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New diverse amphibian and reptile assemblages from the late Neogene of northern Greece provide novel insights into the emergence of extant herpetofaunas of the southern Balkans

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Abstract

We here describe abundant new fossil material of amphibians and reptiles from different late Neogene localities of northern Greece: the Early Pliocene (MN 14) of Spilia 0, Spilia 1, and Spilia 2; the Early Pliocene (MN 15) of Spilia 3, Spilia 4, Spilia 5, and Vevi; and the Late Miocene or Pliocene of Chalicorrema and Rema Marmara. These new late Neogene herpetofaunas are highly diverse, documenting a considerably rich herpetofauna allowing the identification of at least two salamander, seven frog, two turtle, seven lizard, and eight snake taxa. Salamanders are represented by the salamandrid genera *Ommatotriton* and *Ichthyosaura*. Frogs are represented by the bombinatorid *Bombina*, the discoglossids *Latonia* cf. *ragei* and *Latonia* sp., the pelobatid *Pelobates* aff. *praefuscus* and *Pelobates* sp., the ranids *Pelophylax* and *Rana* cf. *dalmatina*, the hylid *Hyla* gr. *arborea*, and the bufonid *Bufo* gr. *viridis*. Turtles are represented by the emydid *Emys* and an indeterminate geoemydid. Lizards are represented by the scincid *Ophiomorus*, two lacertids (one of which potentially pertaining to *Lacerta*), amphisbaenians, agamids, the anguid *Pseudopus*, and a potential varanid. Snakes are represented by the erycid *Eryx*, the natricid *Natrix* aff. *rudabanyaensis*, a small-sized elapid, an "Oriental viper", the colubriforms *Periergophis* and *Paraxenophis*, as well as two further distinct but still indeterminate morphotypes of colubriforms. For the material from Spilia tentatively referred to *Ommatotriton*, this is only the third occurrence in the fossil record globally. The new material of *Ichthyosaura* and *Bombina* mark the first documentation of these genera in the Greek fossil record. Abundant cranial and postcranial material from Spilia is tentatively referred to *Latonia* *ragei*, a taxon previously known from the Early Miocene of Western Europe. The new record of *Pelobates* represents the oldest documented occurrences of the genus in the Greek fossil record. Interestingly, the *Pelobates* from Spilia bears much resemblance to an extinct taxon, *Pelobates* aff. *praefuscus*, which is otherwise known from the Late Miocene of the Caucasus, and not to the extant species that currently inhabits the area. The identification of *Pelophylax* and *Rana* adds to the rather poor Neogene record of ranids from Greece. Particularly for the case of *Rana* cf. *dalmatina* from Spilia 4, this corresponds to the only documented occurrence of this extant taxon in the Greek fossil record. Similarly, the identification of *Hyla* gr. *arborea* in Spilia 1, Spilia 3, and Spilia 4, marks only the third documented occurrence of this genus in the Greek fossil record. The *Bufo* material from Spilia 1,

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Spilia 3, and Spilia 4 represents the first documented fossil occurrence of the extant *Bufo viridis* complex in Greece. The material of *Emys* gr. *orbicularis* from Vevi marks the only known pre-Quaternary record of the genus in Greece and one of the only few Neogene members of the genus known from Europe. The scincid *Ophiomorus* is identified in Spilia 4, known from several cranial and postcranial remains, well outside the extant range of the genus. Practically, the Spilia *Ophiomorus* is only the fourth known fossil occurrence of this extant genus globally and also represents one of its oldest known occurrences. Material from Spilia 1 and Spilia 3 is tentatively referred to cf. *Lacerta* sp., and this would mark the first known occurrence of this emblematic extant genus in the Greek fossil record, denoting the presence of the genus since at least the Early Pliocene. The new amphisbaenian specimens from Spilia 4 add to the recently described single vertebra from the same locality, and represent the youngest occurrence of amphisbaenians from continental Eastern Europe. The new agamid material from Vevi and Chalicorrema add substantially to the record of this group, which was in Greece so far known exclusively from the latest Miocene/earliest Pliocene of Maramena. A similarly important addition is the record of *Pseudopus* from Spilia 4, as this genus had been known in the Greek fossil record only from a very few localities. The potential varanid from Spilia represents one of the few Pliocene occurrences of this group in Europe. We identify *Natrix* aff. *rudabanyaensis* among the material from Spilia 0, Spilia 4, and Vevi, adding to the previously known record of this taxon from Maramena, however, its precise species level assignment should await a revision of Neogene European *Natrix* spp. The find of a small elapid from Spilia 4 represents the youngest occurrence of a coral snake from Europe, extending their stratigraphic range up to the Early Pliocene (MN 14). *Periergophis* and *Paraxenophis*, two bizarre snakes, so far exclusively known from their type locality in Maramena, could be also present here, even if tentatively identified. Most notably, the new material from these localities comprises forms that are now extinct (e.g., *Periergophis* and *Paraxenophis*) or extirpated from Europe (e.g., *Latoria*, *Varanidae*, *Elapidae*) but at the same time also loudly attests the emergence of the extant genera that dominate the extant herpetofaunas of Greece (*Ichthyosaura*, *Bombina*, *Pelobates*, *Pelophylax*, *Rana*, *Hyla*, *Bufo*, *Emys*, *Ophiomorus*, *Lacerta*, *Pseudopus*, *Eryx*, and *Natrix*), for some of which their fossil record is documented here for the first time in the area.

Keywords Anura, Urodela, Testudines, Squamata, Serpentes, Miocene, Pliocene, Greece, Taxonomy, Anatomy

Introduction

Greece harbors one of the most diverse extant herpetofaunas in Europe, with an astonishing array of amphibian and reptile taxa, including multiple endemic genera and species (Sillero et al., 2014; Speybroeck et al., 2020). Molecular evidence, together with the fossil record, have suggested that this current extant herpetofaunal diversity in the region represents the dynamic product of intense evolutionary processes, dispersal and extinction events, climatic and environmental perturbations, and palaeogeographic alterations, which occurred throughout the Cenozoic, but particularly during the past few million years, and which all shaped the extant amphibian and reptilian taxonomic composition across the Greek mainland and islands (e.g., Lymberakis & Poulakakis, 2010; Macaluso et al., 2023a). Nevertheless, the fossil record of amphibians and reptiles in Greece is far from complete, spanning only from the Early Miocene up to the Holocene, but still includes some extinct forms, others that are now extirpated from the European continent, as well as a few representatives of some of the extant genera that currently inhabit the area (see Delfino & Georgalis, 2022; Georgalis & Delfino, 2022a, 2022b; Vlachos, 2022 and references therein).

Such incomplete fossil record of amphibians and reptiles from Greece is apparently hindering our understanding on how and when some taxa became extinct and how and when the currently inhabiting extant taxa appeared and prevailed in the area. This scarcity is particularly true for the Pliocene epoch, as fossil localities of that age from Greece that yielded amphibian and reptile remains are only a few, and these usually comprise only fragmentary remains (Delfino & Georgalis, 2022; Georgalis & Delfino, 2022b; Vlachos, 2022). Nevertheless, the Pliocene represents a quintessential stage in the evolution and emergence of extant taxa, as it succeeds a much warmer Miocene and it commences immediately after one of the most important faunal turnovers and climatic, biogeographic, and palaeogeographic events that hampered Cenozoic Europe, i.e., the Messinian Salinity Crisis (for herpetofaunal studies see Georgalis & Szyndlar, 2022; Georgalis et al., 2019b; Ivanov, 2022; Macaluso et al., 2023a; Villa & Delfino, 2019b). Due to its geographic position, situated at the southern tip of the Balkan Peninsula and at the margins of the European continent with Asia, the area of Greece has been right at the forefront of these prominent late Neogene faunal events and thus offers an unprecedented potential to study their impact on herpetofaunas.

We here describe abundant new fossil material of amphibians and reptiles from the late Neogene of northern Greece. The specimens originate from the Early Pliocene of Spilia [MN 14 (Spilia 0, 1, 2) and MN 15 (Spilia 3, 4, 5)], the Early Pliocene (MN 15) of Vevi, and the Late Miocene or Pliocene of Chalicorrema and Rema Marmara, and all attest for a high diversity of amphibians and reptiles in the late Neogene of the area. Principally, the new material demonstrates the coexistence in the region of a few relict taxa of past, warmer Miocene climates, together with a spectacularly high amount of extant genera, some recognized in the fossil record of the broader area for the first time. The significance of these new fossil occurrences and their bearing on our understanding of the evolution and emergence of extant herpetofaunas, are thoroughly discussed.

Material and methods

All fossil specimens are permanently curated at the collections of UU. Comparative skeletal material of extant amphibians and reptiles was studied in the collections of HNHM, ISEZ, MGPT-MDHC, MNCN, MNHN, NHMW, NMP, PIMUZ, and SME.

Taxonomy follows Dubois et al. (2021) for amphibians, Joyce et al. (2021) for turtles, Pyron et al. (2013), Zheng and Wiens (2016), and Burbrink et al. (2020) for lizards, and Zaher et al. (2009), Pyron et al. (2014), Burbrink et al. (2020), Georgalis and Smith (2020), and Smith and Georgalis (2022) for snakes.

Anatomical terminology follows: Villa et al. (2014) for urodeles (cranial); Ratnikov and Litvinchuk (2007) and Macaluso et al. (2023b) for urodeles (vertebrae); Vater (2003) for urodeles (appendicular); Sanchíz (1998) for anurans (general); Gómez and Turazzini (2016) for anurans (ilia); Joyce and Bell (2004) for turtles; Villa and Delfino (2019a) for lizards (cranial); Tschopp (2016), Georgalis et al. (2018c), and Čerňanský et al. (2019) for lizards (vertebrae); Rage (1984), Szyndlar (1984), and Cundall and Irish (2008) for snakes (cranial); and Rage (1984), Szyndlar (1984), Georgalis et al. (2021b), and Szyndlar and Georgalis (2023) for snakes (vertebrae).

Institutional abbreviations HNHM: Hungarian Natural History Museum, Budapest, Hungary; ISEZ: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; MGPT-MDHC: Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of 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, Czech Republic; PIMUZ: Palaeontological Institute and Museum of the University of Zurich, Switzerland; SME:

Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany; UU: Department of Earth Sciences, University of Utrecht, Utrecht, Netherlands.

Localities

All localities that are the focus of this paper are situated in northern Greece (Fig. 1). The localities of Spilia belong to the Regional Unit of Serres in the Administrative Region of Central Macedonia, the localities of Chalicorrema and Rema Marmara belong to the Regional Unit of Kavala in the Administrative Region of Eastern Macedonia and Thrace, whereas Vevi belongs to the Regional Unit of Florina in the Administrative Region of Western Macedonia.

The localities Spilia 0, 1, 2, 3, 4, 5 are parts of the Spilia Formation in the Strymon Basin (de Bruijn, 1989; van der Meulen & van Kolfschoten, 1986). Spilia 0 and 1 are the oldest, considered MN 14, whereas Spilia 3 and 4 are the youngest, with an age of MN 15 (de Bruijn, 1989; Doukas & Papayianni, 2016; Koufos, 2006, 2013; van der Meulen & van Kolfschoten, 1986). The localities of Spilia 2 and 5 yielded very few fossil specimens and they have not been precisely stratigraphically constrained but it can be tentatively considered that Spilia 2 pertains to MN 14 and Spilia 5 to MN 15 (de Bruijn, 1989). The most abundant amphibian and reptile fossil remains from our sample originate from Spilia 4, Spilia 3, and Spilia 1, whereas the material from Spilia 0 and Spilia 2 is much limited, and only a single specimen comes from Spilia 5. For details on the geology of the Spilia Formation, see Armour-Brown



Fig. 1 Map of Greece, indicating the localities of Spilia [Spilia 0 (MN 14), Spilia 1 (MN 14), Spilia 2 (MN 14), Spilia 3 (MN 15), Spilia 4 (MN 15), and Spilia 5 (MN 15)], Vevi (MN 15), Chalicorrema (Late Miocene or Pliocene), and Rema Marmara (Late Miocene or Pliocene). Map adapted from (https://commons.wikimedia.org/wiki/File:Greece_location_map.svg)

et. al. (1977) and de Bruijn (1989). The only reptile that had been so far documented from Spilia is a single amphibiaenian vertebra described by Georgalis et. al. (2018c) from Spilia 4. Frog remains have also been mentioned from Spilia by Sanchíz (1998), however, they had not been formally described or figured.

Vevi is situated to the east of the city of Florina. The fossil locality pertains to an Early Pliocene age (MN 15; Doukas & Papayianni, 2016). Among amphibians and reptiles, only frog remains have been mentioned, but not described or figured, by Sanchíz (1998).

Chalicerrema and Rema Marmara are located near along the seaside road leading to Kavala. Both these localities pertain to ravines (“rema” meaning “ravine” in Greek) that were situated on roadcuts of the seaside road that was connecting the cities of Thessaloniki and Kavala, discovered during the original fieldwork conducted there during the 1970’s by Hans de Bruijn, Derek Erdbrink (UU), and Constantine Doukas (University of Athens) (C. Doukas, personal communication to GLG, August 2023). Our herein studied material from Chalicerrema and Rema Marmara originates from this original fieldwork. Nevertheless, we found it rather puzzling to spot the precise locations of both these localities. The ambiguity about their exact locations was also hampered by the fact that some ravine names in the area have since been changed or even that some localities that bear particular ravine names are in fact situated in different ravines than the actual ravine with that name (G. Syrides, personal communication to GLG, August 2023)! Chalicerrema (formerly known also as Rema Aslan or Aslani Lakkos; e.g., van der Meulen & van Kolfshoten, 1986) is a locality in the homonymous ravine, which starts from the village Akropotamos and ends SSW to the Aegean Sea (G. Syrides, personal communication to GLG, August 2023). All few herpetofaunal remains from this locality originate from the first layer of this locality [Chalicerrema 1 (formerly known as Rema Aslan 1)]. Moreover, there is a further ambiguity on the exact location of the fossiliferous spot called Rema Marmara, as it is practically a different ravine to the west of the actual ravine Rema Marmara [i.e., between the ravine Chalicerrema and the (real) ravine Rema Marmara; G. Syrides, personal communication to GLG, August 2023]. Both Chalicerrema and Rema Marmara have yielded micromammals (de Bruijn, 1989; Steffens et al., 1979; van der Meulen & van Kolfshoten, 1986). As for the age of these two localities, it cannot be precisely determined. For Chalicerrema, other papers have treated it merely as indeterminate Miocene or Pliocene (e.g., Delfino & Georgalis, 2022; Delfino et al., 2008; Georgalis et al., 2016b; Sanchíz, 1998) or it has even been considered as MN 17, i.e., Early Pleistocene (Doukas & Papayianni, 2016). Rema Marmara has been treated

as Late Miocene in Koufos (2006, 2024), indeterminate Miocene in Delfino and Georgalis (2022) or indeterminate Miocene or Pliocene in Sanchíz (1998). According to van der Meulen and van Kolfshoten (1986) the faunal fossil remains from Rema Marmara appear above vaporates, which were indicative of the Messinian Salinity Crisis or earlier. Based on micromammals, de Bruijn (1989) tentatively regarded the age of Rema Marmara as MN 12 (i.e., Late Miocene). More details about the geology of Rema Marmara can be found in de Bruijn (1989). We tentatively treat here the age of both Chalicerrema and Rema Marmara as Late Miocene or Pliocene. In any case, all these fossiliferous layers in that seaside coast are Neogene, however, some are Miocene and some are Pliocene (G. Syrides, personal communication to GLG, August 2023).

Systematic Palaeontology

Amphibia Blainville, 1816

Urodela Duméril, 1805

Salamandroidea Goldfuss, 1820

Salamandridae Goldfuss, 1820

***Ommatotriton* Gray, 1850**

cf. *Ommatotriton* sp.

Figure 2

Material. *Spilia 4*: three trunk vertebrae (UU SP4 515, UU SP4 516, and UU SP4 720).

Description.

These three vertebrae from *Spilia 4* are rather small (Fig. 2). The largest one, UU SP4 720 (Fig. 2k–n), is 2.8 mm long, whereas the other two are either about 1.5 mm (UU SP4 515; Fig. 2a–e) or 1 mm (UU SP4 516; Fig. 2f–j) in length. They are opisthocelous, with a moderately or well-developed neck separating the anterior condyle from the main body of the vertebral centrum. The anterior surface of the condyle is flat and vertical. The ventral portion of the centrum is broken away in UU SP4 515 (Fig. 2e), but two large subcentral foramina are visible on the ventral surface at least in UU SP4 720 (Fig. 2n). The transverse processes are slender and posterolaterally directed. A very wide foramen is visible anterior to the parapophyses. The ventral and zygapophyseal crests are moderately to well developed. The ventral lamina composed by the ventral crests goes from subtriangular (in UU SP4 515) to rhomboidal (in UU SP4 720). The neural arch is high and dorsally depressed. Posteriorly, it rises distinctly. The arch defines a wide neural canal, which is wider than the anterior condyle in anterior view. The prezygapophyses are badly preserved in UU SP4 720, but are complete in the other two specimens: they are small and elongated, subelliptical in shape and slightly inclined in dorsolateral direction. The straight anterior margin of the neural arch

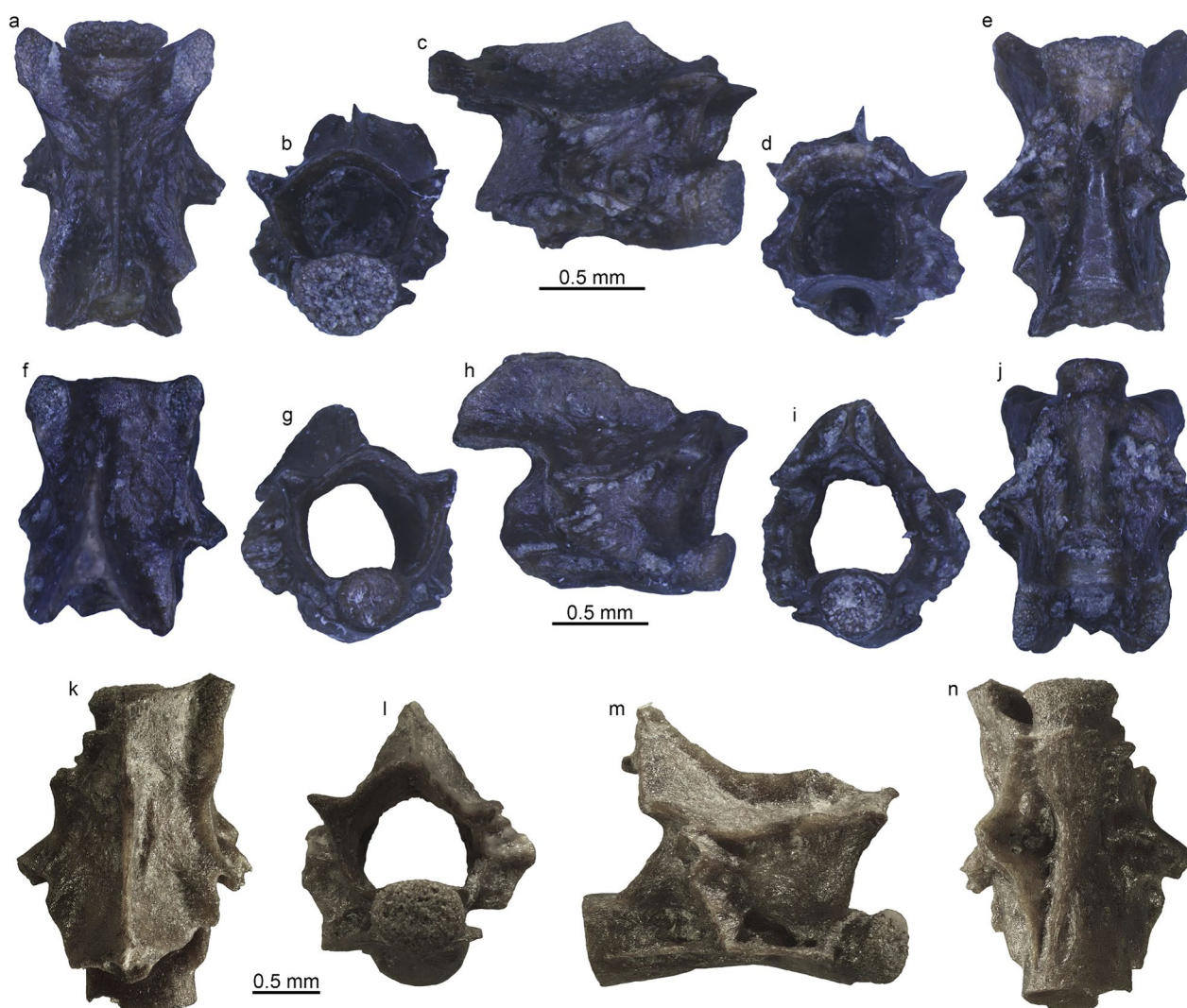


Fig. 2 cf. *Ommatotriton* sp. from Spilia 4. **a–e** Trunk vertebra (UU SP4 515) in dorsal (**a**), anterior (**b**), right lateral (**c**), posterior (**d**), and ventral (**e**) views; **f–j** trunk vertebra (UU SP4 516) in dorsal (**f**), anterior (**g**), right lateral (**h**), posterior (**i**), and ventral (**j**) views; **k–n** trunk vertebra (UU SP4 720) in dorsal (**k**), anterior (**l**), right lateral (**m**), and ventral (**n**) views

is located roughly at the end of their anterior third. The postzygapophyses, on the other hand, are preserved only in UU SP4 516, sharing a similar shape with the prezygapophyses and ending in line with the posterior margin of the neural arch. The neuropophysis is high. Its anterior end is located roughly in line with the posterior end of the prezygapophyses, not far from (but not in contact with) the anterior margin of the neural arch. The anterior margin of the neuropophysis is inclined in UU SP4 515 and straight in UU SP4 516 (not preserved in UU SP4 720). The dorsal margin is sufficiently preserved only in UU SP4 516, which shows a nearly straight dorsal outline in lateral view. A posterior, triangular expanded area touching the posterior margin of the neural arch is visible in the same

specimen, but its presence in the other vertebrae cannot be evaluated due to poor preservation. The posterior end of the arch is completely missing in UU SP4 720, badly preserved in UU SP4 515 and more preserved in UU SP4 516. At least the latter clearly displays a wide, deep and U-shaped notch on the posterior margin. In spite of the poor preservation, the posterior margin of the arch appears slightly wavy in UU SP4 515, but it is not clear whether a real notch was present or not.

Remarks. The referral of these vertebrae to small salamandrids is supported by the opisthocelous centrum and the posterior notch on the neural arch (Ratnikov & Litvinchuk, 2007). The combined presence of high neural crest, high neural arch, well-developed anterior zygapophyseal

crests, and especially the very wide foramen at the base of each parapophysis is diagnostic for *Ommatotriton* (Macaluso et al., 2023b). The remaining morphology is also comparable with the one described for trunk vertebrae of *Ommatotriton ophryticus* (Berthold, 1846) by Ratnikov and Litvinchuk (2007), except mainly for the distinctly smaller size of the Greek fossils. The very wide neural canal of UU SP4 516 could be a juvenile condition, thus accounting for the very small size of at least this vertebra. In any case, we treat our identification as only tentative here due to the significant difference in size of these fossils compared to extant representatives of the genus.

***Ichthyosaura* Sonnini de Manoncourt & Latreille, 1801**

***Ichthyosaura* sp.**

Figure 3

Material. *Spilia* 4: two trunk vertebrae (UU SP4 661 and UU SP4 663).

Description.

The trunk vertebrae are moderately large (Fig. 3). The centrum is opisthocoelous and 3 mm long in the largest specimen (UU SP4 663; Fig. 3f). The anterior condyle has a flat and very poorly ventrally inclined anterior surface and a well-developed neck. In ventral view, a pair of subcentral foramina are visible on each side of the centrum. The anterior ventral crests are moderately developed. The posterior ones are not well preserved in any of the specimens, but in the best cases they appear only slightly less developed than the anterior ones. The transverse processes are slender and posterolaterally directed. A small foramen is present anterior to them. The zygapophyseal crests are well developed and straight. In anterior view, the neural canal is rather high and vaulted, being roughly as large as the anterior condyle. The neural arch is high and rather flat dorsally. In lateral view, the portion dorsal to the level of the

zygapophyses makes up about one third of total height of the vertebrae. In dorsal view, the anterior margin of the arch is concave and has its posteriormost point in correspondence with the end of the anterior fourth of the prezygapophyses. The latter are rather wide, sub-elliptical and very slightly dorsally inclined. In dorsal view, they display diverging medial margins. The neurapophysis is present, starting very far from the anterior margin of the neural arch (posterior to the end of the prezygapophyses). It appears rather low, but this is most probably due to its incomplete status. The posterior margin of the neural arch is damaged, but it is preserved enough in at least some specimens to show that the neurapophysis was in contact with it. No expanded area is visible by the posterior end of the latter.

Remarks. A second, slightly larger, salamandrid taxon is represented in the *Spilia* 4 assemblage, by these vertebrae. The combination of well-developed neck, anteriorly-inclined condyle, high neural arch, neurapophysis in contact with posterior margin of the neural arch, moderately to well-developed ventral and zygapophyseal crests, anterior zygapophyseal crests not bending ventrally to contact parapophyses, small foramen at the base of parapophyses, and elliptical prezygapophyses with diverging medial margins supports an identification as an indeterminate member of the genus *Ichthyosaura* (Macaluso et al., 2023b; Ratnikov & Litvinchuk, 2007). Ratnikov and Litvinchuk (2007) reported a straight anterior margin of the neural arch in *Ichthyosaura alpestris* (Laurenti, 1768) (their *Mesotriton alpestris*), but Macaluso et al. (2023b) mentioned variation in this feature, with precaudal vertebrae of this species displaying either a concave or a straight margin. The concave anterior margin of the neural arch in these vertebrae from *Spilia* is thus not in conflict with an attribution to the genus.

***Urodela* indet.**

Figures 4, 5

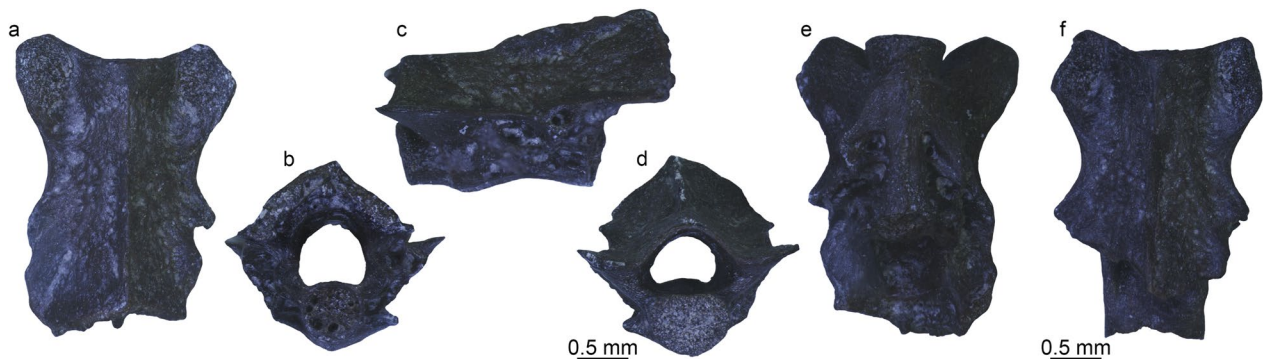


Fig. 3 *Ichthyosaura* sp. from *Spilia* 4. **a–e** Trunk vertebra (UU SP4 661) in dorsal (**a**), posterior (**b**), left lateral (**c**), anterior (**d**), and ventral (**e**) views; **f** trunk vertebra (UU SP4 663) in dorsal view

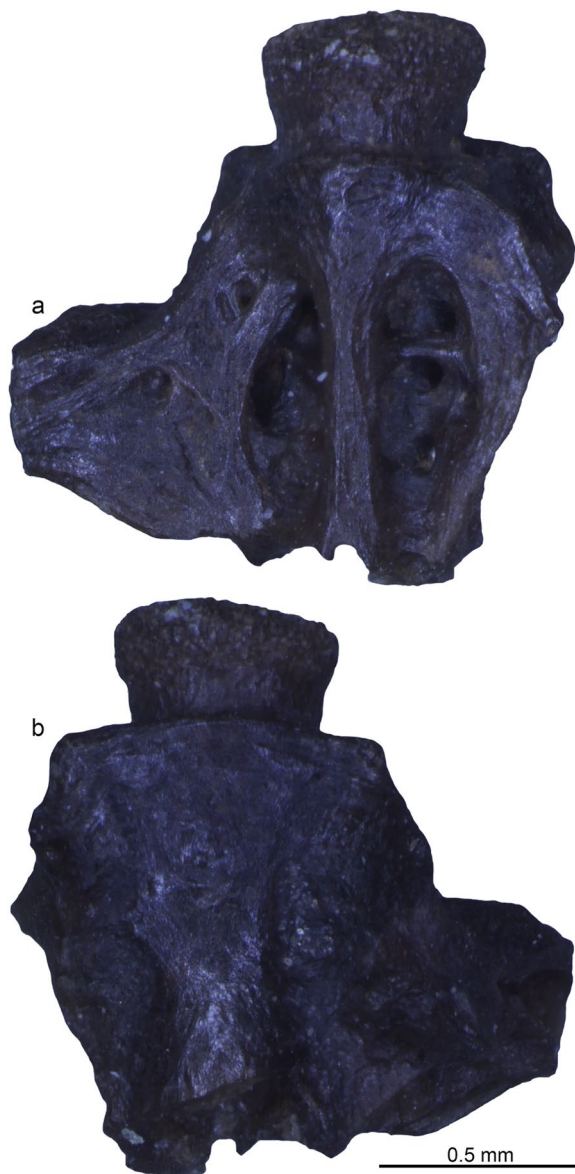


Fig. 4 Urodela indet. from Spilia 1. Trunk vertebra (UU SP1 1068) in dorsal (a) and ventral (b) views

Material. *Spilia 1*: three fragmentary vertebrae (UU SP1 1066–UU SP1 1068) and one humerus (UU SP1 1065); *Spilia 4*: one dentary (UU SP4 687), five trunk vertebrae (UU SP4 662, UU SP4 686, UU SP4 688, UU SP4 717, and UU SP4 718), one caudal vertebra (UU SP4 719), three humeri (UU SP4 665, UU SP4 722, and UU SP4 723), three femora (UU SP4 664, UU SP4 666, and UU SP4 721), and one tibia (UU SP4 667).

Description.

The dentary (UU SP4 687) from Spilia 4 is small (Fig. 5a, b). Only the anterior portion is preserved. The crista dentalis shows a large number of small and closely-spaced

tooth positions. Teeth were pleurodont, but they are not preserved. Medially, the canalis primordialis is almost completely closed in the preserved portion of the dentary; the incisura dentalis is represented only by a very narrow groove, which ends very far from the anterior end of the bone. A deep sulcus dentalis is present dorsally. It strongly deepens posteriorly due to a well-developed dorsal expansion of the bone present medial to the sulcus. Anteriorly, the mandibular symphysis is wide and subcircular, with a somehow flattened medial border. The lateral surface seems to display a very light roughness, but this could be due to taphonomical processes rather than to the presence of a real sculpturing. A line of mental foramina is present at midheight. A very low ridge is present on the ventral surface of the dentary, starting from the symphysis and lowering posteriorly.

The vertebrae from Spilia 1 (Fig. 4) and Spilia 4 (Fig. 5d–f) are too poorly preserved to provide a satisfactory description.

The humeri from Spilia 1 and Spilia 4 are small to medium sized and rather slender. Only the proximal epiphysis is preserved in UU SP1 1065 and UU SP4 665, whereas the other two specimens are complete. The processus dorsalis is preserved only in UU SP1 1065 and UU SP4 723 (Fig. 5g): it is rather short and either pointed (UU SP4 723) or rounded (UU SP1 1065). In anterior view, the crista ventralis is elongated and poorly inclined. The distal epiphysis has a rather deep fossa cubitalis ventralis, whereas the fossa olecrani is very shallow.

The femora from Spilia 4 are also medium sized and slender. UU SP4 666 and UU SP4 721 (Fig. 5h) preserve the proximal half, with a very deep fovea trochlearis, a shallow fovea dorsocaudalis, and a well-developed trochanter. The caput femoris is well ossified. UU SP4 664 preserves the distal epiphysis alone, with a deep fossa intercondylaris.

The small tibia (UU SP4 667) from Spilia 4 is moderately slender (Fig. 5i, j). It carries a very well-developed tibial crest, which reaches the distal epiphysis. The free portion of the crest is missing. The opposite surface of the tibia is smooth, devoid of any ridge.

Remarks. All these remains pertain to urodeles (Francis, 1934; Holman & Stuart, 1991; Macaluso et al., 2020, 2023b; Ratnikov & Litvinchuk, 2007). A more precise identification is hindered either by poor preservation or by the still poorly understood comparative osteology of these amphibians. Nevertheless, they likely belong to one of the two salamandrid urodeles identified from Spilia based on better preserved vertebral material.

Anura Duméril, 1805

Mediogyrinia Lataste, 1878

Bombinatoroidea Gray, 1825

Bombinatoridae Gray, 1825



Fig. 5 Urodela indet. from Spilia 4. **a–c** Right dentary (UU SP4 687) in lateral (**a**), medial (**b**), and dorsal (**c**) views; **d** trunk vertebra (UU SP4 662) in ventral view; **e, f** caudal vertebra (UU SP4 719) in dorsal (**e**) and left lateral (**f**) views; **g** right humerus (UU SP4 723) in anterior view; **h** right femur (UU SP4 721) in anterior view; **i, j** right tibia (UU SP4 667) in posterior (**i**) and dorsal (**j**) views

***Bombina* Oken, 1816**

***Bombina* sp.**

Figure 6

Material. *Chalacorrema*: one sacral vertebra (UU RA 516), one urostyle (UU RA 513), and one humerus (UU RA 504).

Description.

The sacral vertebra UU RA 516 is poorly preserved (Fig. 6a, b). It clearly has a posterior condyle, but the anterior end is missing. The neural canal is dorsoventrally compressed in anterior view. Dorsally, the neural arch has no carina neuralis. Only the right prezygapophysis is well preserved, whereas only the medial end of the left one is preserved. The right prezygapophysis is wide and elliptical in dorsal view. The prezygapophyses are well expanded medially, thus constricting the neural arch in the middle in dorsal view. Anteriorly, a poorly-preserved structure comparable with a pseudozygosphene is visible.

The transverse processes are missing, but their base is wide. The preserved portion of the vertebra is slightly more than 7 mm wide and about 5 mm long.

The urostyle UU RA 513 misses its distal portion (Fig. 6c, d). Anteriorly, it has a single, mediolaterally-widened cotyle. The neural arch is closed dorsally and there is no carina neuralis. Transverse processes are present by the anterior end of the arch, being laminar in lateral view and slightly anteroposteriorly widened in dorsal view. The specimen is about 9.5 mm in length.

The humerus UU RA 504 is well preserved (Fig. 6e, f). It has a straight diaphysis, ending distally with a laterally-shifted and spherical eminentia capitata. The crista paraventralis is absent. The cristae medialis and lateralis are moderately developed, the medial one to a higher extent compared to the lateral one. The well-marked olecranon scar is moderately elongated in a proximodistal direction. The specimen is almost 10 mm in length.



Fig. 6 *Bombina* sp. from Chalicorrema. **a, b** Sacral vertebra (UU RA 516) in dorsal (**a**) and ventral (**b**) views; **c, d** urostyle (UU RA 513) in right lateral (**c**) and dorsal (**d**) views; **e, f** left humerus (UU RA 504) in ventral (**e**) and dorsal (**f**) views

Remarks. These few remains from Chalicorrema share with the genus *Bombina* the following morphological features (Bailon, 1999): the posterior cotyle; the extended transverse processes; the morphology of the prezygapophyses; the possible pseudozygosphene (sacral vertebra); the presence of widened transverse processes; the absence of carina neuralis; the presence of a single anterior cotyle (urostyle); straight diaphysis; the absence of crista paraventralis; and laterally-shifted eminentia capitata (humerus). Accordingly, we refer this material to *Bombina*.

