quercy collections and are further not taxonomically informative, hindering thus the taxonomic validity of the taxon. Indeed, the lithograph of the dentary (Filhol, 1877a,b,c) shows a rather incomplete specimen and only in lingual view, whereas the figured right femur (Filhol, 1877a,b,c) also does not provide any important taxonomic information. The dentary also appears now to be lost (Klembara and Green, 2010), though it would not be surprising if it eventually emerges from the collections of AMNH, as is the case of the holotype of another Filhol's lizard, *Pseudeumeces cadurcensis*, which was only recently rediscovered there (Bolet et al., 2017). Regarding Filhol's femur, its lithograph is rather similar to one femur from Quercy that is currently housed in the collections of MNHN (MNHN.F.QU17626, labeled as "*Necrosaurus* cf. *cayluxi*"; personal observation, October 2016) and it is preliminarily identified as that specimen (Fig. 2B), especially taking into consideration the fact that there is only one damaged area and that this area occupies the same place on the specimen and on the lithograph (Jean-Claude Rage, personal communication, July 2017). I here tentatively consider both Filhol's specimens as representing an indeterminate species of *Palaeovaranus* and assign them to *Palaeovaranus* sp.

## 3. *Melanosauroides giganteus* or *Ophisauriscus eucarinatus*?

In a paper dealing with the fossil lizards from the well known middle Eocene locality of Geiseltal, Germany, Kuhn (1940b) described and named two purported large anguids, aff. *Ophisauriscus* (*Melanosauroides*) *eucarinatus* and *Melanosauroides giganteus*. This case seems strange even at a first glance, as Kuhn (1940b) treated his newly established genus name *Melanosauroides* firstly as a subgenus of his aff. *Ophisauriscus* and, in few pages later, as a valid, distinct genus name. *Ophisauriscus eucarinatus* was established on the basis of GMH CeIV-4021-1933, a hind limb with associated osteoderms (Fig. 3A), whereas another specimen (GMH CeIV-4054-1933) was also tentatively referred to the same taxon (Fig. 3B) (Kuhn, 1940b). This species was only rather briefly described, and only the holotype was figured (Kuhn, 1940b). To the contrary, *Melanosauroides giganteus* was established on a single, but much more complete specimen, GMH CeIII-4139-1933, a disarticulated skeleton, including skull elements (parietal, frontal, quadrate, maxilla, dentary, and jugal) (Fig. 4) and was more extensively described, discussed, and figured in the original publication (Kuhn, 1940b). It is worth noting also that the two type specimens were recovered from different quarries within Geiseltal and as such, they pertain to different ages: the holotype of *Melanosauroides giganteus* originated from the younger (MP 13/?MP 14) Quarry "Cecilie III", whereas the holotype and the other referred specimen of *Ophisauriscus eucarinatus* from the older (MP 13) Quarry "Cecilie IV" (Haubold and Krumbiegel, 1984).

Hoffstetter (1943) was the first to realize the "necrosaurid" affinities of *Melanosauroides giganteus* and he transferred this species into *Necrosaurus*, recombining it as *Necrosaurus giganteus*, but did not discuss at all *Ophisauriscus eucarinatus*. McDowell and Bogert (1954) also accepted congeneric affinities with *Necrosaurus* for *Melanosauroides giganteus*, but they constantly used the incorrect specific epithet "*maximus*" instead of "*giganteus*" throughout their text, apparently verbally confusing it with (the currently considered a glyptosaurine anguid) *Melanosaurus maximus* Gilmore, 1928, from the Eocene of the USA, which they also treated as a close relative of the German taxon. Nevertheless, these authors redescribed the type and only known specimen of *Melanosauroides giganteus* and highlighted important anatomical features, which they regarded as "shinisaur" characteristics (McDowell and Bogert, 1954). In a similar way to Hoffstetter (1943), McDowell and Bogert (1954) totally ignored *Ophisauriscus eucarinatus*. The "necrosaurid" affinities of "*giganteus*" also convinced Kuhn himself, who in a later paper used the binomen *Necrosaurus giganteus*, but still treated his "*eucarinatus*" as an anguid, under the binomen ?*Ophisauriscus eucarinatus* (Kuhn, 1963).

The first authors who compared both these two Geiseltal lizards were Haubold (1977) and Estes (1983). These authors regarded both *Ophisauriscus eucarinatus* and *Melanosauroides giganteus* as conspecific and continued to accept their "necrosaurid" affinities (Haubold, 1977; Estes, 1983). Among the two researchers, Haubold (1977) was the first to formally synonymize these two taxa and, as the first reviser, considered *Necrosaurus giganteus* as the senior synonym and valid name for this species, to which he also referred new cranial material from Geiseltal. However, in an act of nomenclatural inconsistency, Estes (1983) appealed only to page priority in order to render "*eucarinatus*" as the senior synonym of "*giganteus*", even though this criterion has no standing according to ICZN (1999) (see also Georgalis and Joyce, 2017 for a discussion). Estes (1983) also referred to "necrosaurids" another species from Geiseltal, *Eosaniwa koehni*, which was originally described as a varanid by Haubold (1977). Despite the fact that Haubold (1977) was the first reviser, the opinion of Estes (1983) has since been broadly followed by all subsequent authors who dealt with this form again under the combination *Necrosaurus eucarinatus* (e.g. Rage, 1988; Augé, 1993, 2005; Conrad, 2008) and even Haubold and Krumbiegel (1984) mentioned the page priority issue of the species epithet "*eucarinatus*" over "*giganteus*". The only exception to this synonymization was made by Borsuk-Białynicka (1984) who (probably unaware of Estes's [1983] work) followed Haubold (1977) and mentioned this taxon as *Necrosaurus giganteus*, though she casted doubts about its "necrosaurid" affinities.

This nomenclatural misconception that has also important taxonomic implications apparently arose from the influential status of Estes's (1983) compendium, which has served up to now as a standard reference point for squamate palaeontology. However, besides the erroneous usage of the page priority criterion that Estes (1983) applied to overrule the actions of Haubold (1977) as first reviser, the major point is that "*eucarinatus*" was founded upon a rather incomplete specimen that comprises no cranial elements, whereas the holotype of "*giganteus*" includes skull material that bears important diagnostic characters for defining the species. Indeed, all subsequent authors who referred new specimens to "*eucarinatus*" based their referral to shared resemblance among the skull remains (e.g. Augé, 2005), though these elements are only present on the holotype of "*giganteus*". My first hand observation of the above-mentioned specimens at the collections of GMH lead me to consider that the type of *Ophisauriscus eucarinatus* bears no diagnostic features at the species level and as such, I am here suggesting this taxon to be a nomen dubium. Nevertheless, the shape of the osteoderms on the type of *O. eucarinatus* bears the distinctive "necrosaur" morphology of these elements (Estes, 1983; Augé, 2005; see also Smith, 2017 for a discussion about similar osteoderm morphology present also in shinisaurid lizards) and the specimen thus represents an indeterminate species of *Palaeovaranus*, herein referred to as *Palaeovaranus* sp. The same seems to be also the case for GMH CeIV-4054-1933, which was referred to *O. eucarinatus* by Kuhn (1940b). This specimen is also a limb element with several osteoderms, is figured herein for the first time (Fig. 3B), and is also referred to as *Palaeovaranus* sp. To the contrary, *Melanosauroides giganteus* is indeed a valid taxon, with its holotype bearing evident "necrosaur" features on the maxilla, dentary, and shape of teeth. Accordingly, I am here recombining this taxon as *Palaeovaranus giganteus* comb. nov. Notably, the holotype of *Palaeovaranus giganteus* is one of the most complete specimens of the genus *Palaeovaranus*. It is worth noting that despite its name, in a bit sense of taxonomic and nomenclatural irony, *Palaeovaranus giganteus* is smaller than its congener *Palaeovaranus cayluxi*.

It is beyond the scope of this paper to redescribe *Palaeovaranus giganteus* and I simply refer here the diagnostic features provided by Augé (2005), Klembara and Green (2010), and Rage and Augé (2010) for their "*Necrosaurus eucarinatus*", which was in any case partially based on the holotype of *Melanosauroides giganteus*. As such, *Palaeovaranus giganteus* can be differentiated from *Palaeovaranus cayluxi* by the following characters: smaller size, higher tooth number, lateral margins of the parietal which do not meet to form a posterior sagittal ridge, parietal having a narrow extension of the table posteriorly, and osteoderms fused to the dorsal surface of the parietal.

## 4. Palaeovaranidae fam. nov., an enigmatic Paleogene lizard clade

Hoffstetter (1943) established his new family Necrosauridae to accommodate certain large European Paleogene lizards that possessed pointed and recurved ("caniniform") teeth. Varanoid affinities of necrosaurids were firstly challenged by McDowell and Bogert (1954) who considered them as shinisaurids (then nested within Xenosauridae), a suggestion that seemed to convince even Hoffstetter (1954) and only tentatively or partially followed by others (Romer, 1956; Kuhn, 1963; Haubold, 1977). In any case, "necrosaurids" were soon "taxonomically" returned to varanoids by the same author who coined the family name (Hoffstetter, 1962b), and there has since been a consensus, at least for their platynotan affinities: either nested within varanoids (e.g. Hecht and Hoffstetter, 1962; Hoffstetter, 1969; Estes, 1983; Carroll, 1988;

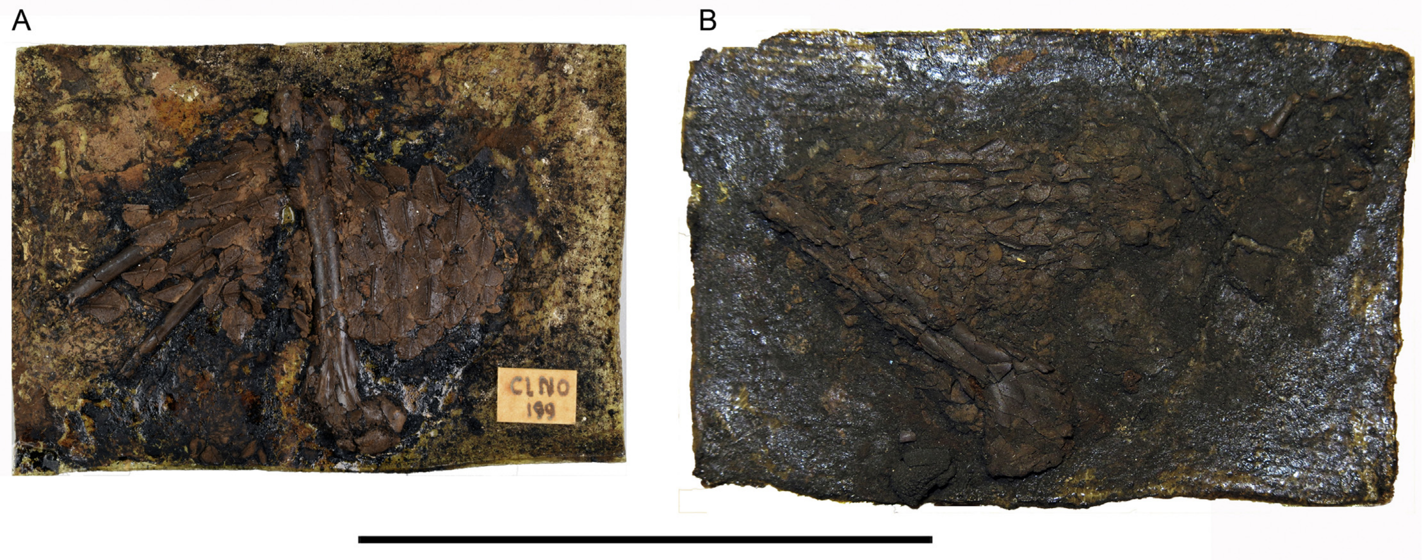

**Fig. 3.** Photographs of the holotype of *Ophisauriscus eucarinatus* (GMH CeIV-4021-1933) (A) and a specimen previously referred to this species (GMH CeIV-4054-1933) (B), both herein attributed to *Palaeovaranus* sp., from the middle Eocene of Geiseltal, Germany. Scale bar = 5 cm. Photographs by G. Georgalis, courtesy of GMH.
*Photographies de l'holotype d'*Ophisauriscus eucarinatus *(GMH CeIV-4021-1933) (A) et d'un spécimen précédemment affecté à cette espèce (GMH CeIV-4054-1933) (B), tous deux attribués dans le présent travail à* Palaeovaranus *sp., de l'Eocène moyen de Geiseltal, Allemagne. Barre d'échelle = 5 cm. Photographies par G. Georgalis, autorisation de GMH.*

**Fig. 4.** Photograph of the holotype of *Melanosauroides giganteus* (GMH CeIII-4139-1933) (herein *Palaeovaranus giganteus*) (A) from the middle Eocene of Geiseltal, Germany. Close up of the maxilla and associated vertebrae (B). Close up of the parietal (C). Scale bar = 5 cm (for A). Photographs by G. Georgalis, courtesy of GMH.
*Photographie de l'holotype de* Melanosauroides giganteus *(GMH CeIII-4139-1933) (dans le présent travail:* Palaeovaranus giganteus*) (A) l'Éocène moyen de Geiseltal, Allemagne. Gros plan du maxillaire et des vertèbres associées (B). Gros plan du pariétal (C). Barre d'échelle = 5 cm (Pour A). Photographies par G. Georgalis, autorisation de GMH.*

Augé, 1990a, 2005; Carroll and Debraga, 1992; Conrad, 2008; Augé and Smith, 2009; Houssaye et al., 2011; Vitt and Caldwell, 2014; Georgalis et al., 2017), or simply representing a paraphyletic assemblage of platynotans (e.g. Borsuk-Białynicka, 1984; Pregill et al., 1986; Cifelli and Nydam, 1995; Lee, 1997; Norell and Gao, 1997; Gao and Norell, 1998; Molnar, 2004; Rieppel et al., 2007; Klembara and Green, 2010; Hong-Yu and Norell, 2013; Bolet, 2017).

The taxonomic content of "necrosaurids" was soon after modified in order to encompass also taxa from geographic areas outside Europe. Indeed, even upon its establishment, the Late Cretaceous North American *Parasaniwa wyomingensis* was already suggested to bear strong resemblance with *Palaeovaranus cayluxi* (Gilmore, 1928). Such a suggestion apparently influenced also Kuhn (1940b) who described and figured new material of *Palaeovaranus cayluxi* from Quercy but he stressed the possibility that these specimens could pertain to *Parasaniwa*. Hoffstetter (1969) also suspected that his European Necrosauridae were rather similar to *Parasaniwa wyomingensis* and another Late Cretaceous North American taxon, *Paraderma bogerti* Estes, 1964. Both of these North American forms were already placed into their own family, Parasaniwidae, by Estes (1964), but the same author soon reassessed his opinion and, in his monumental compendium of fossil lizards, he subsumed Parasaniwidae into Necrosauridae (Estes, 1983). With this taxonomic rearrangement, "necrosaurids" formally ceased to be an exclusively European lineage, but their geographic range was significantly expanded into North America, whereas their stratigraphic distribution went as back as the Cretaceous. This taxonomic action apparently led the way for recognizing more "necrosaurids" in the fossil record of different continents and different epochs. Characteristically, the Late Cretaceous Mongolian form *Parviderma inexacta* Borsuk-Białynicka, 1984, was also originally described as a "necrosaurid", whereas *Ekshmer bissektensis* Nessov, 1981, from the Late Cretaceous (Coniacian) of Uzbekistan, was subsequently referred to the same group (Nessov, 1997). Yadagiri (1986) described his new species *Paikasisaurus indicus* from the Early Jurassic of India, assigning it to Parasaniwidae (apparently ignoring the paper of Estes [1983]), but this taxon is based on extremely fragmentary dentary material and its taxonomic attribution cannot be evaluated. An additional form from the Early Cretaceous (Albian) of Utah has been referred to Necrosauridae by Cifelli and Nydam (1995), with these authors suggesting that this could eventually represent the oldest member of this clade. Besides the problematic *Paikasisaurus indicus*, all these chronologically and geographically disparate forms were mostly characterized by "subpleurodont" (sensu Hoffstetter, 1954), fang-like, and recurved teeth, oval and high keeled osteoderms, and, in several cases, dentition with plicidentine. In order to render a monophyletic Necrosauridae, Augé (2005) proposed a revised diagnosis for this clade, including only the European Paleogene genera *Necrosaurus* and *Eosaniwa*, but also the Asian Cretaceous *Parviderma*.

Considering that I here conclude that *Necrosaurus* is not an available name for zoological nomenclature, the name Necrosauridae is rendered invalid (ICZN, 1999:Article 11.7.1.1), and it is thus necessary to introduce a new name for the immediate clade typified by the genus *Palaeovaranus* Zittel, 1887–1890, and its type species *Palaeovaranus cayluxi* Zittel, 1887–1890. Following the ICZN (1999), I am herein introducing the new name Palaeovaranidae fam. nov., for which I am using a Linnean "family" rank for simplicity purposes. Taking into consideration that the species level taxonomy of the formerly called "necrosaurids" and their affinities within other squamates are still unresolved, I am here defining the monotypic Palaeovaranidae as including only the European Paleogene genus *Palaeovaranus*. As for the diagnosis and the differentiation of Palaeovaranidae from other lizards, I am herein following the one proposed by Augé and Smith (2009) for *Necrosaurus*, adding also characters from the recent studies of Klembara and Green (2010) and Rage and Augé (2015). Accordingly, both Palaeovaranidae and *Palaeovaranus* can be diagnosed on the basis of the combination of the following characters: presence of oval, keeled osteoderms, premaxilla with a long, arched nasal process, non-paired frontal, not narrowed between the orbits, non-paired parietal, no ridges on the ventral surface of the parietal, adductor musculature extending onto dorsal surface of parietal, sometimes with a sagittal crest, intramandibular septum being fused along its ventral border, teeth being trenchant, blade-like, recurved, tooth bases dilated, striated, with plicidentine, tooth replacement alternate and interdental, cervical vertebrae elongate, caudal vertebrae with no autotomic septa, caudal vertebrae with pedicles for articulation with chevron bones located very close to the condyle, and transverse processes of the caudal vertebrae slightly extending anteroposteriorly and being located more posteriorly than in anguines (Augé and Smith, 2009; Klembara and Green, 2010; Rage and Augé, 2015). However, I acknowledge that if future phylogenetic analysis demonstrates that the Cretaceous North American *Parasaniwa* shares indeed close relationships with the European Paleogene *Palaeovaranus*, then the name Parasaniwidae Estes, 1964, is available for that clade as it has priority.

The distribution of Palaeovaranidae and *Palaeovaranus* is confined from the early Eocene to the early Oligocene of Europe. The lineage seems to have become extinct shortly after the so called "Grande Coupure" that exterminated several European herpetofaunal elements at the Eocene–Oligocene boundary (Rage, 1984a, 2013; Augé, 2005). Two potential Paleocene records from Cernay, France (Hoffstetter, 1943, 1962b; Augé, 2005), and Walbeck, Germany (originally *Saniwa* aff. *ensidens* of Kuhn, 1940a; Augé, 1990b), have not been adequately described and their assignment to palaeovaranids should be only considered as tenuous. The new taxonomic scheme, which I am here suggesting, with *Palaeovaranus cayluxi* as the appropriate name over *Necrosaurus cayluxi* and *Palaeovaranus giganteus* being the only other valid referred species of this genus, necessitates an update in the nomenclature and identification of certain other "necrosaurid" occurrences. *Palaeovaranus cayluxi* is only known from France, with various records from the old, non precisely dated collections of Quercy (De Stefano, 1903; Fejérváry, 1935; Kuhn, 1940b; Augé, 1986, 2005), but also from the well-dated late Eocene localities of Sainte Néboule (MP 18) (Rage, 1978; Augé, 1986, 2005), Escamps (MP 19) (Zittel, 1887–1890; Augé, 1986, 2005), and Rosières B (MP 19) (Augé, 2005). In addition, a similar or even conspecific form that has been described as *Necrosaurus* cf. *cayluxi* from the middle Eocene (MP 16) of Le Bretou (Rage, 1988), is here tentatively referred to *Palaeovaranus* cf. *cayluxi*. As far as it concerns *Palaeovaranus giganteus*, apart from its holotype and the referred material from the middle Eocene (MP 13/14) of Geiseltal, Germany (Kuhn, 1940b; Haubold, 1977), this species is also known from the late Eocene of France (La Bouffie, MP 17 [Augé, 1986]; Les Pradigues, MP 17 [Augé, 1986, 2005]; Escamps, MP 19 [Augé, 1986, 2005; Rage, 2013]), and from the old, undated collections of Quercy (Augé, 1986, 2005). I have to admit, however, that the vast majority of all these referrals to the two *Palaeovaranus* species has been made mostly by using phenetic resemblance of the material and not a thorough phylogenetic analysis, so it has to be regarded as provisional.

In addition to the two valid species, *Palaeovaranus cayluxi* and *P. giganteus*, other indeterminate palaeovaranid material that cannot be assigned to the species level but can only be referred to as *Palaeovaranus* sp. is also known from the early Eocene of Belgium (Dormaal, MP 7 [Augé, 1990b, 2005]), the early Eocene of France (Condé-en-Brie, MP 8/9 [Augé, 2005]; La Borie, MP 8/9 [Laurent et al., 2010]), the early Eocene of Spain (Masia de l'Hereuet, MP 8+9 [Bolet, 2017]), the middle Eocene of France (Saint-Maximin, MP 13 [Duffaud and Rage, 1997]), the middle Eocene of Germany (Messel, MP 11 [Keller and Schaal, 1992]), the late Eocene of The United Kingdom (Totland Bay, MP 17 [Klembara and Green, 2010]; Headon Hill, MP 18 [Rage and Ford, 1980]; Osborne, MP 19 [Klembara and Green, 2010]; Hamstead, MP 20/21 [Klembara and Green, 2010]), the early Oligocene of Belgium (Boutersem, MP 21 [Augé and Smith, 2009]; Hoeleden, MP 21 [Hecht and Hoffstetter, 1962]; Hoogbutsel, MP 21 [Hecht and Hoffstetter, 1962]), and the early Oligocene of France (Mas de Got B, MP 22 [Augé, 1986, 2005]; Valbro, MP 22 [Rage and Augé, 2015]). To these, I am adding the original "necrosaurid" material of Filhol (1873, 1876, 1877a,b,c) and Lydekker (1888a) from the Old collections of Quercy, as also the type material of *Odontomophis atavus* Rochebrune, 1884, *Palaeovaranus filholi* De Stefano, 1903, and one of the paralectotypes (MNHN.F.QU16334) of *Pylmophis gracilis* Rochebrune, 1884, also from the old collections of Quercy, the above-mentioned *Ophisauriscus eucarinatus* Kuhn, 1940b, and material referred by Kuhn (1940b) to cf. *Glyptosaurus hillsi*, from the middle Eocene of Geiseltal, Germany, which all show palaeovaranid features, though not adequate to diagnose a taxon at the species level (Hoffstetter, 1946, 1955; Meszoely et al., 1978; Estes, 1983; Rage, 1984b; Augé, 2005). *Odontomophis atavus* was originally established as a scolecophidian snake on the basis of a dentary (Rochebrune, 1884) but it was subsequently demonstrated that it pertains to an indeterminate species of "*Necrosaurus*" (Hoffstetter, 1946, 1955; Rage, 1974, 1984b). *Palaeovaranus filholi* was established upon a large number of specimens, including a maxilla, mandibles, vertebrae, and appendicular elements, and this taxon was mostly differentiated from *Palaeovaranus cayluxi* by its shape and size of teeth and the shape of the glenoid cavity of their vertebrae (De Stefano, 1903), features that are highly variable within lizards. Indeed, the distinctiveness of *Palaeovaranus filholi* has since been strongly criticized (Nopcsa, 1908; Fejérváry, 1918; Estes, 1983; Augé, 2005), though I note that part of the maxillary and/or the mandibular type material could eventually have some taxonomic significance. In any case, it cannot be demonstrated whether the plethora of the syntypes of *Palaeovaranus filholi* belong indeed even to the same species, and the taxon could even represent a chimaera. This problem could be solved through the designation of a lectotype, but pending redescription of this material, I am refraining from acting so. Regarding *Pylmophis gracilis*, this taxon was established as a new snake species from Quercy on the basis of two articulated posteriormost trunk vertebrae, one dentary, and one "mummified" skin (Rochebrune, 1884). Nevertheless, it was subsequently shown by Rage (1974, 1981, 1984b) that the dentary that was part of the original type series belonged in fact to a lizard. The same author also designated one of the specimens as the lectotype (the two articulated posteriormost trunk vertebrae; MNHN.F.QU16335) of *Pylmophis gracilis* in order to resolve the chimaera status of this species and to maintain taxonomic stability (Rage, 1984b). In any case, judging from the published figure of Rochebrune (1884:figure 9 of his plate 2), which depicts the dentary only in labial view, it seems that this specimen could pertain to a palaeovaranid, although the teeth appear to be relatively more slender in comparison with other specimens of this clade. I provisionally refer this specimen to *Palaeovaranus* sp. As for the Geiseltal material that was tentatively referred to the North American taxon cf. *Glyptosaurus hillsi* by Kuhn (1940b), it consisted a specimen with vertebrae and osteoderms that was soon after attributed to *Necrosaurus* sp. by Meszoely et al. (1978) and subsequently to *Necrosaurus eucarinatus* by Estes (1983). I also consider this occurrence as an indeterminate species of *Palaeovaranus*. In all the above-mentioned occurrences, generic attribution to *Palaeovaranus* is mostly made by general, shared morphological features, and thus should not be considered as definite. Furthermore, special caution is needed when dealing with isolated finds, as shinisaurids have recently been described also from the Paleogene of Europe and they have similar osteoderms to those of palaeovaranids (Smith, 2017). Moreover, there are other purported occurrences of this genus that were mentioned by Augé (2005), but they lack any description, figures, or/and repository numbers, and so their taxonomic status cannot therefore be evaluated. Such records are omitted here from further consideration. Additionally, two other Eocene German taxa, *Eosaniwa koehni* Haubold, 1977, from Geiseltal, and *Saniwa feisti* Stritzke, 1983, from Messel, have been variously suggested to represent "necrosaurids" (Estes, 1983; Augé, 1990b, 2005; Rossmann, 2000; Conrad, 2008; Smith, 2017). A redescription of *Eosaniwa koehni* has recently demonstrated that it represents a derived varanoid (Rieppel et al., 2007). Regarding *Saniwa feisti*, this taxon has not yet been redescribed under a modern phylogenetic context, although in recent literature, its originally suggested varanid affinities (Stritzke, 1983) have been questioned, it has generally been considered as a "necrosaurid" (Augé, 1990b, 2005; Rossmann, 2000; Conrad, 2008), and was even referred under the combination *Necrosaurus feisti* by Smith (2017). They are both herein excluded from *Palaeovaranus* and Palaeovaranidae, though most probably they represent allied forms, especially the latter species, which could eventually pertain indeed to *Palaeovaranus*. Lastly, Alifanov (1993) reported the presence of *Necrosaurus* sp. from the late Paleocene of Tsagan-Hushu locality, Mongolia, whereas he further speculated that ecological competition with varanids drove Asian "necrosaurids" to their extinction by the middle Eocene. However, this material was never described and/or figured and as such, I consider its generic assignment as dubious and, in any case, the presence of *Palaeovaranus* in Asia is not justified on the basis of the current evidence.

Of course, the exact affinities and the precise systematic designation of Palaeovaranidae and *Palaeovaranus* are far from resolved. It is beyond the scope of this paper to address these issues, but nevertheless, the clarification of the appropriate nomenclature and the true type material of *Palaeovaranus cayluxi* and *Palaeovaranus giganteus* can serve as the basis for including these taxa into more complete phylogenetic analyses and comparing them with other coeval lizards from the Paleogene of Europe.

I admit that the taxonomic rearrangement I am here suggesting by setting the names *Necrosaurus* and Necrosauridae aside alters drastically the prevailed nomenclature of these lizards but this is necessary in order to follow the disciplines of the ICZN (1999) and maintain taxonomic stability. After all, similar cases are known also for other vertebrate groups, such as the usage of the crocodylian *Boverisuchus* Kuhn, 1938, over the "popular" but apparently invalid *Pristichampsus* Gervais, 1853 (Brochu, 2012). This highlights the need for the reassessment of taxa that were established during the 19th century, as it is probable that "popular" names that are widely used in the modern literature will eventually prove to be nomina nuda or nomina dubia. Nevertheless, even the etymology of *Palaeovaranus* seems to be more appropriate than *Necrosaurus*: Filhol (1876) did not provide any explanation for the name *Necrosaurus*, although Molnar (2004) suggested that the name means "lizards of death". However, I believe that Filhol intended to signify in fact a "νεκρός" ("nekros") (Greek for "dead") and "σαύρα" ("saura") (Greek for "lizard"), i.e., a "dead lizard", which was a common practice of this author for several of his taxa from Quercy (e.g. *Necrodasypus* Filhol, 1894 and *Necromanis* Filhol, 1894). As such, I credit that the valid name *Palaeovaranus* (from the Greek "παλαιός" ["palaeos" = "old"] and the genus name *Varanus*) pays a more appropriate homage to this bizarre lizard, at least in comparison with the almost cynical name *Necrosaurus*.

## 5. Conclusions

Although *Necrosaurus cayluxi* was already identified as a large, fossil lizard since the 19th century (Filhol, 1873, 1876, 1877a, b, c), its exact taxonomic affinities are still unresolved. I here demonstrate that the current nomenclature of this animal is erroneous and that the appropriate name for this lizard from the Phosphorites of Quercy should be *Palaeovaranus cayluxi* and that authorship of this taxon should be attributed to Zittel (1887–1890) and not Filhol. This fact renders Zittel's (1887–1890) described and figured maxilla as the true holotype of this taxon and this specimen should serve as the basis of comparison of *P. cayluxi* with all other finds that have been previously assigned to "necrosaurids". Furthermore, the taxonomic status of *Necrosaurus eucarinatus* from the middle Eocene of Geiseltal, Germany, is clarified and it is demonstrated that it is a nomen dubium, whereas its sympatric *Melanosauroides giganteus* is shown to be a valid taxon, recombined under *Palaeovaranus*. The taxonomic content of *Palaeovaranus* is discussed and the genus includes remains that are known from the early Eocene until the early Oligocene of several localities in Europe. A new clade name, Palaeovaranidae, is herein established to encompass *Palaeovaranus*, though it is acknowledged that the relationships of this group need further assessment, especially in regard with certain North American and Asian forms. A thorough and more comprehensive reading of the old literature is highly advised, as it is expected that certain other species that were established during the 19th century will be eventually demonstrated to be nomina nuda.

## Disclosure of interest

The author declares that he has no competing interest.

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## References

Alifanov, V., 1993. Some peculiarties *(sic)* of the Cretaceous and Palaeogene lizard faunas of the Mongolian People's Republic. Kaupia 3, 9–13.

Anquetin, J., Joyce, W.J., 2014. A reassessment of the Late Jurassic turtle *Eurysternum wagleri* (Eucryptodira, Eurysternidae). Journal of Vertebrate Paleontology 34, 1317–1328.

Augé, M., 1986. Les Lacertiliens (Reptilia, Squamata) de l'Éocène supérieur et de l'Oligocène ouest européen. Thèse 3ème cycle Université Pierre et Marie Curie - Paris VI (inédit), Paris.

Augé, M., 1990a. La faune de lézards et d'Amphisbènes de l'Éocène inférieur de Condé-en-Brie (France). Bulletin du Muséum national d'Histoire naturelle, 4$^e$ série 12, 111–141.

Augé, M., 1990b. La faune de lézards et d'Amphisbènes (Reptilia, Squamata) du gisement de Dormaal (Belgique, Éocène inférieur). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 60, 161–173.

Augé, M., 1993. Repartition et dynamisme des faunes de Lacertilia et d'Amphisbaenia dans l'Éocène Européen. Palaeovertebrata 22, 51–71.

Augé, M., 2003. La faune de Lacertilia (Reptilia, Squamata) de l'Éocène inférieur de Prémontré (Bassin de Paris, France). Geodiversitas 25, 539–574.

Augé, M., 2005. Évolution des lézards du Paléogène en Europe. Mémoires du Muséum national d'Histoire naturelle 192, 1–369.

Augé, M., Smith, R., 2009. An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene–Oligocene transition. Zoological Journal of the Linnean Society 155, 148–170.

Bolet, A., 2017. First early Eocene lizards from Spain and a study of the compositional changes between late Mesozoic and early Cenozoic Iberian lizard assemblages. Palaeontologica Electronica 20.2.20A, 1–22.

Bolet, A., Rage, J.-C., Conrad, J.L., 2017. Rediscovery of the long-lost holotype of the lacertid lizard *Pseudeumeces cadurcensis* (Filhol, 1877). Journal of Vertebrate Paleontology 37, e1315669.

Borsuk-Białynicka, M., 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi desert, Mongolia. Paleontologia Polonica. Results of the Polish-Mongolian Paleontological Expeditions, part X 46, 5–105.

Boulenger, G.A., 1918. Les Lezards Helodermatides de l'Eocène supérieur de la France. Comptes rendus hebdomadaires des séances de l'Académie des Sciences de Paris 166, 889–893.

Brochu, C., 2012. Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103, 1–30.

Broili, F., 1911. 3. Klasse. Reptilia. Reptilien. Kriechtiere. In: Zittel, K.A. (Ed.), Grundzüge der Paläontologie (Paläozoologie). II. Vertebrata. Druck und Verlag von R. Oldenbourg, Munich and Berlin, pp. 179–308.

Carroll, R.L., 1988. Vertebrate paleontology and evolution. W.H. Freeman and Company, New York.

Carroll, R.L., Debraga, M., 1992. Aigialosaurs: Mid-Cretaceous Varanoid lizards. Journal of Vertebrate Paleontology 12, 66–86.

Cifelli, R.L., Nydam, R.L., 1995. Primitive, helodermatid-like platynotan from the Early Cretaceous of Utah. Herpetologica 51, 286–291.

Cifelli, R.L., Nydam, R.L., Gardner, J.D., Weil, A., Eaton, J.G., Kirkland, J.I., Madsen, S.K., 1999. Medial Cretaceous vertebrates from the Cedar Moutain formation, Emery county, Utah: The Mussentuchit local fauna. In: Gillette, D.D. (Ed.), Vertebrate Paleontology in Utah, 99. Utah Geological Survey Miscellaneous Publication, pp. 219–242.

Conrad, J.L., 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bulletin of the American Museum of Natural History 310, 1–182.

Conrad, J.L., Head, J.J., Carrano, M.T., 2014. Unusual soft-tissue preservation of a crocodile lizard (Squamata, Shinisauria) from the Green River Formation (Eocene) and shinisaur relationships. Anatomical Record 297, 545–559.

Conrad, J.L., Rieppel, O., Gauthier, J., Norell, M., 2011. Osteology of *Gobiderma pulchrum* (Monstersauria, Lepidosauria, Reptilia). Bulletin of the American Museum of Natural History 362, 1–88.

Conrad, J.L., Rieppel, O., Grande, L., 2008. Re-assessment of varanid evolution based on new data from Saniwa ensidens Leidy, 1870 (Squamata, Reptilia). American Museum Novitates 3630, 1–15.

De Stefano, G., 1903. I sauri del Quercy appartenenti alla collezione Rossignol. Atti della Societa Italiana di Scienze Naturali e del Museo Civili di Storia Naturale, Milan 42, 382–418.

De Stefano, G., 1905. Appunti sui Batraci e sui Rettili del Quercy appartenenti alla collezione Rossignol. Parte Terza. Coccodrilli–Serpenti–Tartarughe. Bolletino della Società Geologica Italiana 24, 17–67.

Duffaud, S., Rage, J.-C., 1997. Les remplissages karstiques polyphasés (Éocène, Oligocène, Pliocène) de Saint-Maximin (Phosphorites du Gard) et leur apport à la connaissance des faunes européennes, notamment pour l'Éocène moyen (MP 13). 2.–Systématique : Amphibiens et Reptiles. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Institut de Montpellier de l'École Pratique des Hautes Études 21, 729–735.

Dunn, E.R., 1927. Results of the Douglas Burden expedition to the Island of Komodo. I.–Notes on *Varanus komodoensis*. American Museum Novitates 286, 1–10.

Eastman, C.R., 1902. Text-book of Palaeontology. The MacMillan Company, New York.

Estes, R., 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. University of California Publications in Geological Sciences 49, 1–187.

Estes, R., 1983. Sauria Terrestria, Amphisbaenia. In: Wellnhofer, P. (Ed.), Encyclopedia of Paleoherpetology. Gustav Fisher Verlag, Stuttgart/New York.

Fejérváry, de G.J., 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. Annales historico-naturales Musei nationalis hungarici 16, 341–467.

Fejérváry, de G.J., 1935. Further contributions to a monograph of the Megalanidae and Fossil Varanidae, with notes on recent varanians. Annales historico-naturales Musei nationalis hungarici, Pars Zoologica 29, 1–130.

Filhol, H., 1873. Sur les vertébrés fossiles trouvés dans les dépôts de phosphate de chaux du Quercy. Bulletin de la Société Philomathique de Paris, Série 6 (10), 85–89.

Filhol, H., 1876. Sur les reptiles fossiles des phosphorites du Quercy. Bulletin de la Société Philomathique de Paris, Série 6 (11), 27–28.

Filhol, H., 1877a. Recherches sur les Phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères. Pt. II. Annales des Sciences géologiques 8, 1–340.

Filhol, H., 1877b. Recherches sur les phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères. G. Masson, Paris.

Filhol, H., 1877c. Recherches sur les Phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères. Pt. II. Bibliothèque de l'École des hautes études, Section des Sciences naturelles 16, 1–338.

Filhol, H., 1894. Observations concernant quelques mammifères fossiles nouveaux du Quercy. Annales des Sciences Naturelles, Zoologie et Paléontologie 16, 129–150.

Gao, K.-Q., Norell, M.A., 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of anguimorphan lizards. American Museum Novitates 3230, 1–51.

Georgalis, G.L., Joyce, W.G., 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58, 115–208.

Georgalis, G.L., Szyndlar, Z., Kear, B.P., Delfino, M., 2016. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109, 103–116.

Georgalis, G.L., Villa, A., Delfino, M., 2017. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. Journal of Vertebrate Paleontology 37, e1301946.

Gervais, P., 1853. Observations relatives aux reptiles fossiles de France (première partie). Comptes Rendus de l'Académie des Sciences de Paris 36, 374–377.

Gervais, P., 1876. Zoologie et Paléontologie générales. Arthus Bertrand, Paris.

Gilmore, C.W., 1928. The fossil lizards of North America. Memoirs of the National Academy of Sciences 11, 1–197.

Gilmore, C.W., 1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Part II. Lizards. Proceedings of the American Philosophical Society 85, 159–167.

Haubold, H., 1977. Zur Kenntnis der Sauria (Lacertilia) aus dem Eozän des Geiseltals. In: Matthes, H.W., Thaler, B. (Eds.), Eozäne Wirbeltiere des Geiseltales (Wissenschaftliche Beiträge 1977/2), 1977. Martin-Luther-Universität Halle-Wittenberg, Wissenschaftliche Beiträge, pp. 107–112.

Haubold, H., Krumbiegel, G., 1984. Typenkatalog der Wirbeltiere aus dem Eozän des Geiseltals. Martin-Luther-Universität, Halle.

Hecht, M., Hoffstetter, R., 1962. Note préliminaire sur les amphibiens et les squamates du Landénien supérieur et du Tongrien de Belgique. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre 38, 1–30.

Hoffstetter, R., 1943. Varanidae et Necrosauridae fossiles. Bulletin du Muséum national d'Histoire naturelle, Série 2 (15), 134–141.

Hoffstetter, R., 1946. Les Typhlopidae fossiles. Bulletin du Muséum National d'Histoire Naturelle, Série 2 (18), 309–315.

Hoffstetter, R., 1954. Sur la position systématique de *Necrosaurus* : Saurien de l'Éocène européen. Comptes Rendus Sommaires de la Société Géologique de France, Paris 1954, 422–424.

Hoffstetter, R., 1955. Squamates de type moderne. In: Piveteau, J. (Ed.), Traité de Paléontologie, 5. Masson, Paris, pp. 606–662.

Hoffstetter, R., 1962a. Additions à la faune reptilienne de l'Éocène supérieur de Mormont-Saint-Loup (Suisse). Bulletin de la Société Géologique de France 4, 109–117.

Hoffstetter, R., 1962b. Revue des récentes acquisitions concernant l'histoire et la systématique des Squamates. Problèmes actuels de paléontologie-Évolution des Vertébrés. Colloques internationaux du Centre national de la recherche scientifique 104, 243–279.

Hoffstetter, R., 1969. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. Bulletin du Muséum National d'Histoire Naturelle 40, 1051–1064.

Hong-Yu, Y., Norell, M.A., 2013. New materials of *Estesia mongoliensis* (Squamata: Anguimorpha) and the evolution of venom grooves in lizards. American Museum Novitates 3767, 1–31.

Houssaye, A., Bardet, N., Rage, J.-C., Pereda Suberbiola, X., Bouya, B., Amaghzaz, M., Amalik, M., 2011. A review of *Pachyvaranus crassispondylus* Arambourg, 1952, a pachyostotic marine squamate from the latest Cretaceous phosphates of Morocco and Syria. Geological Magazine 148, 237–249.

International Commission on Zoological Nomenclature (ICZN), 1999. International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature, London, Online version http://www.iczn.org/iczn/index.jsp.

Keller, T., Schaal, S., 1992. Lizards: reptiles en route to success. In: Schaal, S., Ziegler, W. (Eds.), Messel: an insight into the history of life and of the earth. Clarendon press, Oxford, pp. 121–133.

Klembara, J., Green, B., 2010. Anguimorph lizards (Squamata, Anguimorpha) from the Middle and Upper Eocene of the Hampshire Basin of Southern England. Journal of Systematic Palaeontology 8, 97–129.

Kuhn, O., 1938. Die Crocodilier aus dem mittleren Eozän des Geiseltales bei Halle. Nova Acta Leopoldina 39, 313–328.

Kuhn, O., 1939a. Die Schlangen (Boidae) aus dem Mitteleozän des Geiseltales. Nova Acta Leopoldina, Neue Folge 7, 119–133.

Kuhn, O., 1939b. Squamata: Lacertilia et Ophidia. Fossilium Catalogus, 1: Animalia, pars 86. Verlag Gustav Feller, Neubrandenburg, 89 p.

Kuhn, O., 1940a. Crocodilier-und Squamatenreste aus dem oberen Paleocän von Walbeck. Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B 1940, 21–25.

Kuhn, O., 1940b. Die Placosauriden und Anguiden aus dem Mittleren Eozän des Geiseltales. Nova Acta Academia Leopoldina 53, 461–486.

Kuhn, O., 1963. Sauria (Supplementum I). Fossilium Catalogus 1: Animalia, Pars 104. W. Junk. The Hague, 1–87.

Laurent, Y., Adnet, S., Bourdon, E., Corbalan, D., Danilo, L., Duffaud, S., Fleury, G., Garcia, G., Godinot, M., Le Roux, G., Maisonnave, C., Métais, G., Mourer-Chauviré, C., Presseq, B., Sigé, B., Solé, F., 2010. La Borie (Saint-Papoul, Aude) : un gisement exceptionnel dans l'Éocène basal du Sud de la France. Bulletin de la Société d'histoire naturelle de Toulouse 146, 89–103.

Lee, M.S., 1997. The phylogeny of varanoid lizards and the affinities of snakes. Philosophical Transaction of the Royal Society of London B 352, 53–91.

Lydekker, R., 1886. Indian Tertiary & post-Tertiary Vertebrata. Siwalik Crocodilia, Lacertilia & Ophidia. Palaeontologia Indica 3, 210–240.

Lydekker, R., 1888a. Catalogue of Fossil Reptiles and Amphibians in the British Museum (Natural History). Part 1. The Orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria. British Museum (Natural History), London.

Lydekker, R., 1888b. Notes on Tertiary Lacertilia and Ophidia. Geological Magazine 5, 110–113.

McDowell, S.B., Bogert, C.M., 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bulletin of the American Museum of Natural History 105, 1–145.

Meszoely, C., Estes, R., Haubold, H., 1978. Eocene anguid lizards from Europe and a revision of the genus *Xestops*. Herpetologica 34, 156–166.

Molnar, R.E., 2004. 2. The long and honorable history of Monitors and their kin. In: Pianka, R.E., King, D., King, R.A. (Eds.), Varanoid Lizards of the World. Indiana University Press, Bloomington, Indiana, pp. 10–67.

Nessov, L.A., 1981. [The discovery of a terrestrial lizard jaw in the Upper Cretaceous of Uzbekistan]. Vestnik Leningradskogo Universiteta 2, 105–107 (in Russian).

Nessov, L.A., 1997. [Cretaceous Non-marine Vertebrates of Northern Eurasia]. Saint Petersburg State University, Institute of Earth Crust, Saint Petersburg (in Russian).

Nopcsa, F., 1908. Zur Kenntnis der fossilen Eidechsen. Beitrage zur Paläontologie und Geologie Osterreich-ungarns und des Orients 21, 33–62.

Norell, M.A., Gao, K., 1997. Braincase and phylogenetic relationships of *Estesia mongoliensis* from the Late Cretaceous of the Gobi desert and the recognition of a new clade of lizards. American Museum Novitates 3211, 1–25.

Nydam, R.L., 2000. A new taxon of Helodermatid-like lizards from the Albian–Cenomanian of Utah. Journal of Vertebrate Paleontology 20, 285–294.

Pregill, G., Gauthier, J.A., Greene, H.W., 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. Transactions of the San Diego Society of Natural History 21, 167–202.

Rage, J.-C., 1974. Les Serpents des Phosphorites du Quercy. Palaeovertebrata 6, 274–303.

Rage, J.-C., 1978. La poche à Phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérior. 5. Squamates. Palaeovertebrata 8, 201–215.

Rage, J.-C., 1981. Les Colubridae (Reptilia, Serpentes) du Néogène français. Le problème des espèces du Miocène de Sansan. Geobios 14, 537–542.

Rage, J.-C., 1984a. La « Grande Coupure » Eocène-Oligocène et les herpétofaunes (Amphibiens et Reptiles) : problèmes du synchronisme des événements paléobiogéographiques. Bulletin de la Société géologique de France 26, 1251–1257.

Rage, J.-C., 1984b. Serpentes. In: Wellnhofer, P. (Ed.), Encyclopedia of paleoherpetology. Gustav Fisher Verlag, Stuttgart/New York.

Rage, J.-C., 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. I Amphibiens et Reptiles. Palaeontographica Abteilung A 205, 3–27.

Rage, J.-C., 2006. The lower vertebrates from the Eocene and Oligocene of the Phosphorites du Quercy (France): an overview. In: Pélissié, T., Sigé, B. (Eds.), 30 millions d'années de biodiversité dynamique dans le paléokarst du Quercy. Journées Bernard Gèze. Strata, 13, pp. 161–173.

Rage, J.-C., 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments 93, 517–534.

Rage, J.-C., Augé, M., 1993. Squamates from the Cenozoic of the western part of Europe. A review. Revue de Paléobiologie, volume spécial 7, 199–216.

Rage, J.-C., Augé, M., 2010. Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. Geobios 43, 253–268.

Rage, J.-C., Augé, M., 2015. Valbro: a new site of vertebrates from the early Oligocene (MP 22) of France (Quercy). III – Amphibians and squamates. Annales de Paléontologie 101, 29–41.

Rage, J.-C., Ford, R.L.E., 1980. Amphibians and squamates from the Upper Eocene of the Isle of Wight. Tertiary Research 3, 47–60.

Rieppel, O., 1980. The phylogeny of anguinomorph lizards. Denkschriften der Schweizerischen naturforschenden Gesellschaft 94, 1–86.

Rieppel, O., Conrad, J.L., Maisano, J.A., 2007. New morphological data for *Eosaniwa koehni* Haubold, 1977 and a revised phylogenetic analysis. Journal of Paleontology 81, 760–769.

Riley, H., Stutchbury, S., 1836. A description of various fossil remains of three distinct saurian animals discovered in the autumn of 1834, in the Magnesian Conglomerate on Durdham Down, near Bristol. Proceedings of the Geological Society of London 2, 397–399.

Rochebrune, de A.T., 1884. Faune ophiologique des Phosphorites du Quercy. Mémoires de la Société des Sciences naturelles de Saône-et-Loire 5, 149–164.

Roger, O., 1898. Wirbelthierreste aus dem Dinotheriensande. II. Theil. Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg in Ausburg 33, 385–396.

Romer, A.S., 1945. Vertebrate paleontology, Second edition. University Chicago Press, Chicago.

Romer, A.S., 1956. Osteology of the reptiles. University Chicago Press, Chicago.

Rossmann, T., 2000. Osteologische Beschreibung von *Geiseltaliellus longicaudus* Kuhn, 1944 (Squamata: Iguanoidea) aus dem Mittleren Eozän der Fossillagerstätten Geiseltal und Grube Messel (Deutschland), mit einer Revision der Gattung *Geiseltaliellus*. Palaeontographica Abteilung A 258, 117–158.

Smith, K.T., 2017. First crocodile-tailed lizard (Squamata: *Pan-Shinisaurus*) from the Paleogene of Europe. Journal of Vertebrate Paleontology 37, e1313743.

Smith, K.T., Gauthier, J.A., 2013. Early Eocene lizards of the Wasatch Formation near Bitter Creek, Wyoming: diversity and paleoenvironment during an interval of global warming. Bulletin of the Peabody Museum of Natural History 54, 135–230.

Stritzke, R., 1983. *Saniwa feisti* n. sp., ein Varanide (Lacertilia, Reptilia) aus dem Mittel-Eozän von Messel bei Darmstadt. Senckenbergiana Lethaea 64, 497–508.

Vitt, L.J., Caldwell, J.P., 2014. Herpetology. An Introductory Biology of Amphibians and Reptiles, 4th ed. Academic Press, Elsevier, Amsterdam.

Weigelt, J., 1929. *Loricotherium Waltheri* ist doch kein Gürteltier, sondern eine Gürtlechse: *Placosaurus Waltheri* n. sp. Jahrbuch des Halleschen Verbandes für die Erforschung der mitteldeutschen Bodenschätze 8, 187–191.

Weithofer, A., 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. Beiträge zur Paläontologie Österreich-Ungarns 6, 225–292.

Yadagiri, P., 1986. Lower Jurassic lower vertebrates from Kota Formation, Pranhita-Godavari Valley, India. Journal of the Palaeontological Soceity of India 31, 89–96.

Zittel, K.A., 1887–1890. Handbuch der Paläontologie. Palaeozoologie. III. Pisces, Amphibia, Reptilia, Aves. Druck und Verlag von R. Oldenbourg, Munchen/Leipsig.

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# New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers

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**Abstract** *Laophis crotaloides* was described by Richard Owen as a new and very large fossil viperid snake species from Greece. The type material is apparently lost and the taxon was mostly neglected for more than a century. We here describe a new partial viperid vertebra, collected from the same locality and of equivalent size to the type material. This vertebra indicates that at least one of the three morphological characters that could be used to diagnose *L. crotaloides* is probably an artifact of the lithographer who prepared the illustration supporting the original description. A revised diagnosis of *L. crotaloides* is provided on the basis of the new specimen. Despite the fragmentary nature of the new vertebra, it confirms the validity of *L. crotaloides*, although its exact relationships within Viperidae remain unknown. The new find supports the presence of a large viperid snake in the early Pliocene of northern Greece, adding further data to the diversity of giant vipers from Europe.

**Keywords** Serpentes · Viperids · Neogene · Greece · Gigantism

## 1 Introduction

In 1857, the eminent British palaeontologist Richard Owen described *Laophis crotaloides*, a new species of viperid snakes, on the basis of 13 large, fossilized vertebrae from Megalo Emvolon, near Thessaloniki, northern Greece. According to Owen, the vertebrae apparently belonged to a very large viperid with striking similarity to modern rattlesnakes (*Crotalus*). Ever since, *Laophis* has been regarded a mystery for ophidian palaeontology, with almost all subsequent authors neglecting it or considering it problematic, even if its proposed dimensions of more than three meters reached mythical standards (Kuhn 1939; Hoffstetter 1955; Rage 1984; Szyndlar 1991; Szyndlar and Rage 2002).

Here we report on a previously undescribed vertebra of a large snake from the same area of the type locality of *L. crotaloides* in northern Greece. Although the vertebra is fragmentary, it shares with the former taxon, overall large size and clear viperid features. This vertebra is here assigned to the species *L. crotaloides* and it currently represents the only available specimen for this taxon. Unfortunately, the fragmentary nature of the new vertebra precludes any precise conclusions about the taxonomic status of this taxon and the affinities of *Laophis* within the other members of the Viperidae cannot be clarified. Nevertheless, this new material confirms the validity of the

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taxon and further points that certain vertebral characters featured in the original description by Owen (1857) were in fact inaccurate. The occurrence and diversity of giant vipers in the European fossil record is discussed.

## 2 Materials and methods

The fossil material described in this study consists of an isolated vertebra that was collected in the early 1980s by Hans de Bruijn and Constantin Doukas in the locality of Megalo Emvolon, Greece. The vertebra is curated in the collections of the Institute of Earth Sciences Utrecht (The Netherlands) under the catalogue number KB3. Institutional Abbreviations are: KB, Karabournou collection of the Institute of Earth Sciences Utrecht (The Netherlands); MDHC, Massimo Delfino herpetological collection, Department of Earth Sciences of the University of Torino (Italy); NHM, The Natural History Museum, London (UK).

## 3 Geological setting and palaeoecology

### 3.1 Geology of Megalo Emvolon

Karabournou (also known as Karabournu, Karaburun or Falaise de Karaburun) is an old name for the modern Megalo Emvolon. Megalo Emvolon is situated in the northern part of the Gonia Formation, very near the city of Thessaloniki in the prefecture of Central Macedonia, northern Greece (Koufos et al. 1991). The Gonia Formation is highly fossiliferous and consists of both lenticular and massively bedded clays, sandstones, marls, and marly limestones (Syrides 1990). The locality of Megalo Emvolon was first discovered by Arambourg in the 1910s and is well known for its large mammals (Arambourg and Piveteau 1929; Koufos 2006). There is not a clear fossiliferous horizon in Megalo Emvolon, but several small fossil concentrations, which are dispersed across the deposits. It comprises three different fossiliferous levels: a lower one, Megalo Emvolon 1 (MEV), situated in the grey argillaceous sands near the bottom of the outcrop near the sea; Megalo Emvolon 2 (MEM), situated around twenty meters above MEV, above a bed with red sands and gravels; and Megalo Emvolon 3 (MEL), situated around ten meters above MEM, near the top of the section (Koufos et al. 1991). The characters of the sediments indicate a rapid deposition and the mammal fossils recovered from MEV, MEM and MEL do not suggest any age differences (Boev and Koufos 2000). Fossils found before the study of Koufos et al. (1991), cannot be accurately assigned to a precise level of Megalo Emvolon. This is also the case for the lost type material of *L. crotaloides*. The Megalo Emvolon section faunistically conforms to the early Pliocene (Zanclean–earliest Piacenzian) late Ruscinian European Land Mammal Zone MN 15, estimated at 4.2–3.2 Ma (Koufos et al. 1991; Koufos 2006).

*Remarks* About the type locality of *L. crotaloides*, Owen (1857:199) just mentioned that Captain Spratt collected these fossils from “Karabournou, on the eastern coast of the Gulf of Salonica” (=Thessaloniki). It is therefore impossible to know exactly from which of the several small fossil concentrations of Megalo Emvolon the snake vertebrae were collected. Captain Thomas Abel Brimage Spratt was heavily interested in fossils and had collected during his voyages with the British Navy across the Mediterranean, numerous specimens from several localities (Maempel 1986). He was also the author of several papers dealing with the geology of the localities he visited (Spratt 1842, 1847). Spratt is known to have visited the Thessaloniki area in March 1854, serving on the ship “Spitfire” (Maempel 1986) and he personally described the geology of the region three years later (Spratt 1857). In this paper, Spratt (1857:183) mentioned that he found the snake vertebrae, along with an indeterminate large mammal, “in the marls at about one mile N. E. of the Cape” (=Megalo Emvolon).

Given that the geology of Megalo Emvolon was not well established until the analysis of Koufos et al. (1991), several authors considered the age of *Laophis* as late Miocene (Zittel 1887–1890; Hoffstetter 1938, 1955; Kuhn 1939, 1963; Romer 1956; Młynarski et al. 1982), while Rage (1984) and Szyndlar (1991) regarded it as latest Miocene or earliest Pliocene.

### 3.2 Palaeoecology of Megalo Emvolon

The mammal fauna of Megalo Emvolon is speciose and relatively well studied. It includes the bovids *Gazella borbonica*, *Koufotragus bailloudi* and *Parabos macedoniae*, the suid *Sus minor*, the equid *Hipparion longipes*, various rodents and lagomorphs, the canid *Nyctereutes donnezani*, as also the cercopithecid *Dolichopithecus ruscinensis* (Arambourg and Piveteau 1929; Steffens et al. 1979; de Bruijn 1984; Koufos et al. 1991; Koufos and Koliadimou 1993; Koufos 1997), all indicative of a late Ruscinian (MN 15) age (Koufos 2006). The avifauna of Megalo Emvolon comprises only one bird fossil, the peafowl *Pavo bravardi* (Boev and Koufos 2000). Reptiles are represented by *L. crotaloides* (the only squamate recovered from the locality) and numerous small and giant tortoises (Bachmayer et al. 1980; Georgalis and Kear 2013). The mammal fauna indicates a semi-arid environment for Megalo Emvolon (Eronen and Rook 2004).

## 4 Systematic palaeontology

Squamata OPPEL 1811.
Serpentes LINNAEUS 1758.
Viperidae OPPEL 1811.

### 4.1 Genus *Laophis* OWEN 1857

*Type species L. crotaloides* OWEN 1857.
*Etymology* Owen (1857) provided a short etymology only for his new genus name: *Laophis* derives from the Greek words Las (Λᾶς), meaning stone in the ancient Doric dialect, and -ophis (ὄφις) denoting snake. Gender is masculine. Interestingly, another genus that shares an identical etymology, *Lithophis* [translated also as "stone snake" in Greek (λίθος + ὄφις)], has a similarly obscure taxonomic status, as it is just represented by a single fragmentary precloacal vertebra from the Eocene of Wyoming, USA (Marsh 1871; Rage 1984).
*Diagnosis* As for *L. crotaloides*, the only known species.

### 4.2 *Laophis crotaloides* OWEN 1857 (Figs. 1, 2a)

*Holotype* 13 precloacal vertebrae (Fig. 1). No catalogue number formally designated (Owen 1857) and the original material is now lost (Rage 1984; Szyndlar 1991; Szyndlar and Rage 2002). Our attempt to relocate the type material of *L. crotaloides* was not successful as well: the type material is not listed in the catalogues of the Natural History Museum in London (NHM) and apparently it is not present in the collections (S. Chapman, pers. comm. to M. D.).

It is impossible to determine if the type material ever entered the collections of the NHM. After the collection of the fossils by Captain Spratt, they were immediately sent to E. Forbes and deposited in the Museum of Economical Geology (later renamed as the Museum of Practical Geology, also known as the Geological Museum), in Jermyn Street, London (Spratt 1857) and apparently it was still present 3 years later, when Owen (1857) studied and published it. It is known, however, that by the end of the nineteenth century, the display cases of the museum were so overcrowded that it became necessary to discard all material not closely connected to the work and purposes of the Geological Survey (NHM Archives, accessed November 2015). It therefore is plausible that the 13 isolated vertebrae of *L. crotaloides* were not considered impressive enough and were discarded. Moreover, the collections of the Museum of Practical Geology are now part of the collections of the Natural History Museum, London and are known to have moved from Jermyn Street to Exhibition Road, South Kensington in 1935. The *L. crotaloides* type material could therefore have been lost during this collection transfer.
*New referred specimen* KB3, an incomplete precloacal vertebra (Fig. 2a).

*Etymology* Species name etymology was not provided in the original description by Owen, but it apparently refers to the rattlesnake genus *Crotalus* (Crotalinae) and -oides (-οειδές) for like. Gender is masculine. As such, the name *L. crotaloides* could translate as the "rattlesnake-like stone snake". We note that the diacritic mark used in the original spelling "*crotaloïdes*" is removed here following ICZN (1999) Article 32.5.2.1.

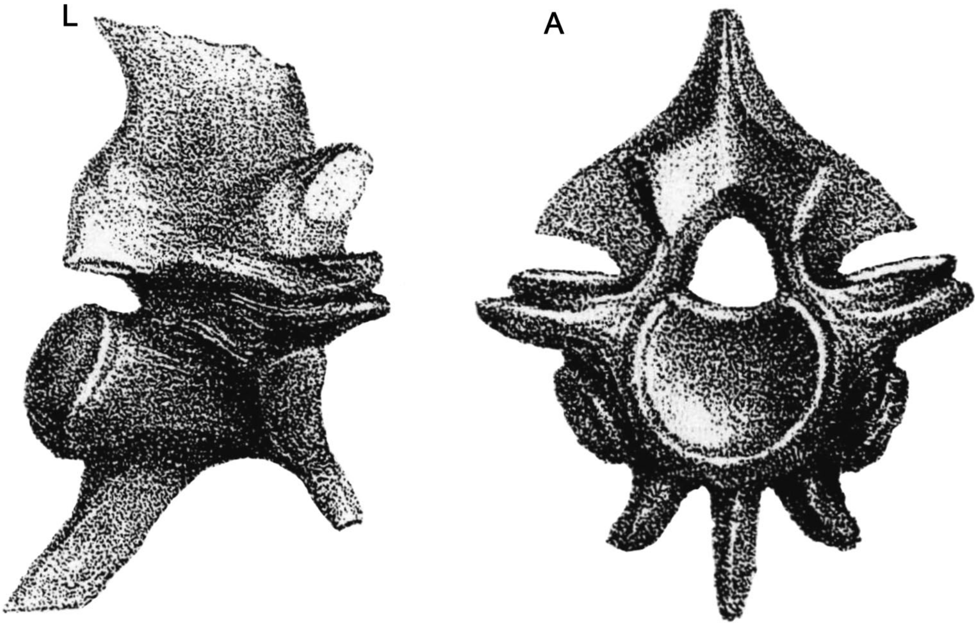


**Fig. 1** Type vertebra of *Laophis crotaloides* modified from the original publication by Owen (1857). Image not to scale (originally depicted by Owen 1857 in natural size). *A* anterior view, *L* lateral view

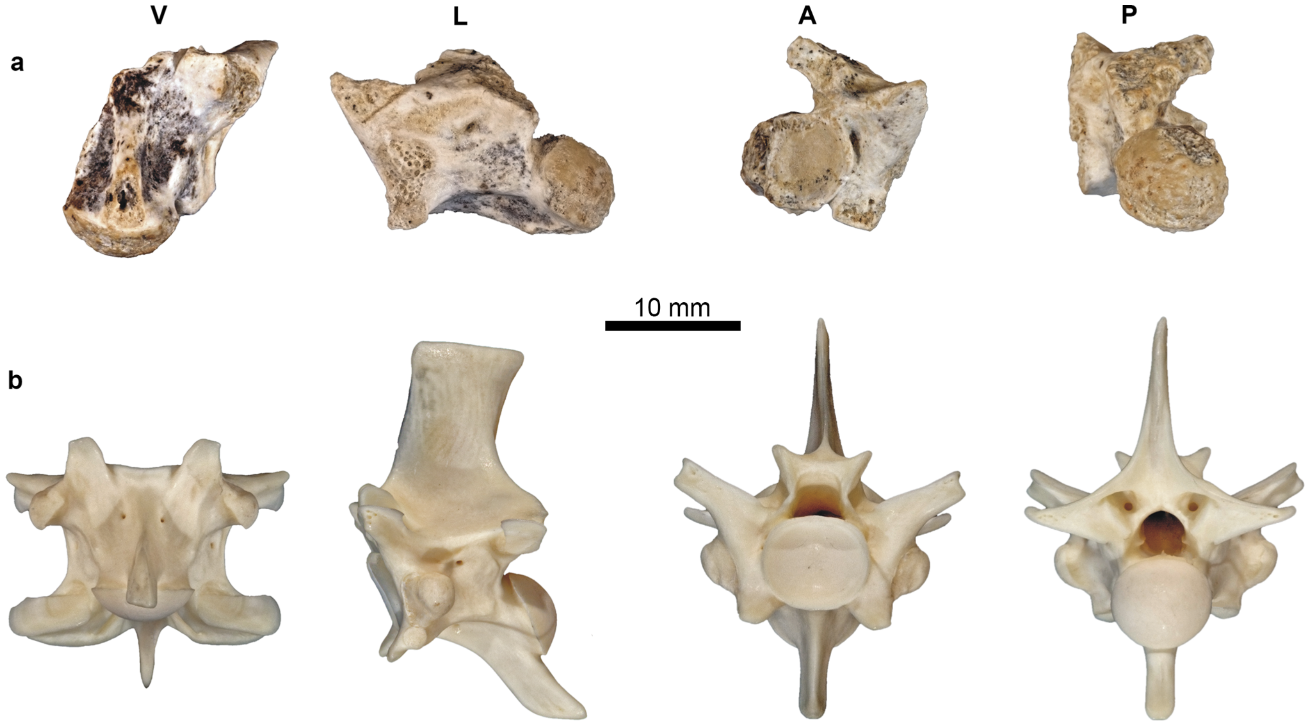


**Fig. 2** **a** Precloacal vertebra KB3, referred to *Laophis crotaloides*. **b** Precloacal vertebra (CL = 11.20 mm) of the extant large viperid *Bitis rhinoceros* (specimen MDHC 100). *Scale bar* 10 mm. *A* anterior view, *L* lateral view, *P* posterior view, *V* ventral view

*Occurrence* Megalo Emvolon (Central Macedonia, Greece), early Pliocene (late Ruscinian MN 15, equivalent to Zanclean to earliest Piacenzian). The taxon is known only from the type locality.

*Differential diagnosis* Taking into account the new specimen, *L. crotaloides* can be referred to the Viperidae on the basis of the proportionally wide cotyle and condyle (the latter of which is quite robust), the probable presence of hypapophysis, a relatively short centrum and, above all, the dorsally tilted prezygapophyseal facets (see characters in Szyndlar 1984, 1991). *L. crotaloides* can be differentiated from all other viperid snakes by the combination of the following characters: very large vertebral size (CL equal or larger than 15 mm); centrum proportionally short and broad in ventral view; cotyle much wider than the neural canal; condyle stout and proportionally large, elliptical in shape and being slightly wider than tall; diapophyses probably more developed than the parapophyses; and well developed parapophyseal processes.

*Remarks* The size, shape, general morphology and overall proportions of the new vertebra KB3 match those of the type material of *L. crotaloides* (see below), but the length of the condylar neck and the thickness of the prezygapophyseal facets are not as developed as shown by Owen (1857).

## 5 Description

### 5.1 The *Laophis crotaloides* type material described by Owen (1857)

In the original description of *L. crotaloides*, Owen (1857: pl. 4) figured one of the 13 vertebrae representing the type material of his new taxon, but only in lateral and anterior views (Fig. 1). According to the original figures, the vertebra appears to be strongly elongated dorsoventrally in lateral view. The centrum is short, whereas the neural spine and the hypapophysis are very large. The zygosphenal roof seems to be concave. The condyle is rather robust. In anterior view, the zygosphenal roof is strongly convex (contra the situation figured in lateral view). The prezygapophyseal articular part is very thick. The cotyle is extremely large, almost twice the size of the neural canal, whereas it seems to be rather concave. As is discussed below, the inconsistency of the features of the zygosphene in anterior and lateral views, as also the long condylar neck, lead Rage (1984) and subsequently Szyndlar (1991) to consider these characters as a product of fantasy of the lithographer.

*Laophis crotaloides* was described by Owen as the largest viperid snake (Szyndlar 1991), indicating a size "between 10 and 12 feet in length" (Owen 1857:199). Thanks to the drawings provided by Owen in natural size, it is possible to estimate several vertebral measurements for the type vertebra of *L. crotaloides*, justifying Owen's claims: the length of the centrum measured in lateral view from the concavity between the dia- and parapophyses is about 15 mm; the height of the vertebra from the tip of the neural spine to the tip of the hypapophysis is of at least about 30 mm (it is not clear if the neural spine was complete) if measured in lateral view and 28 mm if measured in anterior view; the distance between the lateral edges of the prezygapophyses is 32 mm; the cotyle is about 9 mm wide.

### 5.2 Specimen KB3

The vertebra KB3 is fragmentary, having preserved only part of the left prezygapophysis, part of the left half of the neural arch, and slightly more than the left half of the centrum (Fig. 2a). The prezygapophysis preserves part of the articular facet (but it is not possible to evaluate its former shape and that of the prezygapophyseal processes) that appears to be anterolaterally oriented in dorsal view and is dorsally tilted in anterior view. The cotyle is only partially preserved but it was clearly very wide—much wider than the neural canal—and it is accompanied by a small paracotylar foramen placed close to the dorsolateral quadrant of the cotyle (only the left quadrant is preserved). The preserved portion of the cotyle rim, despite a little erosion, clearly indicates that the cotyle does not protrude significantly from the anterior profile of the vertebra. Dia- and parapophysis are nearly entirely eroded but it seems that the former was more developed than the latter. The parapophyseal process was probably well developed as suggested by the remnants of its basis; the medial surface of the process was delimited by a small ridge. In ventral view, the centrum is proportionally short and broad. The centrum length (CL) can be estimated to be 15 mm (slightly higher—about 16.3 mm—if measured in lateral view, from the concavity between the dia- and the parapophysis to the posterior tip of the condyle). The hypapophysis is not preserved with the exception of its anterior, keel-like prolongation. The posterior edge of the hypapophysial root reached the condyle. On each side of the keel, at mid centrum length, there is a tiny subcentral foramen laying in a deep subcentral groove laterally delimited by an evident subcentral ridge. A small lateral foramen is placed at the bottom of a funnel depression. Anterodorsally to this foramen, between the interzygapophyseal ridge and the eroded diapophysis, there is another depression with an elongated shape. The condyle is stout and proportionally large; it is elliptical in shape, being slightly wider (about 7.9 mm) than tall (about 6.4 mm). The ventral edge of the condyle is placed slightly posterior than the dorsal edge. The development of the condylar neck can be evaluated thanks to the landmark represented by the base of the posterior edge of the neural arch: even if it is quite apparent due to the absence of the posterior region of the neural arch, the space between the base of the latter and the anterior edge of the condyle is of about 1 mm and therefore, considering the length of the vertebra, the condylar neck is not significantly different from that of extant snakes, as was (probably erroneously) shown in the original description.

## 6 Discussion

### 6.1 The mystery of *Laophis crotaloides*: taxonomic history, affinities and status

The taxonomic status of *L. crotaloides* has been a mystery for ophidian palaeontology since its original description by Owen in 1857. The fact that the type and previously only known material is considered lost, further hindered and complicated the knowledge of its affinities. As such, *Laophis* was mostly omitted in most subsequent publications regarding fossil snakes, with only few exceptions that treated it as a problematic taxon (Kuhn 1939, 1963; Rage 1984; Szyndlar 1991; Szyndlar and Rage 1999, 2002).

As mentioned above, Owen (1857) described and named the new species *L. crotaloides* on the basis of 13 isolated vertebrae that he compared with those of a number of extant species. He concluded that *L. crotaloides* bore close resemblance to modern vipers; however, the material was sufficiently distinct at the specific level. He further speculated affinities with rattlesnakes (Crotalinae), but he acknowledged that the limited available material could not allow him determine whether the 13 fossil vertebrae originated from the anterior or mid-trunk regions of the snake body and as such, no certain taxonomic conclusions could be made. Owen (1857) strongly emphasized the absolute size of his new taxon, pointing vertebral size similar with large extant pythonids.

There are not many discussions or mentions of *L. crotaloides* in the literature despite the more than 150 years since its original description. Römer (1870) noted that the vertebrae of *L. crotaloides* shared several characteristics with extant *Crotalus.* Rochebrune (1880) cited *L. crotaloides* in his list of fossil snakes, without any further comment. While, the idea of rattlesnake affinities of *L. crotaloides* was not concluded with certainty by Owen, Zittel (1887–1890) listed this taxon in Crotalidae, mentioning also Owen's (1857) size estimate of more than three meters for this taxon. Similar taxonomic affinities were later followed by Hoffstetter (1938), whereas 1 year later, Kuhn (1939) allocated *L. crotaloides* to Crotalidae (=Viperidae sensu lato, under the modern sense), the same family to which he assigned also the extant genus *Vipera* Laurenti, 1768. However, he did not provide any justification for the assignment of *L. crotaloides* to this group (Kuhn 1939). Later, Hoffstetter (1955) stated that *L. crotaloides* displayed indeed the characteristics of the Viperidae and was considered a crotaline snake; however, according to the same author, an alternative allocation of the Greek taxon to viperines, based solely on vertebrae, could not be excluded (Hoffstetter 1955). Romer (1956) made a brief mention on *Laophis* in his list of the genera of Crotalinae. Few years later, in his second edition of his snake volume of the "Fossilium Catalogus", Kuhn (1963) classified all known fossil viperids into two subfamilies, Viperinae and Crotalinae. Apparently influenced by Hoffstetter (1955), he continued to classify *Laophis* (as "? *Laophis* Owen, 1857") among the Crotalinae (Kuhn 1963:34), again with no further comments or justification explaining his decision. Młynarski et al. (1982) mentioned *L. crotaloides* in their description of the Miocene lower vertebrates from Opole, Poland. They referred to its age as Miocene and noted that *L. crotaloides* was the only European fossil snake attributed to Crotalinae known to date, even if it could not be shown with certainty that the taxon was a pit viper. In his complete treatise of fossil snakes, Rage (1984) considered that the characters used by Owen (1857) to establish *L. crotaloides* were widespread among viperids and that differentiation between viperines and crotalines simply on the basis of vertebral morphology was not possible. He additionally, considered the figures of Owen as inaccurate and further concluded that this taxon is a nomen dubium (Rage 1984). Three years later, Zerova et al. (1987) briefly hinted at *L. crotaloides* and briefly discussed the fact that this taxon could belong to crotalines. Later on, Szyndlar (1991) considered that taxonomic allocations of *L. crotaloides* to crotalines were most probably suggested because of erroneous interpretations surrounding its specific epithet. The same author highlighted the large centrum length of the vertebra, further postulated affinities of this taxon with the African genus *Bitis*, based on overall vertebral morphology, and considered the validity of *L. crotaloides* as an open question. In his description of the enigmatic viperid "*Coluber*" *kargii*, Szyndlar (1992) mentioned *L. crotaloides*, briefly stating that its taxonomic distinctiveness from other viperids cannot be demonstrated. Other short references to *L. crotaloides* were made by Rage in Golay et al. (1993) and by Szyndlar (1995) a few years later. Ivanov (1999) mentioned *L. crotaloides*, referring to its age as "lowermost Pliocene", noting also that this taxon was considered by Rage (1984) as a nomen dubium. As his main aim was to describe a fossil pit viper from Ukraine, he cited Szyndlar (1991:245) in assuming that "*Laophis* might have been a *Bitis*-like snake rather than a pit viper", therefore leaving his Ukrainian fossil as the only European pit viper. Subsequently, Szyndlar and Rage (1999) mentioned *L. crotaloides*, noted that its systematic status is unclear, although its assignment to Viperidae is unquestionable. They continued considering this taxon as a nomen dubium. The same authors, three years later, mentioned again *L. crotaloides* in their complete review of the fossil record of viperines (Szyndlar and Rage 2002), noting that its taxonomic status is uncertain. The last published mention of *L. crotaloides* was made by Wallach et al. (2014) who followed Rage (1984) in considering this taxon a nomen dubium.