Alytoidea Fitzinger, 1843

Discoglossidae Günther, 1858

***Latonia* Meyer, 1843**

***Latonia ragei* Hossini, 1993**

Latonia* cf. *ragei

Figures 7, 8, 9, 10, 11, 12

Material. *Spilia 1*: one frontoparietal (UU SP1 1022), four maxillae (UU SP1 1018, UU SP1 1024, UU SP1 1044, and UU SP1 1046), two atlantes (UU SP1 1028), three trunk vertebrae [UU SP1 1021 (two elements) and UU SP1 1027], one urostyle (UU SP1 1134), and five ilia (UU SP1 1017, UU SP1 1026, UU SP1 1110, UU SP1 1133, and UU SP1 1141); *Spilia 3*: one frontoparietal (UU SP3 624), two maxillae (UU SP3 639 and UU SP3 672), four angulars (UU SP3 629–UU SP3 631, and UU SP3 680), one trunk vertebra (UU SP3 628), one sacral vertebra (UU SP3 637), one scapula (UU SP3 632), two humeri (UU SP3 636 and UU SP3 641), and seven ilia (UU SP3

621–UU SP3 623, UU SP3 625–UU SP3 627, and UU SP3 638); *Spilia 4*: five maxillae (UU SP4 523, UU SP3 524, UU SP4 693, and UU SP4 737), four angulars (UU SP4 715 and UU SP4 728), one atlas (UU SP4 525), one trunk vertebra (UU SP4 712), four sacral vertebrae [UU SP4 529 and UU SP4 530 (three elements)], two urostyles (UU SP4 520 and UU SP4 521), two ribs (UU SP4 714), four humeri [UU SP4 517, UU SP4 518, and UU SP4 519 (two elements)], and seven ilia (UU SP4 513, UU SP4 526, UU SP4 528, UU SP4 531, UU SP4 532, and UU SP4 716).

Description.

UU SP1 1022 is a rather large element that most likely represents the anteromedial part of the frontoparietal (Fig. 7a, b). The ventral surface is smooth, whereas the dorsal one is almost completely covered by a dense dermal sculpturing composed by tubercles, which fuses to form longitudinal ridges anteriorly. The bone sections exposed along the broken margins clearly show that the ornamentation was secondarily connected to the frontoparietal table and not directly ossified on it. UU SP3 624 is a fragment of a moderately large frontoparietal, of which only the left anterolateral portion is preserved (Fig. 9a, b). The ventral surface shows part of the incrassatio frontoparietalis, which is long and reaches the anterior end. The lateral margin of the incrassatio is marked by a low and wavy ridge. Lateral to the incrassatio, there is a narrow pars contacta, the lateral portion of which bends ventrally. Anteriorly, the pars contacta develops an anterior horn, provided with a strongly striated ventral

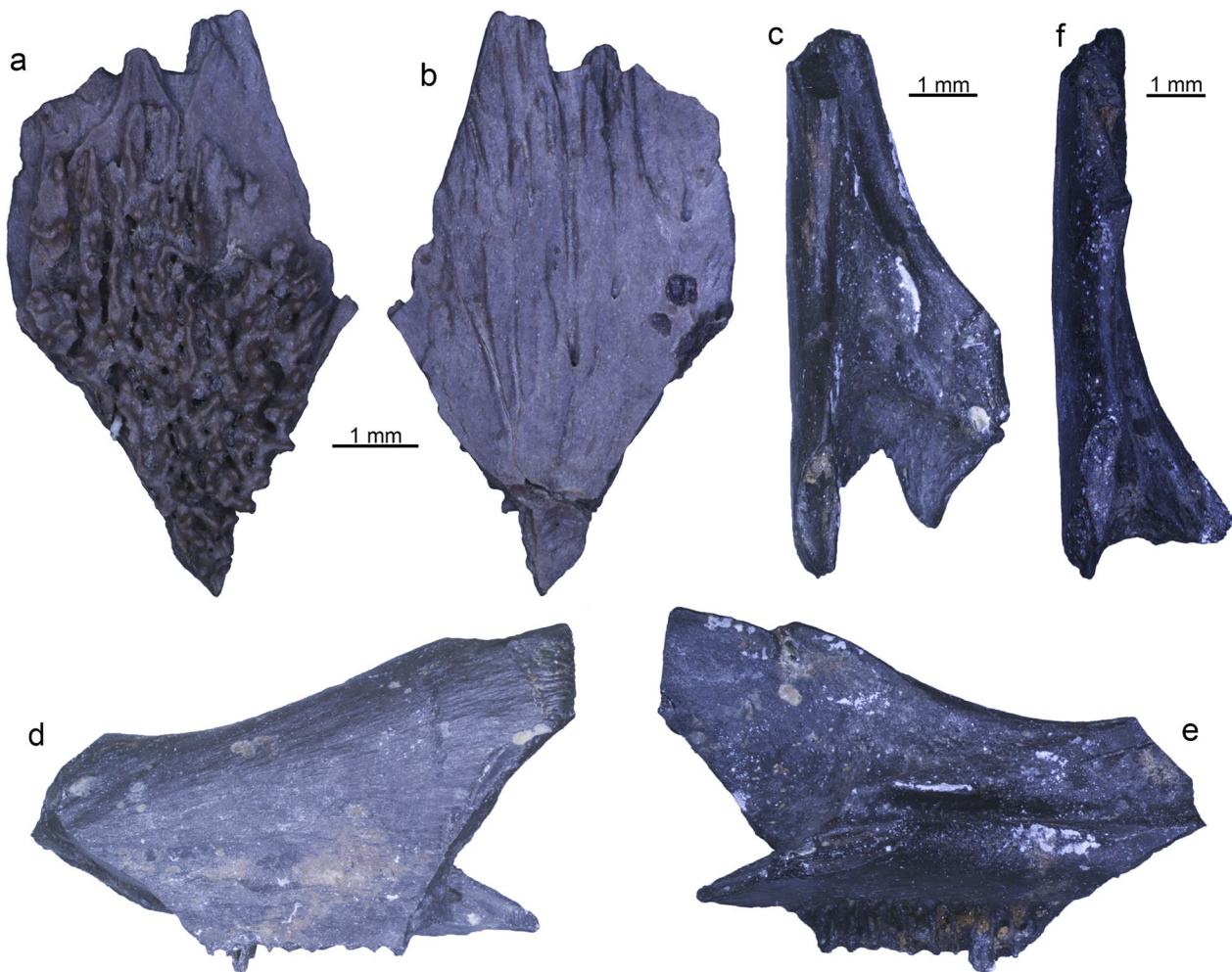


Fig. 7 *Latonia* cf. *ragei* from Spilia 1, cranial elements. **a, b** Fragment of frontoparietal (UU SP1 1022) in dorsal (**a**) and ventral (**b**) views; **c–e** left maxilla (UU SP1 1018) in dorsal (**c**), lateral (**d**) and medial (**e**) views; **f** left maxilla (UU SP1 1044) in dorsal view

surface for the contact with the sphenethmoid. The dorsal surface of the fragment of frontoparietal bears a well-developed dermal sculpturing. The only unsculptured part is the anterior horn. The sculpturing is made up by a moderately dense accumulation of small tubercles. Anteriorly, the tubercles are joined together to form longitudinal ridges. Laterally, the tectum supraorbitale is present, but poorly developed, at least in the preserved portion of the bone.

Several fragments of maxillae are represented in the Spilia localities (Figs. 7c–f, 9c–e, 11). The large UU SP3 639 (Fig. 9c–e) and the moderately large UU SP1 1018 (Fig. 7c–e), UU SP1 1024, and UU SP4 523 (Fig. 11a, b) are the largest ones, whereas the others are slightly smaller. Medially, the maxillae display a mediolaterally short lamina horizontalis, which is rather high in medial view. Ventrally to the lamina, a high number of closely-spaced tooth positions is present. When preserved, the

teeth are clearly pleurodont and cylindrical. When the posterior end is preserved [e.g., UU SP4 523 (Fig. 11a, b) and UU SP4 693 (Fig. 11d)], the tooth row extends slightly posteriorly to the lamina horizontalis. A well-developed processus pterygoideus is preserved only in few specimens (e.g., UU SP1 1044, UU SP3 639, and UU SP4 693), but it was probably present at least in other specimens where the posterior end is not missing also judging from the visible medially-directed curvature of the posterior end of the lamina horizontalis. The posterior depression is present, but not marked by ridges. The margo orbitalis is strongly concave. The lateral surface of the maxillae is smooth. Only UU SP4 523 (Fig. 11b) displays very few and small rugosities towards the posterodorsal corner (i.e., the processus zygomaticomaxillaris). It has to be noted that the other largest specimens, UU SP1 1018, UU SP1 1024, and UU SP3 639, show no sculpturing.

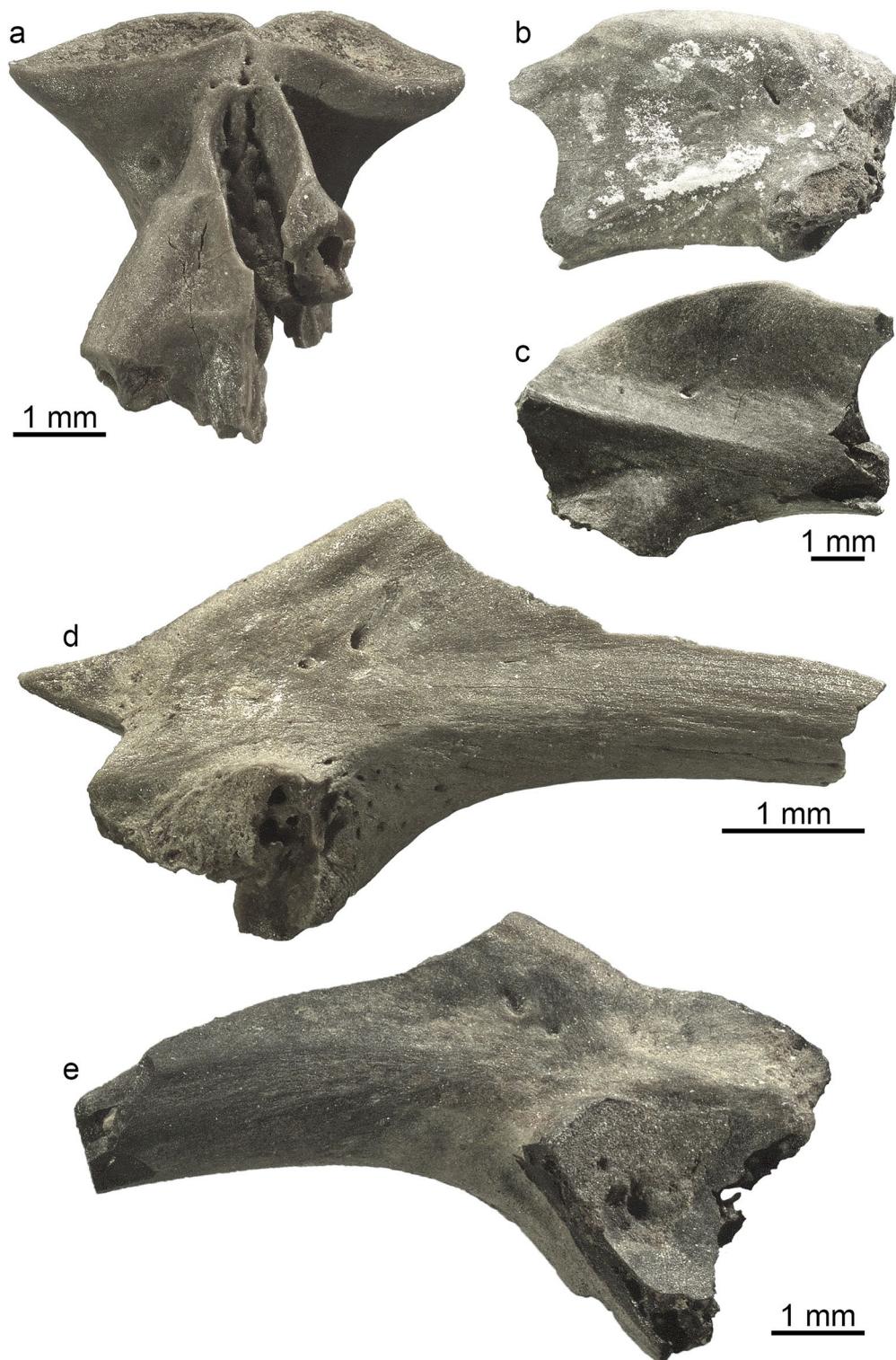


Fig. 8 *Latonia cf. ragei* from Spilia 1, postcranial elements. **a** Urostyle (UU SP1 1134) in dorsal view; **b, c** left ilium (UU SP1 1017) in lateral (**b**) and medial (**c**) views; **d** right ilium (UU SP1 1026) in lateral view; **e** left ilium (UU SP1 1141) in lateral view

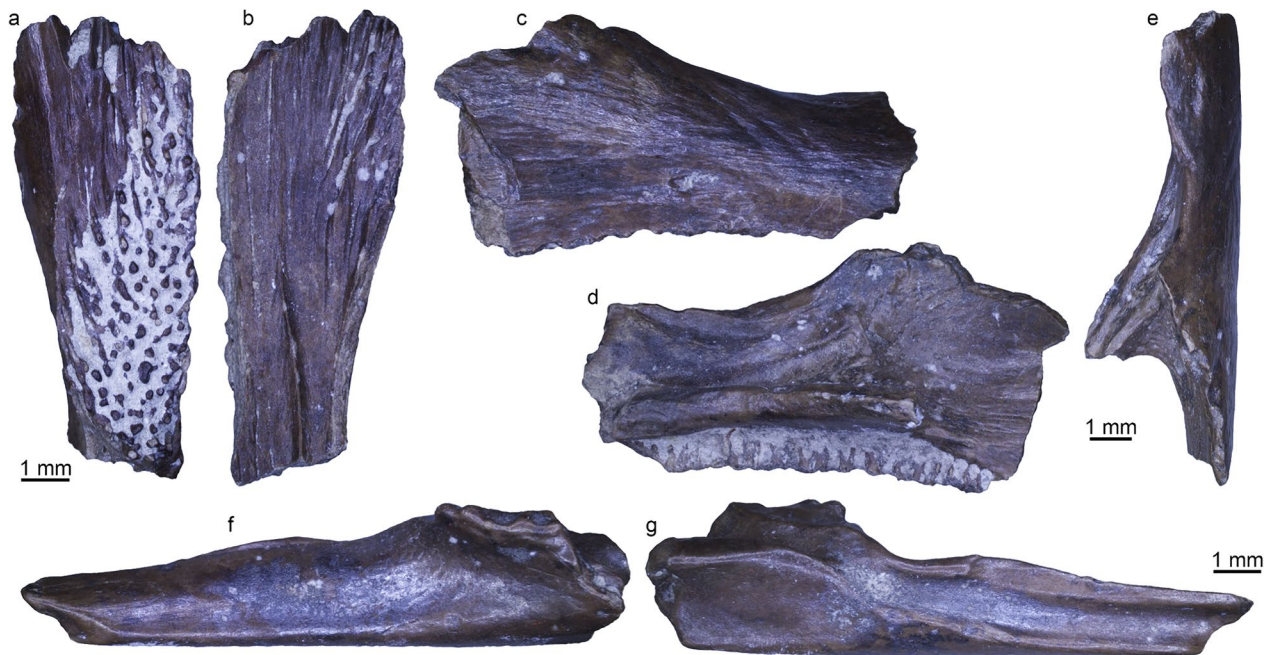


Fig. 9 *Latonia cf. ragei* from Spilia 3, cranial elements. **a, b** Fragment of frontoparietal (UU SP3 624) in dorsal (**a**) and ventral (**b**) views; **c–e** right maxilla (UU SP3 639) in lateral (**c**), medial (**d**), and dorsal (**e**) views; **f, g** right angular (UU SP3 629) in medial (**f**) and lateral (**g**) views

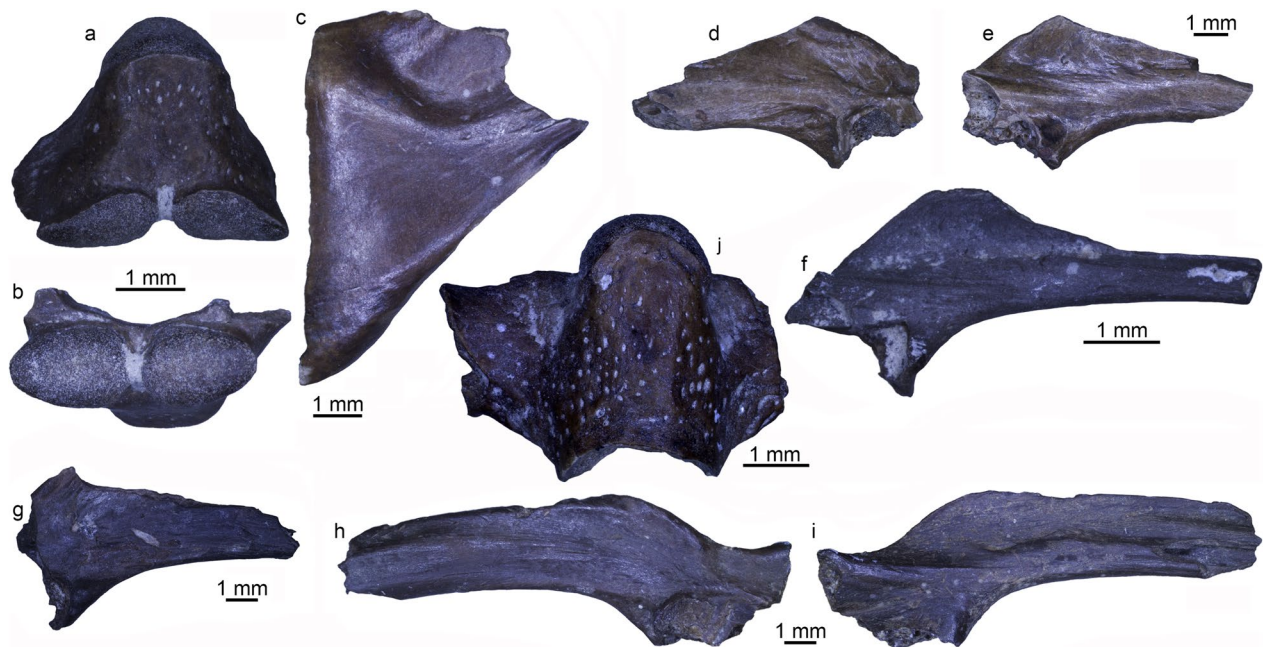


Fig. 10 *Latonia cf. ragei* from Spilia 3, postcranial elements. **a, b** Sacral vertebra (UU SP3 637) in ventral (**a**) and posterior (**b**) views; **c** right scapula (UU SP3 632) in ventral view; **d, e** left ilium (UU SP3 621) in lateral (**d**) and medial (**e**) views; **f** left ilium (UU SP3 622) in medial view; **g** right ilium (UU SP3 625) in lateral view; **h, i** left ilium (UU SP3 638) in lateral (**h**) and medial (**i**) views; **j** trunk vertebra (UU SP3 628) in ventral view

The angulars from Spilia 3 (Fig. 9f, g) and Spilia 4 are medium to moderately large sized. None of them is completely preserved. They carry both a processus

coronoideus and a processus paracoronoideus. The former is distinctly dorsally directed and, when completely preserved, not extended posteriorly. The lateral surface is

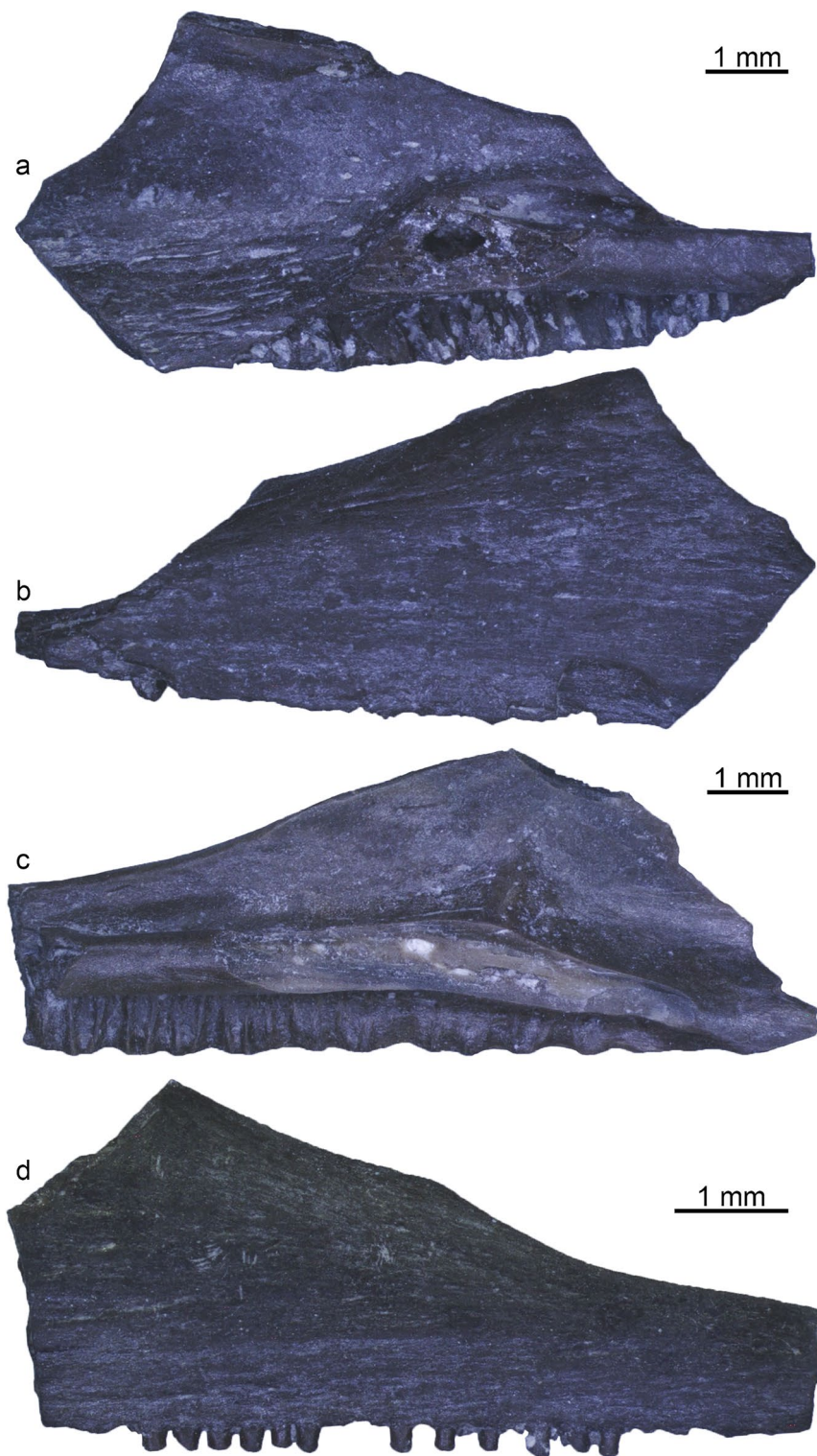


Fig. 11 *Latonia cf. ragei* from Spilia 4, cranial elements. **a, b** Left maxilla (UU SP4 523) in medial (**a**) and lateral (**b**) views; **c** right maxilla (UU SP4 524) in medial view; **d** right maxilla (UU SP4 693) in lateral view

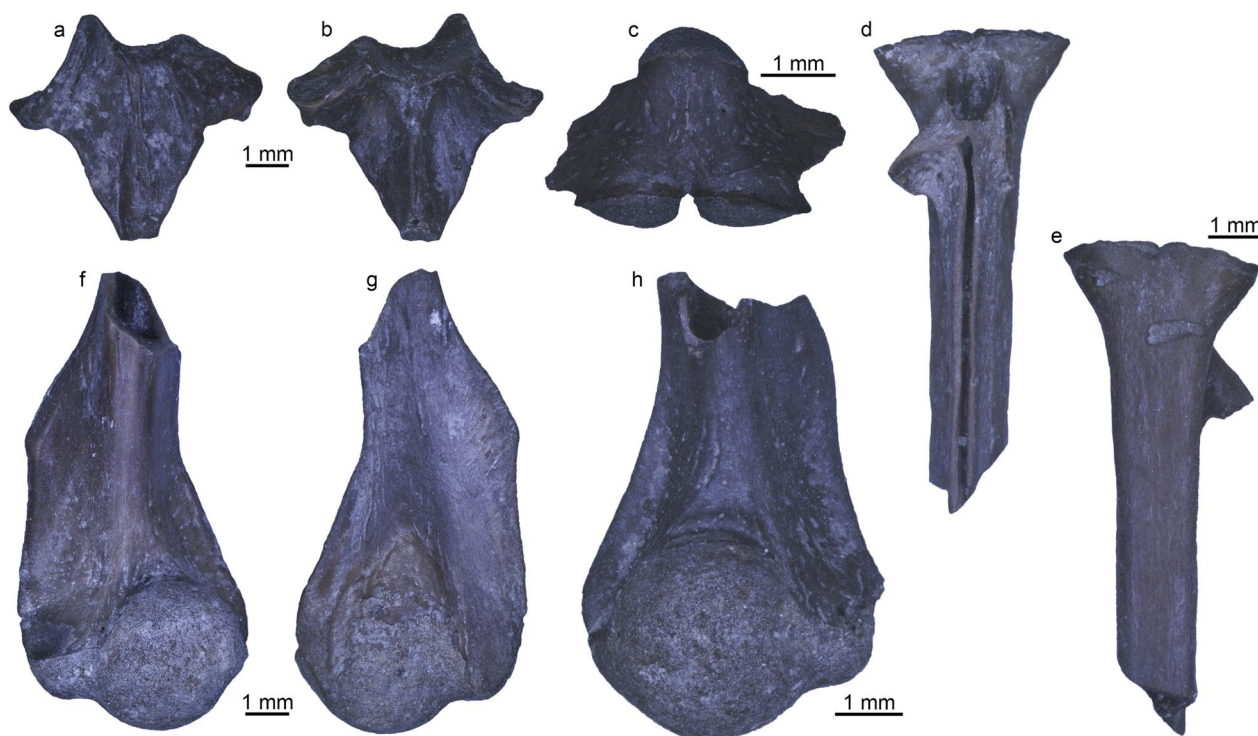


Fig. 12 *Latonia* cf. *ragei* from Spilia 4, postcranial elements. **a, b** One atlas (UU SP4 525) in dorsal (**a**) and ventral (**b**) views; **c** sacral vertebra (UU SP4 529) in ventral view; **d, e** urostyle (UU SP4 520) in dorsal (**d**) and ventral (**e**) views; **f, g** left humerus (UU SP4 517) in ventral (**f**) and dorsal (**g**) views; **h** right humerus (UU SP4 518) in ventral view

characterized by a depressed area marked ventrally by a sharp crista mandibulae externa.

The atlantes from the Spilia localities are not complete and they preserve different portions of this element. UU SP4 525 preserves only the dorsal portion of the neural arch (Fig. 12a, b). It is moderately large and displays a long and robust posterior point. The dorsal surface is smooth, but the remnants of a poorly preserved, low longitudinal ridge are recognisable in the middle. The other atlantes preserved only the centrum and are smaller. They bear two anterior cotyles, which are somehow reniform in anterior view, dorsally inclined and distinctly separated medially by a spatium interglenoidale. Posteriorly, a subcircular cotyle is present. A distinct, variably developed longitudinal ridge stands out on the ventral surface of the centrum.

The trunk vertebrae from the Spilia localities are of medium size (Fig. 10j). Only the opisthocoelous centrum is preserved. It is subcylindrical, with circular anterior condyle and posterior cotyle. The anterior condyle is followed by a poorly distinct neck. In lateral view, the centrum is distinctly ventrally concave.

The sacral vertebrae from Spilia are also medium-sized and preserving the centrum alone (Figs. 10a, b, 12c). They have an anterior condyle, which is elliptical,

and two posterior condyles, which are elliptical as well and well separated. The ventral surface of the sacrals is not distinctly concave in lateral view as it is in the trunk vertebrae.

The urostyles from Spilia are medium to moderately large sized and rather well preserved (Figs. 8a, 12d, e). Anteriorly, they bear two wide and roughly suboval cotyles, which are slightly mediolaterally extended and clearly separated medially. Posteriorly, the urostyle has a moderately high crista dorsalis, which is not closed dorsally for its whole length in UU SP4 521 and closed only by the anterior margin in UU SP4 520 (Fig. 12d, e). Two transverse processes are present by the anterior end of the crista. Their distal ends are missing, but a narrowing is clearly visible. Only the right process in UU SP4 521 and the left one in UU SP4 520 (Fig. 12d, e) extend slightly posteriorly to form a short lamina, but this ends not far from the process itself. The canalis coccygeus is wide and ogival in anterior view.

The ribs from Spilia are medium sized and moderately robust. They are constricted at mid-length and present a distinct process on the dorsal surface.

The single scapula (UU SP3 632) from Spilia 3 is large and fragmentary, preserving the pars suprascapularis

alone (Fig. 10c). The latter is very wide. A very well-developed crista anterior is present.

The humeri from Spilia (Fig. 12f–h) reach a rather large size (but a very small one is also present: UU SP3 636) and preserve only their distal half. The shaft is moderately robust and straight. The spherical eminentia capitata is shifted laterally. The fossa cubitalis ventralis is present, but moderately shallow (somehow slightly deeper in the very small UU SP3 636). The epicondylus ulnaris is large, whereas the radialis one is small. Cristae medialis and lateralis follow the same proportions, with the former distinctly more developed than the other. The olecranon scar is well distinct and elongated.

The ilia from Spilia (Figs. 8b–e, 10d–i) are medium-sized, with only UU SP3 622 (Fig. 10f), UU SP3 623, UU SP4 513, UU SP4 531, and UU SP4 716 being smaller and UU SP1 1017 (Fig. 8b, c), UU SP1 1133, and UU SP3 638 (Fig. 10h, i) being larger. None of them is completely preserved. They have a dorsal crest, which is well preserved only in UU SP3 638 (Fig. 10h, i) and UU SP4 528. In these specimens, the crest is visibly straight (i.e., not medially bending). In the smallest specimens, the posterior end of the dorsal crest merges with a laminar dorsal prominence, not clearly presenting a developed dorsal protuberance in this position. Larger specimens, on the other hand, display a slightly more evident protuberance. The latter is elongated and presents a gently-curving dorsal margin. UU SP3 638 (Fig. 10h, i) and UU SP4 528 clearly shows that the dorsal prominence is not exceeded by the crista dorsalis in height. A distinct tubercular fossa (fossula tuberis superioris sensu Roček, 1994) is not clearly visible in any of the specimens, but few small foramina are present where it should be located. The acetabulum is large and very deep, with a very strongly developed anterior margin. Anterior to the acetabulum, a distinct preacetabular fossa is present in UU SP3 622 (Fig. 10f), UU SP3 623, UU SP3 625 (Fig. 10g), UU SP3 627, UU SP4 513, UU SP4 526, and UU SP4 531, but clearly not in UU SP1 1141 (Fig. 8e) and UU SP4 528. A shallow supraacetabular fossa is visible dorsally in UU SP1 1141 (Fig. 8e), UU SP3 622, and UU SP4 513 and very poorly in UU SP3 638 (Fig. 10h, i), UU SP4 531, and UU SP4 532, but the same area is not preserved in the other specimens. The base of the dorsal acetabular expansion is preserved only in UU SP3 627, UU SP3 638 (Fig. 10h, i), UU SP4 513, UU SP4 526, and UU SP4 531, which show apparently that the angle between the latter and the dorsal prominence is very wide ($>90^\circ$). The ventral acetabular expansion is regularly missing. On the medial side, a wide and deep interiliac groove (sensu Bailon, 1999) is present, but due to breakage an interiliac tubercle is clearly visible only in UU SP1 1141 (Fig. 8e) and UU SP3 627.

Remarks. *Latonia* is well represented in the Spilia localities. Among the diagnostic features reported for this genus by e.g., Roček (1994, 2013) and Syromyatnikova et al. (2019b), we can mention the double processes on the angular and the secondary sculpturing on dermal bones as particularly significant. Compared to the five currently recognized extant and extinct species of the genus (Biton et al., 2013, 2016; Roček, 1994, 2013; Syromyatnikova & Roček, 2019; Syromyatnikova et al., 2019b), the Spilia *Latonia* differs from *Latonia nigriventer* (Mendelssohn & Steinitz, 1943) because of the highly sculptured frontoparietal, from *Latonia seyfriedi* Meyer, 1843 (including *Latonia gigantea* [Lartet, 1851]; Syromyatnikova et al., 2019b) in the smooth maxilla, from *Latonia vertaizoni* (Friant, 1944) in the well-developed coronoid process, and from *Latonia caucasica* Syromyatnikova & Roček, 2019, in the tooth row slightly extending posteriorly. A certain similarity in the significant features reported by Syromyatnikova and Roček (2019) is present between the *Latonia* from Spilia and *Latonia ragei*, at least as far as the elements known for both are concerned. Thus, we tentatively refer these fossils to the latter species. The light rugosities present on the lateral surface of a single maxilla, UU SP4 523, which is otherwise undistinguishable from the other maxillae, are a peculiar feature, worth being highlighted here. However, the taxonomic significance of these rugosities, which do not represent clearly a dermal sculpturing, cannot be clearly evaluated here in the context of *Latonia* species with smooth maxillae.

Latonia sp.

Figures 13, 14

Material. *Vevi*: eight maxillae (UU VE 502–UU VE 509), two pterygoids (UU VE 540 and UU VE 542), nine angulars (UU VE 521–UU VE 528, and UU VE 538), six trunk vertebrae (UU VE 530–UU VE 535), one sacral vertebra (UU VE 529), two urostyles (UU VE 510 and UU VE 511), one coracoid (UU VE 537), one humerus (UU VE 515), six radioulnae (UU VE 513 and UU VE 516–UU VE 520), two ilia (UU VE 536 and UU VE 541), and two tibiofibulae (UU VE 512 and UU VE 514).

Description. Almost all of these bones from *Vevi* are very large and robust, indicative of the presence of a relatively large-sized frog (Figs. 13, 14). However, some smaller specimens are also present, especially among the vertebrae.

The maxillae from *Vevi* have a smooth lateral surface (Fig. 13a–m). The specimens preserve either the anterior end (or part of it) or portions of the bone posterior to the palatine process. The anterior end is very long. Anteriorly, at least UU VE 507 (Fig. 13k), which represents the complete anterior portion, shows a deep articulation for the premaxilla. The medial side of the maxilla has a high lamina horizontalis, which is not developed in medial



Fig. 13 *Latonia* sp. from Vevi, cranial elements. **a, b** Right maxilla (UU VE 502) in lateral (**a**) and medial (**b**) views; **c–e** left maxilla (UU VE 503) in lateral (**c**), medial (**d**), and dorsal (**e**) views; **f–h** right maxilla (UU VE 504) in dorsal (**f**), lateral (**g**), and medial (**h**) views; **i, j** left maxilla (UU VE 505) in lateral (**i**) and medial (**j**) views; **k** left maxilla (UU VE 507) in medial view; **l, m** right maxilla (UU VE 509) in lateral (**l**) and medial (**m**) views; **n** right pterygoid (UU VE 540) in dorsal view; **o** left pterygoid (UU VE 542) in dorsal view; **p–r** right angular (UU VE 521) in lateral (**p**), medial (**q**), and dorsal (**r**) views



Fig. 14 *Latonia* sp. from Vevi, postcranial elements. **a** Trunk vertebra (UU VE 530) in ventral view; **b** trunk vertebra (UU VE 531) in ventral view; **c–g** sacral vertebra (UU VE 529) in anterior (**c**), right lateral (**d**), posterior (**e**), dorsal (**f**), and ventral (**g**) views; **h–j** urostyle (UU VE 510) in dorsal (**h**), ventral (**i**), and left lateral (**j**) views; **k** right coracoid (UU VE 537) in dorsal view; **l–n** left humerus (UU VE 515) in dorsal (**l**), ventral (**m**), and medial (**n**) views; **o, p** left ilium (UU VE 536) in lateral (**o**) and medial (**p**) views; **q** left tibiofibula (UU VE 512) in ventral view; **r** right radioulna (UU VE 513) in medial view; **s, t** right radioulna (UU VE 516) in medial (**s**) and lateral (**t**) views

direction. The lamina ends posteriorly with a well-developed processus pterygoideus. Dorsally, the lamina hosts a deep and narrow groove for the palatoquadrate bar. Ventral to the lamina horizontalis, the alveolar portion bears small, pleurodont and closely-packed teeth. The tooth row ends posteriorly roughly at the level of the processus pterygoideus. The posterior end of the maxillae displays

a distinct posterior depression on the medial surface, but this appears to be not defined anteroventrally by a ridge even in the largest maxillae. The concavity of the margo orbitalis is shallow. The largest and most complete maxillae reach a length of 14.4 mm.

The fragmentary pterygoids from Vevi preserve part of the ramus maxillaris, provided with a well-developed and

rounded ventral flange (Fig. 13n, o). A poorly-developed sculpturing is present on the flange; this is more easily visible on the better-preserved UU VE 540. The largest fragment is 7.4 mm long.

Angulars from Vevi display two rounded processes on the medial side (Fig. 13p–r). The paracoronoid process is small and horizontal. The coronoid process is more developed and subvertical; it continues posteriorly in a laminar and lowering ridge. The sulcus cartilagine Meckeli is very shallow in correspondence with the paracoronoid process, but deepens distinctly at the level of the coronoid one. A sharp crista mandibulae externa is present, marking ventrally a deep lateral depression on the posterior half of the bone. The length of the angulars reaches up to 24.6 mm in the largest and most preserved specimen.

The trunk vertebrae from Vevi are mainly represented by isolated subcylindrical centra, sometimes with a light degree of dorsoventral compression (Fig. 14a, b). These have a cotyle on one end and a condyle on the other. Even though it is not undisputedly possible to define an anterior and a posterior end, the presence of a sort of neck around the condyle hints towards an opisthocoealous condition for these vertebrae. In lateral view, the ventral surface is concave. UU VE 530 (Fig. 14a) and UU VE 531 (Fig. 14b) still bear a single, well-preserved transverse process each, which is robust, short and laterally expanded. The process displays a wide and flat articulation surface for a free rib at its distal end. The length of the largest centrum is 4.8 mm.

The single available sacral vertebra (UU VE 529) from Vevi has an anterior condyle and two posterior condyles (Fig. 14c–g). The anterior condyle is subcircular, whereas the posterior condyles are subelliptical and well separated. In lateral view, the ventral surface of the vertebral centrum is slightly concave. In anterior view, the neural canal is wide and roughly shaped as a mediolaterally-elongated triangle. The dorsal surface of the neural arch is irregular, but a low carina neuralis is visible along its midline. The transverse processes and the prezygapophyses are broken off. The centrum of this vertebra is 5.2 mm long (measured along the midline) and 5.5 mm wide (measured as the maximum width at the posterior condyles).

The urostyles from Vevi possess two anterior fossae condyloideae, which are mediolaterally elongated and contact each other in the middle (Fig. 14h–j). They do not coalesce. The neural arch is poorly preserved in both specimens. Cylindrical transverse processes are present by its anterior end. Each process is followed by a lamina horizontalis. These laminae are very low in UU VE 510 (Fig. 14h–j), but strongly more developed in UU VE 511. The dorsal surface of the neural arch is completely

missing in UU VE 511, but its anterior end is preserved in the other specimen. Based on the latter, it can be observed that there is no crista dorsalis and that the arch opened in a wide dorsal fissure. The longest urostyle is at least 11.3 mm long, but it is not possible to estimate how much of its posterior portion is missing.

The coracoid (UU VE 537) from Vevi misses the pars epicoracoidalis (Fig. 14k). The middle portion is straight and narrow. The pars glenoidalis is very wide. The specimen is 8.9 mm long.

Only the distal half of a humerus (UU VE 515) from Vevi is preserved, in good overall conditions (Fig. 14l–n). The diaphysis is straight and ends distally with a spherical eminentia capitata, which is slightly laterally shifted. A shallow fossa cubitalis ventralis is present. Structures on the medial side (i.e., epicondylus ulnaris and crista medialis) are strongly more developed than those on the lateral side (i.e., epicondylus radialis and crista lateralis). On the dorsal surface of the distal end, the olecranon scar is short, being almost as long as it is wide. The complete length of the fragment reaches 11.6 mm.

Radioulinae from Vevi (Fig. 14r–t) have a massive proximal epiphysis, with a wide but short olecranon. The dorsal surface of the olecranon shows a distinctly rough aspect. The rest of the bone, distal to the collum antebra-chii, is strongly mediolaterally compressed and expands towards the distal end. The sulcus longitudinalis is very shallow, deepening and widening only in its distalmost half. The very wide distal epiphysis is preserved only in UU VE 513 (Fig. 14r). The radial and ulnar portions are mediolaterally compressed. The length of this skeletal element, even though none of the specimens is complete, reaches up to at least 14.2 mm in the largest and most preserved specimen.

The most complete ilium (UU VE 536) from Vevi has a rather high dorsal crest, which merges posteriorly with a poorly distinct and elongated dorsal tubercle (Fig. 14o, p). The dorsal portion of the crest is missing. A distinct tubercular fossa (fossula tuberis superioris sensu Roček, 1994) is not present, but foramina are visible in the corresponding area. Most of the body of the ilium is broken away. The anteroventral part of the acetabular rim is raised. There is no preacetabular fossa. UU VE 541, on the other hand, only preserves the body of the ilium. Laterally, the acetabular fossa is moderately wide and subcircular, with a very high anteroventral portion of the acetabular rim. Both the preacetabular and the supraacetabular fossae are absent. The ventral acetabular expansion is well developed; the dorsal acetabular expansion is broken. On the medial side, a very deep and wide interiliac groove is present. The interiliac tubercle is so well developed to an extent that it is not distinguishable from the medial side of the ventral acetabular expansion.

UU VE 536 is 14.9 mm long (Fig. 14o, p). UU VE 541 is 8.5 mm long and 8.5 mm high.

Both tibiofibulae from Vevi preserve only the proximal half (Fig. 14q). They have a narrow diaphysis, which expands significantly towards the proximal epiphysis. The width of the epiphysis is slightly less than twice the width of the narrowest part of the diaphysis. The epiphysis bears a well-distinct and sharp crista cruris. In proximal view, the articular surfaces of both the tibial and the fibular portions are elliptical. The main axes of these articular surfaces are roughly parallel. The largest specimen is 19.4 mm.

Remarks. A large anuran taxon is represented in Vevi by remains that share a general discoglossine morphology. Presence of both paracoronoid and coronoid processes on the angular, a sulcus cartilagine Meckeli that deepens at the level of the coronoid process, maxillae with a long processus pterygoideus and a distinct medial depression on the posterior end, as well as the pterygoid provided with a ventral flange support an identification of this large discoglossine with a member of the widespread genus *Latonia* (Biton et al., 2013, 2016; Roček, 1994, 2013; Syromyatnikova & Roček, 2019; Syromyatnikova et al., 2019b). A precise specific identification is prevented by the absence in the sample of important elements such as frontoparietals and prooticoccipitals. However, few characters that are currently interpreted as taxonomically significant within *Latonia* (see Roček, 2013; Sorbelli et al., 2021; Syromyatnikova & Roček, 2019; Syromyatnikova et al., 2019b) can be observed. Unsculptured maxillae like those present in the Vevi material characterize all species of the genus, including a possible new species from the Italian Early Pleistocene (Sorbelli et al., 2021), except for *Latonia seyfriedi* (including *Latonia gigantea*; sensu Syromyatnikova et al., 2019b). The maxillary tooth row ending with the lamina horizontalis is reminiscent of (some) specimens of *L. seyfriedi* (reported as *L. gigantea* in Syromyatnikova & Roček, 2019) and *Latonia caucasica*, whereas the coronoid process is unlike *Latonia vertaizoni* in being well developed. In the end, the sculptured ventral flange of the pterygoid is so far only reported for the possible Italian new species (Sorbelli et al., 2021), but detailed description of referred pterygoids are unavailable for most of the extinct *Latonia*. As a matter of fact, apart from the extant *Latonia nigriventer*, this feature can be evaluated only on a single isolated pterygoid attributable to *L. seyfriedi* (Villa et al., 2019; mentioned there as *L. gigantea*), which is unsculptured. Conflicting affinities, therefore, render it difficult to confidently point out possible relations with known taxa, also considering the known variation in at least some of the diagnostic features. More material and a clarification of the validity of diagnostic characters within

Latonia are needed in order to better define the taxonomic identity of the *Latonia* from Vevi.

Discoglossidae indet.

Figure 15

Material. *Chalicorrema*: two urostyles (UU RA 518 and UU RA 519).

Description.

UU RA 518 and UU RA 519 are two fragments of urostyles (Fig. 15). UU RA 519 preserves only part of the shaft (Fig. 15c). It has a low carina neuralis, which is open dorsally with a narrow longitudinal groove. UU RA 518 preserves the anterior end and part of the shaft, but not the carina neuralis (Fig. 15a, b). Anteriorly, it has two mediolaterally-extended cotyles, which merge in the midline. Ventrally, a small point is visible at the confluence between the two cotyles. The fragments UU RA 518 and UU RA 519 are slightly less and slightly more than 10 mm long, respectively.

Remarks. The dorsal fissuring of the neural arch is a feature shared by discoglossid (sensu Dubois et al., 2021) anurans (i.e., *Discoglossus* Otth, 1837, and *Latonia*; Roček, 1994; Biton et al., 2016), to which these two urostyles can be therefore assigned. All other observable features are coherent with such an identification. Nevertheless, the very fragmentary status of the specimens and the absence of other clear discoglossid remains in *Chalicorrema* prevent a more precise referral.

Geobatrachia Ritgen, 1828

Archaeosalientia Roček, 1981

Pelobatoidea Bonaparte, 1850

Pelobatidae Bonaparte, 1850

Pelobates Wagler, 1830

Pelobates praefuscus Khosatzky, 1985

Pelobates aff. *praefuscus*

Figures 16, 17

Material. *Spilia 1*: two humeri (UU SP1 1144); *Spilia 3*: four maxillae (UU SP3 649–UU SP3 652), one frontoparietal (UU SP3 658), three sacro-urostylar complexes (UU SP3 653–UU SP3 655), six humeri (UU SP3 618, UU SP3 633, and UU SP3 642–UU SP3 645), and three ilia (UU SP3 646–UU SP3 648); *Spilia 4*: eight maxillae (UU SP4 669–UU SP4 674 and UU SP4 736), one nasal (UU SP4 675), two frontoparietals (UU SP4 668 and UU SP4 691), one sacro-urostylar complex (UU SP4 676), and one humerus (UU SP4 711).

Description.

These small maxillae from *Spilia* are only partially preserved (Fig. 16a–f). Most of them are represented by a fragment of the mid-posterior portion of the bone, but UU SP3 651, UU SP3 652, and UU SP4 670 (Fig. 16e, f) preserve the area of the processus palatinus and UU SP3 649 (Fig. 16a, b) preserves most of the bone except for the anterior end and the tooth row. The maxillae display



Fig. 15 Discoglossidae indet. from Chalicorrema. **a, b** Urostyle (UU RA 518) in dorsal (**a**) and ventral (**b**) views; **c** urostyle (UU RA 519) in left lateral view

a rather narrow (higher anteriorly) lamina horizontalis, which does not originate a processus pterygoideus posteriorly. The tooth row carries closely-spaced and narrow tooth positions. When the teeth are preserved, these are pleurodont, pedicellated and bicuspid. The tooth row ends in correspondence with the end of the lamina horizontalis in UU SP4 672, but it extends posterior to it in UU SP3 650 (Fig. 16c) and UU SP4 671. The processus palatinus of UU SP3 649 (Fig. 16a, b), UU SP3 651, UU SP3 652, and UU SP4 670 (Fig. 16e, f), though highly damaged, is visibly narrow, anterodorsally projected

and deeply grooved dorsally. The margo orbitalis is gently concave. A distinct dermal sculpturing is present on the lateral surface. The sculpturing is rather sparse [very slightly denser in UU SP4 670 (Fig. 16f) and UU SP4 671] and made up by small tubercles and short ridges.

The nasal (UU SP4 675) from Spilia 4 is of medium size and wide (Fig. 16g, h). The dorsal surface bears a rather sparse dermal sculpturing made up by tubercles and short ridges.

UU SP3 658 (Fig. 16i, j) and UU SP4 668 (Fig. 16k, l) are fragments of frontoparietals, preserving approximately

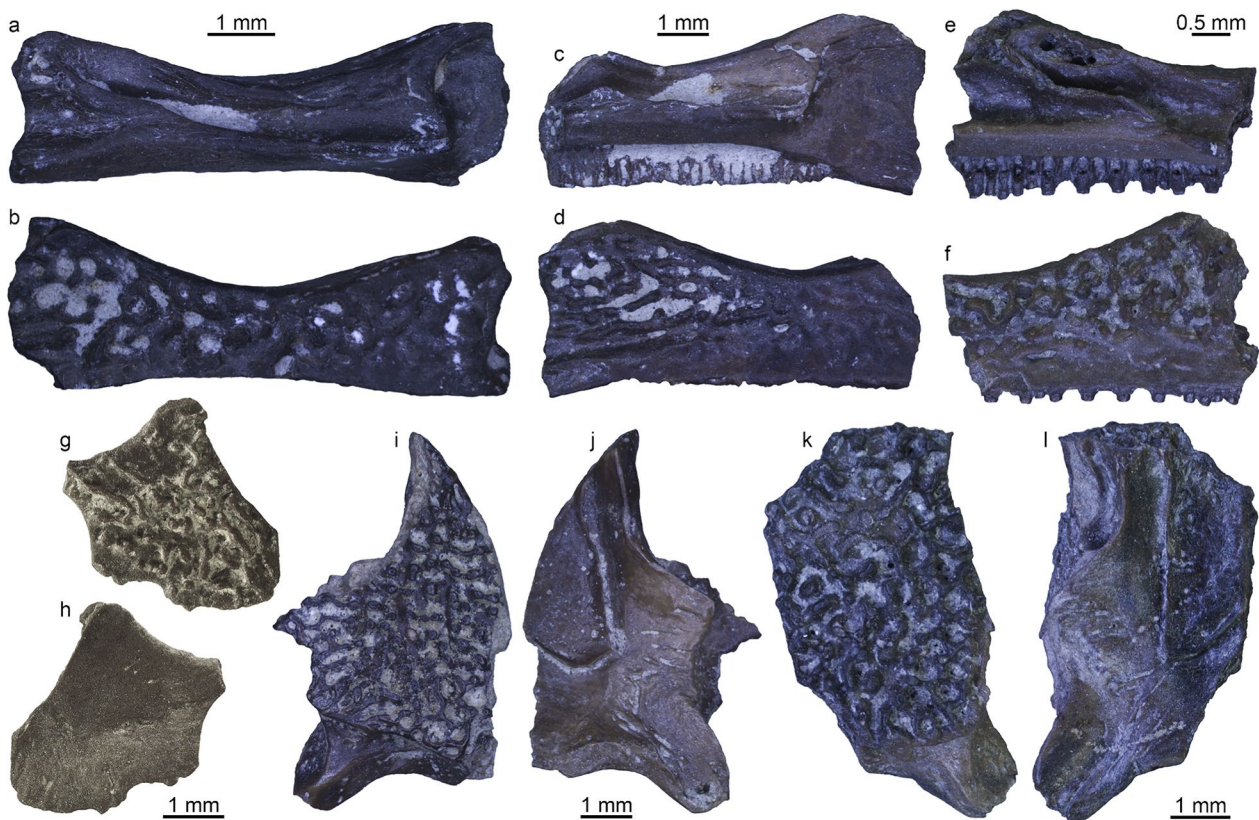


Fig. 16 *Pelobates* aff. *praefuscus* from Spilia 3 (SP3) and Spilia 4 (SP4), cranial elements. **a, b** Right maxilla (UU SP3 649) in medial (**a**) and lateral (**b**) views; **c, d** right maxilla (UU SP3 650) in medial (**c**) and lateral (**d**) views; **e, f** right maxilla (UU SP4 670) in medial (**e**) and lateral (**f**) views; **g, h** left nasal (UU SP4 675) in dorsal (**g**) and ventral (**h**) views; **i, j** frontoparietal (UU SP3 658) in dorsal (**i**) and ventral (**j**) views; **k, l** frontoparietal (UU SP4 668) in dorsal (**k**) and ventral (**l**) views

the left and right posterolateral quarter of the bone respectively. The bone they represent is rather robustly built. On the ventral surface, the posterolateral corner of the incrassatio frontoparietalis is visible: it has a straight lateral margin (slightly sigmoid in the anterior portion in UU SP3 658), whereas the posterior margin has an anteromedial course. Lateral to the incrassatio, there is the rather shallow canalis arteriae orbitonasalis, starting from a wide foramen that is visible in ventral view. The posterior portion of the canalis is open ventrally. A short, wide and distally rounded processus paraoccipitalis is present at the posterolateral corner of the bone. A low and dorsally flat ridge runs longitudinally on the dorsal surface of the latter process. Medial to the base of the same process, the rather wide foramen arteriae occipitalis is not exposed in dorsal view, being visible only in posterior view. UU SP4 691 is also a fragment of frontoparietal, but it preserves the middle portion of the left side of the bone. The canalis arteriae occipitalis is visible, as well as the lateral margin of the incrassatio frontoparietalis, which appears slightly sigmoid in this portion of the bone. The canalis opens ventrally in

its posterior part and is moderately deep. The dorsal surface of all specimens is largely covered by a sparse dermal sculpturing with tubercles and short ridges.

The sacrourostyle complexes from Spilia 3 (Fig. 17a, b) and Spilia 4 (Fig. 17c, d) are poorly preserved and medium to moderately small sized. Most of the urostyle component is missing, but the fusion of the sacral vertebra with the urostyle is still recognizable. The centrum is cylindrical, with an anterior cotyle. The neural canal is dorsoventrally compressed, reniform in anterior view. The neural arch is dorsally flattened, devoid of any developed structure on its dorsal surface. The lateral processes are very anteroposteriorly enlarged, but they are almost completely missing.

The humeri from Spilia preserve only the distal half of the bone (Fig. 17e, f). The shaft is mostly missing and therefore it is not possible to state whether it was straight or curved. The eminentia capitata is slightly laterally shifted. The fossa cubitalis ventralis is moderately deep and opened on the lateral side. The epicondylus ulnaris is almost double in size than the epicondylus radialis. The

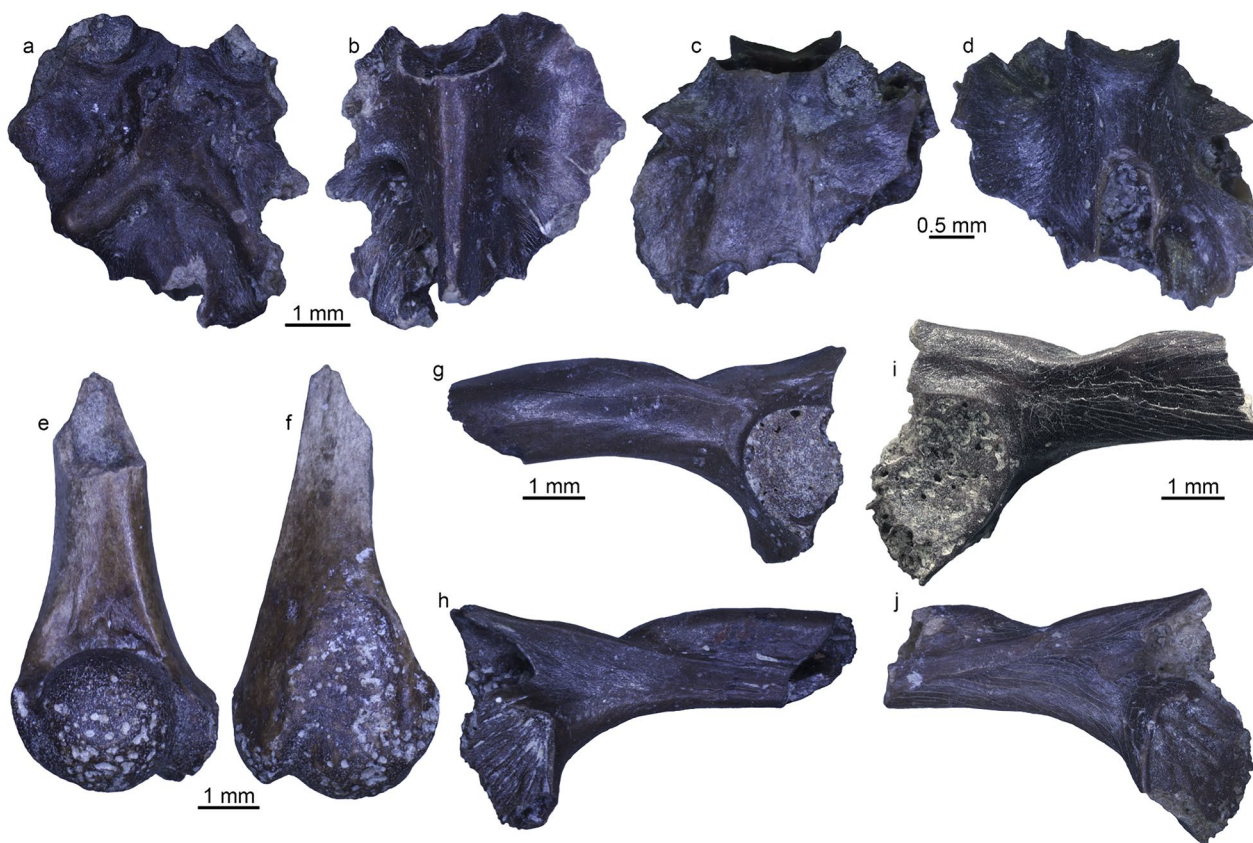


Fig. 17 *Pelobates* aff. *praefuscus* from Spilia 3 (SP3) and Spilia 4 (SP4), postcranial elements. **a, b** Sacrourostyle complex (UU SP3 653) in dorsal (**a**) and ventral (**b**) views; **c, d** sacrourostyle complex (UU SP4 676) in dorsal (**c**) and ventral (**d**) views; **e, f** right humerus (UU SP3 618) in ventral (**e**) and dorsal (**f**) views; **g, h** left ilium (UU SP3 646) in lateral (**g**) and medial (**h**) views; **i, j** right ilium (UU SP3 648) in lateral (**i**) and medial (**j**) views

cristae medialis and lateralis are not developed. The olecranon scar is rather large, but somehow elongated.

The ilia from Spilia are medium sized (Fig. 17g–j). They have no dorsal crest and no dorsal tubercle. The preacetabular and supraacetabular fossae are also absent. The shaft is mostly missing in all specimens. The acetabulum is rather wide and semicircular. The spiral groove is deep. The posteromedial surface of the bone displays a low degree of striation.

Remarks. All these remains show combinations of features typical for *Pelobates* (Bailon, 1999; Roček, 2013). Maxillae, nasal, and frontoparietals have a similar dermal sculpturing, which is coossified with the bone in contrast with that of *Latonia* (Roček, 2013; Syromyatnikova et al., 2019b); in the latter genus, the sculpturing is a true exostosis and arises separately from dermal bones in outer layers of the dermis, fusing only secondarily with the dermal bones (see Georgalis et al., 2023c). The humeri have a shifted eminentia capitata and a laterally-open fossa cubitalis ventralis. The sacrourostyle complexes display an anterior cotyle and strongly-enlarged lateral processes. This sacral morphology is present in

Pelodytes Bonaparte, 1838b, as well, but fusion with the urostyle is absent in this taxon (Bailon, 1999). Iliia have no dorsal crest, no dorsal tubercle, a deep spiral groove (Böhme, 2010), and a striated posteromedial surface. The Spilia *Pelobates* differs from all extant species of the genus in having a ventrally open posterior portion of the canalis arteriae orbitonasalis (Syromyatnikova, 2019). Considering extinct occurrences, it closely recalls *Pelobates* aff. *praefuscus* from the Late Miocene (MN 13) of Solnechnodolsk, Russia, in respect to the frontoparietal characters deemed significant by Syromyatnikova (2019). Similar to the taxon from Solnechnodolsk, the one from Spilia has a pustular sculpturing, a shallow canalis arteriae orbitonasalis (even though this may be slightly deeper at least in UU SP4 691), and the foramen arteriae occipitalis that is both located medial to the processus paraoccipitalis and not visible in dorsal view (even though both these latter features are variable in *Pelobates* aff. *praefuscus* from Solnechnodolsk; Syromyatnikova, 2019). It differs from all other Miocene species in the pustular (i.e., not pit-and-ridges) sculpturing of the cranial bones. *Pelobates praefuscus* has an extremely deep

canalis arteriae orbitonasalis (Syromyatnikova, 2019), in contrast with the *Spilia* taxon. *Pelobates* sp. from the Early Pliocene (MN 14) of Nizhny Vodyanoi, Russia (Syromyatnikova, 2019) also shares affinities with the *Spilia* taxon, but only a few of the frontoparietal features are preserved in elements from this Russian locality. Following Syromyatnikova's (2019) criteria, it appears thus reasonable to identify this Greek pelobatid as *Pelobates* aff. *praefuscus*, in the same way as the Solnechnodolsk occurrence.

Pelobates sp.

Figure 18

Material. *Chalicorrema*: two maxillae (UU RA 509 and UU RA 512) and five sculptured bone fragments (UU RA 510, UU RA 511, UU RA 514, UU RA 515, and UU RA 517).

Description.

The two maxillae from *Chalicorrema* are only partially preserved (Fig. 18a–e). Both are lacking the anterior half of the bone, though UU RA 509 (Fig. 18a–c) preserves a larger portion of the posterior part compared to UU RA 512 (Fig. 18d, e). Medially, there is a narrow lamina horizontalis. In dorsal view, the lamina is not strongly developed in medial direction. The posterior end of the lamina originates a short processus pterygoideus. Ventral to the lamina, the tooth row hosts closely-packed, pedicellate

and pleurodont teeth. The tooth row extends posterior to the processus pterygoideus in UU RA 509 (Fig. 18b), but ends more anterior in UU RA 512 (Fig. 18e). The posterior end of the medial surface of the maxilla has no posterior depression. The processus zygomaticomaxillaris is well developed and distally rounded. The margo orbitalis is deep. The lateral surface hosts a well-developed and rather dense sculpturing, which is coossified to the bone. The sculpturing is made of small tubercles, which are aligned and united in ridges (Fig. 18c, d). UU RA 509 is slightly less than 10 mm long (Fig. 18a–c). Five sculptured bone fragments from *Chalicorrema* (Fig. 18f, i) cannot be clearly recognized as either portions of maxillae or of other bones, but share with UU RA 509 and UU RA 512 the same dermal sculpturing.

Remarks. These sculptured skull bones from *Chalicorrema* are here assigned to *Pelobates* because of the coossified dermal sculpturing made up by tubercles and ridges (Bailon, 1999; Roček, 2013; Syromyatnikova, 2017, 2019). The deep margo orbitalis is shared with species such as *Pelobates cultripipes* (Cuvier, 1829) and *Pelobates syriacus* Boettger, 1889 (Bailon, 1999; Blain et al., 2016), as well as with *Pelobates* aff. *praefuscus* from Caucasus (Syromyatnikova, 2019) and the *Spilia* specimens described above. Due to poor preservation and scarcity of the available material, a more precise identification at species level is here avoided.

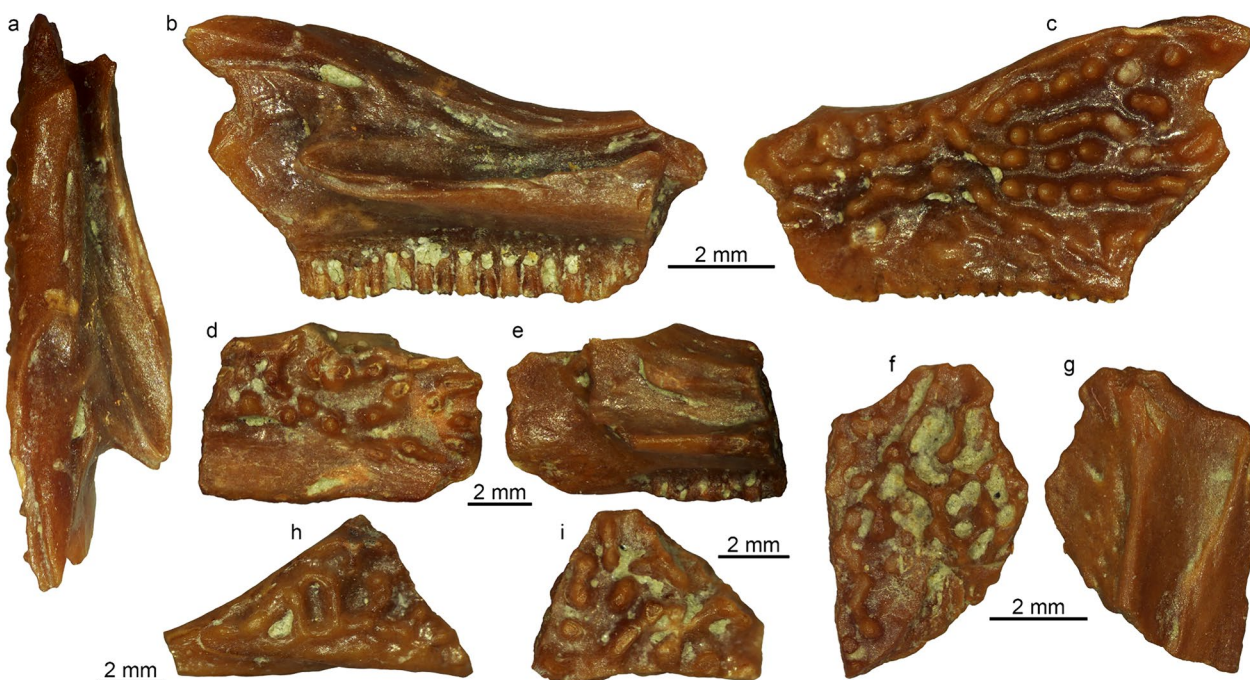


Fig. 18 *Pelobates* sp. from *Chalicorrema*. **a–c** Left maxilla (UU RA 509) in dorsal (**a**), medial (**b**), and lateral (**c**) views; **d, e** left maxilla (UU RA 512) in medial (**d**) and lateral (**e**) views; **f, g** fragment of sculptured skull-roofing bone (UU RA 510) in dorsal (**f**) and ventral (**g**) views; **h** fragment of sculptured bone (UU RA 514) in external view; **i** fragment of sculptured bone (UU RA 517) in external view

Ranomorpha Fejérváry, 1921

Ranoidea Batsch, 1796

Ranidae Batsch, 1796

***Pelophylax* Fitzinger, 1843**

***Pelophylax* sp.**

Figure 19

Material. *Spilia 1*: 13 ilia [UU SP1 1031, UU SP1 1033, and UU SP1 1034 (11 elements)]; *Spilia 4*: one ilium (UU SP4 682).

Description.

These ilia from *Spilia 1* and *Spilia 4* reach a rather large size (Fig. 19), but small specimens are also present (e.g., UU SP1 1031). They bear a high and straight dorsal crest, which is however not completely preserved in any of the specimens. The dorsal tubercle is present, elongated, rather vertically oriented and very well distinct. Its lateral surface is flat. Only in the smallest specimens, the tubercle is slightly less vertical. The body of the ilium has a moderately wide and semicircular acetabulum, a deep supraacetabular fossa, and no preacetabular fossa. The ventral acetabular expansion is well developed. The posterior portion of the body is either broken off or damaged in all specimens, but it appears moderately thick in the best-preserved ones.

Remarks. Considered together, the presence of a high and straight dorsal crest, the well-distinct and vertical dorsal tubercle, and the rather thick posterior portion of the body suggest attribution of these ilia to *Pelophylax* (Bailon, 1999; Gleed-Owen, 1998). A more precise identification is not possible based on such a small sample (Blain et al., 2015).

***Rana* Linnaeus, 1758**

***Rana dalmatina* Fitzinger in Bonaparte, 1838b**

Rana* cf. *dalmatina

Figure 20

Material. *Spilia 4*: one ilium (UU SP4 683).

Description.

The moderately small ilium (UU SP4 683) from *Spilia 4* is rather well preserved, even though most of the shaft is missing (Fig. 20). It has a well-developed dorsal crest and a distinct dorsal tubercle. The tubercle is elongated and shows some low rugosities on its lateral surface. Its dorsalmost point does not exceed the dorsal crest in height. The dorsal acetabular expansion is moderately long and creates an angle wider than 90° with the tubercle. A small supraacetabular fossa is visible between the tubercle and the dorsal expansion. The ventral acetabular expansion is rather well developed. There is no preacetabular fossa. The acetabulum is moderately wide. The medial surface of the body of the ilium does not display any interiliac groove or tubercle. The bone has a narrow and moderately high ilioischial junction.

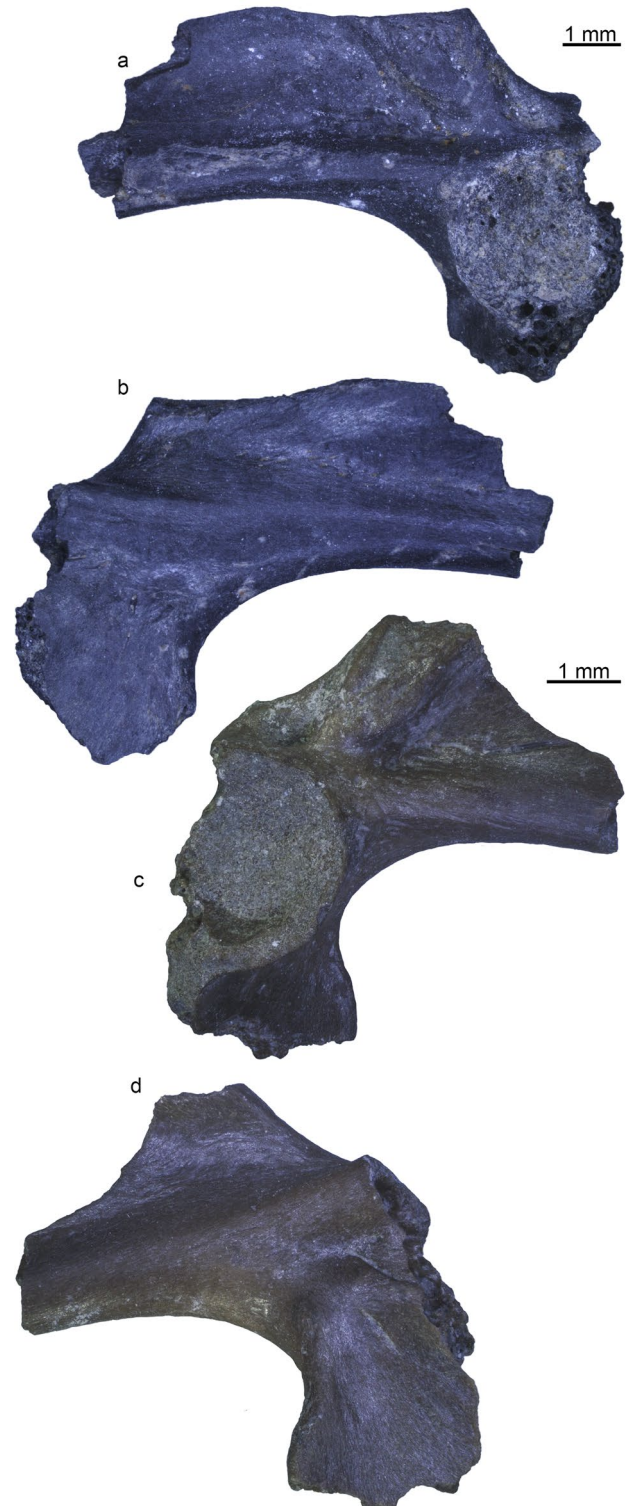


Fig. 19 *Pelophylax* sp. from *Spilia 1* (SP1) and *Spilia 4* (SP4). **a, b** Left ilium (UU SP1 1033) in lateral (**a**) and medial (**b**) views; **c, d** right ilium (UU SP4 682) in lateral (**c**) and medial (**d**) views

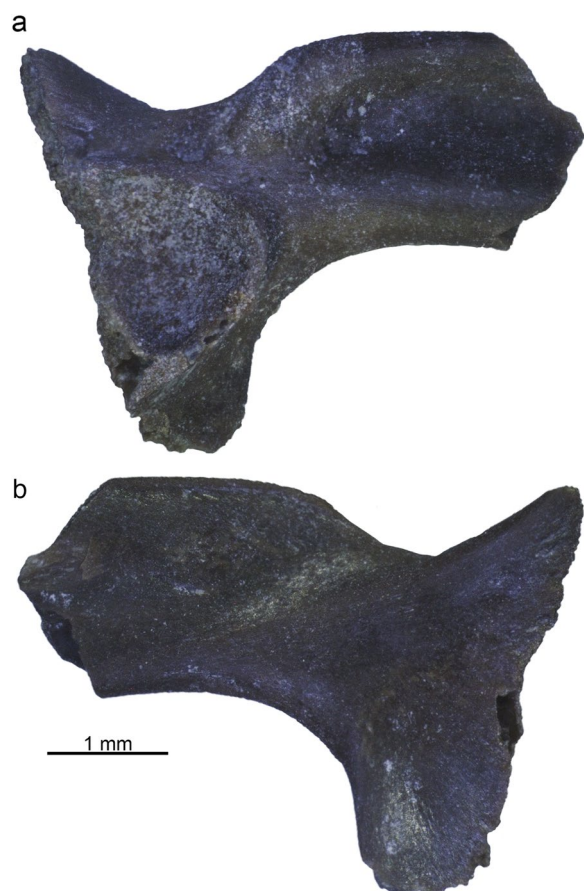


Fig. 20 *Rana* cf. *dalmatina* from Spilia 4. Right ilium (UU SP4 683) in lateral (a) and medial (b) views

Remarks. This ilium from Spilia 4 is assigned to the genus *Rana* because of the following features: well-developed dorsal crest; angle between dorsal tubercle and dorsal acetabular expansion higher than 90°; and high and narrow ilioischiatric junction (Bailon, 1999; Gleed-Owen, 1998; Ratnikov, 2001). More than 100 species of *Rana* are currently recognized (Dubois et al., 2021) and our knowledge of their comparative osteology is extremely limited. Thus, a real identification of this fossil at specific level is not possible, even though some features are useful to discuss. UU SP4 683 differs from *Rana temporaria* Linnaeus, 1758, in the well-developed ventral acetabular expansion (Bailon, 1999). A dorsal crest that is higher than the dorsal tubercle is a feature found in *Rana dalmatina* and *Rana iberica* Boulenger, 1879, but not in *Rana arvalis* Nilsson, 1842, *Rana pyrenaica* Serra-Cobo, 1993, and *Rana temporaria* (Bailon, 1999; Blain & Arribas, 2017). An irregular lateral surface of the dorsal tubercle is reported for *R. arvalis* and *R. temporaria* by Gleed-Owen (1998). The irregularities seem to be present also in Gleed-Owen's drawing of the ilium of *R. dalmatina* (Gleed-Owen, 1998, fig. 5.46a), even though

he did not mention this directly in the text. Similarities between the tubercle of *R. dalmatina* and the irregular one of *R. arvalis* are indeed reported, however (Gleed-Owen, 1998, p. 215), maybe involving the morphology of the lateral surface as well. Our personal observations confirm that rugosities are sometimes present on the tubercle of *R. dalmatina* (AV, pers. obs.), even though this feature appears to be variable. Variation in the roughness/smoothness also occurs in *R. temporaria* (Gleed-Owen, 1998; AV, pers. obs.). Pending a more complete study of the ilial comparative morphology of brown frogs, we here refer UU SP4 683 to *Rana* cf. *dalmatina*, as this species is the one sharing the most similarities with it among the species for which osteological data are available. However, we acknowledge that this identification should only be considered as tentative, awaiting for more information on other species, such as the southern Balkan endemic *Rana graeca* Boulenger, 1891.