Systematic assignment of *L. crotaloides* is hindered by uncertainties surrounding its vertebral anatomy. According to Szyndlar (1991), besides its absolute size, *L. crotaloides* as described and figured by Owen is characterized by two features that distinguish it from other large viperids: very thin parapophyseal processes and the long condylar neck. The referral of KB3 to the same taxon suggests that the condylar neck was erroneously illustrated in Owen's original figures and an elongated condylar neck is not a character of *L. crotaloides*; the shape and size of the parapophyseal processes of KB3 cannot be evaluated because of preservation reasons. Even if KB3 cannot definitively address this question, it indicates that at least one of the potential diagnostic characters of this taxon was probably related to the inaccuracy of the figure accompanying the description. The fact that the drawing provided by Owen (1857) is not accurate is testified by the zygosphenal roof, which, as already reported by Rage (1984) and Szyndlar (1991), is strongly convex in anterior view, but not in lateral view. The extreme thickness of the prezygapophyseal articular part (according to Szyndlar 1991) shown by the figures published by Owen (1857) probably does not reflect the original morphology of the specimen, as suggested by the morphology of KB3.

The taxonomic status of *L. crotaloides* cannot be evaluated with certainty on the basis of the new material, and it is not possible to allocate this taxon to either crotalines or viperines. On the basis of biogeography, however, it seems more plausible that *L. crotaloides* is a viperine, as crotalines are totally absent from the European fossil record, with the exception of a single occurrence in the Miocene of Ukraine (Ivanov 1999). Taxonomic assignment within viperines (true vipers) cannot also be established with certainty. Whether or not *L. crotaloides* had affinities with the "Oriental vipers complex" or *Daboia* (where the largest European species belong; see below) cannot be verified. The absolute large size of the *L. crotaloides* vertebra could indicate strong affinities with the coeval and similarly sized viperids from Mallorca and Layna, Spain (Szyndlar 1988; Bailon et al. 2010; Torres et al. 2014). The large geographic distance between Greece and Spain should

**Table 1** Published occurrences of Greek fossil Viperidae

| Taxon | Locality | Age | References |
|---|---|---|---|
| Viperidae indet. ('oriental vipers complex') | Maramena (Serres) | Latest Miocene (MN 13) | Szyndlar (1995) |
| *Laophis crotaloides* | Megalo Emvolon (Thessaloniki) | Early Pliocene (MN 15) | Owen (1857); this paper |
| Viperidae indet. ('oriental vipers complex') | Tourkobounia 1 (Attica) | Late Pliocene (MN 16) | Szyndlar (1991) |
| *Vipera* cf. *berus* | Laghada B (Kos Island) | Early Pleistocene | Szyndlar (1991) |
| *Vipera* cf. *berus* | Megalopolis (Peloponnese) | Middle Pleistocene | van Vugt (2000) |
| Viperidae indet. ('oriental vipers complex') | Latomi (Chios Island) | Middle Pleistocene | Schneider (1975) and Szyndlar (1991) |
| *Vipera* cf. *ammodytes* | Tourkobounia 2 (Attica) | Middle Pleistocene | Szyndlar (1991) |
| *Vipera* cf. *berus* | Tourkobounia 2 (Attica) | Middle Pleistocene | Szyndlar (1991) |

probably prompt us to be cautious when dealing with such taxonomic assignments, but common faunal elements between Greek and Spanish Pliocene localities could favor this hypothesis. Both Megalo Emvolon and Layna localities share the same *Hipparion* species (Koufos et al. 1991) and as such, affinities of *L. crotaloides* with the large Spanish viperid *Daboia maxima* should not be ruled out. Moreover, the proximity of the Greek localities to western Asia and northern Africa, leaves the possibility that *L. crotaloides* was an immigrant from the East. Large fossil viperids from outside Europe are not sufficiently known, except for certain North American forms (Holman 2000). Judging from palaeobiogeography, affinities of *L. crotaloides* with large African *Bitis* spp. cannot be excluded. Vipers of the latter genus are also known to attain large size, exceeding 170 cm in total length (Spawls et al. 2002; Mallow et al. 2003). In fact, the vertebral morphology of *Bitis* spp. bears the closest resemblance with *L. crotaloides* among all true vipers, as was already noted by Szyndlar (1991). Indeed, mid-trunk vertebrae of both genera "are strongly elongate dorso-ventrally in lateral view, owing to exceptionally long hypapophyses and neural spines together with relatively short centra" (Szyndlar 1991:244). Vertebrae of both *Laophis* (at least as it is shown in the original illustration of Owen) and *Bitis* are more than twice as high (distance between the hypapophyseal tip and neural spine top) as long (centrum length) (Szyndlar 1991) (Fig. 2). *Bitis*, however, has never been recorded from Europe with certainty—two purported records from the Miocene of Hungary (Kormos 1911) and Spain (Piveteau 1927) have since been shown to represent a non-*Bitis* viperid (Szyndlar 1984, 1991) and a colubrid (Szyndlar and Rage 2002) respectively. The African fossil record of squamates, that could potentially include large sized *Bitis* or *Bitis*-like forms, is not adequately sampled (Delfino et al. 2004; Rage and Bailon 2011) and this is unfortunately also the case for the Asian fossil viperids (Szyndlar and Rage 2002). With all the above taken into account, we cannot make any certain conclusions regarding the exact taxonomic affinities of *L. crotaloides* within the Viperidae. However, the taxon should no longer be considered a nomen dubium, as the new vertebra bears a unique combination of characters, above all the very large absolute size (CL more than 15 mm), which can diagnose *L. crotaloides* as a distinct valid species.

## 6.2 Fossil viperid snakes from Greece

Viperids are conspicuous elements of the extant Greek herpetofauna, comprising several species, one of which is endemic (Valakos et al. 2008). Species that currently inhabit Greece include *Vipera ammodytes* LINNAEUS 1758, widespread throughout the Cyclades and Eastern Aegean Islands, *Vipera berus* LINNAEUS 1758, distributed in Macedonia and Thrace, *Vipera ursinii* BONAPARTE 1835, from central and northern Greece, *Montivipera xanthina* (GRAY 1849) in Thrace and Eastern Aegean Islands, and *Macrovipera schweizeri* (WERNER 1935), endemic to Milos Archipelago and Siphnos Island (Valakos et al. 2008).

The past distribution of viperids currently living in Greece is unclear due to the limited available fossil material and the scarcity of the remains, mostly lacking diagnostic features. Nevertheless, fossil viperids have been sporadically recovered from Greek localities (Table 1). Miocene vipers are almost absent from Greek localities, but this should be of no surprise, as reptiles in general are rather rarely documented from that period in Greece (Römer 1870; Richter 1995; Delfino et al. 2008; Georgalis et al. 2013; Georgalis et al. 2016). An indeterminate viperid from Maramena, Central Macedonia, represents an exception, as it is the only Miocene viper from Greece. The Maramena viperid has been assigned to the "Oriental vipers complex" and is believed to have reached a relatively large size (Szyndlar 1995). Apart from *L. crotaloides* and the material from Maramena, the only other Neogene viperid from Greece is recorded from the late Pliocene of Tourkobounia 1 in Attica (Fig. 4b). This has been referred to the "Oriental vipers complex" and represents a rather large taxon, having an estimated centrum length of 10.1 mm (Szyndlar 1991). It is worth noting that Szyndlar (1991:249) dubbed this specimen as "the largest viper known from East European sites." All other fossil occurrences of vipers from Greece represent Pleistocene records that could represent the extant species or indeterminate viperids. Most notable among them is a very large viperid from the Middle Pleistocene of Latomi, Chios Island, which bears strong vertebral resemblance (CL more than 6 mm) with large-sized *Macrovipera lebetina* (Schneider 1975; Nilson and Andrén 1986; Szyndlar 1991), a

**Table 2** Geographic and stratigraphic distribution of the largest European fossil viperids, along with their respective maximum vertebral CL

| Taxon | Locality | Age | Maximum centrum length (CL) (mm) | References |
|---|---|---|---|---|
| *Laophis crotaloides* (KB 3 specimen) | Megalo Emvolon, Greece | Early Pliocene (MN 15) | 16.30 | This study |
| *Laophis crotaloides* (lost holotype) | Megalo Emvolon, Greece | Early Pliocene (MN 15) | 15 | Owen (1857) and Szyndlar (1991) |
| Viperidae indet. ('oriental vipers complex') | Na Burguesa-1 (Mallorca), Spain | Pliocene (MN 15/MN 16) | 15[a] | Torres et al. (2014) |
| Viperidae indet. ('oriental vipers complex') | Calo den Rafelino (Mallorca), Spain | Pliocene (MN 15/MN 16) | 12.70 | Bailon et al. (2010) |
| *Daboia maxima* ('*Daboia* complex') | Layna, Spain | Early Pliocene (MN 15) | 11.80 | Szyndlar (1988) and Szyndlar and Rage (1999) |
| Viperidae indet. ('oriental vipers complex') | Langenau, Germany | Early Miocene (MN 4) | 10.50 | Szyndlar and Rage (1999) |
| Viperidae indet. ('*Daboia* complex') | Vieux-Collonges, France | Early to middle Miocene (MN 4/MN 5) | 10.20 | Szyndlar and Rage (1999) |
| Viperidae indet. ('oriental vipers complex') | Tourkobounia 1, Greece | Late Pliocene (MN 16) | 10.10 | Szyndlar (1991) |
| *Macrovipera lebetina* ('oriental vipers complex') | Aetokremnos, Cyprus | Holocene | 10.07 | Bailon (1999) |
| Viperidae indet. ('Oriental vipers complex') | Vallée de la Canterrane, France | Pliocene (undetermined) | 9.67 | Bailon (1991) |
| *Macrovipera sarmatica* ('oriental vipers complex') | Calfa, Moldova | Late Miocene (MN 9) | 9.40 | Zerova et al. (1987) and Szyndlar (1991) |
| *Macrovipera kuchurganica* ('oriental vipers complex') | Kuchurgan, Ukraine | Early Pliocene (MN 14) | 9.10 | Zerova et al. (1987) and Szyndlar (1991) |
| Viperidae indet. ('oriental vipers complex') | La Grive, France | Middle Miocene (MN 7/MN 8) | 8.70 | Szyndlar and Rage (1999) |
| Viperidae indet. ('oriental vipers complex') | Rustavi, Georgia | Late Miocene (MN 10) | 8.60 | Zerova et al. (1987) and Szyndlar and Rage (2002) |
| Viperidae indet. ('oriental vipers complex') | Artenay, France | Early Miocene (MN 4) | 8.60 | Szyndlar and Rage (1999) |
| Viperidae indet. ('oriental vipers complex') | Iles Medas, Spain | Late Pliocene (MN 16) | 8.40 | Bailon (1991) |
| Viperidae indet. ('oriental vipers complex') | Steinheim, Germany | Middle Miocene (MN 7/MN 8) | 8.30 | Szyndlar and Rage (1999) |
| Viperidae indet. ('oriental vipers complex') | Maramena, Greece | Late Miocene (MN 13) | 8.10 | Szyndlar (1995) |
| Viperidae indet. ('oriental vipers complex') | Sandelzhausen, Germany | Middle Miocene (MN 6) | 8.10 | Szyndlar and Rage (1999) |

[a] It is not possible to know the CL of the Na Burguesa-1 vertebra because it is incomplete. Torres et al. (2014) provide a measurement of the distance from the anterior tip to the prezygapophysis to the posterior tip of the postzygapophysis: 15.1 mm. This distance is smaller than the CL in viperid snakes, a fact that was also reevaluated by additional measurements in the vertebrae of *Agkistrodon piscivorus* (MDHC 103), *Bitis rhinoceros* (MDHC 100) and *Macrovipera lebetina* (MDHC 317)

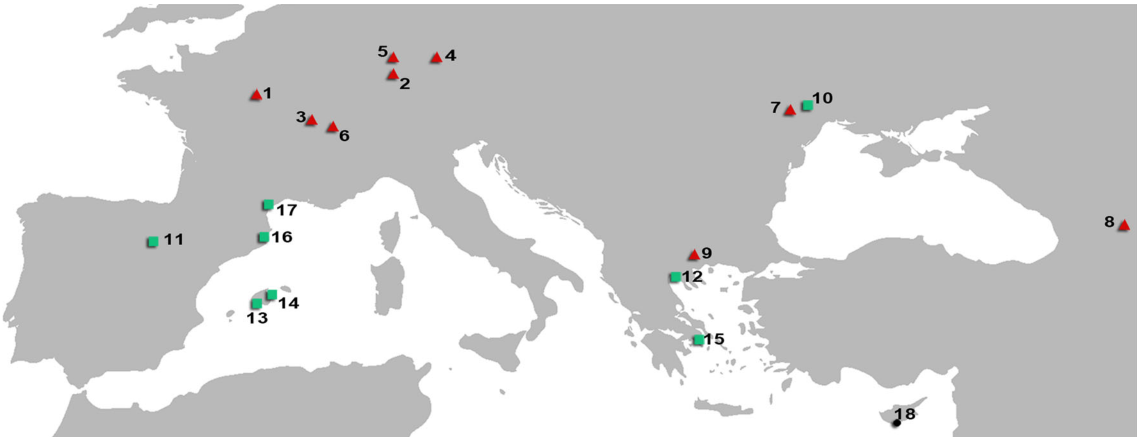


**Fig. 3** Map of Europe, indicating the fossil localities bearing large viperids (CL ≥ 8 mm). *Triangles* represent Miocene, *squares* represent Pliocene and *circles* represent Pleistocene and Holocene localities. *1* Artenay (France), *2* Langenau (Germany), *3* Vieux-Collonges (France), *4* Sandelzhausen (Germany), *5* Steinheim (Germany), *6* La Grive (France), *7* Calfa (Moldova), *8* Rustavi (Georgia), *9* Maramena (Greece), *10* Kuchurgan (Ukraine), *11* Layna (Spain), *12* Megalo Emvolon (Greece), *13* Calo den Rafelino (Spain), *14* Na Burguesa-1 (Spain), *15* Tourkobounia 1 (Greece), *16* Iles Medas (Spain), *17* Vallée de la Canterrane (France), *18* Aetokremnos (Cyprus)

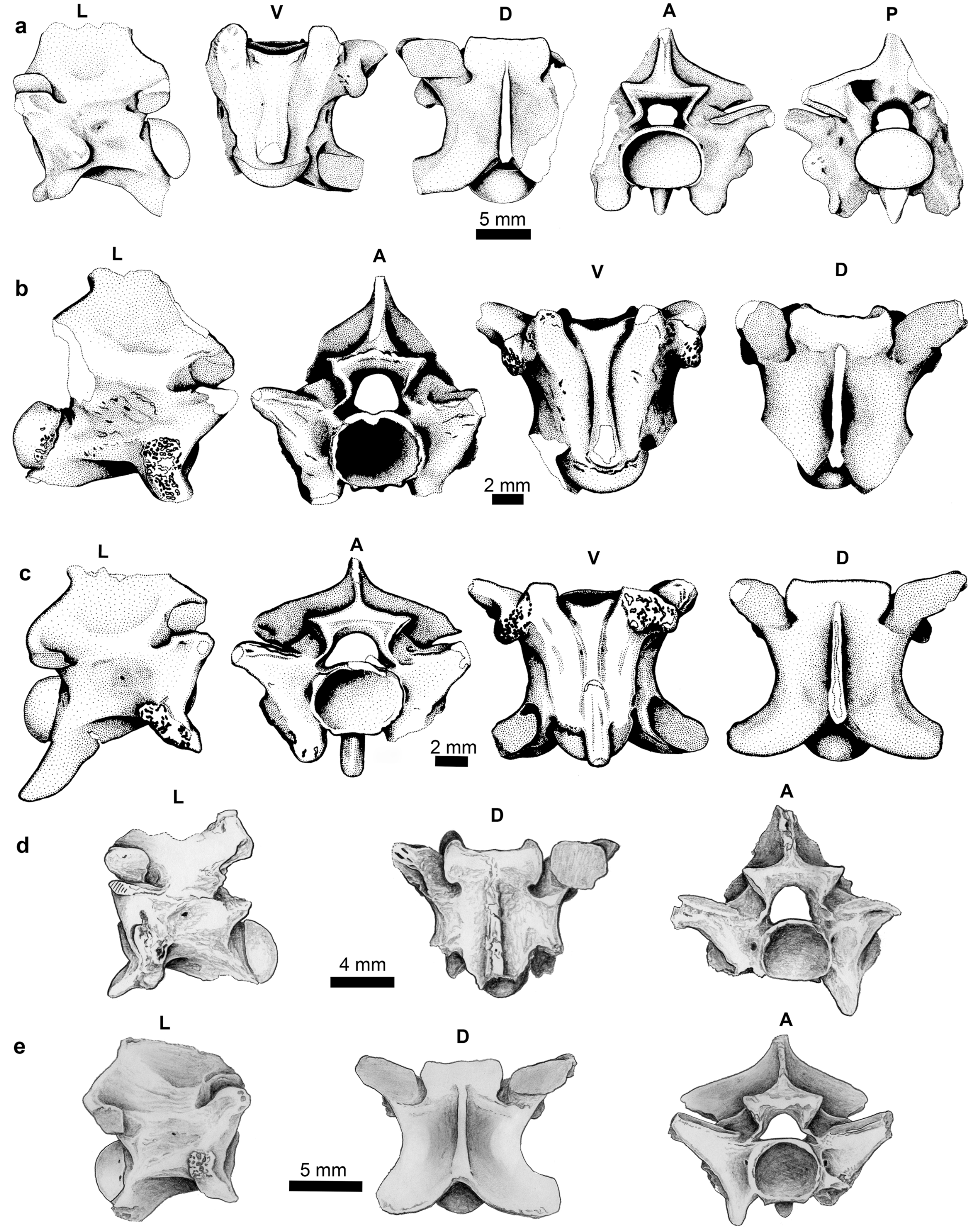
species that does not occur in the extant herpetofauna of the country.

### 6.3 Gigantism among European Viperidae

With a maximum estimated centrum length (CL) of 16.3 mm, the new vertebra of *L. crotaloides* ranks as the largest one among European viperids (Table 2). It is beyond the scope of this paper to provide a size estimation for *L. crotaloides* based on vertebral dimensions. Nevertheless, large to very large body sizes have been documented several times among the fossil record of European vipers (Rage 1984; Szyndlar 1991). Viperid snakes first appeared in Europe during the early Miocene (MN 1) (Kinkelin 1892; Rage 1984; Szyndlar 1987b; Szyndlar and Rage 2002; Čerňanský et al. 2015), becoming quickly widespread throughout the continent (Szyndlar 1991) and achieving large sizes already by the MN 4 (Szyndlar and Rage 1999) (Fig. 3). The appearance of large-sized viperids in Europe slightly coincides with the Miocene Climatic Optimum (Böhme 2003). Regarding the taxonomy of the European viperids to the genus level, several different approaches have appeared in the literature, most of which are based strictly on molecular data (Nilson and Andrén 1986; Herrmann et al. 1992; Lenk et al. 2001), as few or no osteological characters are known that could support such division (Bailon et al. 2010). We follow here the subdivision of viperines according to Szyndlar and Rage (1999) who focused on the morphology of the trunk vertebrae of viperines, a study that could directly apply to fossil specimens. These groupings are the "*Vipera berus* complex", "*Vipera aspis* complex", "Oriental vipers complex" and *Daboia.* The former two comprise relatively small taxa, whereas the latter two comprise the largest ones (Szyndlar and Rage 1999; Bailon et al. 2010).

*Daboia*, an extant Asian genus, is represented in Europe only by *D. maxima* (originally placed in *Vipera*), which was described by Szyndlar (1988) as a new large viperid species from the Pliocene (MN 15) of Layna, Spain (Fig. 4a). This species was initially assigned to the "Oriental vipers complex", as this group is known to possess much larger and relatively shorter vertebral centra, comparing to other European vipers (Szyndlar 1987a, 1988, 1991). However, it is now believed that *Daboia* is excluded from this group, as this genus can be differentiated from the "Oriental vipers complex" on the basis of the trunk vertebrae showing a greater development of the neural spine, which is higher than long (Szyndlar and Rage 1999; Bailon et al. 2010). With a vertebra centrum length and centrum width of 11.80 and 10.32 mm respectively, this Spanish taxon was supposed to be the largest viperine species (Szyndlar and Rage 2002). However, these vertebral dimensions are still smaller than the original type material of *L. crotaloides* and the new referred specimen. Another possible occurrence of *Daboia* in Europe could be an indeterminate large viperid from the early to middle Miocene of Vieux-Collonges, France (Szyndlar and Rage 1999) (Fig. 4e).

The so called "Oriental vipers complex" (genera *Macrovipera* and *Montivipera*) comprises some of the largest viperine species (Szyndlar 1991). This group has currently a very small distribution in Europe, existing only in the easternmost mainland Greece, the Cyclades islands, Cyprus, and European Turkey, but had achieved a much wider distribution during the Neogene (Szyndlar 1991).


a
L
V
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5 mm
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2 mm
d
L
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5 mm

◀ **Fig. 4** Mid-trunk vertebrae of large European fossil viperids. **a** *Daboia maxima* (early Pliocene of Layna, Spain). **b** Viperidae indet. (late Pliocene of Tourkobounia 1, Greece). **c** *Macrovipera kuchurganica* (early Pliocene of Kuchurgan, Ukraine). **d** Viperidae indet. (early Miocene of Langenau, Germany). **e** Viperidae indet. (early Miocene of Vieux-Collonges, France). **a** From Szyndlar 1988; **b**, **c** from Szyndlar 1991; **d**, **e** from Szyndlar and Rage 1999; Images used with permission. *A* anterior view, *D* dorsal view, *L* lateral view, *P* posterior view, *V* ventral view

Species of "Oriental vipers" are differentiated from the much smaller European vipers by having much larger and relatively shorter vertebral centra, relatively higher neural spines and longer hypapophyses (Szyndlar 1987a, 1988). "Oriental vipers" from Europe, achieved a fairly large size already by the early to middle Miocene, as it is documented by large vertebrae from the localities of Langenau, Steinheim and Sandelzhausen (Germany) and La Grive and Artenay (France) (Szyndlar and Rage 1999) (Fig. 4d). They quickly became rather diverse and widespread throughout Europe: apart from the Greek records from Maramena and Tourkobounia 1 that were mentioned above, large "Oriental vipers" are also known from several other localities from the continent. It is worth noting that they are known from both edges of the Mediterranean Europe: in the East, an exceptionally large specimen of *Macrovipera lebetina* from the Neolithic site of Aetokremnos, Cyprus (10th millennium BC) (Bailon 1999), whereas in the West, Bailon et al. (2010) described a fragmentary vertebra belonging to a large "Oriental viper" from Calo del Rafelino of Mallorca. With a centrum length of the trunk vertebra equal to 12.70 mm, the Mallorca viperid is even larger than *Daboia maxima*, whereas the authors suggested a body length of "close or greater than 200 cm" (Bailon et al. 2010:151). More recently, an even larger viperid was described from the Pliocene of Na Burguesa-1, Mallorca (Torres et al. 2014). Large snakes of the 'Oriental vipers complex' have also been recorded from the Pliocene of Iles Medas, Spain and Vallée de la Canterrane, France (Bailon 1991).

Smaller, but still of considerable size, "Oriental viper" taxa have also been reported from the central part of eastern Europe: *Macrovipera sarmatica* and *M. kuchurganica.* The former species, from the late Miocene (MN 9) of Calfa (Kalfa), Moldova is believed to have attained a fairly large size, estimated on the basis of a centrum length of 9.10 mm (Zerova et al. 1987; Szyndlar 1991), whereas the latter originates from the early Pliocene of Kuchurgan, Ukraine, and bears strong resemblance with the extant *Macrovipera lebetina* (Zerova et al. 1987; Szyndlar 1991) (Fig. 4c). As was noted by Szyndlar and Rage (2002), *Macrovipera sarmatica* has also a bizarre taxonomic history: it was published as a new species by its name giving authors, Chkhikvadze and Lungu, in two different papers (Zerova et al. 1987; Lungu et al. 1989)! Zerova et al. (1987) also described another large, but unnamed viperid from Rustavi, Georgia.

Still undescribed specimens of "Oriental vipers" have been repeatedly mentioned in the literature, indicating the broad distribution of these snakes in Europe during the Neogene (Delfino 2002; Szyndlar and Rage 2002). Szyndlar (1988) briefly mentioned an undescribed viperid of "enormous size" from the Pliocene of Vilafant, Spain. The fact, however, that these specimens are still undescribed, hinders establishment of their affinities within Viperidae. Nevertheless, large to giant vipers were widespread in Europe during the Neogene, with their range being contracted only to the Mediterranean edges of the continent by the Pliocene. Large vipers probably did not survive the Plio-Pleistocene in western Europe as there are no post Pliocene fossils from that area, whereas they still survive in the eastern edge of the continent, having extant representatives in the Greek islands (*Macrovipera schweizeri*) and Cyprus (*Macrovipera lebetina*).

## 7 Conclusions

A precloacal vertebra, found in the early Pliocene of Megalo Emvolon, northern Greece, is referred to the enigmatic viperid species *L. crotaloides*, previously described from the same locality. As the type and previously only known material of this taxon is considered lost, the new vertebra described herein represents the sole available specimen for *L. crotaloides.* The vertebra is highly fragmentary, but nevertheless bears a unique combination of characters (very large vertebral size, with CL equal or larger than 15 mm; centrum proportionally short and broad in ventral view; cotyle much wider than the neural canal; condyle stout and proportionally large, elliptical in shape and being slightly wider than tall; diapophyses probably more developed than the parapophyses; and well developed parapophyseal processes) that enables us to diagnose *L. crotaloides.* The exact affinities of this species within the Viperidae still cannot be concluded with certainty, but its specific validity is justified. The presence of a giant viperid snake in the Pliocene of Greece is confirmed. The new specimen further adds to the diversity and distribution of fossil vipers from the country and the giant vipers of Europe in general.

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## References

Arambourg, C., & Piveteau, J. (1929). Les vertebres du Pontien de Salonique. *Annales de Paléontologie, 18*, 59–138.

Bachmayer, F., Młynarski, M., & Symeonidis, N. (1980). Fossile Schildkroten aus dem Pliozan von Megalo Emvolo (Karaburun) bei Saloniki (Griechenland) A. Eine fossile Maurische Landschildkrote (*Testudo* cf. *graeca* Linne) B. Fossile reste von Riesenschilkroten. *Annales Géologiques des Pays Helléniques, 31*, 267–276.

Bailon, S. (1991). Amphibiens et Reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes. *PhD dissertation*, Université de Paris VII, Paris, France, 499 + 89 pp.

Bailon, S. (1999). Toad and snake. In A. H. Simmons (Ed.), *Faunal extinction in an island society* (pp. 182–186). New York: Kluwer Academic/Plenum Publishers.

Bailon, S., Bover, P., Quintana, J., & Alcover, J. A. (2010). First fossil record of *Vipera* Laurenti 1768 "Oriental vipers complex" (Serpentes: Viperidae) from the Early Pliocene of the western Mediterranean islands. *Comptes Rendus Palevol, 9*, 147–154.

Boev, Z., & Koufos, G. (2000). Presence of *Pavo bravardi* (Gervais, 1849) (Aves, Phasianidae) in the Ruscinian locality of Megalo Emvolon, Macedonia, Greece. *Geologica Balcanica, 30*, 69–74.

Böhme, M. (2003). The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology, 195*, 389–401.

Bonaparte, L. (1835). *Iconographia della Fauna Italica per le quattro classi degli animali vertebrati. Tome 2* (264 pp.). Rome: Salviucci.

Čerňanský, A., Rage, J.-C., & Klembara, J. (2015). The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. *Journal of Systematic Palaeontology, 13*, 97–128.

de Bruijn, H. (1984). Remains of the mole-rat *Microspalax odessanus* Topachevski, from Karaburun (Greece, Macedonia) and the family Spalacidae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B, 87*, 417–424.

Delfino, M. (2002). Erpetofaune italiane del Neogene e del Quaternario. *PhD dissertation*, University of Modena and Reggio Emilia, Modena and Reggio Emilia, Italy, 382 pp.

Delfino, M., Kotsakis, T., Arca, M., Tuveri, C., Pitruzella, G., & Rook, L. (2008). Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. *Geodiversitas, 30*, 641–656.

Delfino, M., Segid, A., Yosief, D., Shoshani, J., Rook, L., & Libsekal, Y. (2004). Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression). In E. Abbate, B. Woldehaimanot, Y. Libsekal, T.M. Tecle & L. Rook (Eds.), A step towards human origins. The Buia *Homo* one-million-years ago in the Eritrean Danakil Depression (East Africa) (pp. 51–60). *Rivista Italiana di Paleontologia e Stratigrafia, 110*(supplement) (144 pp). Milano: Università di Milano.

Eronen, J., & Rook, L. (2004). The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *Journal of Human Evolution, 47*, 323–341.

Georgalis, G. L., & Kear, B. P. (2013). The fossil turtles of Greece: an overview of taxonomy and distribution. *Geobios, 46*, 299–311.

Georgalis, G. L., Velitzelos, E., Velitzelos, D., & Kear, B. P. (2013). *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the lower Miocene of northern Greece. In D. Brinkman, P. Holroyd, & J. Gardner (Eds.), *Morphology and evolution of turtles: papers in honor of Eugene S. Gaffney. Volume 3. Pleurodires* (pp. 277–287). Dordrecht: Springer.

Georgalis, G. L., Villa, A., & Delfino, M. (2016). First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. *The Science of Nature, 103*, 12. doi:10.1007/s00114-016-1336-5

Golay, P., Smith, H. M., Broadley, D. G., McCarthy, C., Rage, J.-C., Schätti, B., & Toriba, M. (1993). *Endoglyphs and other major venomous snakes of the world. A checklist* (478 pp.). Geneva: Azemiops Herpetological Data Center.

Gray, J. E. (1849). *Catalogue of the specimens of snakes in the collection of the British Museum* (125 pp.). London: Edward Newman.

Herrmann, H.-W., Joger, U., & Nilson, G. (1992). Phylogeny and systematics of Viperinae snakes. III: resurrection of the genus *Macrovipera* (Reuss, 1927) as suggested by biochemical evidence. *Amphibia-Reptilia, 13*, 375–392.

Hoffstetter, R. (1938). Ophidiens fossiles. *Bulletin de la Société Linnéenne de Lyon, 7*, 230–234.

Hoffstetter, R. (1955). Squamates de type moderne. In J. Piveteau (Ed.), *Traité de Paléontologie, Tome V (Amphibiens, Reptiles, Oiseaux)* (pp. 606–662). Paris: Masson et Cie.

Holman, J. A. (2000). *Fossil snakes of North America. Origin, evolution, distribution, paleoecology* (376 pp.). Bloomington and Indianapolis: Indiana University Press.

ICZN (International Commission on Zoological Nomenclature). (1999). *International code of zoological nomenclature* (4th ed.). London: International Trust for Zoological Nomenclature.

Ivanov, M. (1999). The first European pit viper from the Miocene of Ukraine. *Acta Palaeontologica Polonica, 44*, 327–334.

Kinkelin, F. (1892). Ein fossiler Giftzahn. *Zoologischer Anzeiger, 15*, 93–94.

Kormos, T. (1911). A Polgárdi pliocén csontlelet. *Földtani Közlöny, 41*, 48–64.

Koufos, G. D. (1997). The canids *Eucyon* and *Nyctereutes* from the Ruscinian of Macedonia, Greece. *Palaeontologia i Evolucio, 30–31*, 39–48.

Koufos, G. D. (2006). The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. *Annales Géologiques des Pays Helléniques, 4*, 183–214.

Koufos, G. D., & Koliadimou, K. (1993). Two lagomorphs from the Pliocene of Macedonia (Greece). *Bulletin of the Geological Society of Greece, 28*, 117–129.

Koufos, G., Syrides, G., & Koliadimou, K. (1991). A Pliocene primate from Macedonia. *Journal of Human Evolution, 21*, 283–294.

Kuhn, O. (1939). Squamata: Lacertilia et Ophidia. In W. Quenstedt (Ed.), *Fossilium Catalogus, I: Animalia, pars 86* (122 pp.). Neubrandenburg: Verlag Gustav Feller.

Kuhn, O. (1963). Serpentes (Supplementum I). In F. Westphal (Ed.), *Fossilium Catalogus, I: Animalia, pars 103* (45 pp.). Gravenhage: Uitgeverij Dr. W. Junk.

Laurenti, J. N. (1768). *Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota* *reptilium austracorum*, *quod authoritate et consensu* (217 pp.). Vienna: Joan. Thomae.

Lenk, P., Kalyabina, S., Wink, M., & Joger, U. (2001). Evolutionary relationships among the true vipers (Viperinae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution, 19*, 94–104.

Linnaeus, C. (1758). *Systema Naturae per regna tria naturae*, *secundum classes*, *ordines*, *genera*, *species*, *cum characteribus*, *differentiis*, *synonymis*, *locis* (824 pp.). Stockholm: Laurentii Salvii.

Lungu, A. N., Zerova, G. A., & Chkhikvadze, V. M. (1989). Large lizards and venomous snakes from the middle Sarmatian of Moldavia and significance of the fossil herpetofauna for paleoclimatology. In *Fauna i Flora Mezozoya i Kaynozoya Yuzhnykh Okrain Russkoy Platformy* (pp. 59–69). Kishinev: Izdatelstvo Shtiintsa **(in Russian)**.

Maempel, G. Z. (1986). T.A.B. Spratt (1811–88) and his contribution to maltese geology. *Melita Historica, 9*, 271–308.

Mallow, D., Ludwig, D., & Nilson, G. (2003). *True vipers. Natural history and toxinology of old world vipers* (359 pp.). Malabar: Krieger Publishing Company.

Marsh, O. C. (1871). Description of some new fossil serpents, from the Tertiary deposits of Wyoming. *The American Journal of Science and Arts, series, 3*(1), 322–329.

Młynarski, M., Szyndlar, Z., Estes, R., & Sanchiz, B. (1982). Lower vertebrate fauna from the Miocene of Opole (Poland). *Estudios Geológicos, 38*, 103–119.

Nilson, G., & Andrén, C. (1986). The mountain vipers of the Middle East—the *Vipera xanthina* complex (Reptilia, Viperidae). *Bonner Zoologische Monographien, 20*, 1–90.

Oppel, M. (1811). *Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben* (p. 86). München: Joseph Lindauer.

Owen, R. (1857). On the fossil vertebrae of a Serpent (*Laophis crotaloïdes*, Ow.) discovered by Capt. Spratt, R.N., in a tertiary formation at Salonica. *Quarterly Journal of the Geological Society of London, 13*, 196–199.

Piveteau, J. (1927). Etudes sur quelques amphibiens et reptiles fossiles. 1ère partie. *Annales de Paléontologie, 16*, 61–97.

Rage, J.-C. (1984). Serpentes. In P. Wellnhofer (Ed.), *Encyclopedia of paleoherpetology*, *part 11* (80 pp.). Stuttgart, New York: G. Fischer.

Rage, J.-C., & Bailon, S. (2011). Chapter 16, amphibia and squamata. In T. Harrison (Ed.), *Paleontology and geology of laetoli: human evolution in context. Volume 2: fossil hominins and the associated fauna*, *vertebrate paleobiology and paleontology* (pp. 467–478). New York: Springer.

Richter, A. (1995). The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). *Münchner Geowissenschaften Abhandlungen, 28*, 35–38.

Rochebrune, A. T. de (1880). Revision des ophidiens fossiles du Museum d'Histoire Naturelle. *Nouvelles Archives du Muséum d'Histoire Naturelle*, *2$^{ème}$ Série*, *3*, 271–296.

Romer, A. S. (1956). *Osteology of the reptiles* (772 pp.). Chicago: University of Chicago Press.

Römer, F. (1870). Über *Python euboicus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea. *Zeitschrift der Deutschen Geologischen Gesellschaft, 22*, 582–590.

Schneider, B. (1975). Ein mittelpleistozane Herpetofauna von der Insel Chios, Agais. *Senckenbergiana biologica, 56*, 191–198.

Spawls, S., Howell, K., Drewes, R., & Ashe, J. (2002). *A field guide to reptiles of East Africa* (546 pp.). London and San Diego: Academic Press.

Spratt, T. A. B. (1842). Notices connected with the geology of the island of Rhodes. *Proceedings of the Geological Society of London, 3*, 773–775.

Spratt, T. A. B. (1847). Remarks on the geology of the island of Samos. *Quarterly Journal of the Geological Society of London, 3*, 65–67.

Spratt, T. A. B. (1857). On the freshwater deposits of Euboea, the coast of Greece and Salonika. *Quarterly Journal of the Geological Society of London, 13*, 177–184.

Steffens, P., Bruijn, H. de, Meulenkamp, J. E., & Benda, L. (1979). Field guide to the Neogene of northern Greece (Thessaloniki area and Strimon basin). *Publications of the Department of Geology and Paleontology of the University of Athens series A*, *35*, l–14.

Syrides, G. E. (1990). Lithostratigraphical, biostratigraphical and palaeogeographical study of the Neogene/Quaternary sedimentary formations of Chalkidiki peninsula. *PhD dissertation*, Aristotle University of Thessaloniki, Thessaloniki, Greece, 243 pp. **[in Greek]**

Szyndlar, Z. (1984). Fossil snakes from Poland. *Acta Zoologica Cracoviensia, 28*, 1–156.

Szyndlar, Z. (1987a). Neogene "Oriental vipers" of Europe. In J. J. van Gelder, H. Strichbosch, & P. J. M. Bergers (Eds.), *Proceedings of the 4th ordinary general meeting of the societas europaea herpetologica* (pp. 378–390). Nijmegen: Catholic University.

Szyndlar, Z. (1987b). Snakes from the lower miocene locality of Dolnice (Czechoslovakia). *Journal of Vertebrate Paleontology, 7*, 55–71.

Szyndlar, Z. (1988). Two new extinct species of the genera *Malpolon* and *Vipera* (Reptilia, Serpentes) from the Pliocene of Layna Spain. *Acta Zoologica Cracoviensia, 31*, 687–706.

Szyndlar, Z. (1991). A review of neogene and quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios Geologicos, 47*, 237–266.

Szyndlar, Z. (1992). "*Coluber*" *kargii* von Meyer, 1845 (Serpentes: Viperidae), from the Miocene of Öhningen (Germany). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 1992* (11), 692–700.

Szyndlar, Z. (1995). The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 4. Serpentes (Squamata, Reptilia). *Münchner Geowissenschaften Abhandlungen, 28*, 35–39.

Szyndlar, Z., & Rage, J.-C. (1999). Oldest fossil vipers (Serpentes: Viperidae) from the old World. *Kaupia, 8*, 9–20.

Szyndlar, Z., & Rage, J.-C. (2002). Fossil record of the true vipers. In G. Scuett, M. Hoggren, M. Douglas, & H. Greene (Eds.), *Biology of the vipers* (pp. 419–441). Eagle Mountain: Eagle Mountain Publishing.

Torres E., Bailon, S., Bover, P., & Alcover, J. A. (2014). Sobre la presencia de un vipérido de gran talla perteneciente al complejo de víboras Orientales en el yacimiento de Na Burguesa-1 (Mioceno superior/Plioceno inferior, Mallorca). In R. Royo-Torres, F. J. Verdú & L. Alcalá (Eds.) *XXX Jornadas de Paleontología de la Sociedad Española de Paleontologia Fundamental*, *24*, 237–240. Teruel: Fundación Conjunto Paleontológico de Teruel-Dinópolis.

Valakos, E. D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., & Foufopoulos, J. (2008). *Amphibians and reptiles of Greece* (463 pp.). Frankfurt: Chimaira.

van Vugt, N. (2000). Orbital forcing in late Neogene lacustrine basins from the Mediterranean. A magnetostratigraphic and cyclostratigraphic study. *Geologica Ultraiectina*, *189*, 167.

Wallach, V., Williams, K. L., & Boundy, J. (2014). *Snakes of the world: a catalogue of living and extinct species* (1237 pp.). Boca Raton, London and New York: CRC Press.

Werner, F. (1935). Reptilien der Ägäischen Inseln. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien, 144*, 81–117.

Zerova, G. A., Lungu, A. N., & Chkhikvadze, V. M. (1987). Large fossil vipers from northern Black Seaside and Transcaucasus. *Trudy Zoologicheskogo Instituta, 158*, 89–99.

Zittel, K. A. von (1887–1890). *Handbuch der Paläontologie. Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces*, *Amphibia*, *Reptilia*, *Aves)* (900 pp.). Munich, Leipzig: Oldenbourg.

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ORIGINAL PAPER

# First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group

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**Abstract** The fossil record of Chamaeleonidae is very scarce and any new specimen is therefore considered important for our understanding of the evolutionary and biogeographic history of the group. New specimens from the early Miocene of Aliveri (Evia Island), Greece constitute the only fossils of these lizards from southeastern Europe. Skull roofing material is tentatively attributed to the Czech species *Chamaeleo* cf. *andrusovi*, revealing a range extension for this taxon, whereas tooth-bearing elements are described as indeterminate chamaeleonids. The Aliveri fossils rank well among the oldest known reptiles from Greece, provide evidence for the dispersal routes of chameleons out of Africa towards the European continent and, additionally, imply strong affinities with coeval chamaeleonids from Central Europe.

**Keywords** Chamaeleonidae · Squamata · Miocene · Biogeography · Aliveri

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## Introduction

Chameleons (Squamata, Chamaeleonidae) constitute a rather diverse group with more than 200 species that are now distributed in Africa, Madagascar and several other Indian Ocean islands, southern Asia, Cyprus and southern parts of Mediterranean Europe (Glaw 2015). Cryptic diversity appears to be prominent within the group, with several new species having been described only during the current decade, mostly on the basis of molecular data (Gehring et al. 2011; Crottini et al. 2012; Greenbaum et al. 2012; Stipala et al. 2011, 2012; Tilbury and Tolley 2015). The size range of chamaeleonids is also broad and astonishing, with the larger members of the family surpassing 600 mm in total length (Glaw and Vences 1994), whereas the smallest species rank well among the tiniest known reptiles, both extant (*Brookesia micra*, attaining only 29 mm [Glaw et al. 2012]) and extinct (e.g. *Jucaraseps grandipes* [Bolet and Evans 2012]). The ability of some species to 'change' colour, along with their peculiar external morphology, have gained the attention of the public for centuries and render them readily distinguishable even for non-specialists (Teyssier et al. 2015). Moreover, their bizarre external appearance, acrodont dentition, unique skeletal anatomy, as even their specialized feeding and locomotor habits have long lead herpetologists to consider chameleons as a monophyletic group (Camp 1923; Estes 1983). Their relationships to other squamates, however, are yet not fully resolved, mostly because of the uncertainty of the position of Iguania, but it is widely accepted that Chamaeleonidae constitute a group within the iguanian clade Acrodonta (Estes et al. 1988; Townsend et al. 2004; Kumazawa 2007; Conrad 2008; Vidal and Hedges 2009; Gauthier et al. 2012; Wiens et al. 2012; Pyron et al. 2013; Reeder et al. 2015), even if their affinities with Agamidae are a matter of debate, with different topologies arising on the basis of morphological and molecular data (Bolet and Evans 2013; Tolley and Menegon 2013).

Despite the broad geographic distribution among extant taxa, the fossil record of Chamaeleonidae is rather patchy (Bolet and Evans 2013). A Cretaceous origin of the group is commonly accepted based on molecular data (Tolley et al. 2013), but with their first fossil record dating back to the early Miocene (Moody and Roček 1980; Pickford 1986), such molecular divergence date cannot be thoroughly tested. The dispersal of chamaeleonids to Europe and Asia seems to have occurred later (Bolet and Evans 2013; Tolley et al. 2013); indeed, their Neogene record on the European continent is rather scanty with few, scattered occurrences only across the early to middle Miocene of Central Europe (Moody and Roček 1980; Böhme and Ilg 2003; Čerňanský 2010; Bolet and Evans 2013).

Europe currently harbours two extant taxa of chamaeleonids: *Chamaeleo chamaeleon* (Linnaeus, 1758) and *Chamaeleo africanus* Laurenti, 1768 (Dimaki et al. 2000, 2008, 2015). The Greek distribution of the former species now solely comprises Samos island, as populations inhabiting Crete and Chios seem to have gone extinct recently. It is worth noting, however, that Sillero et al. (2014) reported this species as still present in Crete, considering it allochthonous. The distribution of *C. africanus* in Greece (restricted only to a small region near the town of Pylos, Peloponnese) is the sole European population for this African species and most probably is a product of human introduction during early antiquity (Fig. 2) (Böhme et al. 1998; Kosuch et al. 1999; Dimaki et al. 2000, 2008).

Despite their occurrence in the extant herpetofauna of the country, chamaeleonids have never been previously described from Greek fossil localities. Here, we report on three new chamaeleonid fossils found in the early Miocene (MN 4) locality of Aliveri, Evia Island, which indicate the Neogene existence of these lizards in Greece. One of these specimens is tentatively attributed to the species *Chamaeleo* cf. *andrusovi* Čerňanský, 2010, which was previously known only from the early Miocene of the Czech Republic, whereas the other two specimens represent indeterminate chamaeleonids.

## Geological setting

Aliveri is a fossiliferous locality, located within the Neogene sedimentary basin of Aliveri/Kymi, in Evia (also spelled Euboea) Island in Central Greece. Along with the Gavathas site, Lesvos Island, it has yielded the oldest known Greek Neogene land mammal fauna (Koufos 2006a, b; van den Hoek Ostende et al. 2015). Aliveri was discovered in 1977 and was initially dated to the MN 3 zone (de Bruijn et al. 1980). Nevertheless, there is a general consensus now that it is referable to MN 4 (Doukas 2003; Koufos 2006b; van den Hoek Ostende et al. 2015). More specifically, as was recently stated by van den Hoek Ostende et al. (2015:276), ‘although undeniably an MN 4 assemblage, Aliveri is one of the oldest localities from that MN unit, and presumably co-eval with many of the MN 3 assemblages from western and central Europe’. The age of Aliveri is tentatively estimated between 18 and 17.5 Ma, and corresponds to the Burdigalian stage (Orleanian Continental Stage) (Koufos 2006b; van den Hoek Ostende et al. 2015). A detailed description of the geology of Aliveri is provided by de Bruijn et al. (1980).

The micromammal assemblage of Aliveri is rather diverse and has been the subject of several studies (de Bruijn et al. 1980; van der Meulen and de Bruijn 1982; Schmidt-Kittler 1983; Klein Hofmeijer and de Bruijn 1985, 1988; Doukas 1986; López Martinez 1986; Álvarez Sierra et al. 1987). It includes erinaceids, dimylids, heterosoricids, talpids, soricids, ochotonids, eomyids, many sciurids, cricetids, anomalomyids, spalacids and glirids. Larger mammals are less known, but palaeogalids, equids, palaeomerycids, cervids and bovids are present, as well as the viverrid *Euboictis* (van den Hoek Ostende et al. 2015). As for the herpetofauna of Aliveri, anurans, crocodylians, anguids, lacertids, as well as indeterminate lizards, snakes and turtles are present but have not been described. The study of these amphibians and reptiles will be the subject of a forthcoming publication.

## Material and methods

All three chamaeleonid specimens described herein belong to the collections of the Department of Earth Sciences in the University of Utrecht and are accessioned under the repository numbers UU AL 3501–3503. All specimens were found in the early Miocene locality of Aliveri in three different field seasons, in 1977 (UU AL 3502), 1978 (UU AL 3501), and 1980 (UU AL 3503), led by the University of Utrecht. As with the micromammal material that has also been collected from this locality, all chamaeleonid fossils have been recovered from the underclay of the lignite occurring North of Aliveri, along the eastern edge of the basin where the lignite wedges out against Mesozoic limestones (de Bruijn et al. 1980). For comparison purposes, skeletal material of extant chamaeleonids was studied in the herpetological collections of the University of Torino and the Muséum national d’Histoire naturelle, Paris. Photos of the fossil specimens were taken using the Leica M205 microscope and the Leica application suite V 3.3.0, in the University of Torino.

## Results

### Systematic palaeontology

Reptilia Laurenti 1768
Squamata Oppel, 1811
Iguania Cope, 1864
Acrodonta Cope, 1864
Chamaeleonidae Gray, 1825
*Chamaeleo* Laurenti, 1768
*Chamaeleo* cf. *andrusovi* Čerňanský, 2010
(Fig. 1a, b, c, d)

Material: The specimen here referred to *Chamaeleo* cf. *andrusovi* is a skull roofing bone fragment (UU AL 3501).

Description: UU AL 3501 is a skull roofing bone fragment about 3 × 3 mm in diameter. A comparison with extant chamaeleonid material, stored in the collections of the University of Torino and the Muséum national d'Histoire naturelle, Paris, suggests that the fragment can be part of the circumorbital region (i.e. either a prefrontal or a postorbital), but its fragmentary status prevents a more precise determination. The fragment is flattened and its external surface is covered by an ornamentation made by various small tubercles grouped in four, well-separated and rounded clusters. Two of the four clusters are aligned along one of the margins of the fragment, which is a natural border and not the result of breakage (as the other margins). If our interpretation of the fragment as part of a circumorbital bone is correct, this would be the orbital margin. The inner surface of the specimen is smooth.

Chamaeleonidae indet.
(Fig. 1e–h)

Material: Two additional specimens from the same locality are assigned to Chamaeleonidae, but cannot be attributed to the species level. These two specimens are both tooth bearing bones (UU AL 3502 and UU AL 3503).

Description: UU AL 3502 and UU AL 3503 are very fragmentary tooth-bearing bones. However, they clearly bear acrodont, large and triangular teeth, which are well-spaced and located on the edge of the bones. Two of them are preserved in UU AL 3502 and three of them are visible in UU AL 3503, even if in the latter specimen only one is well preserved. Small accessory cusps are recognizable anteriorly and posteriorly to the main one in one tooth of UU AL 3502 and in two teeth of UU AL 3503. Ventrally directed interdental grooves are present on the lateral surface. Due to the fragmentary nature of both specimens, it is currently impossible to determine whether these two tooth-bearing elements originate from the dentary or the maxilla.

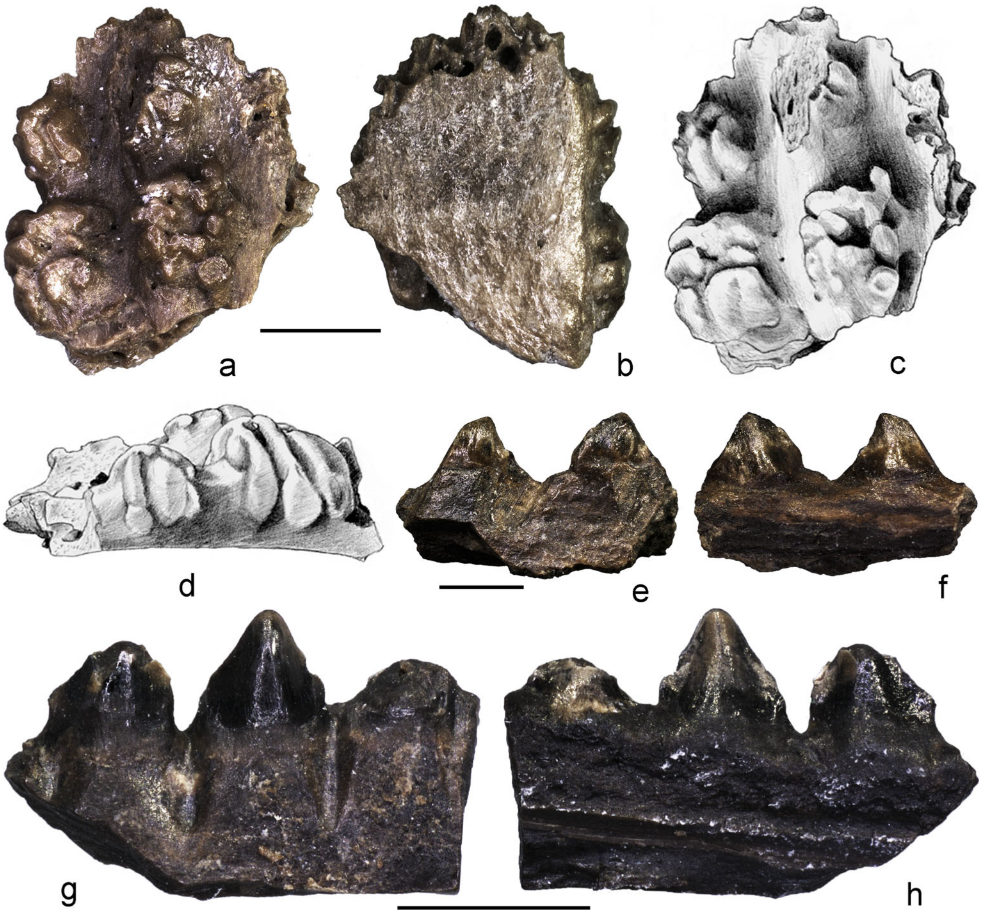

**Fig. 1** Fossil chamaeleonids from Aliveri. **a–d** *Chamaeleo* cf. *andrusovi*: skull roofing bone, UU AL 3501, in external (**a**) and internal (**b**) views, and its interpretative drawing in external (**c**) and lateral (**d**) views. **e–h** Chamaeleonidae indet.: tooth-bearing bones, UU AL 3502 (**e–f**) and UU AL 3503 (**g–h**), in lateral (**e**, **g**) and medial (**f**, **h**) views. *Scale bars* represent 1 mm

### Taxonomic identification

The specimens described herein were preliminarily described in an unpublished report by Delfino (unpublished), who attributed them to Chamaeleonidae indet. On the other hand, Böhme and Ilg (2003) cited for the same locality the presence of *Chamaeleo* cf. *C. caroliquarti* in their online database, without further details or describing any material.

Because of the complex ornamentation and the well-spaced and complex clusters of tubercles (= pustular protuberances of Čerňanský (2010)), the skull bone fragment (UU AL 3501) from Aliveri can be referred to *Chamaeleo* cf. *andrusovi*. In the original diagnosis provided for this species, Čerňanský (2010:609) stated that *C. andrusovi* was a small chamaeleonid, differing from all other taxa in several features, but most notably by 'its typical strongly pustular ornamentation of the external surfaces of the skull roofing bones. Differs from adult *Chamaeleo calyptratus*, *Triceros* (sic) *hoehneli* or *Calumma globifer* in regard to the concentration, distribution and shape of the protuberances—mostly complicated pustular protuberances are moderately spaced and rather evenly distributed, covering the otherwise smooth external surface'. This diagnostic feature appears also in the Greek specimen; therefore, the skull roofing bone is attributed to *Chamaeleo* cf. *andrusovi.*

The two tooth-bearing elements from Aliveri (UU AL 3502 and UU AL 3503) can be attributed to the Chamaeleonidae on the basis of the well-spaced and apically located acrodont teeth (Delfino et al. 2008 and references therein). The identification of chamaeleonid tooth-bearing bones is severely hampered by the widespread, homoplastic features surrounding their anatomy. Generally, the dentaries of Acrodonta share several common features that should prompt us being rather cautious when dealing with taxonomic assignments to either agamids or chamaeleonids (Augé 1997; Delfino et al. 2008; Rage and Bailon 2011). Even if the two fragmentary tooth-bearing bones cannot be identified as portions of maxillae or dentaries, it is worth noting that Čerňanský (2010) has shown that dentaries of chamaeleonids are not diagnostic to the species level. Assigning the tooth-bearing bones to *Chamaeleo* cf. *andrusovi* on just the base of the taxonomic allocation of the skull roofing bone seems premature for the moment, as fossil evidence has shown that distinct chameleon species could have co-existed in sympatry: different morphologies that have been observed among the dentaries of *C. caroliquarti* (Čerňanský 2010) could indicate the existence of more than one chameleon at Dolnice. The fact that *C. caroliquarti* was a very large species (around 500 mm in total length) (Bolet and Evans 2013), whereas *C. andrusovi* was originally described as 'a small species of *Chamaeleo*' (Čerňanský 2010, p. 609), prompts us to leave open the possibility that Dolnice could harbour at least two different chamaeleonid taxa. The idea of two or more sympatric chamaeleonid species in the same locality is reminiscent of a similar situation in several extant species (Raselimanana and Rakotomalala 2003; Tolley and Menegon 2013). Such higher species diversity within a single region has been also recently inferred for fossil chamaeleonids (Dollion et al. 2015). On the other hand, many regions harbour only monospecific communities of extant chamaeleonids (Tolley and Menegon 2013). Taking all these into consideration, whether Aliveri hosted a monospecific chameleon assemblage, or whether multiple sympatric species coexisted, remains only to be revealed on the light of new and more complete specimens from the locality. As such, we refrain from attributing the two tooth-bearing elements to the same species as the skull roofing bone (*Chamaeleo* cf. *andrusovi*) and we thus tentatively consider them as 'Chamaeleonidae indet.'

## Discussion

### The taxonomy of European Neogene chamaeleonids

Six Miocene species have already been named on the basis of rare European fossil remains, which mostly do not comprise overlapping material (Bolet and Evans 2013): *C. caroliquarti* Moody and Roček, 1980, *Chamaeleo bavaricus* Schleich, 1983, *Chamaeleo pfeili* Schleich, 1984, *Chamaeleo simplex* Schleich, 1994, *Chamaeleo sulcodentatus* Schleich, 1994 and *Chamaeleo andrusovi* Čerňanský, 2010. Several anatomical characters appear to be ubiquitous within chamaeleonids, rendering the validity of most of these taxa as tentative or even dubious (Čerňanský 2011). This applies especially to characters in the dentaries of these squamates, which appear to be widespread and indistinguishable from extant representatives. Čerňanský (2010) revised the first named European fossil taxon *C. caroliquarti* and regarded it as a nomen dubium, as he could not differentiate the holotype dentary from several extant taxa, whereas the paratype dentary appeared to belong to a distinct morphotype. We acknowledge here, however, that on several occasions, even fragmentary fossils can bear diagnostic characters. This is the situation, for example, when geometric morphometric approaches are used (Bastir et al. 2014; Cornette et al. 2015), a case study that has also been recently applied to fossil chamaeleonids (Dollion et al. 2015). The latter authors characteristically noted that even small fragments such as parts of the maxilla and the parietal could be useful in taxonomic identification. It is, however, beyond the scope of this paper to evaluate the status of *C. caroliquarti*, and acknowledge that a complete phylogenetic analysis which will, in fact, include enough dentary characters from multiple extant taxa, is needed in order to decipher the systematics of European Neogene chameleons.

## The Aliveri chameleons

The identification of the Aliveri specimens described herein, as chamaeleonids, confirms the presence of this squamate group in the fossil record of Greece. Another purported acrodont taxon, *Uromastyx spinipes* (Daudin, 1802) [= *Uromastyx aegyptia* (Forskål, 1775)] was reported by Mangili (1980) from the Late Pleistocene of Grotta Simonelli in Crete, on the basis of an isolated, 43 mm long, tibia that was not figured and not described in detail, hindering any evaluation of its identity. The location of this fossil is currently unknown. However, since the comparative morphology of lizard tibiae is poorly known, this specimen should be considered an indeterminate squamate. As such, the specimens from Aliveri comprise the sole record of fossil chameleons from Greece.

The taxonomic assignment of the Aliveri skull roofing element as *Chamaeleo* cf. *andrusovi* provides a significant range extension for that species. *C. andrusovi* was until now known only from the early Miocene (MN 4) of Dolnice, Czech Republic (Čerňanský 2010). This new record indicates that this species was widely distributed in the early Miocene of Central and Southern Europe. Such a broad distribution is congruent with that of several extant members of the genus *Chamaeleo* (e.g. *C. chamaeleon* and *C. africanus* are widespread species with populations being adapted to different environments and ecological settings [Dimaki et al. 2000, 2008]). However, the high degree of cryptic speciation in modern chamaeleonids has led to the 'split' of several widespread extant taxa, mostly on the base of molecular data, but with few or no morphological characters that could distinguish them (e.g. Andreone et al. 2001; Nečas et al. 2003, 2005, 2009; Gehring et al. 2010, 2011; Crottini et al. 2012; Greenbaum et al. 2012; Stipala et al. 2011, 2012; Tilbury and Tolley 2015). This fact is further problematic for the fossil record of chamaeleonids, as for their identification we have to rely only on morphological evidence, and no assumption about cryptic speciation within extinct species can be suggested.

It is worth noting that the faunal assemblage of Aliveri is chronologically older than other MN 4 faunas in Europe (van den Hoek Ostende et al. 2015) and that the Greek skull roofing bone assigned to *Chamaeleo* cf. *andrusovi* is therefore older than the conspecific specimens from the type locality of Dolnice, Czech Republic. As such, the Aliveri specimen ranks among the oldest named chamaeleonids of Europe, being only slightly younger than *C. caroliquarti* which has been recorded from the early Miocene (MN 3) localities of Merkur Nord (Czech Republic) and Wintershof West (Germany).

The locality of Aliveri is well known for its rich micromammal fauna. The overall diverse and abundant fauna of flying squirrels suggest a forest biotope (de Bruijn et al. 1980). A relatively humid environment for the locality has also been suggested (van den Hoek Ostende et al. 2015). The new identification of *Chamaeleo* cf. *andrusovi* in Aliveri further confirms the already proposed ecological settings of the locality, as the presence of chamaeleonids is well known to be indicative of warm climates (Moody and Roček 1980) and further suggests relatively dense vegetation (Maul et al. 2011), although several extant genera are known to occur in both closed and open habitats (Tolley et al. 2008; Dollion et al. 2015).

## Palaeobiogeography of the Chamaeleonidae

The biogeographic history of chamaeleonids is hampered by their extremely poor fossil record. Most of the material recovered is fragmentary, thus not permitting identification beyond the family level. Notable exceptions, however, are known to occur, with few exceptional Miocene specimens from Kenya documenting the morphological conservativeness and a relative evolutionary stasis within the group throughout time (Hillenius 1978a; Rieppel et al. 1992). Stem representatives of Chamaeleonidae are not known or at least they have not yet been identified, rendering their early evolutionary history tantalizing and obscure (Bolet and Evans 2013; Simões et al. 2015). Molecular data support a Cretaceous dichotomy between chamaeleonids and other Acrodonta, although the exact dates vary among different researches (Raxworthy et al. 2002; Wiens et al. 2006; Townsend et al. 2011; Bolet and Evans 2013; Dollion et al. 2015). Africa and Madagascar have long been proposed as potential centres of origin for chamaeleonids (Hillenius 1959, 1978b; Blanc 1972; Klaver 1977; Tolley et al. 2013; Dollion et al. 2015). More specifically, Tolley et al. (2013) suggested, on the base of molecular data, that chamaeleonids originated in Africa around the Late Cretaceous, after the break-up of the supercontinent Gondwana, with two independent oceanic dispersals to Madagascar (their modern biodiversity hotspot) during the Palaeocene and the Oligocene. Frustratingly, however, no Cretaceous and Palaeogene fossils are known, and it is characteristic that the first definite known chamaeleonid fossils are documented only in the early Miocene of Africa and Europe (Bolet and Evans 2013; Dollion et al. 2015).

Several enigmatic Palaeogene taxa from Asia bear superficial resemblance with chamaeleonids; however, they are now thought to represent convergent stem acrodonts (Bolet and Evans 2013). It is worth noting here that the taxonomic status of *Anqingosaurus brevicephalus* Hou, 1976 (variously cited also under the incorrect spelling *Anquingosaurus*), an enigmatic species from the Palaeocene of China, is pivotal to our understanding of chamaeleonid evolution. Bolet and Evans (2013, p. 184) doubted the status of *A. brevicephalus* as a chamaeleonid, mentioning characteristically that 'there is nothing to suggest that it is a chameleon'. That being said, there is currently no definite record of a chamaeleonid from the Palaeogene or even the Neogene of Asia. In fact, the only known Asian fossil chamaeleonids are recorded in the Middle Pleistocene of Israel and the Palaeolithic of Lebanon (Haas 1952; Hooijer 1961; Maul et al. 2011; Bolet and Evans 2013), but palaeogeographically Middle East was part of Gondwana and not Asia.

Neogene chameleons in Europe appear to be restricted, both geographically and chronologically, with only few published occurrences from the early to middle Miocene of Czech Republic, Germany and Switzerland, and perhaps also Poland and Spain (Fig. 2) (Moody and Roček 1980; Roček 1984; Schleich 1984; Bolliger 1992; Fejfar and Schleich 1994; Mörs 2002; Böhme and Ilg 2003; Böhme 2010; Čerňanský 2010, 2011; Bolet and Evans 2013). The earliest occurrence of a chamaeleonid in Europe is documented in the early Miocene (MN 3) of Merkur Nord in Czech Republic and Wintershof West in Germany (Čerňanský 2010; Bolet and Evans 2013). A still undescribed chamaeleonid from the early Miocene (MN 3/MN 4) of Agramon, Spain, cited in the online database of Böhme and Ilg (2003), needs further investigation about its exact taxonomic affinities; if it is indeed a chamaeleonid though, then it represents one of the earliest European records of the group. Interestingly, chameleons are neither recovered from the well-known MN 2 squamate fauna of Wiesbaden-Amöneburg (Germany) nor in any other MN 2 European locality, leading Čerňanský et al. (2015) to suggest that their absence in the earliest Miocene is genuine and they only dispersed into Europe shortly thereafter. The presence of chamaeleonids in Central Europe during the early Miocene coincides with the Miocene Climatic Optimum (Böhme 2003), which enabled several other squamate groups to achieve their northernmost distribution (e.g. varanids and cordylids; Bolet and Evans 2013; Delfino et al. 2013). One or more widespread and/or even distinct, sympatric species could be present in the early Miocene of Central Europe at the time of this climatic optimum, as high temperatures favour the diversification of squamates. In any case, the permanence of Miocene chamaeleonids in Europe did not last long as suggested by their last published occurrence in the MN 6 of Ornberg in the Molasse Basin, Switzerland (Bolliger 1992; Čerňanský 2011), whereas an even later occurrence for the group is listed in the online database of Böhme and Ilg

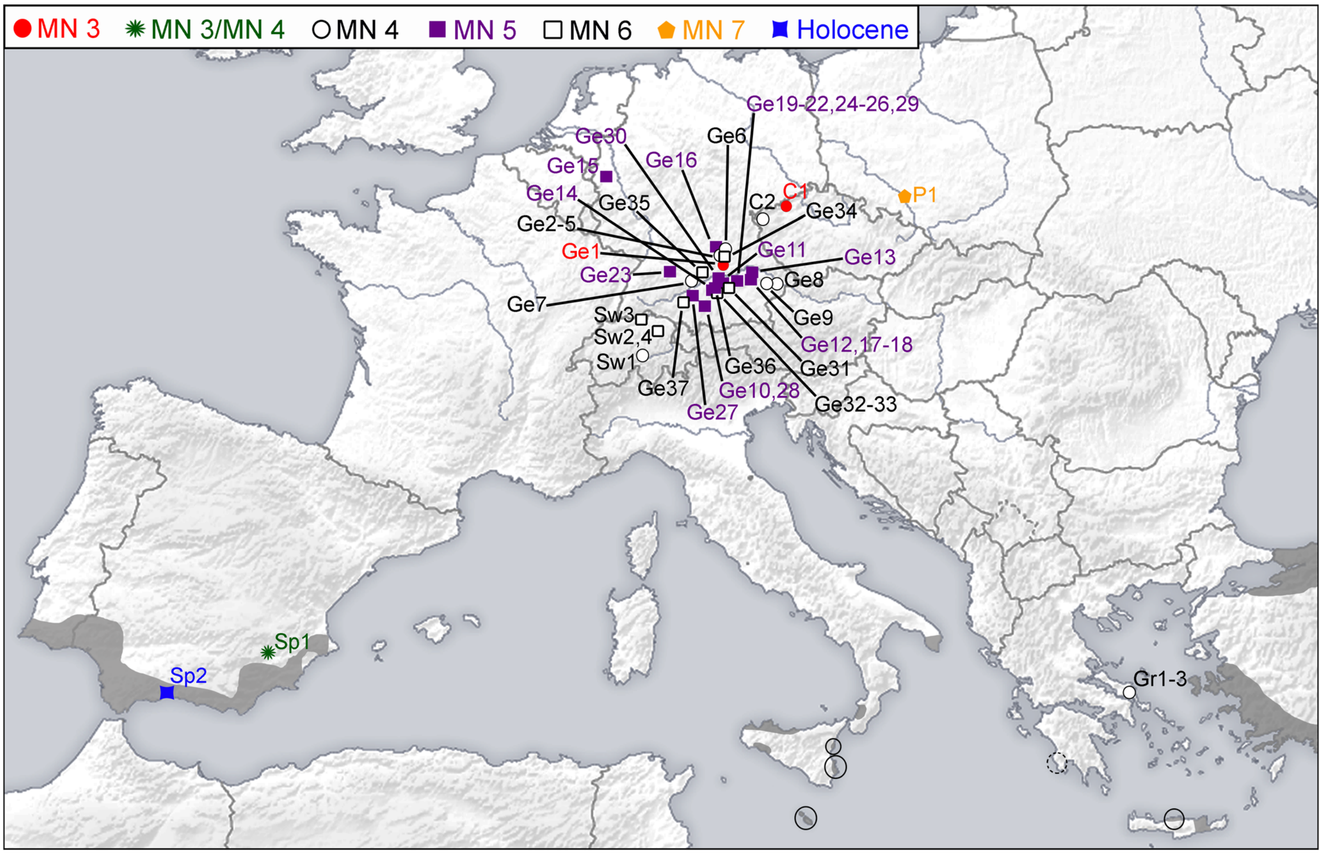

**Fig. 2** Fossil chamaeleonids from Europe. See Online Resource for a list of localities and taxa identified. *Grey and encircled areas* represent the range of extant chameleons in Europe and Western Anatolia, including autochthonous, introduced and recently extinct populations; the *dashed circle* indicates the probably introduced in antiquity population of *C. africanus* near Pylos, whereas the remaining areas refer to *C. chamaeleon*. Distributional data come from Gasc et al. (1997), Sindaco and Jeremčenko (2008), Sperone et al. (2010) and Sillero et al. (2014)

(2003), where an indeterminate reptile that was initially described by Młynarski et al. (1982) from the middle Miocene (MN 7) of Poland is there re-identified as a chamaeleonid. Whatever their last appearance datum, they likely went extinct due to climatic deterioration in Europe and/or ecological competition with newly arrived squamates. Interestingly, a new land bridge has been suggested to exist between Afro-Arabia and Asia during MN 6, which, apparently, favoured a new wave of dispersal of immigrants to Europe (Koufos et al. 2005). Indeed, several African groups are known to have dispersed by this land bridge (e.g. aardvarks) (Koufos et al. 2005; Lehmann 2009), a situation that could have applied also to African squamates. No chamaeleonid fossils are found after the middle Miocene, but a latest immigration event seems to have taken place much more recently, involving the extant species *C. chamaeleon*, which still inhabits several parts of the Mediterranean Europe: a sporadic fossil occurrence from the Holocene of Spain (Talavera and Sanchíz 1983) probably supports this recent wave of dispersal. This latest dispersal event seemingly concerns also the extant Greek populations of *C. chamaeleon* in the islands of Samos and Chios, right adjacent to the coasts of Anatolia; the (recently extinct) population of *C. chamaeleon* in Crete, as also the other extant species occurring in Greece, *C. africanus*, is most probably a product of human introduction during antiquity (Böhme et al. 1998; Dimaki et al. 2015).

With such a scarce fossil record and a rather small temporal and regional European distribution, the dispersal routes of the earliest chamaeleonids remain unclear. Čerňanský et al. (2015) suggested that chamaeleonids (probably along with cordylids) entered Europe no earlier than the MN 3, but they did not suggest any possible route from Africa to Europe. Here we propose three different possible routes (Fig. 3): (i) a marine dispersal from northwestern Africa to southwestern Europe; (ii) a land dispersal from Afro-Arabia to Asia and then via Anatolia to southeastern Europe; and (iii) a land dispersal from Afro-Arabia to Asia and then northwards and eastwards, with an entrance in Europe through Central Asia.

The first scenario involves a marine dispersal from Africa to Europe across the Mediterranean. Such oceanic dispersals are well documented in chamaeleonid biogeographic history with molecular data suggesting multiple waves of colonization in Madagascar, Comoros, Seychelles and Socotra (Tolley et al. 2013; Tolley and Menegon 2013). Squamates in general are considered to be very efficient in trans-oceanic dispersal, with multiple lineages colonizing even the furthest and most remote of the Pacific Ocean islands (Beckon 1992; Fisher 1997; Pregill and Steadman 2004; Zug et al. 2011). These data, along with the extant distribution of chamaeleonids overseas in the Indian Ocean, suggest that the Palaeogene and Early Neogene Mediterranean and Paratethys seas (especially in the western part that is estimated to be rather narrower [Rögl 1999]) should not appear as a severe obstacle for these capable marine navigators. However, their absence from Palaeogene and early Miocene localities from Western Europe could possibly indicate that chamaeleonids did not disperse from this direction. Indeed, the extensive sampling of Western European localities for over a century could probably attest that this absence of chamaeleonids from this region is genuine and not sample biased. The supposed record of an indeterminate chamaeleonid from the early Miocene (MN 3/MN 4) of Agramon is tantalizing, since it could represent the only exception; however, the specimen has not been formally described and its whereabouts are currently unknown (Zbigniew Szyndlar, personal communication, November 2015). We further note here that short-time existing land

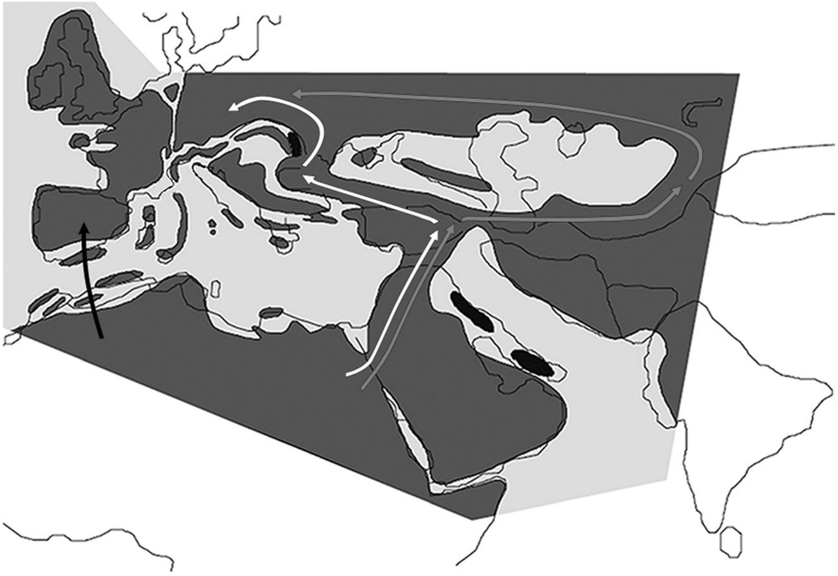

**Fig. 3** Map showing the three biogeographic scenarios described in the text: the first one is represented by a *black arrow*, the second one by *white arrows* and the third one by *grey arrows*. Palaeogeographic map modified from Rögl 1999

connections between Africa and Western Europe have also been suggested (Gheerbrandt and Rage 2006; Zarcone et al. 2010), however, without unveiling any dispersal of chamaeleonids to Europe. A natural or ecological barrier could have prevented these squamates from immigrating to Western Europe either through water rafting or any hypothetical land bridge.

The second scenario involves a land dispersal from Afro-Arabia to Asia and then via Anatolia to Europe. This is supposed to take place in the early Miocene through the so-called *Gomphotherium* Landbridge, a large landmass that arose after the collision of Afro-Arabia with Asia during the MN 3 stage (Rögl 1999; Koufos et al. 2005). This collision provided a connection between Africa and Asia, dividing the huge sea that previously prevented dispersal of terrestrial taxa from Africa to Eurasia. The Afro-Arabian plate acted therefore as a platform for these terrestrial groups that could afterwards use Anatolia and then the Balkans in order to disperse northwards to Central Europe. A similar route had already been mentioned for chameleons by Barbadillo et al. (1997). According to this scenario, Greece seems to have acted as the first 'step' of these African and/or Anatolian immigrants into Europe. Through the '*Gomphotherium* Landbridge', numerous terrestrial tetrapod groups are documented to have dispersed out of Africa, most eminently proboscideans (Rögl 1999; Koufos et al. 2003, 2005). If chameleons used this dispersal scenario, then they were among the first immigrants out of Africa, accompanying proboscideans and other mammal groups; they then rapidly dispersed to Central Europe in a short time interval, as it is shown by the presence of chamaeleonids in Germany and the Czech Republic already by the MN 3 (Roček 1984; Fejfar and Schleich 1994). Interestingly, several other tetrapod groups (e.g. aardvarks, hominoids) dispersed out of Africa much later, using another land bridge that arose during the middle Miocene (MN 6) (Lehmann 2009), but this datum is younger than the majority of fossil occurrences of chamaeleonids in Europe. Different ecological barriers probably existed that prevented or favoured the dispersal of certain groups at different periods.

The third scenario involves a land dispersal of chamaeleonids from Afro-Arabia to Asia and then northwards and entrance in Europe through Central Asia. This should involve again the usage of the '*Gomphotherium* Landbridge' but then after dispersal eastwards and not westwards to the Balkans. We note here that the collision of the Afro-Arabian plate with Asia divided the Paratethys Sea and isolated the Kotsakhurian Sea in the eastern Paratethys region (Fig. 6, in Rögl 1999). This would further put rather severe obstacles in the spread of the African immigrants to the North. Therefore, only a westwards and an eastwards direction for these immigrants would seem possible. If chamaeleonids took the eastward direction, that would mean that they had to disperse to southern Asia, spread to Central Asia and then, after getting around the huge perimeter of the Kotsakhurian Sea, enter Central Europe. That way, their entrance into Europe should take place at the level of the northwestern edge of the Kotsakhurian Sea. However, the ubiquitous absence of chamaeleonid fossils in the several known early Miocene localities from this region does not seem to favour this hypothesis.

We acknowledge that the available fossil material is limited in order to fully support any of the proposed dispersal routes. However, the new Greek specimens provide evidence in favour of our second proposed scenario: a route from Greece towards Central Europe. Moreover, the slightly older age of the Aliveri fauna compared to all other MN 4 European localities, and more specifically from the also chamaeleonid-bearing Dolnice, could indicate a step-wise pathway of these squamates from south to northwards, and hints as Greece being the first European territory to which the group initially arrived from Africa via Anatolia. The presence of chamaeleonids in MN 3 Central European localities (Merkur Nord and Wintershof West), which are slightly older than Aliveri, could indicate that their dispersal and colonization of Europe took place quite fast. The purported record of the chamaeleonid from Agramon (MN 3/MN 4) (Böhme and Ilg 2003), if verified, could hint for very similar dispersal routes of these squamates to proboscideans: the latter group of large mammals are known to have used the *Gomphotherium* Landbridge at the MN 3 stage and rapidly dispersed into the European continent, reaching the Iberian Peninsula at the beginning of MN 4 (Tassy 1990; Koufos et al. 2005). The idea, however, of a combination of both the first and the second biogeographic scenarios should not be ruled out: the presence of chamaeleonids from Aliveri in the Balkan Peninsula, along with that from Agramon in the Iberian Peninsula, may indicate that these squamates could have used different pathways to Europe, from both northwestern and northeastern Africa. Such complex, double or even multiple dispersal events are far from unknown for southern European squamates. To the contrary, they have been well documented for extant gekkotan lizards (Rato et al. 2010, 2011) and Neogene elapid snakes (Szyndlar and Rage 1990). As far as it concerns the latter, the cobra *Naja iberica* from Spain has been described as 'undoubtedly an African invader', which, however, most likely never crossed the Pyrenees barrier and spread to the rest of Europe, which was inhabited by different congeners (Szyndlar and Rage 1990, p. 398). Such barrier could have also prevented early Miocene Iberian chamaeleonids from dispersing northwards, if they indeed ever reached the Peninsula during the early Neogene.

The Aliveri fauna bears a close resemblance to several coeval early Miocene ones from Anatolia, indicating biogeographic correlation and possible dispersal routes (van den Hoek Ostende et al. 2015). Notably, the viverrid *Euboictis* from Aliveri seems to share close affinities with a rather primitive congener form from Sabuncubeli in Anatolia (early MN 3), pointing towards an Asian origin for this mammal group (Koufos et al. 2005; van den Hoek Ostende et al. 2015). In contrast, Aliveri shares with coeval Central European faunas several micromammals, such as the eomyids and the flying squirrels. Curiously, eomyids are not present in the Turkish fossil record and therefore may indicate the existence of an ecological barrier between southern Balkan Peninsula and Anatolia (van den Hoek Ostende et al. 2015). It is also characteristic that the Aliveri rodent *Anomalomys aliveriensis* shares congener species with the early Miocene of Dolnice, Czech Republic, which is also the type locality of *C. andrusovi.* It is therefore obvious that the Aliveri fauna comprised a faunal mosaic of Anatolian and Central European taxa, acting as a biogeographic passage between Anatolia and Central Europe. Frustratingly, however, no chamaeleonid has ever been reported from any of the Anatolian localities (van den Hoek Ostende et al. 2015). More specimens from the early Miocene of Greece and generally from the Balkans and Anatolia are needed in order to fully test our hypothesis about the dispersal routes of chamaeleonids. This is unfortunately hindered by the scarcity of such localities in Greece (Koufos 2006b), as also by the generally limited interest of palaeontologists in fossil reptile finds in the area (Georgalis and Kear 2013). The confirmed presence of chamaeleonids in the early Miocene of Greece, however, allows us to expect that other localities between the MN 3 and MN 4 time intervals in the southern Balkans and Anatolia will also yield similar fossil forms that will only then allow a more accurate reconstruction of the dispersal routes of these charismatic lizards.

*Chamaeleo* cf. *andrusovi* from Aliveri represents only the third reptile species identified from the early Miocene of Greece. Mesozoic and Palaeogene reptiles are yet unknown from this country. *Chamaeleo* cf. *andrusovi*, the pleurodire turtle *Nostimochelone lampra* and the pythonid snake *Python euboicus* are therefore the oldest reptiles in the Greek fossil record (Römer 1870; Georgalis et al. 2013; Georgalis and Kear 2013). As the Aliveri specimens confirm the presence of Chamaeleonidae in the area, it is possible to speculate that several other reptile groups that have a fossil record in the early Neogene of Central Europe, such as cordylids, elapids, boines and choristoderans (Rage 1984; Szyndlar and Rage 1990, 2003; Szyndlar 1991; Evans and Klembara 2005; Rage and Szyndlar 2005; Čerňanský 2012), may be recovered from the Greek localities in the future. Especially for cordylids, it will be rather interesting to test whether this African lizard group (that has an almost identical, restricted fossil distribution in the early Miocene of Central Europe with chamaeleonids [Roček 1984; Čerňanský 2012]) used the same dispersal routes and if they can be identified in Greece and the rest of southeastern Europe as well. Unlike chameleons, however, cordylids are known to have also a Palaeogene fossil record from Europe; therefore, their presence in the same early Miocene localities with chamaeleonids during the climatic optimum could suggest either a continuous presence from the Palaeogene onwards to the Miocene or indeed a Palaeogene extinction and a later dispersal event along with chameleons (Čerňanský 2012). More fossil specimens and a revision of the already named taxa under a modern phylogenetic context are definitely needed in order to shed more light on the European squamate palaeobiogeography.

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## References

Álvarez Sierra MA, Daams R, van der Meulen AJ (1987) The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). 7. The Eomyidae. Proc Koninkl Nederl Akad Wetensc Ser B 90(1):47–56

Andreone F, Mattioli F, Jesu R, Randrianirina JE (2001) Two new chameleons of the genus *Calumma* from north-east Madagascar, with observations on hemipenial morphology in the *Calumma furcifer* group (Reptilia, Squamata, Chamaeleonidae). Herpetol J 11(2):53–68

Augé M (1997) A consideration of the phylogenetic significance of acrodonty. Herpetol J 7:111–113

Barbadillo LJ, García-París M, Sanchiz B (1997) Orígenes y relaciones evolutivas de la herpetofauna ibérica. In: Pleguezuelos JM (ed.) Distribución y Biogeografía de los Anfibios y Reptiles en España y Portugal. Monografías de Herpetología, Vol. 3. Asociación Herpetológica Española y Universidad de Granada, pp 47–100

Bastir M, Böhme M, Sanchiz B (2014) Middle Miocene remains of *Alytes* (Anura, Alytidae) as an example of the unrecognized value of fossil fragments for evolutionary morphology studies. J Vertebr Paleontol 34:69–79

Beckon WM (1992) The giant Pacific geckos of the genus *Gehyra*: morphological variation, distribution, and biogeography. Copeia 1992(2):443–460

Blanc CP (1972) Les reptiles de Madagascar et des îles voisines. In: Battistini R, Vindard G (eds) Biogeography and ecology in Madagascar. Junk, The Hague, The Netherlands, pp 501–614

Böhme M (2003) The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeogr Palaeoclimatol Palaeoecol 195:389–401

Böhme M (2010) Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. Paläontol Z 84:3–41

Böhme M, Ilg A (2003) fosFARbase, www.wahre-staerke.com/ (accessed 1 November 2015)

Böhme W, Bonetti A, Chiras G (1998) The chameleons of the Greek mainland: taxonomic allocation and conservation needs of a second European species (Squamata: Sauria: Chamaeleonidae). Herpetozoa 11(1/2):87–91

Bolet A, Evans SE (2012) A tiny lizard (Lepidosauria, Squamata) from the Lower Cretaceous of Spain. Palaeontol 55(3):491–500

Bolet A, Evans SE (2013) Fossil history of chameleons. In: Tolley KA, Herrel A (eds) The biology of chameleons. University of California Press, Berkeley, pp 175–192

Bolliger T (1992) Kleinsäugerstratigraphie der miozänen Hörnilschüttung (Ostschweiz). Dokum Natur 75:1–297

Camp CL (1923) Classification of the lizards. Bull Am Mus Nat Hist 48: 289–481

Čerňanský A (2010) A revision of chamaeleonids from the Lower Miocene of the Czech Republic with description of a new species of *Chamaeleo* (Squamata, Chamaeleonidae). Geobios 43:605–613

Čerňanský A (2011) A revision of the chameleon species *Chamaeleo pfeili* Schleich (Squamata; Chamaeleonidae) with description of a new material of chamaeleonids from the Miocene deposits of southern Germany. Bulletin of Geosciences, Czech Geological Survey 86(2):275–282

Čerňanský A (2012) The oldest known European Neogene girdled lizard fauna (Squamata, Cordylidae), with comments on Early Miocene immigration of African taxa. Geodiv 34(4):837–848

Čerňanský A, Rage J-C, Klembara J (2015) The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. J Syst Palaeont 13(2):97–128

Conrad JL (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bull Am Mus Nat Hist 310:1–182

Cope ED (1864) On the characters of the higher groups of Reptilia Squamata—and especially of the Diploglossa. Proc Acad Nat Sci Philad 1864:224–231

Cornette R, Herrel A, Stoetzel E, Moulin S, Hutterer R, Denys C, Baylac M (2015) Specific information levels in relation to fragmentation patterns of shrew mandibles: do fragments tell the same story? J Archaeol Sci 53:323–330

Crottini A, Miralles A, Glaw F, Harris DJ, Lima A, Vences M (2012) Description of a new pygmy chameleon (Chamaeleonidae: *Brookesia*) from central Madagascar. Zootaxa 3490:63–74

Daudin FF (1802) Histoire Naturelle, Générale et Particulière des Reptiles; ouvrage faisant suit à l'Histoire naturelle générale et particulière, composée par Leclerc de Buffon; et rédigee par C.S. Sonnini, membre de plusieurs sociétés savantes, vol. 4, F Dufart, Paris

de Bruijn H, van der Meulen AJ, Katsikatsos G (1980) The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 1: the Sciuridae. Proc Koninkl Nederl Akad Wetensc Ser B 83(3):241–261

Delfino M, Kotsakis T, Arca M, Tuveri C, Pitruzzella G, Rook L (2008) Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiv 30(3): 641–656

Delfino M, Rage J-C, Bolet A, Alba DM (2013) Early Miocene dispersal of the lizard *Varanus* into Europe: reassessment of vertebral material from Spain. Act Palaeontol Pol 58(4):731–735

Dimaki M, Valakos ED, Legakis A (2000) Variation in body temperatures of the African Chameleon, *Chamaeleo africanus* Laurenti, 1768 and the Common Chameleon, *Chamaeleo chamaeleon* (Linnaeus, 1758). Belg J Zool 130(Suppl):89–93

Dimaki M, Hundsdörfer AK, Fritz U (2008) Eastern Mediterranean chameleons (*Chamaeleo chamaeleon*, *Ch. africanus*) are distinct. Amphibia-Reptilia 29:535–540

Dimaki M, Chondropoulos B, Legakis A, Valakos E, Vergetopoulos M (2015) New data on the distribution and population density of the African Chameleon, *Chamaeleo africanus* and the Common Chameleon, *Chamaeleo chamaeleon* in Greece. Hyla 2015(1):36–43

Dollion AY, Cornette R, Tolley KA, Boistel R, Euriat A, Boller E, Fernandez V, Stynder D, Herrel A (2015) Morphometric analysis of chameleon fossil fragments from the Early Pliocene of South Africa: a new piece of the chamaeleonid history. Sci Nat 102:2

Doukas CS (1986) The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 5. The insectivores. Proc Koninkl Nederl Akad Wetensc Ser B 89(1):15–38

Doukas CS (2003) The MN4 faunas of Aliveri and Karydia (Greece). Coloq Paleontol 1(2003):127–132

Estes R (1983) Sauria Terrestria, Amphisbaenia. Encyclopedia of Paleoherpetology, part 10a. Gustav Fisher Verlag, Stuttgart/New York

Estes R, de Queiroz K, Gauthier J (1988) Phylogenetic relationships within Squamata. In: Estes R, Pregill G (eds) Phylogenetic relationships of the lizard families: essays commemorating Charles L Camp. Stanford University Press, Stanford, pp 99–118

Evans SE, Klembara J (2005) A choristoderan reptile (Reptilia: Diapsida) from the Lower Miocene of Northwest Bohemia (Czech Republic). J Vertebr Paleont 25:171–184

Fejfar O, Schleich HH (1994) Ein Chamäleonfund aus dem unteren Orleanium des Braunkohlen-Tagebaus Merkur-Nord (Nordböhmen). Cour Forschungsinst Senck 173:167–173

Fisher RN (1997) Dispersal and evolution of the Pacific Basin gekkonid lizards *Gehyra oceanica* and *Gehyra mutilata*. Evol 51(3):906–921

Forskål P (1775) Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium; quae in itinere Orientali observavit Petrus Forskål. Möller, Haunia

Gasc JP, Cabela A, Crnobrnja-Isailovic J, Dolmen D, Grossenbacher K, Haffner P, Lescure J, Martens H, Martinez Rica JP, Maurin H, Oliviera E, Sofianidou TS, Veith M, Zuiderwijk A (1997) Atlas of amphibians and reptiles in Europe. Societas Europea Herpetologica and Museum National d'Histoire Naturelle, Paris

Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB (2012) Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bull Peab Mus Nat Hist 53:3–308

Gehring P-S, Pabijan M, Ratsoavina FM, Köhler J, Vences M, Glaw F (2010) A Tarzan yell for conservation: a new chameleon, *Calumma tarzan* sp. n., proposed as a flagship species for the creation of new nature reserves in Madagascar. Salamandra 46(3):167–179

Gehring P-S, Ratsoavina FM, Vences M, Glaw F (2011) *Calumma vohibola*, a new chameleon species (Squamata: Chamaeleonidae) from the littoral forests of eastern Madagascar. Afr J Herpetol 60(2):130–154

Georgalis GL, Kear BP (2013) The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46:299–311

Georgalis GL, Velitzelos E, Velitzelos D, Kear BP (2013) *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the Lower Miocene of northern Greece. In: Brinkman D, Holroyd P, Gardner J (eds) Morphology and evolution of turtles: papers in honor of Eugene S Gaffney. Vol 3. Pleurodires. Springer, Dordrecht, The Netherlands, pp 277–287

Gheerbrandt E, Rage J-C (2006) Palaeobiogeography of Africa: how distinct from Gondwana and Laurasia. Palaeogeogr Palaeoclimatol Palaeoecol 241:224–246

Glaw F (2015) Taxonomic checklist of chameleons (Squamata: Chamaeleonidae). Vertebr Zool 65(2):167–246

Glaw F, Vences M (1994) A field guide to amphibians and reptiles of Madagascar. 3rd ed, Vences and Glaw Verlag, Koln, Germany

Glaw F, Köhler JR, Townsend TM, Vences M (2012) Rivaling the world's smallest reptiles: discovery of miniaturized and microendemic new species of leaf chameleons (*Brookesia*) from northern Madagascar. PLoS ONE 7(2):e31314

Gray JE (1825) A synopsis of the genera of reptiles and amphibia, with a description of some new species. An Phil 10:193–217

Greenbaum E, Tolley KA, Joma A, Kusamba C (2012) A new species of chameleon (Sauria: Chamaeleonidae: *Kinyongia*), from the northern Albertine Rift, Central Africa. Herpetol 68(1):60–75

Haas G (1952) The fauna of layer B of the Abu Usba Cave. Isr Expl J 2: 35–47

Hillenius D (1959) The differentiation within the genus *Chamaeleo* Laurenti 1768. Beaufortia 8(89):1–92

Hillenius D (1978a) Notes on chameleons. IV: A new chameleon from the Miocene of Fort Ternan, Kenya (Chamaeleonidae, Reptilia). Beaufortia 28:9–15

Hillenius D (1978b) Notes on chameleons. V: the chameleons of North Africa and adjacent countries, *Chamaeleo chamaeleon* (Linnaeus) (Sauria, Chamaeleonidae). Beaufortia 28:37–55.

Hooijer DA (1961) The fossil vertebrates of Ksâr'Akil, a Palaeolithic rock shelter in the Lebanon. Zool Verh 49:3–67

Hou L (1976) New materials of Palaeocene lizards of Anhui. Vertebr Palasiat 14(1):48–52

Klaver CJJ (1977) Comparative lung-morphology in the genus *Chamaeleo* Laurenti, 1768 (Sauria: Chamaeleonidae) with a discussion of taxonomic and zoogeographic implications. Beaufortia 25(327):167–199

Klein Hofmeijer G, de Bruijn H (1985) The mammals from the lower Miocene of Aliveri (Island of Evia, Greece)—the Spalacidae and Anomalomyidae. Proc Koninkl Nederl Akad Wetensc Ser B 88: 185–198

Klein Hofmeijer G, de Bruijn H (1988) The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 8: the Cricetidae. Proc Koninkl Nederl Akad Wetensc Ser B 91(2):185–204

Kosuch J, Vences M, Böhme W (1999) Mitochondrial DNA sequence data support the allocation of Greek mainland chameleons to *Chamaeleo africanus*. Amph-Rept 20:440–443

Koufos GD (2006a) Palaeoecology and chronology of the Vallesian (late Miocene) in the Eastern Mediterranean region. Palaeogeogr Palaeoclimatol Palaeoecol 234(2–4):127–145

Koufos GD (2006b) The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. An Geol Pays Hel 4:183–214

Koufos GD, Zouros N, Mourouzidou O (2003) *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from Lesvos island, Greece; the appearance of deinotheres in the Eastern Mediterranean. Geobios 36:305–315

Koufos GD, Kostopoulos D, Vlachou T (2005) Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belg J Zool 135(2):181–190

Kumazawa Y (2007) Mitochondrial genomes from major lizard families suggest their phylogenetic relationships and ancient radiations. Gene 388:19–26

Laurenti JN (1768) Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu. Joan Thomae, Vienna

Lehmann T (2009) Phylogeny and systematics of the Orycteropodidae (Mammalia, Tubulidentata). Zool J Linn Soc 155:649–702

Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th edn. Laurentius Salvius, Stockholm

López Martinez N (1986) The mammals from the lower Miocene of Aliveri (Island of Evia, Greece). 6. The ochotonid lagomorph *Albertona balkanica* n. gen. n. sp. and its relationships. Proc Koninkl Nederl Akad Wetensc Ser B 89(2):177–194

Mangili G (1980) Fossils reptiles of Simonelli cave. Accad Naz Lincei Probl Attu Sc Cult Quaderno 249:121–122

Maul LC, Smith KT, Barkai R, Barash A, Karkanas P, Shahack-Gross R, Gopher A (2011) Microfaunal remains at Middle Pleistocene Qesem Cave, Israel: preliminary results on small vertebrates, environment and biostratigraphy. J Hum Evol 60(4):464–480

Młynarski M, Szyndlar Z, Estes R, Sanchiz B (1982) Lower vertebrate fauna from the Miocene of Opole (Poland). Estud Geol 38:103–119

Moody S, Roček Z (1980) *Chamaeleo caroliquarti* (Chamaeleonidae, Sauria) a new species from the Lower Miocene of central Europe. Věstnik Ústředniho Ustavu Geologického 55:85–92

Mörs T (2002) Biostratigraphy and paleoecology of continental Tertiary vertebrate faunas in the Lower Rhine Embayment (NW-Germany). Neth J Geosc, Geol Mijn 81:177–183

Mörs T, von der Hocht F, Wutzler B (2000) Die erste Wirbeltierfauna aus der miozänen Braunkohle der niederrheinischen Bucht (Ville-Schichten, Tagebau Hambach). Paläontol Z 74:145–170

Nečas P, Modry D, Slapeta JR (2003) *Chamaeleo* (*Trioceros*) *narraioca* n. sp. (Reptilia: Chamaeleonidae), a new chameleon species from a relict montane forest of Mount Kulal, northern Kenya. Trop Zool 16(1):1–12

Nečas P, Modry D, Slapeta JR (2005) *Chamaeleo* (*Triceros*) *ntunte* n. sp., a new chamaeleon species from Mt. Nyiru, northern Kenya (Squamata: Sauria: Chamaeleonidae). Herpetozoa 18(3/4):125–132

Nečas P, Sindaco R, Kořený L, Kopečná J, Malonza PK, Modry D (2009) *Kinyongia asheorum* sp. n., a new montane chameleon from the Nyiro Range, northern Kenya (Squamata: Chamaeleonidae). Zootaxa 2028:41–50

Oppel M (1811) Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, München

Pickford M (1986) Sediment and fossil preservation in the Nyanza Rift system of Kenya. Geol Soc Spec Pub 25:345–362

Pregill GK, Steadman DW (2004) South Pacific iguanas: human impacts and a new species. J Herpetol 38(1):15–21

Prieto J, Böhme M, Maurer H, Heissig K, Abdul-Aziz H (2009) Biostratigraphy and sedimentology of the Fluviatile Untere Serie (Early and Middle Miocene) in the central part of the North Alpine Foreland Basin: implications for palaeoenvironment and climate. Int J Earth Sci 98(7):1767–1791

Pyron RA, Burbrink FT, Wiens JJ (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evol Biol 13:93

Rage J-C (1984) Serpentes. Handbuch der Palaeoherpetologie, Part 11. Gustav Fischer Verlag, Stuttgart/New York

Rage J-C, Bailon S (2011) Amphibia and Squamata. In: Harrison T (ed) Paleontology and geology of Laetoli: human evolution in context, vol 2, Fossil hominins and the associated fauna. Springer, New York, pp 467–478

Rage J-C, Szyndlar Z (2005) Latest Oligocene-Early Miocene in Europe: Dark Period for booid snakes. Compt R Pal 4:428–435

Raselimanana AP, Rakotomalala D (2003) Chamaeleonidae, chamaeleons. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 960–969

Rato C, Carranza S, Perera A, Carretero MA, Harris DJ (2010) Conflicting patterns of nucleotide diversity between mtDNA and nDNA in the Moorish gecko, *Tarentola mauritanica*. Mol Phyl Evol 56:962–971

Rato C, Carranza A, Harris DJ (2011) When selection deceives phylogeographic interpretation: the case of the Mediterranean house gecko, *Hemidactylus turcicus* (Linnaeus, 1758). Mol Phyl Evol 58:365–373

Raxworthy CJ, Forstner MRJ, Nussbaum RA (2002) Chameleon radiation by oceanic dispersal. Nature 415:784–787

Reeder TW, Townsend TM, Mulcahy DG, Noonan BP, Wood PL Jr, Sites JWJ, Wiens JJ (2015) Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. PLoS ONE 10(3):e0118199

Rieppel O, Walker A, Odhiambo I (1992) A preliminary report on a fossil chamaeleonine (Reptilia: Chamaeleoninae) skull from the Miocene of Kenya. J Herpet 26(1):77–80

Roček Z (1984) Lizards (Reptilia: Sauria) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia). Rozpr Českosl Akad věd, řad matem přír věd 94(1):3–64

Rögl F (1999) Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geol Carpat 50:330–349

Römer F (1870) Über *Python euboicus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea. Z Deuts Geol Ges 22:582–590

Schleich HH (1983) Die mittelmiozane Fossil-Lagerstätte Sandelzhausen 13. *Chamaeleo bavaricus* sp. nov., ein neuer Nachweis aus dem Jungtertiär Süddeutschlands. Mitt Bayer Staatssamml Paläontol Hist Geol 23:77–81

Schleich HH (1984) Neue Reptilienfunde aus dem Tertiär Deutschlands 2. *Chamaeleo pfeili* sp. nov., von der untermiozänen Fossilfundstelle Rauscheröd/Niederbayern (Reptilia, Sauria Chamaeleonidae). Mitt Bayer Staatssamml Paläontol Hist Geol 24:97–103

Schleich HH (1994) Neue Reptilienfunde aus dem Tertiär Deutschlands 15. Neue Funde fossiler Chamäleonen aus dem Neogen Süddeutschlands. Cour Forschungsinst Senckenb 173:175–195

Schmidt-Kittler N (1983) The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). 3. On a new species of *Sivanasua* Pilgrim, 1931 (Feliforma, Carnivora) and the phylogenetic position of this genus. Proc Koninkl Nederl Akad Wetensc Ser B 86(3):301–318

Sillero N, Campos J, Bonardi A, Corti C, Creemers R, Crochet P-A, Crnobrnja Isailović J, Denoël M, Ficetola GF, Gonçalves J, Kuzmin S, Lymberakis P, de Pous P, Rodríguez A, Sindaco R, Speybroeck J, Toxopeus B, Vieites DR, Vences M (2014) Updated distribution and biogeography of amphibians and reptiles of Europe. Amphibia-Reptilia 35:1–31

Simões TR, Wilner E, Caldwell MW, Weinschütz LC, Kellner AWA (2015) A stem acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. Nat Com 6:8149

Sindaco R, Jeremčenko V (2008) The reptiles of the western Palearctic. Vol. 1: annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. In: Belvedere (ed) Monografie della Societas Herpetologica Italica - I

Sperone E, Crescente A, Brunelli E, Paolillo G, Tripepi S (2010) Sightings and successful reproduction of allochthonous reptiles in Calabria. Act Herpetol 5(2):265–273

Stipala J, Lutzmann N, Malonza PK, Borghesio L, Wilkinson P, Godley B, Evans MR (2011) A new species of chameleon (Sauria: Chamaeleonidae) from the highlands of northwest Kenya. Zootaxa 3002:1–16

Stipala J, Lutzmann N, Malonza PK, Wilkinson P, Godley B, Nyamache J, Evans MR (2012) A new species of chameleon (Squamata: Chamaeleonidae) from the Aberdare Mountains in the central highlands of Kenya. Zootaxa 3391:1–22

Szyndlar Z (1991) A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Est Geol 47:103–126

Szyndlar Z, Rage J-C (1990) West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): interrelationships among extinct and extant species. Amphibia-Reptilia 11:385–400

Szyndlar Z, Rage J-C (2003) Non-erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals. Polish Academy of Sciences, Cracow

Talavera R, Sanchíz F (1983) Restos pliocénicos de Camaleón común, *Chamaeleo chamaeleon* (L.) de Málaga. Bol Real Soc Esp Hist Nat (Geolo) 81:81–84

Tassy P (1990) The "Proboscidean datum event": how many proboscideans and how many events. In: Lindsay EH, Fahlbusch V, Mein P (eds) European Neogene mammal chronology. Plenum Press, New York, pp 237–252

Teyssier J, Saenko SV, van der Marel D, Milinkovitch MC (2015) Photonic crystals cause active colour change in chameleons. Nat Com 6:6368

Tilbury CR, Tolley KA (2015) Contributions to the herpetofauna of the Albertine Rift: two new species of chameleon (Sauria: Chamaeleonidae) from an isolated montane forest, south eastern Democratic Republic of Congo. Zootaxa 3905:345–364

Tolley KA, Menegon M (2013) Evolution and biogeography of chameleons. In: Tolley KA, Herrel A (eds) The biology of chameleons. University of California Press, Berkeley, pp 131–147

Tolley KA, Chase BM, Forest F (2008) Speciation and radiations track climate transitions since the Miocene climatic optimum: a case study of southern African chameleons. J Biogeogr 35:1402–1414

Tolley KA, Townsend TM, Vences M (2013) Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. Proc R Soc B 280:20130184

Townsend T, Larson A, Louis EJ, Macey JR (2004) Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. Syst Biol 53:735–757

Townsend TM, Mulcahy DG, Noonan BP, Sites JW Jr, Kuczynski CA, Wiens JJ, Reeder TW (2011) Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. Mol Phyl Evol 61: 363–380

van Den Hoek Ostende LW, Mayda S, Oliver A, Madern A, Hernández-Ballarín V, Peláez-Campomanes P (2015) Aliveri revisited, a biogeographical appraisal of the early Miocene mammals from the eastern Mediterranean. Palaeobiod Palaeoenv 95:271–284

van der Meulen AJ, de Bruijn H (1982) The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2. The Gliridae. Proc Koninkl Nederl Akad Wetensc Ser B 85(4):485–524

Vidal N, Hedges SB (2009) The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. C R Biol 328:1000–1008

Wiens JJ, Brandley MC, Reeder TW (2006) Why does a trait evolve multiple times within a clade? Repeated evolution of snake-like body form in squamate reptiles. Evol 61:123–141

Wiens JJ, Hutter CR, Mulcahy DG, Noonan BP, Townsend TM, Sites JW, Reeder TW (2012) Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. Biol Lett 8:1043–1046

Zarcone G, Petti FM, Cillari A, Di Stefano P, Guzzetta D, Nicosia U (2010) A possible bridge between Adria and Africa: new palaeobiogeographic and stratigraphic constraints on the Mesozoic palaeogeography of the Central Mediterranean area. Earth-Sci Rev 103:154–162

Zug GR, Hamilton AM, Austin CC (2011) A new *Emoia samoensis* group lizard (Squamata: Scincidae) from the Cook Islands, South-central Pacific. Zootaxa 2675:47–57

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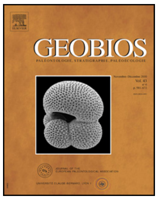

Original article

# Fossil amphibians and reptiles from Plakias, Crete: A glimpse into the earliest late Miocene herpetofaunas of southeastern Europe ☆

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ABSTRACT

Fossil amphibians and reptiles from the earliest late Miocene (early Tortonian, MN 9) of Plakias (Crete, Greece) are described in this paper. Most of the material is fragmentary, precluding precise taxonomic assignment. Nevertheless, the herpetofauna of Plakias is here shown to be diverse, comprising at least six different taxa: an alytid anuran, a crocodilian, two turtles (a pan-trionychid and a geoemydid) and two squamates (an amphisbaenian and a colubroid snake). The crocodilian material represents the first such fossils described from Greece and furthermore, one of the latest occurrences of this group in Europe. The pan-trionychid and the geoemydid represent the oldest occurrences of these groups in Greece and further add to their scarce Miocene record from this country. The first description of a fossil amphisbaenian from Greece is also provided. The new specimens from Plakias add to our knowledge of the Miocene herpetofaunas of southeastern Europe.

## 1. Introduction

Miocene herpetofaunas from Europe are relatively well known (Rage and Augé, 1993; Sanchiz, 1998; Rage and Roček, 2003; Szyndlar and Rage, 2003; Augé, 2005; Danilov, 2005). However, the focus of previous studies is heavily unbalanced toward the herpetofaunas of the western and central parts of the continent, whereas only few papers have dealt with the eastern European ones (Szyndlar and Zerova, 1990; Szyndlar, 1991a,b; Rage and Augé, 1993; Antunes, 1994; Rage and Roček, 2003; Danilov, 2005; Daza et al., 2014). On the other hand, even less is known about the Miocene amphibians and reptiles from southeastern Europe, despite the fact that this region played a pivotal biogeographic role during that period: several dispersals events from both Africa and Asia occurred during this time interval (Rögl, 1999; Koufos et al., 2005). As such, the study of southeastern European localities could clarify important aspects about the biogeography, evolutionary history and extinction events of certain European groups.

Greece harbors a large number of Miocene localities, of which several have been well known and studied for more than a century (Koufos, 2006). However, mammal findings were almost always the main focus of these studies, thereby neglecting other important tetrapod taxa such as amphibians and reptiles. Nevertheless, important fossil findings during the last 160 years have shown a diverse array of Miocene reptiles (Gaudry, 1862–1867; Römer, 1870; Weithofer, 1888; Szalai, 1931; Paraskevaidis, 1955; Bachmayer, 1967; Richter, 1995; Szyndlar, 1995; Georgalis et al., 2013, 2016b; Georgalis and Kear, 2013; Vlachos and Tsoukala, 2014; Vlachos et al., 2015b; Garcia et al., 2016), whereas amphibian fossils remain practically unknown from this time interval in Greece, with only few, sporadic published occurrences (Sanchiz, 1998; Rage and Roček, 2003).

Here we describe new amphibian and reptile findings from the earliest late Miocene (early Tortonian, MN 9) locality of Plakias, on the Island of Crete, southern Greece. The fragmentary nature of these fossils precludes any taxonomic assignment at the species level. Higher level taxonomic determination was possible,

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however, revealing an unexpectedly diverse assemblage consisting of anurans, pan-trionychids, geoemydids, crocodilians, amphisbaenians, and snakes.

**Institutional Abbreviations**: **NHMC**, Natural History Museum and University of Crete, Greece; **UU**, Department of Earth Sciences, University of Utrecht, The Netherlands.

## 2. Geological framework

All specimens described herein were collected from the locality of Plakias (also known under the spelling Plakia). This is an earliest late Miocene locality, situated in the Agios Vasileios municipality, Rethymnon periphery, Island of Crete (Fig. 1). Its exact age was initially believed to be younger than late Astaracian (late MN 7/MN 8; de Bruijn and Meulenkamp, 1972), a suggestion that was tentatively followed by van der Made (1996) and Koufos (2006). However, it was recently shown that the fauna pertains to the Vallesian (early Tortonian, MN 9), with an age of approximately 9.9 Ma (de Bruijn et al., 2012; Koufos and Kostopoulos, 2013). The Plakias Basin is filled with continental deposits characterized by alternations of silty clays, silts, sandstones and conglomerates (de Bruijn et al., 2012). Fossils originate from grayish clays overlying beige to brown clays with calcretes in a shallow gully complex, southeast of Plakias (de Bruijn et al., 2012).

The palaeoherpetofauna of Plakias can neither confirm nor dispute with certainty the suggested age of the locality as Vallesian (MN 9), earliest late Miocene (de Bruijn et al., 2012). However, it is noted that pan-trionychids and crocodilians are better represented in early and middle Miocene localities of Europe, rather than late Miocene ones (Karl, 1999; Delfino and Rossi, 2013). Since none among the Plakias representatives of the herpetofauna can be attributed to the species level, no further age correlation can be safely made. In any case, the age information on the basis of micromammals allows referring the whole faunal assemblage to the earliest late Miocene (MN 9; de Bruijn et al., 2012).

## 3. Material and methods

All the amphibians, crocodilians and squamates, and part of the pan-trionychid and geoemydid material described in this study is housed in the collections of the University of Utrecht (UU). This amphibian and reptile material was collected along with the fossil micromammals that were described by de Bruijn and Meulenkamp (1972) from the first period of fieldwork at Plakias. Part of the geoemydid and the pan-trionychid material belongs to the collections of the Natural History Museum of Crete (NHMC) and represents material that was collected by Kuss in the 1970s. This material was originally in the Geologisch-Paläontologisches Institut der Universität Freiburg, Germany, and later formed part of the collections of the Natural History Museum of Karlsruhe, Germany, before its recent return to the NHMC. This material was studied in the doctoral thesis of one of us (Vlachos, 2015) and is further presented here in the context of the whole herpetofauna of Plakias. It is not possible to determine the exact stratigraphic origin of the material collected by Kuss, as he did not publish anything about it. It has been recently noted, however, that the old (de Bruijn and Meulenkamp, 1972) and new (de Bruijn et al., 2012) micromammal collections of Plakias could "come from slightly different stratigraphic levels" (de Bruijn et al., 2012, p. 61) due to building activity in the area during the last 40 years. However, the same authors noted that "the 25 cm thick grayish silty clay sampled in 2010 seems to be the only bed that contains vertebrate remains" (de Bruijn et al., 2012, p. 61). Following this line of reasoning, and in the absence of conflicting evidence, we treat all the material described herein as originating from the same site.

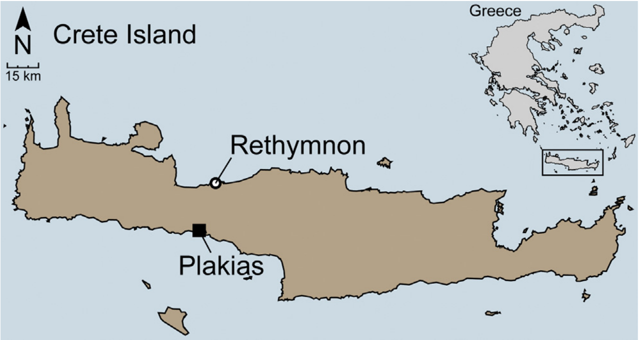


**Fig. 1.** Map of Crete, locating the earliest late Miocene locality of Plakias.

Taxonomy follows Pyron and Wiens (2011) for anurans, Joyce et al. (2004) for turtles, Brochu (2000) for crocodilians, and Gauthier et al. (2012), Pyron et al. (2014), and Wallach et al. (2014) for squamates. Anatomical terminology follows Sanchiz (1998) for anurans, Zangerl (1969) for turtles, Steel (1973) for crocodilians, Estes (1983) for amphisbaenians, and Rage (1984) for snakes.

## 4. Systematic paleontology

Amphibia Linnaeus, 1758
Anura Fischer von Waldheim, 1813
Alytidae Fitzinger, 1843
cf. Alytidae indet.
Fig. 2

**Referred specimens**: UU PL 701, a fragmentary trunk vertebra; UU PL 702, a single, partial tibiofibula.

**Description**: UU PL 701: This trunk vertebra preserves only the centrum and, on both sides, a small, basal portion of the neural arch. The centrum is roughly 2.8 mm long and slightly dorsoventrally flattened. The condyle bears a small, but well-defined condylar neck that is typical of opisthocoelous vertebrae and therefore characterizes the anterior extremity of the centrum. The anterior condyle and the posterior cotyle are rather subcircular.

UU PL 702: The preservational status of this tibiofibula fragment is poor. It preserves only a terminal portion, showing the presence of the two fused elements. Moreover, the fact that this skeletal element has limited diagnostic value hinders a precise identification.

**Remarks**: UU PL 701 can be tentatively referred to the Alytidae on the basis of the condylar neck that marks the condyle. This character has not been described in the literature (e.g., Bailon, 1999) but in our experience, this trait is characteristic for this group of frogs, which at least in some cases have also a comparable size. UU PL 702 is here tentatively referred to the same taxon represented by the co-occurring vertebra. Most probably, the amphibian material presented herein is the same that Sanchiz (1998, p. 168) referred to as "Platkia (*sic.*), Greece, Neogene: Discoglossinae indet. (Sanchiz, unpublished)" (Borja Sanchiz, pers. comm. to GLG, February 2016).

It is beyond the scope of this paper to evaluate the taxonomic affinities of European painted frogs and we follow Frost et al. (2006) in using the term Alytidae for all these amphibians. Despite their confined extant distribution, alytids were once widespread in Europe (Rage and Roček, 2003). In Greece, other fossils attributed to this group have been briefly reported from the Miocene of Aliveri, Ano Metochi, Biodrak, Lefkon, Maramena, Monasteri and Pikermi, the Pliocene of Kardia, Ptolemais and Spilia, and the Miocene or Pliocene of Rema Aslan and Rema Marmara (Rage and Roček, 2003).

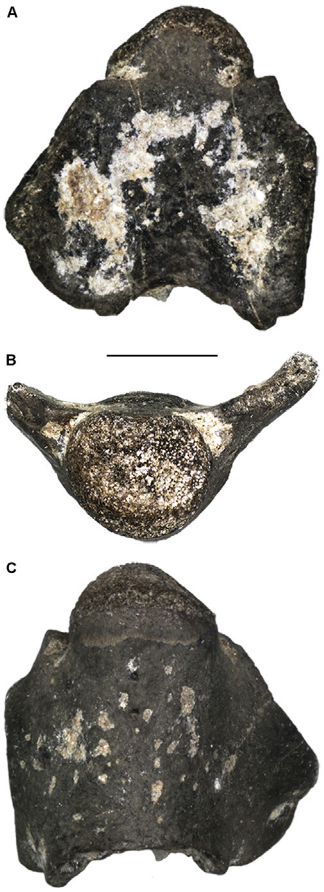


**Fig. 2.** cf. Alytidae from the earliest late Miocene of Plakias: UU PL 701, a trunk vertebra in dorsal (**A**), anterior (**B**) and ventral (**C**) views. Scale bar: 1 mm.

Reptilia Laurenti, 1768
Testudines Batsch, 1788
Pan-Trionychidae Joyce et al., 2004
Pan-Trionychidae indet.
Fig. 3

**Referred specimens**: UU PL 703, costal fragment; UU PL 704, costal fragment; NHMC 21.7.3.1670, neural; NHMC 21.7.3.1671, plastron fragment.

**Description**: NHMC 21.7.3.1670 (Fig. 3(A)): This specimen corresponds to an almost complete neural. Although the specimen is eroded, the shape of the neural appears to be hexagonal with short lateral sides. Dorsally, the distinctive sculpturing is visible, consisting mainly of small pits. Viscerally, the attachment for the vertebra is preserved.

UU PL 703 (Fig. 3(B)): This specimen corresponds to a fragment of a costal, as is shown by the presence of a rib on the visceral part. On the distal side, a part of the rib is apparent as well. Dorsally, the distinctive sculpturing is visible, consisting of small pits that are mainly separated from one another. The anterior and posterior margins of the costal are developed parallel to each other on the preserved part.

UU PL 704 (Fig. 3(C)): This specimen corresponds to a fragment of a costal, as is shown by the presence of the rib on the visceral part. Its morphology is similar to the previously described specimen (UU PL 703), but a larger part of the costal is preserved.

NHMC 21.7.3.1671 (Fig. 3(D)): This specimen most probably corresponds to a process of the plastron. It is long and flattened, with an elliptical cross-section. Further identification is not possible.

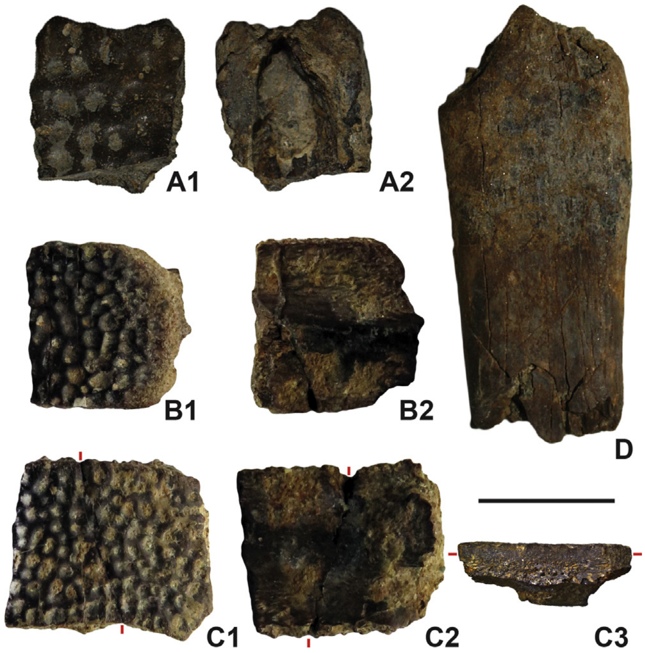


**Fig. 3.** Pan-Trionychidae from the earliest late Miocene of Plakias. **A**. NHMC 21.7.3.1670, fragment of a neural, in dorsal (A1) and visceral (A2) views. **B**. UU PL 703, fragment of a costal in dorsal (B1) and visceral (B2) views. **C**. UU PL 704, fragment of a costal in dorsal (C1) and visceral (C2) views. **D**. NHMC 21.7.3.1671, fragment of plastron in dorsal view. Scale bar: 10 mm.

**Remarks**: The available specimens can be attributed to Pan-Trionychidae based on the presence of sculpturing that covers all metaplastic portions of the shell bones (Vitek and Joyce, 2015). The preserved pan-trionychid material from Plakias consists mainly of carapace fragments and a possible plastron element. Given that the sculpturing pattern is highly variable among soft-shelled turtles, even within individuals of the same species (Gardner and Russell, 1994; Vitek and Joyce, 2015), further identification is not possible. Compared to the only other known fossil pan-trionychid from Greece from the Pliocene of Gefira, northern Greece (Vlachos et al., 2015a), the Plakias specimens pertain to a smaller-sized form, both in regards of carapacial disk length and thickness of the carapace. Another difference between these two Greek occurrences is noted in the sculpturing of the two forms: on the basis of the commonly preserved distal part of the costal, the pits on the Plakias pan-trionychid are mainly separated, whereas in the pan-trionychid from Gefira, they are mostly coalesced, forming continuous grooves. As mentioned above, however, the extreme variability of sculpturing observed within pan-trionychids does not allow us to determine taxonomic differences between the two Greek forms on the basis of this character.

Geoemydidae Theobald, 1868
Genus ***Mauremys*** Gray, 1869
*Mauremys* sp.
Fig. 4

**Referred specimens**: NHMC 21.7.3.1618, part of anterior lobe; NHMC 21.7.3.1619, right xiphiplastron; NHMC 21.7.3.1620, left hypoplastron; NHMC 21.7.3.1621, group of 15 plastral fragments; NHMC 21.7.3.1622-1624, three neurals; NHMC 21.7.3.1625-1626, left hyoplastron fragments; NHMC 21.7.3.1627, right hypoplastron fragment; NHMC 21.7.3.1628, costal fragment; NHMC 21.7.3.1629, right hypoplastron fragment; NHMC 21.7.3.1630-1931, two costal fragments; NHMC 21.7.3.1632, left epiplastron; NHMC 21.7.3.1633, left hyoplastron fragment; NHMC 21.7.3.1634, group of 23 shell fragments; NHMC 21.7.3.1635, right epiplastron; NHMC

21.7.3.1636-1937, two left epiplastra; NHMC 21.7.3.1638-1939, two costal fragments; NHMC 21.7.3.1640, two costals in association; NHMC 21.7.3.1641, right peripheral 1; NHMC 21.7.3.1642, right xiphiplastron fragment; NHMC 21.7.3.1643, right hypoplastron fragment; NHMC 21.7.3.1644, left hyoplastron fragment; NHMC 21.7.3.1645-1947, three costal fragments; NHMC 21.7.3.1648, group of approximately 80 shell fragments; NHMC 21.7.3.1649, neural fragment; NHMC 21.7.3.1650, group of 10 shell fragments; NHMC 21.7.3.1651, neural I; NHMC 21.7.3.1652-1665, 14 costal fragments; NHMC 21.7.3.1666-1668, three peripheral fragments; NHMC 21.7.3.1669, group of 50 shell fragments; UU PL 705, possible hyoplastron fragment.

**Description**: The material consists of numerous shell fragments of relatively good preservation. Most specimens preserve sufficient anatomical information, but several remain indeterminate. The description of the most complete specimens is given below.

Carapace elements (Fig. 4(A–J)). NHMC 21.7.3.1623 (Fig. 4(A)): This specimen corresponds to a complete neural. It is hexagonal, with short anterior lateral sides. It is not crossed by any vertebral sulci, suggesting that it is the second or fourth neural. NHMC 21.7.3.1645 shows a similar morphology (Fig. 4(C)).

NHMC 21.7.3.1622 (Fig. 4(B)): This is a complete neural that is hexagonal, with short lateral sides. It is crossed by the vertebral sulci in the posterior part, suggesting that it is the third or fifth neural.

NHMC 21.7.3.1624 (Fig. 4(D)): This complete neural is quadrangular to rounded, with the anterior part being slightly wider. It is not crossed by any vertebral sulci. Its size is rather small, in comparison to the other neurals described. A dorsal keel is noted longitudinally, suggesting that it could belong to a young individual.

NHMC 21.7.3.1651 (Fig. 4(E)): This specimen corresponds to a complete first neural. It is quadrangular with rounded edges, being longer than wide. The posterior part is crossed by the vertebral sulcus that is not straight.

NHMC 21.7.3.1649 (Fig. 4(F)): This specimen corresponds to a fragment of a neural. It is much wider than long, hexagonal in shape, with shorter anterior lateral sides. As such, it is most probably one of the posterior neurals. Viscerally, the attachment for the vertebra is visible. As it is not crossed by any sulci; it could be either the sixth or seventh neural.

NHMC 21.7.3.1640 (Fig. 4(G)): This specimen corresponds to the medial parts of two successive left costals in association. Both show the long and short medial sutures for the corresponding hexagonal neurals. In the preserved part, the sulci between the vertebrals and the pleurals can be observed.

NHMC 21.7.3.1638 (Fig. 4(H)): This specimen corresponds to an almost complete right costal, missing only the distal part. In medial side, two sutured surfaces are visible, one long and the other short, corresponding to an hexagonal neural. Dorsally, the sulci between the vertebrals are visible, suggesting that this could be the third or fifth costal.

NHMC 21.7.3.1639 (Fig. 4(I)): This specimen corresponds to the medial part of a left costal. In medial side, two sutured surfaces are visible, one long and one short, corresponding to an hexagonal neural. Dorsally, the sulci between the pleurals cross the medial part of this costal, suggesting that this could be the second, fourth or sixth costal.

NHMC 21.7.3.1641 (Fig. 4(J)): This specimen corresponds to an almost complete right peripheral I. Based on the preserved anterior border we can estimate the presence of a wide nuchal notch affecting also the first peripherals. The peripheral is long and narrow. Medially, the vertebral I and the pleural I show a long overlap on the peripheral, whereas the vertebral I contacts marginal II.

Plastron elements (Fig. 4(K–S)). NHMC 21.7.3.1618 (Fig. 4(K)): This specimen corresponds to the right part of the anterior lobe of the plastron, consisting of the right epiplastron and most of the entoplastron. The epiplastron is long and narrow. Viscerally, a long but shallow lip is formed, being concave medially and convex laterally. Anteriorly, a shallow notch is noted. The entoplastron is hexagonal and rounded, being wider posteriorly. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gular/humeral sulcus is slightly convex laterally, and causes a slight constriction in the anterior part of the lobe. The humerals are medially short and laterally longer. The entoplastron is also overlapped by the anterior part of the pectorals. The humero-pectoral sulcus is slightly concave medially.

NHMC 21.7.3.1637 (Fig. 4(L)): This specimen corresponds to a left epiplastron. The epiplastron is long and rather wide. Viscerally, a long lip is formed, being concave medially and convex laterally. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gularo/humeral sulcus is slightly convex laterally. The left epiplastron NHMC 21.7.3.1636 shows a similar morphology.

NHMC 21.7.3.1635 (Fig. 4(M)): This specimen corresponds to a right epiplastron. It is long and rather wide. Viscerally, a long and shallow lip is formed, being concave medially and convex laterally. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is slightly convex laterally and causes a slight constriction in the anterior part of the lobe.

NHMC 21.7.3.1632 (Fig. 4(N)): This is an almost complete left epiplastron, rather long and wide. Viscerally, a short, shallow and slightly concave lip is formed. It is covered medially by the gulars. An irregular growth of a small scute is noted in the anterior end of the gularo-humeral sulcus.

NHMC 21.7.3.1620 (Fig. 4(O)): This specimen corresponds to an almost complete left hypoplastron. The anterior suture, which connects it to the hyoplastron, is straight, whereas the posterior one, which connects it to the xiphiplastron, is slightly convex. The hypoplastron is rather flat. Viscerally, the abdominal forms a wide and slightly convex lip on the posterior lobe. Ventrally, an unusual morphology is noticed. Although the posterior part of the hypoplastron is covered by the abdominal scute, anteriorly there is another sulcus. Such sulcus is apparent also in another specimen from Plakias (NHMC 21.7.3.1643; Fig. 4(P)), a morphology that has not been previously noted in geoemydids. However, the absence of corresponding hyoplastra and the disarticulated nature of the material do not allow us to clarify this character.

NHMC 21.7.3.1643 (Fig. 4(P)): This specimen corresponds to an almost complete right hypoplastron. The anterior suture, which connects it to the hyoplastron, is straight, whereas the posterior one, which connects it to the xiphiplastron, is slightly convex. The hypoplastron is rather flat. Viscerally, the abdominal forms a wide and slightly convex lip on the posterior lobe. In the posterior part, the abdomino-femoral sulcus is clearly visible, whereas in the anterior part the sulcus is not clear as a result of erosion.

NHMC 21.7.3.1619 (Fig. 4(Q)): This specimen corresponds to an almost complete right xiphiplastron. The lateral sides of the posterior lobe are converging posteriorly. On the posterior part, a deep and wide anal notch is formed. The xiphiplastral extremities are rounded. The femorals cover the anterior part of the xiphiplastron, whereas the anals show a somewhat long covering on the posterior part of the lobe. The femoro-anal sulcus is slightly convex, being oriented antero-medially.

NHMC 21.7.3.1642 (Fig. 4(R)): This specimen corresponds to a fragment of the right xiphiplastron. On the basis of the preserved part, the presence of a wide angular anal notch can be estimated. In the anterior part, a short part of the femoro-anal sulcus is noted.

UU PL 705 (Fig. 4(S)): In the collections of UU, this small-sized specimen probably represents a fragment of the left hyoplastron. It preserves a curved sulcus that could be identified as the pectoro-abdominal one. Further identification is not possible, but it is overall similar to the respective material from NHMC and can be attributed to the same taxon as well.

**Remarks**: The specimens can be attributed to Geoemydidae on the basis of the following characters: first neural quadrangular, remaining neurals hexagonal with short anterolateral sides, pectorals medially shorter than the gulars, and deep anal notch. They can be further identified as a member of *Mauremys* on the basis of the contact between vertebral I with marginal II and the entoplastron being crossed by the gulars and the humero-pectoral sulcus (Claude et al., 2007). The *Mauremys* material from Plakias suggests attribution to a single taxon, on the basis of the similar size, surface sculpturing and overall morphology. The combined information of the preserved elements allows the documentation of the morphology of most parts of the shell, indicating a confident assignment to *Mauremys*, but no species determination can be made with certainty.

Based on the available epiplastra, at least three adult individuals are preserved, and a juvenile individual is also present. The unusual morphology noted in the hypoplastra (NHMC 21.7.3.1620 and NHMC 21.7.3.1643) needs to be further investigated, as it has not previously been observed in other geoemydids. However, the absence of corresponding hyoplastra and the disarticulated nature of the material do not allow us to interpret this character. The extended covering of the pleural I and vertebral I on peripheral I distinguishes the Plakias *Mauremys* from the extant *Mauremys caspica* (Gmelin, 1774) and *M. rivulata* (Valenciennes, 1833), as also from the extinct *M. gaudryi* (Depéret, 1885) (Pliocene, France; Hervet, 2003). As such, the Plakias *Mauremys* is more similar to other Miocene terrapins from central and eastern Mediterranean (e.g., *M. campanii* Chesi et al., 2009, from Tuscany, Italy). The narrower neural I, the shape of the entoplastron, having the posterior part shorter than the anterior one, and the shorter pectoral covering on the entoplastron differentiate the Plakias geoemydid from *M. campanii*. The angular anal notch also differentiates the Plakias geoemydid from the roughly similar *M. sarmatica* (Purschke, 1885) from the Miocene of Germany, which has a rounded anal notch (Hervet, 2003). The Plakias terrapin represents the oldest described occurrence of Geoemydidae from Greece, being older than the Allatini (Miocene/Pliocene boundary; Vlachos et al., 2015b) and the Maramena forms (latest Miocene; Gad, 1990; Georgalis and Kear, 2013; Vlachos et al., 2015b), both recovered from northern Greece. All other fossil geoemydid occurrences from Greece are only known from Pleistocene and Holocene remains (Chesi et al., 2007; Georgalis and Kear, 2013).

Crocodylia Gmelin, 1789
Crocodylia indet.
Fig. 5

**Referred specimens**: UU PL 706 to UU PL 732, 27 isolated teeth; UU PL 735 and UU PL 736, two phalanges.

**Description**: UU PL 706-732: Several isolated teeth preserve only a crown that is conical, variably pointed apically, and regularly concave basally. Some of the teeth are only partially preserved; the largest crown is 8.3 mm long. Mesiodistal carinae separate a lingual, slightly concave surface from a labial, slightly convex surface. The carinae are not serrated. Both lingual and labial surfaces can be slightly wrinkled and bear longitudinal ridges. Some of the teeth are slender, long, and pointed, whereas others are more massive and apically blunt.

UU PL 735-736: These two phalanges are elongated elements showing a single roundish articular surface proximally. The best preserved element (UU PL 735) is 18 mm long. Its distal portion is dorsoventrally flattened and laterally provided, on both sides, with a sort of weak keel.

**Remarks**: The morphology of the teeth is fully congruent with that of generalized crocodilians, but does not allow a more precise identification, since in most cases crocodilian teeth are not diagnostic. These are, however, congruent with the morphology of the *Crocodylus* teeth from the late Miocene of Italy (Delfino et al., 2007). Not much can be said about the phalanges, except for the fact that they show standard crocodilian morphology. They are referred to the same taxon as the teeth. The Plakias specimens constitute the first fossils of crocodilians described from Greece, as also one of the last occurrences of this group in the European continent (Table 1).

Squamata Oppel, 1811
Amphisbaenia Gray, 1844
Amphisbaenia indet.
Fig. 6

**Referred specimen**: UU PL 733, a single presacral vertebra.

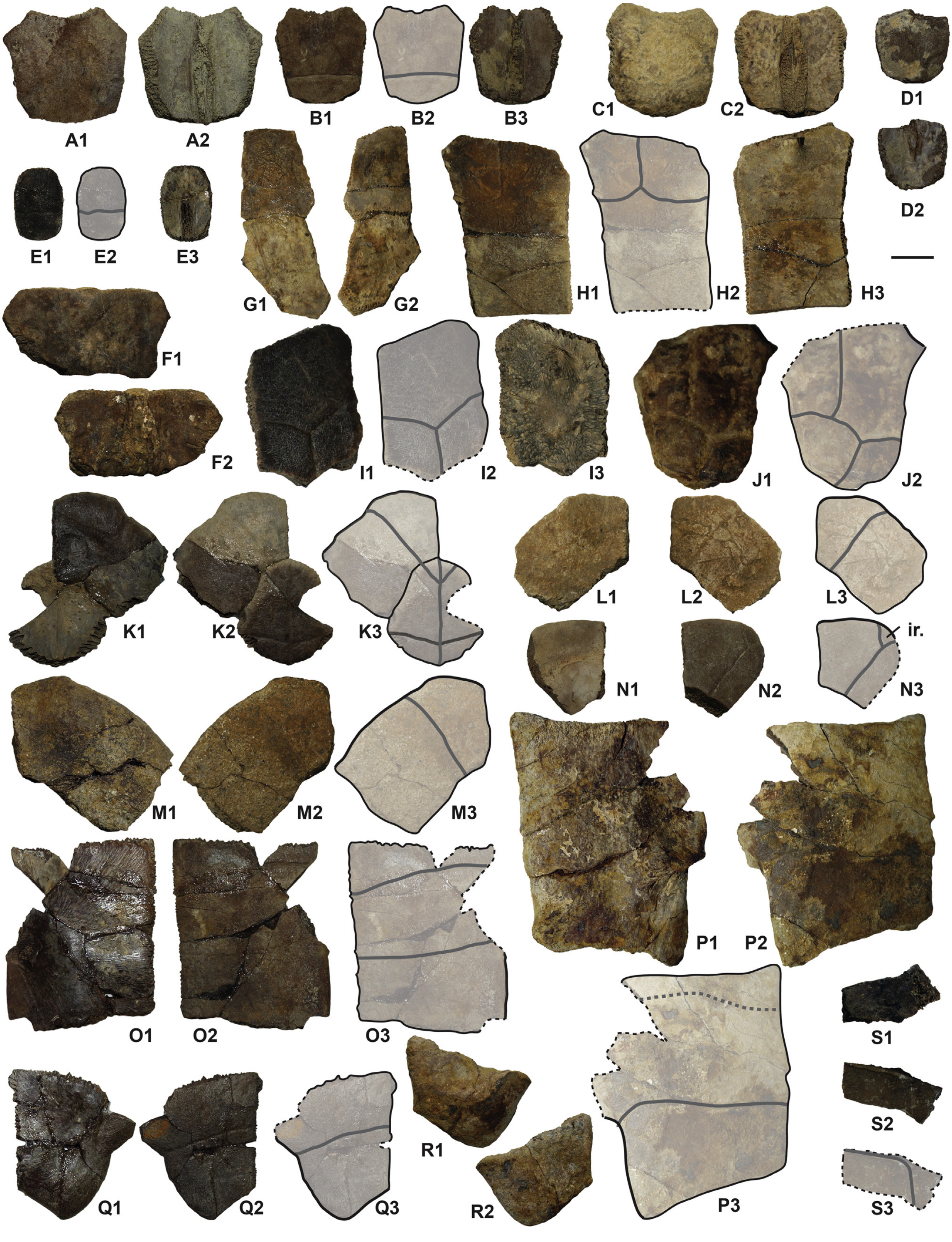
**Description**: The specimen is a rather small, procoelous vertebra with a centrum length of only 1.2 mm. A slight degree of deformation is recognizable in anterior view. The centrum is dorsoventrally compressed and has a flattened ventral surface and subparallel lateral margins. A massive and rounded synapophysis is visible on the right side of the vertebra. In dorsal view, the neural arch is constricted in the middle. Its dorsal surface is flattened and the neural spine is lacking, as well as the zygosphene. Only the right prezygapophysis is preserved: it is roughly sub-elliptical and tilted dorsally about 30°. The prezygapophyseal process is rather short. Neither the posterior end of the neural arch nor the postzygapophyses are preserved.

**Remarks**: The specimen can be attributed to Amphisbaenia on the basis of the combination of the following characters: small size, dorsoventrally compressed centrum with a flattened ventral surface and roughly parallel lateral margins, short and robust prezygapophyses, massive and rounded synapophyses, absence of zygosphene, and a dorsally flattened neural arch lacking a neural spine (Estes, 1983; Delfino, 2003). Amphisbaenians are present in the extant herpetofauna of Greece, with *Blanus* occurring in the Dodecanese Islands (see below, Section 5.2), but they were totally absent in the fossil record of the country. As such, the specimen described herein represents the first known fossil amphisbaenian from Greece. Its affinities with Blanidae, which are the only extant amphisbaenians inhabiting Europe, cannot be tested on the basis of the vertebral morphology: isolated vertebrae of Amphisbaenia do not show significant diagnostic features that would allow for a more precise identification (Estes, 1983). The sole other known fossil amphisbaenian from the Aegean region has been recovered from the Pliocene of Çalta, Turkey (Rage and Sen, 1976). The Çalta amphisbaenian is represented by three vertebrae, none of which was figured or described in detail. As a matter of fact, no further comparison between these specimens can be made.

Also interesting, the vertebra UU PL 733 represents the sole non-snake squamate from Plakias, as other lizards are conspicuously absent. We consider that this absence is due to taphonomic or collection biases and does not reflect the actual lizard palaeodiversity of Plakias.

Serpentes Linnaeus, 1758
Colubroidea Oppel, 1811
?Natricinae Bonaparte, 1838 (*sensu* Szyndlar, 1991b)
?Natricinae indet.
Fig. 7

**Referred specimen**: UU PL 734, a single precloacal vertebra.


A1
A2
B1
B2
B3
C1
C2
D1
D2
E1
E2
E3
G1
G2
H1
H2
H3
F1
F2
I1
I2
I3
J1
J2
K1
K2
K3
L1
L2
L3
ir.
N1
N2
N3
M1
M2
M3
O1
O2
O3
P1
P2
P3
S1
S2
S3
Q1
Q2
Q3
R1
R2

**Description**: The vertebra is fragmentary, with the prezygapophyses, part of the cotyle and part of the neural spine being eroded. The vertebra is procoelous, relatively large and proportionally elongate, with a centrum length of 5.5 mm. The prezygapophyseal processes are not clearly visible, due to the fact that the anterior portion of the vertebra is not well preserved. The cotyle is rather incomplete but appears to be relatively rounded. Only part of the zygosphene is preserved. The condyle is spherical and rather robust, and protrudes significantly from the posterior part of the vertebra. The roof of the zygantrum is visible and appears to be relatively thick. The neural canal is rather large, almost equal in size to the condyle. Synapophyses are divided in diapophyses and parapophyses. The neural spine is broken. The hypapophysis was probably present, however, this cannot be evaluated with certainty. In ventral view, a subcentral foramen is also visible at mid centrum length of the vertebra.

**Remarks**: The specimen can be attributed to Serpentes on the basis of the general vertebral shape and especially the presence of zygantrum and zygosphene (Rage, 1984). The single snake vertebra from Plakias is fragmentary, thus precluding the evaluation of exact taxonomic affinities. However, the probable presence of hypapophysis could indicate that this specimen belongs to either natricines, viperids or elapids. All these three groups have been recorded in the Miocene of Greece (Szyndlar, 1991a,b, 1995; Szyndlar and Rage, 2002; Georgalis et al., 2016a). The combination, however, of a rather elongate centrum, strong subcentral ridge and, probably, a posteriorly vaulted neural spine, prompts us to consider natricine affinities as the most plausible for the Plakias snake. This identification is further supported by direct comparison with numerous skeletons of extant natricine snakes.

## 5. Discussion

### 5.1. Palaeoecology of Plakias

The locality of Plakias is mostly known for its micromammal assemblage (de Bruijn and Meulenkamp, 1972; de Bruijn et al., 2012). This is comprised of erinaceomorphs and soricomorphs eulipotyphlans, and eomyid, sciurid, glirid and murid rodents, whereas larger mammals are known only by an indeterminate suid similar to *Propotamochoerus* (van der Made, 1996; Koufos, 2006; de Bruijn et al., 2012). The presence of at least three distinct taxa of sciurids (Koufos, 2006) indicates the likely presence of a forested environment (de Bruijn et al., 1980), although we acknowledge that several fossil and extant sciurids are ground dwellers (e.g., Viriot et al., 2011). Plant remains and invertebrates are also known from Plakias (de Bruijn et al., 2012). Fossil invertebrates include freshwater gastropods such as *Planorbis* and *Brotia* (de Bruijn et al., 2012), which further suggest the presence of a river or lake system.

The new amphibian and reptile finds from Plakias allow us to draw further conclusions regarding the palaeoecology of this locality. The presence of an alytid frog implies wet habitats, which is the common environment for the extant members of the group (Vitt and Caldwell, 2014). All extant crocodilians are known to be water dwellers, inhabiting river systems, lakes, and even venture into the open sea (Steel, 1973; Britton et al., 2012). The fragmentary nature of the Cretan crocodilian does not allow us to make a proper specific or generic identification, but as the teeth from Plakias bear strong resemblance with certain Neogene finds from the Mediterranean that are assigned to Crocodyloidea or Alligatoroidea, we can infer a similar lifestyle. All extant pan-trionychids are known to be strictly aquatic, and a similar or identical life strategy has been proposed for all fossil taxa of this group as well (Vitek and Joyce, 2015). The occurrence of a geoemydid further indicates the presence of lake and river systems (Busack and Ernst, 1980). The amphisbaenian vertebra is fragmentary and cannot be assigned to the specific level. However, the vast majority of amphisbaenians are fossorial (Kearney, 2003) and as such, a similar, burrowing lifestyle is also proposed for the Cretan representative of this clade. Additionally, the presence of a natricine snake adds a further aquatic or semi-aquatic taxon to the locality (Vitt and Caldwell, 2014).

### 5.2. Biogeography

At least until the late Serravallian (middle Miocene), Crete was located at the southern part of Aegäis, the continental area that united modern Greece with Anatolia, but it was most probably already isolated as an island by the Tortonian (late Miocene), after the opening of the Proto-Aegean Sea (Dermitzakis and Papanikolaou, 1981; Poulakakis et al., 2005). The suggested age of the Plakias fauna as early Tortonian (de Bruijn et al., 2012) coincides with the breakup of the southern Aegean landmass and the early formation of Crete as an island (Poulakakis et al., 2005; fig. 4). As such, we cannot determine with certainty whether Plakias hosted a truly continental fauna or an insular fauna at least partly deriving from the former continental assemblages. However, even if the fauna was an insular one, it should have strong biogeographic affinities with coeval mainland Aegäis faunas.

The micromammal fauna of Plakias bears strong affinities with coeval ones from Central Europe (de Bruijn et al., 2012). The amphibian and reptile fossils described herein provide additional information about the palaeobiogeography of this part of southeastern Europe, as Miocene herpetofaunas are not well documented in that region (Georgalis et al., 2013; Georgalis and Kear, 2013).

The presence of an alytid frog in the late Miocene of Crete is not of biogeographic importance, as this group was widespread throughout Europe during that time interval and has been also found from several other Neogene localities from Greece (Rage and Roček, 2003). All other fossil amphibians from Crete are of Quaternary age (Caloi et al., 1986; Sanchiz, 1998).

The two distinct turtle taxa recovered from Plakias represent the oldest turtles from Crete, as also the oldest occurrences of Geoemydidae and Pan-Trionychidae from Greece known up to date. Overall, turtles were considered up to now to be absent from Neogene localities of Crete, with their only remains known from Pleistocene and Holocene sediments (Bachmayer et al., 1975; Kotsakis, 1977; Brinkerink, 1996; Chesi et al., 2007; Georgalis and Kear, 2013). Although Brinkerink (1996, p. 208) noted that no

**Fig. 4.** *Mauremys* sp. from the earliest late Miocene of Plakias. **A**. NHMC 21.7.3.1623, neural in dorsal (A1) and visceral (A2) views. **B**. NHMC 21.7.3.1622, neural in dorsal (B1), drawing of the dorsal (B2) and visceral (B3) views. **C**. NHMC .7.3.1645, neural in dorsal (C1) and visceral (C2) views. **D**. NHMC .7.3.1624, neural in dorsal (D1) and visceral (D2) views. **E**. NHMC 21.7.3.1651, neural in dorsal (E1), drawing of the dorsal (E2) and visceral (E3) views. **F**. NHMC 21.7.3.1649, neural fragment in dorsal (F1) and visceral (F3) views. **G**. NHMC 21.7.3.1640, two successive costals in dorsal (G1) and visceral (G2) views. **H**. NHMC 21.7.3.1638, costal in dorsal (H1), drawing of the dorsal (H2) and visceral (H3) views. **I**. NHMC 21.7.3.1639, costal fragment in dorsal (I1), drawing of the dorsal (I2) and visceral (I3) views. **J**. NHMC 21.7.3.1641, peripheral in dorsal (J1) and drawing of the dorsal (J2) views. **K**. NHMC 21.7.3.1618, right epiplastron and entoplastron in visceral (K1), ventral (K2) and drawing of the ventral (K3) views. **L**. NHMC 21.7.3.1637, left epiplastron in visceral (L1), ventral (L2) and drawing of the ventral (L3) views. **M**. NHMC 21.7.3.1635, right epiplastron in visceral (M1), ventral (M2) and drawing of the ventral (M3) views. **N**. NHMC 21.7.3.1632, left epiplastron fragment in visceral (N1), ventral (N2) and drawing of the ventral (N3) views. **O**. NHMC 21.7.3.1620, left hypoplastron in visceral (O1), ventral (O2) and drawing of the ventral (O3) views. **P**. NHMC 21.7.3.1643, right hypoplastron in visceral (P1), ventral (P2) and drawing of the ventral (P3) views. **Q**. NHMC 21.7.3.1619, right xiphiplastron in visceral (Q1), ventral (Q2) and drawing of the ventral (Q3) views. **R**. NHMC 21.7.3.1642, right xiphiplastron fragment in visceral (R1) and ventral (R2) views. **S**. UU PL 705, possible hyoplastron fragment in visceral (S1), ventral (S2) and drawing of the ventral (S3) views. Abbreviation: ir, irregular scute growth. Scale bar: 10 mm.