***Rana* sp.**

Figures 21, 22a

Material. *Spilia 1*: six humeri (UU SP1 1035, UU SP1 1038, and UU SP1 1108) and one ilium (UU SP1 1109); *Spilia 3*: one humerus (UU SP3 668); *Spilia 4*: one humerus (UU SP4 684); *Vevi*: two humeri (UU VE 544 and UU VE 545).

Description.

The medium-sized humeri from Spilia are slender and devoid of crista paraventralis (Fig. 21a–c). The spherical eminentia capitata is aligned with the straight shaft. The humerus is provided with a deep fossa cubitalis ventralis, a narrow and elongated olecranon scar, and moderately developed cristae lateralis and medialis. The crista medialis displays a light dorsal bending.

The humeri from Vevi are small and rather slenderly built (Fig. 22a). The proximal half is missing in both cases. The diaphysis is straight. The eminentia capitata is spherical and located in line with the main axis of the bone. The fossa cubitalis ventralis is deep. A moderately-developed crista medialis is present. In medial view, it shows an incipient dorsal bending, which is more evident in UU VE 545. The crista lateralis is absent in UU VE 544 (Fig. 22a), but present as a low ridge in UU VE 545. The epicondylus ulnaris is robust and well ossified in UU VE 545, but partially uncoossified in UU VE 544. The olecranon scar is elongated. UU VE 544 (Fig. 22a) is 8.6 mm long, whereas the length of UU VE 545 is 8.5 mm.

The single ilium (UU SP1 1109) from Spilia 1 is medium-sized (Fig. 21d, e). The shaft is almost completely not preserved, but the base of a dorsal crest is visible. In the same place, there is an evident dorsal tubercle, which is however poorly preserved as well. Posteriorly, the dorsal acetabular expansion is moderately long. The angle composed by the latter and the dorsal tubercle is

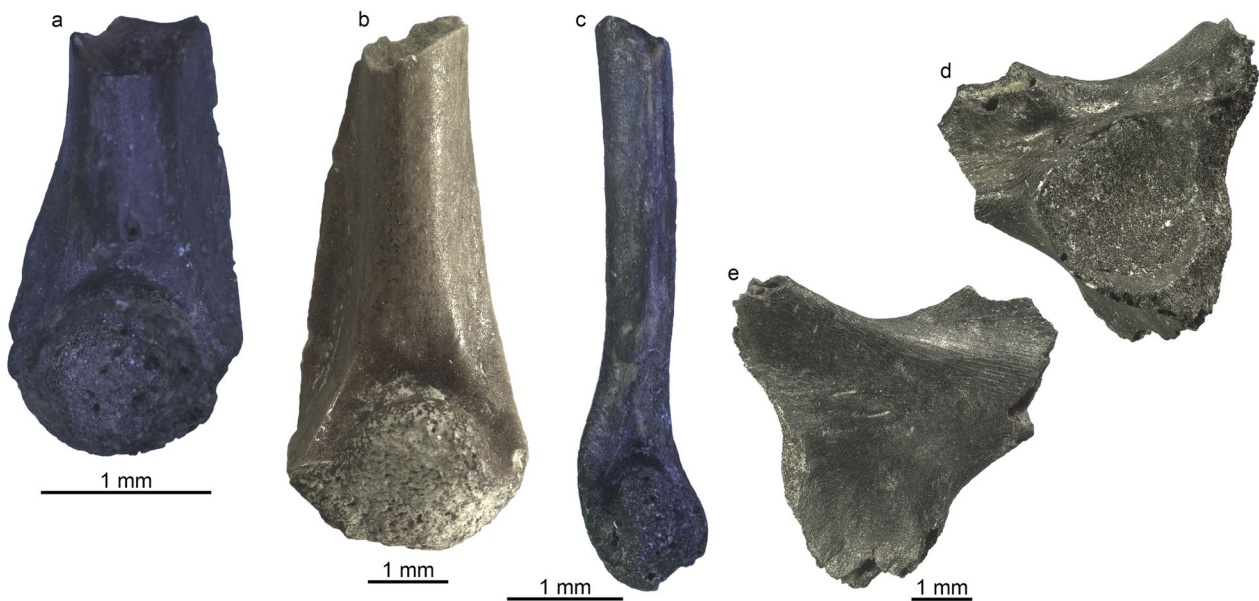


Fig. 21 *Rana* sp. from Spilia 1 (SP1), Spilia 3 (SP3), and Spilia 4 (SP4). **a** Left humerus (UU SP1 1035) in ventral view; **b** left humerus (UU SP3 668) in ventral view; **c** right humerus (UU SP4 684) in ventral view; **d, e** left ilium (UU SP1 1109) in lateral (**d**) and medial (**e**) views

very wide, much more than 90°. The acetabulum is moderately wide. Dorsal to it, there is a rather deep supraacetabular fossa. The ventral acetabular expansion appears short, even though its distal tip is broken. There is no preacetabular fossa. The medial surface is rather flat, without distinct interiliac tubercle or groove. The ilioischiatric junction is high and narrow.

Remarks. These fossils from Spilia share the diagnostic features of brown frogs according to Gleed-Owen (1998) and Bailon (1999), but due to either preservation or absence of known diagnostic features, they cannot be identified more precisely. They might either pertain to the same taxon as UU SP4 683 or to a different brown frog. Similarly, the two humeri from Vevi are referred to brown frogs because of the combination of straight diaphysis, eminentia capitata not shifted laterally, and dorsally-bent crista medialis (see characters in Bailon, 1999).

Ranidae indet.

Figures 22b–f, 23

Material. *Spilia 1*: one sacral vertebra (UU SP1 1143) and three humeri (UU SP1 1115 and UU SP1 1145); *Spilia 4*: one humerus (UU SP4 701); *Vevi*: one coracoid (UU VE 547) and three humeri (UU VE 543, UU VE 546, and UU VE 549).

Description.

The sacral vertebra (UU SP1 1143) from Spilia 1 is small-sized (Fig. 23a). It preserves only the left half of the bone. The centrum has an anterior condyle. Posteriorly, the left posterior condyle is visible, whereas the right

one is missing. The neural arch is slenderly built. The left transverse process is cylindrical.

The coracoid (UU VE 547) from Vevi is small and slender (Fig. 22b, c). It has a narrow and straight middle portion, which expands towards the ends. The medial end, which is the pars epicoracoidalis, is almost twice as wide as the lateral pars glenoidalis. The length of the coracoid, which is almost complete, is 6.2 mm.

The morphology of the humeri from Vevi (Fig. 22d–f) is the same as the one described above for the humeri attributed to *Rana*. The only exception is that these humeri lack a crista medialis. They are well ossified, except for the very thin UU VE 549. The length of the most-preserved one is 7.9 mm.

The humeri from Spilia 1 and Spilia 4 are small and slender (Fig. 23b). They have a straight diaphysis, with no crista paraventralis. The eminentia capitata is spherical and located in line with the diaphysis. The fossa cubitalis ventralis is present. The epicondyles are poorly ossified. Both the crista lateralis and medialis are present, but very poorly developed. On the dorsal side, the olecranon scar is elongated.

Remarks. Sacral vertebrae with an anterior condyle, two posterior condyles, and cylindrical transverse processes, as well as humeri with a straight diaphysis, no crista paraventralis, and a not-shifted eminentia capitata can be assigned to indeterminate ranids (Bailon, 1999). It is not clear whether they could pertain to the brown frogs already identified from Spilia or not. The small size of the humeri, together with the poor development of the cristae and the poorly ossified epicondyles, are indicative of a



Fig. 22 *Rana* sp. from Vevi (a). a Left humerus (UU VE 544) in ventral view. Ranidae indet. from Vevi (b–f). b, c Right coracoid (UU VE 547) in dorsal (b) and ventral (c) views; d, e left humerus (UU VE 543) in ventral (d) and lateral (e) views; f right humerus (UU VE 549) in ventral view

juvenile condition for these elements. As for the indeterminate ranids from Vevi, they may pertain to *Rana* that is present in the locality, also considering the comparable size, but this cannot be stated with certainty.

Hyoidea Rafinesque, 1815
Hylidae Rafinesque, 1815
Hyla Laurenti, 1768
Hyla arborea (Linnaeus, 1758)

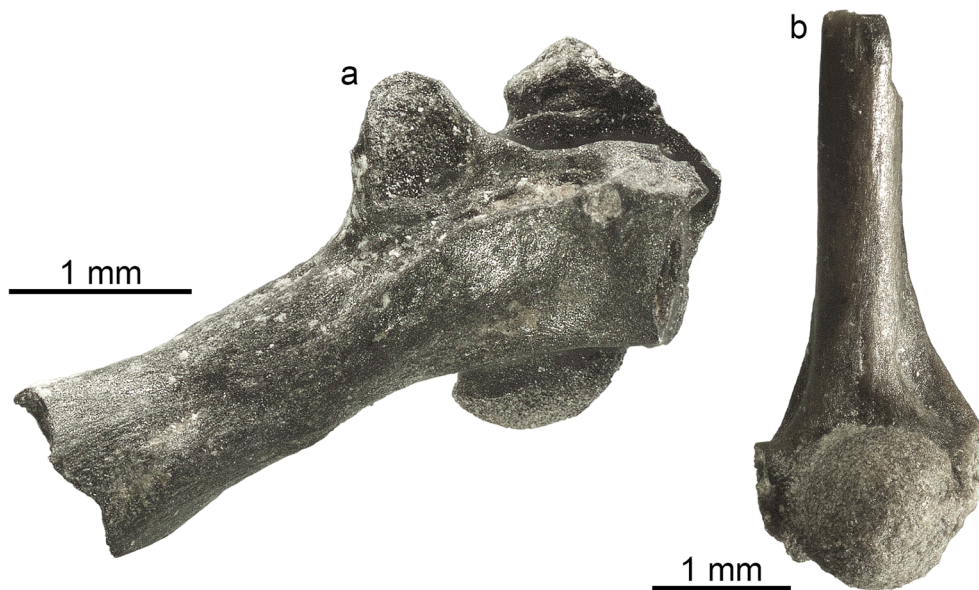


Fig. 23 Ranidae indet. from Spilia 1 (SP1) and Spilia 4 (SP4). **a** Sacral vertebra (UU SP1 1143) in dorsal view; **b** left humerus (UU SP4 701) in ventral view

Hyla gr. arborea

Figure 24

Material. *Spilia 1*: one humerus (UU SP1 1100) and one ilium (UU SP1 1043); *Spilia 3*: one humerus (UU SP3 659) and one ilium (UU SP3 660); *Spilia 4*: one scapula (UU SP4 734) and one humerus (UU SP4 685).

Description.

The poorly preserved scapula (UU SP4 734) from Spilia 4 shows a very slender and elongated body and a cavitas glenoidalis that is easily visible in ventral view.

The processus glenoidalis is broken off, but the processus acromialis is rather slender and straight.

The humeri from the Spilia localities are very small sized and slenderly built (Fig. 24a–c). The diaphysis is straight and devoid of crista paraventralis. The eminentia capitata is clearly laterally displaced compared to the main axis of the diaphysis. The fossa cubitalis ventralis is very deep. The cristae lateralis and medialis are moderately developed. On the dorsal surface, the olecranon scar is poorly visible.

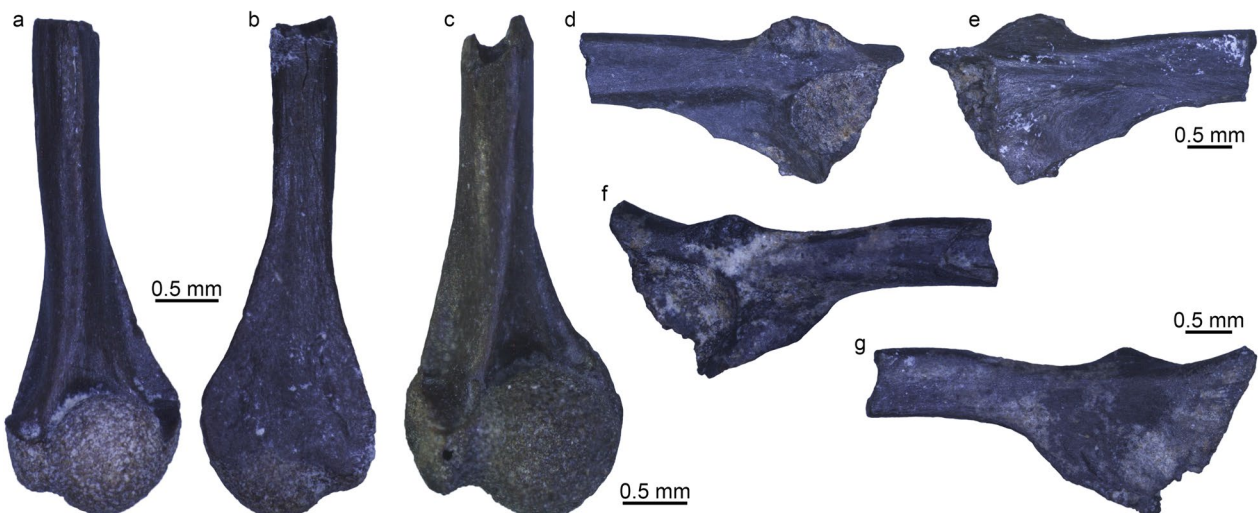


Fig. 24 *Hyla gr. arborea* from Spilia 1 (SP1), Spilia 3 (SP3), and Spilia 4 (SP4). **a, b** Left humerus (UU SP3 659) in ventral (**a**) and dorsal (**b**) views; **c** left humerus (UU SP4 685) in ventral view; **d, e** left ilium (UU SP1 1043) in lateral (**d**) and medial (**e**) views; **f, g** right ilium (UU SP3 660) in lateral (**f**) and medial (**g**) views

The small ilia from Spilia are slenderly built (Fig. 24d–g). They have no dorsal crest, but a well-developed, globular and laterally slanted dorsal tubercle is present. The acetabulum is semicircular. The dorsal acetabular expansion is short. The ventral acetabular expansion is strongly anteroventrally expanded. The lateral surface of the body of the bone is flat.

Remarks. These remains are here assigned to *Hyla* based on the following combination of characters reported as diagnostic by Bailon (1999): slender and elongated scapula with a ventrally-exposed cavitas glenoidalis and a straight processus acromialis; straight humeri devoid of crista paraventralis and provided with a laterally-displaced eminentia capitata, a deep fossa cubitalis ventralis, and a moderately-developed crista radialis; ilia with a globular and laterally-bending dorsal tubercle, an expanded ventral acetabular expansion, and without dorsal crest. All these characters fit well with the European members of the *H. arborea* group (Birbele et al., 2023).

Bufoidea Gray, 1825

Bufoidea Gray, 1825

***Bufo* Rafinesque, 1815**

***Bufo viridis* (Laurenti, 1768)**

Bufo* gr. *viridis

Figure 25

Material. *Spilia 1*: one femur (UU SP1 1057); *Spilia 3*: two ilia (UU SP3 669 and UU SP3 670); *Spilia 4*: two sacral vertebrae (UU SP4 679 and UU SP4 680).

Description.

UU SP4 679 is the best-preserved sacral vertebra from Spilia (Fig. 25a–e). It has a single anterior cotyle, which is elliptical and mediolaterally elongated, and two posterior condyles, subelliptical as well but less elongated. The walls of the neural arch are robustly built. Dorsally, the neural arch bears a sort of pseudozygosphenal structure anteriorly and a distinct neural crest. The transverse processes are broken, but a laterally open fossa is present by their bases. A single prezygapophysis is preserved: it is wide and subcircular. UU SP4 680 is less preserved, but

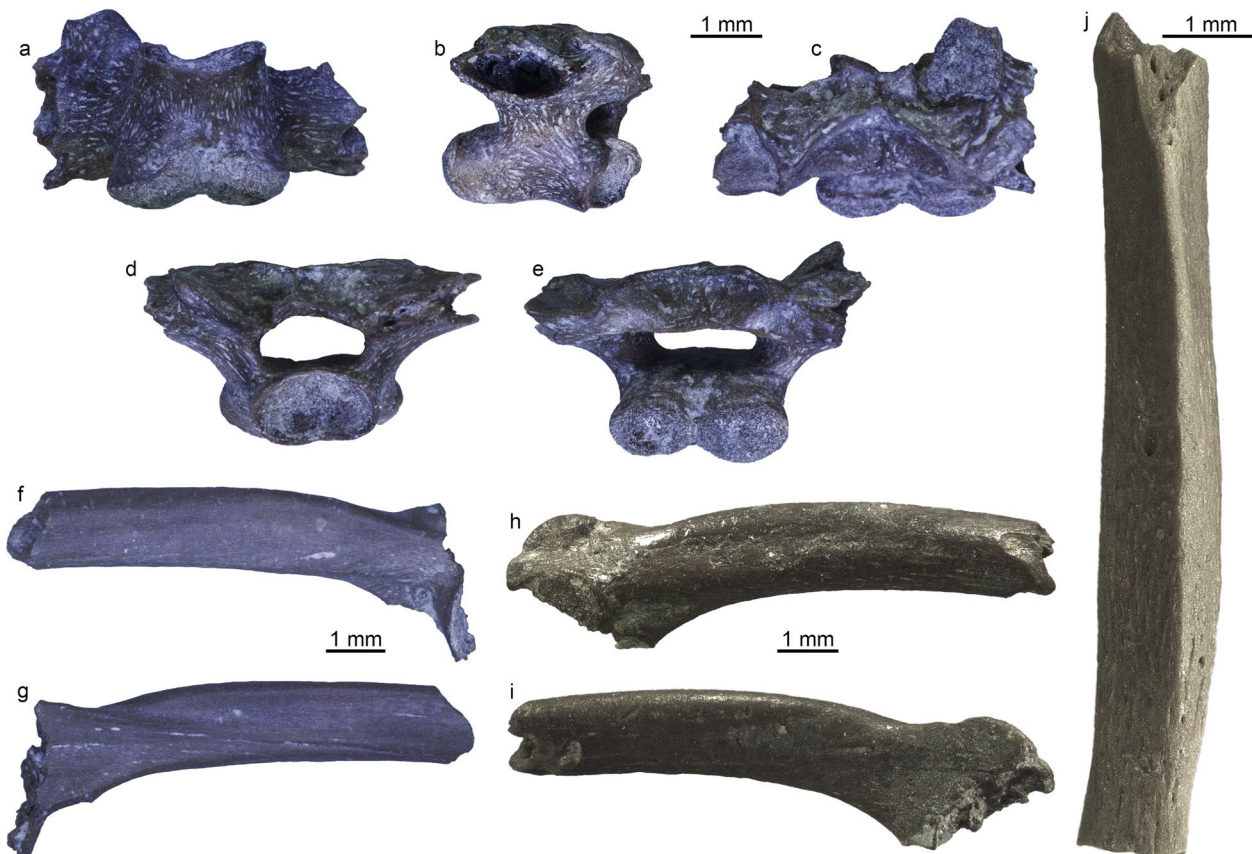


Fig. 25 *Bufo* gr. *viridis* from Spilia 1 (SP1), Spilia 3 (SP3), and Spilia 4 (SP4). **a–e** Sacral vertebra (UU SP4 679) in ventral (**a**), right lateral (**b**), dorsal (**c**), anterior (**d**), and posterior (**e**) views; **f, g** left ilium (UU SP3 669) in lateral (**f**) and medial (**g**) views; **h, i** right ilium (UU SP3 670) in lateral (**h**) and medial (**i**) views; **j** left femur (UU SP1 1057) in medial view

it shares the same morphology. Only the pseudozygosphenal structure is not evidently developed in this second specimen.

The ilia from *Spilia* 3 are moderately small (Fig. 25f, i). They preserve a straight shaft devoid of dorsal crest and a small portion of the body. The dorsal tubercle is better preserved in UU SP3 670 (Fig. 25h, i), displaying a rounded shape with small lobes dorsally. A deep preacetabular fossa is present, being more visible in UU SP3 669 (Fig. 25f, g).

The femur (UU SP1 1057) from *Spilia* 1 is rather small and slender (Fig. 25j). It displays a well-developed and sharp crista femoris.

Remarks. Green toads (*Bufo viridis* complex) are present in the *Spilia* assemblage, identified through the criteria of Bailon (1999) and Ratnikov (2001): sacral vertebrae with an anterior cotyle, two posterior condyles, a distinct neural crest, and a laterally-open fossa close to each transverse process; ilia without dorsal crest, but provided with a multilobed dorsal tubercle and a deep preacetabular fossa; a femur with an undivided crista femoris. A pseudozygosphene is not commonly reported in green toad sacral vertebrae, but it was observed in at least few fossils from the Quaternary of southern Italy (Pirro Nord; M.D., pers. obs.) referred to this clade. The taxonomic significance of this structure in these anurans may be worth further scrutiny. However, the structure observed in UU SP4 679 appears asymmetrical at close inspection, and so it may be interpreted as some sort of anomaly.

Bufonidae indet.

Figures 26, 27

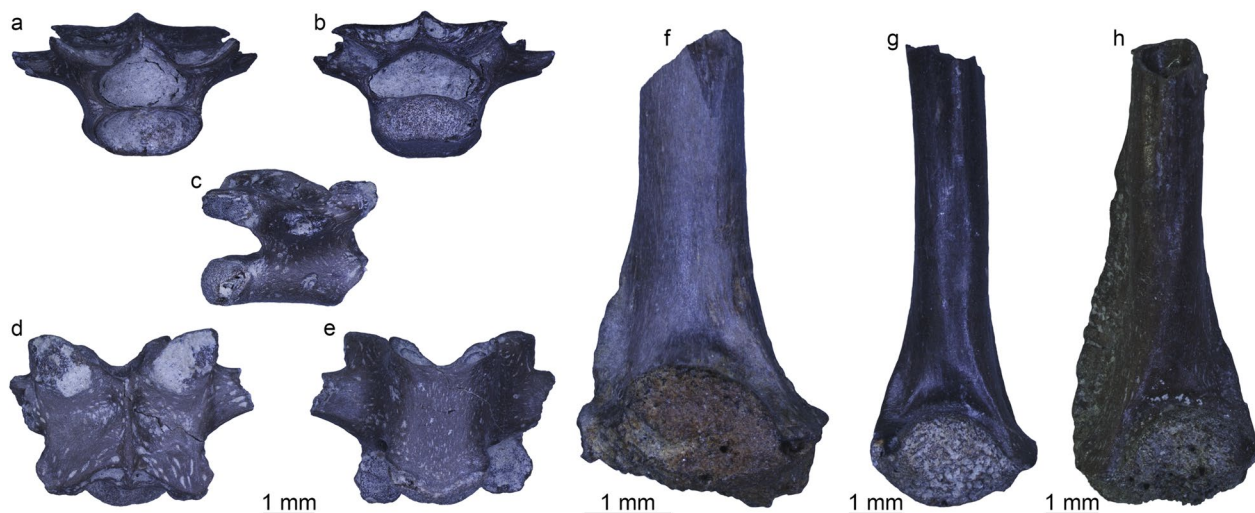


Fig. 26 Bufonidae indet. from *Spilia* 1 (SP1), *Spilia* 3 (SP3), and *Spilia* 4 (SP4). **a–e** Presacral vertebra (UU SP3 661) in anterior (**a**), posterior (**b**), right lateral (**c**), dorsal (**d**), and ventral (**e**) views; **f** right humerus (UU SP1 1041) in ventral view; **g** right humerus (UU SP3 667) in ventral view; **h** left humerus (UU SP4 681) in ventral view

Material. *Chalicorrema*: one sacral vertebra (UU RA 501); *Spilia* 1: one humerus (UU SP1 1041); *Spilia* 3: three trunk vertebrae (UU SP3 661–UU SP3 663) and one humerus (UU SP3 667); *Spilia* 4: one humerus (UU SP4 681).

Description.

The moderately large trunk vertebrae from *Spilia* 3 are robust (Fig. 26a–e). The centrum is procoelous, well individualized and dorsoventrally compressed. The neural arch has robust walls and a flat dorsal surface. A low carina neuralis is present. The transverse processes are located posterior to the prezygapophyses.

UU RA 501 from *Chalicorrema* is the only bufonid element from that locality, representing a small fragment of a sacral vertebra (Fig. 27). In spite of the small size, the vertebra was rather robustly built. Only the left half of the centrum and a small part of the left transverse process are preserved. The centrum has an anterior cotyle. Posteriorly, there is an elliptical condyle. It can be assumed that another, similar condyle was present also on the missing right half of the centrum. The two condyles were not coalescent. The transverse process is too poorly preserved to give any significant morphological information. The fragment has a total centrum length of 2.2 mm.

The humeri from *Spilia* are medium sized (Fig. 26f–h). They have a straight shaft with no crista paraventralis. The eminentia capitata is slightly shifted laterally. A moderately shallow fossa cubitalis ventralis is present. The cristae lateralis and medialis are moderately developed. The distal epiphysis is poorly ossified distally. The olecranon scar is moderately wide.

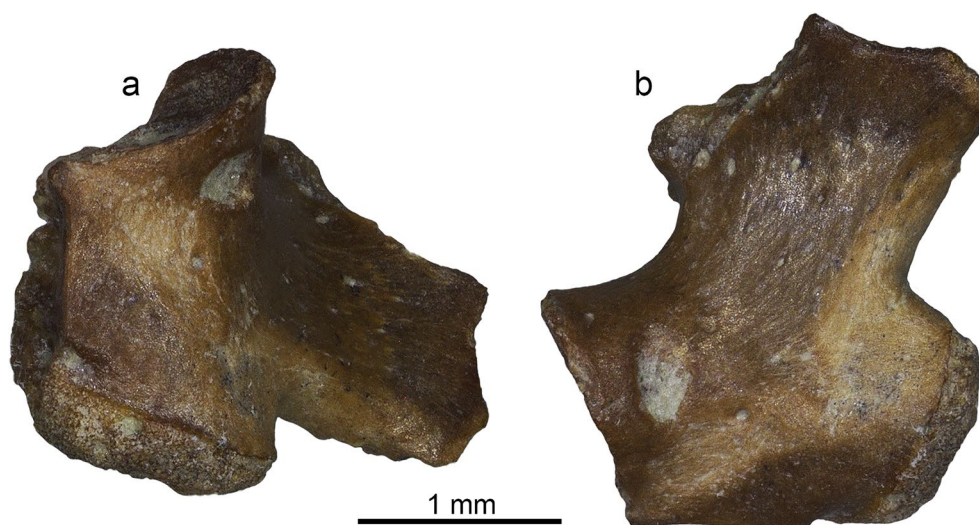


Fig. 27 Bufonidae indet. from Challicorrema. Sacral vertebra (UU RA 501) in ventral (a) and left lateral (b) views

Remarks. These fossils from Spilia share the diagnostic combination of features of bufonid anurans as reported by Bailon (1999). It is not possible, however, to identify them at lower taxonomic level, even though they could pertain to green toads as these are the only bufonids currently known from Spilia. The straight humeral shaft, which is present in males of *Bufo bufo* (Linnaeus, 1758) and *Bufotes viridis* and absent in *Epidalea calamita* (Laurenti, 1768) and females of the preceding taxa according to Bailon (1999), may support this hypothesis.

Similarly, in spite of its very fragmentary status, the sacral vertebra UU RA 501 from Challicorrema can still be assigned to a bufonid anuran, based on the overall robustness, the anterior cotyle, and the well-separated posterior condyles (Bailon, 1999). Further identification is not possible, but the size hints towards either a small species or a juvenile of a larger one.

Anura indet.

Figures 28, 29, 30

Material. *Challicorrema*: one trunk vertebra (UU RA 508), one humerus (UU RA 520), one radioulna (UU RA 506), one femur (UU RA 502), and two tibiofibulae (UU R 503 and UU RA 507); *Rema Marmara*: eight bone fragments (UU RMA 401–UU RMA 405); *Spilia 1*: one premaxilla (UU SP1 1085), 14 maxillae (UU SP1 1045, UU SP1 1051, UU SP1 1052, UU SP1 1055, UU SP1 1056, UU SP1 1060, UU SP1 1062–UU SP1 1064, UU SP1 1111, and UU SP1 1138), six angulars (UU SP1 1106, UU SP1 1117, UU SP1 1139, and UU SP1 1149), one sculptured bone fragment (UU SP1 1020), two atlantes (UU SP1 1039 and UU SP1 1142), 10 trunk vertebrae (UU SP1 1054, UU SP1 1061, and UU SP1 1151), seven fragments of

vertebra (UU SP1 1102, UU SP1 1104, UU SP1 1114, UU SP1 1116, UU SP1 1121, and UU SP1 1128), one sacral vertebra (UU SP1 1040), two urostyles (UU SP1 1137 and UU SP1 1148), one scapula (UU SP1 1124), three coracoids (UU SP1 1025, UU SP1 1118, and UU SP1 1153), 11 humeri (UU SP1 1019, UU SP1 1059, UU SP1 1105, UU SP1 1131, UU SP1 1132, UU SP1 1140, UU SP1 1146, and UU SP1 1147), 16 radioulnae (UU SP1 1050, UU SP1 1099, UU SP1 1103, UU SP1 1113, UU SP1 1122, UU SP1 1130, and UU SP1 1135), 13 ilia (UU SP1 1029, UU SP1 1030, UU SP1 1032, UU SP1 1036, UU SP1 1037, UU SP1 1042, and UU SP1 1123), eight femora (UU SP1 1058, UU SP1 1120, UU SP1 1129, UU SP1 1136, and UU SP1 1152), eight tibiofibulae (UU SP1 1101, UU SP1 1107, UU SP1 1119, UU SP1 1125, and UU SP1 1150), nine phalanges (UU SP1 1047–UU SP1 1049, UU SP1 1053, UU SP1 1112, UU SP1 1126, and UU SP1 1127), and 252 indeterminate elements (UU SP1 1023, UU SP1 1084, UU SP1 1086, UU SP1 1091, and UU SP1 1095); *Spilia 2b*: one radioulna (UU SP2b 503) and one indeterminate element (UU SP2b 502); *Spilia 2d*: one maxilla (UU SP2d 501) and one indeterminate element (UU SP2d 502); *Spilia 3*: one maxilla (UU SP3 671), seven trunk vertebrae (UU SP3 616, UU SP3 656, UU SP3 666, UU SP3 684, and UU SP3 687), three fragments of vertebra (UU SP3 682), one sacral vertebra (UU SP3 619), five urostyles (UU SP3 640, UU SP3 664, UU SP3 665, and UU SP3 686), one scapula (UU SP3 657), two coracoids (UU SP3 690), three humeri (UU SP3 634, UU SP3 635, and UU SP3 689), 25 radioulnae (UU SP3 620 and UU SP3 673), two ilia (UU SP3 688), one ischium (UU SP3 685), one tibiofibula (UU SP3 683), and six indeterminate elements (UU SP3 681 and UU SP3 691); *Spilia 4*: four premaxillae (UU SP4 738), 22



Fig. 28 Anura indet. from Spilia 1 (SP1) and Spilia 2 (SP2). **a–b** Left maxilla (UU SP2d 501) in medial (**a**) and lateral (**b**) views; **c** distal phalanx (UU SP1 1053) in dorsal view; **d** distal phalanx (UU SP1 1126) in dorsal view

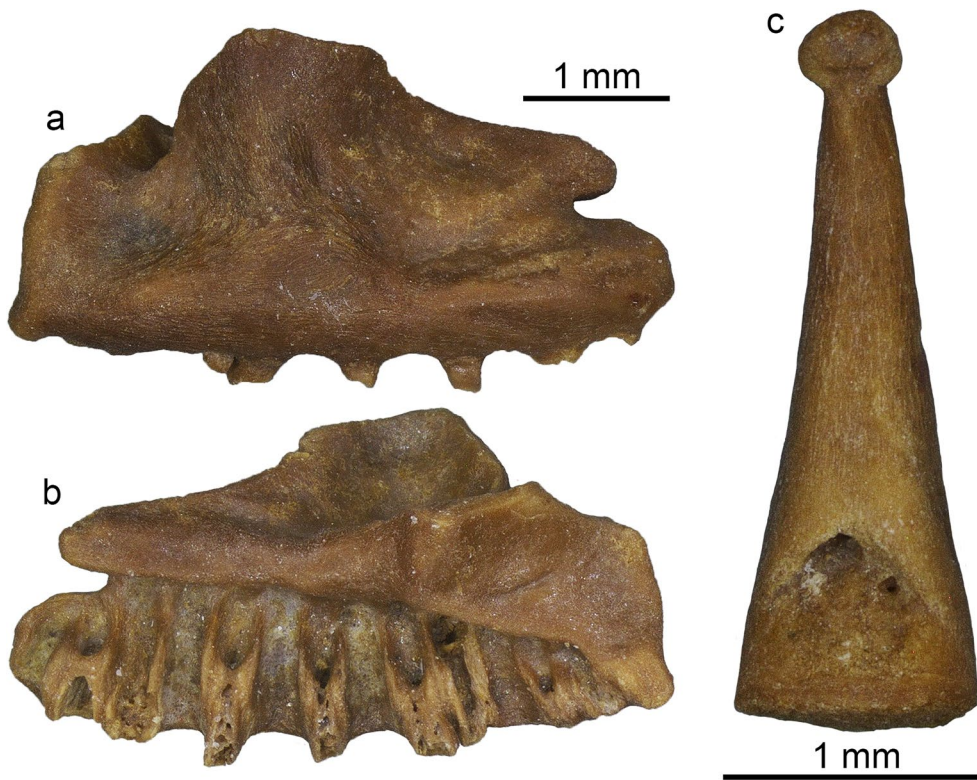


Fig. 29 Anura indet. from Vevi. **a, b** Left premaxilla (UU VE 548) in anterior (**a**) and posterior (**b**) views; **c** Distal phalanx (UU VE 550) in ventral view

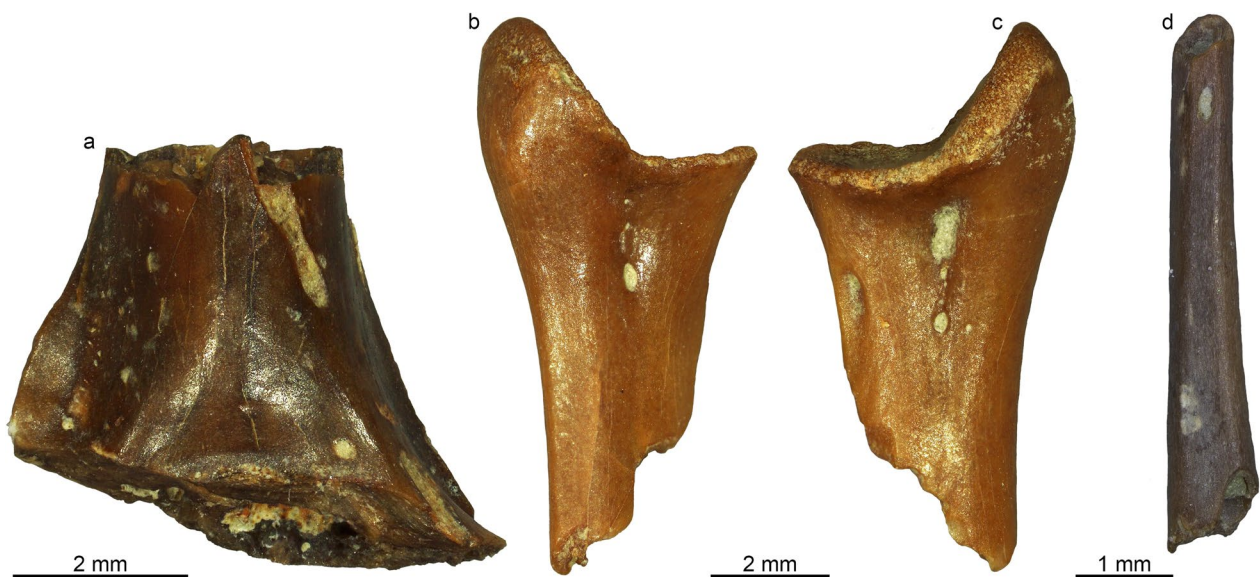


Fig. 30 Anura indet. from Chalicorrema. **a** Left humerus (UU RA 520) in ventral view; **b, c** left radioulna (UU RA 506) in medial (**b**) and lateral (**c**) views; **d** fragment of tibia/fibula (UU RA 503) in medial or lateral view

maxillae (UU SP4 512, UU SP4 689, UU SP4 690, UU SP4 696, and UU SP4 735), eight sculptured fragments (UU SP4 739), four atlantes (UU SP4 698 and UU SP4 731),

33 trunk vertebrae (UU SP4 624 and UU SP4 724), 13 fragments of vertebra (UU SP4 514), two sacral vertebrae (UU SP4 697 and UU SP4 713), four urostyles (UU SP4

522 and UU SP4 725), one scapula (UU SP4 700), five coracoids (UU SP4 677, UU SP4 678, and UU SP4 730), four humeri (UU SP4 699 and UU SP4 729), 10 radioulnae (UU SP4 614, UU SP4 694, and UU SP4 695), two ilia (UU SP4 527 and UU SP4 726), three tibiofibulae (UU SP4 727), two phalanges (UU SP4 732 and UU SP4 733), and 95 indeterminate elements (UU SP4 510 and UU SP4 511); *Vevi*: one premaxilla (UU VE 548), one sacral vertebra (UU VE 570), one humerus (UU VE 569), three radioulnae (UU VE 552), two tibiofibulae (UU VE 539 and UU VE 571), one indeterminate autopodial element (UU VE 572), one phalanx (UU VE 551), and one distal phalanx (UU VE 550).

Description and remarks.

Among the remains from Spilia belonging to indeterminate anurans (Fig. 28), the largest and more robust likely pertain to either *Latonia* or a bufonid. A brief description of the different morphological features encountered in the phalanges from Spilia can be provided. On the whole, the phalanges from Spilia are medium-sized, elongated and rather slender (Fig. 28c, d). They narrow distinctly toward the distal tip. The bulb at the tip is either smooth [eight specimens: UU SP1 1047, UU SP1 1048, UU SP1 1049, UU SP1 1126 (Fig. 28d), UU SP1 1127, and UU SP4 732] or rough [two specimens: UU SP1 1053 (Fig. 28c) and UU SP4 733]. Two lobes are slightly recognizable on the tip of UU SP1 1048, UU SP1 1126, and UU SP1 1127. Specimen UU SP1 1112 is too poorly preserved to recognize the shape of its tip. It is currently not clear, however, to what degree these morphologies have a taxonomical significance.

Similarly, the indeterminate anuran remains from *Vevi* (Fig. 29) pertain perhaps to one of the taxa identified above from the same locality. The distal phalanx (UU VE 550), in particular, is small and slender (Fig. 29c). It has an elongated triangular shape, strongly narrowing distally and ending with a globular tip with no evident lobes. This is similar to phalanxes of *Latonia* figured by Vasilyan (2020, fig. 6), but clear diagnostic features of anuran phalanxes even at supraspecific levels are not known at the moment. We thus refrain from referring this phalanx to the *Vevi Latonia*.

The remains from Chalicorrema are even more fragmentary (Fig. 30). These remains are too poorly preserved to give significant morphological information, allowing precise taxonomic allocation. Similarly, the even fewer remains from Rema Marmara can be assigned to indeterminate anurans, but they cannot be identified more precisely due to either poor preservation or scarce diagnostic value.

Reptilia Laurenti, 1768

Testudines Batsch, 1788 (sensu Joyce et al., 2020a)

Cryptodira Cope, 1868 (sensu Joyce et al., 2020b)
Testudinoidea Fitzinger, 1826 (sensu Joyce et al., 2021)

Emyridae Gray, 1825 (sensu Joyce et al., 2021)

***Emys* Duméril, 1805**

***Emys orbicularis* (Linnaeus, 1758)**

Emys* gr. *orbicularis

Figure 31

Material. *Vevi*: a left epiplastron fragment (UU VE 559), a right hyoplastron fragment (UU VE 567), a left hypoplastron fragment (UU VE 560), and a right xiphiplastron fragment (UU VE 561).

Description.

The fragmentary left epiplastron UU VE 559 preserves on the external surface only part of the gular-humeral sulcus that does not correspond to a notch at the lateral edge of the bone (Fig. 31a–d). On the visceral surface, the preserved portion of the gular pad is low and with a width clearly tapering in medial direction.

Even if only the posterolateral area of the right hyoplastron UU VE 567 is preserved, the axillary buttress is laterally delimited by a relatively smooth area indicating the presence of a ligamental hinge (Fig. 31e–g). The buttress is ventrally marked by the lateral sulcus of the pectoral shield, which is also present at the posterior margin of the element, very close (about 1 mm) to the hyo-hyoplastral contact, represented by a hinge with few large bony interdigitations.

UU VE 560 is a small posterolateral portion of a left hypoplastron (Fig. 31h–j), posterior to the abdominal-femoral sulcus that corresponds to the anterior edge of the fragment (only on the dorsal surface of the element there is a very little segment of the sulcus preserved); the dorsal overlap of the femoral shield is wide and slightly broadening posteriorly.

The right xiphiplastron UU VE 561 preserves only a small portion of the posterolateral region, not including the medial suture but clearly indicating a rather rounded lateral edge of the xiphiplastron and the absence of a deep anal notch (Fig. 31k–m). The area covered by the dorsal overlap of the anal shield is rather tall in the anteriormost-preserved portion and tapers gently in posterior direction.

Remarks. The most diagnostic element is the fragmentary right hyoplastron UU VE 567 because it shows evidence of a ligamental hinge between the plastron and the carapace as well as between the hyoplastron and the hypoplastron. Among the Neogene European turtles, this morphology univocally characterizes the members of the genus *Emys* but does not allow discriminating among the few extinct and extant species so far described (see among others: Fritz et al., 2005, 2011; Hervet, 2000; Młynarski, 1956; Ottonello et al., 2021). The other

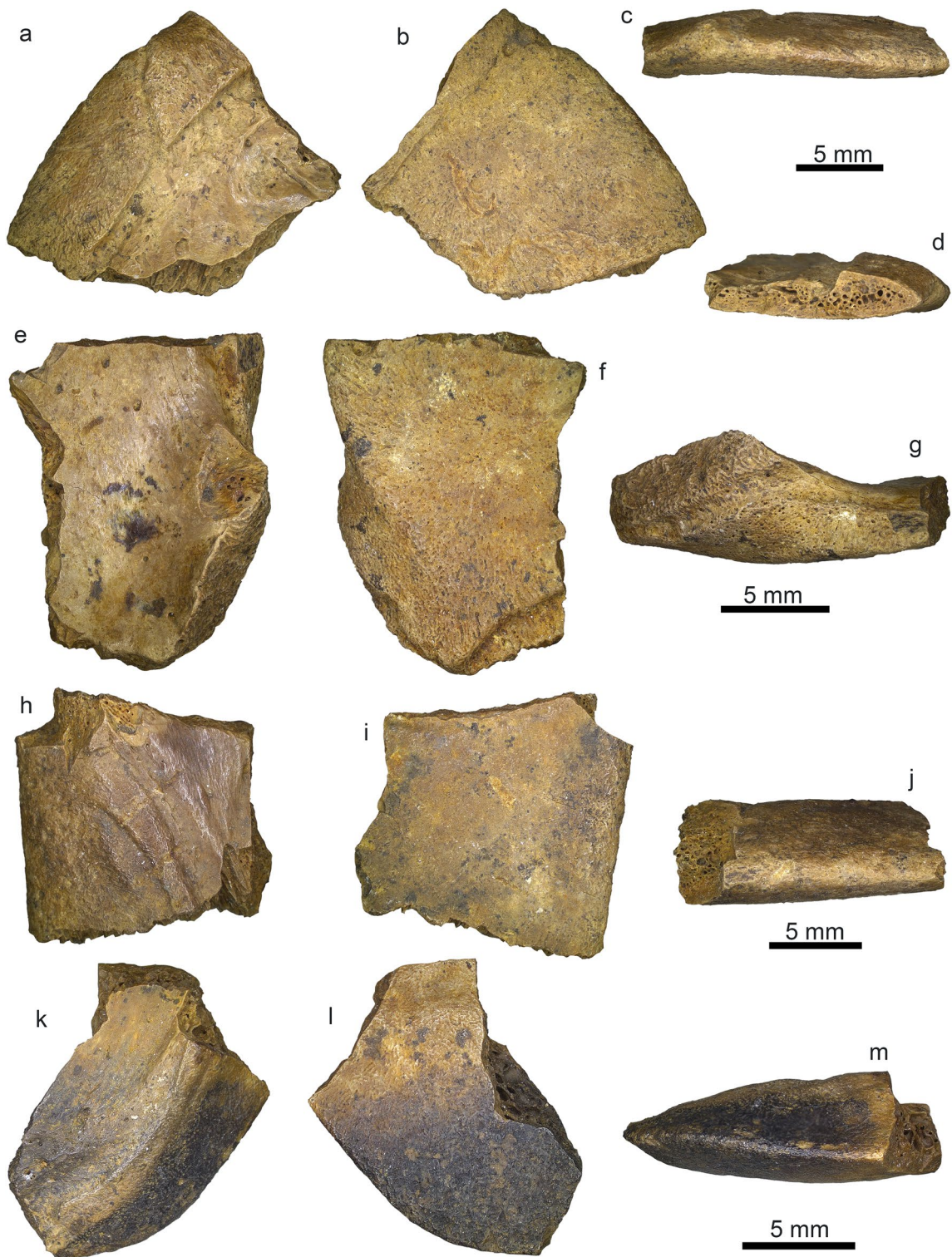


Fig. 31 *Emys gr. orbicularis* from Vevi. **a–d** left epiplastron fragment (UU VE 559) in visceral (**a**), ventral (**b**), anterolateral (**c**), and anteromedial (**d**) views; **e–g** right hyoplastron fragment (UU VE 567) in visceral (**e**), ventral (**f**), and lateral (**g**) views; **h–j** left hypoplastron fragment (UU VE 560) in visceral (**h**), ventral (**i**), and lateral (**j**) views; **k–m** right xiphiplastron fragment (UU VE 561) in visceral (**k**), ventral (**l**), and lateral (**m**) views

elements from Vevi are referred to same taxon based on morphological congruence.

Testuguria Joyce et al., 2004 (sensu Joyce et al., 2021)
Geoemydidae Theobald, 1868 (sensu Joyce et al., 2021)

Geoemydidae indet.

Figure 32

Material. *Vevi*: a left peripheral VII (UU VE 568).

Description.

The seventh left peripheral (UU VE 568) from Vevi (Fig. 32) is complete and characterized by the presence of the following features: marked and high longitudinal ridge (higher posteriorly) on the lateral surface; an evident pore on the inner surface entering the visceral cavity of the shell and opening posteromedially; a U shaped, well-defined and narrow sutural area with the corresponding hyoplastron; clear inguinal scute on the ventral surface, close to the above described sutural area; vertical intermarginal sulcus; pleural-marginal sulcus placed on the peripheral, close to the costal-peripheral suture.

Remarks. UU VE 568 can be easily identified as a geoemydid because of the presence of a musk pore (Hirayama, 1985). Due to the presence of a single element clearly referable to this taxon in the fossil assemblage it is not possible to propose a more precise identification of the Vevi geoemydid. It is, however, worth noting that *Mauremys* Gray, 1869, is the common member of this clade in the European and Greek Neogene (Georgalis & Kear, 2013; Georgalis et al., 2019b; Vlachos, 2022; Vlachos et al., 2019) and it is likely that the Vevi specimen belongs to this genus (though this is not certain; see also “Discussion” below).

Testudinoidea indet.

Figure 33

Material. *Rema Marmara*: a shell fragment (UU RMA 301); *Spilia 1*: two peripherals (UU SP1 1087 and UU SP1 1098), many shell fragments (UU SP1 1070, UU

SP1 1071, UU SP1 1072, UU SP1 1089, UU SP1 1090a, UU SP1 1093a, UU SP1 1096, and UU SP1 1097), a ?coracoid fragment (UU SP1 1074), a scapula/acromion fragment (UU SP1 1088), a scapula (UU SP1 1092), nine ungual phalanges [UU SP1 1075, UU SP1 1076, UU SP1 1077 (six elements), and UU SP1 1094], two cervical vertebrae (UU SP1 1073 and UU SP1 1090b), three caudal vertebrae [UU SP1 1078 and UU SP1 1079 (two elements)], two vertebral fragments (UU SP1 1093b), and an unidentifiable fragment (UU SP1 1080); *Spilia 3*: a shell fragment (UU SP3 678); *Spilia 4*: a carapace fragment (UU SP4 631); *Vevi*: a costal fragment (UU VE 557), a left peripheral I (UU VE 566), four peripherals (UU VE 562–UU VE 565), and three shell fragments (UU VE 558).

Description and remarks.

The costal fragment UU VE 557 (Fig. 33a) from Vevi is rectangular in shape, rather thin and hosts an interpleural sulcus on the external surface; a moderately expressed costal convexity, evident on the visceral surface, gives origin laterally to an apically broken costal process. All the isolated peripherals are non-bridge elements characterized by a pleural-marginal sulcus placed far from the costal-peripheral sulcus. The first left peripheral UU VE 566 is approximately as broad as long and is partly overlapped by the first vertebral scute (Fig. 33d). UU VE 564 shows a deep and well-defined pit for the reception of the costal process of the corresponding costal (Fig. 33b, c). All these elements and fragments from Vevi do not show diagnostic features allowing a precise identification but are characterized by a morphology typical of non-testudinid testudinoids. They likely belong to the taxa identified above on the basis of more diagnostic elements. The first left peripheral UU VE 566 (Fig. 33d) cannot be identified with confidence at genus level because it has a general morphology congruent with both *Emys* and the geoemydid *Mauremys* but, at the same time, different from what reported in the literature for their extant species in being not broader than long as in *Emys orbicularis*

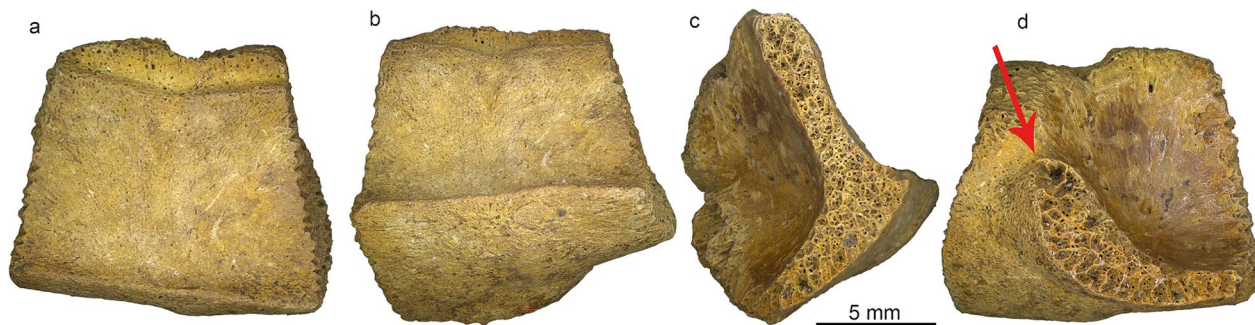


Fig. 32 Geoemydidae from Vevi. Left peripheral (UU VE 568) in dorsolateral (a), ventrolateral (b), posterior (c), and medial (d) views. The arrow indicates the musk pore

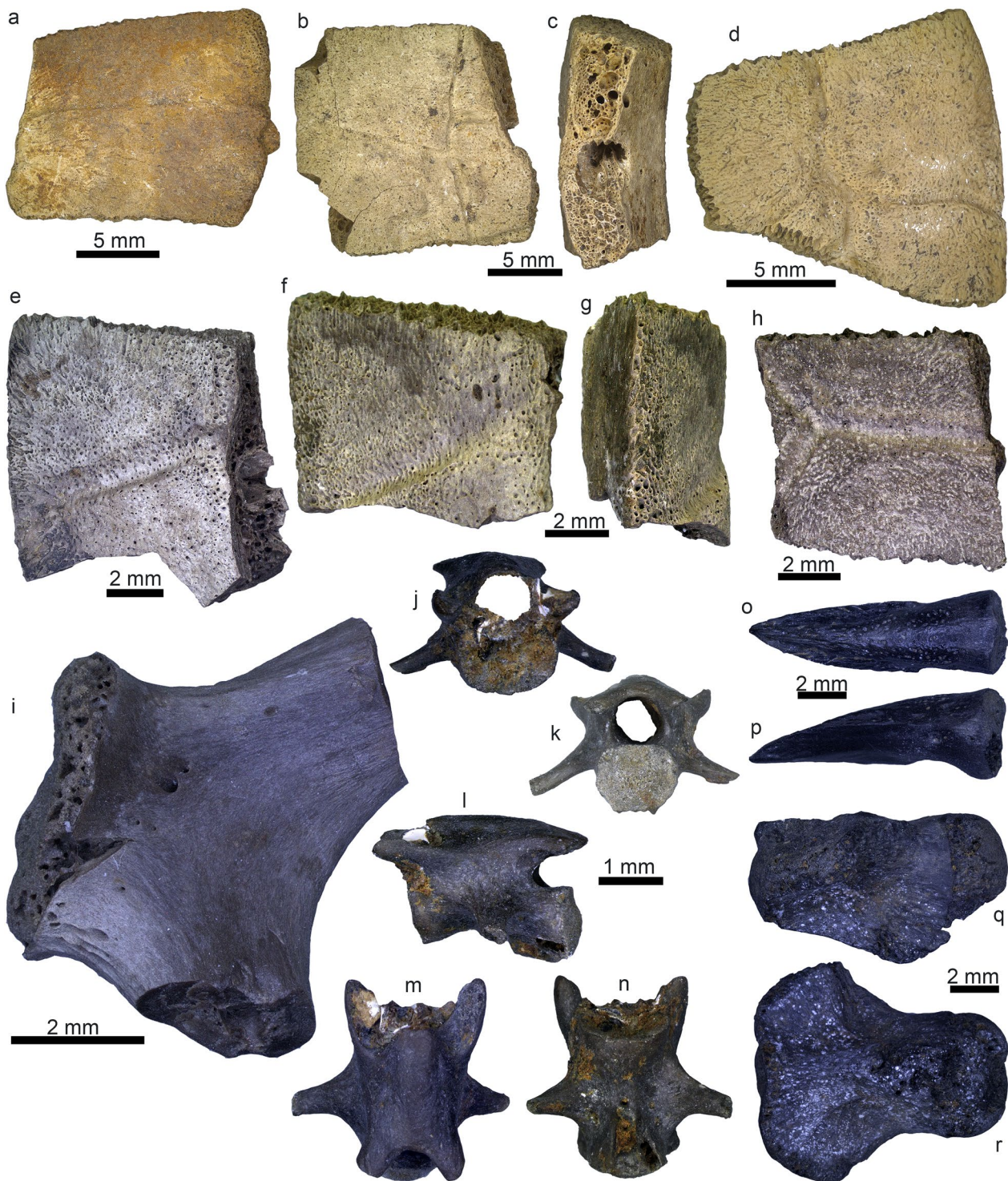


Fig. 33 Testudinoidea indet. from Vevi, Spilia 1 (SP1), and Spilia 4 (SP4). **a** Costal fragment (UU VE 557) in dorsal view; **b–c** peripheral (UU VE 564) in external (**b**) and mediolateral (**c**) views; **d** left peripheral I (UU VE 566) in dorsal view; **e** peripheral (UU SP1 1087) in external view; **f, g** peripheral (UU SP1 1098) in external (**f**) and lateral (**g**) views; **h** carapace fragment (UU SP4 631) in dorsal view; **i** right scapula/acromion fragment (UU SP1 1088) in medial view; **j–n** caudal vertebra (UU SP1 1078) in anterior (**j**), posterior (**k**), left lateral (**l**), dorsal (**m**), and ventral (**n**) views; **o, p** ungual phalanx (UU SP1 1075) in dorsal (**o**) and lateral (**p**) views; **q, r** cervical vertebra (UU SP1 1073) in left lateral (**q**) and ventral (**r**) views

and not longer than broad as in *Mauremys leprosa* (Schweigger, 1812) (see Hervet, 2000).

The specimens from Spilia (Fig. 33e–r) and Rema Marmara are rather fragmentary and do not afford much taxonomic and anatomical insights. The scapula/acromion fragment UU SP1 1088 (Fig. 33i) clearly shows a moderate “neck” at the base of the articular surface. The presence of such sort of “neck” in this specimen could be taxonomically diagnostic at some level, but the presence and development of this character in non-testudinid testudinoids should be better investigated.

Accordingly, we refer all these fragmentary specimens as Testudinoidea indet. Such tentative “superfamily-level” assignment is also supported by a biogeographic rationale [pleurodires are not present in the Late Miocene and Pliocene of Greece (Georgalis & Kear, 2013; Georgalis et al., 2013; Vlachos, 2022) and chelydrids have never been recorded from the country (Georgalis & Kear, 2013; Joyce, 2016; Vlachos, 2022)] as well as the fact that the fossil material certainly does not belong to trionychids, which are characterized by the presence of shell sculpturing and the absence of peripherals (with the exception of *Lissemys* Smith, 1931), pygals, suprapygals, and shell scutes (Delfino et al., 2010; Vitek & Joyce, 2015) and could be potentially represented in the localities here

studied because they were present in the Neogene of the area (Georgalis & Joyce, 2017; Vlachos, 2022).

Squamata Opperl, 1811b

Scincoidea Opperl, 1811b (sensu Pyron et al., 2013)

Scincidae Opperl, 1811b

***Ophiomorus* Duméril & Bibron, 1839**

***Ophiomorus* sp.**

Figure 34

Material. *Spilia* 4: one right dentary (UU SP4 605), 17 trunk vertebrae [UU SP4 575, UU SP4 578, UU SP4 640, UU SP4 641, UU SP4 643, UU SP4 646 (10 elements), and UU SP4 709], one sacral vertebra (UU SP4 625), and one osteoderm (UU SP4 706).

Description.

The small dentary (UU SP4 605) is rather well preserved, missing just the posterior processes (Fig. 34a–c). It is straight, rather slenderly built and rather short, having a complete length of the tooth row of 3.5 mm. The medial side displays a well-developed subdental shelf with a sharp subdental ridge. Medial to the ridge, a deep sulcus dentalis is present. In medial view, the subdental self is rather high, but narrows posteriorly. By the anterior end, there is a narrow and horizontal mandibular symphysis. The Meckelian fossa is wider posteriorly, but

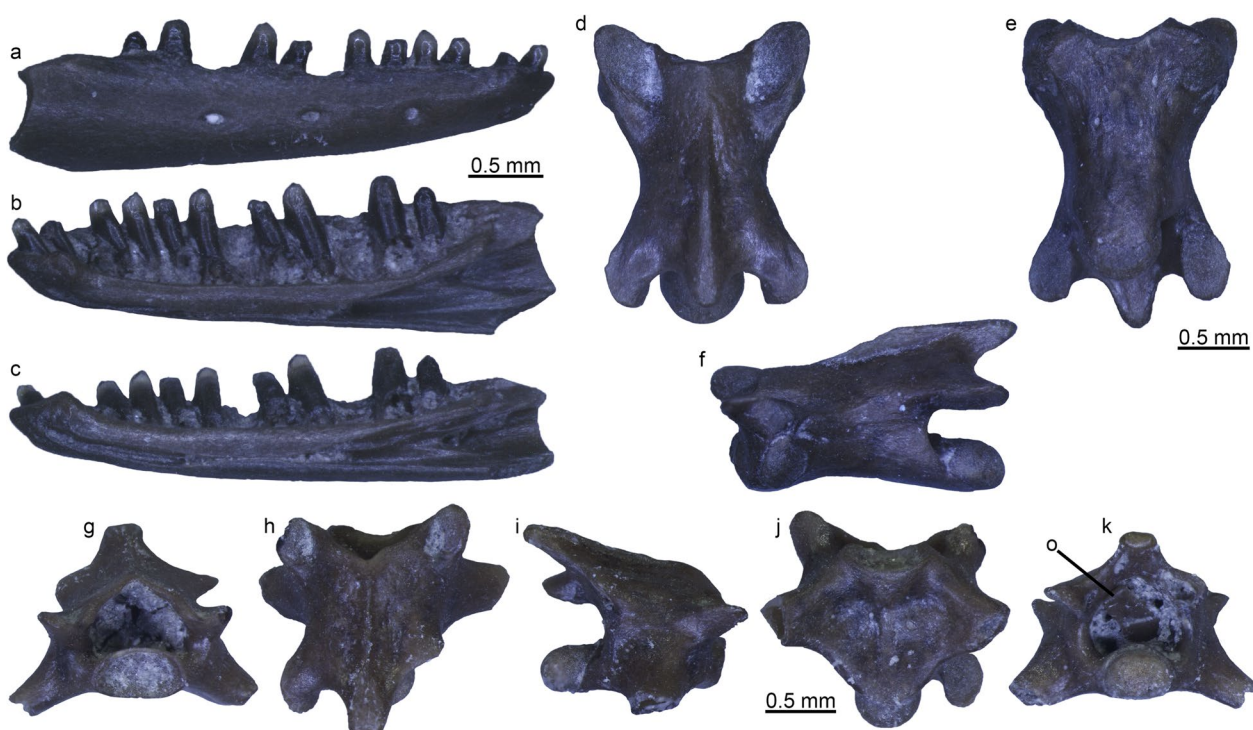


Fig. 34 *Ophiomorus* sp. from Spilia 4. **a–c** Right dentary (UU SP4 605) in lateral (**a**), medial (**b**), and ventromedial (**c**) views; **d–f** trunk vertebra (UU SP4 575) in dorsal (**d**), ventral (**e**), and left lateral (**f**) views; **g–k** sacral vertebra (UU SP4 625) in anterior (**g**), dorsal (**h**), right lateral (**i**), ventral (**j**), and posterior (**k**) views. The osteoderm UU SP4 706 is visible inside the neural canal of UU SP4 625 in posterior view (**l**). **o** osteoderm

very narrow and ventrally exposed in the anterior two thirds of the bone. Due to a medial bending of the ventral margin that bring the latter almost in contact with the subdental shelf, the fossa is represented only by a very narrow groove at mid-length of the bone; no real closure of the fossa is however present. The alveolar foramen is visible in ventral view, being located in correspondence with the second to last (13th) tooth. The ventral margin is straight in medial view. Despite of the breakage, there seems not to be a dorsal bending of the posterior processes. The dentary carries 14 tooth positions, most of them still bearing more or less preserved teeth. The teeth are pleurodont, cylindrical and closely spaced. They are slightly smaller by the anterior and posterior ends of the tooth row, compared to those in the middle. The largest teeth are the ones in positions 10th to 12th, but the size difference is very light. The tooth base is not swollen. In the best-preserved teeth, the crown has both a labial and a lingual cusp. These are rather close, but the cristae originating from them (cristae mesialis and distalis and cristae lingualis anterior and posterior, respectively) are separated by a distinctly wide antrum intercratum, which widens toward the tooth base. The tip of the crown is somehow bent posteromedially. A moderately dense, but very light, striation is present on the lingual side, but not on the labial one. The teeth are exposed laterally for either one third or one half of their height. They are blackish in colour, but the crown is brownish to yellowish. The lateral surface of the dentary is smooth, with four mental foramina, the size of which is homogeneous.

The trunk vertebrae are small sized and elongated (Fig. 34d–f). The centrum length is around 2 mm in all of them. They have a slightly compressed centrum and rounded synapophyses. The sacral vertebra (UU SP4 625; Fig. 34g–k) shares with the trunk vertebrae both the size and general morphology.

UU SP4 706 is a very small and thin osteoderm that was located inside the neural canal of the sacral vertebra UU SP4 625 (Fig. 34k). The osteoderm has an elongated subrectangular shape. The internal surface is smooth, whereas the external one is composed by a smooth gliding surface in the anterior half and a poorly ornamented surface in the posterior one.

Remarks. The scincid nature of the dentary is clearly evidenced by a set of features, among which (Villa & Delfino, 2019a): open and posteriorly-widening Meckelian fossa; subdental ridge present; straight ventral margin; pleurodont teeth provided with labial and lingual cusps, a slightly posteromedially bent crown, and a light striation on the lingual side. The osteoderm (UU SP4 706) is strongly reminiscent in its morphology of one part of the compound osteoderms that are distinctive for skinks (Daza et al., 2024; Estes, 1983; Maliuk et al., 2024;

Williams et al., 2022). This osteoderm was found inside the neural canal of the sacral vertebra UU SP4 625, possibly further supporting a scincid identity for this vertebra as well. Based on preliminary observations on the reference collection available to us, the morphology of all these vertebrae indeed recalls more a scincid condition, and in particular vertebrae of *Ophiomorus* (see also Camaiti et al., 2019, fig. 41). Among extant European skinks, moderately robust teeth without an enlarged crown are present in *Ophiomorus punctatissimus* (Bibron & Bory de Saint-Vincent, 1833) (see Camaiti et al., 2019; Čerňanský et al., 2020; Villa & Delfino, 2019a). A decreasing size in anteriormost and posteriormost teeth is also shared between this species and UU SP4 605, as are a rather high subdental shelf and the posterior position of the alveolar foramen, which is located by the second to last tooth position in the Spilia fossil and at the last position in *O. punctatissimus* (versus a more anteriorly located foramen in other European scincids; Villa & Delfino, 2019a). The tooth count of UU SP4 605 also fits within the range of *O. punctatissimus* (Camaiti et al., 2019; Villa & Delfino, 2019a). UU SP4 605 is also very similar to an isolated dentary from the latest Early Pleistocene of Kaiafas referred to *Ophiomorus* sp. by Villa et al. (2020), except for some minor differences (larger size, one more tooth, and one more mental foramen) and a distinct dorsal bending of the superior posterior process in the latter. The same bending is present in *O. punctatissimus* (Camaiti et al., 2019; Villa & Delfino, 2019a), but it seems to be absent in at least one other representative of the genus (*Ophiomorus tridactylus* [Blyth, 1853]; see Čerňanský et al., 2020, fig. 10A, B). The fossils from Spilia may thus represent a species of *Ophiomorus* different from *O. punctatissimus*, whereas the Kaiafas occurrence might be suggested as a more derived form related to the latter. This could only be confirmed when more morphological information on the other extant *Ophiomorus* species, especially those from the western part of its distribution, are available, though.

Lacertoidea Opper, 1811b (sensu Pyron et al., 2013)

Lacertidae Opper, 1811b

***Lacerta* Linnaeus, 1758**

cf. *Lacerta* sp.

Figure 35

Material. *Spilia 1*: one dentary (UU SP1 1002); *Spilia 3*: one premaxilla (UU SP3 677), two maxillae (UU SP3 606 and UU SP3 609), and two dentaries (UU SP3 602 and UU SP3 603).

Description.

The premaxilla (UU SP3 677) from *Spilia 3* is moderately large-sized (Fig. 35a, b): the preserved width of the broken dental shelf is at least 2.5 mm. It has a rather short and leaf-shaped ascending nasal process. On the external

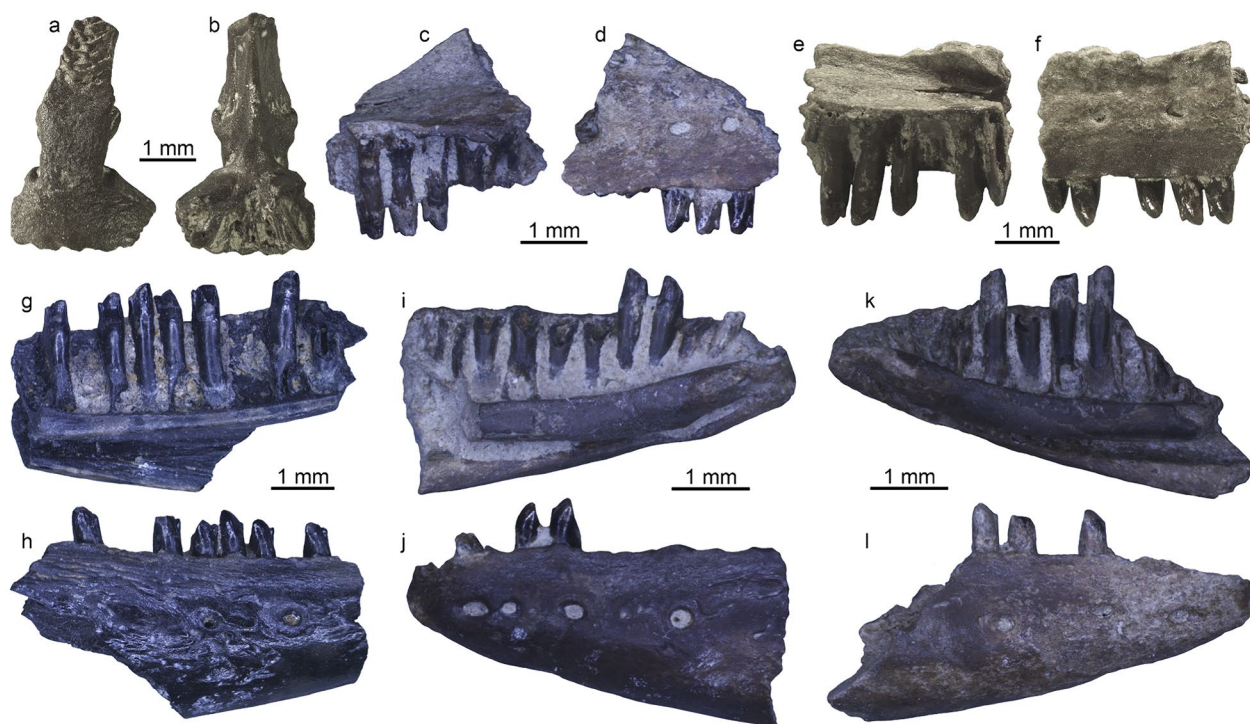


Fig. 35 cf. *Lacerta* sp. from Spilia 1 (SP1) and Spilia 3 (SP3). **a, b** Premaxilla (UU SP3 677) in anterior (**a**) and posterior (**b**) views; **c, d** right maxilla (UU SP3 606) in medial (**c**) and lateral (**d**) views; **e, f** left maxilla (UU SP3 609) in medial (**e**) and lateral (**f**) views; **g, h** right dentary (UU SP1 1002) in medial (**g**) and lateral (**h**) views; **i, j** left dentary (UU SP3 602) in medial (**i**) and lateral (**j**) views; **k, l** right dentary (UU SP3 603) in medial (**k**) and lateral (**l**) views

surface, a strong dermal sculpturing covers the distal half of the process. On the internal surface, the septo-nasal crest is rather sharp; it reaches the dorsal end of the process. The alveolar portion bears at least five pleurodont, cylindrical and slender teeth, none of which is well preserved. The palatal processes are well separated by a middle V-shaped notch, in which the incisive process is lodged.

The fragmentary maxillae from Spilia 3 (Fig. 35c–f) preserve only a small part of the midventral portion of the bone, which is about 3.2 mm in length in UU SP3 609 (Fig. 35e, f) and about 3.7 mm in UU SP3 606 (Fig. 35c, d). They carry pleurodont, closely-spaced, cylindrical, and not expanded teeth, with mono- and bicuspid crowns. On the medial surface of the preserved portion of the facial process of UU SP3 609 (Fig. 35e), a small structure located by the anterodorsal corner of the fragment is most likely the remain of a well-developed carina maxillaris (sensu Müller, 1996). In both specimens, the lateral surface displays two medium-sized ventrolateral foramina and the base of a strong dermal sculpturing cover.