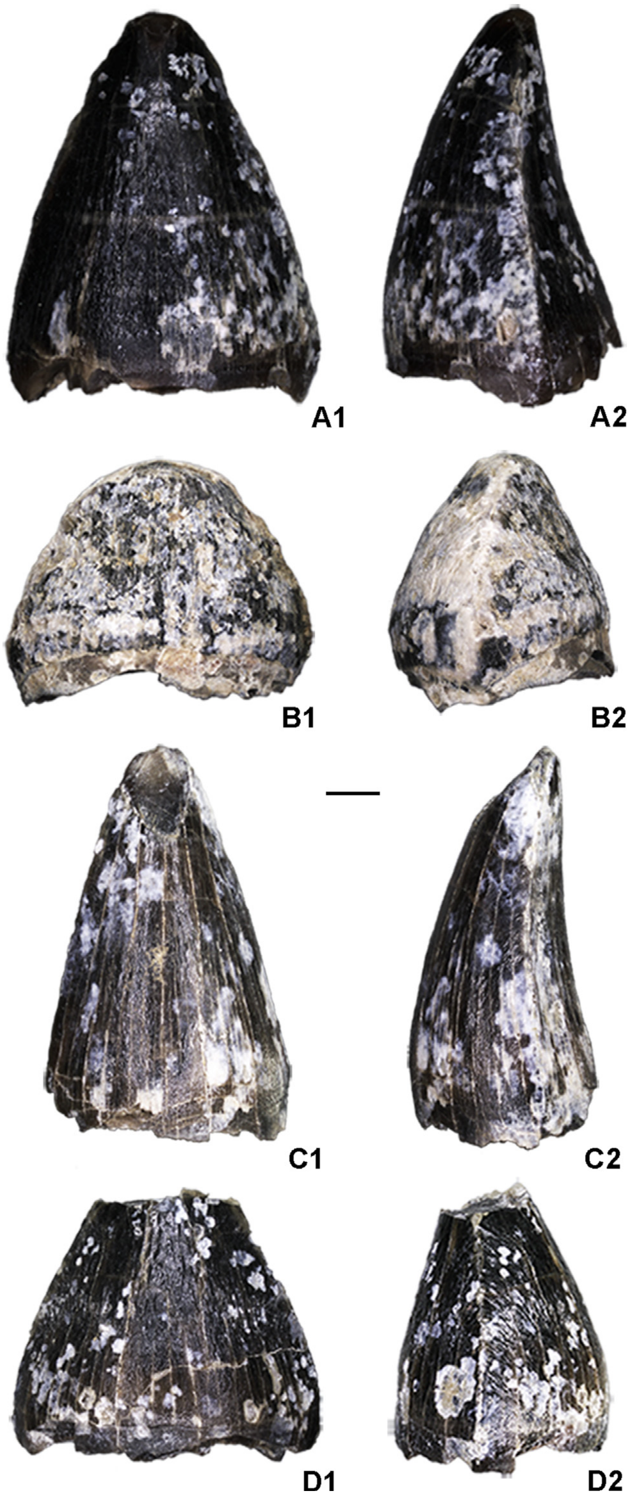


**Fig. 5.** Crocodylia from the earliest late Miocene of Plakias. **A**. UU PL 706, isolated tooth in labial (A1) and mesial (A2) views. **B**. UU PL 707, isolated tooth in labial (B1) and mesial (B2) views. **C**. UU PL 708, isolated tooth in labial (C1) and mesial (C2) views. **D**. UU PL 709, isolated tooth in labial (D1) and mesial (D2) views. Scale bar: 1 mm.

turtles are known from pre-Pleistocene sites from Crete, he pointed out the potential of the site of Plakias. The presence of pan-trionychids in the early late Miocene of Greece represents the oldest record and the second only occurrence of this group from the country, which was otherwise only known from the Pliocene of northern Greece (Vlachos et al., 2015a). Pan-trionychids are widespread throughout Europe during the Neogene (Hummel, 1932; Młynarski, 1976; Danilov, 2005; Karl, 1999); however, their alpha taxonomy has not been settled with certainty, mostly because of the homoplastic characters that are observed in their morphology (Vitek and Joyce, 2015). Curiously also, Miocene pan-trionychids were totally absent until now from Greece, despite the wealth of fossil localities of that age in the country and extensive sampling (Georgalis and Kear, 2013). The new specimens from Plakias could probably indicate that this absence was not genuine and that pan-trionychids will be subsequently found in other Greek Miocene localities. This is further supported by the presence of pan-trionychids in the Miocene of Bulgaria (Pamouktchiev et al., 1998; Georgalis and Kear, 2013) and Anatolia (Staesche et al., 2007). Affinities of the new Cretan pan-trionychid with the Bulgarian and Anatolian forms cannot be established due to the fragmentary nature of the new specimens. Other, relatively geographically close Miocene pan-trionychids are also known from Cyprus (Hadjisterkotis et al., 2000), Egypt (Lapparent de Broin, 2000), and Italy and Malta (Kotsakis, 1985). The Plakias geoemydid adds to the Miocene diversity of this group in southeastern Europe. Additionally, this pre-Messinian occurrence of *Mauremys* further corroborates the suggestion of Chesi et al. (2009) for warm and wet conditions during that period in southern Mediterranean Europe.

Crocodilians are conspicuous elements in several Miocene faunas across European localities (among others, Ginsburg and Bulot, 1997; Kotsakis et al., 2004; Delfino et al., 2007; Delfino and Rook, 2008; Martin, 2010; Martin and Gross, 2011; Delfino and Rossi, 2013). However, they are relatively scarce by the late Miocene and were apparently absent from southeastern Europe and Anatolia (Böhme, 2003; Sen et al., 2011). The youngest up to date published records of crocodilians from Europe are known from the latest Miocene of Italy (Table 1), as supposed occurrences from the late Miocene and Pliocene of Spain and Portugal have not been accompanied by descriptions or figures, and are here considered anecdotal (Delfino et al., 2007). The taxon *Diplocynodon levantinicum* from Bulgaria, was initially thought to be of Pliocene age (Huene and Nikoloff, 1963), whereas it was later treated questionably as late Miocene (Delfino and Rossi, 2013), but its type locality is now believed to pertain most probably to the middle Miocene (Sen et al., 2011). With the exception of the slender snouted forms attributed to *Tomistoma* (Capellini, 1890; Vianna and Moraes, 1945), several late Miocene occurrences are considered to be members of *Crocodylus* or at least cf. *Crocodylus* (Delfino et al., 2007; Delfino and Rook, 2008; Delfino and Rossi, 2013) that possibly dispersed from Africa well before the Messinian Salinity Crisis (Delfino et al., 2007). Interestingly also, Gargano and Scontrone, that yielded *Crocodylus* remains, were palaeoislands during the latest Miocene; we can thus speculate that the Cretan crocodilian could also belong to the same lineage and had originated through a similar dispersal route from Africa. Whatever the case, the isolated teeth from Plakias represent the first crocodilians from Greece to be formally described and one of a few late Miocene occurrences of this group in Europe.

Our knowledge of squamate biogeography during the Miocene of Europe is hindered by the lack of consensus surrounding the taxonomy and phylogenetic relationships of its representatives. This is especially true for the southeastern European localities, from where only few specimens have been recovered, most of which originating from classic, well known mammal-bearing sites (Gaudry, 1862–1867; Weithofer, 1888; Richter, 1995; Georgalis et al., 2016b). The presence of a natricine in the late Miocene of Plakias adds to the already known diversity of this widespread snake group (Szyndlar, 1991b), and in fact, represents one of the southernmost fossil occurrences of colubroids in Europe. Whether the Plakias snake bears close affinities with other Neogene

**Table 1**
Youngest occurrences of crocodilians in Europe.

| Taxon | Age | Locality | Reference |
|---|---|---|---|
| *Crocodylus* sp. | Latest Messinian (or even early Zanclean, depending on the age of the Terre Rosse from Gargano) | Gargano, Apulia, Italy | Delfino et al. (2007) |
| Crocodylia indet. | Late Messinian | Cava del Monticino, Brisighella, Emilia-Romagna, Italy | Rook et al. (2015) |
| *Tomistoma calaritanus* | Tortonian–Messinian | Is Mirrionis, Sardinia, Italy | Capellini (1890) |
| Crocodylia indet. | Late Tortonian | Fiume Santo, Sardinia, Italy | Abbazzi et al. (2008) |
| cf. *Crocodylus* sp. (type of *Crocodylus bambolii*) | Tortonian | Montabamboli-Casteani-Ribolla, Tuscany, Italy | Delfino and Rook (2008) |
| *Tomistoma* cf. *lusitanica* | Tortonian | Olhos de Agua, Algarve, Portugal | Vianna and Moraes (1945) |
| Crocodylia indet. (*Diplocynodon* sp.) | Tortonian | Soblay, Ain, France | Ménouret and Mein (2008) |
| Crocodylia indet. | Early Tortonian | Plakias, Crete, Greece | This paper |
| cf. *Crocodylus* sp. | Early Tortonian | Scontrone, Abruzzo, Italy | Rustioni et al. (1993) and Delfino and Rossi (2013) |

natricines from southeastern Europe (e.g., the natricine from Maramena described by Szyndlar, 1995) cannot be tested due to the fragmentary nature of the single known specimen. Furthermore, the Plakias natricine represents the sole Neogene record of snakes from Crete, as all other fossil occurrences from the island are confined to Pleistocene and Holocene sediments (Holman, 1998). Amphisbaenians are well known from several Miocene European localities, but almost only from the western and central parts of the continent (Roček, 1984; Bolet et al., 2014; Čerňanský et al., 2015), whereas they have never been described from the Balkan Peninsula and eastern Europe in general (Delfino, 2003), with the single exception of a blanid from the middle Miocene of Tauţ, Romania (Venczel and Ştiucă, 2008). After the end of the Miocene, the distribution of amphisbaenians in Europe became gradually restricted to its Mediterranean margins, becoming extinct from most regions after the Pleistocene and surviving today only in the Iberian Peninsula and few Greek Islands (Delfino, 1997; Delfino and Bailon, 2000). Amphisbaenians are represented in the Greek extant herpetofauna solely by the species *Blanus strauchi* (Bedriaga, 1884), which is distributed in the islands of Samos, Fournoi, Leros, Kos, Symi, Rhodes, and Kastellorizon (Valakos et al., 2008). *Blanus* occurs also in the adjacent Anatolia, represented by *B. strauchi* and two additional, recently described or revalidated species: *B. alexandri* Sindaco, Kornilios, Sacchi and Lymberakis, 2014, and *B. aporus* Werner, 1898. So far, the Anatolian fossil record of amphisbaenians is also poor, consisting of only a single record from the Pliocene of Çalta (Rage and Sen, 1976; Delfino, 1997). Whether or not the

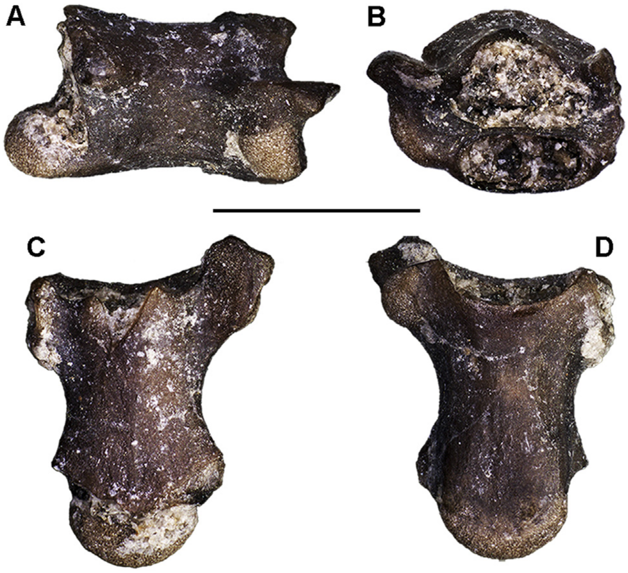


**Fig. 6.** Amphisbaenia from the earliest late Miocene of Plakias: UU PL 733, presacral vertebra in right lateral (**A**), anterior (**B**), dorsal (**C**) and ventral (**D**) views. Scale bar: 1 mm.

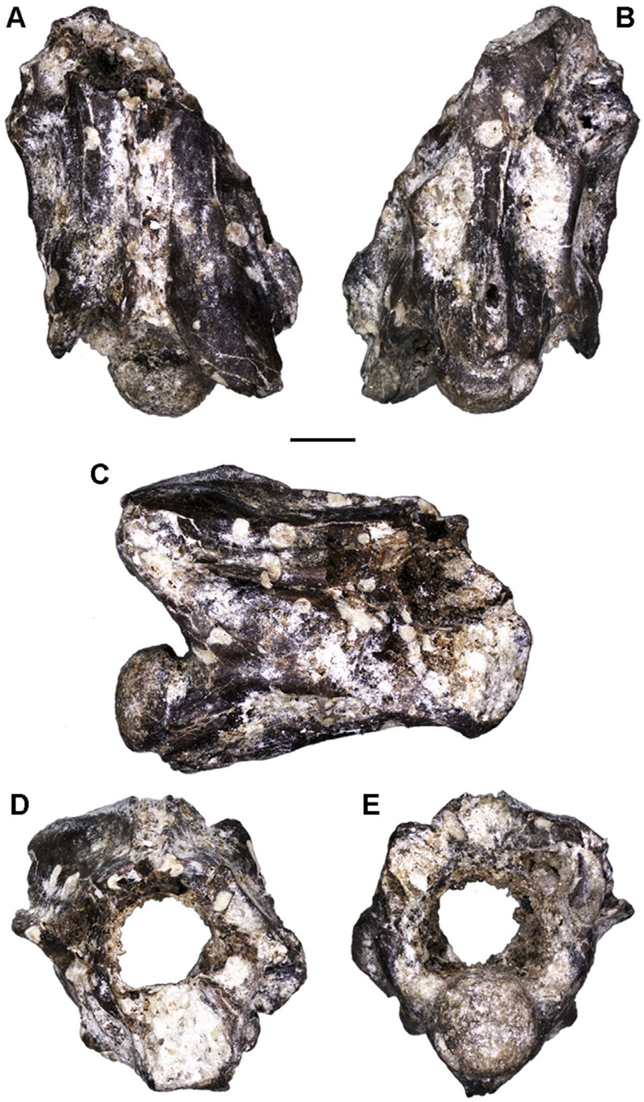


**Fig. 7.** ?Natricinae from the earliest late Miocene of Plakias: UU PL 734, precloacal vertebra in dorsal (**A**), ventral (**B**), right lateral (**C**), anterior (**D**) and posterior (**E**) views. Scale bar: 1 mm.

Plakias specimen represents a species of *Blanus* cannot be evaluated on the basis of vertebral characters. It is, however, probable that the Plakias amphisbaenian does belong to *Blanus*, as members of this genus have a wide Miocene distribution in western and Central Europe (Bolet et al., 2014; Čerňanský et al., 2015) and the disjunct extant restricted distribution in the western and eastern edges of the continent has been in fact interpreted as relics of an initially continuous range in southern Europe (Alexander, 1966; Delfino, 2003), a situation that has also been observed for other squamate groups such as erycid and elapid snakes (Szyndlar, 1991a,b; Rage, 2013). In fact, Greece and in general the southern Balkans have been suggested as acting as a refugium for multiple squamate groups such as scolecophidians, erycids, the large anguid *Pseudopus*, and the so called "oriental vipers" (Delfino, 2003), which all have their sole extant European populations only in that region (Sindaco and Jeremčenko, 2008). However, an alternative hypothesis of the Plakias amphisbaenian sharing affinities with African ones should also be taken into consideration, due to the geographical proximity of Crete to Africa and the unexpected but now well-known marine dispersal capabilities of these squamates (Kearney, 2003; Longrich et al., 2015). Nevertheless, such hypothesis remains severely hindered by the poor fossil record of African squamates (Rage, 2003; Delfino et al., 2004). Pending the discovery of more complete material from Plakias that could ideally comprise cranial elements that bear diagnostic features, no further biogeographic correlations of the Cretan amphisbaenian with European, Anatolian or African taxa can be made with certainty.

## 6. Conclusions

The herpetofauna of Plakias described in this paper includes the oldest amphibians and reptiles from the Island of Crete and represents one of the southernmost fossil herpetofaunas of Europe. The alytid frog presented herein adds to the known record of this group from the Miocene of southern Europe. The crocodilians are the first described from the country and represent one of the youngest occurrences of this group in Europe. Turtles include two distinct taxa: a geoemydid and a pan-trionychid, both representing the oldest occurrences of these groups from Greece. The single colubroid snake specimen adds further to the published record of Miocene snakes from Greece, whereas the amphisbaenian vertebra from Plakias represents the first described fossil of this group from the country, suggesting that amphisbaenians had a continuous range in the northern Mediterranean area. The herpetofauna of Plakias is shown to be diverse. Overall, it further adds to our knowledge of the Miocene herpetofaunas of southeastern Europe, a region in which amphibian and reptile fossils are still not adequately known.

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## References

Abbazzi, L., Delfino, M., Gallai, G., Trebini, L., Rook, L., 2008. New data on the vertebrate assemblage of Fiume Santo (North-western Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinia paleobioprovince. Palaeontology 51, 425–451.

Alexander, A.A., 1966. Taxonomy and variation of *Blanus strauchi* (Amphisbaenia Reptilia). Copeia 1966, 205–224.

Antunes, M.T., 1994. On Western Europe Miocene gavials (Crocodylia): their paleogeography, migrations and climatic significance. Comunicações do Instituto Geológico e Mineiro 80, 57–69.

Augé, M., 2005. Evolution des lézards du Paléogène en Europe. Publications Scientifiques du Muséum, Mémoires du Muséum national d'histoire naturelle, Paris 192, 1–369.

Bachmayer, F., 1967. Eine Riesenschildkröte aus den altpliozänen Schichten von Pikermi (Griechenland). Annales Géologiques des Pays Helléniques 19, 512–526.

Bachmayer, F., Brinkerink, J., Symeonidis, N., 1975. Pleistozäne Schildkröten aus Höhlen der Insel Kreta. Annales Géologiques des Pays Helléniques 27, 110–121.

Bailon, S., 1999. Différenciation ostéologique des anoures (Amphibia Anura) de France. Fiches d'ostéologie animale pour l'archéologie (C. Varia) 1, 1–41.

Batsch, A.J.G.C., 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen, Erster Theil. Allgemeine Geschichte der Natur; besondre der Säugthiere, Vögel, Amphibien und Fische. Akademische Buchhandlung, Jena.

Bedriaga, J., 1884. Nachträgliche Bemerkung über *Amphisbaena strauchi* v. Bedr. Zoologischer Anzeiger 7, 346.

Böhme, M., 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 195, 389–401.

Bolet, A., Delfino, M., Fortuny, J., Almécija, S., Robles, J.M., Alba, D.M., 2014. An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards. PLOS ONE 9, e98082.

Bonaparte, C.L., 1832–1841. Iconographia della fauna Italica per le quattro classi degli animali vertebrati. 2. Anfibi. Tipografia Salviucci, Roma.

Brinkerink, H.P., 1996. Tortoises and turtles from the Pleistocene of Crete. In: Reese, D.S. (Ed.), Pleistocene and Holocene Fauna of Crete and Its First Settlers. Monographs in World Archaeology 28. Prehistory Press, pp. 207–210.

Britton, A.R.C., Whitaker, R., Whitaker, N., 2012. Here be a Dragon: exceptional size in a saltwater crocodile (*Crocodylus porosus*) from the Philippines. Herpetological Review 43, 541–546.

Brochu, C.A., 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. Copeia 2000, 657–673.

Busack, S.D., Ernst, C.H., 1980. Variation in Mediterranean populations of *Mauremys* Gray, 1869 (Reptilia, Testudines Emydidae). Annals of the Carnegie Museum 49, 251–264.

Caloi, L., Kotsakis, T., Palombo, M.R., 1986. La fauna a vertebrati terrestri del Pleistocene delle isole del Mediterraneo. Geologia Romana 25, 235–256.

Capellini, G., 1890. Sul coccodrilliano garialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel 1868. Rendicondi Reale Accademia Lincei (Ser. 4) 6 (I sem.), 149–151.

Čerňanský, A., Rage, J.-C., Klembara, J., 2015. The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. Journal of Systematic Palaeontology 13, 97–128.

Chesi, F., Delfino, M., Abbazzi, L., Carboni, S., Lecca, L., Rook, L., 2007. New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia Testudines) in the central Mediterranean. Rivista Italiana di Paleontologia e Stratigrafia 113, 287–297.

Chesi, F., Delfino, M., Rook, L., 2009. Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover. Journal of Paleontology 83, 379–388.

Claude, J., Tong, H., Suteethorn, V., 2007. Turtles from the late Eocene–early Oligocene of the Krabi Basin (Thailand). Bulletin de la société géologique de France Série 1 178, 305–316.

Danilov, I.G., 2005. Die fossilen Schildkröten Europas. Part 9. In: Fritz, U. (Ed.), Handbuch der Reptilien und Amphibien Europas. Part 3/IIIB: Schildkröten (Testudines) II. AULA-Verlag GmbH, Wiebelsheim, pp. 329–448.

Daza, J.D., Bauer, A.M., Snively, E., 2014. On the gekkotan fossil record. Anatomical Record 297, 433–462.

de Bruijn, H., Doukas, C.S., van den Hoek Ostende, L.W., Zachariasse, W.J., 2012. New finds of rodents and insectivores from the Upper Miocene at Plakias (Crete Greece). Swiss Journal of Palaeontology 131, 61–75.

de Bruijn, H., Meulenkamp, J.E., 1972. Late Miocene rodents from the Pandanassa formation (Prov. Rethymnon), Crete, Greece. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B 75, 54–60.

de Bruijn, H., van der Meulen, A.J., Katsikatsos, G., 1980. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 1: The Sciuridae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B 83, 241–261.

Delfino, M., 1997. *Blanus* from the early Pleistocene of southern Italy: another small tessera from a big mosaic. In: Böhme, I.W., Bischoff, W., Ziegler, T. (Eds.), Herpetologica Bonnensis. SEH, Bonn, pp. 89–97.

Delfino, M., 2003. A Pleistocene amphisbaenian from Sicily. Amphibia-Reptilia 24, 407–414.

Delfino, M., Bailon, S., 2000. Early Pleistocene herpetofauna from Cava Dell' Erba and Cava Pirro (Apulia Southern Italy). Herpetological Journal 10, 95–110.

Delfino, M., Böhme, M., Rook, L., 2007. First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy). Zoological Journal of the Linnean Society London 149, 293–307.

Delfino, M., Rook, L., 2008. African crocodylians in the late Neogene of Europe: a revision of *Crocodylus bambolii* Ristori 1890. Journal of Paleontology 82, 336–343.

Delfino, M., Rossi, M.A., 2013. Fossil crocodylid remains from Scontrone (Tortonian Southern Italy) and the late Neogene Mediterranean biogeography of crocodylians. Geobios 46, 25–31.

Delfino, M., Segid, A., Yosief, D., Shoshani, J., Rook, L., Libsekal, Y., 2004. Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression). In: Abbate, E., Woldehaimanot, B., Libsekal, Y., Tecle, T.M., Rook, L. (Eds.), A Step Towards Human Origins. The Buia *Homo* One-Million-Years Ago in the Eritrean Danakil Depression (East Africa). Rivista Italiana di Paleontologia e Stratigrafia 110 (Suppl.), 51–60.

Depéret, C., 1885. Description géologique du bassin tertiaire du Roussillon. Annales des Sciences Géologiques 17, 1–272.

Dermitzakis, D.M., Papanikolaou, D.J., 1981. Paleogeography and geodynamics of the Aegean region during the Neogene. Annales Géologiques des Pays Helléniques 30, 245–289.

Estes, R., 1983. Sauria Terrestria, Amphisbaenia. In: Wellnhofer, P. (Ed.), Encyclopedia of Paleoherpetology, Part 10a. G. Fischer Verlag, Stuttgart.

Fischer von Waldheim, G., 1813. Zoognosia. Tabulis Synopticis Illustrata,. Usum Praelectionum Academiae Imperialis Medico-Chirurgicae Mosquensis Edita, Ed. 3, vol. 1. Nicolai Sergeidis Vsevolozsky, Moscow.

Fitzinger, L.J.F.J., 1843. Systema Reptilium. Fasciculus Primus. Braumüller et Seidel, Vienna.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P.E., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C., 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History 297, 1–370.

Gad, J., 1990. Nachweis einer Schildkröte des *Mauremys–Ocadia*–Komplexes aus dem Obermiozän von Nordgriechenland. Salamandra 26, 311–313.

Garcia, G., Kostopoulos, D.S., Valentin, X., Koufos, G.D., 2016. Testudines. In: Koufos, G.D., Kostopoulos, D.S. (Eds.), Palaeontology of the Upper Miocene Vertebrate Localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Geobios 49, 23–27.

Gardner, J.D., Russell, A.P., 1994. Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen 193, 209–244.

Gaudry, A., 1862–1867. Animaux fossiles et géologie de l'Attique. Savy, Paris.

Gauthier, J.A., Kearney, M., Maisano, J.A., Rieppel, O., Behike, A.D.B., 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History 53, 3–308.

Georgalis, G.L., Kear, B.P., 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46, 299–311.

Georgalis, G.L., Szyndlar, Z., Kear, B.P., Delfino, M., 2016a. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109, 103–116.

Georgalis, G.L., Velitzelos, E., Velitzelos, D.E., Kear, B.P., 2013. *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the lower Miocene of northern Greece. In: Brinkman, D.B., Holroyd, P.A., Gardner, J.D. (Eds.), Morphology and Evolution of Turtles. Springer, Dordrecht, pp. 277–287.

Georgalis, G.L., Villa, A., Delfino, M., 2016b. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature 103, 12.

Ginsburg, L., Bulot, C., 1997. Les *Diplocynodon* (Reptilia Crocodylia) de l'Orléanien (Miocène inférieur à moyen) de France. Geodiversitas 19, 107–128.

Gmelin, J.F., 1789. Tom. I. Pars III. In: Beer, G.E. (Ed.), Caroli a Linné, Systema Naturae. Leipzig, pp. 1033–1516.

Gmelin, S.G., 1774. Reise durch Rußland zur Untersuchung der drey Natur-Reiche. Kaiserliche Akademie der Wissenschaften, St. Petersbourg.

Gray, J.E., 1844. Catalogue of the Tortoises, Crocodiles, and Amphisbaenians, in the Collection of the British Museum. Trustees of the British Museum, London.

Gray, J.E., 1869. Description of *Mauremys laniaria*, a new freshwater tortoise. Proceedings of the Zoological Society of London 1869, 499–500.

Hadjisterkotis, E., Kassapis, I., Klerides, N., 2000. Paleontological evidence for the presence of *Trionyx* sp. on Cyprus, with new information on living and alien species of terrapins. Newsletter, Hellenic Zoological Society 33, 8–10.

Hervet, S., 2003. Le groupe «*Palaeochelys* sensu lato–*Mauremys*» dans le contexte systématique des Testudinoidea aquatiques du Tertiaire d'Europe occidentale: Apports à la biostratigraphie et à la paléobiogéographie (Ph.D. thesis). Muséum National d'Histoire Naturelle, Paris.

Holman, A.J., 1998. Pleistocene amphibians and reptiles in Britain and Europe. In: Oxford Monographs on Geology and Geophysics 38. Oxford University Press, New York, Oxford.

Huene, F., von Nikoloff, I., 1963. Ein pliozänes krokodil in Bulgarien. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 118, 266–271.

Hummel, K., 1932. Trionychia fossilia. In: Questedt, W. (Ed.), Fossilium Catalogus I: Animalia. Junk, W., Berlin.

Joyce, W.G., Parham, J.F., Gauthier, J.A., 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology 78, 989–1013.

Karl, H.V., 1999. Die Zoogeographie der känozoischen Weichschildkröte *Trionyx-triunguis* Forskål 1775 (Testudines: Trionychidae). JoanneaGeologie und Paläontologie Graz 1, 27–60.

Kearney, M., 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17, 1–74.

Kotsakis, T., 1977. I resti di anfibi e rettili pleistocenici della grotta 'Bate' (Rethymnon Creta). Atti della Accademia Nazionale dei Lincei 63, 571–582.

Kotsakis, T., 1985. Les Trionychidae (Testudinata Reptilia) fossiles de l'Italie. Bollettino della Società Paleontologica Italiana 24, 161–168.

Kotsakis, T., Delfino, M., Piras, P., 2004. Italian Cenozoic crocodilians: taxa, timing and biogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 210, 67–87.

Koufos, G.D., 2006. The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. Annales Géologiques des Pays Helléniques 4, 183–214.

Koufos, G.D., Kostopoulos, D.S., 2013. First report of *Brachypotherium* Roger 1904 (Rhinocerotidae, Mammalia) in the Middle Miocene of Greece. Geodiversitas 35, 629–641.

Koufos, G.D., Kostopoulos, D., Vlachou, T., 2005. Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belgian Journal of Zoology 135, 181–190.

de Lapparent de Broin, F., 2000. African chelonians from the Jurassic to present: phases of development and preliminary catalogue of the fossil record. Palaeontologia Africana 36, 43–82.

Laurenti, J.N., 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu. Joan. Thomae, Vienna.

Linnaeus, C., 1758. Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Laurenti Salvii, Holmiae 1, 1–823.

Longrich, N.R., Vinther, J., Pyron, R.A., Pisani, D., Gauthier, J.A., 2015. Biogeography of worm lizards (Amphisbaenia) driven by end-Cretaceous mass extinction. Proceedings of the Royal Society B: Biological Sciences 282, 20143034.

Martin, J.E., 2010. A new species of *Diplocynodon* (Crocodylia, Alligatoroidea) from the Late Eocene of the Massif Central France, and the evolution of the genus in the climatic context of the Late Palaeogene. Geological Magazine 147, 596–610.

Martin, J.E., Gross, M., 2011. Taxonomic clarification of *Diplocynodon* Pomel, 1847 (Crocodilia) from the Miocene of Styria, Austria. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 261, 177–193.

Ménouret, B., Mein, P., 2008. Les vertébrés du Miocène supérieur de Soblay (Ain, France) Document des Laboratoires de Géologie de Lyon, UFR des sciences de la Terre. Université Claude Bernard-Lyon 1 165, 1–97.

Młynarski, M., 1976. Testudines. In: Kuhn, O. (Ed.), Encyclopedia of Paleoherpetology, Part 7. G. Fischer Verlag, Stuttgart.

Oppel, M., 1811. Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, München.

Pamouktchiev, A., Lapparent de Broin, F.de, Anguelov, A., 1998. Nouvelle trouvaille de tortue fossile en Bulgarie. Annuaire de l'Université de Sofia «St. Kliment Ohridski»' Faculté de Géologie et Géographie, Livre 1. Géologie 90, 5–8.

Paraskevaidis, I., 1955. Zwei Schildkröten reste aus dem Obermiozän von Chios. Annales Géologiques des Pays Helléniques 6, 133–141.

Poulakakis, N., Lymberakis, P., Tsigenopoulos, C.S., Magoulas, A., Mylonas, M., 2005. Phylogenetic relationships and evolutionary history of snake-eyed skink *Ablepharus kitaibelii* (Sauria: Scincidae). Molecular Phylogenetics and Evolution 34, 245–256.

Purschke, C.A., 1885. *Clemmys sarmatica* n. sp. aus dem Tegel von Hernals bei Wien. Denkschriften der Kaiserlichen Akademie der Wissenschaften/Mathematisch-Naturwissenschaftliche Classe 50, 185–192.

Pyron, R.A., Reynolds, R.G., Burbrink, F.T., 2014. A taxonomic revision of boas (Serpentes Boidae). Zootaxa 3846, 249–260.

Pyron, R.A., Wiens, J.J., 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. Molecular Phylogenetics and Evolution 61, 543–583.

Rage, J.-C., 1984. Serpentes. In: Wellnhofer, P. (Ed.), Encyclopedia of Paleoherpetology, Part 11. G. Fischer Verlag, Stuttgart, New York.

Rage, J.-C., 2003. Squamate reptiles from the early Miocene of Arrisdrift (Namibia). Memoir of the Geological Society of Namibia (Ministry of Mines and Energy). Windhoek 19, 43–50.

Rage, J.-C., 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments 93, 517–534.

Rage, J.-C., Augé, M., 1993. Squamates from the Cenozoic of the western part of Europe. A review. Revue de Paléobiologie volume spécial 7, 199–216.

Rage, J.-C., Roček, Z., 2003. Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. Amphibia-Reptilia 24, 133–177.

Rage, J.-C., Sen, S., 1976. Les Amphibiens et les Reptiles du Pliocène supérieur de Calta (Turquie). Géologie méditerranéenne 3, 127–134.

Richter, A., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian–Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata Reptilia). Münchner Geowissenschaftliche Abhandlungen 28, 35–38.

Roček, Z., 1984. Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia). Rozpravy Ceskoslovenské Akademie Ved. Rada Matematickych a prírodních Ved 94, 3–69.

Rögl, F., 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologia Carpathica 50, 330–349.

Römer, F., 1870. Über *Python euboicus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea. Zeitschrift der Deutschen Geologischen Gesellschaft 22, 582–590.

Rook, L., Delfino, M., Sami, M., 2015. I vertebrati fossili della cava del Monticino di Brisighella: una finestra sui popolamenti continentali del Mediterraneo nel Miocene superiore, I gessi di Brisighella e Rontana. Memorie dell'Istituto Italiano di Speleologia s. II 28, 79–100.

Rustioni, M., Mazza, P., Azzaroli, A., Boscagli, G., Cozzini, F., Di Vito, E., Masseti, M., Pisano, M., 1993. Miocene vertebrate remains from Scontrone, National Park of Abruzzi, Central Italy. Rendiconti della Accademia Nazionale dei Lincei, Classe di Scienze Fisiche Matematiche e Naturali 9, 227–237.

Sanchiz, B., 1998. Salientia. In: Wellnhofer, P. (Ed.), Encyclopedia of Paleoherpetology, Part 4. Friedrich Pfeil, Munich.

Sen, S., Antoine, P.O., Varol, B., Ayyildiz, T., Sözeri, K., 2011. Giant rhinoceros *Paraceratherium* and other vertebrates from Oligocene and middle Miocene deposits of the Kağızman-Tuzluca Basin, Eastern Turkey. Naturwissenschaften 98, 407–423.

Sindaco, R., Jeremčenko, V., 2008. The Reptiles of the Western Palearctic. Vol. 1 Annotated Checklist and Distributional Atlas of the Turtles, Crocodiles, Amphisbaenians and Lizards of Europe, North Africa, Middle East and Central Asia. Monografie della Societas Herpetologica Italica I, Belvedere, Latina.

Sindaco, R., Kornilios, P., Sacchi, R., Lymberakis, P., 2014. Taxonomic reassessment of *Blanus strauchi* (Bedriaga, 1884) (Squamata: Amphisbaenia: Blanidae), with the description of a new species from south-east Anatolia (Turkey). Zootaxa 3795, 311–326.

Staesche, K., Karl, H.-V., Staesche, U., 2007. Fossile Schildkröten aus der Türkei. Geologisches Jahrbuch Reihe B 98, 91–149.

Steel, R., 1973. Crocodylia. In: Kuhn, O. (Ed.), Encyclopedia of Paleoherpetology, Part 16. G. Fischer Verlag, Stuttgart, Portland.

Szalai, T., 1931. Schildkrötenstudien: I. *Testudo schafferi* nov. sp., eine Riesenschildkröte aus dem Pliozän von Samos. Annalen des Naturhistorischen Museums in Wien 46, 153–157.

Szyndlar, Z., 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos 47, 103–126.

Szyndlar, Z., 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estudios Geológicos 47, 237–266.

Szyndlar, Z., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian–Ruscinian Boundary (Neogene). 4. Serpentes (Squamata Reptilia). Münchner Geowissenschaftliche Abhandlungen 28, 35–39.

Szyndlar, Z., Rage, J.-C., 2002. Fossil record of the true vipers. In: Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H.W. (Eds.), Biology of the Vipers. Eagle Mountain Publicing, Eagle Moutain, pp. 419–444.

Szyndlar, Z., Rage, J.-C., 2003. Non-erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow.

Szyndlar, Z., Zerova, G., 1990. Neogene cobras of the genus *Naja* (Serpentes: Elapidae) of East Europe. Annalen des Naturhistorischen Museums in Wien 91A, 53–61.

Theobald Jr., W., 1868. Catalogue of Reptiles in the Museum of the Asiatic Society of Bengal. Journal of the Asiatic Society, Extra Number.

Valakos, E.D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., Foufopoulos, J., 2008. Amphibians and Reptiles of Greece, Edition Chimaira. Serpents Tale, Frankfurt.

Valenciennes, A., 1833. *Chelonia pelasgorum*, *Emys hellenica*, *Emys iberica*, *Emys rivulata*. In: Bory de Saint-Vincent, J.B. (Ed.), Expédition Scientifique de Morée. Travaux de la Section des Sciences Physiques. Zoologie. Levrault, F.G., Paris.

van der Made, J., 1996. Pre-Pleistocene land mammals from Crete. In: Reese, D.S. (Ed.), Pleistocene and Holocene Fauna of Crete and Its First Settlers. Monographs in World Archaeology 28. Prehistory Press, pp. 69–79.

Venczel, M., Ştiucă, E., 2008. Late middle Miocene amphibians and squamate reptiles from Tauţ, Romania. Geodiversitas 30, 731–763.

Vianna, A., Moraes, A., 1945. Sur un crâne de crocodile fossile découvert dans le Miocène de Lisbonne. Boletim de la Sociedade Geológica de Portugal 4, 161–170.

Viriot, L., Pelaez-Campomanes, P., Vignaud, P., Andossa, L., Mackaye, H.T., Brunet, M., 2011. A new xerinae (Rodentia, Sciuridae) from the late Miocene of Toros-Menalla (Chad). Journal of Vertebrate Paleontology 31, 844–848.

Vitek, N.S., Joyce, W.G., 2015. A review of the fossil record of New World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 56, 185–244.

Vitt, L.J., Caldwell, J.P., 2014. Herpetology. An Introductory Biology of Amphibians and Reptiles, 4th ed. Academic Press, Elsevier, Amsterdam.

Vlachos, E., 2015. The Fossil Chelonians of Greece. Systematics – Evolution – Stratigraphy – Palaeoecology. (Ph.D. thesis). Aristotle University of Thessaloniki, Greece.

Vlachos, E., Cerda, I., Tsoukala, E., 2015a. The first record of a soft-shelled turtle (Testudines: Pan-Trionychidae) from southern Balkans (Pliocene, Gefira N. Greece) and new information from bone histology. The Science of Nature 102, 45.

Vlachos, E., Kotsakis, T., Delfino, M., 2015b. The chelonians from the latest Miocene–earliest Pliocene localities of Allatini and Pylea (East Thessaloniki, Macedonia Greece). Comptes Rendus Palevol 14, 187–205.

Vlachos, E., Tsoukala, E., 2014. *Testudo* cf. *graeca* from the new Late Miocene locality of Platania (Drama basin N. Greece) and a reappraisal of previously published specimens. Bulletin of the Geological Society of Greece XLVIII 27–40.

Wallach, V., Williams, K.L., Boundy, J., 2014. Snakes of the World: A Catalogue of Living and Extinct Species. CRC Press, Boca Raton.

Weithofer, A., 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. Beiträge zur Paläontologie Österreich-Ungarns 6, 225–292.

Werner, F., 1898. Über einige neue Reptilien und einen neuen Frosch aus dem cilicischen Taurus. Zoologischer Anzeiger 21, 217–223.

Zangerl, R., 1969. The turtle shell. In: Bellairs d', A.A., Parsons, T.S. (Eds.), The Biology of the Reptilia 1, Morphology A. Academic Press, London, New York, pp. 311–339.

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# Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece

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**ABSTRACT**
We here describe a new squamate fauna from the late Miocene (Messinian, MN 13) of Ano Metochi, northern Greece. The lizard fauna of Ano Metochi is here shown to be rather diverse, consisting of lacertids, anguids, and potential cordylids, while snakes are also abundant, consisting of scolecophidians, natricines and at least two different colubrines. If our identification is correct, the Ano Metochi cordylids are the first ones identified from Greece and they are also the youngest representatives of this group in Europe. A previously described scincoid from the adjacent locality of Maramena is here tentatively also referred to cordylids, strengthening a long term survival of this group until at least the latest Miocene. The scolecophidian from Ano Metochi cannot be attributed with certainty to either typhlopids or leptotyphlopids, which still inhabit the Mediterranean region. The find nevertheless adds further to the poor fossil record of these snakes. Comparison of the Ano Metochi herpetofauna with that of the adjacent locality of Maramena reveals similarities, but also striking differences among their squamate compositions.

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## Introduction

Fossil squamate faunas from the southeastern edges of Europe are not well studied, despite the fact that they could play a pivotal role in our understanding of the biogeography and systematics of these reptiles. As such, although fossil lizards and snakes have been known from Greece since the nineteenth century (Owen 1857; Römer 1870; Weithofer 1888), they have only been sparsely documented (Schneider 1975; Szyndlar and Zerova 1990; Georgalis, Szyndlar et al. 2016; Georgalis, Villa, Delfino 2016).

The focus of this paper is the squamate fauna of the late Miocene (Messinian, MN 13) Ano Metochi-2 and Ano Metochi-3 localities in northern Greece. Fossil reptiles from Ano Metochi were previously undescribed, with the exception of an indeterminate natricine briefly mentioned by Szyndlar (1991b), and an agamid listed, erroneously, by Delfino et al. (2008, map in Figure 1) and Blain et al. (2016, map in Figure 4) (see Discussion below). The fossils described herein pertain to a diverse array of lizards and snakes and all originate from Ano Metochi-2 and Ano Metochi-3, two adjacent localities that were up to now mostly known for their micromammals (de Bruijn 1989; Koufos 2006).

*Institutional Abbreviations*: MDHC, Massimo Delfino Herpetological Collection, University of Torino, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; NHMW, Naturhistorisches Museum, Vienna, Austria; UU, University of Utrecht, Utrecht, Netherlands.

## Materials and methods

All specimens described herein belong to the collection of the UU. Comparative material includes multiple skeletons of extant lizards and snakes housed in the MDHC, MNHN, MNCN and NHMW.

## Geological and palaeoecological settings

Ano Metochi is situated next to the city of Serres, in the Serres Basin, Central Macedonia, northern Greece (Figure 1). Fossils have been found in two different localities, namely Ano Metochi-2 and Ano Metochi-3 (hereafter abbreviated as AM-2 and AM-3). The fossiliferous level of both AM-2 and AM-3, as well as that of the adjacent locality of Maramena, belong to the Lefkon Formation, characterized by conglomerates containing pebbles of schist, gneiss and granite (de Bruijn 1989). The geology of the Lefkon Formation and the adjacent ones (Georgios Formation and Spilia Formation) within the Serres Basis is described in detail by de Bruijn (1989). AM-2 and AM-3 are currently considered to be coeval and to be late Miocene (Messinian, MN 13) in age, whereas the adjacent Maramena is only slightly younger (MN 13 / 14) (Koufos 2006). Ano Metochi is mostly known for its diverse micromammal fauna, comprising lagomorphs, and sciurid, petauristid, cricetid, murid, gerbillid, spalacid and glirid rodents (de Bruijn 1989; Koufos 2006). Among large mammals, only the giraffid *Helladotherium* and two bovids, *Prostrepsiceros woodwardi* and an indeterminate species

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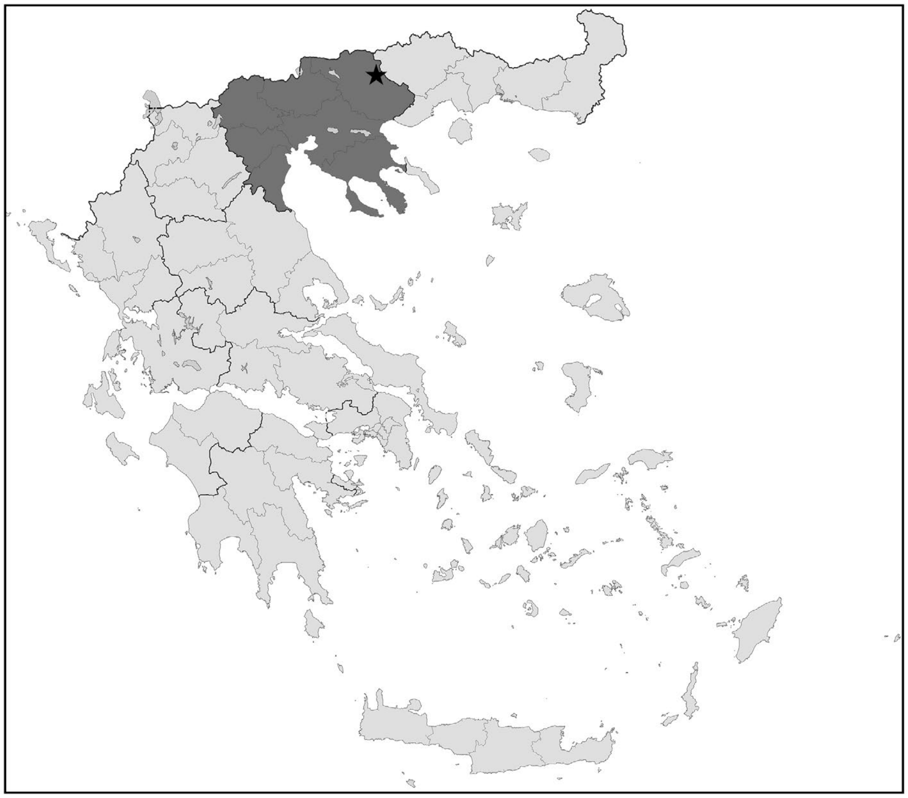

**Figure 1.** Map of Greece, indicating the localities of Ano Metochi (AM-2 and AM-3) studied in this paper.

of *Gazella*, have been reported so far from from Ano Metochi (Koufos 2006). Interestingly, different palaeoenvironments have been suggested for AM-2 and AM-3 on the basis of their micromammal fauna, with the former being considered to pertain to a wet and forest landscape, whereas the latter corresponding to a more dry and open environment (de Bruijn 1989).

Systematic Palaeontology

Squamata Oppel, 1811

Lacertidae Oppel, 1811

Lacertidae indet (Figure 2).

*Material*. AM-2: one fragment of a maxilla (UU AM2 501), three dentaries (UU AM2 502, UU AM2 503 and UU AM2 504), and two fragments of tooth-bearing bones (UU AM2 505). AM-3: one premaxilla (UU AM3 501), one maxilla (UU AM3 502) and one dentary (UU AM3 503).

*Description*. The premaxilla (UU AM3 501) is almost complete, lacking only the dorsal tip of the ascending nasal process. It is small-sized, with an alveolar plate that is 2.1 mm wide. It bears seven pleurodont, cylindrical and slender teeth, whose crown is not preserved. The postero-lateral tips of the palatal process are broken, but they are clearly separated by a wide and V-shaped notch. The incisive process is poorly developed. The ascending nasal process tends to slightly widen dorsally, but it does not show a leaf-shaped or an arrow-shaped morphology; its lateral margins are roughly subparallel in anterior view. A distinct septonasal crest is visible on the posterior surface of the process, whereas the anterior one is smooth.

The maxillae (UU AM3 502 and UU AM2 501) are represented by small fragments (UU AM3 502 is 3 mm in length, whereas UU AM2 501 is roughly 4.5 mm in length) bearing pleurodont, cylindrical and slender teeth. Ten tooth positions are recognizable in UU AM3 502, but only four teeth are preserved; all of them are bicuspid. UU AM2 501, on the other hand, bears three teeth and three empty tooth positions. In the latter specimen, tooth crowns are rather eroded, but one of the teeth seems to show two small accessory cusps by the sides of the main one. On the dorsal surface of the palatal shelf of both maxillae there is a very large superior dental foramen, followed by a wide and deep groove. The lateral surface of the fragments is smooth, with two ventrolateral foramina in both of them. Moreover, it is distinctly concave in UU AM2 501.

UU AM3 503, UU AM2 502, UU AM2 503 and UU AM2 504 are partially preserved dentaries, with missing the anteriormost and posteriormost parts. The length of the preserved portion of the specimens is 3.3 mm (UU AM3 503), 6.3 mm (UU AM2 502), 3 mm (UU AM2 503) and 6.7 mm (UU AM2 504). The dentaries are characterized by heterodont dentition and bear pleurodont and cylindrical teeth. Eight tooth positions are visible in UU AM3 503, ten in UU AM2 502, nine in UU AM2 503 and sixteen in UU AM2 504. The preserved teeth can be mono-, bi- or tricuspid. All teeth protrude well above the labial wall of the jaw. Also, teeth increase in basal diameter along the row, with the anteriormost having a narrower diameter than the posteriormost ones. The Meckelian fossa is moderately wide and opens medio-ventrally on the medial side of the bone. The lateral surface is smooth, with only three (Lac 002 and UU AM2 503) or six (UU AM2 504) labial foramina (not preserved in UU AM2 503), of which one is rather enlarged in UU AM3 503.

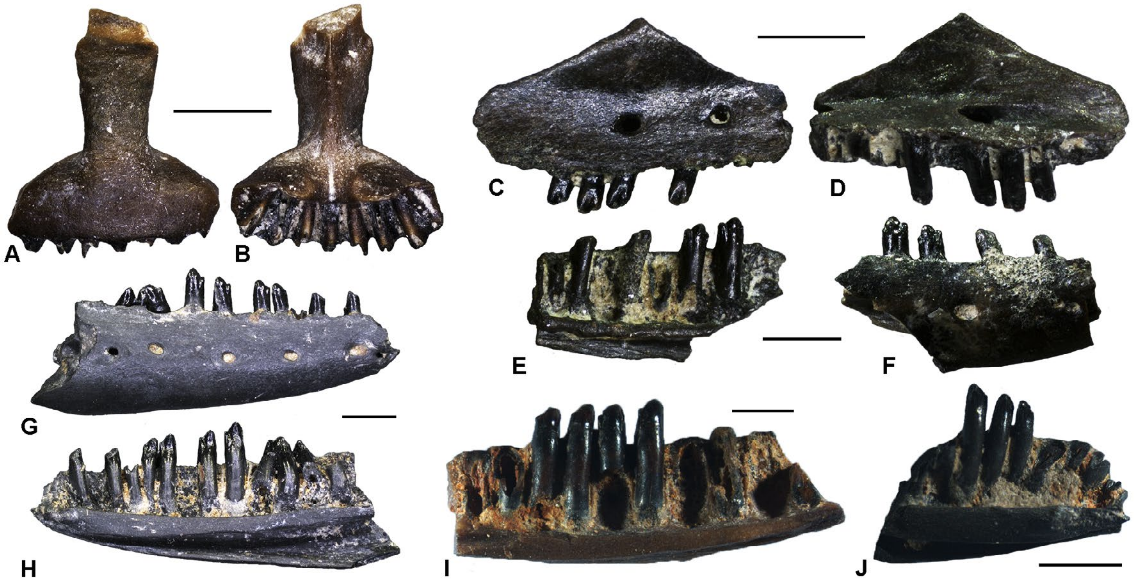

**Figure 2.** Lacertidae indet.: premaxilla (UU AM3 501) in anterior (A) and posterior (B) views; right maxilla (UU AM3 502) in lateral (C) and medial (D) views; right dentary (UU AM3 503) in medial (E) and lateral (F) views; right dentary (UU AM2 504) in lateral (G) and medial (H) views; right dentary (UU AM2 502) in medial (I) view; left dentary (UU AM2 503) in medial (J) view. Scale bars = 1 mm.

The fragments of tooth-bearing bones are small-sized and poorly preserved. They bear pleurodont, cylindrical, slender and bicuspid teeth.

*Remarks*. The morphology of the teeth allows assignment of UU AM3 502, UU AM3 503 and UU AM3 501 to Lacertidae (Bailon 1991). The width of the alveolar plate of UU AM3 501 fits within the ranges defined by Barahona and Barbadillo (1997) for *Iberolacerta bonnali*, *Podarcis bocagei*, *Podarcis hispanicus*, and *Podarcis muralis* (1.6 mm-2 mm) and for *Acanthodactylus erythrurus*, *Iberolacerta cyreni*, *Iberolacerta monticola*, and *Psammodromus algirus* (2.3–2.4 mm). Moreover, according to the latter authors, seven tooth positions are a characteristic feature of the premaxillae of *A. erythrurus*, *I. bonnali*, *Po. bocagei*, *Po. hispanicus*, and *Po. muralis*, whereas the parallel lateral margins are typical of those of *Algyroides marchi*, *I. bonnali*, *Po. bocagei*, *Po. hispanicus*, *Po. muralis*, *Ps. algirus*, and *Psammodromus hispanicus* (Barahona and Barbadillo 1997). Accordingly so, UU AM3 501 seems to show affinities with the genus *Podarcis* and with *I. bonnali*. However, it has to be noted that the work of Barahona and Barbadillo (1997) is based only on Iberian lacertids and little is known about the comparative osteology of the small species inhabiting the eastern part of Europe today. Following a cautious approach, we can therefore attribute this specimen to a small-sized indeterminate lacertid, even if the possibility that it belongs to a juvenile of some other, larger species cannot be totally ruled out. As for UU AM3 502, UU AM3 503 and all the remains from AM-2, their fragmentary nature precludes any taxonomic assignment with certainty, but their size is consistent with a small-sized taxon. We cannot thus exclude neither the possibility that the material coming from the two localities pertains to the same taxon, nor that they represent two distinct lacertids from Ano Metochi.

Scincoidea Oppel, 1811

Cordylidae Gray, 1837

?Cordylidae indet (Figure 3).

*Material*. AM-2: one maxilla (UU AM2 507), two dentaries (UU AM2 508 and UU AM2 509), and one fragment of tooth-bearing bone (UU AM2 510). AM-3: two right maxillae (UU AM3 505, UU AM3 506) and one left maxilla (UU AM3 507).

*Description*. The four maxillae (UU AM2 507, UU AM3 505, UU AM3 506, and UU AM3 507; UU AM3 506 is broken into two portions) are not complete, but are moderately large in size (lengths are 7 mm for UU AM3 505, 5 mm for UU AM3 507, 8 mm for UU AM3 506, and 3.5 mm-long for UU AM2 507). They bear moderately robust, pleurodont and cylindrical teeth, whose crowns are blunt and show lingual and labial longitudinal cusps separated by a groove (similar to the morphotype F of Kosma 2004). Moreover, the crowns are slightly curved in posteromedial direction and present striae on the lingual side. The preserved tooth positions are 10 for UU AM3 507, 13 for UU AM3 505, 20 for UU AM3 506, 6 for UU AM2 507, and all teeth are closely spaced. UU AM3 506, the most complete specimen, shows a low arched ridge on the medial surface of the anterior half of the facial process and a deep and moderately large superior dental foramen followed by a shallow groove. A similar superior dental foramen is visible also in UU AM3 507. In UU AM2 507, the arched ridge is well developed. The lateral surface of all specimens is smooth, with only a number of ventrolateral foramina (three in UU AM2 507, five in UU AM3 507 and seven in UU AM3 505 and UU AM3 506).

Tooth morphology of the two incomplete dentaries (UU AM2 507 and UU AM2 509) is similar to the above described maxillae, even if teeth are slightly more slender. Both specimens still preserve 9 tooth positions only. UU AM2 508 is 3.8 mm-long, whereas UU AM2 509 is 3.4 mm in length. Both specimens are fragmentary and lack the posterior half, but UU AM2 509 preserves a narrow and horizontal mandibular symphysis. The Meckelian fossa is open medially. The lateral surface is smooth, with two (UU AM2 509) or four (UU AM2 508) labial foramina.

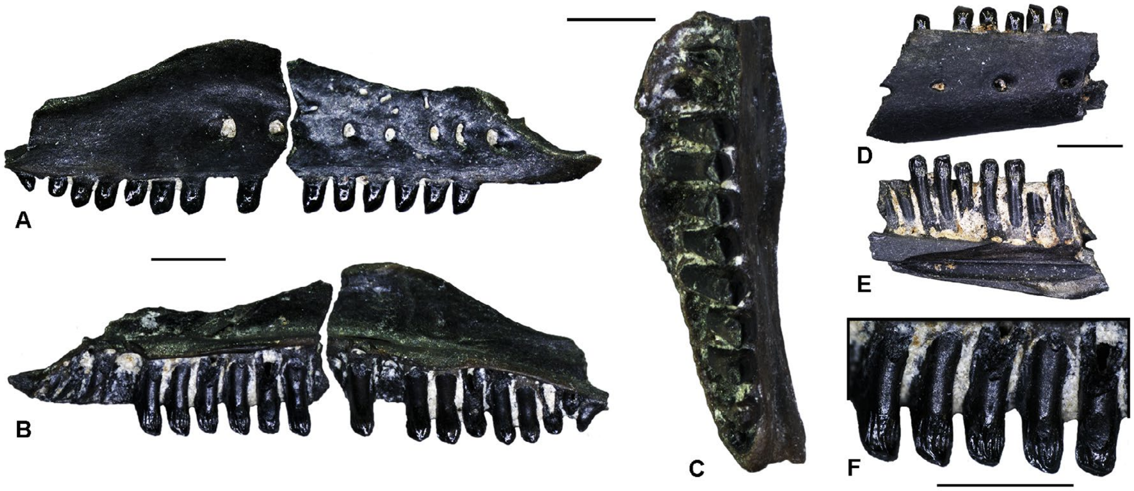

**Figure 3.** ?Cordylidae indet.: right maxilla (UU AM3 506) in lateral (A) and medial (B) views; left maxilla (UU AM3 507) in ventral (C) view; rigth dentary (UU AM2 508) in lateral (D) and medial (E) views; close-up of the teeth of UU AM3 506 in lingual view (F). Scale bars = 1 mm.

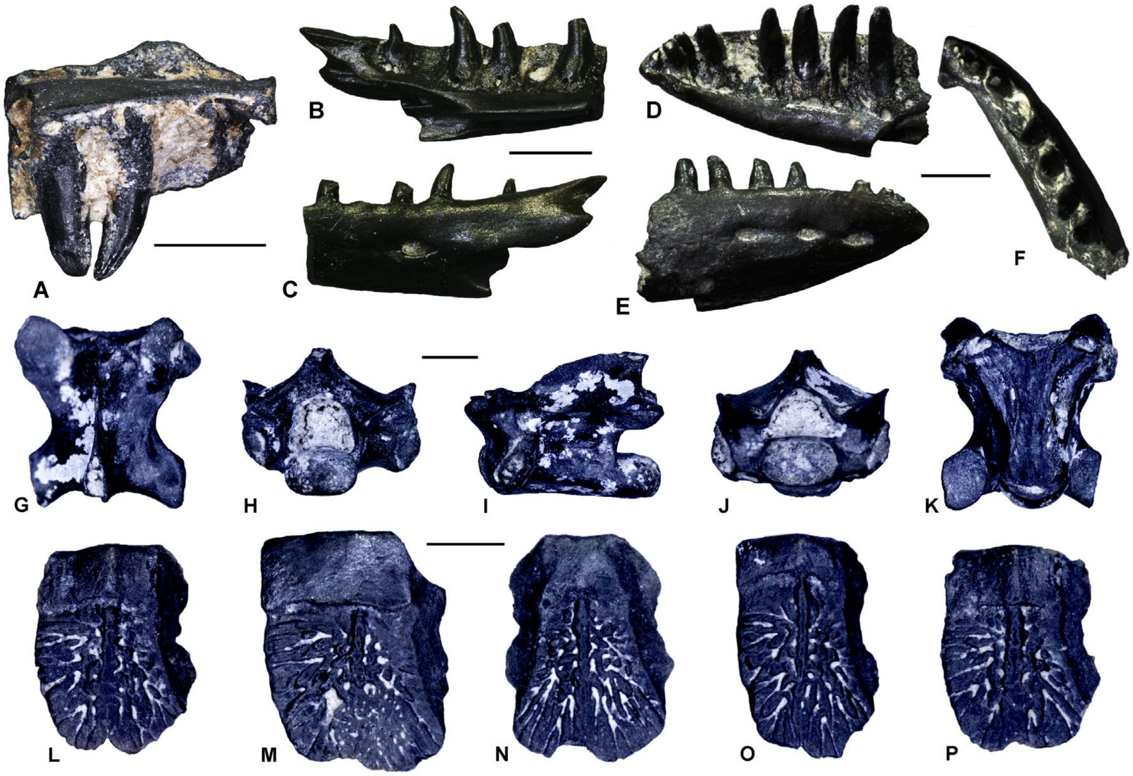

**Figure 4.** *Ophisaurus* sp.: left maxilla (UU AM2 512) in medial view (A); left dentary (UU AM3 510) in medial (B) and lateral (C) views; right dentary (UU AM3 512) in medial (D), lateral (E) and dorsal (F) views; presacral vertebra (UU AM3 513) in dorsal (G), posterior (H), left lateral (I), anterior (J) and ventral (K) views. Anguidae indet.: osteoderm (UU AM3 515) in dorsal (L) view; osteoderm (UU AM3 516) in dorsal (M) view; osteoderm (UU AM3 517) in dorsal (N) view; osteoderm (UU AM3 518) in dorsal (O) view; osteoderm (UU AM3 519) in dorsal (P) view. Scale bars = 1 mm.

UU AM2 510 is a small fragment of tooth-bearing bone, which bears two teeth that are morphologically similar to the ones of UU AM2 507. It cannot be determined with certainty whether this material pertains to a dentary or a maxilla.

*Remarks*. Pleurodont implantation, cylindrical shape and bicuspid crown provided with lingual and labial longitudinal cusps and with striae on the lingual side are typical of the teeth of Scincoidea (sensu Estes et al. 1988 and Gauthier et al. 2012), including Cordyliformes (Cordylidae and Gerrhosauridae) and Scincidae *sensu lato* (Kosma 2004). In gerrhosaurids, the striation is usually absent or poorly developed (Kosma 2004). A large number of cordylids and scincids, on the other hand, show this feature (Kosma 2004), but the distinction between the two families is often difficult (Čerňanský 2012). However, the remains from Ano Metochi, despite being incomplete have more robust teeth than those usually present in scincids and the striation is usually less distinct in the latter clade (Kosma 2004). Moreover, the above-described tooth morphology is similar to those shown by a left dentary from the early Miocene of Switzerland, figured by Jost et al. (2015, Figure 6(h)) and attributed to *Bavaricordylus* sp., as also by a right dentary from the early Miocene of Czech Republic, assigned to aff. *Palaeocordylus bohemicus* by Čerňanský (2012). Accordingly so, we here tentatively attribute the above described specimens from Ano Metochi to indeterminate cordylids. Interestingly, the scincoid taxon from the late Miocene of the nearby Maramena, described by Richter (1995, Figure 1(c) and (d)) as 'Scincoidea Incertae Sedis' bears strong resemblance with our Ano Metochi specimens, especially in terms of tooth morphology and the arrangement of the striae, and is here also tentatively referred to Cordylidae. Indeed, such a resemblance of the Maramena scincoid with primitive cordyliforms was already suggested by Richter (1995), who noted a similar arrangement pattern of the main striae of the teeth. In any case, if our identification is correct, these latest Miocene Greek forms from Ano Metochi and Maramena represent the youngest occurrence of Cordylidae from Europe.

Anguimorpha Fürbringer, 1900
Anguidae Gray, 1825
Anguinae Gray, 1825
*Ophisaurus* Daudin, 1803
*Ophisaurus* sp (Figure 4).

*Material*. AM-2: one fragment of a maxilla (UU AM2 512). AM-3: four dentaries (UU AM3 509, UU AM3 510, UU AM3 511 and UU AM3 512), 51 presacral vertebrae (UU AM3 513).

*Description*. UU AM2 512 is a rather small fragment of maxilla, carrying two sub-pleurodont teeth. A third, empty tooth position is visible. The preserved teeth are slender and slightly enlarged in their basis. One of them preserves the tip, which is pointed and slightly bending in posteromedial direction. There are no clear striae, but two sharp carinae are present both in the anterior and the posterior sides of the tip. The lateral surface of the fragment is slightly concave and bears two ventrolateral foramina.

The dentaries (UU AM3 509, UU AM3 510, UU AM3 511 and UU AM3 512) are small-sized and incomplete. UU AM3 512 represents the anterior end, UU AM3 510 is represented only by the posterior portion, UU AM3 511 preserves only the dorsal part of the posterior portion and UU AM3 509 lacks both the anterior and the posterior ends. All specimens are 4 mm in length, except for UU AM3 511 which is smaller (2.8 mm long). They bear sub-pleurodont, canine-like teeth, which are slightly posteromedially curved by their tip and slightly enlarged by their base. Teeth of UU AM3 512 are slightly more cylindrical and less enlarged. No striae can be seen on the lingual side of the teeth. Number of preserved tooth positions is 5 in UU AM3 511, 6 in UU AM3 510, 8 in UU AM3 509 and 9 in UU AM3 512. The Meckelian fossa (not preserved in UU AM3 511) is moderately narrow and opens ventromedially in UU AM3 509 and UU AM3 510, but only ventrally in UU AM3 512, since a ventral expansion of the subdental shelf covers it laterally. The lateral surface is smooth, except for the presence of the mental foramina (one in UU AM3 510 and UU AM3 511, three in UU AM3 512 and four in UU AM3 509) and of a deep articulation surface for the angular. The mandibular symphysis (preserved only in UU AM3 512) is narrow and almost horizontal; its posterior end develops medially forming a short triangular expansion. The end of the intramandibular septum is visible in UU AM3 510 and UU AM3 511: it is located by the second posteriormost tooth position in the former and by the third posteriormost one in the latter. The posterior end of the same specimens presents a well developed coronoid process (although broken by the tip in the latter) and a less developed surangular process, separated by a moderately shallow coronoid incisure. The angular process (preserved only in UU AM3 510) seems not to develop beyond the posterior margin of the articulation surface with the angular, even though its tip could be broken. The surangular spine seems to be present but its posterior end is always broken and the splenial spine, when preserved, is poorly developed.

Presacral vertebrae (UU AM3 513) are small (centrum length 1.9–4 mm) and have a dorsoventrally compressed centrum with distinctly convergent lateral margins. The neural canal is subtriangular in anterior view and the prezygapophyses and postzygapophyses are rounded and strongly tilted dorsally (about 45°). A well developed neural spine is present on the dorsal surface of the neural arch.

*Remarks*. The dorsoventrally compressed vertebral centrum with convergent lateral marginsclearly hint for the presence of a non-*Anguis* anguine taxon in Ano Metochi (Estes 1983). Furthermore, in a comparative study of the lower jaw of extant anguine genera, Klembara et al. (2014) stated that the presence of a surangular spine and of cylindrical and conical (canine-like) teeth slightly bending posteriorly by their tip distinguish dentaries of *Ophisaurus* from those of *Anguis* and *Pseudopus* (note that the latter authors considered *Dopasia* as a junior synonym of *Ophisaurus*; this taxonomic opinion is also followed here). The dentaries from Ano Metochi clearly do not belong to any of the extant species of the genus because of the absence of striae on the lingual side of the teeth and the poorly developed angular process (Klembara et al. 2014). Moreover, they can be differentiated from the extant species *Ophisaurus koellikeri* on the basis of their pointed end of the surangular process, from *Ophisaurus ventralis* on the basis of their coronoid process being longer than the surangular process, and from *Ophisaurus attenuatus*, *Ophisaurus compressus*, *Ophisaurus mimicus* and *O. ventralis* by the fact that the latter species have all their teeth slender (Klembara et al. 2014). Among fossil taxa, three species of *Ophisaurus* (including *Dopasia*) and related forms have been established on the basis of dentaries from the Oligocene of the Phosphorites du Quercy, France: *Ophisaurus coderetensis*, *Ophisaurus frayssensis* and *Ophisaurus roqueprunensis* (Augé 1992, 2005), with the former two having been recently reallocated to their own genus, *Ophisauromimus* (Čerňanský et al. in press). The dentaries from AM-3 differ from *Ophisauromimus coderetensis* in having a less marked coronoid incisure, from *Ophisauromimus frayssensis* in having a smaller size and less enlarged teeth, and from *Ophisaurus roqueprunensis* in having a surangular process shorter than the coronoid one and less enlarged teeth (Augé 1992, 2005). Eastern and Central European species of *Ophisaurus* have been erected based on parietals and therefore it is not possible to state if dentaries from AM-3 could belong to them or not. However, they differ from the ones attributed by Roček (1984) to *Ophisaurus* cf. *spinari* from Dolnice (early Miocene, MN 4), Czech Republic, because of shorter angular and surangular processes. The overall morphology of the herein described dentaries is similar to the one of those attributed to the 'Anguinae morphotype 2' from Merkur-Nord (early Miocene, MN 3), Czech Republic (Klembara

**Figure 5.** Scolecophidia indet.: precloacal vertebra (UU AM3 521) in dorsal (A), posterior (B), right lateral (C), anterior (D) and ventral (E) views. Scale bar = 1 mm.

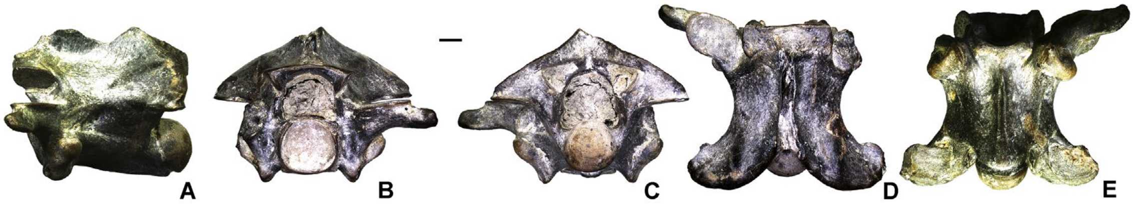

**Figure 6.** cf. *Dolichophis* sp.: precloacal vertebra (UU AM3 522) in left lateral (A), anterior (B), posterior (C), dorsal (D) and ventral (E) views. Scale bar = 1 mm.

2014) and to *Ophisaurus* sp. from Polgárdi (late Miocene, MN 13), Hungary (Venczel 2006). The latter locality has also yielded vertebrae and osteoderms that are similar in size and morphology to the ones from Ano Metochi (Venczel 2006).

Anguidae indet (Figure 4).

*Material*. AM-2: one fragment of an osteoderm (UU AM2 513). AM-3: 25 caudal vertebrae (UU AM3 514), and 41 osteoderms (UU AM3 515-UU AM3 520).

*Description*. Caudal vertebrae are small-sized (centrum length of the largest one is 3.9 mm). Their centrum is dorsoventrally compressed and bears the proximal portions of fused haemapophyses. The autotomy plane is present.

Osteoderms (UU AM2 513 and UU AM3 515-UU AM3 520) are small, but moderately thick. They are subrectangular in shape and they show a low keel in the middle of their ornamented external surface. In UU AM2 513, the keel is distinct and sharp.

*Remarks*. The subrectangular and thick osteoderms provided with a keel on the external surface indicates that they belong to a non-*Anguis* anguine. Furthermore, although it appears most probable that both osteoderms and caudal vertebrae belong to the same taxon described above (*Ophisaurus* sp.), this cannot be shown with certainty. We therefore refrain from formally assigning these elements to *Ophisaurus*, leaving even open the slight possibility that there is a second anguid present in Ano Metochi.

Serpentes Linnaeus, 1758

Scolecophidia Duméril et Bibron, 1844

Scolecophidia indet (Figure 5).

*Material*. AM-3: one precloacal vertebra (UU AM3 521).

*Description*. The precloacal vertebra UU AM3 521 is rather small, with a centrum length of only 1.2 mm, and is missing the anterior and posterior margins of the neural arch, the left prezygapophysis and postzygapophysis, as well as the left synapophysis. The right prezygapophysis and postzygapophysis, the right synapophysis and the condyle are partially incomplete. The preserved postzygapophysis seems to be rather long and enlarged, extending well beyond the level of the condyle in ventral view. The anterior tip of prezygapophysis forms an angle of less than 10° with the posterior tip of the postzygapophysis. The vertebra bears no hypapophysis or haemal keel. The neural arch is depressed and lacks a neural spine. The synapophysis is of hemispherical shape. Both cotyle and condyle are rather flattened dorsoventrally and their form is therefore strongly elliptical. No paracotylar foramina are present. As is common in scolecophidians, the neural canal is proportionally large, being much wider above the level of the cotyle, than below the level of the zygosphene. In lateral view, a large lateral foramen can be seen. There are two ventral foramina, of which one is rather enlarged.

*Remarks*. Rage (1984) and Szyndlar (1985, 1991a) discussed the uniform morphology of scolecophidian vertebrae that hinders their taxonomy. Their conservative vertebral anatomy has resulted in just a single named taxon of this clade from the whole European fossil record, '*Typhlops*' *grivensis* (Hoffstetter 1946; Rage 1984). As is the case with most other Paleogene and Neogene European scolecophidians, the new Greek scolecophidian cannot be assigned with certainty to either Typhlopidae or Leptotyphlopidae. Moreover, the indeterminate scolecophidian from the Pliocene of Çalta, Turkey, described by Rage and Sen (1976) was not figured, and as such, no comparison with the Ano Metochi form can be made. The rather long and enlarged postzygapophyses of the new Greek vertebra, extending well beyond the level of the condyle in ventral view, seem to be distinctive; however, the current lack of knowledge regarding the anatomy and variability of scolecophidian vertebrae, hinders the potential taxonomic value of such a character. Whatever the case, the new vertebra described in this paper, is one among only a handful of known Neogene occurrences of the group worldwide (Mead 2013).

Alethinophidia Nopcsa, 1923

Colubridae Oppel, 1811

Colubrinae Oppel, 1811 (sensu Szyndlar, 1991a)

*Dolichophis* Gistel, 1868

cf. *Dolichophis* sp (Figure 6).

*Material*. AM-3: seven precloacal vertebrae (UU AM3 522–UU AM3 528).

*Description*. The neural spine is only partially preserved in all vertebrae, but it appears that it was longer than high. The neural arch is vaulted. The centrum of the vertebrae is relatively elongated anteroposteriorly. The synapophyses are clearly differentiated into parapophyses and diapophyses, with the former being larger than the latter. Lateral foramina are present. The subcentral ridges and the haemal keel are prominent. In dorsal view, the neural spine appears to be thinner anteriorly than posteriorly. The zygosphene is slightly crenate and no median lobe is present, while the two lateral lobes are rather prominent. The prezygapophyseal articular facets are large and have a relatively oval shape. The prezygapophyseal processes are pointed distally. In anterior view, the neural canal is rather broad, being wider than the cotyle. The zygosphenal roof is thick. In posterior view, the postzygapophyseal processes are marked by small foramina. The zygantrum appears to be wider than the condyle, with the latter being slightly depressed.

*Remarks*. The presence or absence of a hypapophysis in the mid-trunk vertebrae has been considered as the most significant character in distinguishing colubrine from natricine snakes (Szyndlar 1984, 1991a, 1991b). The specimens UU AM3 522–UU AM3 528 can be assigned to Colubrinae (sensu Szyndlar 1991b) by the combination of the following features: lightly built morphology, presence of haemal keel (and not of hypapophysis), synapophyses clearly divided into diapophyses and parapophyses, presence of lateral foramina, straight interzygapophyseal ridge, and straight subcentral ridge. Judging from the size of the largest vertebrae (CL: 6.2 mm for UU AM3 522, 5.9 mm for UU AM3 523, and 5.08 mm for UU AM3 524), the material pertains to a relatively large-sized colubrine snake, and it further bears strong resemblance with the extant *Dolichophis*, as also with '*Coluber*' *caspioides*, a species originally described from the early Miocene of Petersbuch 2 (Szyndlar and Schleich 1993), with an additional referred form from the early Miocene of Merkur-Nord, Czech Republic (Ivanov 2002). It is worth noting that recently Szyndlar (2012) suggested that '*Coluber*' *caspioides* should be probably referred, along with its similartaxa '*C.*' *suevicus*, '*C.*' *dolnicensis* and '*C.*' *pouchetii*, to the extant genus *Dolichophis*, although he did not formally establish new generic combinations for his proposal. This option was later also followed by Venczel and Hír (2015) who described a similar form as '*Coluber*' cf. *caspioides* from the middle Miocene of Litke 1, Hungary, although they also hesitated to formally assign this taxon to *Dolichophis*. In any case, the Ano Metochi large colubrine described herein bears strong vertebral resemblance to the complex '*Coluber*' *caspioides* - '*C.*' *suevicus* - '*C.*' *dolnicensis* - '*C.*' *pouchetii*, and is here tentatively assigned to cf. *Dolichophis*, rather than to the wastebasket taxon '*Coluber*'.

Colubrinae indet (Figure 7).

*Material*. AM-3: eight precloacal vertebrae (UU AM3 529–UU AM3 538).

*Description*. The centrum is longer than wide. The neural spine is variably damaged in most specimens. The lateral foramina are distinct and they occur in deep depressions just ventral to the interzygapophyseal ridges. Synapophyses are clearly divided into parapophyses and diapophyses, with the former being rather laterally directed. In dorsal view, the zygosphene is variably convex or slightly crenate. The prezygapophyseal articular facets are rather broad. The prezygapophyseal processes of the largest vertebrae are rather short. In ventral view, the haemal keel continues anteriorly toward the base of the cotyle. Subcentral foramina are either present or absent, and there are even two small ones in UU AM3 531. The subcentral ridges are short and they are arched dorsally. In anterior view, the zygosphene roof is arched. Paracotylar foramina, when present, are situated in a deep depression next to the cotyle. Cotyle and condyle are slightly depressed and have an oval shape, in anterior and posterior views respectively.