The dentaries from Spilia 1 and Spilia 3 are also medium sized, even though poorly preserved (Fig. 35g–l). The preserved portion, which represents either part of

the middle portion of the bone (UU SP1 1002; Fig. 35g, h) or its anterior end (other specimens), is 7 mm (UU SP1 1002), 5.4 mm (UU SP3 602; Fig. 35i, j) or about 6.2 mm (UU SP3 603; Fig. 35k, l). A moderately high subdental shelf is present medially, showing a subdental ridge and a shallow sulcus dentalis dorsally. The shelf narrows posteriorly in UU SP1 1002 (Fig. 35i). Anteriorly, the subdental shelf ends in a narrow and subhorizontal mandibular symphysis. The Meckelian fossa is narrow anteriorly, but enlarges posteriorly. The ventral margin of the dentary is convex. The teeth are pleurodont, cylindrical, closely spaced and not expanded. The most preserved teeth display either a mono- or a bicuspid crown. The lateral surface of the dentary is smooth, with few mental foramina.

Remarks. The morphological features displayed by these fossil remains from Spilia allow their attribution to a lacertid lizard, the size of which is comparable with that of a medium-sized taxon. Significant features supporting the lacertid nature of these remains are (Augé, 2005; Čerňanský & Syromyatnikova, 2019; Čerňanský et al., 2016; Villa & Delfino, 2019a): the V-shaped notch of the premaxilla; the presence of a subdental ridge associated with a sulcus dentalis; the wide and open Meckelian fossa; the convex ventral margin of the dentaries; and the heterodont dentition composed of pleurodont and either

mono- or bicuspid teeth. The short and leaf-shaped nasal process of the premaxilla is found in *Lacerta*, *Timon* Tschudi, 1836, and *Zootoca* Wagler, 1830, among extant European lacertids (Barahona & Barbadillo, 1997; Villa & Delfino, 2019a). Premaxillae of *Zootoca* are generally smaller than the one from Spilia, whereas those of adult *Timon* are distinctly larger. UU SP3 677 fits on the other hand within the size range of *Lacerta* (Villa & Delfino, 2019a), to which the herein-described medium-sized fossils could therefore be related. It has to be noted, however, that an identification based mainly on size should be treated with caution and considered only as tentative. Čerňanský and Syromyatnikova (2019) reported a very wide nasal process in *Lacerta agilis* Linnaeus, 1758, and a less wide process in other species of *Lacerta*. If the Spilia premaxilla indeed belonged to *Lacerta*, the moderate width of its nasal process would suggest that it does not pertain to the former taxon.

Lacertidae indet. (small-sized)

Figure 36

Material. *Spilia 4*: one coronoid (UU SP4 704).

Description.

This coronoid (UU SP4 704) from Spilia 4 is very small (Fig. 36). Both the anterior and posterior tips are broken. The anterior half is clearly divided into an anteromedial and a labial processes. The latter is smaller than the former, but not reduced. The coronoid process is well developed and dorsally directed, with a rounded distal end. The posteromedial process is wide. A short and rounded posterior process is present, thus defining a distinct notch on the posterior margin of the coronoid. A well-developed coronoid ridge stands out on the medial side

of the bone. In dorsal view, a clear medial concavity is recognizable.

Remarks. UU SP4 704 clearly pertains to a lacertid lizard due to the following combination of features (Villa & Delfino, 2019a): not reduced labial process; wide posteromedial process; clear medial concavity in dorsal view; presence of the posterior process. The dorsally-directed coronoid process is a widely distributed feature in lacertids, thus not allowing a precise identification of this isolated element. However, it is indicative of an adult condition (Villa & Delfino, 2019a). Given its very small size, UU SP4 704 is therefore evidence for the presence in the Spilia 4 assemblage of a second lacertid taxon, the adults of which were small in size.

Lacertidae indet.

Figures 37, 38

Material. *Spilia 1*: one dentary (UU SP1 1001); *Spilia 3*: two dentaries (UU SP3 608 and UU SP3 610) and one fragment of indeterminate tooth bearing bone (UU SP3 607); *Spilia 4*: one maxilla (UU SP4 638), five dentaries (UU SP4 603, UU SP4 604, UU SP4 611, UU SP4 636, and UU SP4 637), and two fragments of indeterminate tooth bearing bones (UU SP4 504 and UU SP4 650); *Rema Marmara*: two dentaries (UU RMA 302 and UU RMA 303).

Description.

The fragment of a left maxilla (UU SP4 638) from Spilia 4 is small and poorly preserved (Fig. 37a, b). It carries pleurodont, cylindrical, closely-spaced and bicuspid teeth. A wide and posteriorly directed supradental foramen is preserved. The preserved portion of the lateral surface is smooth, with few moderately large, ventrolateral foramina.

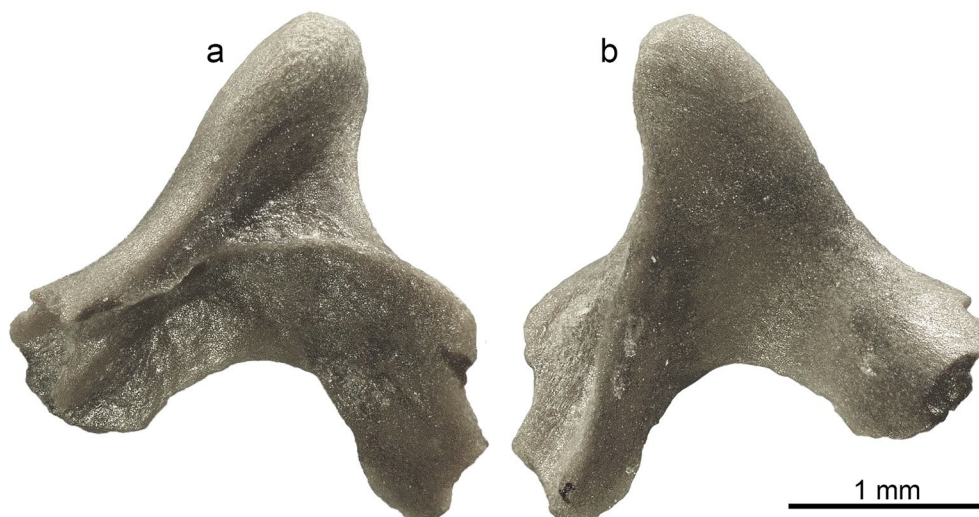


Fig. 36 Lacertidae indet. (small-sized) from Spilia 4. Left coronoid (UU SP4 704) in lateral (a) and medial (b) views

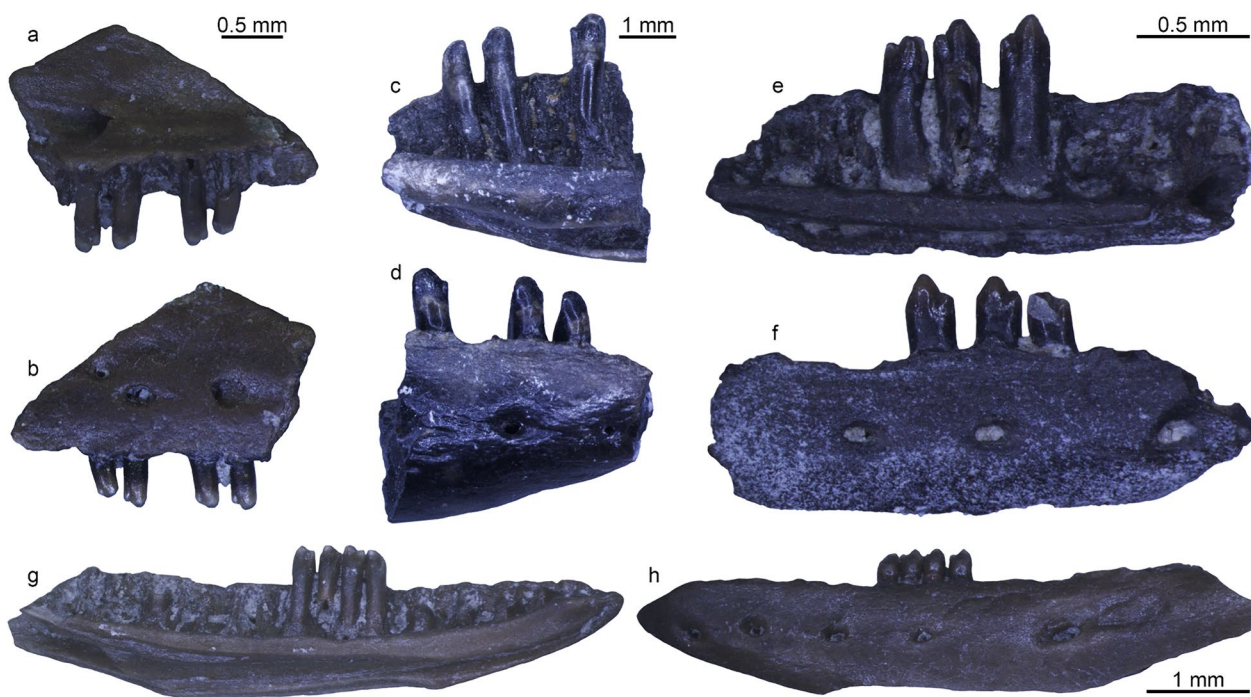


Fig. 37 Lacertidae indet. from Spilia 1 (SP1), Spilia 3 (SP3), and Spilia 4 (SP4). **a, b** Left maxilla (UU SP4 638) in medial (**a**) and lateral (**b**) views; **c, d** right dentary (UU SP1 1001) in medial (**c**) and lateral (**d**) views; **e, f** right dentary (UU SP3 610) in medial (**e**) and lateral (**f**) views; **g, h** left dentary (UU SP4 603) in medial (**g**) and lateral (**h**) views

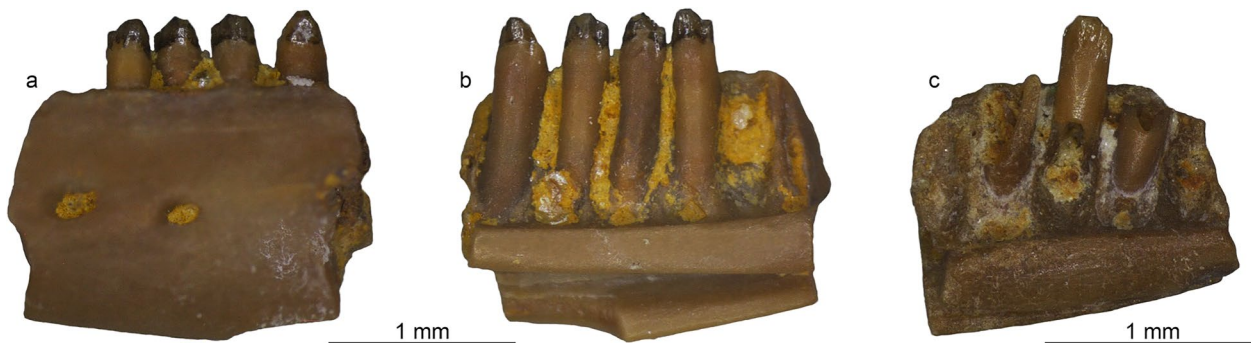


Fig. 38 Lacertidae indet. from Rema Marmara. **a, b** Left dentary (UU RMA 302) in lateral (**a**) and medial (**b**) views; **c** left dentary (UU RMA 303) in medial view

The dentaries from the Spilia localities (Fig. 37c–h) are small and very fragmentary, with the exception of UU SP4 603 that preserves most of the tooth row (Fig. 37g, h). Their teeth are similar to those of the maxilla, but they can be either bi- or tricuspid. They bear a narrow subdental shelf with a distinct subdental ridge. The mandibular symphysis, preserved in UU SP4 603 (Fig. 37g, h) and UU SP4 636, is narrow and subhorizontal. The Meckelian fossa is wide and medially open. When preserved, the ventral margin of the bone is convex. The lateral surface is smooth, with few mental foramina. UU SP4

603 bears five mental foramina (the posteriormost one being slightly larger than the others) and at least 24 tooth positions (Fig. 37g, h). The alveolar foramen is located roughly between the 22nd and the 23rd tooth positions.

Other tooth bearing bones from Spilia carry pleurodont, cylindrical and closely-spaced teeth, which are bicuspid. Tooth bases are not swollen. The fragments are rather small and not so robustly built.

The two small fragments of dentaries from Rema Marmara are very poorly preserved (Fig. 38). Both represent only a small portion of the middle part of the bone, likely

originally located close to the anterior end. Medially, the Meckelian fossa is open. The opening faces medially in UU RMA 302 (Fig. 38b) and more ventrally in UU RMA 303 (Fig. 38c), indicating that the latter fragment was located more anteriorly than the former one in origin. This is also supported by the height of the subdental shelf, which is proportionally high in both fragments, but to a higher degree in UU RMA 303 (Fig. 38c). The shelf clearly narrows posteriorly in UU RMA 302 (Fig. 38b). Dorsally, the subdental shelf bears a subdental ridge and a sulcus dentalis. The ventral margin of the bone is convex. The lateral surface is smooth, with few small mental foramina. Both fragments preserve a few teeth, together with empty tooth positions. UU RMA 302 displays four well-preserved teeth, plus a single empty tooth position (Fig. 38a, b). On the other hand, UU RMA 303 hosts only one well-preserved tooth (even though the crown is rather worn), two fragments of tooth bases, as well as two empty tooth positions (Fig. 38c). The preserved teeth are closely spaced, pleurodont, slender, and cylindrical. The tooth bases are not expanded. In all teeth, the crowns bear a large main cusp and a smaller accessory cusp located mesially. This accessory cusp is less evident in the posteriormost tooth of UU RMA 302 (Fig. 38a, b) and in the single well-preserved one of UU RMA 303 (Fig. 38c), either because of lower development of the cusp itself or wearing. Striae are visible on the lingual side of the crown, but not on the labial one. In both specimens, about one third of tooth height is laterally exposed.

Remarks. The fossil remains from Spilia all share lacertid features, particularly in the tooth morphology. However, their preservational status does not allow a clear identification. The smallest specimens may pertain to the above-mentioned small taxon that was present at Spilia, but it is not possible to confidently exclude that these elements are juveniles of the larger one and so they are here identified only as indeterminate lacertids. The two dentary fragments from Rema Marmara clearly belong to indeterminate lacertids, due to their tooth morphology, the presence of an open Meckelian fossa and a subdental ridge, and the convex ventral margin (Augé, 2005; Černanský & Syromyatnikova, 2019; Villa & Delfino, 2019a). The very poor preservation of the specimen hinders any further identification.

Amphisbaenia Gray, 1844

Amphisbaenia indet.

Figure 39

Material. *Spilia 4*: one cervical vertebra (UU SP4 617) and 19 trunk vertebrae (UU SP4 572–UU SP4 574, UU SP4 576, UU SP4 577, UU SP4 579, UU SP4 580, UU SP4 616, UU SP4 639, UU SP4 645, UU SP4 653, and UU SP4 707).

Description.

UU SP4 617 is a very small vertebral centrum of a cervical vertebra, with a centrum length of around 1.3 mm

(Fig. 39a). The centrum is rather short and procoelous. Ventrally, a short hypapophysis is present, being distally pointed and posteroventrally directed. Cotyle and condyle are rather mediolaterally elongated, but not strongly dorsoventrally compressed. The synapophyses are preserved, appearing massive and rather subcircular. A single prezygapophysis, the left one, is also preserved: it is small and subcircular.

The trunk vertebrae are small and short (Fig. 39b–w). They have a procoelous centrum with a centrum length reaching 2.5 mm. The centrum is dorsoventrally compressed, with a slight degree of variation in the degree of compression. The ventral surface is smooth and rather flat, with no keel. The subcentral foramina are small and located very laterally, in correspondence of the lateral margins of the centrum. The lateral margins are distinctly concave in ventral view. The synapophyses are moderately massive and subcircular. In anterior view, the neural arch is either flattened dorsally or slightly more elevated. There is no neural spine, except for a very small and low hint of it in UU SP4 576 (Fig. 39g) and UU SP4 653 (Fig. 39p, q) close to the posterior end of the neural arch. In these latter specimens, the neural arch is more elevated than in the others. Distinct postzygoprezygapophyseal laminae are visible laterally. The posterior margin of the neural arch is generally devoid of any real notch, but in UU SP4 639 two very small projections of the margin originate a very small concavity (Fig. 39j, l). Zygapophyses are moderately small, subcircular and slightly dorsally inclined. A very small hint of prezygapophyseal process is present in some specimens, such as UU SP4 573 (Fig. 39d).

Remarks. The general morphology of these trunk vertebrae recalls that of a previously described amphisbaenian vertebra from Spilia 4 (UU SP4 501), which was assigned to *Amphisbaenia* indet. by Georgalis et al. (2018c). Thus, they can be assigned to amphisbaenians as well based on the same combination of characters, i.e., dorsoventrally compressed centrum with a flat ventral surface and roughly parallel lateral margins, massive and rounded synapophyses, absence of zygosphenes, and a dorsally weakly convex neural arch lacking a neural spine, and presence (at least in some vertebrae) of small prezygapophyseal processes (see Georgalis et al., 2018c). The cervical vertebra pertains to a worm lizard as well, due to the massive and circular synapophyses, the mediolaterally elongated cotyle and condyle, and the very small size. A confident attribution of amphisbaenian vertebrae even at family level is currently considered not possible. Still, few features displayed by the Spilia vertebrae are worth discussing. A neural spine is generally absent in amphisbaenians, with very few exceptions (Kearney, 2003; Rage et al., 2013). When present, the

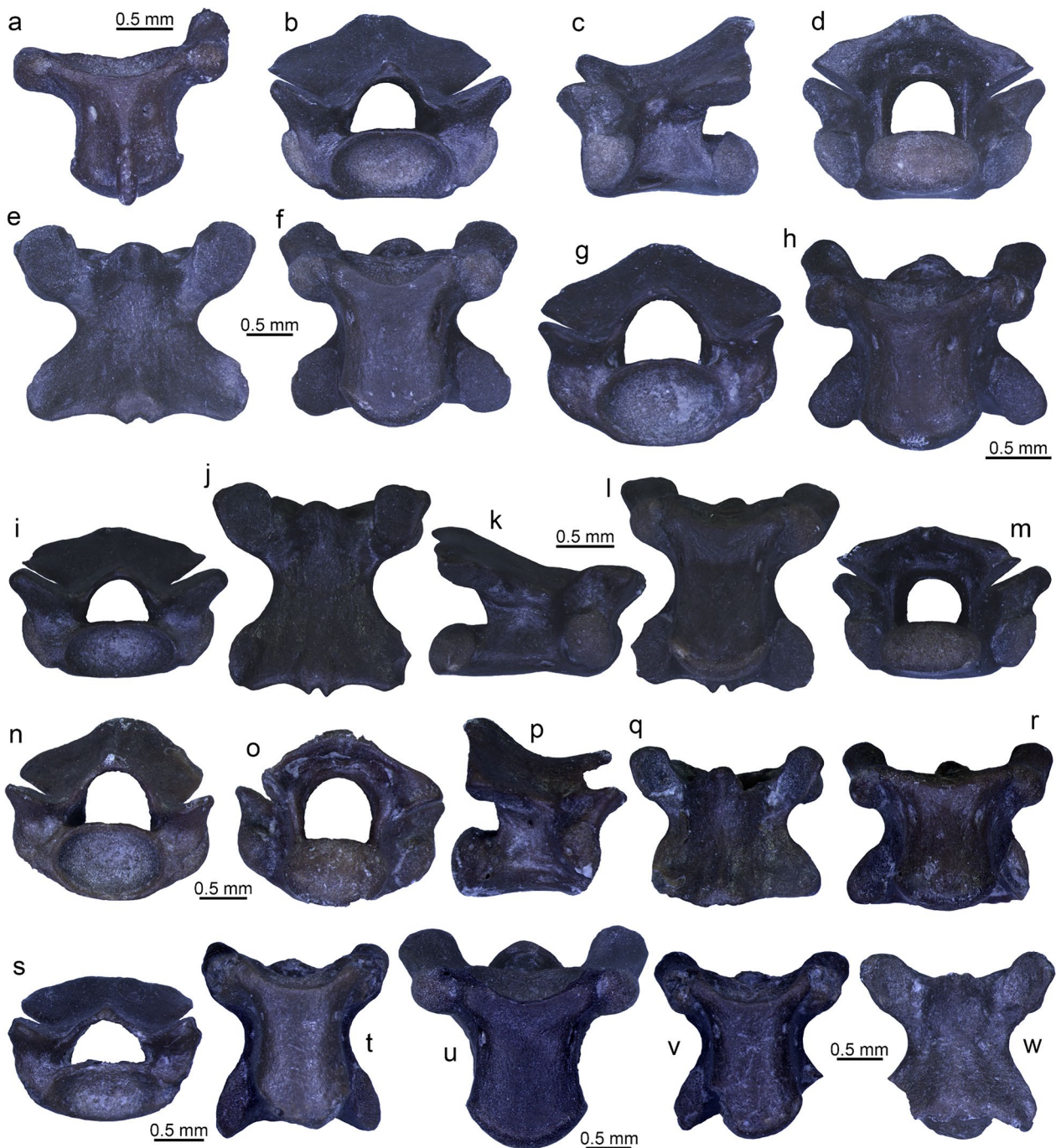


Fig. 39 Amphisbaenia indet. from Spilia 4. **a** Cervical vertebra (UU SP4 617) in ventral view; **b–f** trunk vertebra (UU SP4 573) in anterior (**b**), left lateral (**c**), posterior (**d**), dorsal (**e**), and ventral (**f**) views; **g, h** trunk vertebra (UU SP4 576) in anterior (**g**) and ventral (**h**) views; **i–m** trunk vertebra (UU SP4 639) in anterior (**i**), dorsal (**j**), right lateral (**k**), ventral (**l**), and posterior (**m**) views; **n–r** trunk vertebra (UU SP4 653) in anterior (**n**), posterior (**o**), right lateral (**p**), dorsal (**q**), and ventral (**r**) views; **s, t** trunk vertebra (UU SP4 574) in anterior (**s**) and ventral (**t**) views; **u** trunk vertebra (UU SP4 579) in ventral view; **v, w** trunk vertebra (UU SP4 572) in ventral (**v**) and dorsal (**w**) views

spine is described as small but distinct, which might contrast with the condition in the Spilia specimens displaying only a very poorly developed hint. Moreover, it has to

be noted that, in the amphisbaenian material from Spilia, the spine hint is regularly found on slightly shorter vertebrae further characterized by a more elevated neural arch

and a less compressed centrum, when compared to the rest of the sample. Whether this reflects the presence of two different taxa or just intracolumnar variation cannot be evaluated here. A similar statement may hold true for the small projections shown by UU SP4 639.

Scincoidea or Lacertoidea indet.

Figure 40

Material. *Spilia 3*: two dentaries (UU SP3 604 and UU SP3 605); *Spilia 5*: one right dentary (UU SP5 101).

Description.

These specimens from *Spilia* are represented by fragments of dentary of different sizes (Fig. 40). They are poorly preserved, but clearly display a subdental ridge and pleurodont, cylindrical and closely spaced teeth. All the preserved teeth miss their crown. The Meckelian fossa is open medially and rather wide. The lateral surface is smooth, with one or more wide mental foramina. UU SP3 604 preserves the anterior end, with a subhorizontal mandibular symphysis.

Remarks. The presence of a subdental ridge, combined with pleurodont teeth and an open Meckelian fossa, is a feature of “Scincomorpha” (Evans, 2008). This group is currently considered paraphyletic, however, and so we here assign these dentaries to either indeterminate Lacertoidea or Scincoidea following modern taxonomies of squamates (e.g., Burbrink et al., 2020; Jones et al., 2013; Pyron, 2017; Pyron et al.,

2013; Streicher & Wiens, 2017; Zheng & Wiens, 2016 [partly]) or alternatively known under the terminology Scinciformata and Laterata respectively in other recent works (e.g., Burbrink et al., 2020; Vidal & Hedges, 2005 [partly]).

Iguania Cuvier, 1817

Agamidae Spix, 1825

Agaminae Spix, 1825

Agaminae indet.

Figure 41

Material. *Chalicorrema*: one right maxilla (UU RA 403), three dentaries (UU RA 427–UU RA 429), two fragments of indeterminate tooth bearing bones (UU RA 401 and UU RA 402), and five caudal vertebrae (UU RA 404 and UU RA 430–UU RA 433).

Description.

UU RA 403 is a small bone fragment, representing the anterior end of the anterior premaxillary process of a right maxilla (Fig. 41a, b). In dorsal view, it has a straight anterior margin. There is no anterolateral process. An anteromedial process could, on the other hand, have been present in origin, but an evident breakage in the related area of the specimen hinders a clear evaluation of its possible development. The dorsal surface of the anterior premaxillary process is strongly concave. The specimen bears a single, well-preserved first tooth, plus fragments of a second one posteriorly. The tooth is subpleurodont,



Fig. 40 Scincoidea or Lacertoidea indet. from *Spilia 3* (SP3) and *Spilia 5* (SP5). **a, b** Right dentary (UU SP5 101) in medial (**a**) and lateral (**b**) views; **c, d** left dentary (UU SP3 605) in lateral (**c**) and medial (**d**) views



Fig. 41 Agaminae indet. from Chalicorrema. **a, b** Left maxilla (UU RA 403) in medial (**a**) and lateral (**b**) views; **c–e** right dentary (UU RA 427) in medial (**c**), lateral (**d**), and dorsal (**e**) views; **f, g** right dentary (UU RA 428) in lateral (**f**) and medial (**g**) views; **h, i** right dentary (UU RA 429) in medial (**h**) and lateral (**i**) views; **j** fragment of tooth bearing bone (UU RA 402) in medial view; **k, l** caudal vertebra (UU RA 430) in dorsal (**k**) and ventral (**l**) views

straight and pointed. It has no striation and an unswollen base. In spite of being very poorly preserved, the second tooth also has a subpleurodont implantation. The complete specimen is 2.4 mm long.

Three anterior portions of dentaries are present in our material from Chalicorrema (Fig. 41c–i). UU RA 428 (Fig. 41f, g) only preserves the anteriormost tip, where the subpleurodont teeth are located, whereas the other two specimens display also part of the acrodon part of the tooth row. In medial view, all specimens present a high subdental table. The table is not distinctly developed medially in dorsal view, and bears no subdental ridge. The Meckelian fossa is narrow and opens ventromedially. Anteriorly, the mandibular symphysis is wide. The ventral margin of the dentaries is straight. The lateral surface is smooth, with few anteroposteriorly-aligned mental foramina. In both most well-preserved dentaries, at least

five foramina can be counted; these increase in width towards the posterior. The dentition is heterodont, with two subpleurodont teeth followed by acrodon ones. UU RA 427 (Fig. 41c–e) and UU RA 429 (Fig. 41h, i) preserve five and three acrodon tooth positions, respectively. Only the first subpleurodont teeth in UU RA 428 (Fig. 41f, g) and UU RA 429 (Fig. 41h, i) are complete, whereas the second ones in these specimens and both ones in UU RA 427 (Fig. 41c–e) preserve only their bases. The most preserved subpleurodont teeth are straight, conical, non-striated, and with a rounded tip. A slightly-swollen base is visible in the first tooth of UU RA 428 (Fig. 41f, g). On both UU RA 427 (Fig. 41c–e) and UU RA 428 (Fig. 41f, g), the first subpleurodont tooth is clearly larger than the second one, whereas it is the opposite in UU RA 429 (Fig. 41h, i). The acrodon teeth are triangular and closely packed. Ventrally, they extend to cover the underlying bone. Only in UU RA

427, distinct interdental grooves are present between each pair of acrodont teeth on the lateral surface of the bone (Fig. 41d). The most preserved dentary, UU RA 427, is slightly more than 10 mm long (Fig. 41c–e).

The two fragments of indeterminate tooth bearing bones from Chalicorrema are too poorly preserved to be assigned to either maxillae or dentaries (Fig. 41j). They are rather small. UU RA 402 carries one subpleurodont tooth and one acrodont tooth, whereas UU RA 401 carries two acrodont teeth and a small fragment of a third one. The subpleurodont tooth is pointed, not swollen, and slightly posteromedially curved by the tip. It has no striae. The acrodont ones extend on the lingual margin of the related tooth bearing bone. They are less preserved in UU RA 401 than in UU RA 402. In the latter specimen, the acrodont teeth are small and triangular, with no distinct accessory cusps. Teeth of UU RA 401 are larger, representing either a more posterior portion of the tooth row or an older individual. The total length of UU RA 401 is 3.0 mm, whereas it is 2.0 mm in UU RA 402.

The caudal vertebrae from Chalicorrema are slenderly built and elongated (Fig. 41k, l). They have wide and subelliptical anterior cotyle and posterior condyle. In anterior view, the neural canal is small, being roughly half as high as the cotyle. When preserved, the zygapophyses have subovoid and subvertical facets. The ventral surface of the centrum is smooth, with no traces of haemapophyses or pedicles for the chevron bone. There is no autotomy plane. The bases of laminar transverse processes are preserved in at least some vertebrae, being located roughly at mid-length. The longest and most-preserved vertebra is slightly less than 10 mm long.

Remarks. An agamid is represented in the Chalicorrema assemblage by a few fragmentary fossils. The main character supporting this identification for the tooth bearing bones is the presence of both (sub)pleurodont and acrodont teeth in the dentition (Augé, 2005; Blain et al., 2014; Delfino et al., 2008; Georgalis et al., 2023a; Moody, 1980; Smith, 2011; Smith et al., 2011; Villa & Delfino, 2019a). Another character that is commonly used to discriminate agamids from chamaeleonids is the extension of the acrodont teeth onto the lingual surface of the tooth bearing bone (Evans et al., 2002; Georgalis et al., 2023a; Villa & Delfino, 2019a). The validity of the latter distinction was doubted by Rage and Bailon (2011), but there is no evidence indicating the presence of a chamaeleonid in Chalicorrema and thus we here refer the only tooth bearing bone fragment not presenting subpleurodont teeth to the same taxon as the other specimens due to comparable size and overall morphology of the acrodont teeth. The presence of two subpleurodont teeth is indicative of an agamine identity of this taxon (Maul et al., 2011). The caudal vertebrae are also attributed to Agaminae due to

shared morphology with comparative specimens at our disposal (in i.e., overall elongated shape, subelliptical anterior cotyle, subvertical prezygapophyses). The poor preservation of the remains does not allow a more precise identification. Smith et al. (2016) reported sexual dimorphism in the size of subpleurodont teeth in the agamid *Stellagama stellio* (Linnaeus, 1758), with the second tooth being larger than the first one in males. Even though identification of the Chalicorrema material is limited to the suprageneric rank, a similar variation in tooth size is observed in the three dentaries available, possibly suggesting a comparable dimorphism.

Agamidae indet.

Figure 42

Material. Vevi: one fragment of tooth bearing bone (UU VE 501).

Description. The fragment of tooth bearing bone (UU VE 501) from Vevi cannot be clearly assigned to a specific element, likely being either part of a maxilla or a dentary. It bears two acrodont teeth, which are triangular and

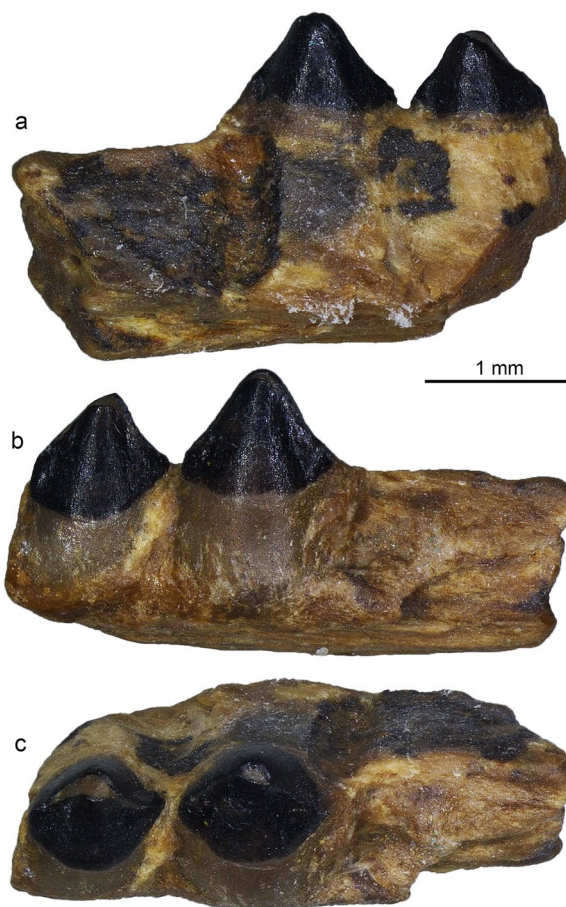


Fig. 42 Agamidae indet. from Vevi. Fragment of tooth bearing bone (UU VE 501) in lateral (a), medial (b), and dorsal (c) views

provided with an incipient accessory cusp on both mesial and distal sides (Fig. 42). A low degree of wearing possibly due to tooth abrasion is visible, thus giving a rounded shape to the tip of both teeth. No distinct striae are visible on the labial and lingual sides. The medial side of the tooth base expands ventrally to cover the alveolar surface of the tooth bearing bone. The two teeth are separated by a distinct space. On the lateral side of the tooth bearing bone there are two vertical, deep and wide interdental grooves. The fragment is 3.8 mm long.

Remarks. The bone fragment from Vevi is here referred to an agamid lizard because of the widely-separated acrodont teeth, which expand ventrally on the medial side of the bone (Delfino et al., 2008; Evans et al., 2002; Georgalis et al., 2023a; Villa & Delfino, 2019a; but note possible variability, regarding features also present in chamaeleonids, reported by Rage & Bailon, 2011 and Georgalis et al., 2023a). A more precise determination of this Vevi fragment within Agamidae is not possible. It could be likely that the Vevi specimen could pertain to Agaminae, as is the more complete material from Chalicorrema described above.

Anguimorpha Fürbringer, 1900
Anguidae Gray, 1825

Anguinae Gray, 1825

***Pseudopus* Merrem, 1820**

***Pseudopus* sp.**

Figure 43

Material. *Spilia* 4: eight trunk vertebrae (UU SP4 569–UU SP4 571, UU SP4 590, UU SP4 591, UU SP4 627, UU SP4 632, and UU SP4 633), one cloacal vertebra (UU SP4 584), and 14 caudal vertebrae (UU SP4 581–UU SP4 583, UU SP4 585–UU SP4 589, UU SP4 634, and UU SP4 635).

Description.

A few trunk vertebrae are present in the sample from *Spilia* 4 (Fig. 43). UU SP4 570 is a rather complete trunk vertebra of medium size and with a robustly-built aspect (Fig. 43f–j). The vertebral centrum is procoelous, dorsoventrally compressed and 5 mm long. The ventral surface is flat and the lateral margins are oblique and straight in ventral view. In anterior view, the neural canal is roughly as high as the cotyle. The synapophyses are dorsoventrally elongated. The zygapophyses are wide, elliptical and dorsally inclined of slightly less than 45°. The dorsal surface of the neural arch carries a well-developed neural spine, running for the entire length of the arch and ending posteriorly with a slightly expanded area. UU SP4 569 (Fig. 43a–e) and UU SP4 632 are slightly less

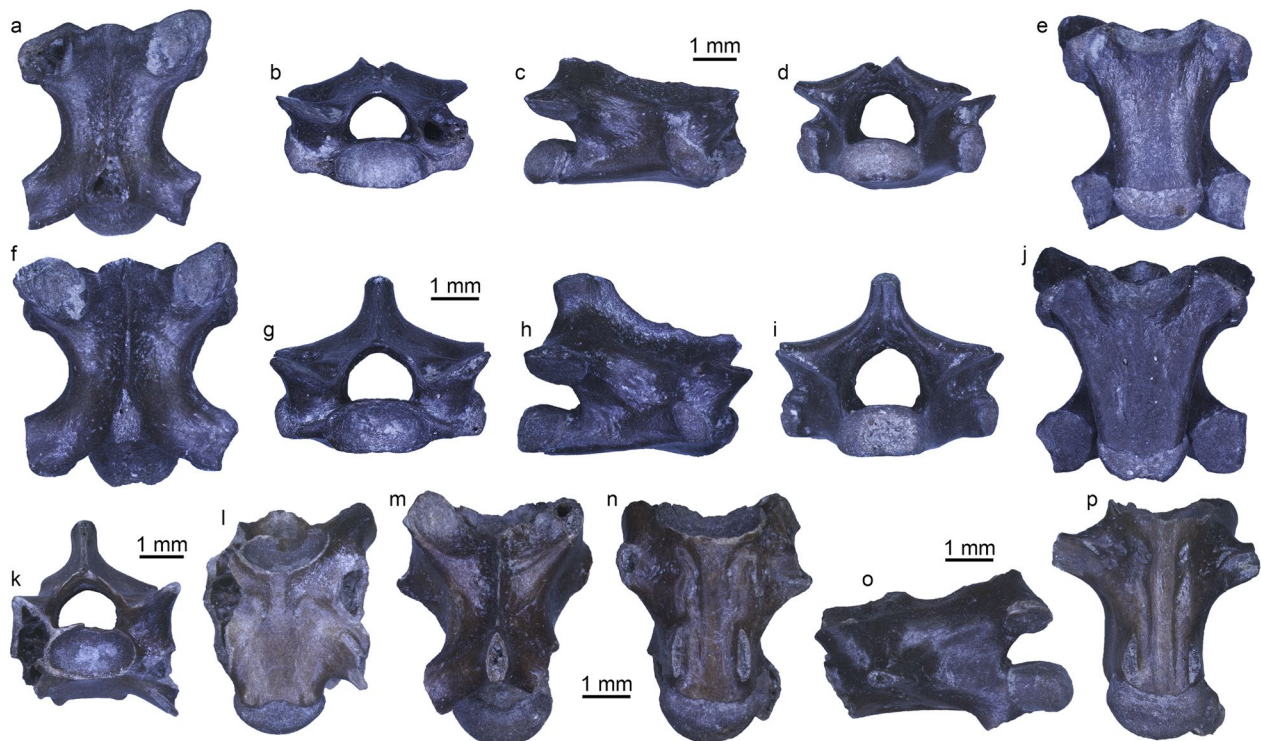


Fig. 43 *Pseudopus* sp. from *Spilia* 4. **a–e** Trunk vertebra (UU SP4 569) in dorsal (**a**), anterior (**b**), right lateral (**c**), posterior (**d**), and ventral (**e**) views; **f–j** trunk vertebra (UU SP4 570) in dorsal (**f**), anterior (**g**), right lateral (**h**), posterior (**i**), and ventral (**j**) views; **k, l** cloacal vertebra (UU SP4 584) in anterior (**k**) and ventral (**l**) views; **m, n** caudal vertebra (UU SP4 585) in dorsal (**m**) and ventral (**n**) views; **o, p** caudal vertebra (UU SP4 588) in left lateral (**o**) and ventral (**p**) views

preserved, but they share with UU SP4 570 both the same morphology and size. UU SP4 571, UU SP4 590, UU SP4 591, and UU SP4 627 are also similar, with the single exception of slightly concave lateral margins in ventral view.