*Remarks*. These vertebrae are attributed to Colubrinae by the combination of the absence of hypapophysis and presence of haemal keel, lightly built morphology, synapophyses clearly divided into diapophyses and parapophyses, presence of lateral foramina, straight interzygapophyseal ridge, and straight subcentral ridge (Szyndlar 1984, 1991a). This material corresponds to a smaller-sized and different colubrine taxon than the larger cf. *Dolichophis* sp. described above. Apart from their absolute size, the two Ano Metochi colubrines can be also distinguished from each other, by differences in their zygantral roof, prezygapophyseal and postzygapophyseal morphology.

Natricinae Bonaparte 1838 (sensu Szyndlar, 1991b)

*Natrix* Laurenti, 1768

*Natrix* sp (Figure 7).

*Material*. AM-2: 24 precloacal vertebrae (UU AM2 515). AM-3: 94 vertebrae (UU AM3 539), one compound bone (UU AM3 540), and one quadrate (UU AM3 541).

*Description*. All vertebrae bear well developed hypapophyses. In ventral view, the centrum is flattened and clearly delimited by prominent subcentral ridges. In several vertebrae, there are two enlarged subcentral foramina, located in both sides of the keel, at the middle of the centrum. Synapophyses are clearly divided into diapophyses and parapophyses bearing parapophyseal processes. The latter seem prominent and project anteroventrally. Prezygapophyseal processes are stout and the prezygapophyseal articular facets are oval shaped. The zygosphene is rather narrow and in dorsal view it appears to be slightly crenate. Both cotyle and condyle are rather rounded and enlarged, being larger than the neural canal. The neural spine variably damaged in all specimens, with few only exceptions. In all cases, the neural spine is longer than high in lateral view. Lateral foramina are enlarged.

The compound bone (UU AM3 540) lacks the anteriormost portion. The mandibular fossa is rather deep. The medial flange of the mandibular fossa is low. The labial flange is concave. The upper border of the labial flange is rather thickened.

In posterolateral view, the quadrate (UU AM3 541) is wide and flat. The bone is wider in the proximity of the trochlea quadrati and it expands towards the dorsal crest. The stapedial process is small and is indistinctly demarcated from the bone. The dorsal crest is thin and lacks the dorsoventral widening. The quadrate crest is prominent especially at middle length.

*Remarks*. The trunk vertebrae are assigned to Natricinae and in particular to the genus *Natrix*, on the basis of the presence of hypapophysis and the shape of the neural spine, the cranial margin of which overhangs anteriorly and the caudal margin overhangs posteriorly (Szyndlar 1984, 1991b; Ivanov 2002). The quadrate is assigned to the genus *Natrix* on the basis of the presence of the thin dorsal crest and the small stapedial process that is indistinctly demarcated from the bone (Ivanov 2002). The compound bone and the vertebral morphology are reminiscent

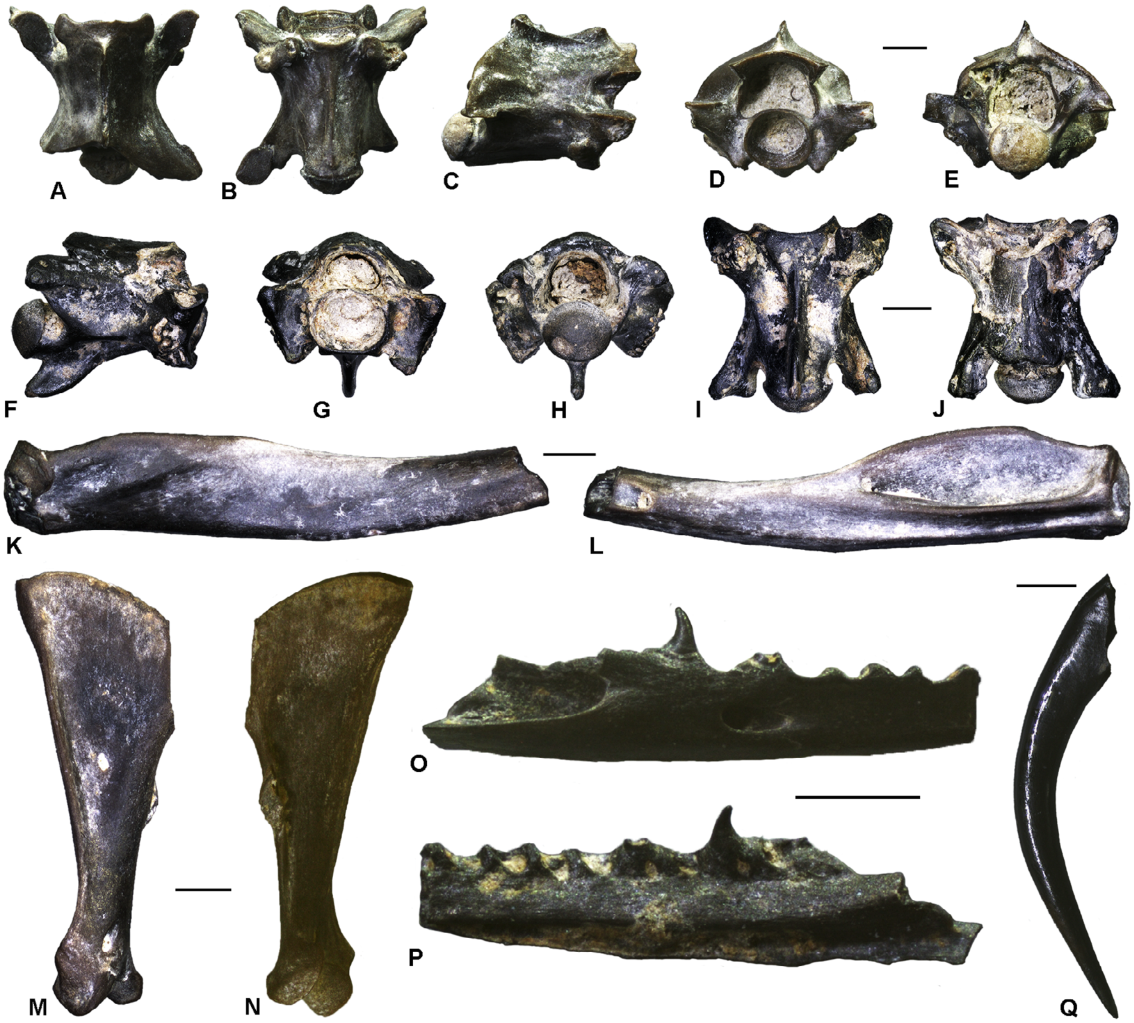

**Figure 7.** Colubrinae indet.: precloacal vertebra (UU AM3 529) in dorsal (A), ventral (B), right lateral (C), anterior (D) and posterior (E) views. *Natrix* sp.: precloacal vertebra (UU AM2 515) in right lateral (F), anterior (G), posterior (H), ventral (I) and dorsal (J) views; right compound bone (UU AM3 540) in medial (K) and lateral (L) views; left quadrate (UU AM3 541) in posterolateral (M) and anteromedial (N) views. Serpentes indet.: right dentary (UU AM2 516) in lateral (O) and medial (P) views; fang (UU AM3 547) (Q). Scale bars = 1 mm.

to *Natrix longivertebrata* and *N.* aff. *longivertebrata* from the Pliocene of Poland and the Miocene of France respectively (Szyndlar 1984; Rage and Szyndlar 1986).

Serpentes indet (Figure 7).

*Material*. AM-2: one dentary (UU AM2 516), 35 precloacal vertebrae (UU AM2 517) and 11 caudal vertebrae (UU AM2 518). AM-3: four dentaries (UU AM3 542-UU AM3 545), one ?compound bone (UU AM3 546), several isolated fangs (UU AM3 547), 130 precloacal vertebrae (UU AM3 548), 46 caudal vertebrae (UU AM3 549), and 14 ribs (UU AM3 550).

*Remarks*. These various cranial and postcranial elements are either fragmentary or bear no clear diagnostic features that allow us to attribute them to any clade or make any proper identification. They are all considered to pertain to indeterminate snakes, that could belong also to one of the above described forms.

Squamata indet.

*Material*. AM-2: one fragment of a dentary (UU AM2 519), one fragment of tooth-bearing bone (UU AM2 520), one vertebra (UU AM2 521), and one fragment of a femur (UU AM2 522). AM-3: one fragment of a pterygoid (UU AM3 551), four vertebrae (UU AM3 552), two humeri (UU AM3 553 and UU AM3 554), and one ilium (UU AM3 555).

*Remarks*. Similarly to the case of the indeterminate snakes that was discussed above, this material does not bear diagnostic characters for identification beyond Squamata, and is here considered to pertain to indeterminate lizards (aka non-snake squamates).

## Discussion

### *Biogeography*

The Ano Metochi squamate fauna is quite diverse, being comprised of at least seven different species of lizards and snakes. Furthermore, this is one of a few only Miocene squamate localities described so far from Greece (Römer 1870; Weithofer 1888; Conrad et al. 2012; Georgalis, Villa and Delfino 2016; Georgalis, Villa, Vlachos et al. in press).

The purported presence of an agamid at AM-3, previously listed by Delfino et al. (2008) and Blain et al. (2016), is based on the misidentification of a specimen (UU AM3 557) belonging to a cyprinid fish. A similar erroneous attribution of a fish bone from the Pleistocene of Hungary to an agamid lizard was made by Meszoely and Gasparik (2002), as later noted by Rage (2013), prompting that cautiousness should be taken when identifying acrodont lizards.

With the exception of the probable cordylids, all squamate clades (lacertids, anguids, scolecophidians, colubrines and natricines) recovered from Ano Metochi still have extant representatives in Greece (Valakos et al. 2008; Sillero et al. 2014). On the other hand, fossil cordylids have never been described from that country and are now confined solely to Africa.

The fossil locality Maramena, which is located few kilometres away from Ano Metochi, provides a meaningful comparison, although it is slightly younger (MN 13/14). Maramena contains agamids, anguids (*Ophisaurus*), lacertids, scincoids (tentatively referred herein to cordylids), elapids and viperids (of the 'Oriental vipers complex') (Richter 1995; Szyndlar 1995). According to this faunal composition, lacertids and *Ophisaurus* are present in both Ano Metochi and Maramena. Also, as was noted above, the scincoid from Maramena described by Richter (1995) as 'Scincoidea Incertae Sedis' is here tentatively referred to Cordylidae, thus marking the shared presence of this clade in both Ano Metochi and Maramena. As such, it is obvious that lacertids, cordylids and *Ophisaurus* share a common presence in the late Miocene of the Serres Basin, reaching at least the Mio-Pliocene boundary. On the other hand, agamids, elapids and 'Oriental vipers' are absent from the MN 13 stage (Ano Metochi) of the Serres Basin, whereas these clades are recovered at the end of MN 13 or the beginning of MN 14 (Maramena). Additionally, scolecophidians are present at the MN 13 stage, are then absent at the end of MN 13 or beginning of MN 14, and appear again in the Greek fossil record in the Plio-Pleistocene (Szyndlar 1991a). Agamids, scolecophidians and 'Oriental vipers' are still members of the Greek extant herpetofauna (Sillero et al. 2014), although it has not been clearly demonstrated that the distribution of the former is natural or due to anthropogenic factors in antiquity (Delfino et al. 2008). However, taking into consideration only these two localities, it is difficult to attest whether such faunal absences are genuine or simply an artifact of preservation or collection. Agamids have a wide distribution during the late Miocene of southern Europe, and are readily identified among lizard remains due to their characteristic acrodont dentition (Delfino et al. 2008). Scolecophidians are relatively small, their remains are difficult to collect, and they therefore have a poor fossil record (Mead 2013; Colombero et al. 2014), so it is possible that their absence in Maramena is due to preservation or collection biases. However, the case of elapids and 'Oriental vipers' is more complicated. These snake groups have several records from Miocene localities across Europe that are older than Maramena and Ano Metochi (Szyndlar and Rage 1990, 2002; Georgalis, Szyndlar et al. 2016a). The first descriptions of these groups from Greece is only in the late Miocene (MN 13 / 14) of Maramena (Szyndlar 1995), with elapids being recorded from the country also in the Pliocene and probably Pleistocene (Szyndlar 1991b), whereas 'Oriental vipers' are still members of the extant herpetofauna (Georgalis, Szyndlar et al. 2016). It is worth noting that elapids are also mentioned (without any description or figure) in a species list from the also northern Greek locality of 'Ravin de la Pluie' (MN 10) (de Bonis et al. 1991), and it is therefore impossible to reassess such a record or the correctness of its identity. As such, we can speculate that the absence of elapids and 'Oriental vipers' from Ano Metochi is genuine. In any case, however, this absence does not necessitate that these snake groups did not disperse to Greece prior to MN 13 (age of Ano Metochi). It is possible, in fact, that ecological factors did not favour the presence of cobras and large vipers at Ano Metochi.

## ***The rise and fall of European girdled lizards***

Girdled lizards (Cordylidae) constitute a bizarre clade of heavily armored squamates that are now confined to sub-saharan Africa. Despite their restricted extant distribution, the clade achieved a much wider distribution in the past, as it is demonstrated by its fossil record. Fossil cordylids are known with certainty from the early Miocene of The Czech Republic (Roček 1984; Čerňanský 2012) and Germany (Kosma 2004), and the middle Miocene (MN 5) of Austria (Böhme 2002), Germany (Böhme 2010) and Switzerland (Jost et al. 2015). In addition, certain occurrences from the Paleogene of Europe have been variously suggested as having affinities with cordyliforms. These include *Eocordyla mathisi* from the middle and late Eocene of France (Augé 2005), and '*Lacerta*' *rottensis* from the late Oligocene of Germany (von Meyer 1856; Böhme and Lang 1991), as also other, unnamed forms from the late Eocene of Spain (Bolet and Evans 2013) and the late Oligocene of France (Augé and Rage 1995). The strong morphological resemblance of cordylid and scincid fossil remains may account for this low diversity and the poor record of the former clade. Future revisions may therefore show that several putative 'scincids' belong in fact to cordyliforms. In any case, the disjunct fossil distribution of cordyliforms has hindered our understanding of their palaeobiogeography. Different scenarios were created to explain their origins in Europe: either a continuous persistence of cordyliforms in Europe from the Eocene until the Miocene, or a late Paleogene extinction event of the primitive cordyliforms and then a re-dispersal of cordylids from Africa during the early Miocene, following the so-called '*Gomphotherium* Landbridge' (Čerňanský 2012; Georgalis, Villa, Delfino 2016). The Ano Metochi cordylids cannot favor either of these scenarios. On the other hand, however, they reveal that cordyliforms persisted in Europe for much longer than what was previously thought, since up to now their younger described fossils had been recovered from the middle Miocene (MN 5) of Central Europe (Rage 2013). Therefore, if our identification of the herein described specimens is correct, the occurrence of cordylids in the much younger strata of the late Miocene Ano Metochi (MN 13) and the tentative referral of the Maramena (MN 13/14) form to this clade, implies a much longer survivorship and a possible withdrawal of their range to the southeastern margins of the continent. Interestingly, it seems that the Miocene southern Europe has variously marked the last occurrences for other reptile clades as well, as it has been previously suggested for podocnemidoidean turtles (Georgalis et al. 2013; Georgalis and Kear 2013) and somehow for crocodiles, even if in the latter case, dispersal from Africa is likely (Delfino and Rossi, 2013). The long term survival of cordylids could be explained by taking into consideration the ecology of extant girdled lizards, which mostly shelter in rock crevices or burrows (Bauer 1998), although Čerňanský (2012) considered that alternative ecological lifestyles for extinct cordylids could also be possible.

### *The diversity of* Ophisaurus *in the Neogene of Europe*

*Anguis* and *Pseudopus* are the only anguines that currently inhabit Europe, whereas species of *Ophisaurus* (*sensu lato*) are still present in northern Africa, southern Asia and North America. The main distinction between elements of *Pseudopus* and *Ophisaurus* is based on the tooth and parietal morphology, with the former genus distinguished by molariform posterior teeth, parietal characterized by an anterior branch of the parietal crest medially developed and the absence of a distinct parietal notch, whereas the latter bearing canine-like teeth, an anterior branch of the parietal crest laterally developed and a distinct parietal notch (Klembara 1979, 1981; Klembara et al. 2014). Klembara (1981) also mentioned some differences in the vertebral morphology of *Pseudopus* and *Ophisaurus*, with the vertebrae of the former being more robust and having straight lateral margins in the centrum, rather than concave ones as is the case for the latter genus. Despite their absence in the extant European herpetofauna, a large amount of *Ophisaurus* or *Ophisaurus*-like forms have been described from the fossil record of Europe, with their first appearance during the early Eocene of France (Augé et al. 1997). Since then, they continued to be present in several European Paleogene localities (Rage and Ford 1980; Augé 1992; Augé and Rage 1995; Böhme 2008; Augé and Smith 2009; Klembara and Green 2010; Čerňanský et al. 2016). Whether all these forms, however, constitute a single monophyletic lineage remains yet to be tested on the basis of complete phylogenetic analysis. During the Miocene *Ophisaurus* or *Ophisaurus*-like forms became widespread throughout Europe. Their remains have up to this date been recovered from Austria (Böhme 2002; Miklas-Tempfer 2003; Böhme and Vasilyan 2014), The Czech Republic (Klembara 1979, 1981, 2014; Roček 1984), France (Augé and Rage 2000; Rage and Bailon 2005), Germany (Jörg 1965; Prieto et al. 2009; Böhme 2010; Čerňanský et al. 2015), Hungary (Venczel 2006; Venczel and Hír 2015), Italy (Delfino 2002; Venczel and Sanchiz 2006; Rook et al. 2015), Portugal (Antunes and Mein 1981; Crespo 2001), Romania (Hír and Venczel 2005; Venczel et al. 2005; Venczel and Ştiucă 2008), Slovakia (Klembara 1986), Spain (Murelaga et al. 2002; Blain 2005), and Switzerland (Jost et al. 2015; Mennecart et al. 2016). Following the end of the Miocene the clade is in demise and their Pliocene record is scarce (Bailon 1989; Čerňanský 2011; Delfino et al. 2011). The last occurrence on the continent is reported from the Pleistocene of France (Clot et al. 1976) and Spain (Blain and Bailon 2010). The presence of *Ophisaurus* in Ano Metochi, along with the previously published record from Maramena, further confirms that, during the late Miocene, the genus had a widespread distribution across Europe, being also present in the southeastern margins of the continent. Greece is currently inhabited by four distinct anguid species: *Anguis graeca*, *Anguis fragilis*, *Anguis cephallonica*, and the largest European lizard, *Pseudopus apodus* (Sindaco and Jeremcenko, 2008; Gvoždík et al. 2010; Sillero et al. 2014).

### *The Neogene scolecophidians of Europe*

Scolecophidians still occur in the extant Greek herpetofauna with *Xerotyphlops vermicularis*, which is also the sole representative of Typhlopidae in Europe. Leptotyphlopidae are not members of the extant European fauna, but still occur in the adjacent Asia Minor (Adalsteinsson et al. 2012). In Europe, fossil scolecophidians are first described from the early Eocene of Dormaal, Belgium (Hecht and Hoffstetter 1962). After that, the clade is totally absent until the early Miocene, when it is recorded in France, Spain and The Czech Republic (Alférez and Brea 1981; Szyndlar 1987; Rage and Bailon 2005). During the Miocene and until the Pleistocene, scolecophidians have been sporadically recovered from localities across Europe (Szyndlar 1985; Hír and Venczel 2005; Szyndlar 2005; Venczel et al. 2005; Venczel and Ştiucă 2008; Venczel 2011; Colombero et al. 2014), showing a post-Pliocene southward-directed decreasing trend of their range to the southeastern edges of Europe (Szyndlar 1991a; Rage 2013). This decrease in their range fully reflects their extant European distribution (southern Balkan Peninsula only), and is also consistent with similar southern European 'refugia' observed in other disparate reptile clades, such as erycine booids (Szyndlar 1991a; Rage 2013), and 'Oriental vipers' (Szyndlar and Rage 2002; Georgalis, Szyndlar et al. 2016). Fossil scolecophidians were already known from Greece, but they had only been recovered from Plio-Pleistocene sediments (Szyndlar 1991a). Thus, the new Ano Metochi form adds to the poor global Neogene record of the clade (Mead 2013).

Frustratingly, due to their conservative vertebral morphology and the scarcity of extant scolecophidian skeletal descriptions, it is rather difficult to attribute these occurrences to either typhlopids or leptotyphlopids. Moreover, the previously considered widespread extant genus *Typhlops,* has now been split into several genera on the basis of external morphology and strong molecular data, with *Typhlops sensu stricto* being now confined to the Caribbean, and the sole extant European representative assigned to its own genus, *Xerotyphlops*, along with three other species from the Sahara, Socotra Islands and southwestern Asia (Hedges et al. 2014; Pyron and Wallach 2014). This fact leaves the generic status of the until now single named species '*Typhlops*' *grivensis* Hoffstetter, 1946 as uncertain, an attribution that was already first questioned by Rage (1984) who treated this taxon as ?*Typhlops grivensis*. We thus here treat the generic attribution of '*T.*' *grivensis* in quotation marks, pending a redescription of the latter species.

## Conclusions

Specimens of fossil squamates are described from the late Miocene (MN 13) of Ano Metochi, northern Greece. Systematic study of the material documents a diverse fauna consisting of lacertid, possible cordylid and anguid lizards, and scolecophidian, colubrine and natricine snakes that, with the exception of the latter constitute the oldest from Greece. The remains that were the origin of the erroneous identification of agamid lizards in previous publications have been here referred to cyprinid fish. A previously described scincoid from the adjacent locality of Maramena is herein tentatively referred to Cordylidae. The probable occurrence of girdled lizards (Cordylidae) in the latest Miocene of Greece is remarkable, as it constitutes the youngest records of the clade from Europe, implying a long term survivorship of a group that was previously thought to have become extinct around the middle Miocene (MN 5). The scolecophidian from Ano Metochi cannot be assigned to either Typhlopidae or Leptotyphlopidae, but adds to the poorly documented diversity of worm snakes. Comparison of the squamate faunas of the adjacent localities Ano Metochi and Maramena reveals shared faunal elements but also notable absences among these localities. The analysis and detailed description of the squamate remains from Ano Metochi allows us to expand and correct the knowledge of the reptile assemblage of this locality (previously limited to brief faunal lists) and therefore to enhance our understanding of Miocene reptile faunas of southeastern Europe.

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## References

Adalsteinsson SA, Branch WR, Trape S, Vitt LJ, Hedges SB. 2012. Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata). Zootaxa. 2244:1–50.

Alférez DF, Brea LP. 1981. Estudio preliminar de los restos de Peces, Anfibios y Reptiles del yacimiento mioceno de Córcoles (Guadalajara) [Preliminary study of the remains of fish, amphibians and reptiles in the Miocene deposit of Córcoles (Guadalajara)]. Boletin de la Real Sociedad Española de Historia Natural, Seccion Geologia. 79:5–20.

Antunes MT, Mein P. 1981. Vertébrés du miocène moyen de Amor (Leiria) - importance stratigraphique [The Vertebrates from the middle Miocene of Amor (Leiria) - stratigraphic importance]. Ciências da Terra. 6:169–188.

Augé ML. 1992. Une espéce nouvelle ďOphisaurus (Lacertilia, Anguidae) de lOligocène des phosphorites du Quercy [One new species of Ophisaurus (Lacertilia, Anguidae) from the Oligocene of the Phosphorites of Quercy]. Révision de la sous-famille des Anguinae Paläontol Z 66:159–175.

Augé ML. 2005. Evolution des lézards du Paléogène en Europe [Evolution of lizards from the Paleogene of Europe]. Mémoires du Muséum national d'Histoire naturelle. 192:3–369.

Augé M, Rage J-C. 1995. Le Garouillas et les sites contemporains (Oligocene, MP 25) des Phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertebres. 2. Amphibiens et squamates [Le Garouillas and the contemporary sites (Oligocene, MP 25) from the Phosphorites of Quercy (Lot, Tarn-et-Garonne, France). 2. Amphibians and squamates]. Palaeontographica Abt A. 236:11–32.

Augé M, Rage J-C. 2000. Les Squamates (Reptilia) du Miocène moyen de Sansan [The squamates (Reptilia) from the middle Miocene of Sansan]. In: Ginsburg L, editor. La faune miocène de Sansan et son environnement [The Miocene fauna of Sansan and its environment]. Paris: Muséum national d'Histoire naturelle; p. 263–313.

Augé M, Smith R. 2009. An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene-Oligocene transition. Zool J Linn Soc. 155:148–170.

Augé M, Duffaud S, Lappatrent de Broin F, Rage J-C, Vasse D. 1997. Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin parisien): une herpétofaune de référence pour l'Eocène inférieur [The amphibians and reptiles of Prémontré (Cuisian, Paris Basin): one reference herpetofauna for the early Eocene]. Géologie de la France. 1:23–33.

Bailon S. 1989. Les amphibiens et les reptiles du Pliocène Supérieur de Balaruc II (Hérault, France) [Amphibians and reptiles from the Upper Pliocene of Balaruc II (Hérault, France)]. Palaeovertebrata. 19:7–28.

Bailon S. 1991. Amphibiens et Reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes [Amphibians and reptiles from the Pliocene and Quaternary of France and Spain] [PhD dissertation]. Paris: Université de Paris VII.

Barahona F, Barbadillo LJ. 1997. Identification of some Iberian lacertids using skull characters. Rev Esp Herpetol. 11:47–62.

Bauer AM. 1998. Lizards. In: Cogger HG, Zweifel RG, editors. Encyclopedia of Reptiles and Amphibians. San Diego (CA): Academic Press; p. 126–173.

Blain H-A. 2005. Contribution de la paléoherpétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne [Contribution of the palaeoherpetofauna (Amphibia & Squamata) to the knowledge of climate change and landscape of the upper Pliocene and the Middle Pleistocene of Spain] [PhD dissertation]. Paris: Muséum national d'Histoire naturelle.

Blain H-A, Bailon S. 2010. Anfibios y escamosos del Pleistoceno inferior de Barranco León y de Fuente Nueva 3 (Orce, Andalucía, España) [Amphibians and squamates from the lower Pleistocene of Barranco León y de Fuente Nueva 3 (Orce, Andalucía, Spain)]. In: Toro I, Martínez-Navarro B, Agustí J, editors. Ocupaciones humanas durante el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza [Human occupation during the lower and Middle Pleistocene of Cuenca de Guadix-Baza]. Arqueología Monografías. Junta de Andalucía: Sevilla; p. 165–183.

Blain H-A, Bailon S, Agustí J. 2016. The geographical and chronological pattern of herpetofaunal Pleistocene extinctions on the Iberian Peninsula. C R Palevol. 15:761–744.

Böhme M. 2002. Lower Vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin - palaeoecological, environmental and palaeoclimatical implications. Beiträge zur Paläontologie. 27:339–354.

Böhme M. 2008. Ectothermic vertebrates (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) from the Upper Oligocene of Oberleichtersbach (Northern Bavaria, Germany). Cour Forsch-Inst Senckenberg. 260:161–183.

Böhme M. 2010. Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. Paläontol Z. 84:3–41.

Böhme W, Lang M. 1991. The reptilian fauna of the Late Oligocene locality Rott near Bonn (Germany) with special reference to the taxonomic assignment of "*Lacerta rottensis*" Von Meyer, 1856. Neues Jahrb Geol Palaontol Abh Monatshefte H. 9:515–525.

Böhme M, Vasilyan D. 2014. Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). Palaeobiod Palaeoenv. 94:21–40.

Bolet A, Evans SE. 2013. Lizards and amphisbaenians (Reptilia, Squamata) from the late Eocene of Sossís (Catalonia, Spain). Palaentol Electronica. 16:1–23.

Bonaparte CL. 1832–1841. *Iconographia della fauna Italica per le quattro classi degli animali vertebrati*. Vol. 2. Anfibi. Rome (Italy): Dalla Tipografia Salviucci.

Čerňanský A. 2011. New finds of the Neogene lizard and snake fauna (Squamata: Lacertilia; Serpentes) from the Slovak Republic. Biologia. 66:899–911.

Čerňanský A. 2012. The oldest known European Neogene girdled lizard fauna (Squamata, Cordylidae), with comments on Early Miocene immigration of African taxa. Geodiversitas. 34:837–848.

Čerňanský A, Rage J-C, Klembara J. 2015. The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. J Syst Palaeontol. 13:97–128.

Čerňanský A, Klembara J, Müller J. In press. The new rare record of the late Oligocene lizards and amphisbaenians from Germany and its impact on our knowledge of the European terminal Palaeogene. Palaeobiod Palaeoenv. doi:10.1007/s12549-015-0226-8.

Clot A, Chaline J, Jammot D, Mourer-Chauviré J, Rage J-C. 1976. Montousse 5 (Hautes-Pyrenees), un nouveau remplissage de fissure a faune de vertebres du Pleistocene inferieur [Montousse 5 (Hautes-Pyrenees), one new fissure filling with a vertebrate fauna from the lower Pleistocene]. Geobios. 9:511–514.

Colombero S, Angelone C, Bonelli E, Carnevale G, Cavallo O, Delfino M, Giuntelli P, Mazza P, Pavia G, Pavia M, Repetto G. 2014. The Messinian vertebrate assemblages of Verduno (NW Italy): another brick for a latest Miocene bridge across the Mediterranean. Neues Jahrb Geol Palaontol Abh Monatschefte. 272:287–324.

Crespo EG. 2001. Paleoherpetofauna de Portugal [Palaeoherpetofauna of Portugal]. Publicações Avulsas, 2° Série, numero 7. Lisbon (Portugal): Museu Bocage.

Conrad JL, Balcarcel AM, Mehling CM. 2012. Earliest example of a giant monitor lizard (*Varanus*, Varanidae, Squamata). PLoS ONE. 7(8):e41767.

de Bonis L, Bouvrain G, Geraads D, Koufos G. 1991. Diversity and paleoecology of Greek late Miocene mammalian faunas. Palaeogeogr Palaeoclimatol Palaeoecol. 91:99–121.

de Bruijn H. 1989. Smaller mammals from the Upper Miocene and lower Pliocene of the Strimon basin, Greece. Part 1. Rodentia and Lagomorpha. Boll Soc Paleontol Ital. 28:189–195.

Delfino M. 2002. Erpetofaune italiane del Neogene e del Quaternario [Italian herpetofaunas from the Neogene and the Quaternary] [PhD dissertation]. [Modena (Italy)]: University of Modena and Reggio Emilia.

Delfino M, Rossi MA. 2013. Fossil crocodylid remains from Scontrone (Tortonian, Southern Italy) and the late Neogene Mediterranean biogeography of crocodylians. Geobios. 46:25–31.

Delfino M, Kotsakis T, Arca M, Tuveri C, Pitruzzella G, Rook L. 2008. Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiversitas. 30:641–656.

Delfino M, Bailon S, Pitruzzella G. 2011. The late Pliocene amphibians and reptiles from “Capo Mannu D1 Local Fauna” (Mandriola, Sardinia, Italy). Geodiversitas. 33:357–382.

Estes R. 1983. Sauria Terrestria, Amphisbaenia. In: Wellnhofer P, editor. Encyclopedia of Paleoherpetology. Stuttgart / New York: Gustav Fisher Verlag; 249 pp.

Estes R, de Queiroz K, Gauthier J. 1988. Phylogenetic relationships within Squamata. In: Estes R, Pregill G, editors. Phylogenetic Relationships of the Lizard Families. Stanford: Stanford University Press; p. 119–282.

Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bull Peab Mus Nat Hist. 53:3–308.

Georgalis GL, Kear BP. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios. 46:299–311.

Georgalis GL, Velitzelos E, Velitzelos, D, Kear BP. 2013. *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the lower Miocene of northern Greece. In: Brinkman D, Holroyd P, Gardner J, editors. Morphology and evolution of turtles: papers in honor of Eugene S Gaffney Volume 3 Pleurodires. Dordrecht (The Netherlands): Springer; p. 277–287.

Georgalis GL, Szyndlar Z, Kear BP, Delfino M. 2016. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences. 109:113–116.

Georgalis GL, Villa A, Delfino M. 2016. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. Sci Nat. 103:12.

Georgalis GL, Villa A, Vlachos E, Delfino M. In Press. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios. (accepted).

Gvoždík V, Jandzik D, Lymberakis P, Jablonski D, Moravec J. 2010. Slow worm, *Anguis fragilis* (Reptilia: Anguidae) as a species complex: genetic structure reveals deep divergences. Mol Phylogenet Evol. 55:460–472.

Hecht M, Hoffstetter R. 1962. Note préliminaire sur les amphibiens et les squamates du Landenien supérieur et du Tongrien de Belgique [A preliminary note on the amphibians and the squamates from the Landenians and the Tongrian of Belgium]. Bulletin de l’Institut royal des Sciences naturelles de Belgique. 38:1–30.

Hedges SB, Marion AB, Lipp KM, Marin J, Vidal N. 2014. A taxonomic framework for typhlopid snakes from the Caribbean and other regions (Reptilia, Squamata). Caribb Herpetol. 49:1–61.

Hír J, Venczel M. 2005. New middle Miocene vertebrate localities from Subpiatră (Bihor District, Romania). Acta Palaeontologica Romaniae. 5:211–221.

Hoffstetter R. 1946. Les Typhlopidae fossiles [The fossil Typhlopidae]. Bulletin du Muséum National d’Histoire Naturelle, Paris (Série 2) 18:309–315.

Ivanov M. 2002. The oldest known Miocene fauna from Central Europe: Merkur-North locality. Czech Republic Acta Palaeontol Pol. 47:513–534.

Jörg E. 1965. *Ophisaurus acuminatus* nov. spec. (Anguidae, Rept.) von der pontischen Wirbeltier-Fundstatte Hewenegg Hegau [*Ophisaurus acuminatus* nov. spec. (Anguidae, Rept.) from the Pontian of Wirbeltier-Fundstatte Hewenegg Hegau]. Beiträge zur naturkundlichen Forschungen in SW. Deutschland. 24:21–30.

Jost J, Kälin D, Börner S, Vasilyan D, Lawver D, Reichenbacher B. 2015. Vertebrate microfossils from the Upper Freshwater Molasse in the Swiss Molasse Basin: Implications for the evolution of the North Alpine Foreland Basin during the Miocene Climate Optimum. Palaeogeogr Palaeoclimatol Palaeoecol. 426:22–33.

Klembara J. 1979. Neue Funde der Gattungen *Ophisaurus* und *Anguis* (Squamata, Reptilia) aus dem Untermiozan Westbohmens (CSSR) [New finds of the genera *Ophisaurus* and *Anguis* (Squamata, Reptilia) from the Lower Miocene of West Bohemia (CSSR)]. Vestnik Ustrednıho ustavu geologickeho. 54:163–169.

Klembara J. 1981. Beiträg zur Kenntnis der Subfamilie Anguinae (Reptilia, Anguidae) [Contribution to the knowledge of the subfamily Anguinae]. Acta Univ Carol, Geol. 2:121–168.

Klembara J. 1986. New finds of the genus *Ophisaurus* (Reptilia, Anguidae) from the Miocene of Western Slovakia (Czechoslovakia). Acta Univ Carol, Geol, Špinar. 2:187–203.

Klembara J. 2014. New finds of anguines (Squamata, Anguidae) from the Early Miocene of Northwest Bohemia (Czech Republic). Paläontol Z. 89:171–195.

Klembara J, Green B. 2010. Anguimorph lizards (Squamata, Anguimorpha) from the Middle and Upper Eocene of the Hampshire Basin of Southern England. J Syst Palaeontol. 8:97–129.

Klembara J, Hain M, Dobiašová K. 2014. Comparative Anatomy of the Lower Jaw and Dentition of Pseudopus apodus and the Interrelationships of Species of Subfamily Anguinae (Anguimorpha, Anguidae). Anat Rec. 297:516–544.

Kosma R. 2004. The dentitions of recent and fossil scincomorphan lizards (Lacertilia, Squamata) - systematics, functional morphology, paleocology [PhD dissertation]. [Hannover (Germany)]: University of Hannover.

Koufos GD. 2006. The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. Ann Geol des Pays Helleniques. 4:183–214.

Laurenti, JN. 1768. Austriaci Viennensis specimen medicum, exhibens synopsin reptilium emendatam cum experimentis ca Venena et antidota reptilium Austriacorum quod authoritate et consensu. Vienna (Austria): Joannis Thomae de Trattnern, Caes. Reg. Maj. Aulae Typographi et Bibliopolae.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus 1, Pars 1. Stockholm (Sweden): Laurentii Salvius.

Mead J. 2013. Scolecophidia (Serpentes) of the Late Oligocene and Early Miocene, North America, and a fossil history overview. Geobios. 46:225–231.

Mennecart B, Yerly B, Mojon P-O, Angelone C, Maridet O, Böhme M, Pirkenseer C. 2016. A new Late Agenian (MN2a, Early Miocene) fossil assemblage from Wallenried (Molasse Basin, Canton Fribourg, Switzerland). Paläontol Z. 90:101–123.

Meszoely CAM, Gasparik M. 2002. First record of an agamid lizard from the Pleistocene of Hungary. Fragm Palaeontol Hung. 20:1–2.

Miklas-Tempfer PM. 2003. The Miocene Herpetofaunas of Grund (Caudata; Chelonii, Sauria, Serpentes) and Mühlbach am Manhartsberg (Chelonii, Sauria, Amphisbaenia, Serpentes), Lower Austria. Ann Naturhist Mus Wien. 104A:195–235.

Murelaga X, Pereda-Suberbiola X, Lapparent de Broin F, Rage J-C, Duffaud S, Astibia H. Badiola A.. 2002. Amphibians and reptiles from the Early Miocene of the Bardenas Reales of Navarre (Ebro Basin, Iberian Peninsula). Geobios. 35:347–365.

Nopcsa F. 1923. Die Familien der Reptilien [The families of the Reptiles]. Fortschritte der Geologie und Paläontologie. 2:1–210.

Oppel M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodom einer Naturgeschichte derselben. München (Germany): Joseph Lindauer Verlag.

Owen R. 1857. On the fossil vertebrae of a Serpent (*Laophis crotaloïdes*, Ow.) discovered by Capt. Spratt, R.N., in a tertiary formation at Salonica. Quarterly Journal of the Geological Society of London. 13:196–199.

Prieto J, Böhme M, Maurer H, Heissig K, Abdul-Aziz H. 2009. Biostratigraphy and sedimentology of the Fluviatile Untere Serie (Early and Middle Miocene) in the central part of the North Alpine Foreland Basin: implications for palaeoenvironment and climate. Int J Earth Sci. 98:1767–1791.

Pyron RA, Wallach V. 2014. Systematics of the blindsnakes (Serpentes: Scolecophidia: Typhlopoidea) based on molecular and morphological evidence. Zootaxa. 3829:1–081.

Rage J-C. 1984. Serpentes. In: Wellnhofer P, editor. Encyclopedia of paleoherpetology. Stuttgart / New York: Gustav Fisher Verlag.

Rage J-C. 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiod Palaeoenv. 93:517–534.

Rage J-C, Bailon S. 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). Geodiversitas. 27:413–441.

Rage J-C, Ford RLE. 1980. Amphibians and squamates from the Upper Eocene of the Isle of Wight. Tertiary Research. 3:47–60.

Rage J-C, Sen S. 1976. Les Amphibiens et les Reptiles du Pliocène supérieur de Çalta (Turquie) [The amphibians and the reptiles from the upper Pliocene of Çalta (Turkey)]. Géologie méditerranéenne. 3:127–134.

Rage J-C, Szyndlar Z. 1986. *Natrix longivertebrata* from the European Neogene, a snake with one of the longest known stratigraphic ranges. Neues Jahrb Geol Palaontol Mh. 1986:56–64.

Richter A. 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). Münchner Geowiss Abh. 28:35–38.

Roček Z. 1984. Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia). Rozpravy Ceskoslovenské Akademie Ved, Rada matematickych a prirodnich Ved. 94:1–66.

Römer F. 1870. Über *Python euboicus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea [On *Python euboicus*, a fossil giant snake from the tertiary shale of Kumi in the island of Euboea]. Z Dtsch geol Gesell. 22:582–590.

Rook L, Delfino M, Sami M. 2015. I vertebrati fossili della cava del Monticino di Brisighella: una finestra sui popolamenti continentali del Mediterraneo nel Miocene superiore. I gessi di Brisighella e Rontana [The fossil vertebrates from the cave of Monticino di Brisighella: one window to the Mediterranean continental populations in the upper Miocene: the sediments of Brisighella and Rontana]. Memorie dell'Istituto Italiano di Speleologia s II, 28:79–100.

Schneider B. 1975. Ein mittelpleistozane Herpetofauna von der Insel Chios, Agais [A middle Pleistocene herpetofauna from the island of Chios, Aegean]. Senckenb Biol. 56:191–198.

Sillero N, Campos J, Bonardi A, Corti C, Creemers R, Crochet P-A, Crnobrnja Isailović J, Denoël M, Ficetola GF, Gonçalves J, et al. 2014. Updated distribution and biogeography of amphibians and reptiles of Europe. Amphibia-Reptilia. 35:1–31.

Sindaco R, Jeremčenko V. 2008. The reptiles of the western Palearctic Vol 1: annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. Belvedere: Monografie della Societas Herpetologica Italica I.

Szyndlar Z. 1984. Fossil snakes from Poland. Acta Zoologica Cracoviensia. 28:1–156.

Szyndlar Z. 1985. Ophidian fauna (Reptilia, Serpentes) from the Uppermost Miocene of Algora (Spain). Estud Geol. 41:447–465.

Szyndlar Z. 1987. Snakes from the lower Miocene locality of Dolnice (Czechoslovakia). J Vert Paleontol. 7:55–71.

Szyndlar Z. 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae. Colubrinae Estud Geol. 47:103–126.

Szyndlar Z. 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae. Viperidae Estud Geol. 47:237–266.

Szyndlar Z. 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 4. Serpentes (Squamata, Reptilia). Münchner Geowiss Abh. 28:35–39.

Szyndlar Z. 2005. Snake fauna from the Late Miocene of Rudabánya. In: Bernor RL, Kordos L, Rook L, editors. Multidisciplinary research at Rudabánya Palaeontogr ital 90:31–52.

Szyndlar Z. 2012. Early Oligocene to Pliocene Colubridae of Europe: a review. Bull Soc géol France. 183:661–681.

Szyndlar Z, Rage J-C. 1990. West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): interrelationships among extinct and extant species. Amphibia-Reptilia. 11:385–400.

Szyndlar Z, Rage J-C. 2002. Fossil record of the true vipers. In: Schuett G, Hoggren M, Douglas M, Greene H, editors. Biology of the Vipers. Eagle Mountain: Eagle Mountain Publishing; p. 419–441.

Szyndlar Z, Schleich HH. 1993. Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern Germany. Stuttgarter Beiträge zur Naturkunde B. 192:1–47.

Szyndlar Z, Zerova G. 1990. Neogene cobras of the genus *Naja* (Serpentes: Elapidae) of East Europe. Ann Naturhist Mus Wien. 91A:53–61.

Valakos ED, Pafilis P, Sotiropoulos K, Lymberakis P, Maragou P, Foufopoulos J. 2008. Amphibians and reptiles of Greece. Frankfurt (Germany): Chimaira.

Venczel M. 2006. Lizards from the late Miocene of Polgárdi (W-Hungary). Nymphaea: Folia naturae Bihariae 33:25–38.

Venczel M. 2011. Middle-Late Miocene snakes from the Pannonian basin. Acta Palaeontologica Romaniae. 7:343–349.

Venczel M, Hír J. 2015. Lissamphibians and squamate reptiles from the early middle Miocene of Litke. Northern Hungary Geobios. 48:491–504.

Venczel M, Sanchíz B. 2006. Lower Miocene Amphibians and Reptiles from Oschiri (Sardinia, Italy). Hantkeniana. 5:72–75.

Venczel M, Ştiucă E. 2008. Late middle Miocene amphibians and squamate reptiles from Tauţ. Romania Geodiversitas. 30:731–763.

Venczel M, Hir J, Huza RR, Popa E, Golban G. 2005. A new Middle Miocene vertebrate fauna from Subpiatră (Bihor County, Romania). Nymphaea: Folia naturae Bihariae. 32:23–38.

von Meyer H. 1856. Letter on various fossil vertebrates. Neues Jahrb Geol Palaontol Abh. 1856:824–829.

Weithofer A. 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen [Contribution to the knowledge of the fauna of Pikermi in Athens]. Beiträge zur Paläontologie Österreich-Ungarns. 6:225–292.

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ARTICLE

# THE LAST EUROPEAN VARANID: DEMISE AND EXTINCTION OF MONITOR LIZARDS (SQUAMATA, VARANIDAE) FROM EUROPE

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ABSTRACT—Remains of a varanid lizard from the middle Pleistocene of the Tourkobounia 5 locality near Athens, Greece are described. The new material comprises cranial elements only (one maxilla, one dentary, and one tooth) and is attributed to *Varanus*, the genus to which all European Neogene varanid occurrences have been assigned. Previously, the youngest undisputed varanid from Europe had been recovered from upper Pliocene sediments. The new Greek fossils therefore constitute the youngest records of this clade from the continent. Despite being fragmentary, this new material enhances our understanding of the cranial anatomy of the last European monitor lizards and is clearly not referable to the extant *Varanus griseus* or *Varanus niloticus*, the only species that could be taken into consideration on a present-day geographic basis. However, these fossils could represent a survivor of the monitor lizards of Asian origin that inhabited Europe during the Neogene.

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## INTRODUCTION

Monitor lizards (Varanidae) constitute a diverse clade of squamates that inhabit Africa, southern continental Asia, the Philippines, Indonesia and adjacent islands, and Australia (Pianka et al., 2004). This clade contains more than 70 extant species, with new ones being frequently described (Doughty et al., 2014; Maryan et al., 2014; Weijola et al., 2016). Varanids range greatly in size and include the largest known terrestrial lizards ( = non-snake squamates), both extinct and extant (Pianka et al., 2004). Despite their wide extant distribution, their fossil record is sparse. The first varanids are identified with certainty in the early Eocene of western Europe. The clade is present there in the Paleogene and throughout the Neogene, whereas it has few, sporadic occurrences in the Paleogene of North America, the Paleogene, Neogene, and Quaternary of Africa and Asia, and the Neogene and Quaternary of Australia (Estes, 1983; Delfino et al., 2004; Pianka et al., 2004; Smith et al., 2008; Holmes et al., 2010). Although scarce, fossil varanids have been known since the middle of the 19th century (Gaudry, 1862). Their European pre-Pleistocene record is by far the most abundant, with specimens having been recovered from several localities across the continent (Fejérváry, 1918, 1935; Pianka et al., 2004; Delfino et al., 2013).

In this paper, we describe new varanid cranial material from the middle Pleistocene of Tourkobounia 5, near Athens, Greece, that represents the youngest record of Varanidae from Europe and confirms a longer survivorship and later extinction of monitor lizards on this continent.

**Institutional Abbreviations—MDHC**, Department of Earth Sciences, University of Turin, Turin, Italy; **MNCN**, Museo Nacional de Ciencias Naturales–CSIC, Madrid, Spain; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **SMF**, Senckenberg Museum, Frankfurt, Germany; **TMP**, Royal Tyrrell Museum, Drumheller, Alberta, Canada; **UU**, collection of the University of Utrecht; **ZFMK**, Zoologisches Forschungsmuseum Koenig, Bonn, Germany.

## MATERIALS AND METHODS

All varanid specimens described in this paper were found at the earliest middle Pleistocene locality of Tourkobounia 5, near Athens, Greece. They are part of the collection of the University of Utrecht. Comparative material of extant varanids was studied at MDHC, MNCN, MNHN, SMF, TMP, and ZFMK.

The following specimens of extant species of *Varanus* were studied: *Varanus acanthurus* (SMF 11639, SMF 11642, ZFMK 5225, ZFMK 54252), *Varanus albigularis* (SMF 11543, SMF 21573, SMF 26580, SMF 34049, SMF 40162, SMF 54758, ZFMK 5138, ZFMK 83428), *Varanus beccarii* (SMF 11637), *Varanus bengalensis* (MNHN 1883–1828, MNHN 1886–634, MNHN 1886–649, SMF 11550, SMF 11554, SMF 32956, SMF 40160, SMF 40179, SMF 60428, SMF 63456, SMF 71569, SMF 71570, TMP 85.16.5, TMP 90.7.360, ZFMK 14872, ZFMK14873, ZFMK 59018, ZFMK 70425), *Varanus caudolineatus* (SMF 40086), *Varanus cumingi* (SMF 11577, SMF 76293), *Varanus doreanus* (SMF 32290, ZFMK 83429), *Varanus dumerilii* (SMF 11556, TMP 90.7.271, TMP 90.7.272, TMP 90.7.362, SMF 11557, ZFMK 14876, ZFMK 14877), *Varanus eremius* (SMF 11648), *Varanus exanthematicus* (MDHC 335, MNHN 1910–7, MNHM 1952–132, SMF 11544, SMF 11545, SMF 33260, SMF 33261, SMF 40161, ZFMK 14884, ZFMK 17528, ZFMK 21652, ZFMK 38432, ZFMK 63663, ZFMK 63664, ZFMK 76976, ZFMK 76977), *Varanus flavescens*

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(MNHN 1964–51, SMF 11546, SMF 54157, ZFMK 14878, ZFMK 21653), *Varanus giganteus* (SMF 53263, ZFMK 14882, ZFMK 84341), *Varanus gilleni* (SMF 11627), *Varanus glebopalma* (ZFMK 54847), *Varanus gouldi* (SMF 11620, SMF 53276, SMF 59018, ZFMK 14885), *Varanus grayi* (SMF 72156), *Varanus griseus* (MNHN 1880–4, MNHN 1888–196, MNHN 1895–366, MNHN 1909–402, MNHN 1973–105, SMF 32911, SMF 33205, SMF 33206, SMF 33254, SMF 33255, SMF 33256, SMF 33257, SMF 33702, SMF 40163, SMF 70678, SMF 74486, SMF 79190, TMP 90.7.47, ZFMK 7848, ZFMK 14883, ZFMK 21657, ZFMK 53533), *Varanus indicus* (SMF 32180, TMP 90.7.45, ZFMK 14863, ZFMK 14864, ZFMK 14865, ZFMK 14866, ZFMK 14867, ZFMK 14881), *Varanus jobiensis* (SMF 75817), *Varanus komodoensis* (SMF 23189, SMF 37209, SMF 57555, SMF 57556, SMF 68133, ZFMK 64698), *Varanus marmoratus* (SMF 11571), *Varanus mertensi* (SMF 53275), *Varanus mitchelli* (ZFMK 54250), *Varanus niloticus* (MNCN 40853, MNHN 1887–909, MNHN 1909–20, MNHN 1921–260, MNHN 1921–260 bis, MNHN 1934–339, MNHN 1964–50, MNHN 2005–62, SMF 11615, SMF 11618, SMF 26579, SMF 32250, SMF 32909, SMF 33251, SMF 33252, SMF 33253, SMF 34427, SMF 46912, SMF 47171, SMF 53197, SMF 83055, SMF 83056, TMP 90.7.31, ZFMK 70424, ZFMK 14887, ZFMK 14888, ZFMK 21655, ZFMK 21656, ZFMK 7847), *Varanus ornatus* (SMF 36173, SMF 54117, ZFMK 14889, ZFMK 87629), *Varanus prasinus* (SMF 11626, SMF 69454, ZFMK 14868, ZFMK 14869, ZFMK 14870, ZFMK 14871, ZFMK 14874, ZFMK 14875, ZFMK 54845, ZFMK 54846, ZFMK 76978, ZFMK 7929), *Varanus rudicollis* (MNHN 1973-108, SMF 40207, SMF 59216, SMF 59239, SMF 59242, SMF 67586, TMP 90.7.361, ZFMK 5229, ZFMK 53534, ZFMK 54253), *Varanus salvator* (MNHN 1886–284, MNHN 1888–198, MNHN 1977–04, SMF 11563, SMF 32807, SMF 32908, SMF 33126, SMF 33127, SMF 33128, SMF 33129, SMF 33130, SMF 33131, SMF 33132, SMF 33133, SMF 33134, SMF 35148, SMF 40175, SMF 40176, SMF 40177, SMF 40178, SMF 66647, SMF 69440, SMF 72158, SMF 81057, SMF 86676, SMF 90068, TMP 90.7.221, TMP 90.7.223, TMP 90.7.269, TMP 90.7.273, TMP 90.7.274, ZFMK 14859, ZFMK 14860, ZFMK 14861, ZFMK 21651, ZFMK 70190, ZFMK 70205, ZFMK 70433, ZFMK 91955), *Varanus salvadorii* (SMF 57878, SMF 58064, SMF 67670, ZFMK 90996, ZFMK 90997), *Varanus semirex* (ZFMK 54247, ZFMK 54248, ZFMK 54249), *Varanus similis* (ZFMK 54251, ZFMK 59027), *Varanus spenceri* (SMF 53277), *Varanus storri* (ZFMK 14880, ZFMK 54848, ZFMK 54849), *Varanus timorensis* (TMP 90.7.38, ZFMK 14886, ZFMK 10000), *Varanus tristis* (SMF 11630), and *Varanus varius* (TMP 1997.030.0340).

## LOCALITY

Tourkobounia is a fossiliferous fissure fill near Athens, Greece, that consists of five distinct fossiliferous sites, namely, Tourkobounia 1, 2, 3, 4, and 5, spanning from the late Pliocene to the middle Pleistocene. Tourkobounia 1 comprises the oldest fauna, with a late Pliocene age (MN 16), Tourkobounia 2 is earliest early Pleistocene, whereas Tourkobounia 3, 4, and 5 are considered to pertain to the latest early to earliest middle Pleistocene (Symeonidis and de Vos, 1976; Symeonidis and Zapfe, 1976; Reumer and Doukas, 1985). The geological settings of the Tourkobounia locality were described in detail by Sindowski (1951), de Bruijn and van der Meulen (1975), and Symeonidis and de Vos (1976). A diverse micromammal fauna has been described from the middle Pleistocene site of Tourkobounia 5, comprising chiropterans, erinaceomorph and soricomorph eulipotyphlans, rodents, and lagomorphs, but macromammals are restricted to a felid and a cervid (Symeonidis and de Vos, 1976; Reumer and Doukas, 1985).

Among reptiles from Tourkobounia 5, only a few snakes have been briefly described to date. These include an indeterminate scolecophidian, the natricine *Natrix* sp., and the colubrines *Elaphe quatuorlineata* and *Zamenis longissimus* (Szyndlar, 1991a, 1991b). The herpetofauna from this fossil locality will be described elsewhere.

## SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768
SQUAMATA Oppel, 1811
VARANIDAE Gray, 1827 (sensu Estes et al., 1988)
*VARANUS* Merrem, 1820
*VARANUS* sp.
(Figs. 1, 2)

**Material**—UU TB5 1001, one right maxilla (Fig. 1); UU TB5 1002, one partial right dentary (Fig. 2A, B); UU TB5 1003, one isolated tooth (Fig. 2C, D).

## ANATOMICAL DESCRIPTION

**Right Maxilla**—The maxilla (UU TB5 1001) is fragmentary, lacking the anterior region (probably the region corresponding to the first three tooth positions) and the posterior tip (Fig. 1). The preserved part is moderately robust and 17 mm long. The facial process is not fully preserved, but its anterior, ascending edge develops a medial lamina that shows a distinct ventromedial fold. On the dorsal surface of this fold, there is a wide and slightly anteroposteriorly elongated vomeronasal foramen. The foramen is flanked laterally by a ridge-like structure (a lappet), which marks the dorsal edge of the medial lamina. Because it is broken, the degree of development of this lappet cannot be determined. Because of its presence, however, the vomeronasal foramen opens at the base of the medial side of the anterior premaxillary process. A very low ridge is also visible on the dorsal surface of the lateral margin of the same process. The palatal shelf is broken, but a large superior dental foramen is visible by the posterior end of the fragment. The contact between the ventromedial fold and the palatal shelf forms a large, posteriorly open cavity. Five complete tooth positions are preserved (a sixth position may have been present posteriorly). Two of them house well-preserved teeth. The most posterior position is occupied by the base of a third tooth. The most anterior, incomplete position bears a small basal portion of another tooth. The teeth are subpleurodont, elongated, conical, and pointed. Their tips are slightly posteromedially recurved and slightly labiolingually compressed, and their bases are slightly swollen lingually. Unserrated carinae are present on their anterior and posterior margins. Striations indicating infolding of dentine are present on the bases both lingually and labially. A spongy tissue connects the teeth to the alveolar portion of the maxilla. The longest tooth is roughly 4 mm in length. The lateral surface of the maxilla is smooth, with a row of six anteroposteriorly aligned ventrolateral foramina near the alveolar margin. Most foramina are small, but the posterior-most one is much larger than the others. Near the anterior end of the maxilla, a rather large foramen opens posterolaterally above the line of ventrolateral foramina.

**Right Dentary**—The fragmentary dentary (UU TB5 1002), lacking the anterior portion and the posterior processes (Fig. 2A, B), is 15.7 mm long. The Meckelian fossa is wide and entirely open medially. The subdental ridge is broken, and it is not possible to determine to what extent it originally covered the fossa. Four complete tooth positions and a partial anterior fifth are preserved. The bases of two teeth are preserved. They are connected to the bone by a spongy tissue and show striae on both the lingual and the labial surfaces. The posterior opening of the alveolar canal is located by the last tooth position, and the intramandibular septum continues posteriorly as a ridge fused to the wall of the Meckelian fossa. Although it is partially broken, the superior posterior process appears to bend distinctly dorsally.

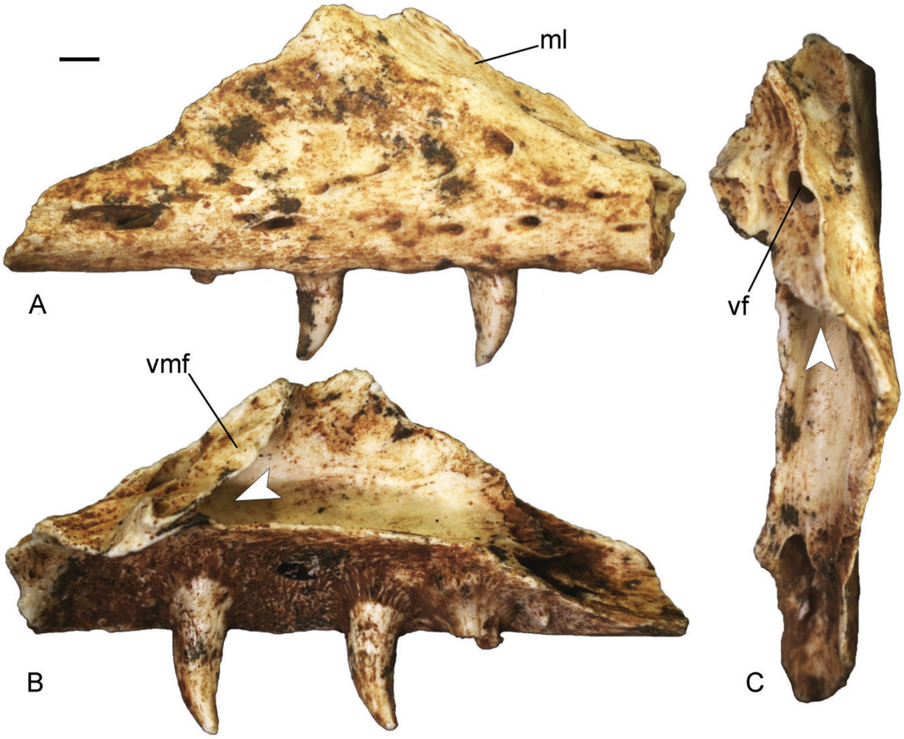

FIGURE 1. *Varanus* sp. Right maxilla (UU TB5 1001) in **A,** lateral, **B,** medial and **C,** dorsal views. White arrowheads mark the cavity between the ventromedial fold and the palatal shelf. **Abbreviations**: **ml**, medial lamina; **vf**, vomeronasal foramen; **vmf**, ventromedial fold. Scale bar equals 1 mm.

The lateral surface is smooth, with two large mental foramina. The ventral margin of the dentary is straight in medial view.

**Tooth**—The isolated tooth (UU TB5 1003) is subpleurodont, elongated, and conical, with a length of 3.9 mm (Fig. 2C, D). It has an enlarged base, a pointed tip, and sharp, unserrated carinae on both the anterior and posterior sides. The distal half of the tooth is labiolingually compressed, whereas the base is slightly swollen lingually. The latter portion shows distinct striae on both the labial and the lingual surfaces. The contact surface with the tooth-bearing bone is elliptical and oblique, showing a spongy structure.

## TAXONOMIC IDENTIFICATION

Trenchant and keeled or globular teeth, provided with spongy tissue for the connection with their tooth-bearing bone, and striation of the surface of the teeth near their base (indicating the presence of plicidentine, i.e., the infolding of the dentine and enamel at the basal portion of the tooth) are typical features of the clade Varanoidea (e.g., Estes, 1983; Bailon, 1991; Kearney and Rieppel, 2006; Pianka et al., 2004; Luan et al., 2009). Moreover, certain features of the new Greek material exclude its referral to the non-varanid varanoids (helodermatids, necrosaurids, and lanthanotids). In *Heloderma*, striae due to the development of plicidentine are less extended towards the tip of the teeth in comparison with *Varanus* (Kearney and Rieppel, 2006). In addition, the spongy tissue at the tooth base of helodermatids does not fully close the pulp cavity, as it does in *Varanus* and in the isolated tooth described herein (Kearney and Rieppel, 2006). In *Lanthanotus*, striae are less developed towards the tip, whereas the shapes of the teeth, maxilla, and the dentary are very different than those of the new fossil material (McDowell and Bogert, 1954; Kearney and Rieppel, 2006). In necrosaurids, the presence of plicidentine is highly probable, but the anatomy of the maxilla and the dentary, and dental shape, is distinct (Augé, 2005; Augé and Smith, 2009). Moreover, in terms of the

FIGURE 2. *Varanus* sp. Right dentary (UU TB5 1002) in **A**, medial and **B**, lateral views; isolated tooth (UU TB5 1003) in **C**, medial and **D**, labial views. Scale bars equal 1 mm.

European fossil record, lanthanotids are totally absent, whereas helodermatids and necrosaurids are confined strictly to the Paleogene (Rage, 2013). Within varanids, European fossils have only been attributed to the genera *Saniwa* and *Varanus*. The differentiation between the two is mostly based on stratigraphic rationale and osteological features of bones other than maxillae or dentaries, but a longer posterior process of the maxilla is generally present in *Saniwa* (Estes, 1983). In any case, members of *Saniwa* are completely absent from Europe after the Eocene (Augé, 2005), and *Varanus* is the only valid varanoid genus that has been reported from European Neogene localities to date (Delfino et al., 2013). *Varanus* is also the sole recognized genus of Quaternary and extant varanids (Pianka et al., 2004). Furthermore, the morphology of the Tourkobounia 5 specimens is consistent with attribution to *Varanus*, so the material can be confidently referred to this genus.

The morphology of the maxilla is different from that of the two extant species that could have potentially extended their range to Greece in the Middle Pleistocene: *Varanus niloticus* (Linnaeus, 1766) and *Varanus griseus* (Daudin, 1803). The former is characterized, along with all the other African taxa (*Varanus ornatus* Gray, 1845, *Varanus exanthematicus* Bosc, 1792, and *Varanus albigularis* Daudin, 1802), by posterior globular teeth in adult individuals (D'Amore, 2015), whereas *V. griseus*, among others, is characterized by the absence of the medial lamina that is clearly developed in UU TB5 1001 on the sloping anterior edge of the facial process. The presence of this lamina in UU TB5 1001 is congruent with that of the extinct *Varanus marathonensis* Weithofer, 1888, from the late Miocene of Pikermi (also near Athens), as well as that of several extant Asian taxa, but the preservational status and the poor knowledge of the osteology of extant species precludes any specific identification.

## DISCUSSION AND CONCLUSIONS

Varanids first appear in the European fossil record during the Eocene. They are totally absent from the Oligocene faunas of the continent and seem to appear again after the early Miocene (Rage, 2013). It remains plausible that these former European Paleogene varanids were victims of the 'Grande Coupure,' going extinct at the end of the Eocene and that the Miocene forms are the product of a younger wave of dispersal (Augé, 1993; Rage, 2013). On the basis of the available data, however, this cannot be demonstrated with certainty. In any case, all Neogene European varanids appear to be members of *Varanus*, and they seem to have dispersed into Europe around the early Miocene (Delfino et al., 2013; Čerňanský et al., 2015). In fact, the earliest evidence of the genus on the European continent is recorded in the early Miocene of Spain (Delfino et al., 2013). Whether these early Miocene immigrants originated directly from Africa (Holmes et al., 2010) or have Asian affinities (Conrad et al., 2012; Vidal et al., 2012; Rage, 2013) cannot be demonstrated with certainty. The occurrence of *Varanus*-like forms in the late Eocene and early Oligocene of Egypt (Smith et al., 2008; Holmes et al., 2010) favors an African origin, but the Asian record is too poor to offer any insights. The fact that the maxilla from Tourkobounia 5 does not show any relationship with extant African taxa (*V. albigularis*, *V. exanthematicus*, *V. griseus*, *V. niloticus*, *V. ornatus*) suggests Asian affinities, as already reported for the extinct *Varanus amnhophilis* Conrad et al., 2012, from the late Miocene of Samos (Conrad et al., 2012).

Whatever their exact origin may have been, *Varanus* spp. rapidly achieved a wide distribution throughout Europe during the Miocene. Fossils attributed to this genus have been described from localities in several countries, including Austria, Germany, Greece, Hungary, Italy, Moldova, Portugal, Romania, Spain, and Ukraine (Weithofer, 1888; Roger, 1898, 1900; Fejérváry, 1918, 1935; Hoffstetter, 1969; Antunes and Rage, 1974; Antunes and Mein, 1981; Lungu et al., 1983; Zerova and Chkhikvadze, 1986; Delfino, 2002; Hír and Venczel, 2005; Rage and Bailon, 2005; Venczel, 2005, 2006; Conrad et al., 2012; Delfino et al., 2013; Böhme and Vasilyan, 2014; Colombero et al., 2014; Venczel and Hír, 2015). During the Pliocene, there is an apparent contraction in their distribution, because described specimens are known only from Hungary (Bolkay, 1913; Fejérváry, 1918), France (Bailon, 1991; Bailon and Blain, 2007), and Spain (Sanz, 1977; Bailon, 1992). Reports of Pliocene varanids from Moldova and Ukraine (Zerova and Chkhikvadze, 1986) lack descriptions, figures, and collection numbers and are thus here excluded from consideration. Otherwise, the last reported occurrence of a varanid from the European continent is known from the late Pliocene (MN 16) of Beremend 1, Hungary, part of the type material of *Varanus deserticolus* (Bolkay, 1913; Rage, 2013). This taxon was established by Bolkay (1913) on the basis of fragments of a dentary and a vertebra. The vertebra, however, was later shown to belong to a large anguid (Fejérváry, 1918; Fejérváry-Lángh, 1923; Estes, 1983), whereas the dentary indeed has varanid affinities and was considered as being similar to *Varanus marathonensis* from the late Miocene of Pikermi (Fejérváry, 1918; Estes, 1983).

Outside Europe, the last reliable occurrence of a varanid from the northern part of the Mediterranean is known from the late Pliocene of Çalta, Turkey (Rage and Sen, 1976). This material has been attributed to the Miocene taxon *V. marathonensis* and pertains to a fairly large animal (about 2.5 m) (Rage and Sen, 1976). The available material from Çalta consists solely of vertebrae and as such cannot be directly compared with the Tourkobounia 5 varanid. The much smaller size of the Greek specimens may differentiate it from the older Çalta form, but the large foramina present in the former material could suggest a juvenile condition (see below), rendering the basis for such a taxonomic distinction equivocal.

There are two purported occurrences of varanids from the Pleistocene of Europe. The first supposed varanid is from the Late Pleistocene of Arene Candide, Italy (Morelli, 1891). The only known specimen is now considered lost (Delfino, 2002), and its identification as a varanid has been questioned multiple times (Estes, 1983; Holman, 1998; Delfino, 2002). Delfino (2002) noted that this fossil could belong to a large-sized *Timon*-like lacertid, but owing to some differences between the figured specimen and the standard lacertid lower jaw morphology, he preferred to consider it only as an undetermined lizard. We accept this view herein. The second purported European Pleistocene varanid is from the Middle Pleistocene of the Petralona cave, northern Greece. This specimen was initially mentioned as *Varanus* aff. *marathonis* (sic) by Sickenberg (1971), with Kretzoi and Poulianos (1981) referring to this as '*Varanus intermedius* Bolkay.' However, this material has never been formally described or figured, and no repository number has been given. Moreover, even the measurements of the supposed two specimens (vertebra: 270 mm; phalanx: 340 mm) are apparently erroneous. Even in terms of nomenclature, the Petralona specimen is problematic: Sickenberg (1971) constantly referred to it with an erroneous spelling of *V. marathonensis*, whereas Kretzoi and Poulianos (1981) apparently referred to what is actually *Ophisaurus intermedius* Bolkay, 1913, a large anguid, now considered a junior synonym of *Pseudopus pannonicus* (Fejérváry-Lángh, 1923; Estes, 1983). In any case, after personal investigation from one of us (GLG), we were not able to locate this purported varanid material in the collection where it is supposedly kept (Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki, Greece), and this occurrence is therefore herein considered as anecdotal.

Given that the two previously reported specimens can be disregarded, the Tourkobounia 5 specimens described herein represent the sole substantiated occurrence of varanids from the Pleistocene of Europe, indicating that this clade survived much longer in this region than previously thought. The documented restricted distribution of varanids during the European Pliocene clearly reveals that the clade was already in decline, and the absence of younger specimens had been used to infer a possible extinction by the end of that epoch (Bailon and Blain, 2007; Rage, 2013). Judging from their fossil record, it seems that Pliocene varanids were not restricted to the southern margins of Europe but were also present in the central portions of the continent (Hungary). The persistence of varanids in the Pliocene of both south and central Europe is thus consistent with that of other thermophilic taxa that occurred at that time in both regions, such as scolecophidians, erycine booids, and elapids (Rage, 2013). The new Greek *Varanus* shows that monitor lizards inhabited Europe at least until the middle Pleistocene. It thus seems that Pleistocene European varanids showed a southward contraction of their range, as is the case of other thermophilic taxa, such as agamids, the large anguid *Pseudopus*, amphisbaenians, scolecophidians, erycines, and 'Oriental vipers' (Szyndlar, 1991a; Delfino, 1997; Delfino et al., 2008; Georgalis et al., 2016). With the available data in hand, it is difficult to conclude with certainty whether climatic change was the only driving force behind the disappearance of varanids from Europe. Additional factors, such as interactions with other taxa (e.g., predation and competition), may have played a role in their final demise. It is worth noting that, although represented by very few remains possibly belonging to a single individual (the size of the maxilla and the dentary is comparable), the monitor lizard from Tourkobounia seems to be significantly smaller than *V. amnhophilis*, which was reported to reach more than 600 mm in snout-vent length, and *V. marathonensis*, both also known from cranial material (Fejérváry, 1918; Rage and Sen, 1976; Pianka et al., 2004; Conrad et al., 2012). Judging from the presence of a clearly developed medial lamina in the maxilla of the Tourkobounia 5 form, also observed in *V. marathonensis* (Weithofer, 1888), it seems plausible that they both belong to the same lineage. This considerable size reduction between the Miocene and the Pleistocene forms could be tentatively regarded as a survival adaptation of the last European monitor lizards, in an effort to face the lower temperatures of the Pleistocene, in comparison with those of their Neogene predecessors. Such size reduction after extinction events (known as the 'Lilliput effect'; Urbanek, 1993) has been observed in distantly related tetrapod clades (Smith, 1995; Tverdokhlebov et al., 2002). On the other hand, other European reptile clades are known to have reached considerably larger sizes during the Plio–Pleistocene, such as the anguid *Pseudopus pannonicus* (Klembara, 2012) and giant tortoises (Georgalis and Kear, 2013). Furthermore, the alternative possibility that the specimens described herein belong to a juvenile cannot be excluded. According to Evans (2008), a change in size of the nerve foramina is one of the major ontogenetic changes occurring in the lizard skull, with juveniles having larger foramina that separate into smaller ones during growth. The large foramina on the lateral surfaces of both the maxilla UU TB5 1001 and the dentary UU TB5 1002 could be interpreted as a juvenile condition. Only the discovery of more Pleistocene varanids from Europe will eventually resolve these questions.

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## LITERATURE CITED

Antunes, M. T., and P. Mein. 1981. Vertébrés du miocène moyen de Amor (Leiria)—importance stratigraphique. Ciências da Terra 6:169–188.

Antunes, M. T., and J.-C. Rage. 1974. Notes sur la géologie et la paléontologie du Miocène de Lisbonne. XIV: quelques Squamata (Reptilia). Boletim da Sociedade Geológica de Portugal 19:47–60.

Augé, M. 1993. Repartition et dynamisme des faunes de lacertilia et d'amphisbaenia dans l'Eocene Europeen. Palaeovertebrata 22:51–71.

Augé, M., 2005. Evolution des lézards du Paléogène en Europe. Publications Scientifiques du Muséum, Mémoires du Muséum national d'Histoire naturelle, Paris 192:1–369.

Augé, M., and R. Smith. 2009. An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene–Oligocene transition. Zoological Journal of the Linnean Society 155:148–170.

Bailon, S. 1991. Amphibiens et reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes. Doctoral dissertation, Université de Paris VII, Paris, France, 499 pp.

Bailon, S. 1992. Escamosos (Reptilia) fósiles del yacimiento de Moreda (Plioceno medio/superior, Granada). Revista Española de Paleontología, Extra 7(Suppl 3):11–15.

Bailon, S., and H.-A. Blain. 2007. Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pléistocène. Quaternaire 18:55–63.

Böhme, M., and D. Vasilyan. 2014. Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). Palaeobiodiversity and Palaeoenvironments 94:21–40.

Bolkay, J. 1913. Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. Mittheilungen aus dem Jahrbuche der königlichen Ungarischen geologischen Reichsanstalt 21:217–230.

Bosc, L. 1792. *Lacerta exanthematica*. Actes de la Société d'Histoire Naturelle de Paris 1:1–25.

Bruijn, H. de, and A. J. van der Meulen. 1975. The Early Pleistocene rodents from Tourkobounia-1 (Athens, Greece) I and II. Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B 78:314–338.

Čerňanský, A., J.-C. Rage, and J. Klembara. 2015. The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. Journal of Systematic Palaeontology 13:97–128.

Colombero, S., C. Angelone, E. Bonelli, G. Carnevale, O. Cavallo, M. Delfino, P. Giuntelli, P. Mazza, G. Pavia, M. Pavia, and G. Repetto. 2014. The Messinian vertebrate assemblages of Verduno (NW Italy): another brick for a latest Miocene bridge across the Mediterranean. Neues Jahrbuch für Geologie und Paläontologie, Monatschefte 272:287–234.

Conrad, J. L., A. M. Balcarcel, and C. M. Mehling. 2012. Earliest example of a giant monitor lizard (*Varanus*, Varanidae, Squamata). PLoS ONE 7:e41767.