The morphology of the cloacal vertebra (UU SP4 584) recalls that of the trunk vertebrae (Fig. 43k, l). It has a centrum length of 4 mm.

The caudal vertebrae from Spilia 4 are robustly built and medium sized (Fig. 43m–p). They are procoelous and have a dorsoventrally compressed centrum, provided with fused and narrow haemapophyses on the ventral side. The latter are not preserved in any of the fossil remains, however, their bases are still visible. There is no precondylar constriction and no complete autotomy plane is generally visible. Only few specimens still present an unfused plane on the ventral side of the vertebra. The caudal vertebrae are provided with wide zygapophyses, which are elliptical and dorsally inclined of slightly less than 45°. Dorsally, there is a laminar neural spine that expands posteriorly. In no case the transverse processes

are completely preserved, but a small foramen passing through their bases is visible in at least some of the specimens.

Remarks. The presence of *Pseudopus* in the Spilia assemblage is testified by anguid trunk vertebrae with a robust morphological construction, straight and posteriorly convergent lateral margins of the centrum, and neural canal that is not higher than the cotyle in anterior view (Čerňanský et al., 2019; Klembara, 1981). The caudal vertebrae are attributed to the same taxon because of the similar robustness and the partial or complete fusion of the autotomy plane (Etheridge, 1967; Loréal et al., 2023). A specific attribution of the material is not possible in the absence of cranial elements, but trunk vertebrae with concave margins of the centrum can be recognized as juveniles (Čerňanský et al., 2019; Klembara, 1981).

(non-*Anguis*) Anguinae indet.

Figures 44, 45

Material. *Chalicorrema*: six osteoderms (UU RA 421–UU RA 426); *Spilia 4*: 25 osteoderms (UU SP4 502, UU

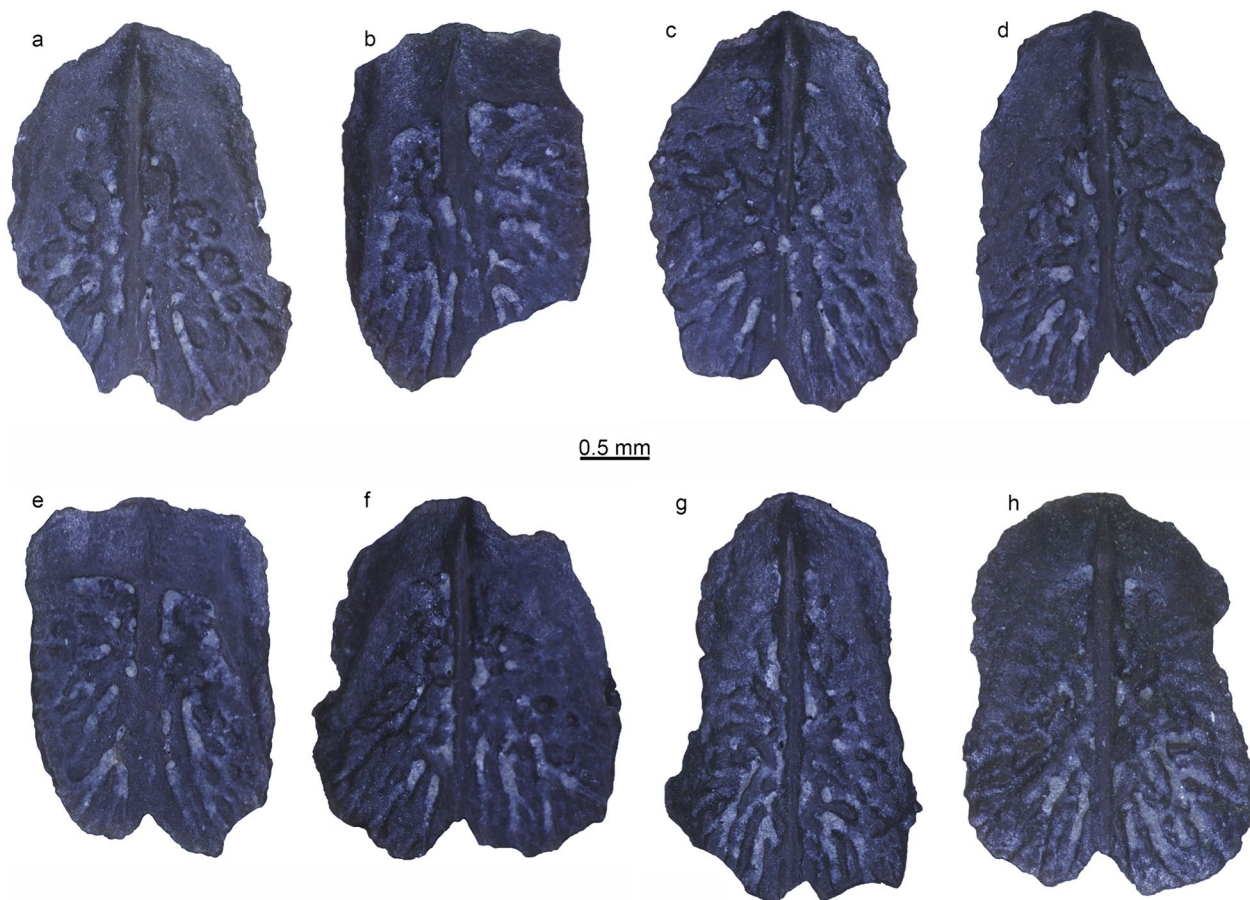


Fig. 44 (Non-*Anguis*) Anguinae indet. from Spilia 4. Osteoderms (a UU SP4 593; b UU SP4 594; c UU SP4 595; d UU SP4 596; e UU SP4 597; f UU SP4 598; g UU SP4 600; h UU SP4 647), all shown in external view

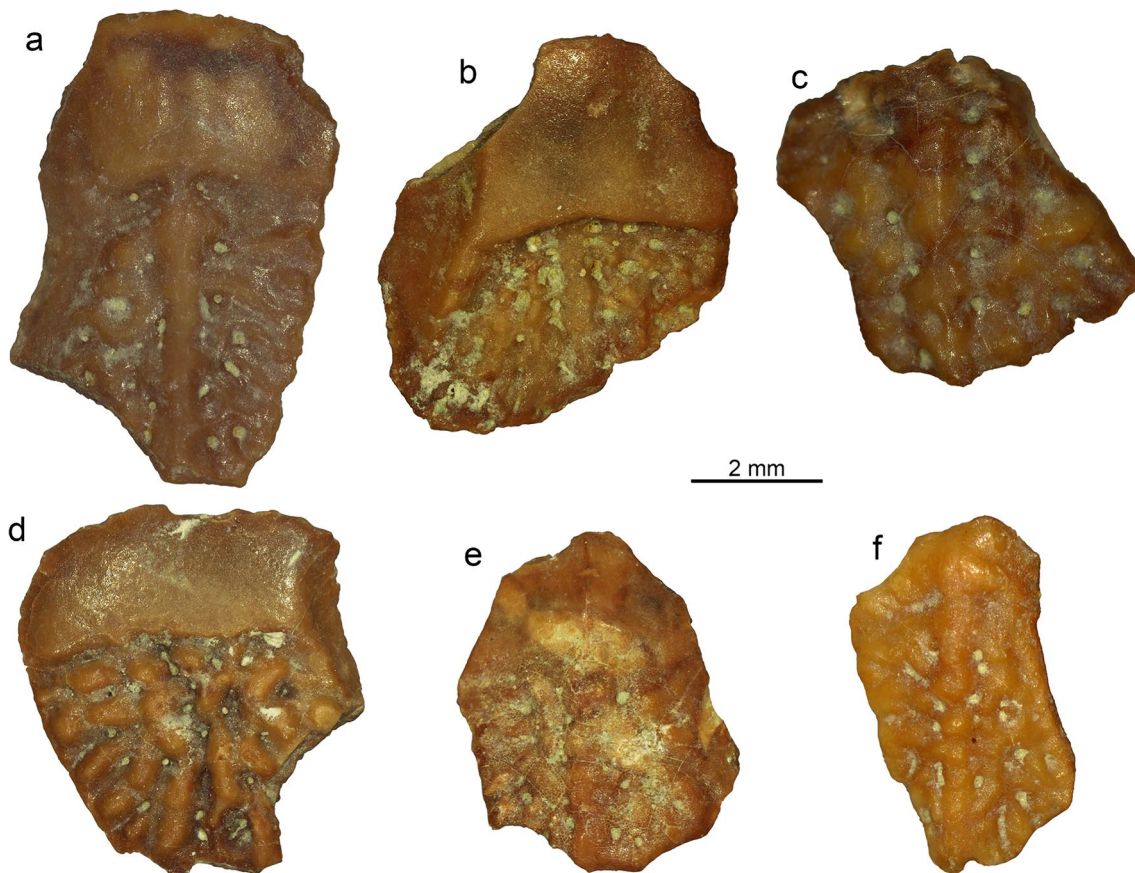


Fig. 45 (Non-*Anguis*) Anguinae indet. from Challicorrema. Osteoderms (a UU RA 421; b UU RA 422; c UU RA 425; d UU RA 423; e UU RA 424; and f UU RA 426), all shown in external view

SP4 503, UU SP4 592–UU SP4 602, and UU SP4 647–UU SP4 649) and one caudal vertebra (UU SP4 705).

Description.

The osteoderms from Spilia 4 are small- to medium-sized, squared and only moderately robust (Fig. 44). They display a smooth gliding surface, a vermicular sculpturing, and most of them also a low longitudinal keel on the external side.

The six osteoderms from Challicorrema are large-sized and robust, with either a subrectangular or subpentagonal shape (Fig. 45). The external surface is covered with a vermicular sculpturing except for the smooth surface where the osteoderms were covered by the preceding ones. A low longitudinal keel is visible on at least some of the osteoderms.

UU SP4 705 from Spilia 4 represents only the posterior condyle of a caudal vertebra. The condyle is dorsoventrally compressed, with no precondylar constriction. The bases of the fused and narrow haemapophyses are visible.

Remarks. Squared and robust osteoderms, sometimes provided with a keel, are confidently referred to

non-*Anguis* anguine lizards, as osteoderms of the genus *Anguis* Linnaeus, 1758, are characterized by an oval or irregular shape and bear no keels (Delfino et al., 2011; Hoffstetter, 1962; Holman, 1998; Klembara & Green, 2010). As such, these osteoderms are evidence of the presence in Challicorrema and Spilia 4 of a non-*Anguis* taxon. Accordingly, they could potentially pertain to either the genera *Pseudopus* described above or *Ophisaurus* Daudin, 1803, but in any case, a more precise determination is not possible. Particularly for the case of the osteoderms from Spilia 4, it seems most likely that they pertain to *Pseudopus*, as that taxon is well documented in that locality by the above-described vertebral material.

As for the fragmentary caudal vertebra UU SP4 705 from Spilia 4, the fused and narrow haemapophyses, the dorsoventral compression, and the absence of a precondylar constriction allow its assignment to an indeterminate anguid, but the very poor preservation hinders any further comment. This is also here referred to non-*Anguis* anguines and most likely to *Pseudopus*, as this is the only anguid known from that locality.

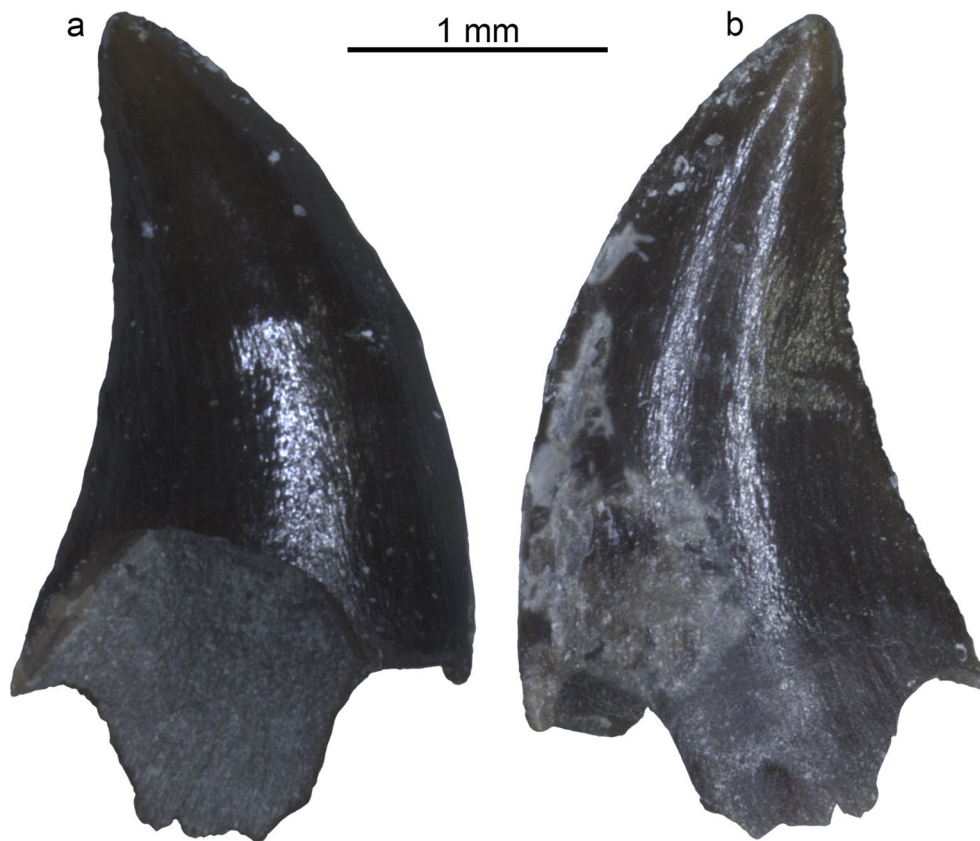


Fig. 46 cf. *Varanidae* indet. from Spilia 4. Isolated tooth (UU SP4 506) in lingual (a) and labial (b) views

Varanidae Gray, 1827 (sensu Estes et al., 1988)
cf. Varanidae indet.

Figure 46

Material. *Spilia 4*: one isolated tooth (UU SP4 506).

Description. This isolated tooth from Spilia 4 misses its proximal part (Fig. 46). The preserved portion is 3.1 mm in length. The tooth is strongly labiolingually compressed, slightly curved posteriorly, canine-like and pointed. It is smooth, without longitudinal grooves. The mesial and distal cutting edges are slightly serrated, with the distal one being more serrated than the mesial one.

Remarks. The single and partial tooth from Spilia 4 is tentatively attributed to an indeterminate monitor lizard because of the overall similarity between it and the general morphology of varanid teeth: labiolingual compression that encompasses the pulp cavity, presence of serrated carinae, posterior bending (Bhullar & Smith, 2008; Bullet, 1942; Georgalis et al., 2023b; Ivanov et al., 2018; Peyer, 1929; Villa et al., 2018). Nevertheless, the attribution cannot be confidently confirmed because of the missing tooth base, the absence of which hinders the recognition of the main apomorphy of varanoid teeth (namely, the presence of plicidentine; Estes et al., 1988; Georgalis & Scheyer, 2019; Kearney & Rieppel,

2006). Remarkable is also the absence of grooves in the preserved portion of the basal area of the tooth; such grooves are generally associated with the presence of the plicidentine (see for example Villa et al., 2021, fig. 17a–d). Nevertheless, the labiolingual tooth crown compression, with mesial and distal carinae is considered a synapomorphy of the varanoid genera *Lanthanotus* Steindachner, 1878, and *Varanus*, with the latter genus having this compression extending to the tooth base and being visible in the pulp cavity (Bhullar & Smith, 2008; Georgalis et al., 2023b). Most of the tooth base is not preserved in the Spilia tooth, but nevertheless it seems that the pulp cavity is compressed, a feature typical of *Varanus* (Georgalis et al., 2023b).

(non-snake) Squamata indet.

Figure 47

Material. *Chalicorrema*: one fragment of indeterminate tooth bearing bone (UU RA 405); *Spilia 3*: one cervical vertebra (UU SP3 615); *Spilia 4*: three quadrates (UU SP4 608, UU SP4 612, and UU SP4 613), one indeterminate cranial element (UU SP4 692), one axis (UU SP4 626), three trunk vertebrae (UU SP4 642, UU SP4 644, and UU SP4 710), two sacral vertebrae (UU SP4 703,



Fig. 47 Non-snake Squamata indet. from Chalicorrema and Spilia 4. **a, b** Fragment of tooth bearing bone (UU RA 405) in medial (**a**) and lateral (**b**) views; **c–e** left quadrate (UU SP4 608) in posterior (**c**), medial (**d**), and anterior (**e**) views; **f–h** right quadrate (UU SP4 613) in posterior (**f**), medial (**g**), and anterior (**h**) views; **i–k** left quadrate (UU SP4 612) in lateral (**i**), medial (**j**), and posterior (**k**) views; **l** caudal vertebra (UU SP4 656) in ventral view; **m** left humerus (UU SP4 610) in posteroventral view

708), three caudal vertebrae (UU SP4 621, UU SP4 628, and UU SP4 656), five ribs (UU SP4 505), two humeri (UU SP4 607 and UU SP4 610), and five femora (UU SP4 609, UU SP4 651, UU SP4 652, and UU SP4 702).

Description and remarks.

The fossil remains from Spilia 3 and Spilia 4 pertain to lizards, but they cannot be confidently identified because of either an overall poor preservation or the current lack of data on the comparative postcranial osteology of these reptiles.

The three quadrate fragments from Spilia 4 (UU SP4 608, UU SP4 612, and UU SP4 613) only preserve the pillar, which is narrow and straight and expands dorsally and ventrally (Fig. 47c–k). In all three specimens, a low medial lamina is present but the lateral lamina is broken off.

The humerus (UU SP4 610) from Spilia 4 (Fig. 47m), as well as most femora, are very small, but well ossified. They could thus pertain to the small-sized lacertid identified based on the above-described coronoid UU SP4 704. The other humerus (UU SP4 607) is also very small, but its epiphyses are not ossified, thus suggesting it belonged to a juvenile. At least one rather large femur (part of UU SP4 702) is also present, possibly attributable to the medium-sized lacertid.

The trunk vertebrae from Spilia 4 are small, with a centrum length ranging from 1.8 to 1.9 mm. They are poorly elongated and have a not compressed centrum. This morphology is more similar to the one of lacertid vertebrae, among non-snake squamates from Spilia. Pending a real detailed comparative analysis of the vertebrae of these squamates, however, this possible identification should just remain tentative.

It is also worth noticing the specimen UU SP4 656 (Fig. 47l). This is a medium-sized caudal vertebra, with a not compressed, procoelous centrum. The centrum length is about 3.5 mm and both cotyle and condyle are circular. There is no precondylar constriction. The ventral surface of the centrum is distinctly keeled and posteriorly it displays two small articular surfaces for the chevron bone located immediately anterior to the posterior condyle. The left transverse process is better preserved than the right one, even though the distal half is still missing. The autotomy plane is not visible. The neural arch is poorly preserved. A laminar neural spine is present, but broken. The suboval left prezygapophysis is preserved, with a slight dorsal inclination in anterior view. On the lateral surface of the neural arch, a very low but distinct postzygaprezygapophyseal lamina is visible. This morphology fits well with caudals of lacertids, thus suggesting that this vertebra could pertain to the medium-sized one (cf. *Lacerta* sp.) identified in Spilia based on cranial bones. UU SP4 621 and UU SP4 628 are smaller (centrum length around 3 mm and 2.5 mm respectively) and less preserved, but the morphology is more or less the same. They could pertain to indeterminate lacertids as well.

As for the single element from Chalicorrema, this specimen (UU RA 405) is a fragment of tooth bearing bone (Fig. 47a, b). It is either part of a maxilla or a dentary, but this cannot be clearly stated. It carries seven tooth positions, two of which are still occupied by moderately preserved teeth. The teeth are pleurodont, cylindrical, slender and closely spaced. The tooth base is not swollen. Both teeth have a poorly preserved crown, thus hindering a clear recognition of the morphology. The crown of the (probably) most anterior tooth appears rounded, but this is due to breakage and wearing. The other tooth seems to display a small anterior cusp mesially, but, at a closer inspection, this comes out as an artifact due to breakage. The fragment is 4.0 mm long. According to this description, it is obvious that a third lizard taxon, a small lizard with a pleurodont dentition, is also present in the Chalicorrema fossil assemblage, but its taxonomy cannot be confidently stated based on this single and very poorly preserved specimen. Considering what is preserved of its tooth morphology and the fossil record of non-snake squamates in the Neogene of Europe, teeth of this element appear more similar to those of lacertid and scincoid lizards, and maybe to a lesser degree, gekkotans. However, a clear attribution is not possible for the moment, and we only refer this fossil to an indeterminate lizard, different from the above-described agamine and anguine from that locality.

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Constrictores Oppel, 1811a (sensu Georgalis & Smith, 2020)

Booidea Gray, 1825 (sensu Pyron et al., 2014)

Erycidae Bonaparte, 1831 (sensu Pyron et al., 2014)

Eryx Daudin, 1803

cf. *Eryx* sp.

Figure 48

Material. *Spilia 4*: an anterior trunk vertebra (UU SP4 533).

Description.

The vertebra (UU SP4 533) is very fragmentary, missing most of the zygosphenes and neural spine, as well as parts of the condyle and the hypapophysis (Fig. 48). In anterior view (Fig. 48a), the zygosphenes are almost totally damaged and its shape cannot be discerned. The neural canal is large. The prezygapophyses are much dorsally inclined, extended at around the mid-height level of the neural canal. The cotyle is large and oval-shaped (its dorsal roof is damaged). There seem to be no paracotylar foramina. The paradiapophyses extend slightly below the ventral level of the cotyle. In posterior view (Fig. 48b), the neural arch is depressed, with a vaulting ratio (sensu Georgalis et al., 2021b) equal to 0.44. The condyle is rather eroded, preserving mostly the condylar base. In dorsal

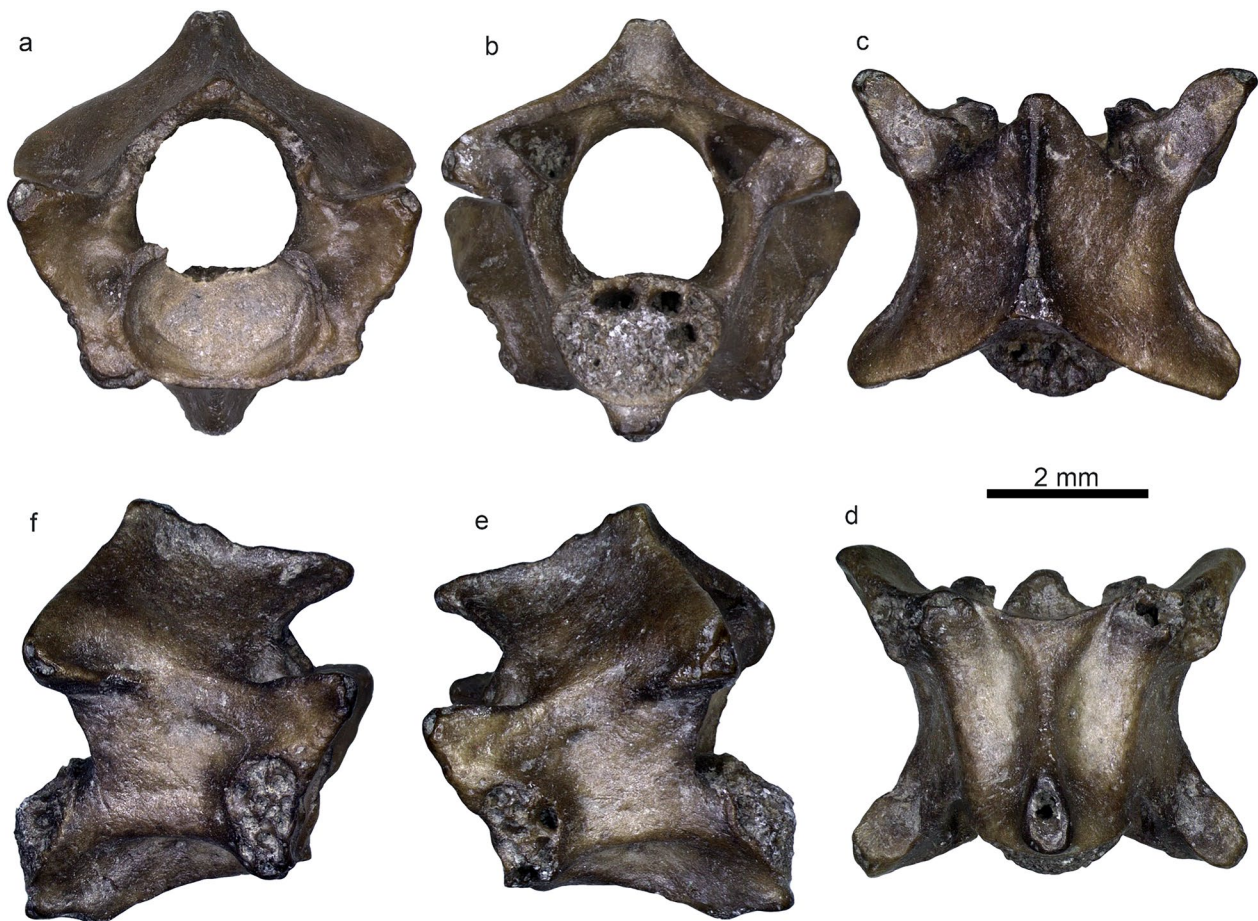


Fig. 48 cf. *Eryx* sp. from Spilia 4. Anterior trunk vertebra (UU SP4 533) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

view (Fig. 48c), the prezygapophyses extend anterolaterally. The prezygapophyseal accessory processes are short. The interzygapophyseal constriction is deep. The posterior median notch of the neural arch is deep. In ventral view (Fig. 48d), the centrum is slightly wider than long (ratio centrum length to neural arch width: 1.03). The hypapophysis covers the whole midline of the centrum. The subcentral grooves are deep. The paradiapophyses are partially eroded but there is no clear distinction among the diapophyseal and parapophyseal portions. The postzygapophyseal articular facets are elongated and oval. In lateral view (Fig. 48e, f), the neural spine is rather damaged and therefore its overall shape and height cannot be assessed. A single lateral foramen is situated below each interzygapophyseal ridge. The subcentral ridges are slightly convex. The hypapophysis is damaged but from the preserved part, it is evident that it was more posteriorly directed; the preserved part also denotes that this element is considerably thick at around the posterior half of the centrum. Judging from the presence of

hypapophysis, the vertebra pertains to the anterior trunk region of the column, whereas the very large neural canal implies for earlier ontogenetic stage (perhaps juvenile).

Remarks. This specimen was previously mentioned but not described or figured by Szyndlar (1991a). It is tentatively considered an anterior trunk vertebra of the erycid genus *Eryx* based on the wider than long centrum, presence of short prezygapophyseal accessory processes, the much dorsally inclined prezygapophyses in anterior view, with prezygapophyseal articular facets situated above the base of the neural canal, the absence of paracotylar foramina, the dorsoventrally compressed neural arch, the interzygapophyseal ridges strongly sloping anteriorly in lateral view, the thin hypapophysis in ventral view, and the relatively small size (Szyndlar & Georgalis, 2023). Nevertheless, the most diagnostic part of the erycid vertebral column lies within the caudal series, which is characterized by an extreme peculiar morphology (see Szyndlar & Georgalis, 2023). As such, and taking also into consideration

the fragmentary nature of the specimen, the *Spilia* 4 vertebra is only tentatively referred to *Eryx*.

Caenophidia Hoffstetter, 1939

Colubroidea Zaher, Graziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009

Colubriformes Schlegel, 1837 (sensu Zaher et al., 2009)

Remarks. Following current taxonomic schemes, Colubriformes includes Pareidae Romer, 1956, Colubroidea Opper, 1811b, Elapoidea Boié, 1827, and Viperoida Opper, 1811b (Burbrink et al., 2020; Zaher et al., 2009, 2019). Among these, Pareidae are currently distributed to southern Asia (Wallach et al., 2014) and have never been documented in the fossil record of Europe. Certain taxa from the European fossil record cannot still be precisely determined as belonging to either colubroids, elapoids, and viperoids, and they are assigned as Colubriformes incertae sedis.

Traditionally, in the literature most caenophidians that lacked hypapophyses in their mid- and posterior trunk vertebrae were collectively referred as “Colubrinae” or “colubrines” (e.g., Rage, 1984; Szyndlar, 1984, 1991a, 2012). Nevertheless, recent advances in our understanding of snake phylogenetic relationships have demonstrated that this is a paraphyletic assemblage. As such, the colubroid families of colubrids and dipsadids, and the elapoid family of psammophiids, which all share the absence of hypapophyses in mid- and posterior trunk vertebrae and have a European fossil record, are in fact distantly related (see Georgalis & Scheyer, 2022; Georgalis & Szyndlar, 2022; Georgalis et al., 2019a, 2019b; Ivanov, 2022; Zaher et al., 2019). As such, we prefer to use the term Colubriformes for all these forms, unless for the case that we can somehow exclude affinities with the elapoid lineage of psammophiidae, and then we can more precisely refer them to Colubroidea (see below). The cases of *Periergophis* and *Paraxenophis* described here from *Spilia* can only be assigned to Colubriformes incertae sedis (see below).

Colubroidea Opper, 1811b (sensu Zaher et al., 2009)

Remarks. Following current taxonomic schemes, Colubroidea includes Colubridae Opper, 1811b, Natricidae, Dipsadidae Bonaparte, 1838a, Calamariidae Bonaparte, 1838a, and Pseudoxenodontidae McDowell, 1987 (Burbrink et al., 2020; Zaher et al., 2009, 2019). The latter two are currently distributed in southeastern Asia and have never been found in the European fossil record.

Natricidae Bonaparte, 1838a

***Natrix* Laurenti, 1768**

***Natrix rudabanyaensis* Szyndlar, 2005**

Natrix* aff. *rudabanyaensis

Figures 49, 50, 51, 52

Material: *Spilia* 0: 12 trunk vertebrae (UU SP0 153–UU SP0 164) and one caudal vertebra (UU SP0 165); *Spilia* 1: one caudal vertebra (UU SP1 1012); *Spilia* 4: 19 trunk vertebrae [UU SP4 565, UU SP4 566, and UU SP4 568 (17 vertebrae)]; *Vevi*: Four anterior trunk vertebrae (UU VE 603–UU VE 606), 10 mid-trunk vertebrae (UU VE 607–UU VE 616), three posterior trunk vertebrae (UU VE 617–UU VE 619), and nine caudal vertebrae (UU VE 620–UU VE 628).

Description.

The description of the trunk vertebrae is mainly based on the specimens from *Vevi*, which are more complete (Fig. 49). The vertebrae are lightly built. All specimens are at least partially fragmentary with the neural spine broken off close to its base (but see Fig. 51g for a perfectly preserved neural spine of a single specimen from *Spilia* 0). In lateral view (Fig. 49a, f, k, n), the anterior margin of the neural spine of the best-preserved mid-trunk vertebra (UU VE 607) extends anteriorly to the level of the posterior margin of the zygosphenal facet. The zygosphenal facet is markedly large and rhomboid. There is a distinct blunt ridge developed at the posterior margin of the zygosphenal facet which extends from the base of the anterior neural spine base. The well-developed interzygapophyseal ridges are usually sharp. The lateral foramen is situated close below the interzygapophyseal ridge. The dorsally arched subcentral ridges are prominent. The diapophyses are well-separated from the equally sized parapophyses. The anteriorly directed parapophyseal processes are moderately long and they are well-separated from the parapophyseal facets. The only preserved complete hypapophysis of one specimen (UU VE 609) is sigmoid with blunt distal tip situated slightly anterior to the posterior margin of the condyle (Fig. 49k). The condyle is developed on a rather short condylar neck. In dorsal view (Fig. 49b, g, o), the zygosphenon has pointed lateral lobes and a rather wide medial lobe. The prezygapophyseal articular facets are widely oval; however, prezygapophyseal accessory processes are broken off close to their base. The epizygapophyseal spines are moderately developed but sometimes they are indistinct as a result of surface abrasion. The posterior median notch of the neural arch is rather deep. The diapophyses are directed posterolaterally. In ventral view (Fig. 49c, l, p), the hypapophysis extends anteriorly to form the triangular anterior keel with small subcotylar tubercles developed at the base of the cotylar rim. Their distal tip is directed posterolaterally. The converging subcentral ridges are straight and wide subcentral grooves occur between those ridges and narrow (almost sharp) hypapophysis. In posterior trunk vertebrae (UU VE 617; Fig. 49p), the sharp subcentral ridges are



Fig. 49 *Matrix* aff. *rudabanyaensis* from Vevi, trunk vertebrae. **a–e** Anterior trunk vertebra (UU VE 603) in right lateral (**a**), dorsal (**b**), ventral (**c**), anterior (**d**), and posterior (**e**) views; **f–j** mid-trunk vertebra (UU VE 607) in left lateral (**f**), dorsal (**g**), ventral (**h**), anterior (**i**), and posterior (**j**) views; **k–m** mid-trunk vertebra (UU VE 609) in left lateral (**k**), ventral (**l**), and anterior (**m**) views. **n–p** Posterior trunk vertebra (UU VE 617) in left lateral (**n**), dorsal (**o**), and ventral (**p**) views

markedly developed and the subcentral grooves are rather deep. Subcentral foramina are very small. The postzygapophyseal articular facets are irregularly shaped. In anterior view (Fig. 49d, i, m), the thin zygosphenal roof is straight with a ventrally bent medial lobe. The zygosphenal facets are slightly uplifted above the zygosphenal roof. The neural canal is sub-squared with rather small lateral sinuses. Paracotylar foramina are situated in depressions on either side of the rounded cotylar rims. In posterior view (Fig. 49e, j), the neural arch is moderately vaulted, with a vaulting ratio

(sensu Georgalis et al., 2021b) ranging between 0.32 and 0.39. The zygantrum is wide. The number of small parazygantral foramina is variable from 1 to 3 on either side. The small condyle is almost orbicular with its ventral margin slightly depressed.