D'Amore, D. C. 2015. Illustrating ontogenetic change in the dentition of the Nile monitor lizard, *Varanus niloticus*: a case study in the application of geometric morphometric methods for the quantification of shape–size heterodonty. Journal of Anatomy 226:403–419.

Daudin, F. 1802. Histoire Naturelle, Générale et Particulière des Reptiles; ouvrage faisant suit à l'Histoire naturelle générale et particulière, composée par Leclerc de Buffon; et rédigee par C.S. Sonnini, membre de plusieurs sociétés savantes, vol. 4. F. Dufart, Paris, 397 pp.

Daudin, F. 1803. Histoire Naturelle des Reptiles, vol. 8. F. Dufart, Paris, 439 pp.

Delfino, M. 1997. *Blanus* from the early Pleistocene of southern Italy: another small tessera from a big mosaic; pp. 89–97 in I. W. Böhme, W. Bischoff, and T. Ziegler (eds.), Herpetologica Bonnensis. SEH, Bonn, Germany.

Delfino, M. 2002. Erpetofaune italiane del Neogene e del Quaternario. Doctoral Thesis, University of Modena and Reggio Emilia, Modena and Reggio Emilia, Italy, 382 pp.

Delfino, M., J.-C. Rage, A. Bolet, and D. M. Alba. 2013. Early Miocene dispersal of the lizard *Varanus* into Europe: reassessment of vertebral material from Spain. Acta Palaeontologica Polonica 58:731–735.

Delfino, M., T. Kotsakis, M. Arca, C. Tuveri, G. Pitruzzella, and L. Rook. 2008. Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiversitas 30:641–656.

Delfino, M., A. Segid, D. Yosief, J. Shoshani, L. Rook, and Y. Libsekal. 2004. Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression). Rivista Italiana di Paleontologia e Stratigrafia 110:51–60.

Doughty, P., L. Kealley, A. Fitch, and S. C. Donnellan. 2014. A new diminutive species of *Varanus* from the Dampier Peninsula, western Kimberley region, Western Australia. Records of the Western Australian Museum 29:128–140.

Estes, R. 1983. Sauria Terrestria, Amphisbaenia. Encyclopedia of Paleoherpetology, Part 10a. Gustav Fisher Verlag, Stuttgart and New York, 249 pp.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata; pp. 99–118 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L Camp. Stanford University Press, Stanford, California.

Evans, S. E. 2008. The skull of lizards and tuatara; pp. 1–347 in C. Gans, A. S. Gaunt, and K. Adler (eds.), Biology of the Reptilia, Volume 20, The Skull of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Fejérváry, G. J. de. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. Annales Musei Nationales Hungarici, Pars Zoologica 16:341–467.

Fejérváry, G. J. de. 1935. Further contributions to a monograph of the Megalanidae and Fossil Varanidae, with notes on recent varanians. Annales Musei Nationales Hungarici, Pars Zoologica 29:1–130.

Fejérváry-Lángh, A. M. 1923. Beiträge zu einer Monographie der fossilen Ophisaurier. Palaeontologia Hungarica 1:123–220.

Gaudry, A. 1862. Note sur les débris d'oiseaux et de reptiles trouvés à Pikermi, Grèce, suivie de quelques remarques de paléontologie générale. Bulletin de la Société Géologique de France 19:629–640.

Georgalis, G. L., and B. P. Kear. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46:299–311.

Georgalis, G. L., Z. Szyndlar, B. P. Kear, and M. Delfino. 2016. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109:103–116.

Gray, J. E. 1827. A synopsis of the genera of saurian reptiles, in which some new genera are indicated and others reviewed by actual examination. The Philosophical Magazine, or Annals of Chemistry, Mathematics, Astronomy, Natural History, and General Science 2:54–58.

Hír, J., and M. Venczel. 2005. New middle Miocene vertebrate localities from Subpiatră (Bihor District, Romania). Acta Palaeontologica Romaniae 5:211–221.

Hoffstetter, R. 1969. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. Bulletin du Muséum National d'Histoire Naturelle 40:1051–1064.

Holman, A. J. 1998. Pleistocene Amphibians and Reptiles in Britain and Europe. Oxford University Press, New York, 254 pp.

Holmes, R. B., A. M. Murray, Y. S. Attia, E. L. Simons, and P. Chatrath. 2010. Oldest known *Varanus* (Squamata: Varanidae) from the Upper Eocene and Lower Oligocene of Egypt: support for an African origin of the genus. Palaeontology 53:1099–1110.

Kearney, M., and O. Rieppel. 2006. An investigation into the occurrence of plicidentine in the teeth of squamate reptiles. Copeia 2006:337–350.

Klembara, J. 2012. A new species of *Pseudopus* (Squamata, Anguidae) from the early Miocene of Northwest Bohemia (Czech Republic). Journal of Vertebrate Paleontology 32:854–866.

Kretzoi, M., and N. Poulianos. 1981. Remarks on the middle and lower Pleistocene vertebrate fauna in the Petralona Cave. Anthropos (Athens) 8:57–72.

Laurenti, J. N. 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu. Joan Thomae, Vienna, 217 pp.

Luan, X., C. Walker, S. Dangaria, Y. Ito, R. Druzinsky, K. Jarosius, H. Lesot, and O. Rieppel. 2009. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontium. Evolution & Development 11:247–259.

Lungu, A. N., G. A. Zerova, and V. M. Chkhikvadze. 1983. [Primary evidence on the Miocene *Varanus* of the North Black Sea litoral]. Bulletin of the Academy of Sciences of the Georgian SSR 110:417–420. [Russian, with English summary]

Maryan, B., P. M. Oliver, A. J. Fitch, and M. O'Connell. 2014. Molecular and morphological assessment of *Varanus pilbarensis* (Squamata: Varanidae), with a description of a new species from the southern Pilbara, Western Australia. Zootaxa 3768:139–158.

McDowell, S. B., and C. M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of anguinomorphan lizards. Bulletin of the American Museum of Natural History 105:1–142.

Merrem, B. 1820. Versuch eines Systems der Amphibien, vol. 8. J. C. Krieger, Marburg, 189 pp.

Morelli, N. 1891. Resti organici rinvenuti nella caverna delle Arene Candide presso Finalmarina. Atti della Società Ligustica di Scienze Naturali e Geografiche 2:171–205.

Oppel, M. 1811. Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, Munich, 86 pp.

Pianka, R. E., D. King, and R. A. King. 2004. Varanoid Lizards of the World. Indiana University Press, Bloomington, Indiana, 587 pp.

Rage, J.-C. 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments 93:517–534.

Rage, J.-C., and S. Bailon. 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). Geodiversitas 27:413–441.

Rage, J.-C., and S. Sen. 1976. Les amphibiens et les reptiles du Pliocène supérieur de Çalta (Turquie). Géologie méditerranéenne 3:127–134.

Reumer, J. W. F., and C. S. Doukas. 1985. Early Pleistocene Insectivora (Mammalia) from Tourkobounia (Athens, Greece). Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B 88:111–121.

Roger, O. 1898. Wirbelthierreste aus dem Dinotheriensande, II. Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg (a. V.) in Augsburg 33:385–396.

Roger, O. 1900. Wirbelthierreste aus dem Dinotheriensande, III. Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg (a. V.) in Augsburg 34:53–70.

Sanz, J. 1977. Presencia de *Varanus* (Sauria, Reptilia) en el Plioceno de Layna (Soria). Trabajos sobre Neogeno-Cuaternario 8:113–125.

Sickenberg, O. 1971. Revision der Wirbeltierfauna der Höhle Petralona. Annales Géologiques des Pays Hélleniques 23:230–264.

Sindowski, K. H. 1951. Zur Geologie des Lykabettos-Turkowuni-Gebietes bei Athen, mit einem Beitrag über frühdiluviale Wirbeltierfunde aus Spalten. Annales Géologiques des Pays Hélleniques 3:11–21.

Smith, K. T., B.-A. S. Bhullar, and P. A. Holroyd. 2008. Earliest African record of the *Varanus* stem-clade (Squamata: Varanidae) from the early Oligocene of Egypt. Journal of Vertebrate Paleontology 28:909–913.

Smith, R. M. H. 1995. Changing fluvial environments across the Permian–Triassic boundary in the Karoo Basin, South Africa, and possible causes of tetrapod extinctions. Palaeogeography, Palaeoclimatology, Palaeoecology 117:81–104.

Symeonidis, N. K., and J. de Vos. 1976. Großsäugerfunde aus den plistozänen Spaltenfüllungen von Turkovunia in Athen. Annales Géologiques des Pays Hélleniques 28:135–144.

Symeonidis, N., and H. Zapfe. 1976. Primatenzahne (Cercopithecidae) aus einer Pleistozänen Spaltenfullung im Steibruch Tourkobounia, Athen. Annales Géologiques des Pays Hélleniques 28:207–214.

Szyndlar, Z. 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos 47:103–126.

Szyndlar, Z. 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estudios Geológicos 47:237–266.

Tverdokhlebov, V. P., G. I. Tverdokhlebova, M. V. Surkov, and M. J. Benton. 2002. Tetrapod localities from the Triassic of the SE of European Russia. Earth Science Reviews 60:1–66.

Urbanek, A. 1993. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. Historical Biology 7:29–50.

Venczel, M. 2005. A new Middle Miocene vertebrate fauna from Subpiatră. Nymphaea, Folia naturae Bihariae 32:23–38.

Venczel, M. 2006. Lizards from the Late Miocene of Polgárdi (W. Hungary). Nymphaea, Folia naturae Bihariae 33:25–38.

Venczel, M., and J. Hír. 2015. Lissamphibians and squamate reptiles from the early middle Miocene of Litke, Northern Hungary. Geobios 48:491–504.

Vidal, N., J. Marin, J. Sassi, F. U. Battistuzzi, S. Donnellan, A. J. Fitch, B. G. Fry, F. J. Vonk, R. C. Rodriguez de la Vega, A. Couloux, and S. B. Hedges. 2012. Molecular evidence for an Asian origin of monitor lizards followed by Tertiary dispersals to Africa and Australasia. Biology Letters 8:853–855.

Weijola, V., S. C. Donnellan, and C. Lindqvist. 2016. A new blue-tailed Monitor lizard (Reptilia, Squamata, *Varanus*) of the *Varanus indicus* group from Mussau Island, Papua New Guinea. ZooKeys 568:129–154.

Weithofer, A. 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. Beiträge zur Paläontologie Österreich-Ungarns 6:225–292.

Zerova, G. A., and V. M. Chkhikvadze. 1986. Neogene varanids of the USSR; pp. 689–694 in Z. Roček (ed.), Studies in Herpetology. Charles University of Prague, Prague, Czech Republic.

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# First fossil find of the *Blanus strauchi* complex (Amphisbaenia, Blanidae) from the Miocene of Anatolia

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Worm lizards (Amphisbaenia) constitute a bizarre and specialized clade of mostly limbless, burrowing reptiles and whose exact affinities within other squamates have not yet been fully resolved, with different phylogenetic topologies arising on the basis of external morphology and/or skeletal anatomy (Estes et al., 1988; Kearney, 2003; Conrad, 2008; Gauthier et al., 2012), molecular data (Townsend et al., 2004; Vidal and Hedges, 2009; Pyron et al., 2013; Reeder et al., 2015), and fossil finds (Müller et al., 2011; Čerňanský et al., 2015a; Tałanda, 2016), with a sister group relationship with lacertids seeming probable (Townsend et al., 2004; Vidal and Hedges, 2005; Müller et al., 2011; Čerňanský et al., 2015a). *Blanus* is an amphisbaenian genus, long placed within Amphisbaenidae, until being recently reallocated in its own family, Blanidae, by Kearney (2003) who further suggested a basal position within Amphisbaenia as a whole. The genus currently comprises eight extant species, all limbless forms, with a rather disjunct circum-Mediterranean distribution (Sindaco and Jeremčenko, 2008). Two species complexes are currently recognized, a western one, the *Blanus cinereus* complex, distributed in the Iberian Peninsula and northwestern Africa (Albert et al., 2007; Albert and Fernández, 2009), and an eastern one, the *Blanus strauchi* complex, distributed in southern Anatolia, some islands of the Aegean Sea, and parts of Iraq, Syria, Lebanon, and Israel (Sindaco et al., 2014). This disjuct distribution of extant *Blanus* is apparently the relic of a much wider distribution, as it is revealed from fossils attributed to blanids originating from different European localities dating as back as the early Eocene (Augé, 2005, 2012; Folie et al., 2013) and continuing until the Quaternary (Delfino, 1997, 2003). As far as it concerns the genus *Blanus*, its earliest occurrence is represented by the type material of *Blanus thomaskelleri* Čerňanský, Rage and Klembara, 2015b, from the early Miocene (MN 2, Aquitanian) of Amöneburg, Germany, whereas additional finds from Oschiri, Sardinia, Italy, referred by Venczel and Sanchiz (2006) to *Blanus gracilis* (Roček, 1984), could be even older as age estimations of the latter locality range between MN 1 and MN 5. Whereas fossils of *Blanus* are relatively common in central and western Europe (Bolet et al., 2014), they appear to be absent from the eastern Mediterranean region. Indeed, as it concerns the Iberian *Blanus cinereus* complex, its fossil remains are well known and are readily identifiable (Blain et al., 2007), but this is not the case for *B. strauchi* complex, fossils of which were up to now totally unknown (Villa et al., 2017). Furthermore, blanids can only be identified in the fossil record on the basis of cranial remains, as amphisbaenian vertebrae, which are frequently found in the European Neogene, cannot be identified with certainty to the family level (Estes, 1983; but see Augé [2012] for vertebrae of certain Paleogene amphisbaenians). The only two up to now published records of fossil amphisbaenians from the eastern Mediterranean are based exclusively on vertebrae remains and originate from the Miocene of Plakias, Greece (Georgalis et al., 2016b) and the Pliocene of Çalta, Turkey (Rage and Sen, 1976). As such, although on the basis of a biogeographic rationale these two records probably belong to blanids, no such assignment can be made with certainty, especially regarding the fact that the latter material was never figured or adequately described. Here we describe a cranial element from the middle Miocene locality of Gebeceler, Turkey, that corresponds to the first fossil find of a member of the *Blanus strauchi* complex and the sole confirmed fossil occurrence of the genus *Blanus* in the eastern Mediterranean region.

**Institutional Abbreviations**— **EUNMH PV,** Natural History Museum of Ege University in Izmir, Turkey; **MNCN,** Museo Nacional de Ciencias Naturales, Madrid, Spain; **NHMC,** Natural History Museum of Crete, Herakleion, Greece; **NHMW,** Naturhistorisches Museum Wien, Vienna, Austria.

## MATERIALS AND METHODS

The amphisbaenian dentary described herein originates from the middle Miocene locality of Gebeceler, Turkey. The material is permanently housed at the collections of the EUNMH PV and is accessioned under the number 17151. Comparative skeletal material of extant blanid specimens include specimens housed in the collections of MNCN, NHMC, and NHMW, as also published figures in Schleich (1985), Folie et al. (2013), and Bolet et al. (2014).

Figure 1. Map of Turkey and nearby regions, indicating the range of the extant *Blanus strauchi* complex (circles) and the fossil locality of Gebeceler (star). The distribution of extant taxa follows Tok et al. (2012) and Sindaco et al. (2014).

## LOCALITY

Gebeceler Formation characterizes a middle Miocene continental deposition situated at the Afyon region (western Turkey) (Fig. 1). The Formation is composed of alluvial deposits at its base that grade upwards into volcanosedimentary lacustrine sediments. It comprises syn-sedimentary volcanoclastic units of alkaline volcanism and ends to a silicified limestone facies with a 40 meter thickness. At the basement of the lacustrine unit, the Gebeceler fossil locality is exposed, characterized by fine clastics that represent lacustrine shore-zone sedimentation. The greenish, massive sandstone-claystone level has yielded a local mammalian fauna, consisting of the rhinocerotid *Hispanotherium grimmi*, the equid *Anchitherium* sp., and the ruminants *Triceromeryx* sp. and *Micromeryx flourensianus* (Saraç, 2003). Recently, the fauna was revised by Mayda et al. (2013) with the rhinocerotid and ruminant remains being subsequently attributed to *Caementodon* cf. *caucasicum*, a new species of *Giraffokeryx*, and *Hispanomeryx* sp. respectively, and a new spalacid record, *Sinapospalax* cf. *berdikensis*, was added. The latter micromammal from Gebeceler provides further support for assigning the age of the locality to the late MN 6 or most probably to the base of MN 7/8 zones. This is also in agreement with the age of the Susuz-Yaylacılar locality (MN 7/8) (Sickenberg et al., 1975), which is located at the upper levels of the Gebeceler Formation.

## SYSTEMATIC PALAEONTOLOGY

### REPTILIA Laurenti, 1768
### SQUAMATA Oppel, 1811
### AMPHISBAENIA Gray, 1844

### BLANIDAE Kearney, 2003
### *BLANUS* Wagler, 1830
### *BLANUS STRAUCHI* (Bedriaga, 1884)
### *Blanus* cf. *strauchi*
(Fig. 2)

**Material—** EUNMH PV-17151, one right dentary (Fig. 2).

**Description—** EUNMH PV-17151 represents a right dentary. The specimen is relatively small, with a maximum length of 3.6 mm. Its anteriormost portion, including the edge of the symphysis is not preserved. The dentary bears six complete teeth, one other incomplete tooth, but it seems that there is also one other tooth position in the anterior part of the specimen. As such, the total number of teeth should equal to eight. Dentition is subpleurodont and highly heterodont, with all teeth differing between each other in terms of shape, height and base diameter. The second preserved tooth (occupying the third tooth position in life), which is not complete, seems to have been large, judging from the diameter of its base. All teeth are monocuspid, conical, robust, slightly recurved, though not all of them at the same degree, and bear no striations. The apices of the teeth are orientated dorsally. The fifth preserved tooth (the sixth in life) is the largest and most robust. The posteriormost tooth is the smallest one. Resorption pits are present and are circular in shape. The dentary heightens posteriorly. The coronoid process is not preserved and therefore, its extent cannot be assessed but on the basis of the curvature of the coronoid facet, which is also incomplete, it does not seem to have been high. In lingual view, the Meckel's groove is fully open, relatively narrow in the anterior part of the dentary but wide at the posterior part (after the fifth preserved tooth), and forms a narrow groove that runs parallel to the ventral border of the bone. The interdental distance is relatively large (as is common for *Blanus strauchi* and the extinct *Blanus gracilis*), with the exception of the first two preserved teeth which are rather closely spaced. Above the Meckel's groove, there is a rather prominent and thickened subdental shelf (sensu Rage and Augé, 2010), that only narrows at the level of the posteriormost tooth and its ventral margin is relatively curved, especially at the level of the fifth preserved tooth. There is an acute angle formed between the ventral margins of the dentary and the posterior portion of the symphysis. The ventral margin of the dentary is relatively concave. The intramandibular septum is preserved. In labial view, there are two

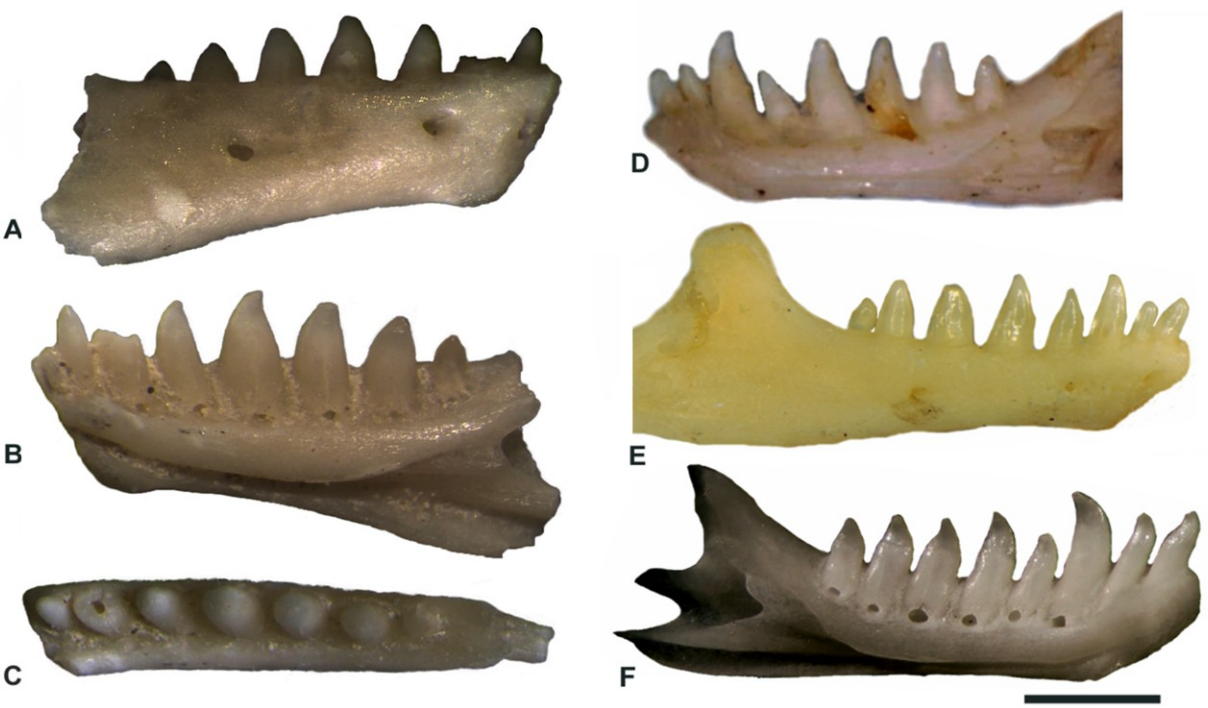

Figure 2. Dentaries of extinct and extant *Blanus* spp. **A, B, C,** right dentary (EUNMH PV-17151) of *Blanus* cf. *strauchi* from the middle Miocene of Gebeceler, Turkey, in labial **(A)**, lingual **(B)**, and dorsal **(C)** views; **D,** right dentary (NHMC 80.3.111.24) of an extant, freshly dissected, *B. strauchi* from Nisyros Island, Greece, in lingual view; **E,** right dentary (NHMW 18352:7) of an extant *B. strauchi* from Dodurga, Turkey, in labial view; **F,** left dentary (MNCN 16533) of an extant *B. cinereus* from San Agustín de Guadalix, Madrid, Spain, in lingual view. Scale bar represents 1 mm.

rather enlarged labial foramina, one at the level of the interdental gap between the second and third preserved teeth, the other at the level of the interdental gap between the fifth and the sixth ones. An additional, poorly preserved labial foramen seems also to be probably present just anterior to the level of the first preserved tooth. In dorsal view, the dentary is slightly convex labially. The sulcus dentalis is not much expanded medially.

## DISCUSSION

The Gebeceler dentary can be safely attributed to *Blanus* on the basis of the shape of the teeth (conical, robustly built and slightly recurved, with their apices orientated dorsally) and the low number of teeth (probably eight), of which the third one is enlarged, all features characteristic of the genus (Gans and Montero, 2008; Bolet et al., 2014; Čerňanský et al., 2015b).

Eight fossil taxa have been attributed to Blanidae, all from the European continent. The early Eocene taxon *Blanosaurus primeocaenus* Folie, Smith and Smith, 2013, from Belgium and France, and the middle Eocene *Cuvieribaena carlgansi* Čerňanský, Augé and Rage, 2015a, and *Louisamphisbaena ferox* Augé, 2012, both from France, have been suggested to represent the earliest named blanids (Augé, 2012; Folie et al., 2013; Čerňanský et al., 2015a), extending the fossil record of the clade well back into the Paleogene. Furthermore, the Paleogene record of the group appears not to be confined to these two taxa, as it can be judged by several other finds across the Eocene of France (Augé, 2012) and Spain (Bolet and Evans 2013), and the Oligocene of France (Rage and Augé 2015) and Germany (Schleich, 1988; Čerňanský et al. 2016). Whether these Paleogene forms belong indeed to blanids, however, remains to be tested only on the basis of more complete material and an extensive phylogenetic analysis that will include multiple fossil amphisbaenians. During the Neogene, blanids appear to have been diverse, especially across the Miocene. Named forms include: *Blanus antiquus* Schleich, 1985, from the middle Miocene of Austria, France, and Germany (Schleich, 1985; Böhme, 1999; Miklas-Tempfer, 2003), *Blanus gracilis* (Roček, 1984) from the early Miocene of The Czech Republic and Italy (Roček, 1984; Venczel and Sanchiz, 2006), *Blanus mendezi* Bolet, Delfino, Fortuny, Almécija, Robles, and Alba, 2014, from the middle Miocene of Spain (Bolet et al., 2014), *Blanus thomaskelleri* Čerňanský, Rage and Klembara, 2015b, from the early Miocene of Germany and The Czech Republic (Čerňanský et al., 2015b), and *Palaeoblanus tobieni* Schleich, 1988, from the early Miocene of Germany (Schleich, 1988). The new Gebeceler blanid described herein appears to be quite distinct from the Paleogene taxa in terms of general shape, robustness of teeth, and curvature of the ventral margin of the dentary, and besides, lacks the amblyodont dentition and the increasing size of teeth towards the symphysis, features that are characteristic of *C. carlgansi*. Among the Miocene taxa, resemblance is more notable. However, the new Anatolian form can be readily differentiated from *Palaeoblanus tobieni*, as in the latter taxon the first tooth is the most enlarged and bears dorsoventral slopes on its tooth crowns (Schleich, 1988; Čerňanský et al., 2015b). In comparison with *Blanus antiquus* and *Blanus mendezi*, it can be distinguished mostly by the shape of teeth, the thickness of the subdental shelf, size of interdental gaps, and different degree of heterodonty. In terms of size, the Gebeceler form approaches mostly *Blanus gracilis*, which is characterized by a rather small dentary size (Roček, 1984). This fact is further interesting, taking into consideration that the latter species was considered as the probable sister group of *Blanus strauchi* by Bolet et al. (2014). The geographically most proximal fossil blanid to our new find is the material described as *Blanus* cf. *gracilis* from the middle Miocene of Romania (Venczel and Ştiucă, 2008). This is also distinct from EUNMH PV-17151 in terms of thickness of the subdental shelf, curvature of the ventral margin of the dentary, and shape of teeth, although these characters may be related to intraspecific variability. Referral of blanid material from the early Pleistocene Apulia, southern Italy, to *Blanus* cf. *strauchi* by Holman (1998) was soon after shown to be erroneous by Delfino and Bailon (2000) who described in detail and figured that material. As far as it concerns the extant taxa, EUNMPH PV-17151 can only be provisionally differentiated from *Blanus strauchi* by its higher robustness of its teeth, thicker subdental shelf, and a more recurved ventral margin of the dentary, and from *Blanus cinereus* by different shape and curvature of teeth, a larger interdental gap, and a more opened Meckel's groove at the posterior part of the dentary (Fig. 2). Nevertheless, these differences should be taken with caution, as there is large variability observed within extant blanids, and moreover, dentaries appear to have less diagnostic characters in comparison with maxillae (Bolet et al., 2014). Indeed, features such as the shape, curvature, robustness, and number of dentary teeth appear to be highly variable in extant *Blanus* spp., with different tooth counts observed, ranging between seven and even nine (Bailon, 1991; Čerňanský and Venczel, 2011; Bolet et al., 2014). Besides, a splenial is not present in the new Anatolian fossil, however, this element has been occasionally observed in certain specimens of *Blanus cinereus* (e.g. Blain et al., 2007) and as such, this feature is subjected to individual variation and has no taxonomic utility. Furthermore, the splenial is usually an easily disarticulated bone, and as such, its absence from a specimen should not account for a genuine absence from that individual in life. The coronoid process, a feature that has often been used to diagnose extinct taxa (e.g. Roček 1984; Čerňanský et al., 2015b), is not preserved in the Anatolian specimen.

The new fossil find described herein originates from a locality that is only situated few kilometers outside the known geographic range of the extant *Blanus strauchi* complex in Anatolia (Fig. 1). It is worth noting that a significant amount of cryptic variation has been observed in this complex (as is also the situation in the *Blanus cinereus* complex) and as such it has recently been split by Sindaco et al. (2014) into distinct species: the nominal species *Blanus strauchi* (Bedriaga, 1884) (with two subspecies, *Blanus strauchi strauchi* and *Blanus strauchi bedriagae* [Boulenger, 1884]), distributed in western and southwestern Anatolia and certain islands of the eastern Aegean Sea (Samos, Fournoi, Leros, Kos, Symi, Pserimos, Telendos, Nisyros, Rhodes, and Kastellorizon), *Blanus aporus* Werner, 1898, distributed in southcentral and southeastern Anatolia, and *Blanus alexandri* Sindaco, Kornilios, Sacchi, and Lymberakis, 2014, from southeastern Anatolia and parts of Syria, Iraq, and maybe Israel (Sindaco et al., 2014). Nevertheless, these taxa were defined solely on the basis of molecular data and/or external morphology, and their skeletal differentiation (if any exists) is not known. Regarding the great extent of variability observed in both extant and extinct blanids that was discussed above, we are here reluctant in naming EUNMPH PV-17151 as a new taxon, and considering its overall resemblance with the extant members of the *Blanus strauchi* complex, and using also a biogeographic rationale, we refer this specimen to *Blanus* cf. *strauchi*. Of course, we denote here that the assignment of this Miocene specimen as *Blanus* cf. *strauchi* does not necessarily indicate that the fossil form has closer affinities with *Blanus strauchi* sensu stricto than with its cryptic Anatolian congeners *B. aporus* and *B. alexandri*. Rather than that, we use this taxonomic allocation as a convenience for denoting assignment of the fossil material to the *Blanus strauchi* complex.

The new *Blanus* from Gebeceler confirms the presence of the *B. strauchi* complex in Anatolia as back as at least the middle Miocene (MN 6 or MN 7/8), and further represents the sole verified occurrence of the genus in the eastern Mediterranean. Additionally, the new find represents the only Miocene squamate currently described from Turkey, with the only exception of recently reported anguid finds (Čerňanský et al., 2017). Frustratingly, the scarceness of fossil squamate material from Anatolia and the southern Balkans hinders our understanding of the palaeobiogeography of Blanidae. The wide distribution of *Blanus* spp. in central Europe during the early and middle Miocene is contradicted by the modern disjunct geographic range of the genus; however, the recent find of *B. mendezi* in the middle Miocene of Spain (Bolet et al., 2014), along with the new middle Miocene Turkish *Blanus* described herein, both confirm a much wider distribution and reveal that the present range of the genus was already inhabited by at least as back as that time. In any case, a post-Miocene southward constriction of the blanid geographic range, as has been variously suggested (e.g. Delfino, 2003), is also supported here, and is reminiscent of the case of certain other European reptile clades, such as agamids, large-sized anguids, scolecophidians, booids, “Oriental vipers”, geoemydids, giant testudinids, and pan-trionychids (Szyndlar, 1991; Bailon and Blain, 2007; Chesi et al., 2007; Delfino et al., 2008; Georgalis and Kear, 2013; Rage, 2013; Georgalis et al., 2016a, 2017; Georgalis and Joyce, 2017). More fossil squamates from Anatolia are definitely needed in order to clarify palaeobiogeographic assumptions, as this region has repeatedly acted as a “refugium” for multiple reptile groups, a fact also suggested by its current herpetofaunal synthesys and molecular data (Kornilios et al., 2011).

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## LITERATURE CITED

Albert, E. M., and A. Fernández. 2009. Evidence of cryptic speciation in a fossorial reptile: description of a new species of *Blanus* (Squamata: Amphisbaenia: Blanidae) from the Iberian Peninsula. Zootaxa 2234:56–68.

Albert, E.M., R. Zardoya, and M. García-París. 2007. Phylogeographical and speciation patterns in subterranean worm lizards of the genus *Blanus* (Amphisbaenia: Blanidae). Molecular Ecology 16:1519–1531.

Augé, M. 2005. Evolution des lézards du Paléogène en Europe. Publications Scientifiques du Muséum, Mémoires du Muséum national d'Histoire naturelle, Paris 192:1–369.

Augé, M. 2012. Amphisbaenians from the European Eocene: a biogeographical review. Palaeobiodiversity and Palaeoenvironments 92:425–443.

Bailon, S. 1991. Amphibiens et reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes. Doctoral thesis, Université de Paris VII, Paris, France.

Bailon, S., and H.-A. Blain. 2007. Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pléistocène. Quaternaire 18:55–63.

Bedriaga, J. 1884. Nachträgliche Bemerkung über *Amphisbaena strauchi* v. Bedr. Zoologischer Anzeiger 7:346.

Blain, H.-A., S. Bailon, and J. Agusti. 2007. Anurans and squamate reptiles from the latest early Pleistocene of Almenara-Casablanca-3 (Castellón, East of Spain). Systematic, climatic and environmental considerations. Geodiversitas 29:269–295.

Böhme, M. 1999. Doppelschleichen (Sauria, Amphisbaenidae) aus dem Untermiozän von Stubersheim 3 (Süddeutschland). Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 39:85–90.

Bolet, A., M. Delfino, J. Fortuny, S. Almécija, J.M. Robles, and D.M. Alba. 2014. An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards. PLoS One 9:e98082.

Bolet, A. and S. E. Evans. 2013. Lizards and amphisbaenians (Reptilia, Squamata) from the late Eocene of Sossís (Catalonia, Spain). Palaentologia Electronica 16:1–23.

Boulenger, G. A. 1884. Descriptions of new species of reptiles and batrachians in the British Museum. Annals and Magazine of Natural History, 5th Series 13:396–398.

Čerňanský, A., M. Augé, and J.-C. Rage. 2015a. A complete mandible of a new Amphisbaenian reptile (Squamata, Amphisbaenia) from the late Middle Eocene (Bartonian, MP 16) of France. Journal of Vertebrate Paleontology 35:e902379.

Čerňanský, A., J. Klembara, and J. Müller. 2016. The new rare record of the late Oligocene lizards and amphisbaenians from Germany and its impact on our knowledge of the European terminal Palaeogene. Palaeobiodiversity and Palaeoenvironments 96:559–587.

Čerňanský, A., J.-C. Rage, and J. Klembara. 2015b. The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. Journal of Systematic Palaeontology 13:97–128.

Čerňanský, A., D. Vasilyan, G. L. Georgalis, P. Joniak, S. Mayda, and J. Klembara. 2017. The first records of fossil anguines (Squamata; Anguidae) from the Oligocene and Miocene localities of Turkey. Swiss Journal of Geosciences 110:741–751.

Čerňanský, A., and M. Venczel. 2011. An amphisbaenid reptile (Squamata, Amphisbaenidae) from the Lower Miocene of Northwest Bohemia (MN 3, Czech Republic). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 260:73–77.

Chesi, F., M. Delfino, L. Abbazzi, S. Carboni, L. Lecca, and L. Rook. 2007. New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia, Testudines) in the Central Mediterranean. Rivista Italiana di Paleontologia e Stratigrafia 113:287–297.

Conrad, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bulletin of the American Museum of Natural History 310:1–182.

Delfino, M. 1997. *Blanus* from the early Pleistocene of southern Italy: another small tessera from a big mosaic; pp. 89–97 in I. W. Böhme, W. Bischoff, and T. Ziegler (eds.), Herpetologica Bonnensis, SEH, Bonn.

Delfino, M., 2003. A Pleistocene amphisbaenian from Sicily. Amphibia-Reptilia 24:407–414.

Delfino, M., and S. Bailon. 2000. Early Pleistocene herpetofauna from Cava Dell' Erba and Cava Pirro (Apulia, Southern Italy). Herpetological Journal 10:95–110.

Delfino, M., T. Kotsakis, M. Arca, C. Tuveri, G. Pitruzzella, and L. Rook. 2008. Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiversitas 30:641–656.

Estes, R. 1983. Sauria Terrestria, Amphisbaenia. Encyclopedia of Paleoherpetology, part 10a. Gustav Fisher Verlag, Stuttgart, New York, 249 pp.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata; pp 99–118 in R. Estes, and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L Camp. Stanford University Press, Stanford.

Folie, A., R. Smith, and T. Smith. 2013. New amphisbaenian lizards from the Early Paleogene of Europe and their implications for the early evolution of modern amphisbaenians. Geologica Belgica 16:227–235.

Gans, C. and R. Montero. 2008. An Atlas of Amphisbaenian Skull Anatomy; pp 621–738 in C. Gans, A. S. Gaunt, and K. Adler (eds.), Biology of the Reptilia. Vol. 21. The Skull and Appendicular Locomotor Apparatus of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca.

Gauthier, J.A., Kearney, M., Maisano, J.A., Rieppel, O., Behike, A.D.B., 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History 53:3–308.

Georgalis, G. L., and W. G. Joyce. 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58:115–208.

Georgalis, G. L., and B. P. Kear. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46:299–311.

Georgalis, G. L., Z. Szyndlar, B. P. Kear, and M. Delfino. 2016a. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109:103–116.

Georgalis, G. L., A. Villa, and M. Delfino. 2017. Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. Historical Biology 29:730–742.

Georgalis, G. L., A. Villa, E. Vlachos, and M. Delfino. 2016b. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49:433–444.

Holman, A. J. 1998. Pleistocene Amphibians and Reptiles in Britain and Europe. Oxford University Press, New York, 254 pp.

Kearney, M. 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17:1–74.

Kornilios, P., Ç. Ilgaz, Y. Kumlutaş, S. Giokas, S. Fraguedakis-Tsolis, and B. Chondropoulos. 2011. The role of Anatolian refugia in herpetofaunal diversity: an mtDNA analysis of *Typhlops vermicularis* Merrem, 1820 (Squamata, Typhlopidae). Amphibia-Reptilia 32 :351–363.

Laurenti, J. N. 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu. Joan Thomae, Vienna, 217 pp.

Mayda, S., F. Göktaş, A. S. Tesakov, T. Kaya,V. Titov, and K. Halaçlar. 2013. A new middle Miocene mammalian fauna from Afyon-Gebeceler (Western Turkey). 66th Turkish Geology Symposium. Abstracts Book 470–471.

Miklas-Tempfer, P. M. 2003. The Miocene Herpetofaunas of Grund (Caudata; Chelonii, Sauria, Serpentes) and Mühlbach am Manhartsberg (Chelonii, Sauria, Amphisbaenia, Serpentes), Lower Austria. Annalen des Naturhistorischen Museums in Wien 104:195–235.

Müller, J., C. A. Hipsley, J. J. Head, N. Kardjilov, A. Hilger, M. Wuttke, and R. Reisz. 2011. Eocene lizard from Germany reveals amphisbaenian origins. Nature 473:364–367.

Oppel, M. 1811. Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, München, 86 pp.

Pyron, R. A., F. T. Burbrink, J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:93.

Rage, J.-C. 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments 93:517–534.

Rage, J.-C., and M. Augé. 2010. Squamate reptiles from the middle Eocene of Lissieu France). A landmark in the middle Eocene of Europe. Geobios 43:253–268.

Rage, J.-C., and M. Augé. 2015. Valbro: A new site of vertebrates from the early Oligocene (MP 22) of France (Quercy). III – Amphibians and squamates. Annales de Paleontologie 101:29–41.

Rage, J.-C., and S. Sen. 1976. Les Amphibiens et les Reptiles du Pliocène supérieur de Çalta (Turquie). Géologie méditerranéenne 3:127–134.

Reeder, T. W., T. M. Townsend, D. G. Mulcahy, B. P. Noonan, P. L. Wood Jr., J. W. Sites Jr., and J. J. Wiens. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. PLoS ONE 10:e0118199.

Roček, Z. 1984. Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia). Rozpravy Ceskoslovenské Akademie Ved, Rada Matematickych a prírodních Ved 94:3–69.

Saraç, G. 2003. Türkiye Omurgalı Fosil Yatakları. Scientific Report No. 10609. General Directorate of the Mineral Research and Exploration of Turkey (MTA), Ankara 208 pp.

Schleich, H.-H. 1985. Neue Reptilienfunde aus dem Tertiär Deutschlands 3. Erstnachweis von Doppelschleichen (*Blanus antiquus* sp. nov.) aus dem Mittelmiozän Süddeutschlands. Münchner Geowissenschaftliche Abhandlungen Reihe A 4:1–16.

Schleich, H.-H. 1988. Neue Reptilienfunde aus dem Tertiär Deutschlands. 8. *Palaeoblanus tobieni* n. gen., n. sp. - neue Doppelschleichen aus dem Tertiär Deutschlands. Paläontologische Zeitschrift 62:95–105.

Sindaco, R., and V. K. Jeremčenko. 2008. The reptiles of the Western Palearctic. 1. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. Monografie della Societas Herpetologica Italica, I. Edizioni Belvedere, Latina (Italy), 580 pp.

Sindaco, R., P. Kornilios, R. Sacchi, and P. Lymberakis. 2014. Taxonomic reassessment of *Blanus strauchi* (Bedriaga, 1884) (Squamata: Amphisbaenia: Blanidae), with the description of a new species from south-east Anatolia (Turkey). Zootaxa 3795:311–326.

Staesche, K. 1975. Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten. Geologisches Jahrbuch, Series B 15:1–167.

Szyndlar, Z. 1991. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos 47:103–126.

Tałanda, M. 2016. Cretaceous roots of the amphisbaenian lizards. Zoologica Scripta 45:1–8.

Tok, C. V., M. Tosunoğlu, D. Ayaz, K. Çiçek, and H. S. Mutlu. 2012. New records of the Anatolian Worm Lizard, *Blanus strauchi* (Bedriaga, 1884), from Turkey (Squamata: Amphisbaenia: Blanidae). Herpetozoa 24:107–111.

Townsend, T. M., A. Larson, E. Louis, and J. R. Macey. 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. Systematic Biology 53:735–757.

Venczel, M., and B. Sanchíz. 2006. Lower Miocene Amphibians and Reptiles from Oschiri (Sardinia, Italy). Hantkeniana 5:72–75.

Venczel, M., and E. Ştiucă. 2008. Late middle Miocene amphibians and squamate reptiles from Tauţ, Romania. Geodiversitas 30:731–763.

Vidal, N., and B. S. Hedges. 2009. The molecular evolutionary tree of lizards, snakes, and amphisbaenians. Comptes Rendus Biologies 332:129–139.

Villa, A., E. Tschopp, G. L. Georgalis, and M. Delfino. 2017. Osteology, fossil record and palaeodiversity of the European lizards. Amphibia-Reptilia 38:79–88.

Wagler, J. G. 1830. Natürliches System der Amphibien, mit vorangehender Classification der Saügthiere und Vögel. J. G. Cotta, Munich.

Werner, F. 1898. Über einige neue Reptilien und einen neuen Frosch aus dem cilicischen Taurus. Zoologischer Anzeiger 21:217–223.

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# Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece)

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## Abstract

We here describe lizards and snakes from the late Miocene (MN 10) of Ravin de la Pluie, near Thessaloniki, Greece, a locality widely known for its hominoid primate *Ouranopithecus macedoniensis*. The new finds comprise two large-sized lizards (a probable anguine and a varanid) and two snakes (an elapid and a small-sized "colubrine"). Even if the material is represented by few specimens, this is the first record of squamates from the late Miocene MN 10 biozone of southeastern Europe and the third only for the whole continent. The importance of the varanid vertebrae for systematic attributions is discussed. The new varanid limb elements described herein rank among the few such specimens in the fossil record of monitor lizards. Judging from the new and previously published varanid appendicular material, we suggest that Neogene monitor lizards from Europe possessed comparatively short and robustly built limbs. Distinctive scars on one of the limb elements are interpreted as bite marks of a predator or scavenger, offering insights on the palaeoecology of the herpetofauna of the locality.

**Keywords** Squamata · Neogene · Greece · Biogeography · Taxonomy

**Abbreviations**

| | |
|---|---|
| HNHM | Hungarian Museum of Natural History, Budapest, Hungary |
| LGPUT | Laboratory of Geology and Palaeontology of the University of Thessaloniki, Thessaloniki, Greece |
| MDHC | Massimo Delfino herpetological collection, Department of Earth Sciences of the University of Torino, Torino, Italy |
| MNCN | Museo Nacional de Ciencias Naturales, Madrid, Spain |
| MNHN | Muséum national d'Histoire naturelle, Paris, France |
| NHMW | Naturhistorisches Museum Wien, Vienna, Austria |
| RPl | Ravin de la Pluie locality, Greece |
| ZZSiD | Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland |

## 1 Introduction

The late Miocene fossiliferous localities of the Axios River valley, near Thessaloniki, Greece, span from the early Vallesian (MN 9) to the late Turolian (MN 13), and have yielded a significant amount of fossil mammals since their initial discovery at the beginning of the twentieth century (Arambourg and Piveteau 1929; Koufos 2006 and references therein). The abundance of fossil material and the geographic position of the Axios valley along the route between Anatolia and the Balkan Peninsula, renders this region crucial to our understanding of late Miocene vertebrate dispersals. Frustratingly, the main focus of

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palaeontological research has centered on mammals, which are by far the most abundant. Lizards and snakes, on the other hand, had never been described from the Axios Valley so far.

We here describe the first squamates, (i.e., lizards and snakes), from the late Miocene (MN 10) locality of Ravin de la Pluie, which is located in the Axios Valley and is primarily known for its hominoid primate *Ouranopithecus macedoniensis* (Koufos 2006). The specimens described herein are the first reptiles known from Ravin de la Pluie, with the exception of few testudinid turtles (Arambourg and Piveteau 1929; Garcia et al. 2011; Georgalis and Kear 2013). These new lizards and snakes are the only ones recorded from the late Vallesian MN 10 zone of southeastern Europe, and as such, provide significant biogeographical data. Among the material, there are appendicular remains that pertain to varanid lizards, and these elements are compared with all the few other limb fossils that have been attributed to this clade from the Neogene of Europe. The importance of the varanid vertebrae for taxonomic purposes is also addressed.

## 2 Materials and methods

All specimens described herein are permanently curated at the collections of LGPUT and accessioned under the "RPl" acronym. Part of this material was simply mentioned, but not described or figured, in a preliminary faunal list of de Bonis et al. (1992), where they reported the presence of "Boidae indet." and "*Palaeonaja* sp.". Our investigation of the material, however, concluded that no booid is present in this collection, and most probably this was a misidentification of the colubrid described below or some other specimen, which remained still unprepared at that time. The presence of an elapid snake in Ravin de la Pluie is here confirmed, though this taxon is described as *Naja* sp., considering that the usage of the genus name *Palaeonaja* is now considered obsolete (see below). Comparative material includes numerous skeletons of extant squamates housed in HNHM, MDHC, MNCN, MNHN, NHMW, and ZZSiD.

## 3 Geological setting and palaeoecology

The locality Ravin de la Pluie, (hereafter RPl) is situated near the village of Nea Messimvria in Axios Valley, about 25 km west of Thessaloniki city. It is located into the Nea Messimvria Formation and more exactly in the upper parts of the Formation, which is rather thick and consists mainly of sands, gravels, loose or hard conglomerates and red clay. Ravin de la Pluie is a well-known locality because of its rich mammal fauna and mainly the presence of the hominoid *Ouranopithecus macedoniensis*. Apart from *O. macedoniensis*, the RPl mammal fauna includes the erinaceid *Palerinaceus* sp., the sciurid *Spermophilinus* sp., the murid *Progonomys cathalai*, the hyaenids *Adcrocuta eximia leptorhyncha*, *Hyaenictis* sp., *Protictitherium thessalonikensis*, and *Protictitherium* aff. *intermedium*, the mustelid *Eomellivora wimani*, the felid *Metailurus parvulus*, the gomphotheriid *Choerolophodon pentelici*, the deinotheriid *Deinotherium giganteum*, the equids *Hipparion macedonicum* and *Hipparion* cf. *sebastopolitanum*, an indeterminate rhinocerotid, the giraffids *Palaeogiraffa major*, *Palaeotragus* cf. *coelophrys*, *Palaeotragus* cf. *rouenii*, and *Bohlinia* cf. *attica*, and the bovids *Mesembriacerus melentisi*, *Palaeoryx* sp., *Prostrepsiceros vallesiensis*, and *Samotragus praecursor* (Koufos 2006, 2012a, b). The study of the fauna suggests a late Vallesian, MN 10 age, with more exactly magnetostratigraphic correlations providing an estimated age of ~ 9.3 Ma (Koufos 2013).

Several studies, using various methods, have been carried out for the determination of the Vallesian palaeoenvironment of Axios Valley; the conditions were warm and dry, and the landscape was an open savannah-like with low vegetation (small trees, bushes, shrubs) and a thick herbaceous layer (e.g., de Bonis et al. 1992, 1999; Koufos 2006; Merceron et al. 2007; Rey et al. 2013). This is consistent with the palaeoecology of the herpetofauna of RPl. Varanids, large anguids, and elapids occupy a wide range of palaeoenvironments, ranging from savannah grasslands, deserts and forests (e.g., Pianka et al. 2004; Čerňanský et al. 2017a). However, the combination of the reptilian fauna of Ravin de la Pluie and the generally large size of its taxa, along with the associated mammalian fauna, lead us to consider a savannah grassland as the most plausible ecological setting of the locality.

## 4 Systematic palaeontology

Squamata OPPEL, 1811
Anguimorpha FÜRBRINGER, 1900
Anguidae GRAY, 1825
Anguinae GRAY, 1825
?Anguinae indet.

*Material.* – One caudal vertebra (RPl 299) (Fig. 1).

*Description.* – RPl 299 is a well preserved caudal vertebra. The vertebra is procoelous and relatively large-sized, with a centrum length of 11 mm. Both cotyle and condyle are dorsoventrally depressed, with the former being larger than the latter. In lateral view, the cotyle is orientated relatively anteroventrally. Two robust haemapophyses are

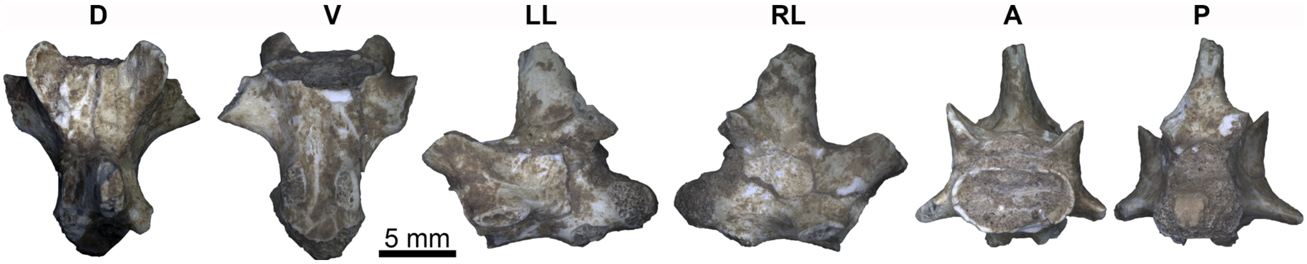

**Fig. 1** ?Anguinae indet. from the late Miocene (MN 10) of Ravin de la Pluie. Caudal vertebra (RPl 299). *A* anterior view, *D* dorsal view, *LL* left lateral view, *P* posterior view, *RL* right lateral view, *V* ventral view

present and fused to the ventral surface of the centrum. Their posterior borders are relatively close to the condyle but are clearly separated from it. Only their bases are preserved. They are compressed mediolaterally but are not laminar. The neural canal is subtriangular in anterior view. The neural arch has its anterior end dorsally flattened but it becomes gradually more arched in its posterior portion. Striae are present on the neural arch. The neural spine is rather high in lateral view, confined only to the posterior portion of the neural arch, and becomes gradually thinner at its dorsal tip. The transverse processes are large and flattened, although both their edges are damaged. There is no visible autotomic fracture plane. Prezygapophyseal articular facets are broadened, flattened and tilted dorsally at 50° in anterior view. Their main axis is directed anteriorly.

*Remarks.* – By certain aspects, caudal vertebrae of large anguids resemble strongly those of varanids (e.g., Estes 1983). Among the distinctive features of the two clades, the haemapophyses (= chevrons) of varanids are articulated on two pedicles, whereas those of anguids are fused to the centrum. More specifically, in *Varanus*, each pedicle ends as an articular facet that faces posteroventrally, but in RPl 299, the remains that are close to the condyle cannot be considered to be such pedicles. They have no posteroventrally oriented facets, though their ends are apparently broken. As such, they are considered to be bases of broken fused-haemapophyses. Concerning the morphology of the neural spine, most, but not all, caudal vertebrae of anguines have tubular and posteriorly inclined neural spines. However, the two or three anteriormost caudal vertebrae of anguines (as also the sacral ones) have laterally compressed and vertical (or almost vertical) neural spines similar to those of varanids (personal observation by JCR and GLG on specimens of *Pseudopus apodus* and *Ophisaurus harti* in MNHN; see also a caudal vertebra of *Pseudopus pannonicus* illustrated in Fejérváry-Lángh (1923: plate III, Fig. 3), where the neural spine is not tubular but compressed laterally and almost vertical). On the other hand, we admit that the morphology and thickness of the haemapophyses, the orientation and thickness of the transverse processes, and the almost vertical angle of the neural spine of RPl 299, are features that are observable in the posterior caudal vertebrae of large-sized varanids. Additionally, a potential varanid attribution of RPl 299 would be further supported by the absolute size of the vertebra, along with what could be an indication of precondylar constriction (seen in ventral view), though the latter is most probably due to erosion and not a real feature of the specimen. Accordingly, the caudal vertebra RPl 299 is tentatively assigned to Anguidae, although we acknowledge the fact that it may in fact pertain to Varanidae, which also occur in this locality (see below). If RPl 299 belongs indeed to an anguid, then it should be assigned to Anguinae on the basis of the well forwarded haemapophyses fused to the centrum (Miklas-Tempfer 2003), taking also into consideration the total absence of the sole other known European anguid clade, Glyptosaurinae, after the late Eocene in the continent (Augé 2005; Rage 2013). Attribution of anguine caudal vertebrae to the species or genus level is not possible (e.g., Čerňanský et al. 2017a, b; Georgalis et al. 2017a). Nevertheless, and if the anguid identity of the specimen is correct, we here suggest possible affinities with *Pseudopus pannonicus* (Kormos, 1911), a widespread Mio-Pliocene taxon, characterized among others by its large size (Klembara and Rummel 2018). Such taxonomic allocation, however, is only based on the rather large size of RPl 299, taking also into consideration a geographic and stratigraphic rationale, and thus should only be considered as tentative.

Platynota DUMÉRIL AND BIBRON, 1839
Varanidae GRAY, 1827 (sensu ESTES ET AL., 1988)
*Varanus* MERREM, 1820
*Varanus* sp.

*Material.* – Two presacral vertebrae (RPl 297–298) (Fig. 2); a humerus (RPl 295) (Fig. 3a, b, d); a tibia (RPl 296) (Fig. 3e, f).

*Description.*

*Presacral vertebrae.* – RPl 297 is a robust trunk vertebra, with a centrum length of 13 mm, missing the right prezygapophysis, right synapophysis, and part of the neural

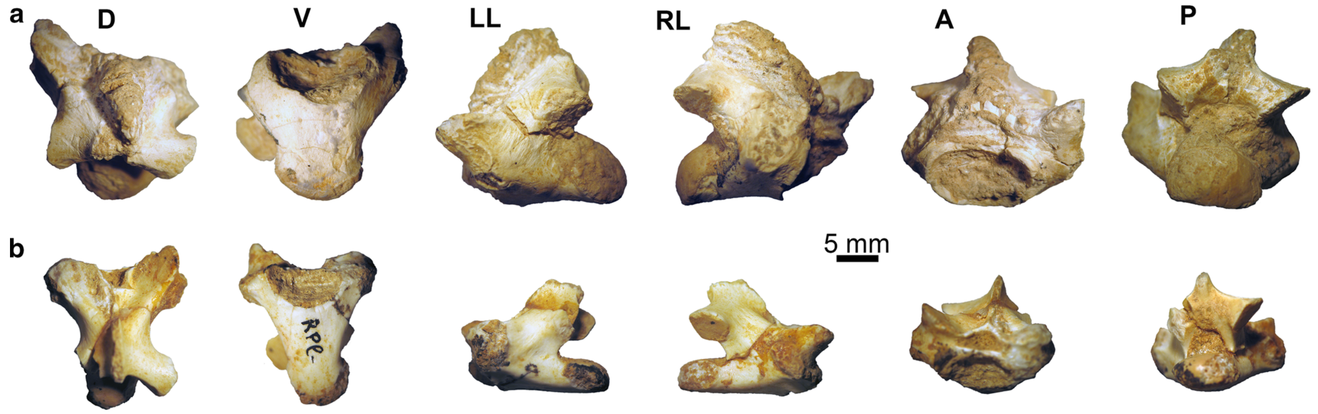

**Fig. 2** *Varanus* sp. from the late Miocene (MN 10) of Ravin de la Pluie. **a** Presacral vertebra (RPl 297); **b** Presacral vertebra (RPl 298). *A* anterior view, *D* dorsal view, *LL* left lateral view, *P* posterior view, *RL* right lateral view, *V* ventral view

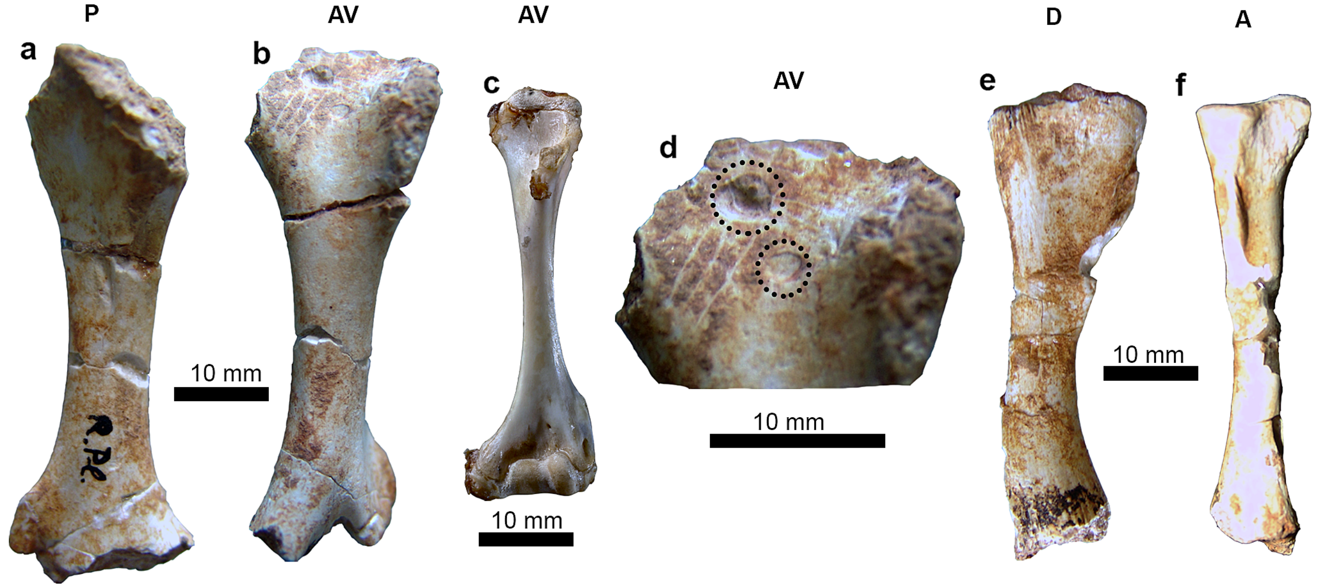

**Fig. 3** *Varanus* sp. from the late Miocene (MN 10) of Ravin de la Pluie and extant *Varanus griseus*. **a**, **b** Left humerus (RPl 295) of *Varanus* sp. from RPl; **c** left humerus of an extant adult, small sized (total length about 60 cm), *Varanus griseus* from northern Africa (MNHN uncatalogued); **d** magnification of the proximal part of the humerus (RPl 295) of *Varanus* sp. from RPl, with dotted circles indicating the two most prominent bite marks; **e**, **f** right tibia (RPl 296) of *Varanus* sp. from RPl. Orientation of the bones follows Russell and Bauer (2008). Note the difference in the stoutness among the humeri of the extant and the Miocene *Varanus* and the difference in torsion between RPLl 295 and the humerus of *V. griseus*. The distal extremities show the same face, but the proximal ends are oriented differently. *A* anterior view, *AV* anteroventral view, *D* dorsal view, *P* posterior view, *V* ventral view

spine. RPl 298 is also a presacral vertebra, with a centrum length of 12 mm, much less robust than the former specimen, but it is much better preserved, missing only the top portion of the neural spine, part of the left prezygapophysis, left synapophysis, and most of the left postzygapophysis. For the sake of convenience, as centrum length we here regard only the measurement between the tip of the condyle and the ventral margin of the cotyle (minimum centrum length of Bailon and Rage 1994). Both vertebrae are procoelous, and in ventral view, the centrum is triangular in shape. In lateral view the centrum is slightly convex ventrally, just prior to the level of the condyle in RPl 297, but it is relatively straight ventrally in RPl 298. The ventral surface of the centrum in both vertebrae is generally smooth, but two rather small ventral foramina are present in RPl 297. A precondylar constriction is clearly present in both vertebrae. Both cotyle and condyle are dorsoventrally depressed, with the former being larger than the latter. The cotyle faces anteroventrally so that, in ventral view, the inner surface of the cotyle is largely visible. The condyle is strongly inclined posterodorsally in lateral view, and it is oval-shaped in posterior view, with a horizontal main axis. The ventral edge of the condyle is close to the posterior edge of the centrum so that only a little portion of the condyle is visible in ventral view. The prezygapophyseal facets are clearly dorsally tilted and they extend anteriorly well beyond the level of the cotyle. Judging from RPl 298, where they are much better preserved, the prezygapophyseal facets are large and oval-shaped. The anterior edge of the neural arch is low and the arch gradually increases in height posteriorly. A distinct, though not fully preserved, pars tectiformis is present in the anterior part of the neural arch. There seems to be a groove between the pars tectiformis and the margins of the prezygapophyses. The posterior edge of the neural arch is relatively well preserved in both vertebrae, with posterodorsal edges inclined quite steeply in posterior view, especially observable in RPl 297. No "pseudozygosphene" or "pseudozygantrum" is present in anterior and posterior views in any of the two vertebrae. The postzygapophyses are well preserved in RPl 297 (only the right one is complete in RPl 298) and they are enlarged and tilted dorsally at about 45°. The texture of the lateral and dorsal surfaces of the vertebrae shows distinct fibrous striae. The neural spine is broken and its height cannot be determined, although it is better preserved in RPl 298. It seems though that its base was developed along most of the posterior length of the neural arch. The neural canal is relatively rounded or rectangular-shaped posteriorly, whereas anteriorly it is dorsally arched and ventrally flattened. Synapophyses are not well preserved in both specimens. Only the left synapophysis of RPl 297 is present, but highly eroded (no diapophysis and parapophysis can be defined), but its extent denotes that it must have been relatively massive in life, whereas in RPl 298 the right synapophysis is also eroded but there are remnants of diapophysis and parapophysis.

*Humerus.* – RPl 295 is a left humerus whose extremities are severely damaged. More specifically, the proximal end lacks the humeral condyle and the lateral and medial tuberosities, whereas the condyles of the distal extremity are broken away. The bone is stoutly built. The proximal extremity was likely slightly wider than the distal end. The torsion of the bone appears to be moderate. The dorsal face of the diaphysis is flattened. On the anteroventral face, the proximal extremity forms a broad, shallow depression (bicipital fossa of Russell and Bauer 2008) that is limited laterally by the bases of the broken off deltopectoral and humeral crests. The distal extremity comprises the bases of the epicondyles, which limit the relatively small radioulnar fossa (fossette sus-trochléenne of Lécuru 1969). The entepicondyle is damaged, but its remaining base shows that it was larger than the ectepicondyle. A short ectepicondylar ridge extends proximally to the ectepicondyle. The presence of an ectepicondylar foramen is not certain. A notch in the broken distal extremity of the ectepicondylar ridge, visible in posterior aspect, may correspond to the proximal part of this foramen, but this cannot be confirmed. On the anteroventral face of the proximal extremity, groove-shaped cuts are present and could probably indicate bite marks from a predator or a scavenger.

*Tibia.* – RPl 296 represents a right tibia. It is stout and slightly sigmoid in dorsal aspect. Both extremities are eroded but are not markedly broken away. The proximal extremity expands more widely than the distal one. The diaphysis is somewhat compressed dorsoventrally so that it appears to be narrower in anterior or posterior views than in dorsal or ventral views. The proximal half of the diaphysis bears a well-developed ventral crest, which projects anteriorly. There is no other crest or process on this specimen.

*Remarks.* – The two presacral vertebrae RPl 297 and 298 can be attributed to Varanidae on the basis of: (1) the presence of a well demarcated anterior part (pars tectiformis) on the neural arch, (2) the morphology of the ventral surface of the centrum that is widened anteriorly and convex ventrally in cross section, and (3) the shape of the condyle that is strongly depressed, with its articular surface facing mainly dorsally (Rage and Bailon 2005). The two RPl vertebrae can be further assigned to *Varanus* on the basis of the prominent precondylar constriction and the presence of striae on the neural arch (Bailon and Rage 1994; Smith et al. 2008; Delfino et al. 2013). Such generic attribution is also strongly consistent with a biogeographic rationale, as *Varanus* is the sole recognized genus of varanids from the European Neogene and Quaternary (Georgalis et al. 2017b). It is worth noting that due to the anteroventral orientation of the cotyle in the vertebrae of *Varanus* [a feature also present in helodermatids (Augé 2005)], two different centrum lengths can be estimated, one minimum (length between the tip of the condyle and the ventral margin of the cotyle) and one maximum (between the tip of the condyle and the dorsal margin of the cotyle) (Bailon and Rage 1994; Delfino et al. 2013).

Appendicular elements of European fossil varanids have been only rarely documented and figured in the literature, with only few exceptions (e.g., de Fejérváry 1918; Sanz 1977; Venczel 2006). Their documentation is further hindered by the conservative nature of the morphology of the lizard limb elements, in addition to the scarcity of extant squamate skeletons in herpetological collections (Bell and Mead 2014). As such, the new limb elements from RPl add to the appendicular fossil record of varanids, though they are not significantly informative from a taxonomic point of view. The similar size and stoutness of the humerus and tibia suggest that they might belong to the same individual, which is consistent with their relative length (taking into account the poor condition of the extremities of both bones, the humerus was likely slightly longer than the tibia). On the other hand, the two bones are clearly more robust, less slender than those of extant *Varanus* of similar sizes, and even somewhat larger, which could even cast doubt on their referral to *Varanus*. However, the RPl fauna includes only two large-sized lizards, a potential large anguine and *Varanus*, with the former being limbless. In addition, various features are consistent with *Varanus*. On the humerus, the diaphysis is flattened, the proximal extremity was apparently slightly wider than the distal one, the bicipital fossa is shallow and broad, the entepicondyle is clearly larger than the ectepicondyle, and the ectepicondylar crest is well developed (Lécuru 1969; Russell and Bauer 2008). Moreover, the ventral crest of the tibia is strong. The distinctive scars on the humerus (Fig. 3c), one of which is deeper than the others, most probably originate from bite marks of a predator or a scavenger, and thus offer an insight into the palaeoecology of the area. Their size and shape is not consistent with bite marks from other varanids, so they do not probably originate from some kind of intraspecific fight. Instead, they more seem to correspond to the teeth of the hyaenid *Protictitherium*, which also occurs at the same locality. So far, the only similar record concerned predation or scavenging of varanid lizards on other taxa (e.g., Molnar 2004), but the opposite case with other fossil taxa preying or scavenging upon monitor lizards was up to now undocumented. As such, if our suggestion is correct, then this is the first recorded case of predation or scavenging upon fossil varanids.

Serpentes LINNAEUS, 1758
Alethinophidia NOPCSA, 1923
Colubridae OPPEL, 1811
“Colubrinae” OPPEL, 1811 (sensu SZYNDLAR, 1991a)
“Colubrinae” indet.

*Material.* – A series of incomplete vertebrae embedded in matrix (RPl 302) (Fig. 4).

*Description.* – RPl 302 is a series of few, probably articulated but rather eroded vertebrae. All vertebrae are rather small, with the largest one attaining a centrum length of only 4 mm. The first vertebrae of the series bear a white sediment colour, whereas the rest bear a black one. Their centrum is slightly longer than wide. On the ventral side of the vertebrae, a haemal keel is present, it is broad and poorly defined laterally, but its posterior limit is clearly marked and pointed. There is no sign of a hypapophysis. All synapophyses are damaged. Only in the first vertebra, a prezygapophysis is preserved, visible only in ventral view. The condyle is rounded.

*Remarks.* – The centrum of the vertebrae in RPl 302 is reminiscent of both booids and colubrids. However, the small vertebral size and the marked posterior edge of the haemal keel make colubrid affinities as more plausible. Among colubrids, the presence or absence of a hypapophysis in the mid- and posterior trunk vertebrae has been considered as the most significant character in distinguishing “colubrine” from natricine snakes (Szyndlar 1991a, b, 2012). It is well recognized though that this traditional practice is more like a convenience rather than pragmatic taxonomy, as other European colubrids (sensu lato), now erected to family level, like psammophiids, also lack hypapophyses in their trunk vertebrae. Consequently, we follow the approach of Szyndlar (1991a, b, 2012) in using the term “Colubrinae” in quotation marks, denoting the presence of a non-natricine colubrid. Nevertheless, the RPl “colubrine” specimen is rather eroded and it is not possible to deduct a more accurate taxonomic attribution.

Elapidae BOIÉ, 1827
*Naja* LAURENTI, 1768
*Naja romani* (HOFFSTETTER, 1939)
*Naja* cf. *romani*

*Material.* – Two precloacal vertebrae (RPl 300–301) (Fig. 5a, b).

*Description.* – RPl 300 is a large and rather robust precloacal (probably mid-trunk or posterior trunk) vertebra with a centrum length of 10 mm, missing its neural spine,

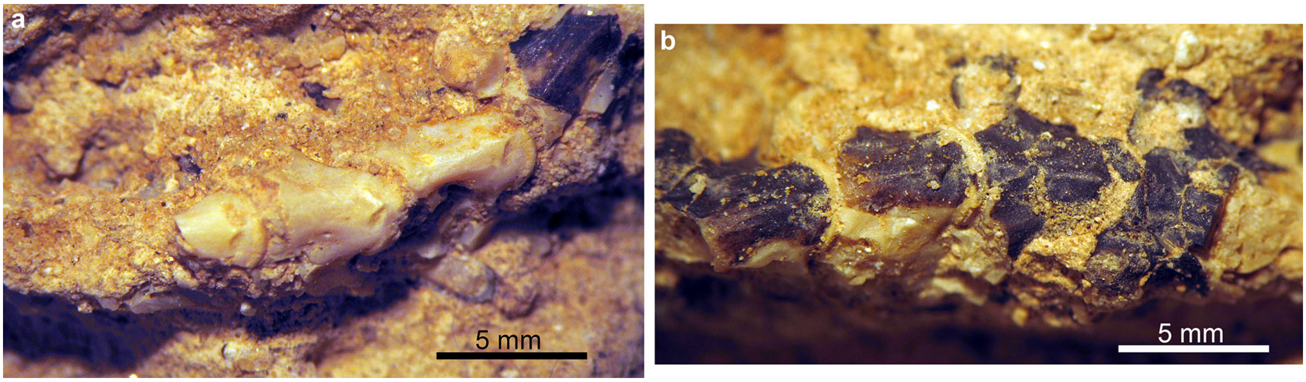

**Fig. 4** “Colubrinae” indet. from the late Miocene (MN 10) of Ravin de la Pluie. **a** Portion of the matrix with articulated vertebrae (RPl 302). **b** Different portion of the same matrix with articulated vertebrae (RPl 302)

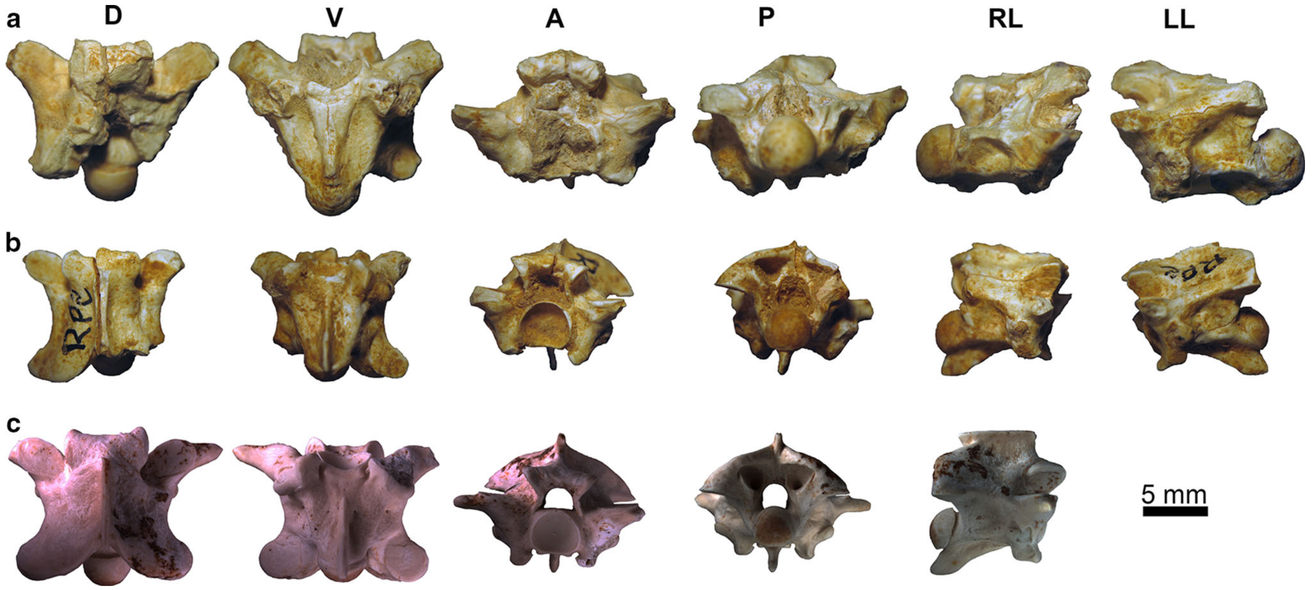

**Fig. 5** *Naja* cf. *romani* from the late Miocene (MN 10) of Ravin de la Pluie and *Naja romani* from the late Miocene (MN 11) of Kohfidisch, Austria. **a** Precloacal vertebra (RPl 300) of *Naja* cf. *romani* from RPl; **b** Precloacal vertebra (RPl 301) of *Naja* cf. *romani* from RPl; **c** Precloacal vertebra (NHMW 2004z0038.0009) of *Naja romani* from Kohfidisch (courtesy of NHMW). *A* anterior view, *D* dorsal view, *LL* left lateral view, *P* posterior view, *RL* right lateral view, *V* ventral view

right postzygapophysis, and parts of the neural arch, synapophyses, and hypapophysis. RPl 301 is a smaller precloacal vertebra, with a centrum length of 8 mm, missing most of its neural spine and the right postzygapophysis. The centrum is triangular in shape and rather broad, especially in the case of RPl 300. The zygosphene is slightly convex in anterior view, whereas in dorsal view, it is slightly crenate in RPl 301 and concave in RPl 300. The neural arch is vaulted and wide in posterior view in RPl 301, but is eroded in RPl 300. The height of the neural spine cannot be evaluated in any of the specimens, as this element is damaged in RPl 300 and only remnants of its base are still present in RPl 301. Nevertheless, it seems that the neural spine extended much of the surface of the neural arch, at least in the case of RPl 301. In lateral view, the interzygapophyseal ridges are prominent. Lateral foramina are present in both vertebrae and are situated in deep depressions. In lateral view, the subcentral ridges are relatively straight over most portion of the vertebra, but become arched dorsally at the level above the hypapophysis. In ventral view, the subcentral ridges are prominent and the subcentral grooves are deep. The keel that prolongs the hypapophysis anteriorly is rather thick in RPl 300 and thin in RPl 301. The hypapohysis is complete in RPl 301 but only its base is preserved in RPl 300. In RPl 301, it is laterally compressed and strongly inclined posteriorly, with its posterior tip being obtuse and situated below the level of the condyle. Prezygapophyses are robust and thick in RPl 300 but not so prominent in RPl 301. In both cases, however, they are produced laterally and only rather slightly inclined dorsally. Prezygapophyseal articular facets are rather wide and oval-shaped. Prezygapophyseal processes are mostly eroded in both vertebrae and, as such, their extent cannot be evaluated. Synapophyses are distinctly divided into diapophyses and parapophyses. These are relatively eroded in RPl 300, but judging from RPl 301 where they are much better preserved, diapophyses are robust and hemisphaerical, parapophyses are wide and relatively flat, whereas parapophyseal processes are directed anteroventrally. Cotyle is rounded, rather large, and relatively deep, especially in the case of RPl 301. Paracotylar foramina are small, situated at the inner margins of deep depressions next to the cotyle. Condyle is rather robust and almost hemisphaerical.

*Remarks.* – The presence of hypapophyses in the mid-trunk vertebrae is an important feature shared by relatively closely related snake clades, such as natricines, elapids, and viperids (Szyndlar 1991a, b), but also distant clades such as acrochordids and bolyeriids. The latter two clades, though, have never been recorded from Europe. RPl 300 and 301 have a relatively large size for natricine snakes. Apart from size, the two vertebrae can be precluded from association with natricines, on the basis on general shape and the shape and inclination of hypapophysis and parapophyses (Szyndlar 1991a, b). Furthermore, the sizes of the cotyle and the condyle do not fit those of viperids, as in the latter clade, the cotyle and condyle are larger (Szyndlar and Rage 1999, 2002; Georgalis et al. 2016a). Moreover, in viperids, the neural arch, in posterior view, is more depressed, and in large vipers (i.e., the “Oriental vipers complex”) it is even flattened (Szyndlar and Rage 1999, 2002; Georgalis et al. 2016a). In addition, the morphology of the ventral face of the centrum and the laterally compressed hypapophysis are characteristic of elapids, and they are clearly consistent with the "*Naja* group" (Szyndlar and Zerova 1990; Szyndlar 1991b). Unfortunately the prezygapophyseal accessory processes, which could be informative for a more precise taxonomic allocation of the specimens, are poorly preserved in both RPl 300 and 301. The morphology of the zygosphene (with three lobes in the smaller vertebra and the median lobe disappearing in the larger one) is consistent with that of *Naja romani*, a widespread species from the Miocene of Europe (Fig. 5c). Accordingly, the new Axios cobra is provisionally referred to this taxon. Differences in the size and shape of RPl 300 and 301 are attributed to ontogenetic or intracolumnar variation.

## 5 Discussion

### 5.1 Palaeobiogeography

The new fossil lizards and snakes from RPl described herein fill an important gap into our knowledge of Eastern Mediterranean Miocene squamate faunas, as this material is the first recorded from the MN 10 zone from southeastern Europe and only the third such record from the whole continent. Indeed, in terms of herpetofaunas, MN 10 is a poorly recorded zone, with only two other European squamate-bearing localities pertaining to that age. These two other localities are Vösendorf, Austria, which has yielded a small-sized anguine, a lacertid, and a "colubrine" (the latter originally erroneously identified as an anilioid) (Papp et al. 1953), and Soblay, France, which has yielded an erycid snake (Demarcq et al. 1983). Even more frustratingly, this latter record from France was simply mentioned but never described or figured, and it cannot now be located. Within southeastern Europe, the new squamate finds (varanids, anguids, "colubrines" and elapids) from RPl rank chronologically intermediate between those from Plakias (Crete Island) (MN 9) (amphisbaenians and natricines; Georgalis et al. 2016b) and those from Pikermi (varanids; Gaudry 1862, 1862–1867; Weithofer 1888) and Mytilinii (Samos Island) (varanids; Conrad et al. 2012) (both MN 12). Considering the different faunal composition between Plakias, Ravin de la Pluie, Pikermi, and Samos, this does not necessarily indicate real absence of certain clades from these localities, but most probably reflects different ecological settings or preservational and collection bias.

The common presence of varanids in Ravin de la Pluie, Pikermi, and Samos, clearly indicates that monitor lizards were geographically widespread in the Greek area at least between the MN 10 to MN 12. Whether this geographic distribution was also reflected by high taxonomic richness of varanids, though, as it is currently indicated by different species known from skull elements in Pikermi (*Varanus marathonensis* Weithofer, 1888) and Samos (*Varanus amnhophilis* Conrad et al., 2012), cannot be evaluated with certainty, as there is no varanid cranial material from RPl, and, moreover, the type material of *V. marathonensis* needs to be reassessed under modern taxonomic and phylogenetic concepts. The presence of several sympatric varanid taxa in various modern herpetofaunas (Pianka et al. 2004) offers, at least, ecological support for envisaging the scenario of more than one late Miocene varanids inhabiting southeastern Europe. In any case, varanids have persisted in the Greek area for a much longer period, until at least the Middle Pleistocene, judging from recently described cranial remains from Tourkobounia 5, near Athens, which also represent the youngest occurrence of monitor lizards from Europe (Georgalis et al. 2017b).

Anguids have so far been described from the Miocene of Greece in the localities of Ano Metochi (MN 13) (Georgalis et al. 2017a) and Maramena (MN 13/14) (Richter 1995), both situated in the Serres Basin in northern Greece. However, in both latter localities, anguids are represented by relatively small-sized forms, probably allied with *Ophisaurus*. As such, if the caudal vertebra from RPl belongs indeed to anguids, then it denotes the presence of a rather large-sized animal, probably allied with the largest known anguine lizard, *Pseudopus pannonicus*. Late Miocene occurrences of this widespread taxon or similar giant forms are known from Austria (Bachmayer and Młynarski 1977), Hungary (Kormos 1911; Fejérváry-Lángh 1923; Klembara 1981; Venczel 2006), Italy (Kotsakis 1989), Ukraine (Fejérváry-Lángh 1923), and probably Slovakia (Čerňanský 2011). Giant anguids with supposed affinities with *P. pannonicus* continued to inhabit Europe during the Pliocene (Fejérváry-Lángh 1923; Młynarski 1956, 1964; Bachmayer and Młynarski 1977; Młynarski et al. 1984; Delfino 2002; Blain and Bailon 2006; Čerňanský et al. 2017a), persisting even until the Pleistocene (Bolkay 1913). Whether all these Miocene, Pliocene, and Pleistocene specimens belong indeed to a single species or they are different taxa of a species complex of giant anguids, remains to be tested through a comprehensive revision of all this material. As such, if our identification is correct, this new specimen demonstrates for the first time the presence of "giant" anguids in Greece. It is worth noting that the largest extant lizard from Europe, *Pseudopus apodus*, shares strong affinities with its Miocene giant relative, *P. pannonicus*, and is still a significant component of the living herpetofauna of the RPl area.

Two fossil snakes have been identified in the collection of squamates from Ravin de la Pluie. Of these, the "colubrine" is not adequately preserved and its exact taxonomic affinities cannot be further elucidated. As such, it is of no relevant significance for biogeographic considerations, but nevertheless adds to the previously poor Miocene record of Greek "colubrines", which to date comprises only material from localities within the Serres Basin (Szyndlar 1991a, 1995; Georgalis et al. 2017a). Among extant non-natricine colubrids, both colubrines (sensu stricto) and psammophiids [i.e., *Malpolon insignitus* (Geoffroy-Saint-Hilaire, 1827)] inhabit today the area of the Axios valley. On the other hand, the new fossil cobra (i.e., Elapidae) from RPl represents the earliest occurrence of elapids in Greece, which were otherwise exclusively known from the late Miocene of Maramena (Szyndlar 1991b, 1995) and the late Pliocene of Tourkobounia 1, near Athens (Szyndlar and Zerova 1990). Additional material from the Middle Pleistocene of Chios Island that was described by Schneider (1975) as a cobra, was subsequently suggested to belong to another snake lineage (Szyndlar 1991b). We agree with this view herein, and judging from the available figure of Schneider (1975), we consider this to be most probably a natricine snake. Cobras seem to be rather widespread in the European Neogene (Szyndlar and Rage 1990). Traditionally considered to represent an endemic, distinct genus (*Palaeonaja*) (Hoffstetter 1939; Rage and Sen 1976; Alberdi et al. 1981; Rage 1984), it was subsequently demonstrated that it in fact has strong affinities with the Asiatic stock of the extant *Naja* (Szyndlar and Rage 1990), a view that was subsequently followed by most authors (e.g., Szyndlar and Zerova 1990; Szyndlar and Schleich 1993; Szyndlar 1991b, 2005), with the notable exception of Wallach et al. (2014) who assigned all European fossil taxa to the African *Afronaja*, without, however, providing justification for their new taxonomic allocation. We herein follow the prevailing view that the Neogene cobras from Europe are all assigned to *Naja*. Apart from Greece, other known late Miocene occurrences of *Naja* include Austria (Bachmayer and Szyndlar 1985; Szyndlar and Zerova 1990), Hungary (Szyndlar 2005), Spain (Alberdi et al. 1981; Szyndlar 1985), and Ukraine (Szyndlar and Zerova 1990). Most likely, the Axios valley cobra could be conspecific with the widespread European taxon *Naja romani*, as the two forms share resemblance in terms of general shape and size (Fig. 5). Due to the incomplete nature of both RPl vertebrae, however, we treat this referral to the specific level as tentative. In any case, the new RPl cobra adds to the known stratigraphic and geographic distribution of these snakes into the Neogene of Europe.

## 5.2 The taxonomic problem of varanid vertebrae

The vertebrae of monitor lizards (Varanidae) are characterized by certain features that render feasible their taxonomic identification, even when dealing with isolated remains. As such, vertebrae represent the most abundant remains in the varanid fossil record (Estes 1983; Molnar 2004; Georgalis et al. 2017b). It is even characteristic that the first confirmed fossil varanid find from Europe was a large trunk vertebra (MNHN.F.PIK3715) from the late Miocene of Pikermi, originally described by Gaudry (1862, 1862–1867) as a "Reptile du groupe des Varans", that was subsequently referred to *Varanus marathonensis* by Weithofer (1888).

Whereas certain features of varanid vertebrae render them identifiable at the family or also at the genus level, differences among the most distinctive characters, such as the degree of the precondylar constriction and the angle of the anteroventral orientation of the cotyle, have been traditionally used in fossil squamate literature as taxonomically important features for monitor lizards, even as diagnostic for specific distinction (e.g., Roger 1898; Nopcsa 1908; Hoffstetter 1969; Lungu et al. 1983; Zerova and Chkhikvadze 1986). As a consequence, the following varanid species have been established exclusively on the basis of vertebrae from the European Cenozoic: *Saniwa orsmaelensis* Dollo, 1923, from the early Eocene (MP 7) of Belgium, *Iberovaranus catalaunicus* Hoffstetter, 1969, from the early Miocene (MN 4) of Spain, *Varanus hofmanni* Roger, 1898, from the middle–late Miocene (MN 6–MN 9) of Germany, *Varanus lungui* Zerova and Chkhikvadze, 1986, from the middle Miocene (MN 7/8) of Moldova, *Varanus tyrasiensis* Zerova and Chkhikvadze in Lungu et al. (1983), also from the middle Miocene (MN 7/8) of Moldova, *Varanus atticus* Nopcsa, 1908, from the late Miocene (MN 12) of Greece, and *Varanus semjonovi* Zerova in Zerova and Chkhikvadze (1986), from the late Miocene (MN 12) of Ukraine. To these, we add also *Varanus deserticolus* Bolkay, 1913, from the late Pliocene (MN 16) of Hungary, which is in fact a chimaera, typified by a varanid dentary and an anguid vertebra (see Georgalis et al. 2017b for further discussion), so it is not considered as exclusively established on vertebral material.

However, it has since been shown that the above mentioned purported diagnostic features (degree of the precondylar constriction and the angle of the anteroventral orientation of the cotyle) are highly variable among varanid vertebrae and they should only be considered with cautiousness upon dealing with taxonomic identifications (Smith et al. 2008; Holmes et al. 2010; Delfino et al. 2013). As such, the validity of most of these names is problematic or at least tentative. *Iberovaranus catalaunicus* has recently been shown to fall within the vertebral variability of *Varanus* and the name has been suggested to be a nomen dubium (Delfino et al. 2013). *Varanus atticus* is typified by the large vertebra from Pikermi that was originally described by Gaudry (1862, 1862–1867), and is now generally accepted as a synonym of *V. marathonensis*, which was established by Weithofer (1888) also from Pikermi, but on the basis of cranial material (e.g., de Fejérváry 1918; Rage and Sen 1976; Estes 1983; Molnar 2004). *Varanus lungui* and *V. tyrasiensis* are coeval and rather approximate geographically, whereas the Ukrainian *V. semjonovi* is younger than the two aforementioned Moldavian taxa but originates practically from the same region. *Varanus hofmanni* is generally treated as a valid taxon, with several other occurrences being provisionally referred to this species from the Miocene of France (Hoffstetter 1969), Hungary (Venczel 2006), and Spain (Hoffstetter 1969); as it is an important, historical taxon, its status needs to be reassessed. The status of *Saniwa orsmaelensis* is more clear: this Paleogene species is generally treated as valid (e.g., Hecht and Hoffstetter 1962; Augé 1990, 2005; Smith et al. 2008). Indeed, the vertebrae of *Saniwa* (currently the sole valid genus of European Paleogene varanids; Augé 2005) seem to be distinct from those of *Varanus* by, among others, the presence of a pseudozygosphene and a straight posterior border of the neural arch between the postzygapophyses (this line is V-shaped in *Varanus*) (Estes 1983; Rage and Augé 2003; Malakhov 2005; Smith et al. 2008).

The two RPl varanid vertebrae differ between them in terms of size, shape, length and extent of pre- and postzygapophyses, and slightly in their degree of precondylar constriction. Nevertheless, this does not imply that they belong to different varanid taxa, but rather that these differences most probably result from ontogenetic or intracolumnar variation (i.e., pertaining to different portions of the trunk region). Interestingly, both RPl vertebrae are much smaller than the stratigraphically younger one belonging to the *Varanus* originally described by Gaudry (1862, 1862–1867) from the late Miocene (MN 12) of Pikermi, that is generally referred to *V. marathonensis*. They further differ from the Pikermi specimen in terms of general shape, degree of precondylar constriction, angle of anteroventral orientation of the cotyle, extent and inclination of prezygapophyses, depression of cotyle and condyle, and size and shape of neural canal. Whether, however, the RPl varanid represents a distinct, smaller and potentially ancestral species to *V. marathonensis*, remains to be elucidated with the study of intraspecific variation among extant varanids and the potential recognition of phylogenetically important characters in these skeletal elements.

### 5.3 Limb morphology of the European Neogene *Varanus*

The limb bones (a left humerus and a right tibia) from the locality of RPl, which are referred to *Varanus*, are clearly more stoutly built than those of similarly-sized extant species of the same genus. The same observation concerns all other so far published limb elements (i.e., only four) from the Neogene of Europe that have been allocated to *Varanus*. These bones consisted so far solely of an ulna, a humerus, a femur, and a phalanx (de Fejérváry 1918; Sanz 1977; Venczel 2006). The ulna and femur were recovered from the latest Miocene (MN 13) of Polgárdi, Hungary, and were referred to as *Varanus* cf. *hofmanni* by Venczel (2006). The humerus, was identified as *Varanus* sp. and originates from the late Pliocene (MN 15) of Layna, Spain (Sanz 1977). The phalanx originates from the early Pliocene (MN 15) of Csarnóta, Hungary, that was referred by de Fejérváry (1918) to *Varanus marathonensis*. Judging from the new Greek material and the published figures of all the above mentioned appendicular remains from Spain and Hungary, it seems that all known limb elements of *Varanus* from the Neogene of Europe are much thicker and stouter than those of the living species (ratio of length/thickness in Miocene forms is lower than in recent forms). This suggests that monitor lizards (i.e., *Varanus*) were represented during the Neogene of Europe by species with relatively short and stocky limbs. Judging from the wide stratigraphic and geographic distribution of short-limbed varanids in the Neogene of Europe, we tentatively suggest that this character was also apparent in all coeval forms from the continent. As such, it would not be surprising that *Varanus marathonensis* from Pikermi and its allied coeval forms from the Neogene of Europe, that are currently not known from any appendicular elements, could have also possessed this distinctive short and robust limb morphology that is apparent at least in the RPl, Polgárdi, and Layna varanids. Obviously, the small number of available specimens does not permit any definite conclusions. The recovery of more fossil limb bones of varanids and a more thorough investigation of the skeletal anatomy of the extant taxa is highly recommended.

## 6 Conclusions

We here describe new finds of lizards and snakes from the late Miocene of Ravin de la Pluie, a locality mostly known for its hominoid *Ouranopithecus macedoniensis*. The new finds represent the first record of fossil squamates from the Axios valley. The fauna is relatively not diverse, with a general trend towards large-sized taxa, though this is most probably an artifact of taphonomy and collection bias. Lizards include the varanid *Varanus* sp. and a probable large anguid. Snakes include the elapid *Naja* cf. *romani* and a small-sized "colubrine". The new squamates from RPl fill a gap in the biogeography and stratigraphy of these reptiles, as they are the first records of lizards and snakes from the late Miocene MN 10 biozone of southeastern Europe, and they complement the knowledge provided by the rare coeval records from the whole continent. The RPl finds further expand the known distribution records of varanids and elapids from southeastern Europe. The potential taxonomic credibility of varanid vertebrae is discussed, with implications about the validity of certain European monitor lizard taxa. The new varanid limb bones from RPl rank among the few such elements in the European record and indicate the presence of robust legs for the European Neogene monitor lizards. The identification of distinctive scars on the RPl varanid humerus corresponds probably to bite marks of a mammalian predator or a scavenger, and offers an insight into the palaeoecology of the locality.

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## References

Alberdi, M. T., Morales, J., Moya, S., & Sanchiz, B. (1981). Macrovertebrados (Reptilia y Mammalia) del yacimiento finimioceno de Librilla (Murcia). *Estudios Geológicos, 37,* 307–312.

Arambourg, C., & Piveteau, J. (1929). Les Vertébrés du Pontien de Salonique. *Annales de Paléontologie, 18,* 59–138.

Augé, M. (1990). La faune de lézards et d'Amphisbènes (Reptilia, Squamata) du gisement de Dormaal (Belgique, Eocène inférieur). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, 60,* 161–173.

Augé, M. (2005). Evolution des lézards du Paléogène en Europe. *Mémoires du Muséum national d'Histoire naturelle, Paris, 192,* 1–369.

Bachmayer, F., & Młynarski, M. (1977). Bemerkungen über die fossilen *Ophisaurus*-Reste (Reptilia, Anguinae) von Österreich und Polen. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematischnaturwissenschaftliche Klasse Abteilung, 1*(186), 285–299.

Bachmayer, F., & Szyndlar, Z. (1985). Ophidians (Reptilia: Serpentes) from the Kohfidisch fissures of Burgenland, Austria. *Annalen des Naturhistorischen Museums Wien, A, 87,* 79–100.

Bailon, S., & Rage, J.-C. (1994). Squamates Néogènes et Pléistocènes du Rift occidental, Ouganda. In B. Senut & M. Pickford (Eds.), *Geology and palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 2: Palaeobiology* (Vol. 29, pp. 129–135). Orléans: CIFEG Occasional Publications.

Bell, C. J., & Mead, J. I. (2014). Not enough skeletons in the closet: Collections-based anatomical research in an age of conservation conscience. *Anatomical Record, 297,* 344–348.

Blain, S., & Bailon, H.-A. (2006). Catalogue of Spanish Plio-Pleistocene amphibians and squamate reptiles from the Museu de Geologia de Barcelona. *Trabajos del Museo Geologico Barcelona, 14,* 61–80.

Boié, F. (1827). *Bemerkungen über Merrem's Versuch eines Systems der Amphibien, 1-ste Lieferung: Ophidier* (Vol. 20, pp. 508–566). Leipzig: Isis von Oken.

Bolkay, J. (1913). Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. *Mittheilungen aus dem Jahrbuche der königlichen Ungarischen geologischen Reichsanstalt, 21,* 217–230.

Čerňanský, A. (2011). New finds of the Neogene lizard and snake fauna (Squamata: Lacertilia; Serpentes) from the Slovak Republic. *Biologia, 66,* 899–911.

Čerňanský, A., Szyndlar, Z., & Mörs, T. (2017a). Fossil squamate faunas from the Neogene of Hambach (northwestern Germany). *Palaeobiodiversity and Palaeoenvironments, 97,* 329–354.

Čerňanský, A., Vasilyan, D., Georgalis, G. L., Joniak, P., Mayda, S., & Klembara, J. (2017b). First record of fossil anguines (Squamata; Anguidae) from the Oligocene and Miocene of Turkey. *Swiss Journal of Geosciences, 110,* 741–751.

Conrad, J. L., Balcarcel, A. M., & Mehling, C. M. (2012). Earliest example of a giant monitor lizard (*Varanus*, Varanidae, Squamata). *PLoS ONE, 7,* e41767.

de Bonis, L., Bouvrain, G., Geraads, D., & Koufos, G. (1992). Diversity and paleoecology of Greek late Miocene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology, 91,* 99–121.

de Bonis, L., Bouvrain, G., & Koufos, G. D. (1999). Palaeoenvironments of the hominoid primate *Ouranopithecus* in the late Miocene deposits of Macedonia, Greece. In J. Agusti, L. Rook, & P. Andrews (Eds.), *Hominoid evolution and climatic change in Europe, vol. I. The evolution of the Neogene terrestrial ecosystems in Europe* (pp. 205–237). London: Cambridge University Press.

de Fejérváry, G. J. (1918). Contributions to a monography on fossil Varanidae and on Megalanidae. *Annales Historico-Naturales Musei Nationalis Hungarici, 16,* 341–467.

Delfino, M. (2002). Erpetofaune italiane del Neogene e del Quaternario. PhD dissertation, University of Modena and Reggio Emilia, Modena and Reggio Emilia, Italy.

Delfino, M., Rage, J.-C., Bolet, A., & Alba, D. M. (2013). Early Miocene dispersal of the lizard *Varanus* into Europe: Reassessment of vertebral material from Spain. *Acta Palaeontologica Polonica, 58,* 731–735.

Demarcq, G., Ballesio, R., Rage, J.-C., Guérin, C., Mein, P., & Méon, H. (1983). Données paléoclimatiques du Néogène de la Vallée du Rhône (France). *Palaeogeography, Palaeoclimatology, Palaeoecology, 42,* 247–272.

Dollo, L. (1923). *Saniwa orsmaelensis*, varanidé nouveau du Landénien supérieur d'Orsmael (Brabant). *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie, 33,* 76–82.

Duméril, A. M. C., & Bibron, G. (1839). *Erpétologie générale ou histoire naturelle complète des reptiles*. Paris: Roret.

Estes, R. (1983). Sauria terrestria, Amphisbaenia. In P. Wellnhofer (Ed.), *Encyclopedia of paleoherpetology, part 10a*. Stuttgart: Gustav Fischer Verlag.

Estes, R., de Queiroz, K., & Gauthier, J. A. (1988). Phylogenetic relationships within Squamata. In R. Estes & G. K. Pregill (Eds.), *Phylogenetic relationships of the lizard families: Essays commemorating C.L. Camp* (pp. 119–281). Stanford: Stanford University Press.

Fejérváry-Lángh, A. M. (1923). Beiträge zu einer Monographie der fossilen Ophisaurier. *Palaeontologia Hungarica, 1,* 123–220.

Fürbringer, M. (1900). Zur vergleichenden anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Zeitschrift, 34,* 215–718.

Garcia, G., Lapparent de Broin, F. de, Bonis, L. de, Koufos, G. D., Valentin, X., Kostopoulos, D., & Merceron, G. (2011). A new terrestrial Testudinidae from the Late Miocene hominoid locality "Ravin de la Pluie" (Axios Valley, Macedonia, Greece). In A. Van der Geer & A. Athanassiou, A. (Eds.), *9th Annual Meeting of the European Association of Vertebrate Palaeontologists, Program and Abstracts* (pp. 26–27). Heraklion: Natural History Museum of Crete.

Gaudry, A. (1862). Note sur les débris d'Oiseaux et de Reptiles trouvés à Pikermi, Grèce, suivie de quelques remarques de paléontologie générale. *Bulletin de la Société Géologique de France*, *19*, 629–640.

Gaudry, A. (1862–1867). *Animaux fossiles et géologie de l'Attique*. Paris: Savy.

Geoffroy-Saint-Hilaire, I. (1827). Description des reptiles qui se trouvent en Égypte. In M. J. C. L. de Savigny (Ed.), *Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée Française. Histoire naturelle. Tome premier. Partie première* (pp. 121–160). Paris: Imprimerie Impériale.

Georgalis, G. L., & Kear, B. P. (2013). The fossil turtles of Greece: An overview of taxonomy and distribution. *Geobios, 46,* 299–311.

Georgalis, G. L., Szyndlar, Z., Kear, B. P., & Delfino, M. (2016a). New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. *Swiss Journal of Geosciences, 109,* 103–116.

Georgalis, G. L., Villa, A., & Delfino, M. (2017a). Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. *Historical Biology, 29,* 730–742.

Georgalis, G. L., Villa, A., & Delfino, M. (2017b). The last European varanid: Demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. *Journal of Vertebrate Paleontology, 37,* e1301946.

Georgalis, G. L., Villa, A., Vlachos, E., & Delfino, M. (2016b). Fossil amphibians and reptiles from Plakias, Crete: A glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. *Geobios, 49,* 433–444.

Gray, J. E. (1825). A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. *Annals of Philosophy, Series, 2*(10), 193–217.

Gray, J. E. (1827). A synopsis of the genera of saurian reptiles, in which some new genera are indicated and others reviewed by actual examination. *The Philosophical Magazine, or Annals of Chemistry, Mathematics, Astronomy, Natural History, and General Science, 2,* 54–58.

Hecht, M., & Hoffstetter, R. (1962). Note préliminaire sur les amphibiens et les squamates du Landénien supérieur et du Tongrien de Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 38,* 1–30.

Hoffstetter, R. (1939). Contribution à l'étude des Elapidae actuels et fossiles et de l'ostéologie des Ophidiens. *Archives du Muséum d'Histoire Naturelle de Lyon, 15,* 1–78.

Hoffstetter, R. (1969). Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. *Bulletin du Muséum National d'Histoire Naturelle, 40,* 1051–1064.

Holmes, R. B., Murray, A. M., Attia, Y. S., Simons, E. L., & Chatrath, P. (2010). Oldest known *Varanus* (Squamata: Varanidae) from the Upper Eocene and Lower Oligocene of Egypt: Support for an African origin of the genus. *Palaeontology, 53,* 1099–1110.

Klembara, J. (1981). Beitrag zur Kenntnis der Subfamilie Anguinae (Reptilia, Anguidae). *Acta Universitatis Carolinae, Geologica, 2,* 121–168.

Klembara, J., & Rummel, M. (2018). New material of *Ophisaurus*, *Anguis* and *Pseudopus* (Squamata, Anguidae, Anguinae) from the Miocene of the Czech Republic and Germany and systematic revision and palaeobiogeography of the Cenozoic Anguinae. *Geological Magazine, 155,* 20–44.

Kormos, T. (1911). *A Polgárdi pliocén csontlelet. Földtani Közlöny, 41,* 48–64.

Kotsakis, T. (1989). Late Turolian amphibians and reptiles from Brisighella (northern Italy): Preliminary report. *Bollettino della Societa Palaeontologica Italiana, 28,* 277–280.

Koufos, G. D. (2006). The Neogene mammal localities of Greece: Faunas, chronology, and biostratigraphy. *Annales Géologiques des Pays Helléniques, 4,* 183–214.

Koufos, G. D. (2012a). A new protictithere from the late Miocene hominoid locality Ravin de la Pluie of Axios Valley (Macedonia, Greece). *Paläontologische Zeitschrift, 86,* 219–229.

Koufos, G. D. (2012b). New material of Carnivora (Mammalia) from the Late Miocene of Axios Valley, Macedonia, Greece. *Comptes Rendus Palevol, 11,* 49–64.

Koufos, G. D. (2013). Neogene mammal biostratigraphy and chronology of Greece. In X. Wang, L. J. Flynn, & M. Fortelius (Eds.), *Fossil mammals of Asia. Neogene biostratigraphy and chronology* (pp. 595–621). New York: Columbia University Press.

Laurenti, J. N. (1768). *Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu*. Vienna: Joan. Thomae nob. De Trattnern.

Lécuru, S. (1969). Etude morphologique de l'humérus des lacertiliens. *Annales des Sciences naturelles, Zoologie et Biologie animale, 11,* 515–558.

Linnaeus, C. (1758). *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Stockholm: Laurentii Salvii.

Lungu, A. N., Zerova, G. A., & Chkhikvadze, V. M. (1983). Primary evidence on the Miocene *Varanus* of the North Black Sea litoral. *Bulletin of the Academy of Sciences of the Georgian SSR, 110,* 417–420.

Malakhov, D. V. (2005). The early Miocene herpetofauna of Ayakoz (Eastern Kazakhstan). *Biota, 6,* 29–35.

Merceron, G., Blondel, C., Viriot, L., Koufos, G. D., & de Bonis, L. (2007). Dental microwear analysis of bovids from the Vallesian (late Miocene) of Axios valley in Greece: Reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea). *Geodiversitas, 29,* 421–433.

Merrem, B. (1820). *Versuch eines systems der Amphibien* (Vol. 8). Marburg: J. C. Krieger.

Miklas-Tempfer, P. M. (2003). The Miocene Herpetofaunas of Grund (Caudata; Chelonii, Sauria, Serpentes) and Mühlbach am Manhartsberg (Chelonii, Sauria, Amphisbaenia, Serpentes), Lower Austria. *Annalen des Naturhistorischen Museums in Wien, 104A,* 195–235.

Młynarski, M. (1956). Lizards from the Pliocene of Poland. Part VI. Study of the Tertiary bone-breccia fauna from Węze near Działoszyn in Poland. *Acta Palaeontologica Polonica, 1,* 135–152.

Młynarski, M. (1964). Die jungpliozane Reptilienfauna von Rębielice Królewskie, Polen. *Senckenbergiana biologica, 45,* 325–347.

Młynarski, M., Szyndlar, Z., Estes, R., & Sanchiz, B. (1984). Amphibians and reptiles from the Pliocene locality of Weze II near Działoszyn (Poland). *Acta Palaeontologica Polonica, 29,* 209–227.

Molnar, R. E. (2004). Part 2. The long and honorable history of monitors and their kin. In R. E. Pianka, D. King, & R. A. King (Eds.), *Varanoid lizards of the world* (pp. 10–67). Bloomington: Indiana University Press.

Nopcsa, F. (1908). Zur Kenntnis der fossilen Eidechsen. *Beitrage zur Paläontologie und Geologie Osterreich-ungarns und des Orients, 21,* 33–62.

Nopcsa, F. (1923). Die Familien der Reptilien. *Fortschritte der Geologie und Paläontologie, 2,* 1–210.

Oppel, M. (1811). *Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben* (p. 86). München: Joseph Lindauer.

Papp, A., Thenius, E., Berger, W., & Weinfurter, E. (1953). Vösendorf—ein Lebensbild aus dem Pannon des Wiener Beckens. Ein Beitrag zur Geologie und Paläontologie der unterpliozänen Congerienschichten des südlichen Wiener Beckens. *Mitteilungen der Geologischen Gesellschaft in Wien, 46,* 1–109.

Pianka, R. E., King, D., & King, R. A. (2004). *Varanoid lizards of the world*. Bloomington: Indiana University Press.

Rage, J.-C. (1984). Serpentes. In P. Wellnhofer (Ed.), *Encyclopedia of paleoherpetology, part 11*. Stuttgart: Gustav Fischer Verlag.

Rage, J.-C. (2013). Mesozoic and Cenozoic squamates of Europe. *Palaeobiodiversity and Palaeoenvironments, 93,* 517–534.

Rage, J.-C., & Augé, M. (2003). Amphibians and squamate reptiles from the lower Eocene of Silveirinha (Portugal). *Ciências da Terra (UNL), 15,* 103–116.

Rage, J.-C., & Bailon, S. (2005). Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). *Geodiversitas, 27,* 413–441.

Rage, J.-C., & Sen, S. (1976). Les Amphibiens et les Reptiles du Pliocène supérieur de Çalta (Turquie). *Géologie méditerranéenne, 3,* 127–134.

Rey, K., Amiot, R., Lécuyer, C., Koufos, G. D., Martineau, F., Fourel, F., et al. (2013). Late Miocene climatic and environmental variations in northern Greece inferred from stable isotope compositions (δ18O, δ13C) of equid teeth apatite. *Palaeogeography, Palaeoclimatology, Palaeoecology, 388,* 48–57.

Richter, A. (1995). The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). *Münchner Geowissenchaften Abhandlungen, 28,* 35–38.

Roger, O. (1898). Wirbelthierreste aus dem Dinotheriensande, II. Theil. *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg in Ausburg, 33,* 385–396.

Russell, A. P., & Bauer, A. M. (2008). The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. In C. Gans, A. S. Gaunt, & K. Adler (Eds.), *Biology of the reptilia: The skull and appendicular locomotor apparatus of Lepidosauria, Volume 21, Morphology 1* (pp. 1–465). Ithaca: Society for the Study of Amphibians and Reptiles.

Sanz, J. (1977). Presencia de *Varanus* (Sauria, Reptilia) en el Plioceno de Layna (Soria). *Trabajos sobre Neogeno-Cuaternario, 8,* 113–125.

Schneider, B. (1975). Ein mittelpleistozäne Herpetofauna von der Insel Chios, Ägäis. *Senckenbergiana biologica, 56,* 191–198.

Smith, K. T., Bhullar, B.-A. S., & Holroyd, P. A. (2008). Earliest African record of the *Varanus* stem-clade (Squamata: Varanidae) from the early Oligocene of Egypt. *Journal of Vertebrate Paleontology, 28,* 909–913.

Szyndlar, Z. (1985). Ophidian fauna (Reptilia, Serpentes) from the uppermost Miocene of Algora (Spain). *Estudios Geológicos, 41,* 447–465.

Szyndlar, Z. (1991a). A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. *Estudios Geológicos, 47,* 103–126.

Szyndlar, Z. (1991b). A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios Geológicos, 47,* 237–266.

Szyndlar, Z. (1995). The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 4. Serpentes (Squamata, Reptilia). *Münchner Geowissenschaftliche Abhandlungen, Reihe A, 28,* 35–39.

Szyndlar, Z. (2005). Snake fauna from the Late Miocene of Rudabánya. In: R. L. Bernor, L. Kordos, & L. Rook (Eds.), Multidisciplinary research at Rudabánya. *Palaeontographia Italica*, *90*, 31–52.

Szyndlar, Z. (2012). Early Oligocene to Pliocene Colubridae of Europe: A review. *Bulletin de la Societe Geologique de France, 183,* 661–681.

Szyndlar, Z., & Rage, J.-C. (1990). West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): Interrelationships among extinct and extant species. *Amphibia-Reptilia, 11,* 385–400.

Szyndlar, Z., & Rage, J.-C. (1999). Oldest fossil vipers (Serpentes: Viperidae) from the old World. *Kaupia, 8,* 9–20.

Szyndlar, Z., & Rage, J.-C. (2002). Fossil record of the true vipers. In G. Schuett, M. Hoggren, M. Douglas, & H. Greene (Eds.), *Biology of the vipers* (pp. 419–441). Eagle Mountain: Eagle Mountain Publishing.

Szyndlar, Z., & Schleich, H. H. (1993). Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern Germany. *Stuttgarter Beiträge zur Naturkunde B, 192,* 1–47.

Szyndlar, Z., & Zerova, G. (1990). Neogene cobras of the genus *Naja* (Serpentes: Elapidae) of East Europe. *Annalen des Naturhistorischen Museums in Wien, 91A,* 53–61.

Venczel, M. (2006). Lizards from the Late Miocene of Polgárdi (W. Hungary). *Nymphaea, Folia naturae Bihariae, 33,* 25–38.

Wallach, V., Williams, K. L., & Boundy, J. (2014). *Snakes of the world: A catalogue of living and extinct species*. Boca Raton: CRC Press.

Weithofer, A. (1888). Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. *Beiträge zur Paläontologie Österreich-Ungarns, 6,* 225–292.

Zerova, G. A., & Chkhikvadze, V. M. (1986). Neogene Varanids of the USSR. In Z. Roček (Ed.), *Studies in Herpetology* (pp. 689–694). Prague: Charles University of Prague.

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# Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia – bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe

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**ABSTRACT**

We here describe new remains of amphibians and reptiles from the early Miocene (MN 4) of two different Greek localities, Aliveri and Karydia. The newly described material consists of urodelans, alytids, indeterminate anurans, turtles, crocodylians, lacertids, indeterminate scincomorphs, anguids, colubrids, viperids, and indeterminate snakes. The presence of the frog *Latonia* cf. *gigantea* in Greece is documented for the first time. Additionally, the presence of viperids in Aliveri implies a much wider distribution for these snakes during the early Miocene of Europe. Of special interest is the presence of a peculiar colubrid that seems to possess a hitherto unknown vertebral structure, which is herein defined as the 'paracentral ridge'. Although incomplete, the new material has important taxonomic and biogeographic implications, as it enhances our understanding of southeastern European herpetofaunas from the early Miocene, a time period that was characterised by major dispersal and extinction events and climatic change that affected the whole continent.

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## Introduction

The early Miocene was an important time interval for European vertebrate faunas, as it witnessed major dispersal events from both Africa and Asia, but also important climatic changes characterised by higher temperatures, all resulting in the emergence of new palaeoenvironments, extinction events, and drastic faunal turnovers (Rögl 1999; Böhme 2003). The most important studies about these early Miocene events have so far focused primarily on mammals (e.g. Koufos et al. 2005), but knowledge of the respective coeval amphibians and reptiles is far more limited and poorly documented (Ivanov 2001; Delfino et al. 2003; Rage and Roček 2003; Čerňanský 2012; Rage 2013). The situation is even more puzzling for the southeastern portions of Europe, where the known early Miocene herpetofauna is limited to only few sporadic occurrences (Đurić 2016; Georgalis et al. 2013; Georgalis, Villa and Delfino 2016; Vasileiadou et al. 2017).

We try here to fill this gap by describing new fossil amphibians and reptiles from two distinct Greek localities, Aliveri and Karydia, both pertaining to the MN 4 zone (Burdigalian, early Miocene). Up to now, only a chamaeleonid lizard (*Chamaeleo* cf. *andrusovi*) had been described from Aliveri (Georgalis, Villa and Delfino 2016). The turtles from both localities were only preliminarily mentioned with no descriptions or figures by Georgalis and Kear (2013) as 'Emydidae (?) indet.' (for Aliveri-2) and 'Testudinata indet.' (for Karydia-2). We analyze the taxonomic affinities of the new Aliveri and Karydia specimens and additionally discuss biogeographic implications that enhance our comprehension of the herpetofaunas of southeastern Europe.

*Abbreviations*: AL1a, Aliveri 1a Site; AL1b, Aliveri 1b Site; AL1980NQ, Aliveri 1980 New Quarry Site; AL2, Aliveri 2 Site; AMPG, Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Athens, Greece; HNHM, Hungarian Natural History Museum, Budapest, Hungary; KR2, Karydia-2 Locality; MDHC, Massimo Delfino Herpetological Collection, University of Torino, Torino, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMP, Národní Muzeum Praha, Prague, The Czech Republic; UU, University of Utrecht, Utrecht, The Netherlands; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

## Materials and methods

The majority of specimens described herein belongs to the collection of the UU, whereas the remaining of the described material belongs to the AMPG. Comparative material includes multiple skeletons of extant frogs, salamanders, turtles, lizards, and snakes held in HNHM, MDHC, MNCN, MNHN, NHMW, NMP, and ZZSiD.

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## Geological settings

The fossiliferous localities of Aliveri and Karydia, together with those of Gavathas and Lapsarna (both on Lesvos Island), Nostimo (Western Macedonia), and possibly of Kalimeriani (Euboea Island), are among the few early Miocene localities in Greece that have yielded fossils of terrestrial vertebrates (Koufos et al. 2003; Koufos 2006; Vasileiadou and Zouros 2012; Georgalis et al. 2013; Koufos 2013; Georgalis, Villa and Delfino 2016; Vasileiadou et al. 2017).

The locality of Aliveri is situated on the island of Euboea (or Evia) in the administrative region of Central Greece (Figure 1) and was discovered in 1977 by a Dutch-Greek team consisting of Albert van der Meulen, Hans de Bruijn and Georgios Katsikatsos (de Bruijn and van der Meulen 1979; Doukas 2003; van den Hoek Ostende et al. 2015). The Aliveri locality represents a lignitic pit in the Neogene Kymi-Aliveri Basin (de Bruijn et al. 1980). The fossil material from the Aliveri locality originates from four different sites, Aliveri 1a, Aliveri 1b, Aliveri 2, and Aliveri 1980 New Quarry. All of these sites are considered coeval. Unfortunately, the locality is not accessible anymore due to housing development in the area. Recently, van den Hoek Ostende et al. (2015) revised the fauna of Aliveri and also provided a history of past discoveries and studies. Though initially correlated to the MN 3 zone (de Bruijn et al. 1980), the fauna of Aliveri is now referred to earliest MN 4, with an estimated age between 18 and 17.5 Ma (Koufos 2006; van den Hoek Ostende et al. 2015). According to van den Hoek Ostende et al. (2015), the Aliveri assemblage is unique in representing the earliest European Neogene locality documenting the co-occurrence of eastern immigrants that include the rodents *Cricetodon*, *Eumyarion*, *Democricetodon*, *Megacricetodon*, and the insectivore *Galerix symeonidisi*, in combination with the presence of European taxa. Besides the abundant micromammal taxa, large mammals are also known, being represented by the equid *Anchitherium*, two species of the palaeomerycid *Lagomeryx*, the bovid *Eotragus*, and the carnivorans *Euboictis aliveriensis* and *Palaeogale* sp. (van den Hoek Ostende et al. 2015). As for the herpetofauna, up to now, only chamaeleonid lizards have been described from Aliveri (Georgalis, Villa and Delfino 2016), whereas turtles were only briefly mentioned by Georgalis and Kear (2013).

The locality of Karydia is situated in northeastern Greece, in the administrative region of East Macedonia and Thrace (Figure 1). It is located northeast of the town of Komotini, about 800 m south of the Karydia village, and was discovered in 1989 by Hans de Bruijn and Dimitris Foussekis (Doukas 2005). The locality belongs to the Neogene sedimentary sequence of the Thrace Basin. According to Doukas and van den Hoek Ostende (2006), the material was collected from a clay quarry, from three fossiliferous levels around a hill (Karydia-1, -2, and -3 [herein dubbed as KR1–KR3]), and all levels are considered synchronous, although the lithology indicates a slightly older age for KR3. Similarly to Aliveri, the Karydia assemblage is attributed to MN 4. However, the rodent fauna implies a younger age for Karydia. Theocharopoulos (2000) argued that *Democricetodon franconicus* from Aliveri is more primitive than conspecific material from Karydia, indicating a slightly younger age for the latter locality. A slightly younger age for Karydia is also supported by the more advanced evolutionary stage of the rodents *Cricetodon* and *Anomalomys*, and the presence in Karydia of *Ligerimys* instead of *Pseudotheridomys* (Doukas 2003; Koufos 2006; van den Hoek Ostende et al. 2015). The younger age of Karydia relative to that of Aliveri, is also supported by insectivores, as the former locality is characterised by the presence of *Galerix kostakii*, a species considered as a descendant of *G. symeonidisi*, the latter being present in Aliveri (Doukas and van den Hoek Ostende 2006). Similarly to Aliveri, Karydia shares

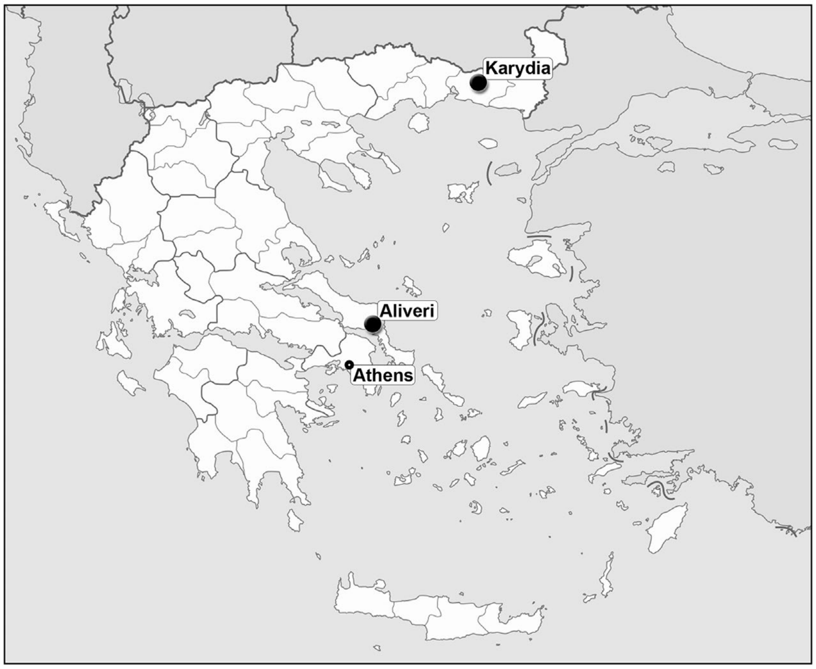

**Figure 1.** Map of Greece with indication of the localities of Aliveri and Karydia. Source: https://commons.wikimedia.org/wiki/File:Greece_location_map.svg

certain congeneric mammal taxa with early Miocene Anatolian localities (e.g. de Bruijn, 2017). No large mammals are known from Karydia and no herpetofauna has been described to date either. It should be highlighted that Karydia has produced far less fossil material in comparison to Aliveri.

Systematic Palaeontology

Amphibia Blainville, 1816

Urodela Duméril, 1806

Urodela indet. (Figure 2)

*Material*. KR3: a tibia (AMPG KR3 037).

*Description*. The tibia is medium-sized, with a total length of 6 mm (Figure 2). It is moderately slender and presents a well-developed tibial crest, whose free portion is broken off. A second low ridge is visible on the ventral surface of the bone, running along its entire length.

*Remarks*. This single, isolated tibia is fully comparable with a medium-sized urodelan in terms of general morphology. A lack of detailed knowledge about the skeletal anatomy of modern salamanders, however, hinders identifying further taxonomic significant features of the Karydia fossil element.

Anura Fischer von Waldheim, 1813

Alytidae Fitzinger, 1843

*Latonia* Meyer, 1843

*Latonia gigantea* (Lartet, 1851)

*Latonia* cf. *gigantea* (Figure 3)

*Material*. KR3: 15 maxillae (AMPG KR3 004, AMPG KR3 005, AMPG KR3 014–AMPG KR3 016, AMPG KR3 027, AMPG KR3 030, AMPG KR3 048–AMPG KR3 055), a frontoparietal (AMPG KR3 038), two praearticulars (AMPG KR3 028 and AMPG KR3 029), two trunk vertebrae (AMPG KR3 031 and AMPG KR3 033), a sacral vertebra (AMPG KR3 032), and four ilia (AMPG KR3 011, AMPG KR3 026, AMPG KR3 044, and AMPG KR3 045).

*Description*.

*Maxillae*. These elements are small and incomplete (Figure 3(A)–(F)). The longest fragments, AMPG KR3 005 and AMPG KR3 015, slightly exceed 5 and 6 mm respectively. The lateral surface is generally smooth. Only AMPG KR3 015 shows a light dermal ornamentation made up by small and indistinct tubercles along the high processus zygomaticomaxillaris, but the presence, or not, of a similar ornamentation in the other specimen cannot be discerned since this part of the bone is missing. Some of the Karydia-3 specimens (e.g. AMPG KR3 005) preserve, at least partially, the anterior end and the processus palatinus. The latter is narrow, anteriorly inclined and gutter-shaped. The portion of the maxilla anterior to the processus palatinus is rather long, being delimited laterally by a high lamina anterior. The lamina horizontalis narrows towards the anterior end. Its dorsal surface displays a rather deep and narrow fossa maxillaris just anterior to the processus palatinus. The posterior end is preserved, at least partially, only in AMPG KR3 015, AMPG KR3 016, and AMPG KR3 027. In these specimens, the lamina horizontalis slightly narrows towards the posterior end and develops a rather long and slender processus pterygoideus. The tooth row extends posteriorly to the end of the lamina horizontalis. A shallow posterior depression is recognizable, including a narrow foramen by its contact with the lamina horizontalis. The depression is not marked by ridges anteriorly. The margo orbitalis is strongly concave.

*Frontoparietal*. The fragmentary frontoparietal is rather small, with a total preserved length of roughly 4 mm (Figure 3(G)–(H)). The anterior end of the bone is missing, whereas posteriorly the bone misses the entire left corner, most of the right processus paraoccipitalis and the right lateral margin. In the entire preserved portion of the bone, the facies dorsalis is rather distinctly narrower than the pars contacta, and the tectum supraorbitale

**Figure 2.** Urodela indet. from Karydia-3: left tibia (AMPG KR3 037) in dorsal (A), ventral (B), lateral (C) and medial (D) views. Scale bar = 1 mm. Abbreviations: tc, tibial crest.

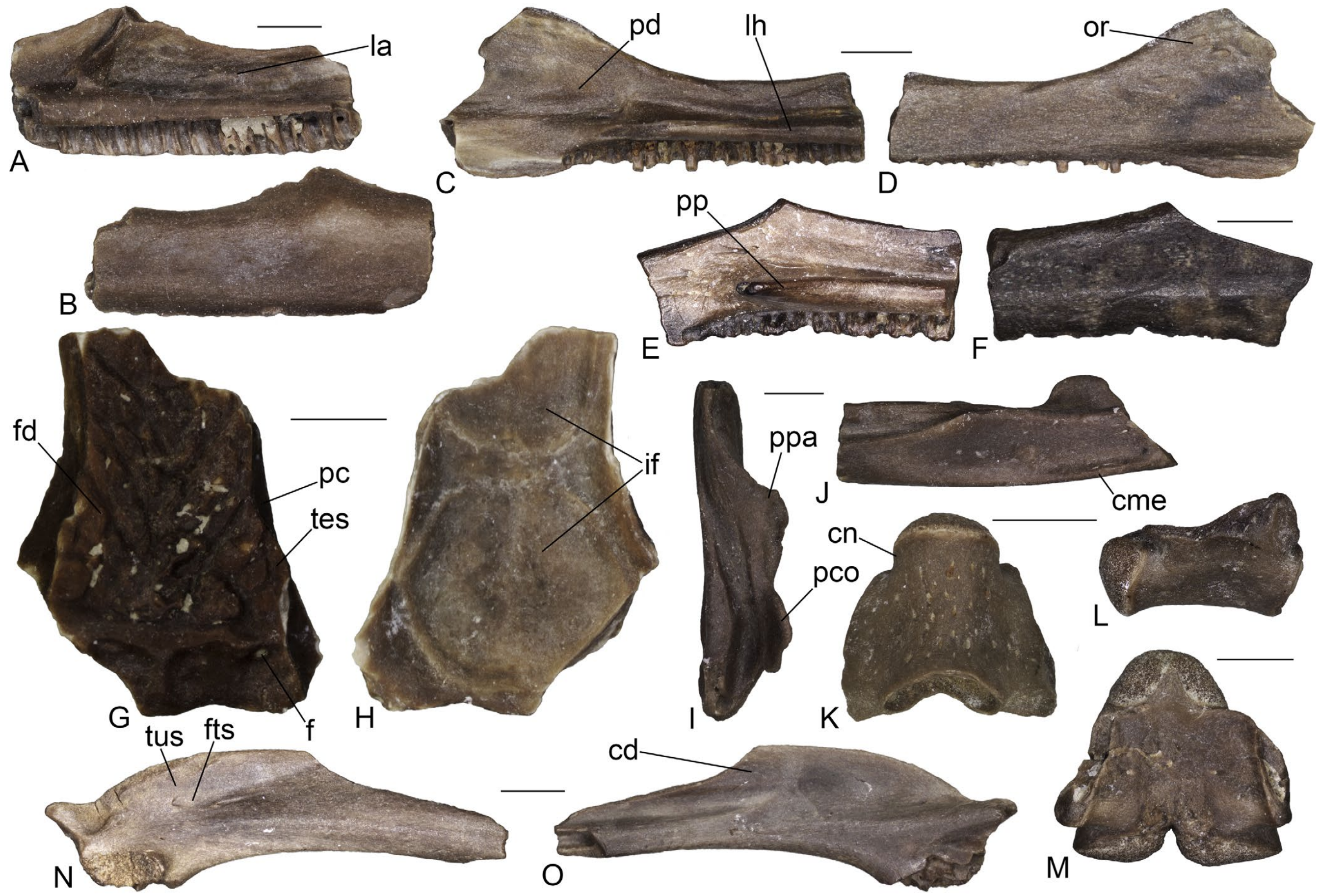

**Figure 3.** *Latonia* cf. *gigantea* from Karydia-3: left maxilla (AMPG KR3 005) in medial (A) and lateral (B) views; left maxilla (AMPG KR3 015) in medial (C) and lateral (D) views; left maxilla (AMPG KR3 016) in medial (E) and lateral (F) views; frontoparietal (AMPG KR3 038) in dorsal (G) in ventral (H) views; left praearticular in dorsal (I) and lateral (J) views; trunk vertebra (AMPG KR3 033) in ventral (K) and left lateral (L) views; sacral vertebra (AMPG KR3 032) in dorsal view (M); right ilium (AMPG KR3 011) in lateral (N) and medial (O) views.
Scale bars = 1 mm. Abbreviations: cd, crista dorsalis; cme, crista mandibulae externa; cn, condylar neck; f, foramen; fd, facies dorsalis; fts, fossula tuberis superioris; if, incrassatio frontoparietalis; la, lamina anterior; lh, lamina horizontalis; or, ornamentation; pc, pars contacta; pco, processus coronoideus; pd, posterior depression; pp, processus pterygoideus; ppa, processus paracoronoideus; tes, tectum supraorbitale; tus, tuber superior.

appears to be developed only as a rather low lamina by each side of the posterior end of the facies dorsalis. The latter is covered by a moderate dermal ornamentation consisting of low tubercles and grooves. The degree of development of the ornamentation tends to fade both anteriorly and towards the lateral sides. Posteriorly to the facies dorsalis, a rather low longitudinal ridge is present in the middle of the smooth posterior area of the dorsal surface of the frontoparietal. By the end of this ridge, a processus posterior is not developed. A sharper ridge runs also at the middle of the dorsal surface of the preserved portion of the processus paraoccipitalis. Medially to the contact between the facies dorsalis and the latter ridge, a small foramen is visible that might represent the opening for the occipital artery. On the lateral sides, the pars contacta is laminar and ventrolaterally extended. On the ventral surface, the incrassatio frontoparietalis is clearly divided into an anterior and a posterior portion, even though the margins of these two portions are poorly marked. Both portions are large. Only the posterior portion of the incrassatio is completely preserved, showing a circular shape. The surface of the incrassatio frontoparietalis is smooth.

*Praearticulars*. These elements are rather small-sized (Figure 3(I)–(J)). They have a slender and horizontal processus paracoronoideus followed posteriorly by a slender and vertically oriented processus coronoideus. The latter is completely damaged in AMPG KR3 029, but its base is visible, attesting its original presence. The rather narrow sulcus pro cartilago Meckeli is rather shallow anteriorly, but it deepens strongly by the processus coronoideus. The lateral surface displays a large and deep depression, marked ventrally by a sharp crista mandibulae externa. The extremitas spatulata is missing.

*Trunk vertebrae*. They are small sized and represented only by the centrum (Figure 3(K)–(L)). The centrum is ophisthocoelous and displays a distinct condylar neck. The shape of the centrum is rather cylindrical, but a slight ventral concavity is visible in lateral view. The concavity is more evident in AMPG KR3 033, however, it is distinctly smaller in AMPG KR3 031. Small portions of the rather thin lateral walls of the neural arch are also preserved in both specimens.

*Sacral vertebra*. This element also preserves only the vertebral centrum (Figure 3(M)). It has an anterior condyle and two posterior condyles. Its size is comparable with the largest trunk vertebra. The condyles are dorsoventrally compressed and the centrum is ventrally flattened.

*Ilia*. These elements are rather small. AMPG KR3 011 preserves most of the shaft, but only a small part of the acetabular portion (Figure 3(N)–(O)). A moderately high crista dorsalis is present. Its anterior half is missing, but the preserved portion seems to display a medial bending anteriorly. The posterior end of the crista is characterised by a poorly marked and anteroposteriorly elongated tuber superior. A shallow fossula tuberis superioris (sensu Roček 1994) is present, housing a small foramen. The supracetabular fossa is deep. Most of the acetabulum is missing, but its anterior margin was strongly raised laterally and seems to have been prominent. Both the partes ascendens and descendens are almost completely broken off, but a deep interiliac groove is still visible in medial view. The other specimens are less well-preserved, but their morphology is fully comparable with that of AMPG KR3 011.

*Remarks*. Maxillae with a long and slender processus pterygoideus and a medial depressed area in the posterior portion, together with prearticulars possessing a processus paracoronoideus associated to the processus coronoideus clearly attest the presence of the discoglossine *Latonia* in Karydia-3 (Roček 1994, 2013). Other, similar-sized remains showing discoglossine features, such as opisthocoelous vertebrae and ilia with a medially-bending crista dorsalis and an interiliac groove, can also be assigned to the same taxon (Roček 1994, 2013; Bailon 1999). The attribution of the frontoparietal from KR3 to *Latonia* is supported by its unpaired nature and the split incrassatio frontoparietalis with a circular posterior portion, but the presence of a foramen for the occipital artery is rather unusual, since this feature is reported to be absent in representatives of the genus (Roček 1994, 2013; Rage and Hossini 2000). Nevertheless, the general morphology of the frontoparietal is fully comparable with early ontogenetic stages of *Latonia gigantea*, as described by Roček (1994) and Rage and Hossini (2000). In particular, the most significant similarities are the narrow facies dorsalis if compared with the pars contacta, the laminar and ventrolaterally-developed pars contacta, and the poorly-marked margins of the incrassatio frontoparietalis. The small size of the specimen also agrees with a juvenile condition, even though the ornamentation, consisting of low tubercles instead of pits and ridges, might suggest it was not a postmetamorphic individual, but rather a subadult (Roček 1994, 2013). The identification as a rather young specimen of *L. gigantea* might be also valid for at least the maxilla AMPG KR3 015, based on the presence of low developed tubercles on the processus zygomaticomaxillaris and the absence of the ridge marking the anterior part of the medial depression in adults (Roček 1994, 2013). Given the small size and the overall similar morphology shown by the other specimens, it seems possible that all discoglossine fossils from Karydia-3 might belong to young individuals of *L. gigantea*. Nevertheless, the presence of a foramen for the occipital artery on the frontoparietal is rather puzzling, and, as such, the identification is here considered only tentative.

cf. *Latonia* sp. (Figure 4A–G)

*Material*. AL1a: an atlas (UU AL 3593). AL1980NQ: three maxillae (UU AL 3552, UU AL 3555, and UU AL 3596), and a right ilium (UU AL 3598).

*Description*.

*Maxillae*. All maxillae from Aliveri are represented by small fragments, the largest one (UU AL 3552) being roughly 4 mm in total length (Figure 4(A)–(B)). They preserve only part of the middle portion of the bone. In medial view, a mediolaterally short and medially convex lamina horizontalis is visible, marking the crista dentalis dorsally. The latter bears pleurodont, closely-spaced, and cylindrical teeth, of which none is completely preserved. The number of preserved tooth-positions is at least 12 in UU AL 3552. The dorsal surface of the lamina horizontalis is marked by a narrow and rather deep groove. The preserved portion of the lateral surface is smooth in all specimens. Certain morphological features, such as the shape of the lamina horizontalis, the tooth morphology, and the smooth lateral surface resemble the specimens from Karydia-3, described above as *Latonia* cf. *gigantea*.

*Atlas*. The atlas from Aliveri preserves only the vertebral centrum (Figure 4(C)–(E)). It is small-sized, strongly dorso-ventrally

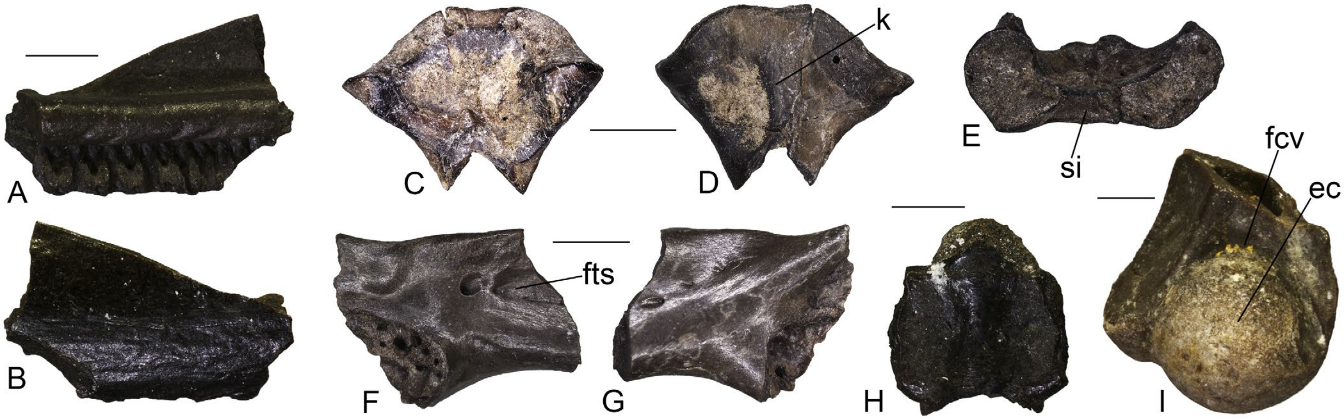

**Figure 4.** cf. *Latonia* sp. from Aliveri (A–G): left maxilla (UU AL 3552) in medial (A) and lateral (B) views; atlas (UU AL 3593) in dorsal (C), ventral (D) and anterior (E) views; right ilium (UU AL 3598) in lateral (F) and medial (G) views. Anura indet. from Aliveri (H): trunk vertebra (UU AL 3553) in dorsal view (H). Anura indet. from Karydia-2 (I): left humerus (UU KR2 5015) in ventral view (I).
Scale bars = 1 mm.Abbreviations: ec, eminentia capitata; fcv, fossa cubitalis ventralis; fts, fossula tuberis superioris; k, keel; si, spatium interglenoidale.

compressed, and has a subcircular posterior cotyle. Anteriorly, two kidney-shaped cotyles are present. They are moderately large and dorsoventrally inclined in anterior view. They are not in contact, since a moderately wide spatium interglenoidale separates them in the middle. A robust keel is visible on the ventral surface of the centrum.

*Ilium*. The small ilium from Aliveri preserves part of the acetabular portion and the base of the shaft (Figure 4(F)–(G)). On the dorsal margin, part of a rather poorly marked tuber superior is preserved. In life, it was probably confluent with a crista dorsalis, which is now missing. Even though the pars ascendens is missing, the angle between the latter and the tuber superior is rather obtuse in lateral view. Two foramina, a strongly larger posterior one and a rather small anterior one, are visible on the lateral surface of the bone; they are located in a rather shallow fossula tuberis superioris. There is no supracetabular fossa. The acetabulum is strongly eroded, but its anteroventral margin is prominent laterally. The preacetabular area is not expanded. Because the ileoischiadic junction is not preserved, it is not possible to discern whether the interiliac tubercle and groove were present.

*Remarks*. In spite of their fragmentary nature, a clear similarity of these specimens is recognizable with *Latonia*. In particular, the Aliveri specimens resemble *Latonia* in the shape of the lamina horizontalis of the maxillae, the ventral keel, the dorsoventrally inclined and medially separated anterior cotyles of the atlas, the poorly-marked tuber superior, the obtuse angle between the tuber and the pars ascendens, and the presence of a fossula tuberis superioris with foramina located into the latter on the ilium (Roček 1994, 2013; Biton et al. 2016). Among discoglossine alytids, a certain similarity is apparent in at least some bones between *Latonia* and *Discoglossus* (e.g. the ilium; Roček 1994; Biton et al. 2016), but the Aliveri fossils cannot be assigned to the latter genus due to the fact that the maxillae bear a more slender lamina horizontalis and the ilia have a more prominent tuber superior forming a less obtuse angle with the pars ascendens (Roček 1994; Bailon 1999; Biton et al. 2016). Due to the poor preservational condition and the scarcity of the fossil material, we here prefer to identify these specimens only tentatively, avoiding also any specific identification, pending the possible discovery of new remains in the future.

Anura indet. (Figure 4H–I)

*Material*. AL1a: an ilium (UU AL 3595), a trunk vertebra (UU AL 3553), and three indeterminate elements (UU AL 3554, UU AL 3594). AL1980NQ: an indeterminate element (UU AL 3597). KR2: a left humerus (UU KR2 5015) and a fragment of radioulna (UU KR2 5016). KR3: a premaxilla (AMPG KR3 003), an ilium (AMPG KR3 024), and eight phalanxes (AMPG KR3 006 and AMPG KR3 023).

*Description and remarks*. These anuran remains from Aliveri are too fragmentary to allow for rigorous identification. Among them, the sole known, small (roughly 2.7 mm long) trunk vertebra (UU AL 3553) could probably belong to the above described cf. *Latonia* sp. on the basis of the cylindrical shape of the centrum. However, the specimen is incomplete and only the cylindrical vertebral centrum is preserved (Figure 4(H)). It displays a cotyle and a condyle, both circular in shape, but since a clear condylar neck is not recognizable, it is not possible to state whether the vertebra was opisthocoelous or procoelous in life. As such, we refrain from formally referring it to cf. *Latonia* and treat this vertebra as an indeterminate anuran. Furthermore, the recognition of the condylar neck is also hindered by a distinct lateral development of the condyle on both sides, possibly indicating a rather high degree of lateral movement of the articulating vertebrae. The respective material from Karydia-2 is relatively better preserved: a medium-sized humerus preserving only the distal epiphysis and a small and very poorly preserved fragment of a radioulna can be assigned only to an indeterminate anuran. The humerus displays a sphaerical eminentia capitata and a moderately deep fossa cubitalis ventralis (Figure 4(I)). The epicondylus ulnaris is robustly built. The epicondylus radialis, on the other hand, is rather small and displays a distinct tubercle on the ventral surface, which is separated from the eminentia capitata by a narrow groove. The bases of both the cristae lateralis and medialis are well developed. On the dorsal surface, the olecranon scar is not recognizable. The fossil remains from Karydia-3 are fragmentary and lack diagnostic characters to the family level, and as such, are here also identified as indeterminate anurans.

Reptilia Laurenti, 1768

Testudines Batsch, 1788

Testudines indet. (Figure 5)

*Material*. AL2: two shell fragments (UU AL 3504–UU AL 3505). KR2: three shell fragments (UU KR2 5001–UU KR2 5003).

*Description*. The two fragments from Aliveri can be joined together in a single, larger fragment (about one square cm) that comes from a chelonian shell (Figure 5(A)–(F)). This identification is supported by the presence of a smooth visceral and a finely vermiculated external surface characterised by a scute sulcus. Moreover, two of the edges of this larger fragment host the typical chelonian sutures. The three small fragments from Karydia are characterised by being thin (2–4 mm) and provided with a rather smooth (visceral) surface and a slightly rough opposite (external) surface (Figure 5(G)–(M)). With the exception of UU KR2 5002, the fragments show a sutural surface on at least one edge. Growth marks are visible on the slightly vermicular external surface of UU KR2 5001. UU KR2 5002 hosts a straight sulcus on the dorsal surface and shows a very modest convexity on its ventral surface, suggesting that this fragment could originate from a costal bone. A rather thin, elongated tubercle, associated with the presence of sutures at three edges, could indicate that UU KR2 5003 is a small fragmentary costal bone as well.

*Remarks*. The material from Aliveri and Karydia is too fragmentary to permit a precise identification of the shell elements. Four clades of non-marine turtles are known from the early Miocene of this region: pan-testudinoids (sensu Joyce et al. 2004), podocnemidoideans, pan-chelydrids, and pan-trionychids (Georgalis and Kear 2013; Georgalis et al. 2013; Joyce 2016; Georgalis and Joyce 2017). The absence of a sculpturing pattern clearly denotes that the material described herein does not pertain to pan-trionychids (Georgalis and Joyce 2017). The general morphology is reminiscent of pan-testudinoids but podocnemidoidean and chelydrid affinities cannot be excluded. Therefore, the material from both localities is herein referred to Testudines indet.

Crocodylia Gmelin, 1789

Crocodylia indet. (Figure 6)

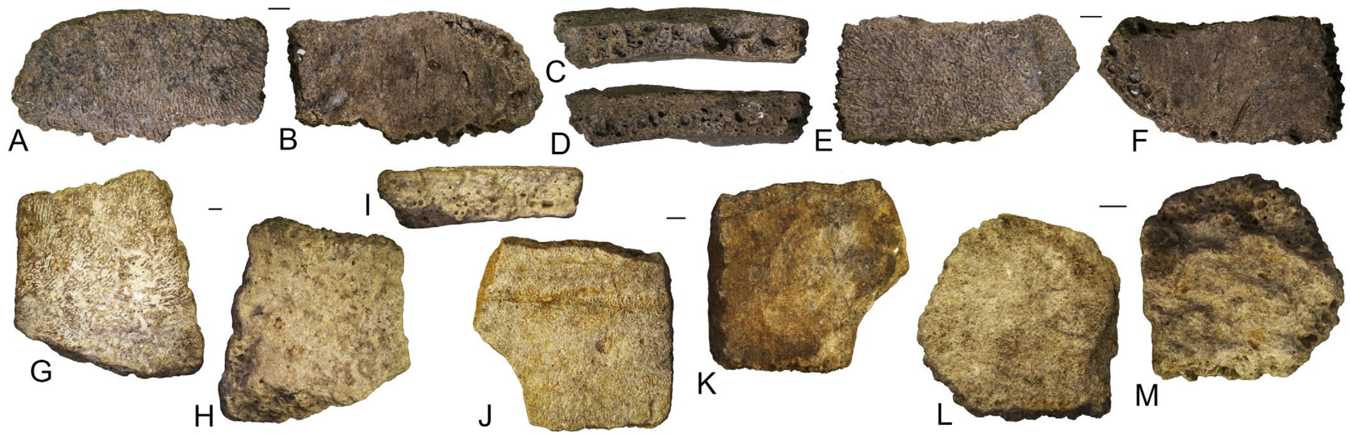

**Figure 5.** Testudines indet. from Aliveri (A–F): shell fragment (UU AL 3504) in external (A), visceral (B), and lateral (C) views; shell fragment (UU AL 3505) in lateral (D), external (E), and visceral (F) views. Testudines indet. from Karydia-2 (G–M): shell fragment (UU KR2 5001) in external (G), visceral (H), and lateral (I); shell fragment, probably a costal (UU KR2 5002) in external (J) and visceral (K) views; shell fragment, probably a costal (UU KR2 5003) in dorsal (L) and ventral (M) views.
Scale bars = 1 mm.

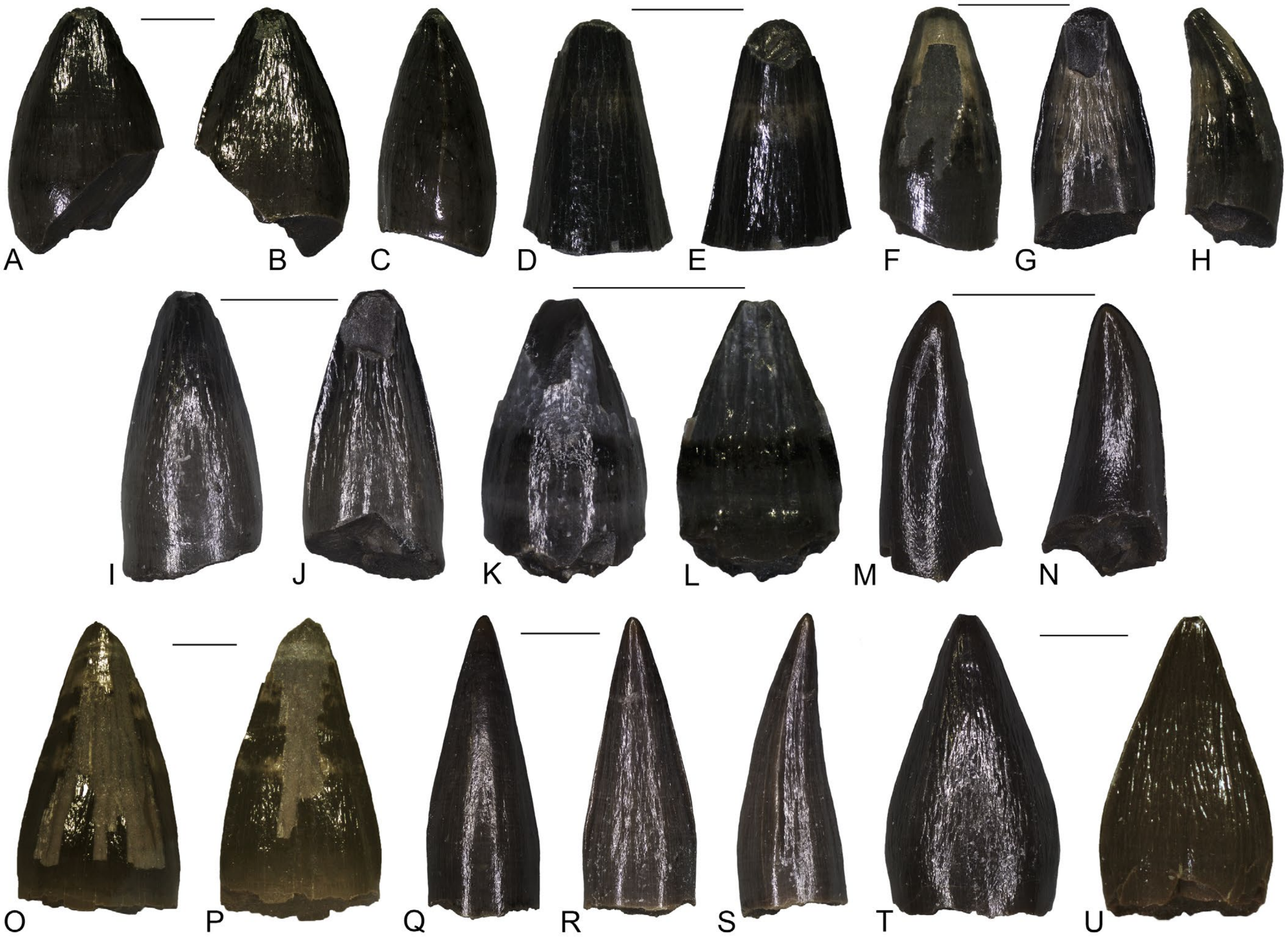

**Figure 6.** Crocodylia indet. from Aliveri: tooth (UU AL 3536) in labial (A), lingual (B), and mesial (C) views; tooth (UU AL 3537) in labial (D) and lingual (E) views; tooth (UU AL 3538) in labial (F), lingual (G), and mesial (H) views; tooth (UU AL 3539) in labial (I) and lingual (J) views; tooth (UU AL 3540) in labial (K) and lingual (L) views; tooth (UU AL 3541) in labial (M) and lingual (N) views; tooth (UU AL 3576) in labial (O) and lingual (P) views; tooth (UU AL 3577) in labial (Q), lingual (R), and mesial (S) views; tooth (UU AL 3578) in labial (T) and lingual (U) views.
Scale bars = 1 mm.

*Material*. AL1a: six isolated teeth (UU AL 3536–UU AL 3541). AL1b: ten isolated teeth (UU AL 3576–UU AL 3585). AL1980NQ: an isolated tooth (UU AL 3556).

*Description*. All teeth from Aliveri share the following characters: small size (the largest, UU AL 3539, is 2.5 cm long), unserrated mesiodistal carinae, rather acute shape (UU AL 3536 is slightly more massive than the others), lingual surface slightly concave, labial surface slightly convex, smooth lingual and labial surfaces, absence of root, and a concave base (Figure 6). UU AL 3537 is the tip of a slightly larger tooth, but shares with the other specimens all the characters available on the preserved portion of the tooth.

*Remarks*. Isolated crocodylian teeth are not diagnostic at a lower taxonomic level (Delfino et al. 2007; Čerňanský et al. 2012; Georgalis, Villa, Vlachos et al. 2016) and therefore the Aliveri material can only be referred to Crocodylia indet. The small size of the teeth and the fact that their root was likely reabsorbed could indicate that they were shed by small individuals (there is no clear evidence of breakage of the root; Frey and Monninger 2010).

Squamata Oppel, 1811
Acrodonta Cope, 1864
Chamaeleonidae Gray, 1825
*Chamaeleo* Laurenti, 1768
*Chamaeleo andrusovi* Čerňanský, 2010
*Chamaeleo* cf. *andrusovi*

*Material*. AL1a: a skull roofing bone (UU AL 3501).

*Remarks*. The chamaeleonids from Aliveri were extensively described by Georgalis, Villa and Delfino (2016) and the reader is referred to that paper for further details. Although they probably all pertain to the same species, only the skull roofing bone possessed enough diagnostic characters for a species determination and was accordingly referred to *Chamaeleo* cf. *andrusovi*, whereas the tooth bearing bones were simply considered as indeterminate chamaeleonids. No further chamaeleonid material has been recovered from Aliveri.

Chamaeleonidae indet.

*Material*. AL1b: a fragment of tooth-bearing bone (UU AL 3502); AL1980NQ: a fragment of tooth-bearing bone (UU AL 3503).

*Remarks*. See *Chamaeleo andrusovi* above.

Scincomorpha Camp, 1923 (sensu Estes et al. 1988)
Lacertidae Oppel, 1811
Lacertidae indet. (Figure 7A–G)

*Material*. AL1a: a fragment of tooth-bearing bone (UU AL 3520). AL1b: a dentary (UU AL 3586) and five fragments of tooth-bearing bones (UU AL 3557–UU AL 3561). AL1980NQ: a fragment of tooth-bearing bone (UU AL 3542). KR3: two maxillae (AMPG KR3 017–AMPG KR3 018) and an isolated tooth (AMPG KR3 007).

**Figure 7.** Lacertidae indet. from Karydia-3 (A–D): left maxilla (AMPG KR3 017) in medial (A) and lateral (B) views; left maxilla (AMPG KR3 018) in medial (C) and lateral (D) views. Lacertidae indet. from Aliveri (E–G): fragment of tooth-bearing bone (UU AL 3557) in medial view (E); fragment of tooth-bearing bone (UU AL 3558) in medial view (F); fragment of tooth-bearing bone (UU AL 3559) in medial view (G). Scincomorpha indet. from Aliveri (H–I): left dentary (UU AL 3519) in medial (H) and lateral (I) views; Scincomorpha indet. from Karydia-3 (J): right dentary (AMPG KR3 010) in medial view (J).
Scale bars = 1 mm. Abbreviations: app, anterior premaxillary process; or, ornamentation; sr, subdental ridge.

*Description*.

*Maxillae*. The lacertid maxillae from KR3 are rather small, fragmentary, and represent only the anterior end of the bone (Figure 7(A)–(D)). The anterior premaxillary process has short anterolateral and anteromedial processes separated by a shallow concavity. Dorsally, the vomeronasal foramen is moderately large and housed in a shallow concave area. It seems that a lappet is absent on the dorsal surface of the anteromedial process. In spite of the strong fragmentary nature of the specimens, a dermal ornamentation appears to be present on the lateral surface of the facial process, at least in AMPG KR3 018 (Figure 7(D)). Ventrally to the ornamentation, some ventrolateral foramina are present. Teeth are pleurodont, cylindrical, narrow, and closely spaced. AMPG KR3 017 preserves three teeth, whereas AMPG KR3 018 has four preserved teeth plus two empty tooth positions. Only one tooth preserves a monocuspid crown in the former specimen, whereas a bicuspid condition is recognizable in all teeth of the latter except for the anteriormost one in which the crown is not preserved.

*Dentary*. The dentary UU AL 3586 preserves only part of the middle portion of the bone. It is 4 mm in length. The Meckelian fossa is wide and opens medially. Teeth are pleurodont but no one is preserved. A moderately slender subdental ridge is present. The ventral margin is distinctly convex in medial view. The labial surface is smooth, though a light roughness seems to be present, however, this could be due to taphonomical reasons. Two mental foramina are present.

*Tooth bearing elements*. The fragments of indeterminate tooth bearing bones bear pleurodont, cylindrical, mono-, bi- and tricuspid teeth, which generally show wear (Figure 7(E)–(G)). Teeth of the largest specimens (UU AL 3557 and UU AL 3559) are hypertrophied.

*Isolated tooth*. AMPG KR3 007 is a single pleurodont and cylindrical tooth. It has a bicuspid crown, with a large main cusp and a smaller accessory cusp.

*Remarks*. The heterodont dentition of these tooth bearing bones from Aliveri is indicative of lacertid affinities (Bailon 1991), though they cannot be more precisely identified due to their poor preservational condition. In spite of the absence of well-preserved teeth, the Aliveri dentary is also assigned to the same taxon because of the convex ventral margin, which is also found in lacertids (AV, pers. obs.). It should be noted that the morphology of the hypertrophied teeth in UU AL 3557 and UU AL 3559 could be reminiscent of certain amblyodont lacertids from the Paleogene and early Neogene of western Europe (Augé 2005), but the Aliveri lizards cannot be attributed to the latter forms, as in amblyodont lizards, the crown is blunt and rounded, and as such, the cusps should be either totally absent or, in some cases, poorly marked.

The overall morphology of the KR3 specimens is consistent with an identification as undetermined lacertids (Bailon 1991; Barahona 1996). Similarly to the Aliveri lacertids, it is difficult to clearly identify the remains at a specific or even generic level, due to their poor preservational status. Nevertheless, their size would suggest the presence of a small-sized taxon in Karydia-3. The presence of the distinct dermal ornamentation on AMPG KR3 018 could testify that, at least this specimen pertains to an adult, and not to a juvenile of a larger species.

Scincomorpha indet. (Figure 7(H)–(J))

*Material*. AL1a: three dentaries (UU AL 3519, UU AL 3521, and UU AL 3524). AL1980NQ: a dentary (UU AL 3549). KR3: a dentary (AMPG KR3 010).

*Description*. The specimens from Aliveri are poorly preserved fragments of dentaries, with a total length of 3.5 mm (UU AL 3519), slightly less than 5 mm (UU AL 3521), roughly 2.5 mm (UU AL 3524), and roughly 3 mm (UU AL 3549) respectively. In medial view, the dentaries display a slender (UU AL 3519) or moderately thick (all other specimens) subdental ridge and a medially open Meckelian fossa. The ventral margin of the bone is missing in all specimens except for UU AL 3549, in which it appears rather straight. At least four (in UU AL 3519), seven (in UU AL 3524) and ten (in UU AL 3521) tooth positions are recognizable, but teeth are preserved only in UU AL 3519 (all four of them) and 3524 (a single one). Teeth appear to have been slender, cylindrical and pleurodont. Teeth of UU AL 3519 are strongly eroded at the tip, but appear to have a peculiar, rather abrupt constriction towards the dorsal level of the dentary (Figure 7(H)–(I)), however, it cannot be ascertained whether this was a true feature in life or is simply an artifact of taphonomy and preservation. The preserved tooth of UU AL 3524 is monocuspid. UU AL 3549 preserves the anterior end, displaying a narrow and subhorizontal mandibular symphysis. The lateral surface is smooth, carrying some mental foramina, in all specimens except for UU AL 3519, where it is slightly rugged.

The dentary fragment from Karydia-3 (AMPG KR3 010) displays a moderately thick subdental ridge on its medial side (Figure 7(J)). The Meckel's groove is open and narrows anteriorly. The ventral margin of the fragment is mostly broken off. The alveolar portion carries 10 tooth positions, but the teeth are not preserved. Nevertheless, they were pleurodont, closely spaced and rather narrow. The lateral surface is smooth, with at least four mental foramina. The total length of the fragment is 6 mm.

*Remarks*. The presence of a subdental ridge on the medial side discriminates dentaries of scincomorph lizards from those of anguimorphs, but it is also present in iguanians and gekkotans (Evans 2008). Nevertheless, the combination of an open Meckel's groove and the pleurodont dentition allow us to exclude an attribution of these dentaries to the latter two groups, rather favouring a scincomorph (sensu Estes et al. 1988) assignment. The preservational condition of the specimens from Aliveri hinders a taxonomic attribution at the family level, but the presence of more than one taxon might be suggested by the difference in the smoothness of the lateral surface of the dentaries. Regarding the Karydia-3 material, if our identification of the other scincomorphs described above as adults of a small lacertid is correct, then the larger size of this dentary might suggest the presence of a second, though still indeterminate, scincomorph taxon in that locality.

Anguimorpha Fürbringer, 1900
Anguidae Gray, 1825
Anguinae Gray, 1825
*Ophisaurus* Daudin, 1803
cf. *Ophisaurus* sp. (Figure 8A–D)

*Material*. KR3: a tooth (AMPG KR3 035) and a trunk vertebra (AMPG KR3 034).

*Description*.

*Tooth*. The isolated tooth is rather small and pointed, even though the tip is broken (Figure 8(A)). It has a conical, roughly

**Figure 8.** cf. *Ophisaurus* sp. from Karydia-3 (A–D): isolated tooth (AMPG KR3 035) in medial view (A); trunk vertebra (AMPG KR3 034) in dorsal (B), ventral (C), and left lateral (D) views. non-*Anguis* Anguinae indet. from Aliveri (E–G): osteoderm (UU AL 3506) in external view (E); osteoderm (UU AL 3516) in external view (F); osteoderm (UU AL 3545) in external view (G); non-*Anguis* Anguinae indet. from Karydia-2 (H–I): osteoderm (UU KR2 5007) in external view (H); osteoderm (UU KR2 5008) in external view (I); non-*Anguis* Anguinae indet. from Karydia-3 (J–L): osteoderm (AMPG KR3 002) in external view (J); osteoderm (AMPG KR3 039) in external view (K); osteoderm (AMPG KR3 040) in external view (L).

Scale bars = 1 mm, except for A, in which it is 0.5 mm. Abbreviations: lk, longitudinal keel; s, synapophysis.

canine shape. The tooth base is not swollen and the apex is not curved. No striae are present. There are small and sharp carinae both anteriorly and posteriorly.

*Trunk vertebra*. The vertebra is procoelous and rather fragmentary as only the left side is preserved (Figure 8(B)–(D)). The neural arch is completely missing, as well as the posterior condyle. The preserved portion of the centrum is roughly 4 mm long. The centrum is dorsoventrally compressed and has a flat ventral surface. Despite the absence of the condyle, a precondylar constriction does not seem to be present. The left lateral margin of the centrum is oblique and slightly concave in ventral view. The left synapophysisis is eroded, but it is distinctly dorsoventrally elongated. The left prezygapophysis is subelliptical and slightly dorsally tilted.

*Remarks*. The morphology of both AMPG KR3 034 and AMPG KR3 035 is reminiscent of that of *Ophisaurus*. As far as the vertebra is concerned, its attribution to *Ophisaurus* is supported by the compressed centrum with no precondylar constriction, an oblique and concave lateral margin, and a flat ventral surface (Klembara 1981; Estes 1983). The isolated tooth, on the other hand, resembles *Ophisaurus* in its conical shape and the absence of a strong curvature (Klembara et al. 2014). Despite the fact that extant species of *Ophisaurus* are reported to have striated tooth crowns, fossil remains with unstriated *Ophisaurus*-like dentition are also known (e.g. Anguine morphotype I from Merkur-Nord; Klembara 2015). An attribution of these two fossils from KR3 to *Ophisaurus* seems therefore possible, but due to scarcity of material and its poor preservational status we here prefer to treat this identification with caution.

non-*Anguis* Anguinae indet. (Figure 8E–L)

*Material*. AL1a: 60 osteoderms (UU AL 3506–UU AL 3518). AL1b: 14 osteoderms (UU AL 3562–UU AL 3575). AL1980NQ: 22 osteoderms (UU AL 3543–UU AL 3548). KR2: seven osteoderms (UU KR2 5006–UU KR2 5013). KR3: 11 osteoderms (AMPG KR3 001, AMPG KR3 002, AMPG KR3 008, AMPG KR3 019, AMPG KR3 039–AMPG KR3 043, AMPG KR3 046, AMPG KR3 047, AMPG KR3 056, and AMPG KR3 057).

*Description*. Osteoderms from Aliveri are small, but rather thick and robust (Figure 8(E)–(G)). They show an external surface with a smooth gliding portion, a vermicular ornamentation and a well-developed longitudinal keel on the external surface. The most well preserved ones are subrectangular in shape.

Osteoderms from Karydia-2 are similar to those from Aliveri. They are small, but robustly-built (Figure 8(H)–(I)). The external surface shows a smooth gliding portion, a vermicular ornamentation on the rest of the surface, and a well-evident longitudinal keel. Osteoderms from Karydia-3 are small and subrectangular in shape (Figure 8(J)–(L)). They display a vermicular ornamentation and, with the sole exception of AMPG KR3 008, a longitudinal keel on the external surface. Similar to the osteoderms from Aliveri and Karydia-2, they also show a smooth gliding portion in their external surface.

*Remarks*. The presence of anguids in Aliveri and Karydia is testified by a large number of osteoderms showing the typical vermicular ornamentation on the external surface. The thickness, the presence of a keel, and the subrectangular shape are found in non-*Anguis* anguine taxa (i.e. either *Pseudopus* or *Ophisaurus*), in contrast to smaller, rounded and unkeeled osteoderms in *Anguis* (Delfino et al. 2011). Regarding the osteoderms from KR3, it is most probable that they pertain to cf. *Ophisaurus* sp. that was described above from that locality.

Serpentes Linnaeus, 1758
Alethinophidia Nopcsa, 1923
Colubridae Oppel, 1811
Colubridae indet. (Figure 9)

*Material*. AL1980NQ: an anterior trunk vertebra (UU AL 3590). KR2: a posterior trunk vertebra (UU KR2 5018), a posterior trunk vertebra (UU KR2 5019), a caudal vertebra (UU KR2 5025), and a fragmentary vertebra (UU KR2 5020). KR3: a fragment of a trunk vertebra (AMPG KR3 020).

*Description*. The trunk vertebrae from both Aliveri and Karydia are incomplete, lacking zygapophyses and synapophyses. The best-preserved specimen, a posterior trunk vertebra (UU KR2

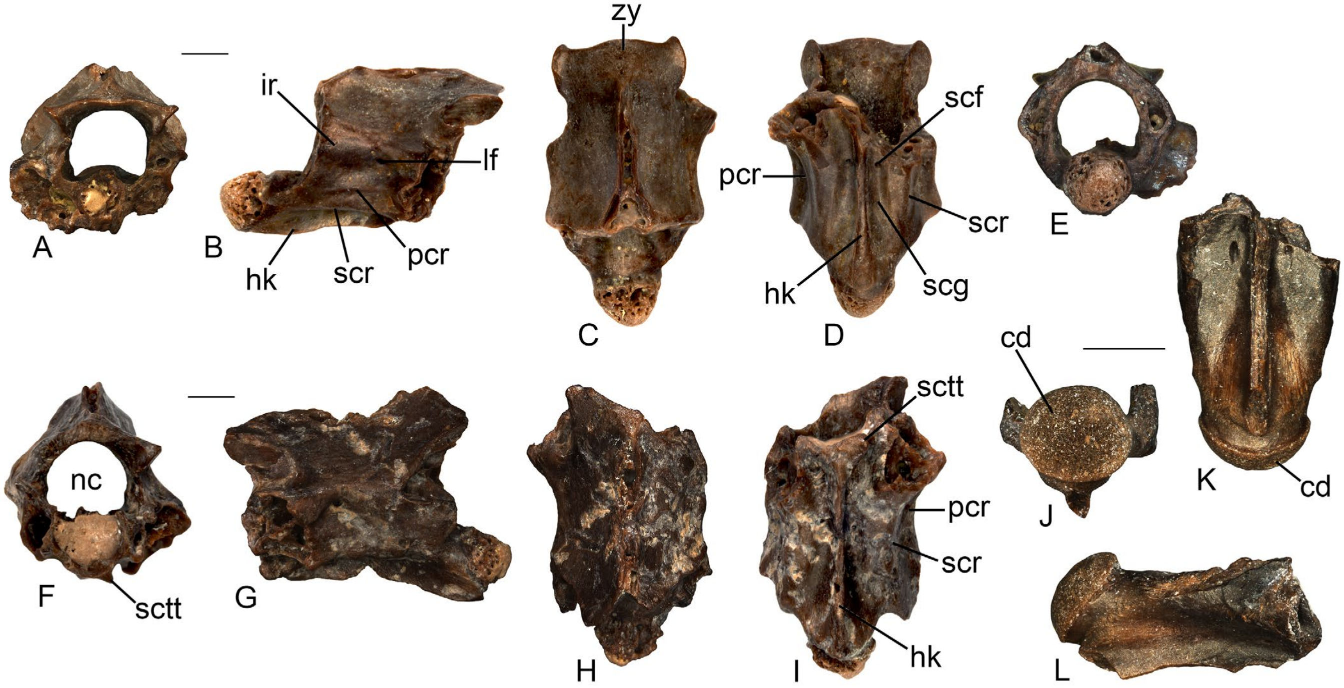

**Figure 9.** Colubridae indet. from Karydia-2 (A–I): posterior trunk vertebra (UU KR2 5018) in anterior (A), right lateral (B), dorsal (C), ventral (D), and posterior (E) views; posterior trunk vertebra (UU KR2 5019) in anterior (F), left lateral (G), dorsal (H), and ventral (I) views; Colubridae indet. from Aliveri (J–L): anterior trunk vertebra (UU AL 3590) in posterior (J), ventral (K), and right lateral (L) views.
Scale bars = 1 mm. Abbreviations: cd, condyle; hk, haemal keel; ir, interzygapophyseal ridge; lf, lateral foramen; nc, neural canal; pcr, paracentral ridge; scf, subcentral foramen; scg, subcentral groove; scr, subcentral ridge; sctt, subcotylar tubercle; zy, zygosphene.

5018), possesses a relatively small zygosphenal facet of oval to sigmoid outline in lateral view (Figure 9(A)–(E)). A large lateral foramen is situated below the rather sharp interzygapophyseal ridge. Its orifice occurs in the vicinity of the dorsal margin of the rather deep and anteroposteriorly slightly enlarged wide depression. The ventral margin of the depression is bordered by a peculiar, distinct sharp crest, which extends from the caudal margin of the unpreserved synapophysis as far as the two thirds of the length of the subcentral ridge. This highly distinct ridge that lies between and almost parallel to the interzygapophyseal and the subcentral ridges is herein termed as 'paracentral ridge'. The subcentral ridges are rather prominent. They are straight and extend as far as the posterior border of the pedicle. Due to the incomplete nature of the specimen, it cannot be certain whether the vertebra possessed a haemal keel or a hypapophysis, although the former structure (haemal keel) seems to have been more probable. The rather narrow haemal keel (or short hypapophysis) is broken off close to its base. In dorsal view, the zygosphene has distinct lateral lobes and a wide medial lobe. The base of the neural spine rises rather anteriorly, at about half of the length of the zygosphenal facet. In ventral view, the subcentral grooves are rather deep. The subcentral foramina are rather large and are situated at the base of the significantly thin haemal keel/hypapophysis. Their orifices are directed anteriorly. The posterior section of the haemal keel/hypapophysis is situated on a triangular-shaped elevation, this feature providing relative support for the presence of a haemal keel instead of a hypapophysis. The anterior portion of the haemal keel/hypapophysis of the second posterior trunk vertebra from Karydia (UU KR2 5019) is triangular, with distinct subcotylar tubercles, though only the left one is preserved (Figure 9(F)–(I)). In anterior view, the zygosphenal lip is vaulted dorsally. The neural canal is rounded with short but distinct lateral sinuses. The cotyle, partially preserved in one vertebra, seems to have been most probably circular. UU AL 3590 is an anterior trunk vertebra and is rather incomplete (Figure 9(J)–(L)). Similarly to UU KR2 5018, it is also characterised by a large depth of the subcentral grooves.

*Remarks*. The vertebrae can be attributed to Colubridae on the basis of their gracile structure, their longer than wide centrum, the narrow haemal keel (or hypapophysis), the distinct subcentral ridges and subcentral grooves, and the gracile zygosphene (Rage 1984; Szyndlar 1984, 1991a, 1991b; LaDuke 1991; Holman 2000). This taxonomic attribution is further supported by the fact that, although the anterior margin of all vertebrae is damaged, the distinct foramen in one specimen (UU KR2 5018) situated on the right side in anterior view indicates that paracotylar foramina were probably present. Due to the damaged ventral portions of all vertebrae, it is not possible to determine whether the structure on the ventral surface of the centrum represents a haemal keel or a hypapophysis, although the presence of the former structure (haemal keel) might be more probable. As such, we refrain from assigning the Aliveri and Karydia colubrids to either 'colubrines' or 'natricines' (sensu Szyndlar 1984, 1991a, 1991b), although we must further acknowledge here that the presence or absence of a hypapophysis throughout the vertebral column is a widespread and variable feature and it should be dealt with high caution, when dealing with taxonomic designations and attributions (Pyron et al. 2013; Head et al. 2016).

Whereas the caudal vertebra UU KR2 5025 and the two vertebral fragments (UU KR2 5020 and AMPG KR3 020) are not informative, the other three colubrid specimens (UU AL 3590, UU KR2 5018, and UU KR2 5019) are characterised by a combination of peculiar features and therefore, enable us to provisionally identify them as belonging to the same taxon. More particularly, the most striking features of this taxon are: (1) in lateral view, a highly distinct ridge, herein defined with the newly introduced term 'paracentral ridge', which is situated above the subcentral ridge and extends from the posterior margin of the diapophysis up to about half of the centrum length; (2) in ventral view, an almost triangular and rather highly elevated surface surrounding the posterior part of the haemal keel (or hypapophysis); (3) a prominent, deep and narrow haemal keel (or hypapophysis) with the ventral margin being sharp along its entire length; (4) prominent subcentral grooves; (5) rather sharp subcentral ridges which are strongly built; (6) rather large subcentral foramina with their orifices directed anteriorly; (7) large lateral foramina, situated in deep depressions; and (8) in dorsal view, a trilobate zygosphene, with distinct lateral lobes. The herein newly defined 'paracentral ridge' appears to be a unique feature and in fact has never been previously described in fossil or extant snakes (e.g. Szyndlar 1984, 1991a, 1991b; Holman 2000; Szyndlar 2005; LaDuke 1991). It is worth noting that in certain colubrids, the anterior portion of the subcentral ridge forms sometimes an elongate triangle whose tip is directed posteriorly, as if the ridge was forked anteriorly in two branches, a ventro-medial and a dorso-lateral one (J-C. Rage, pers. comm., December 2017). The paracentral ridge that is observed in our Greek fossil material, however, does not correspond to that case, as it clearly does not form a triangle and is not united with the subcentral ridge, and is also well projecting across most of the vertebra's lateral surface. Furthermore, we do not consider that this, apparently apomorphic, feature is the product of a pathology, since it is present symmetrically in both lateral views of the vertebrae and is present in both specimens from Karydia (not preserved in the Aliveri specimen). We were only able to identify a similar, but not identical, feature in the trunk vertebrae of the extant Asian snake *Boiga* sp. (specimen MDHC 137), although it is differently shaped and not as prominent as in the Greek fossils. Curiously, this feature on the vertebrae of *Boiga* was not mentioned at all by Ikeda (2007), and it cannot also be ascertained from the photographs provided in that publication. Of course, we are not implying a close relationship among *Boiga* and the Greek colubrid solely on the basis of this feature. Besides, their vertebrae are rather different in terms of general shape, size, and shape of vertebral structures. In any case, the presence of this unique feature, the paracentral ridge, and the combination of the other characters described above probably denote that the colubrid from Karydia and Aliveri is a new taxon. However, on the basis of the scarceness of the material and the rather incomplete and fragmentary nature of all specimens, we refrain from naming it as a new species.

Viperidae Oppel, 1811

Viperidae indet. (Figure 10)

*Material*. AL1a: an incomplete fang (UU AL 3592).

*Description*. The fang is incomplete and has its base unpreserved. The apical termination is slightly curved, with a wide pulpal cavity and venom canal situated anteriorly in central position (Figure 10). In dorsal view, the base of the entrance orifice, which

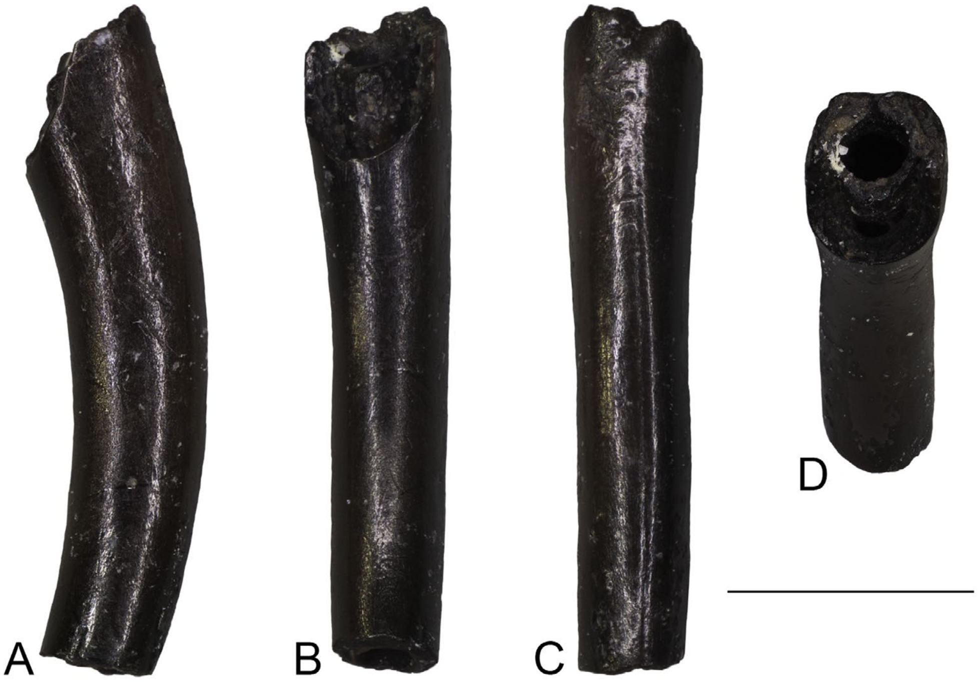

**Figure 10.** Viperidae indet. from Aliveri: isolated fang (UU AL 3592) in lateral (A), posterior (B), anterior (C), and dorsal (D) views. Scale bars = 1 mm.

is situated in the anteriormost proximal part of the fragment, is indicated by the distinction of the dentine folds which form the anterior closure of the venom canal (Figure 10(D)). In anterior view, there is a distinct suture close to the distal termination of the fragment. This suture turns proximally into a narrow groove, which diminishes in front of the entrance orifice base where the fang surface is completely smooth. The discharge orifice is not preserved. A wide groove occurs on either lateral side of the fang along its entire length.

*Remarks*. The single, isolated fang from Aliveri can be assigned to viperids on the basis of the presence of a venom canal which originated from the dentine folding throughout ontogeny. This mode of venom canal development is typical for viperids (Jackson 2002; Zahradnicek et al. 2008). The fangs of elapid snakes differ by the presence of a distinct anterior groove connecting entrance and discharge orifices (Kuch et al. 2006). The distinct lateral grooves which stretch along the entire length of the fragment are rather unusual in viperids although short lateral grooves frequently occur in both crotalines and viperines at the vicinity of the fang base (see Figure 2 in Ivanov 1999; MI, pers. obs.). The preserved specimen from Aliveri is too fragmentary for a more precise determination at the subfamily level. However,

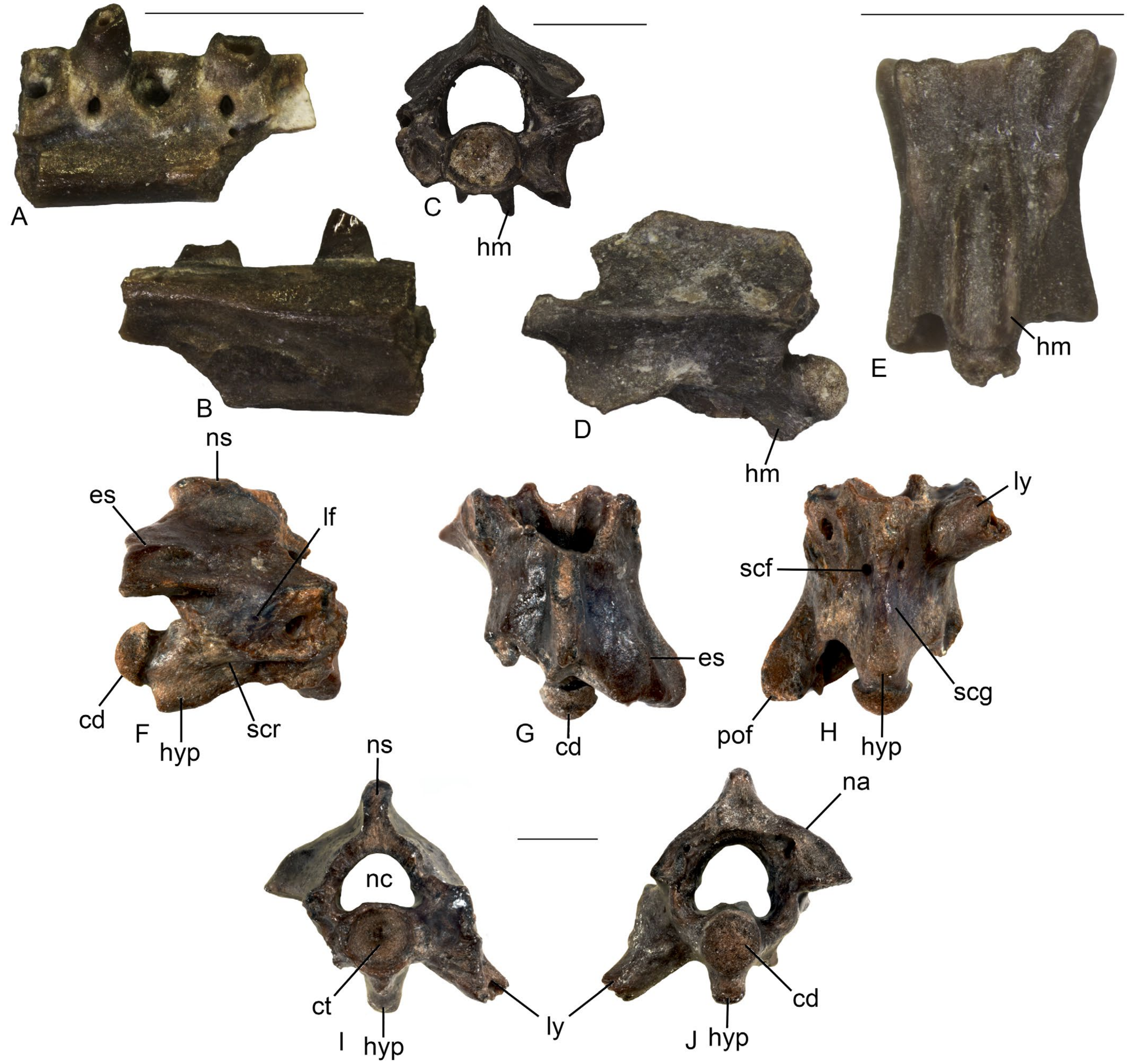

**Figure 11.** Serpentes indet. from Aliveri (A–B): fragment of the anterior part of a left pterygoid (UU AL 3529) in medial (A) and labial (B) views. Serpentes indet. from Karydia-3 (C–E): posterior caudal vertebra (AMPG KR3 021) in anterior (C) and left lateral (D) views; posterior caudal vertebra (AMPG KR3 022) in ventral (E) view. Serpentes indet. from Karydia-2 (F–J): cloacal or anterior caudal vertebra (UU KR2 5022) in right lateral (F), dorsal (G), ventral (H), anterior (I), and posterior (J) views.
Scale bars = 1 mm. Abbreviations: cd, condyle; ct, cotyle; es, epizygapophyseal spine; hm, haemapophysis; hyp, hypapophysis; lf, lateral foramen; ly, lymphapophysis; nc, neural canal; ns, neural spine; pof, postzygapophyseal facet; scf, subcentral foramen; scg, subcentral groove; scr, subcentral ridge.

a possible taxonomic attribution to Viperinae could be indirectly supported by a biogeographic rationale, as Crotalinae are only known in Europe with certainty from the late Miocene (MN 9) of Ukraine (Ivanov 1999).

Serpentes indet. (Figure 11)

*Material*. AL1a: a fragment of the anterior part of a left pterygoid (UU AL 3529). AL1980NQ: a vertebra (UU AL 3591). KR2: a cloacal or anterior caudal vertebra (UU KR2 5022), two fragmentary vertebrae (UU KR2 5023 and UU KR2 5024), and a cloacal or anterior caudal vertebra (UU KR2 5021). KR3: a fragment of a pterygoid (AMPG KR3 013), and two posterior caudal vertebrae (AMPG KR3 021 and AMPG KR3 022).

*Remarks*. These cranial and postcranial remains from Aliveri and Karydia are too fragmentary and incomplete to permit a more precise identification within snakes. It is worth noting, however, that one of these specimens, UU KR2 5022, seems to demonstrate a mixed character set between colubroids and booids (Figure 11(F)–(J)). This vertebra most probably originates from the cloacal region, as it can be judged by the presence of a strongly built, short hypapophysis and the preserved base of the ventral ramus of the left lymphapophysis, although an alternative origin from the anterior caudal region cannot be excluded. The relatively massive structure of the vertebra UU KR2 5022, with a strongly built neural spine and short hypapophysis, as well as the absence of paracotylar foramina, is reminiscent of certain Booidea (e.g. Rage 1984; Szyndlar and Rage 2003), but the ratio of a centrum length/neural arch width >1 and a condyle situated on a rather long neck are not typical for cloacal vertebrae of Booidea and are mostly characterising colubroids (e.g. Rage 1984). To make things even more complicated, several non-pythonid booids, both extinct (e.g. *Bavarioboa*) and extant (e.g. *Boa*), are also known to possess paracotylar foramina, in at least some of their vertebrae (Szyndlar and Rage 2003), rendering obscure the taxonomic reliability of this character. As such, we herein refrain from identifying UU KR2 5022 as a booid and prefer to refer it as Serpentes indet.

Squamata indet.

*Material*. AL1a: four fragments of tooth-bearing bones (UU AL 3522, UU AL 3523, UU AL 3525, and UU AL 3526), a caudal vertebra (UU AL 3527), and fragments of a vertebra and a maxilla (UU AL 3528). AL1b: a pterygoid (UU AL 3588) and a humerus (UU AL 3589). KR3: a caudal vertebra (AMPG KR3 025) and an osteoderm (AMPG KR3 009).

*Remarks*. The above mentioned specimens from Aliveri are either too poorly preserved or they lack significant diagnostic features for a more precise taxonomic attribution. As such, they are attributed only to indeterminate squamates. Similarly, the two specimens from Karydia-3 represent skeletal elements of lizards that are considered not to bear significant diagnostic features. Nevertheless, the caudal vertebra is rather small-sized (centrum length is less than 2 mm) and could therefore belong to the previously mentioned small-sized lacertid. The osteoderm, on the other hand, is different from anguid ones in shape, general morphology and ornamentation, being more similar to supraocular osteoderms of, e.g. lacertids. Given that, it could also belong to that clade.

## Discussion

### *Biogeographic implications of the Aliveri and Karydia herpetofaunas*

Both Aliveri and Karydia share common herpetofaunal elements, such as alytids, lacertids, and colubrids (Table 1). Notably, however, crocodylians, chamaeleonids, and viperids are known from Aliveri but are absent from Karydia, whereas the opposite case is known for salamanders. Of course, with the limited material currently available, it is not possible to state whether such faunistic differences among the two localities are indeed genuine and could imply ecological differences, or they are simply biased by taphonomical or incomplete collection factors. Definitely, however, the fact that Karydia has yielded significantly lower amount of fossil specimens in comparison with Aliveri might partially explain such faunistic differences among the two localities.

**Table 1.** Known occurrences of amphibians and reptiles in the early Miocene of Greece.

| | Aliveri (MN 4a) | Karydia (MN 4a) | Kymi (MN 3/4) | Nostimo (Burdigalian) | Lapsarna (?MN 3) |
|---|---|---|---|---|---|
| ?*Mioproteus* sp. | | | | | + |
| Urodela indet. | | + | | | |
| *Latonia* cf. *gigantea* | | + | | | |
| cf. *Latonia* sp. | + | | | | |
| Anura indet. | + | + | | | + |
| *Nostimochelone lampra* | | | | + | |
| Testudines indet. | + | + | | | |
| Crocodylia indet. | + | + | | | + |
| *Chamaeleo* cf. *andrusovi* and Chamaeleonidae indet. | + | | | | |
| Lacertidae indet. | + | + | | | + |
| Scincomorpha indet. | + | + | | | |
| cf. *Ophisaurus* sp. | | + | | | |
| Anguinae indet. | + | + | | | |
| *Python euboicus* | | | + | | |
| ?Natricinae indet. | | | | | + |
| Colubridae indet. | + | + | | | |
| Viperidae indet. | + | | | | |
| Serpentes indet. | + | + | | | + |
| Squamata indet. (non-snake squamates) | + | + | | | + |

Data from: Aliveri-Georgalis, Villa, and Delfino (2016b) and this paper; Karydia-this paper; Kymi-Römer (1870); Nostimo-Georgalis et al. (2013); Lapsarna Vasileiadou et al. 2017.

The single known salamander element from Karydia is not informative for a precise taxonomic identification, but still represents, along with a recently described probable proteid from Lapsarna (Lesvos) (Vasileiadou et al. 2017), the oldest urodelan remains from Greece, both being also the sole Neogene occurrences from the country. The frog remains from Karydia (and potentially also Aliveri) document the presence of *Latonia* for the first time in Greece and are fully concordant with the widespread European range of that genus during the early Neogene (Roček 1994; see also below). The fragmentary nature of the Aliveri and Karydia turtle specimens does not permit any further biogeographic assumption, but nevertheless, these constitute the oldest such remains from Greece, along with the holotype of *Nostimochelone lampra* from the Burdigalian of Nostimo (administrative region of Western Macedonia) (Georgalis et al. 2013). Crocodylians are rather rare in the Greek fossil record, and as such, they had only recently been described for the first time from the late Miocene of Plakias (Crete) (Georgalis, Villa, Vlachos et al. 2016) and soon after from the early Miocene of Lapsarna (Lesvos) (Vasileiadou et al. 2017). In any case, the new Aliveri remains demonstrate that crocodylians were more widespread in the early Miocene of the region, a situation consistent with similar finds from the Oligo-Miocene of Turkey (Schleich 1994; Sen et al. 2011). As for the lizards, the presence of a chamaeleonid in Aliveri was recently shown to support a probable Greek pathway for this African clade that could have used the '*Gomphotherium* Landbridge' for its dispersal (Georgalis, Villa and Delfino 2016). Newly described chamaeleonid remains from the early Miocene (MN 4) of Sibnica, Serbia (Đurić 2016) suggest that chameleons were more widespread faunal elements in the southern Balkan localities of that time, than what was previously thought. This clade is still absent from the as of yet poor fossil record of squamates from Anatolia. The herein described lacertids from Aliveri and Karydia, along with the recently described Lapsarna material (Vasileiadou et al. 2017), demonstrate that these lizards were already widespread in Greece already by the early Miocene and would since then continue to be a common element of the Greek herpetofaunas. Indeed, lacertids were also described from late Miocene localities of the region (Richter 1995; Georgalis et al. 2017a) and they are currently the dominant (in terms of diversity) reptile group on the European continent (Arnold et al. 2007; Sindaco and Jeremčenko 2008). The Aliveri and Karydia anguids are the oldest representatives of this clade from Greece, though they have been described from the early Miocene of Sibnica, Serbia (Đurić 2016) and various coeval localities from Turkey (Čerňanský et al. 2017), confirming their wide distribution in the area already by the early Neogene. The apparently bizarre colubrid snake from Karydia and its potentially conspecific form from Aliveri seem to possess unique autapomophies that are otherwise unknown in extinct and extant European snakes, most significantly the presence of a new vertebral feature that is herein termed as 'paracentral ridge'. The skeletal anatomy of extant African and Asian snakes is poorly documented so it is currently impossible to identify the presence of a paracentral ridge in modern taxa and to assess its potential diagnostic importance. Considering, however, that this feature is totally absent in all European extinct and extant snakes, it seems plausible that the herein newly described early Miocene Greek colubrids could represent a shortly lived radiation with African or Asian origin. The isolated snake fang from Aliveri denotes the presence of viperid snakes in Greece already by the early Miocene, being the oldest representative from that clade in the region, a presence that culminated with the magnificent *Laophis crotaloides* Owen 1857, one of the largest known viperids, from the Pliocene of Thessaloniki area (Georgalis, Szyndlar, et al. 2016).

### *Frogs of the genus* **Latonia** *in the early Neogene of southeastern Europe*

*Latonia* is a genus of discoglossine alytid frogs that thrived in Europe from the late Oligocene up to the early Pleistocene (Roček 1994, 2013; Delfino 2002), becoming the most common alytid in the continent during the Miocene. The genus may have also been present during the early Oligocene, considering a mention of *Latonia* aff. *vertaizoni* from Quercy (Rage 2006), however, this material is undescribed and still awaits a formal documentation. Starting from the Pliocene, the European range of *Latonia* underwent a southward directed contraction, which eventually resulted in its local extirpation during the Pleistocene. It has been suggested that this extinction event has been linked to Pleistocene climate change (Roček 1994). Nevertheless, *Latonia* has been documented in the early Pleistocene of Anatolia (Vasilyan et al. 2014) and it is also now known that the genus has survived in the Middle East, where the only extant representative, *Latonia nigriventer* (Mendelssohn and Steinitz 1943) still exists, being its sole living representative (Biton et al. 2013, 2016). Although several taxa have been assigned to this genus, it is now generally accepted that only four valid extinct species are known from Europe (Roček 1994): *Latonia seyfriedi* Meyer, 1843 (type species), *Latonia gigantea* (Lartet, 1851), *Latonia ragei* Hossini, 1993, and *Latonia vertaizoni* (Friant, 1944).

The remains of *Latonia* from Karydia-3 share a similar morphology and size with juveniles of *Latonia gigantea*, notwithstanding the possible presence of the foramen for the occipital artery. Assuming that our attribution of these fossils to *Latonia* cf. *gigantea* is correct, Karydia-3 would be one of the southernmost localities from which this species (or at least a morphologically rather similar form) is reported. As a matter of fact, the new Greek occurrence adds to the tentatively attributed remains from the Gargano palaeoisland in Southern Italy (Delfino 2002) and to the recently described remains from Catalonia in the Iberian Peninsula (Villa et al. 2017). This supports the hypothesis that the seemingly poor representation of *L. gigantea* in the Mediterranean area, compared with the fossil record of that species in the rest of Europe (Roček 1994, 2013), might be an artifact of either misidentification or overlooking of fossil remains, rather than a real absence from the area. Further studies on *Latonia* remains that are currently unassigned to the species level and originate from other localities in the southern European peninsulas might shed more light on this issue. Indeed, recently described remains (an ilium and an urostyle) from the early Miocene of Sibnica, Serbia, have been attributed to *Latonia* cf. *gigantea* (Đurić 2016), though they were not figured and, as such, we cannot confirm their identity. It has to be noted, however, that neither ilia nor urostyles are usually considered diagnostic for *Latonia* species, and therefore the identification of the Serbian material must be treated with caution. Moreover, remains from Karydia-3 could also represent the oldest occurrence of the species, given that this locality is considered as probably slightly older than both Dolnice (Czech Republic) and Günzburg (Germany), from which the oldest published remains of *Latonia gigantea* are currently known (Roček 1994, 2013; Böhme 2003).

In any case, the herein-described *Latonia* fossils represent the first published occurrences of the genus in Greece. Its tentative identification from Aliveri, located relatively far from Karydia (more than 300 km straightline distance), suggests a rather widespread distribution of these anurans in the southern part of the Balkan Peninsula during the early Miocene, a view that is also corroborated by their possible presence in the coeval Serbian locality of Sibnica. Nevertheless, whether the Aliveri remains pertain indeed to *Latonia*, needs to be confirmed by more diagnostic material from this or at least from other coeval sites nearby.

### *Early Miocene herpetofaunas from southeastern Europe*

The early Miocene is a rather important time interval for the herpetofaunas of Europe, as it witnesses the transition between the Oligocene to the Miocene and, therefore, records the turning point between a relatively cool and dry Oligocene stage towards a much warmer and humid climate in the early Miocene (Rage and Roček 2003; Rage 2013; Čerňanský et al. 2015). Moreover, this epoch coincides with a wave of new immigrant vertebrate taxa that penetrated to Europe, affecting dramatically the autochthonous faunas of the continent (Ivanov 2001; Rage and Roček 2003; Čerňanský 2012). Several Asian terrestrial taxa are known to have dispersed to Europe during the early Miocene, among which also reptiles (Ivanov 2001; Szyndlar 2012). Moreover, a large number of these dispersals seems to have been facilitated by the collision of the Afro-Arabian plate which created the so called '*Gomphotherium* Landbridge' and allowed a wave of African terrestrial immigrants to enter Eurasia. This event took place at around the MN 3 zone of the early Miocene and, as the name readily suggests, resulted in the establishment of a land contact between northeastern Afro-Arabia and Eurasia, diminishing thus, the marine barrier that was previously separating them (Rögl 1999; Koufos et al. 2005; Georgalis, Villa and Delfino 2016). This new land corridor acted as a platform that enabled dispersals between Eurasia and Afro-Arabia. This dispersal event caused radical faunal turnovers, ecological changes, substitutions, and extinctions across Europe. Several tetrapod terrestrial taxa are known to have dispersed from the Afro-Arabian continent to Europe, through Anatolia and the Balkan Peninsula, among which numerous mammal clades (e.g. Koufos et al. 2003, 2005), but also reptiles, such as chamaeleonids and cordylids (Čerňanský 2012; Georgalis, Villa and Delfino 2016). The opposite kind of dispersal, with a direction from Europe to Africa, has been suggested also for other reptiles, such as the anguine *Ophisaurus* (Blain et al. 2013; Čerňanský et al. 2017). Moreover, the Miocene Climatic Optimum, the beginning of which coincides at around that time period, favored the northward expansion of several thermophilic taxa, such as chamaeleonids, cordylids, and several crocodylians and turtles, that all reached their northernmost distribution by that time (Roček 1984; Böhme 2003; Čerňanský 2010). As a consequence, new clades of amphibians and reptiles appeared in the early Miocene Europe for the first time, or reappeared after millions of years after their last occurrence, whereas other clades were inevitably driven to their final demise and extinction. Two amphibian clades, bufonids and pelodytids, that had been recorded from Europe in the Paleocene and Eocene respectively, but not known then after, reappeared again in the continent, with new representatives at the early Miocene (Rage 2003, 2012; Rage and Roček 2003). Notably also, hylid frogs appeared in Europe during the early Miocene (MN 4) for the first time (Rage and Roček 2003). Moreover, various extant reptile genera, such as the turtle *Rafetus*, the lizards *Pseudopus* and *Varanus*, and the snakes *Naja* and *Python*, made their first European appearance during the early Miocene (Szyndlar and Rage 2003; Klembara 2012; Delfino et al. 2013; Rage 2013; Georgalis and Joyce 2017; Georgalis et al. 2017b; Ivanov et al. 2017), although their exact origins are not yet fully resolved. The case of *Varanus* is rather interesting, as it marks the reappearance of varanids in Europe, considering that this clade was represented in the Paleogene of the continent by a different genus (*Saniwa*) but had become extinct during the late Eocene (Rage 2013; Georgalis et al., 2017b). Shinisaur lizards became totally extinct in Europe at the early Miocene, with their last, sporadic occurrences recorded from the Czech Republic and Germany (Klembara 2008; Čerňanský et al. 2015). Viperids and elapids became brand new representatives for the European snake fauna, as they appeared for the first time in the continent at the earliest Miocene (Kuch et al. 2006; Rage 2013; Čerňanský et al. 2015; Georgalis, Szyndlar, et al. 2016). In parallel, colubrids began to thrive since then, towards an unbalanced competition with booids, the snake group that was dominant during the Paleogene (Szyndlar 2012). The diversity drop within Booidea was rather severe, being labeled in the literature as the 'Dark Period of booid snakes', and spanning from the latest Oligocene to the earliest Miocene (Szyndlar and Rage 2003; Rage and Szyndlar 2005). Finally, the enigmatic Choristodera, an ancient reptile lineage that originated in the Triassic, made its last global appearance in the fossil record during the early Miocene (MN 3) of the Czech Republic (Evans and Klembara 2005).

However, there is still a large gap in our knowledge of early Miocene herpetofaunas of Europe, which is mostly caused by the relative scarcity of localities of this age (especially Aquitanian) in the continent (Čerňanský et al. 2015, 2016). Few earliest Miocene (Aquitanian) localities have produced amphibian and/or reptile remains, the majority of which are turtles. Amphibians, crocodylians, and squamates have far more seldom occurrences, mostly consisting of fragmentary remains. The situation appears to be relatively better for the Burdigalian record, where several localities are known from Central and Western Europe, with far more amphibian and reptile finds and thus providing a better comprehension of their herpetofauna. This scarcity of localities severely hinders our understanding of important events that took place at that time interval. Furthermore, the exact biogeographic routes of the dispersals events that took place at that time are not yet well defined, as this fact is dramatically hampered by a huge gap in our knowledge of southeastern Europe's early Miocene faunas.

Greek localities from this age interval are rather rare and incompletely studied (Koufos 2006). Moreover, in most of these cases, fossil herpetofauna is not the main target of field work or study, being frequently neglected in favor of mammal finds (Georgalis, Villa, Vlachos et al. 2016). As such, up to that date only few records of early Miocene amphibians and reptiles have been described from Greece (Römer 1870; Georgalis et al. 2013; Georgalis, Villa and Delfino 2016; Vasileiadou et al. 2017) (Table 1). The situation is rather similar in adjacent regions, with only few early Miocene amphibians and reptiles described up to date from southern Balkans (Đurić 2016) and Anatolia (Čerňanský et al. 2017). This is rather frustrating, considering that various biogeographic scenaria, dispersal routes, and potential ecological refugia, altogether highlight the important role of the Greek area at around the early Miocene. Several Asian and African amphibian and reptile groups are inferred to have used Greece as the corridor towards their European expansion, whereas certain northern taxa are believed to have moved southwards during climatic deterioration.

So far, the majority of early Miocene herpetofaunal elements from Greece consists mostly of rather fragmentary remains with no apparent taxonomic usefulness, but important specimens have, nevertheless, been recovered. No amphibian and just two reptile taxa from Greece have been named from this time interval: *Python euboicus* Römer 1870; and *Nostimochelone lampra* Georgalis et al., 2012 (for 2013), both known only from their holotypes in their type localities. Additionally, only two other forms have been referred to the species level *Chamaeleo* cf. *andrusovi* from Aliveri (Georgalis, Villa and Delfino 2016) and the herein described Karydia material attributed to *Latonia* cf. *gigantea*. *Python euboicus* is a large sized pythonid snake from the early Miocene of Kymi, Euboea (Römer 1870). The age of Kymi was initially thought to be from the MN 3 zone, but recently it has been suggested that it is from the MN 4 (Szyndlar and Rage 2003). The unfortunate fact that the rather complete holotype skeleton (and only known specimen) is lost hinders the exact taxonomic status and phylogenetic affinities of this taxon. *Nostimochelone lampra* is a podocnemidoidean pleurodire turtle from the early Miocene (Burdigalian) of Nostimo, northwestern Greece (Georgalis et al. 2013). Apart from being the first and only known pleurodire from the region, *Nostimochelone lampra* represents also one of the youngest representatives of this group for the whole European continent (Georgalis and Kear 2013; Georgalis et al. 2013). The recently described chamaeleonid material from Aliveri (*Chamaeleo* cf. *andrusovi*) was shown to bear strong resemblance with roughly coeval forms from the Czech Republic, highlighting a possible dispersal pathway of these lizards from Africa to Anatolia and from there to Greece and then to Central Europe (Georgalis, Villa and Delfino 2016). Therefore, fossil amphibians and reptiles from the localities of Kymi, Nostimo, Lapsarna, Aliveri, and Karydia fill thus an important gap into the early Miocene Greek herpetofaunal vacuum and, as such, are crucial for the understanding of the evolution, taxonomy, and biogeography of these groups in Europe.

## Conclusions

We herein describe fossil amphibians and reptiles from two early Miocene (MN 4) Greek localities, Aliveri and Karydia. Together, these two herpetofaunas have yielded a relatively diverse assemblage consisting of urodelans, alytids, indeterminate anurans, turtles, crocodylians, chamaeleonids, lacertids, indeterminate scincomorphs, anguids, colubrids, viperids, and indeterminate snakes. The frog *Latonia* cf. *gigantea* is described from Greece for the first time and provides implications about the distribution and evolution of that amphibian lineage in Europe. The presence of a viperid in Aliveri denotes that this snake clade achieved a much wider distribution already during the early Neogene of Europe, than what was previously thought. We additionally identify a colubrid that is characterised by a unique combination of features and above all, the presence of an as yet unknown vertebral structure in the lateral walls of the centrum, for which we here introduce the term 'paracentral ridge'. The palaeobiogeography of the European herpetofauna during the early Miocene is discussed. Multiple dispersal events from both Asia and Africa, in combination with major climatic changes (beginning of the Miocene Thermal Maximum) resulted in appearances of new immigrant taxa, extinction events, and significant faunal turnovers that all drastically altered European herpetofaunas. The geographic position of Greece at the edge of southeastern Europe played an important role in dispersals that were facilitated through the collision of the Afro-Arabian plate with Eurasia and the emergence of the '*Gomphotherium* Landbridge' during the early Miocene. The newly described specimens from Aliveri and Karydia partially fill a gap into our knowledge of the early Miocene amphibians and reptiles from this region.

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## References

Arnold EN, Arribas O, Carranza S. 2007. Systematics of the palaearctic and oriental lizard tribe C. Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa. 1430:1–86.

Augé ML. 2005. Evolution des lézards du Paléogène en Europe [Evolution of lizards from the Paleogene of Europe]. Mém Mus Natl d'Hist Nat. 192:3–369.

Bailon S. 1991. Amphibiens et Reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes [Amphibians and reptiles from the Pliocene and Quaternary of France and Spain] [PhD dissertation]. Paris: Université de Paris VII.

Bailon S. 1999. Différenciation ostéologique des anoures (Amphibia, Anura) de France [Osteological differentiation of anurans (Amphibia, Anura) from France]. In: Desse J, Desse-Berset N, editors. Fiches d'ostéologie animale pour l'Archéologie [Animal Osteology Sheets for Archeology], Série C: Varia, 1. Antibes: APDCA; p. 1–41.

Barahona FF. 1996. Osteología craneal de lacértidos de la Península Ibérica e Islas Canarias: análisis sistemático filogenético [Cranial osteology of lacertids from the Iberian Peninsula: systematic and phylogenetic analysis]. [PhD dissertation]. Madrid: Universidad Autónoma de Madrid.

Batsch AJGC. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen, Erster Theil Allgemeine Geschichte der Natur; besondre der Saügthiere, Vögel, Amphibien und Fische. Jena: Akademische Buchhandlung.

Biton R, Geffen E, Vences M, Cohen O, Bailon S, Rabinovich R, Malka Y, Oron T, Boistel R, Brumfeld V, Gafny S. 2013. The rediscovered Hula painted frog is a living fossil. Nat Commun. 4:1959.

Biton R, Boistel R, Rabinovich R, Gafny S, Brumfeld V, Bailon S. 2016. Osteological observations on the alytid anuran *Latonia nigriventer* with comments on functional morphology, biogeography, and evolutionary history. J Morphol. 277:1131–1145.

Blain H-A, Agustí J, López-García JM, Haddoumi H, Aouraghe H, Hammouti K, Pérez-González A, Chacón MG, Sala R. 2013. Amphibians and squamate reptiles from the late Miocene (Vallesian) of eastern Morocco (Guefaït-1, Jerada Province). J Vertebr Paleontol. 33:804–816.

de Blainville HM. 1816. Prodrome d'une nouvelle distribution systématique du règne animal. Bull Sci Soc Philom Paris. 8:113–124.

Böhme M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeogr Palaeoclimatol Palaeoecol. 195:389–401.

de Bruijn H. 2017. A new stage in the evolution of the mole rats (Rodentia, Spalacinae) from the Early Miocene of northern Greece. Hist Biol. 29:571–575.

de Bruijn H, van der Meulen AJ. 1979. A review of the Neogene rodent succesion in Greece. Ann Geol des Pays Helleniques. 1979:207–217.

de Bruijn H, van der Meulen AJ, Katsikatsos G. 1980. The mammals from the lower Miocene of Aliveri (Island of Evia, Greece) 1. The Sciuridae. Proc Koninkl Nederl Akad Wetensc Ser B. 83:241–261.

Camp CL. 1923. Classification of the lizards. Bul Am Mus Nat Hist. 48:289–481.

Čerňanský A. 2010. A revision of chamaeleonids from the Lower Miocene of the Czech Republic with description of a new species of *Chamaeleo* (Squamata, Chamaeleonidae). Geobios. 43:605–613.

Čerňanský A. 2012. The oldest known European Neogene girdled lizard fauna (Squamata, Cordylidae), with comments on Early Miocene immigration of African taxa. Geodiversitas. 34:837–848.

Čerňanský A, Tóth C, Šurka J. 2012. Crocodylian and turtle finds from the Lower Miocene of the Baňa Dolina mine in Veľký Krtíš (Slovakia). Acta Geol Slovaca. 4:113–123. [in Slovak with English summary].

Čerňanský A, Rage J-C, Klembara J. 2015. The early miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. J Syst Palaeontol. 13:97–128.

Čerňanský A, Klembara J, Smith KT. 2016. Fossil lizard from central Europe resolves the origin of large body size and herbivory in giant Canary Island lacertids. Zool J Linn Soc. 176:861–877.

Čerňanský A, Vasilyan D, Georgalis GL, Joniak P, Mayda S, Klembara J. 2017. First record of fossil anguines (Squamata; Anguidae) from the Oligocene and Miocene of Turkey. Swiss J Geosci. 110:741–751.

Cope ED. 1864. On the characters of the higher groups of Reptilia Squamata – and especially of the Diploglossa. Proc Acad Nat Sci Philad. 1864:224–231.

Daudin FM. 1803. Histoire naturelle, générale et particulière des reptiles: ouvrage faisant suite à l'Histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par CS Sonnini Tome septième. Paris: F. Dufart; 436 pp.

Delfino M. 2002. Erpetofaune italiane del Neogene e del Quaternario [Italian herpetofaunas from the Neogene and the Quaternary] [PhD dissertation]. Modena (Italy): University of Modena and Reggio Emilia.

Delfino M, Rage J-C, Rook L. 2003. Tertiary mammal turnover phenomena: what happened to the herpetofauna? In: Reumer JWF, Wessels W, editors. Distribution and migration of Tertiary mammals in Eurasia, a volume in honour of Hans de Bruijn. Deinsea. 10, p. 153–161.

Delfino M, Böhme M, Rook L. 2007. First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy). Zool J Linn Soc. 149:293–307.

Delfino M, Bailon S, Pitruzzella G. 2011. The Late Pliocene amphibians and reptiles from "Capo Mannu D1 Local Fauna" (Mandriola, Sardinia, Italy). Geodiversitas. 33:357–382.

Delfino M, Rage J-C, Bolet A, Alba DM. 2013. Early Miocene dispersal of the lizard *Varanus* into Europe: reassessment of vertebral material from Spain. Acta Palaeontol Pol. 58:731–735.

Doukas CS. 2003. The MN4 faunas of Aliveri and Karydia (Greece). Coloquios de Paleontología, Volumen Extraordinario. 1:127–132.

Doukas CS. 2005. Greece. In: van den Hoek Ostende LW, Doukas CS, Reumer JWF, editors. The fossil record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I Scripta Geologica Special Issue. 5, p. 99–112.

Doukas CS, van den Hoek Ostende LW. 2006. Insectivores (Erinaceomorpha, Soricomorpha; Mammalia) from Karydia and Komotini (Thrace, Greece; MN 4/5). Beiträge zur Paläontologie. 30:109–131.

Duméril AMC. 1806. Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques. Paris: Allais; p. 544.

Đurić D. 2016. The Early Miocene herpetofauna (Amphibia and Squamata) from Sibnica, Serbia. In: Marković Z, Milivojević M, editors. The Neogene of Sibnica and vicinity (Levač basin, Central Serbia) Part 1. Belgrade. Natural History Museum in Belgrade Special issue; p. 57–61.

Estes R. 1983. Sauria Terrestria, Amphisbaenia. In: Wellnhofer P, editor. Encyclopedia of paleoherpetology. Stuttgart: Gustav Fisher Verlag; 249 pp.

Estes R, de Queiroz K, Gauthier J. 1988. Phylogenetic relationships within Squamata. In: Estes R, Pregill G, editors. Phylogenetic relationships of the lizard families. Stanford, CA: Stanford University Press; p. 119–282.

Evans SE. 2008. The skull of lizards and tuatara. In: Gans C, Gaunt AS, Adler K, editors. Biology of the reptilia volume 20 the skull of Lepidosauria. Ithaca (NY): Society for the Study of Amphibians and Reptiles; p. 1–347.

Evans SE, Klembara J. 2005. A choristoderan reptile (Reptilia: Diapsida) from the Lower Miocene of Northwest Bohemia (Czech Republic). J Vertebr Paleontol. 25:171–184.

Fischer von Waldheim G. 1813. Zoognosia tabulis synopticis illustrata usum praelectionum academiae imperialis medico-chirurgicae mosquensis edita. Vol. 1. Moscow: Nicolai Sergeidis Vsevolozsky.

Fitzinger LJFJ. 1843. Systema Reptilium. Fasciculus Primus. Vienna: Braumüller et Seidel.

Frey E, Monninger S. 2010. Lost in action–the isolated crocodilian teeth from Enspel and their interpretive value. Palaeobiodivers Palaeoenviron. 90:65–81.

Friant M. 1944. Caractères anatomiques d'un batracien oligocène de la Limagne, le *Prodiscoglossus vertaizoni* nov. gen. nov. spec [Anatomical characters of an Oligocene batrachian from Limagne, *Prodiscoglossus vertaizoni* nov. gen. nov. sp]. C R Hebd Seances Acad Sci. 219:561–562.

Fürbringer M. 1900. Zur vergleichenden anatomie des Brustschulterapparates und der Schultermuskeln. Jenaische Z. 34:215–718.

Georgalis GL, Joyce WG. 2017. A review of the fossil record of old world turtles of the clade *Pan-Trionychidae*. Bull Peab Mus Nat Hist. 58:115–208.

Georgalis GL, Kear BP. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios. 46:299–311.

Georgalis GL, Velitzelos E, Velitzelos D, Kear BP. 2013. *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the lower Miocene of northern Greece. In: Brinkman D, Holroyd P, Gardner J, editors. Morphology and evolution of turtles: papers in honor of Eugene S Gaffney Volume 3 Pleurodires. Dordrecht (The Netherlands): Springer; p. 277–287.

Georgalis GL, Szyndlar Z, Kear BP, Delfino M. 2016. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss J Geosci. 109:103–116.

Georgalis GL, Villa A, Delfino M. 2016. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. Sci Nat. 103:47.

Georgalis GL, Villa A, Vlachos E, Delfino M. 2016. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios. 49:433–444.

Georgalis GL, Villa A, Delfino M. 2017a. Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. Hist Biol. 29:730–742.

Georgalis GL, Villa A, Delfino M. 2017b. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. J Vertebr Paleontol. 37:e1301946.

Gmelin JF. 1789. Tom. I. Pars III. In: Beer GE, editors, Caroli a Linné, Systema Naturae. Leipzig: Impensis Georg. Emanuel. Beer. p. 1033–1516.

Gray JE. 1825. A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. Ann Philos Ser. 2(10):193–217.

Head JJ, Mahlow K, Müller J. 2016. Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidea, Colubridae. Palaeontol Electronica. 19.2.2FC:1–21.

van den Hoek Ostende LW, Mayda S, Oliver A, Madern A, Hernández-Ballarín V, Peláez-Campomanes P. 2015. Aliveri revisited, a biogeographical appraisal of the early Miocene mammals from the eastern Mediterranean. Palaeobiodivers Palaeoenviron. 95:271–284.

Holman JA. 2000. Fossil snakes of North America: origin, evolution, distribution, paleoecology. Bloomington: Indiana University Press. 357 pp.

Hossini S. 1993. A new species of *Latonia* (Anura, Discoglossidae) from the lower Miocene of France. Amphibia-Reptilia. 14:237–245.

Ikeda T. 2007. A comparative morphological study of vertebrae of snakes occurring in Japan and adjacent regions. Curr Herpetol. 26:13–34.

Ivanov M. 1999. The first European pit viper from the Miocene of Ukraine. Acta Palaeontol Pol. 44:327–334.

Ivanov M. 2001. Changes in the composition of the European snake fauna during the early Miocene and at the early/middle Miocene transition. Paläontol Z. 74:563–573.

Ivanov M, Ruta M, Klembara J, Böhme M. 2017. A new species of *Varanus* (Anguimorpha: Varanidae) from the early Miocene of the Czech Republic, and its relationships and palaeoecology. J Syst Palaeontol 1–31.

Jackson K. 2002. How tubular venom conducting fangs are formed. J Morphol. 252:291–297.

Joyce WG. 2016. A review of the fossil record of turtles of the clade pan-chelydridae. Bull Peab Mus Nat Hist. 57:21–56.

Joyce WG, Parham JF, Gauthier JA. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. J Paleontol. 78:989–1013.

Klembara J. 1981. Beiträgzurkenntnis der subfamilie Anguinae (Reptilia, Anguidae). Acta Univ Carol – Geol. 2:121–168.

Klembara J. 2008. A new anguimorph lizard from the lower miocene of north-west bohemia, czech republic. Palaeontology. 51:81–94.

Klembara J. 2012. A new species of *Pseudopus* (Squamata, Anguidae) from the early Miocene of Northwest Bohemia (Czech Republic). J Vertebr Paleontol. 32:854–866.

Klembara J. 2015. New finds of anguines (Squamata, Anguidae) from the Early Miocene of Northwest Bohemia (Czech Republic). Paläontol Z. 89:171–195.

Klembara J, Hain M, Dobiašová K. 2014. Comparative Anatomy of the Lower Jaw and Dentition of *Pseudopus apodus* and the Interrelationships of Species of Subfamily Anguinae (Anguimorpha, Anguidae). Anat Rec. 297:516–544.

Koufos GD. 2006. The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. Ann Geol des Pays Helleniques. 4:183–214.

Koufos G. 2013. Neogene mammal biostratigraphy and chronology of Greece. In: Wang X, Flynn LJ, Fortelius M, editors. Fossils mammals of Asia: neogene biostratigraphy and chronology. New York (NY): Columbia University Press; p. 595–626.

Koufos GD, Zouros N, Mourouzidou O. 2003. *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from Lesvos island, Greece; the appearance of deinotheres in the eastern Mediterranean. Geobios. 36:305–315.

Koufos GD, Kostopoulos D, Vlachou T. 2005. Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belg J Zool. 135:181–190.

Kuch U, Müller J, Mödden C, Mebs D. 2006. Snake fangs from the Lower Miocene of Germany: evolutionary stability of perfect weapons. Naturwissenschaften. 93:84–87.

LaDuke TC. 1991. The fossil snakes of Pit 91, Rancho la Brea, California. Contrib Sci Nat Hist Mus Los Angeles County. 424:1–28.

Lartet E. 1851. Notice sur la colline de Sansan, suivie d'une récapitulation des diverses espèces d'animaux vertébrés fossiles, trouvés soit à Sansan, soit dans d'autres gisements du terrain tertiaire miocène dans le Bassins-Pyrénéen. Auch: J.-A. Portes; 42 pp.

Laurenti JN. 1768. Austriaci Viennensis specimen medicum, exhibens synopsin reptilium emendatam cum experimentis ca Venena et antidota reptilium Austriacorum quod authoritate et consensu. Vienna (Austria): Joannis Thomae de Trattnern, Caes. Reg. Maj. Aulae Typographi et Bibliopolae.

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis Tomus 1, Pars 1. Stockholm (Sweden): Laurentii Salvius.

Mendelssohn H, Steinitz H. 1943. A new frog from palestine. Copeia. 1943:231–233.

von Meyer H. 1843. Mittheilungen an Professor Bronn gerichtet. Neues Jahrb Mineral Geognosie. 1843:579–590.

Nopcsa F. 1923. Die Familien der Reptilien [The families of the Reptiles]. Fortschritte Geol Paläontologie. 2:1–210.

Oppel M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodom einer Naturgeschichte derselben. München (Germany): Joseph Lindauer Verlag.

Owen R. 1857. On the fossil vertebrae of a Serpent (*Laophis crotaloïdes*, Ow.) discovered by Capt. Spratt, R.N., in a tertiary formation at Salonica. Q J Geol Soc London. 13:196–199.

Pyron RA, Burbrink FT, Wiens JJ. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evol Biol. 13:93.

Rage J-C. 1984. Serpentes In: Wellnhofer P, editor. Encyclopedia of paleoherpetology. Stuttgart: Gustav Fisher Verlag; 80 pp.

Rage J-C. 2003. Oldest Bufonidae (Amphibia, Anura) from the Old World: a bufonid from the Paleocene of France. J Vertebr Paleontol. 23:462–463.

Rage J-C. 2006. The lower vertebrates from the Eocene and Oligocene of the Phosphorites du Quercy (France): an overview. Strata. 13:161–173.

Rage JC. 2012. Amphibians and squamates in the Eocene of Europe: what do they tell us? Palaeobiodivers Palaeoenviron. 92:445–457.

Rage J-C. 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodivers Palaeoenviron. 93:517–534.

Rage J-C, Hossini S. 2000. Les Amphibiens du Miocène moyen de Sansan. Mém Mus Natl d'Hist Nat. 183:177–217.

Rage J-C, Roček Z. 2003. Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. Amphibia-Reptilia. 24:133–167.

Rage J-C, Szyndlar Z. 2005. Latest Oligocene-Early Miocene in Europe: Dark Period for booid snakes. C R Palevol. 4:428–435.

Richter A. 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). Münchner Geowiss Abh. 28:35–38.

Roček Z. 1984. Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia). Rozpravy Ceskoslovenské Akademie Ved, Rada Matematickych a prírodních Ved. 94:3–69.

Roček Z. 1994. Taxonomy and distribution of tertiary discoglossids (Anura) of the genus *Latonia* v. Meyer, 1843. Geobios. 27:717–751.

Roček Z. 2013. Mesozoic and Tertiary Anura of Laurasia. Palaeobiodivers Palaeoenviron. 93:397–439.

Rögl F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geol Carpathica. 50:330–349.

Römer F. 1870. Über *Python Euboïcus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea [On *Python Euboïcus*, a fossil giant snake from the tertiary shale of Kumi in the island of Euboea]. Z Dtsch geol Gesell. 22:582–590.

Schleich HH. 1994. Fossil Schildkröten- und Krokodilreste aus dem Tertiär Thrakiens (W-Türkei). Cour Forsch-Inst Senckenberg. 173:137–151.

Sen S, Antoine PO, Varol B, Ayyildiz T, Sözeri K. 2011. Giant rhinoceros *Paraceratherium* and other vertebrates from Oligocene and middle Miocene deposits of the Kağızman-Tuzluca Basin, Eastern Turkey. Naturwissenschaften. 98:407–423.

Sindaco R, Jeremčenko V. 2008. The Reptiles of the Western Palearctic Vol 1 Annotated Checklist and Distributional Atlas of the Turtles, Crocodiles, Amphisbaenians and Lizards of Europe, North Africa, Middle East and Central Asia. Belvedere: Monografie della Societas Herpetologica Italica I.

Szyndlar Z. 1984. Fossil snakes from Poland. Acta Zool Cracov. 28:1–156.

Szyndlar Z. 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae. Colubrinae Estud Geol. 47:103–126.

Szyndlar Z. 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae. Viperidae Estud Geol. 47:237–266.

Szyndlar Z. 2005. Snake fauna from the Late Miocene of Rudabánya. In: Bernor RL, Kordos L, Rook L, editors. Multidisciplinary research at Rudabánya Palaeontogr Ital. 90, p. 31–52.

Szyndlar Z. 2012. Early Oligocene to Pliocene Colubridae of Europe: a review. Bull Soc Géol France. 183:661–681.

Szyndlar Z, Rage J-C. 2003. Non-erycine Booidea from the Oligocene and Miocene of Europe. Kraków: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences; 111 pp.

Theocharopoulos CD. 2000. Late Oligocene-Middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys* n. gen. from the Eastern Mediterranean area. Gaia. 8:1–113.

Vasileiadou K, Zouros N. 2012. Early Miocene micromammals from the Lesvos Petrified Forest (Greece): preliminary results. Palaeobiodivers Palaeoenviron. 92:249–264.

Vasileiadou K, Böhme M, Neubauer TA, Georgalis GL, Syrides GE, Papadopoulou L, Zouros N. 2017. Early Miocene gastropod and ectothermic vertebrate remains from the Lesvos Petrified Forest (Greece). Pal Z 91(4):541–564.

Vasilyan D, Schneider S, Bayraktutan MS, Şen Ş. 2014. Early Pleistocene freshwater communities and rodents from the Pasinler Basin (Erzurum Province, north-eastern Turkey). Turkish J Earth Sci. 23:293–307.

Villa A, Delfino M, Luján ÀH, Almécija S, Alba DM. 2017. First record of *Latonia gigantea* (Anura, Alytidae) from the Iberian Peninsula. Hist Biol 1–12.

Zahradnicek O, Horacek I, Tucker AS. 2008. Viperous fangs: development and evolution of the venom canal. Mech Dev. 125:786–796.