Trunk vertebrae from *Spilia* (Figs. 51, 52a–e) are in most cases more fragmentary than those from Vevi. Nevertheless, they still afford some anatomical observations. In one specimen (UU SP4 565; Fig. 52a–c) from *Spilia* 4, the hypapophysis is complete, projecting ventrally and its

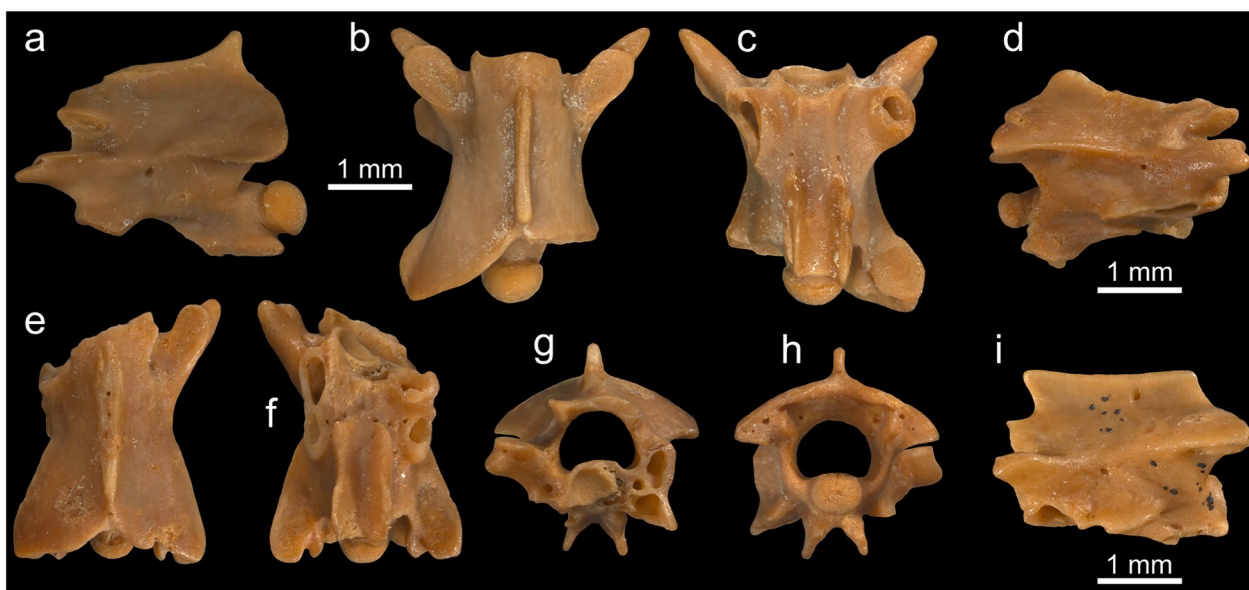


Fig. 50 *Natrix* aff. *rudabanyaensis* from Vevi, caudal vertebrae. **a–c** Anterior caudal vertebra (UU VE 620) in left lateral (**a**), dorsal (**b**), and ventral (**c**) views. **d–h** Caudal vertebra in right lateral (**d**), dorsal (**e**), ventral (**f**), anterior (**g**), and posterior (**h**) views; **i** posterior caudal vertebra (UU VE 621) in left lateral left view

termination does not extend posteriorly from the condyle. Some variation exists among the shape and direction of the neural spine: in one specimen (UU SP4 566; Fig. 52d, e) from Spilia 4, the posterior margin of the neural spine strongly overhangs posteriorly, whereas in a vertebra from Spilia 0 (UU SP0 154; Fig. 51g), the neural spine has its anterior margin straight to slightly anteriorly inclined and its posterior margin posteriorly inclined, and in another vertebra from the latter locality (UU SP0 158; Fig. 51a) it seems that both anterior and posterior margins of the neural spine are almost straight. The neural arch of the Spilia trunk vertebrae is moderately depressed, with a vaulting ratio (sensu Georgalis et al., 2021b) ranging between 0.34 and 0.39.

The available caudal vertebrae from Vevi (Fig. 50), Spilia 0, and Spilia 1 (Fig. 52f) are fragmentary with broken off pleurapophyses and haemapophyses. In lateral view (Fig. 50d, i), the neural spine is about twice longer than high in more anteriorly located caudal vertebrae whereas in posterior caudal vertebrae the neural spine is about three to four times longer than high. In the single caudal vertebra (UU SP1 1012) from Spilia 1, the neural spine has its anterodorsal margin strongly inclined anteriorly (Fig. 52f). In dorsal view (Fig. 50b, e), the zygosphene has distinct lateral lobes and a wide medial lobe. Prezygapophyseal articular facets are oval with their axis elongated anterolaterally. Prezygapophyseal accessory processes are pointed distally and about half of the length of the prezygapophyseal articular facets or they are shorter. In ventral view (Fig. 50c, f), pleurapophyses

of anterior caudal vertebrae have narrow base and the preserved portions of pleurapophyses indicate that they were laterally rather than antero-laterally directed. In posterior caudal vertebrae the pleurapophyses with wide base are directed anteriorly. There is a distinct, posteriorly directed spur developed on the posterior margin of the pleurapophysis base.

Remarks. The hypapophysis-bearing trunk vertebrae with triangular anterior keel, elongated centrum and well-developed epizygapophyseal spines correspond to a typical natrixid morphology (Ivanov, 2002; Szyndlar, 1984, 1991b, 2005; Szyndlar & Schleich, 1993). The referral to the genus *Natrix* is based on the following combination of features in mid-trunk vertebrae: 1, the neural spine is high; 2, the vertebrae with elongated centrum are cylindrical in shape; 3, the prezygapophyseal accessory processes are well developed; 4, the parapophyseal processes are moderately long and directed anteriorly rather than anteroventrally; 5, the hypapophysis is sigmoid with rounded distal tip. There are four extinct valid species of *Natrix* in the European Neogene: *Natrix merkurensis* Ivanov, 2002 (MN 3a–?MN 4; Ivanov, 2002; Rage & Bailon, 2005), *Natrix sansaniensis* (Lartet, 1851) (MN 3a–MN 4 and MN 6; Augé & Rage, 2000; Ivanov, 2002; Szyndlar & Schleich, 1993), *Natrix rudabanyaensis* (MN 9; Szyndlar, 2005), and *Natrix longivertebra* Szyndlar, 1984 (widespread from the Early Miocene up to the Late Pliocene; Ivanov, 2022; Rage & Szyndlar, 1986; Szyndlar, 1984, 1991b; Vasilyan et al., 2022). A further species, *Neonatrix natrixoides* Augé & Rage, 2000, from the Early and Middle Miocene (MN 4

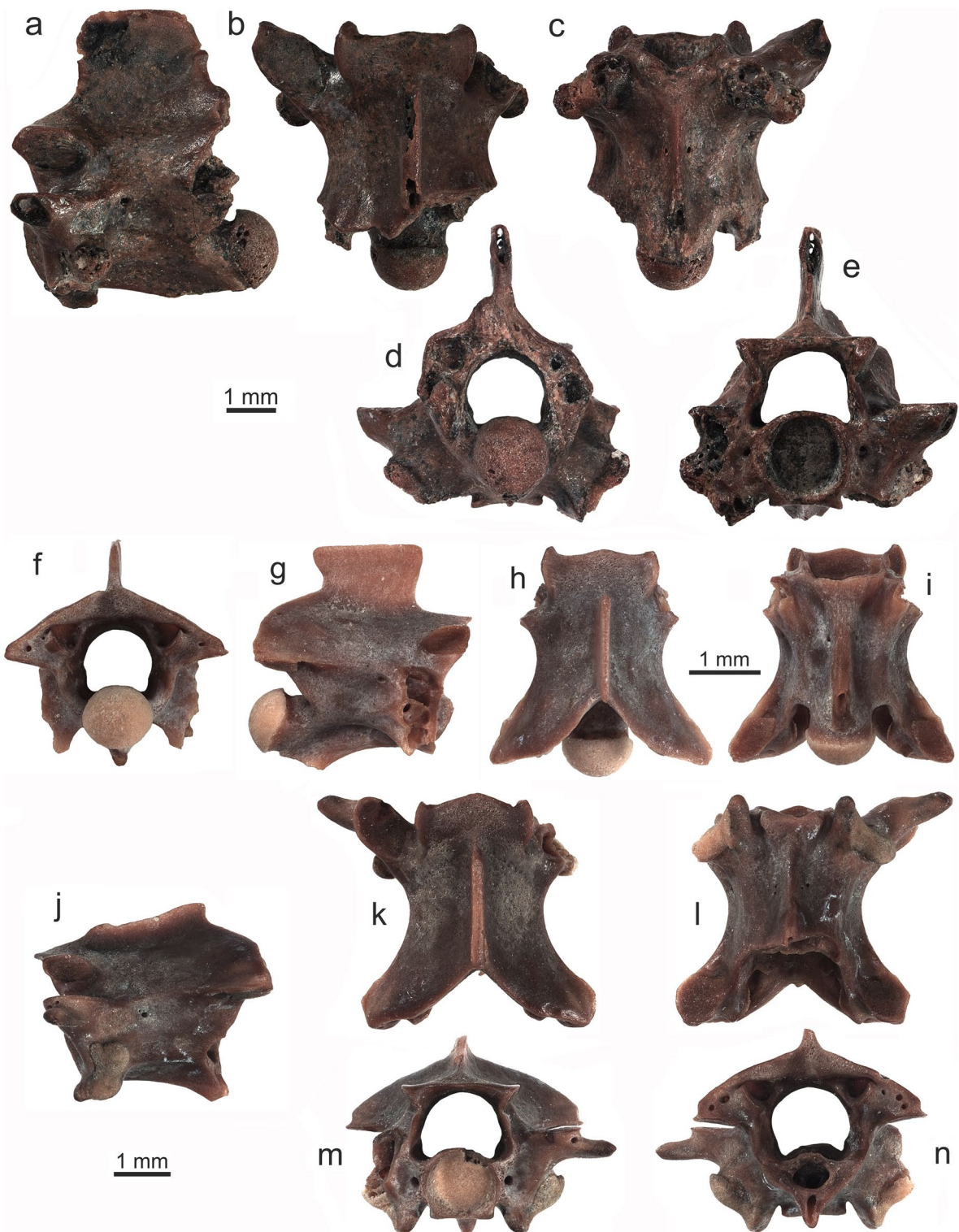


Fig. 51 *Natrix aff. rudabanyaensis* from Spilia 0. **a–e** Anterior trunk vertebra (UU SP0 158) in left lateral (**a**), dorsal (**b**), ventral (**c**), posterior (**d**), and anterior (**e**) views; **f–i** trunk vertebra (UU SP0 154) in posterior (**f**), right lateral (**g**), dorsal (**h**), and ventral (**i**) views; **j–n** trunk vertebra (UU SP0 153) in left lateral (**j**), dorsal (**k**), ventral (**l**), anterior (**m**), and posterior (**n**) views

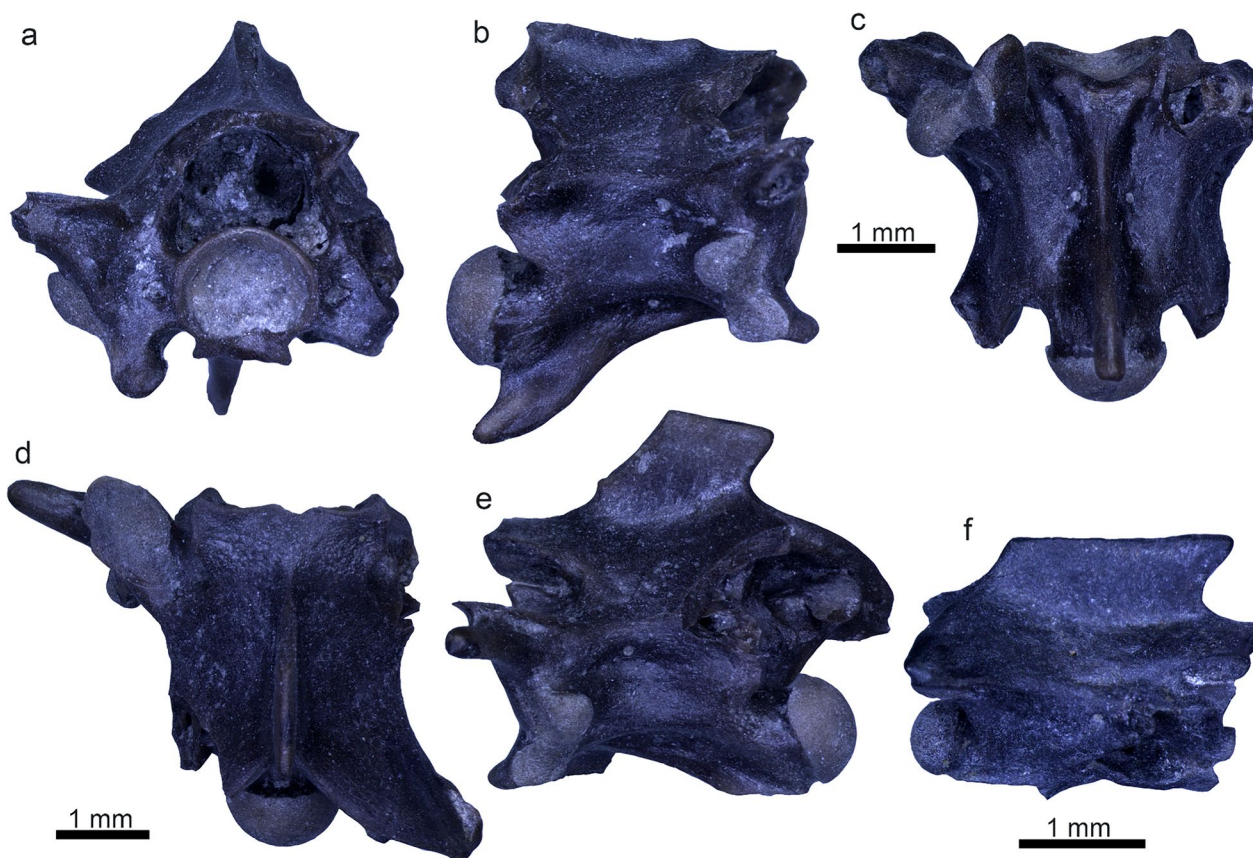


Fig. 52 *Natrix* aff. *rudabanyaensis* from Spilia 1 (SP1) and Spilia 4 (SP4). **a–c** Trunk vertebra (UU SP4 565) in anterior (**a**), right lateral (**b**), and ventral (**c**) views; **d–e** trunk vertebra (UU SP4 566) in dorsal (**d**) and left lateral (**e**) views; **f** caudal vertebra (UU SP1 1012) in right lateral view

and MN 5) of France (Augé & Rage, 2000; Rage & Bailon, 2005), was considered a member of the genus *Natrix* by Szyndlar (2005, 2012); however, its rather short hypapophysis is unusual for *Natrix*, and therefore, even generic allocation of that species is uncertain (Ivanov, 2022). The *Natrix* vertebrae from Vevi and Spilia particularly resemble those of *N. rudabanyaensis* by the following combination of features (see Szyndlar, 2005): 1, relatively small dimensions; 2, moderately elongated centrum; 3, elongated prezygapophyseal articular facets; 4, prezygapophyseal accessory processes long and moderately flattened dorsoventrally. However, the parapophyseal processes of *N. aff. rudabanyaensis* from Vevi and Spilia are shorter and the epizygapophyseal spines are less distinct, compared to those of *N. rudabanyaensis* from the Late Miocene of Rudabanya (Szyndlar, 2005). Admittedly, several vertebral features that are used to differentiate Neogene *Natrix* spp. are subjected to intracolumnar and intraspecific variation or are anyway widespread among natricids. A proper taxonomic referral of this Greek form can only be made once the taxonomy and diagnosis, and intracolumnar variation of the Neogene European species of *Natrix* is better

assessed and revised, something that is well beyond the scope of the present study. For these reasons, we only tentatively refer the Greek material as *Natrix* aff. *rudabanyaensis*, as is the case with the material from Maramena that was recently described by Georgalis et al. (2019b).

?Natricidae indet.

Figures 53, 54, 55

Material. *Chalicorrema*: three trunk vertebrae (UU RA 408–UU RA 410); *Spilia 0*: two trunk vertebrae (UU SP0 151 and UU SP0 152); *Spilia 2b*: one trunk vertebra (UU SP2b 501); *Vevi*: one anterior trunk vertebra (UU VE 601).

Description. All hypapophysis-bearing trunk vertebrae from *Chalicorrema* are rather fragmentary (Fig. 53). In the best-preserved anterior trunk vertebra (UU RA 408; Fig. 53a–c), only the centrum with broken off distal tip of the hypapophysis and incomplete neural arch is present. In lateral view (Fig. 53a), the short interzygapophyseal ridge is well developed. A small lateral foramen is situated in a shallow depression close below the interzygapophyseal ridge. The subcentral ridges are arched dorsally and extend from the base of a non-preserved parapophysis up to the

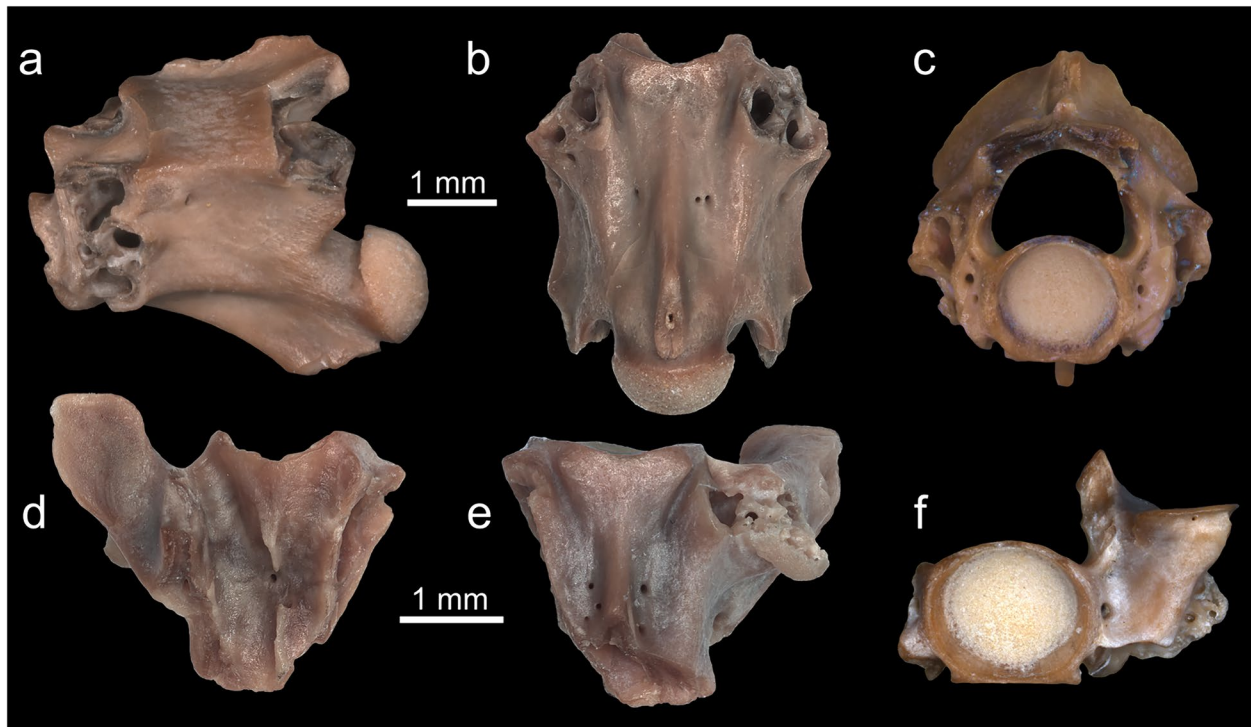


Fig. 53 ?Natricidae indet. from Chalicorrema. **a–c** Trunk vertebra (UU RA 408) in left lateral (**a**), ventral (**b**), and anterior (**c**) views; **d–f** trunk vertebra (UU RA 409) in dorsal (**d**), ventral (**e**), and anterior (**f**) views

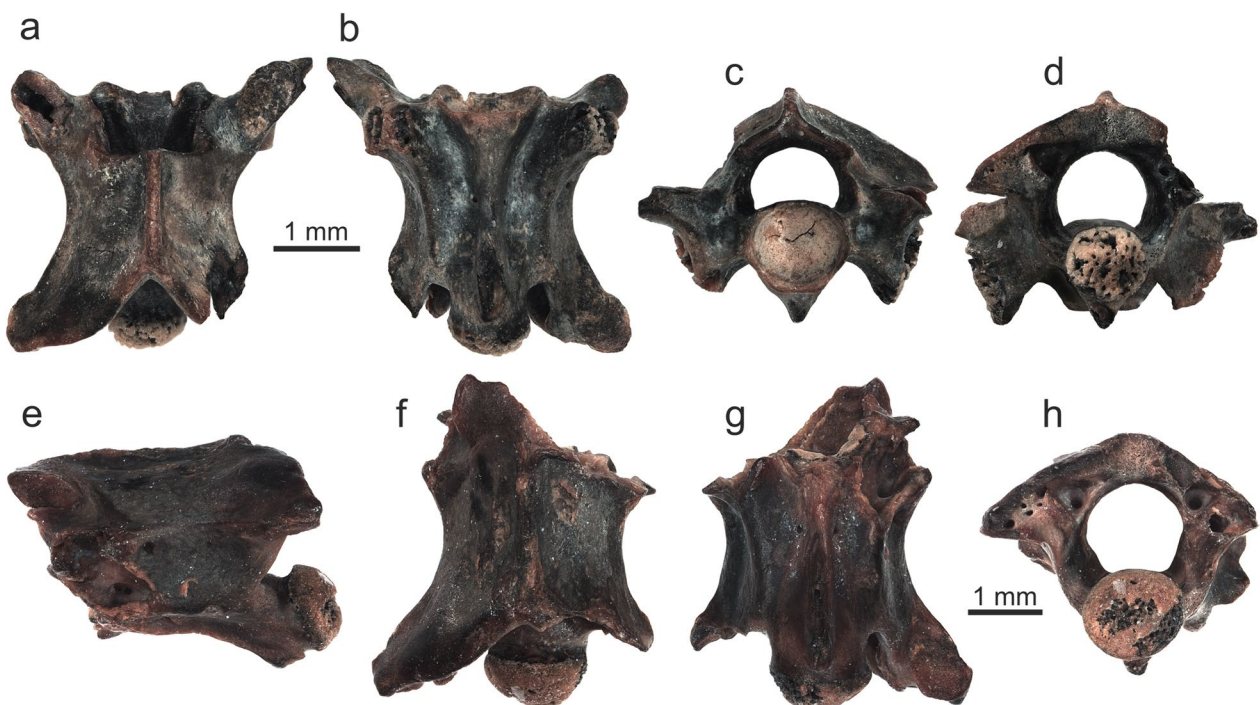


Fig. 54 ?Natricidae indet. from Spilia 0. **a–d** Mid-trunk vertebra (UU SP0 151) in dorsal (**a**), ventral (**b**), anterior (**c**), and posterior (**d**) views; **e–h** mid-trunk vertebra (UU SP0 152) in left lateral (**e**), dorsal (**f**), ventral (**g**), and posterior (**h**) views

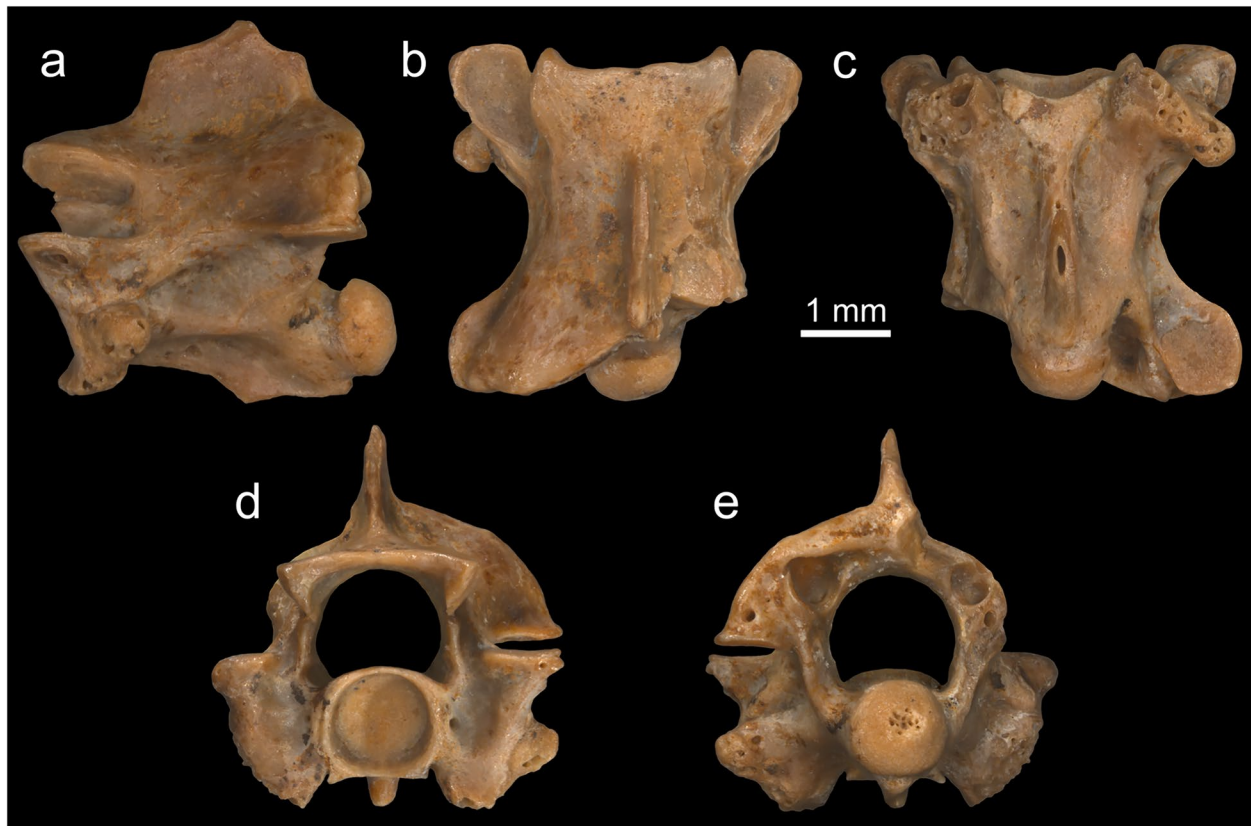


Fig. 55 ?Natricidae indet. from Vevi. Anterior trunk vertebra (UU VE 601) in left lateral (a), dorsal (b), ventral (c), anterior (d), and posterior (e) views

vicinity of the base of the short condylar neck. In dorsal view (Fig. 53d), the only preserved left prezygapophyseal articular facet of one fragment (UU RA 409) is irregularly oval to subtriangular in outline. The prezygapophyseal accessory processes, broken off at their wide base, were most probably well developed in life. In ventral view (Fig. 53b, e), the subcentral grooves are narrow. Subcentral ridges extend parallel along their entire length. The hypapophysis extends to the close vicinity of the cotylar rim but moderately developed triangular expansion of its base occurs anterior to minute subcentral foramina. Small subcotylar tubercles are developed close behind the base of the cotylar rim. The subcentral foramina are situated in the middle of the centrum length, the left one is doubled in UU RA 408 (Fig. 53b) but multiple foramina (three on the right side plus two on the left side) occur in UU RA 409 (Fig. 53e). The condyle is relatively small. In anterior view (Fig. 53c, f), the neural canal is rounded with wide lateral sinuses. The paracotylar foramina, situated in narrow depressions on either side of the circular cotylar rim, are either doubled with upper foramen larger than the lower one (UU RA 408; Fig. 53c). However, only one large single left paracotylar foramen is present in one specimen (UU RA 409; Fig. 53f). The ventral border of the cotylar rim is flat in this specimen (Fig. 53f).

The few vertebrae from Spilia 0 and Spilia 2 are rather fragmentary (Fig. 54). They all possess hypapophyses, which are, however, much incomplete in all specimens. Neural spines, paradiapophyses, and parts of the prezygapophyses are much damaged in all specimens.

The single specimen from Vevi (UU VE 601) represents an anterior trunk vertebra (Fig. 55). Its right side is damaged with broken off right postzygapophysis, incomplete prezygapophyses, and the right paradiapophysis eroded. In lateral view (Fig. 55a), the neural spine rises at the level of the posterior margin of the zygosphenal facets. The neural spine is high with its basal anterior margin inclined slightly posteriorly whereas its posterior margin is inclined anteriorly. The distal termination of the neural spine is not preserved. The long axis of the strongly elongated zygosphenal facet is directed anteriorly rather than anterodorsally. The anteroventrally directed lamina, situated below the interzygapophyseal ridge, forms the dorsal limitation of the wide depression ventrally limited by a straight subcentral ridge. A large lateral foramen is situated close to the dorsal margin of this depression. The diapophysis is well separated from the parapophysis. The parapophyseal process is short but its anterior termination is slightly eroded. The condyle is separated from the

centrum by a wide groove. The anterior keel of the hypapophysis is only moderately inclined in ventral direction but this inclination is well developed in the middle of the centrum length indicating most probably posteroventral inclination of the distal tip of the hypapophysis. In anterior view (Fig. 55d), the neural arch bears no epizygapophyseal spines. The neural canal is rounded with shallow lateral sinuses. The zygosphenal lip is slightly arched dorsally with straight medial part. The prezygapophyses are horizontal with broken off prezygapophyseal accessory processes. Paracotylar foramina are situated in depressions on either side of the cotyle. The cotyle is rounded with slightly depressed ventral margin. The only complete right subcotylar tubercle occurs at the base of the cotyle. In posterior view (Fig. 55e), the neural arch is strongly vaulted, with a vaulting ratio (sensu Georgalis et al., 2021b) equal to 0.52. A very large parazygantral foramen is situated near the edge of the postzygapophysis.

Remarks. All poorly preserved fragments of trunk vertebrae from *Chalicorrema* possess hypapophyses. The well-developed subcentral grooves and ridges in the best-preserved vertebra indicate that this vertebra did not belong to the anterior trunk region. Although all hypapophyses are broken off close to their base, the anterior keel of the hypapophysis is triangular (UU RA 408, UU RA 409) with small subcotylar tubercles which frequently occurs in *Natricidae* (e.g., Szyndlar & Schleich, 1993; Szyndlar, 1984, 1991b, 2005). The only preserved left prezygapophysis of UU RA 409 is horizontal in anterior view. Although the anterior keel of the hypapophysis is reminiscent of that of *Natrix* aff.

rudabanyaensis described above from Spilia and Vevi (see above), even an assignation of the *Chalicorrema* snakes to *Natricidae* is not safe and it should be eventually confirmed solely by better preserved material.

As for the few specimens from Spilia 0 and Spilia 2, all preserved vertebrae are too fragmentary with broken off hypapophyses, neural spines and paradiapophyses (Fig. 54). The elongated centrum, the presence of hypapophysis with distinct triangular anterior keel, as well as the presence of short epizygapophyseal ridges enable identification of these fragmentary vertebrae as possibly belonging to *Natricidae* (Head, 2005; Ivanov, 2002; Szyndlar, 1984, 1991b). Although an assignation of this material to the genus *Natrix*, already identified in Spilia 0 on the basis of several more complete specimens, seems probable, the absence of important diagnostic structures hinders even an exact family-level identification.

As for the Vevi specimen, this anterior trunk vertebra (UU VE 601) possesses a triangular anterior keel with distinct subcotylar tubercles and almost straight subcentral ridges in lateral view (Fig. 55). The first two features typically occur in large specimens of *Natrix*-like snakes. Thus, we tentatively assign UU VE 601 to ?*Natricidae* indet.

Colubroidea indet.

Figures 56, 57, 58

Material. *Spilia 0*: Two anterior trunk vertebrae (UU SP0 166 and UU SP0 167); *Spilia 4*: an anterior trunk vertebra (UU SP4 507) and one trunk vertebra (UU SP4 618); *Vevi*: a mid-trunk vertebra (UU VE 602).

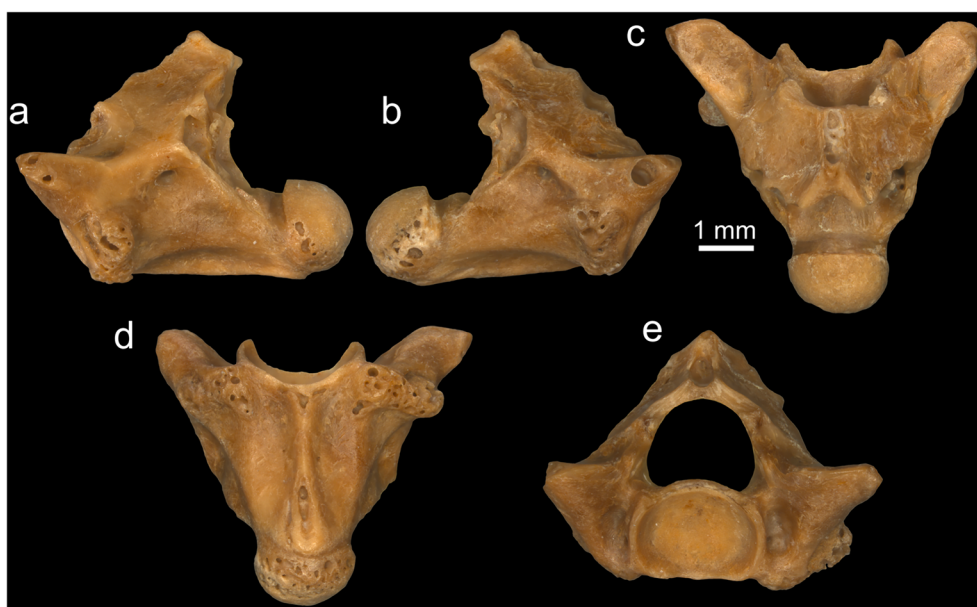


Fig. 56 Colubroidea indet. from Vevi. Mid-trunk vertebra (UU VE 602) in left lateral (a), right lateral (b), dorsal (c), ventral (d), and anterior (e) views

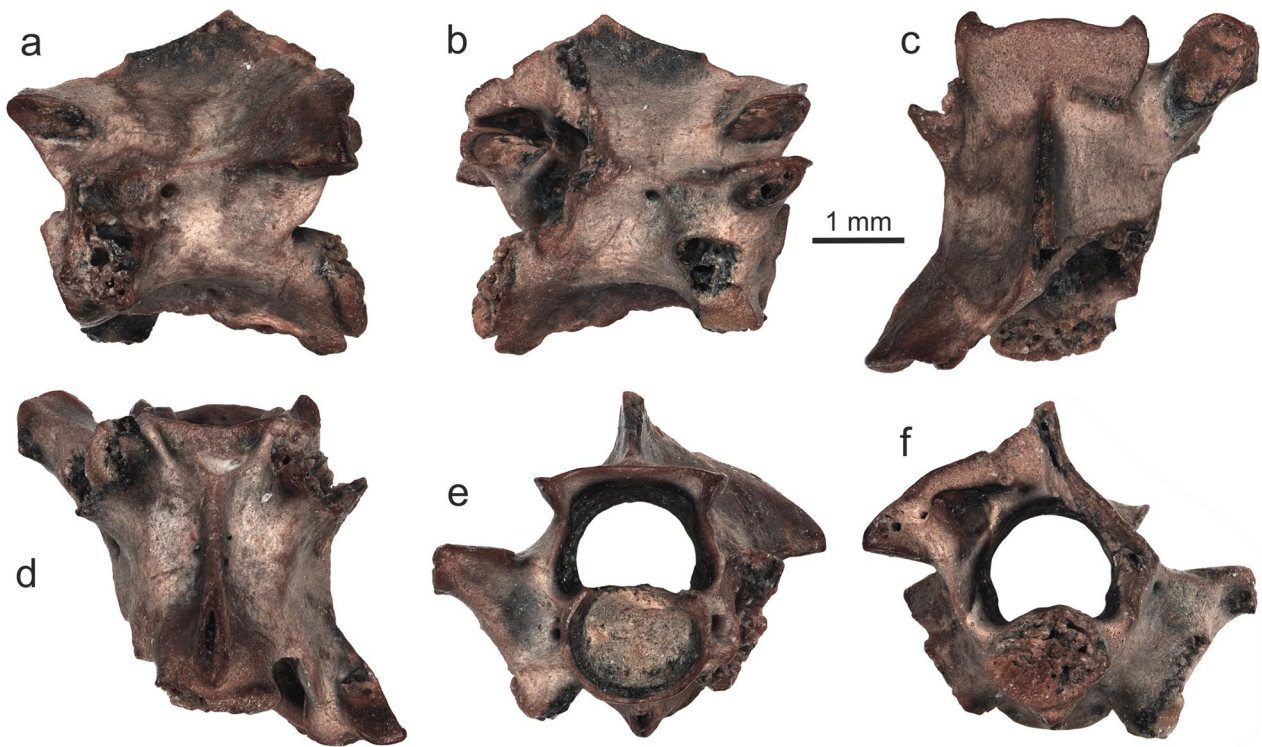


Fig. 57 Colubroidea indet. from Spilia 0. **a–f** Trunk vertebra (UU SP0 166) in left lateral (**a**), right lateral (**b**), dorsal (**c**), ventral (**d**), anterior (**e**), and posterior (**f**) views

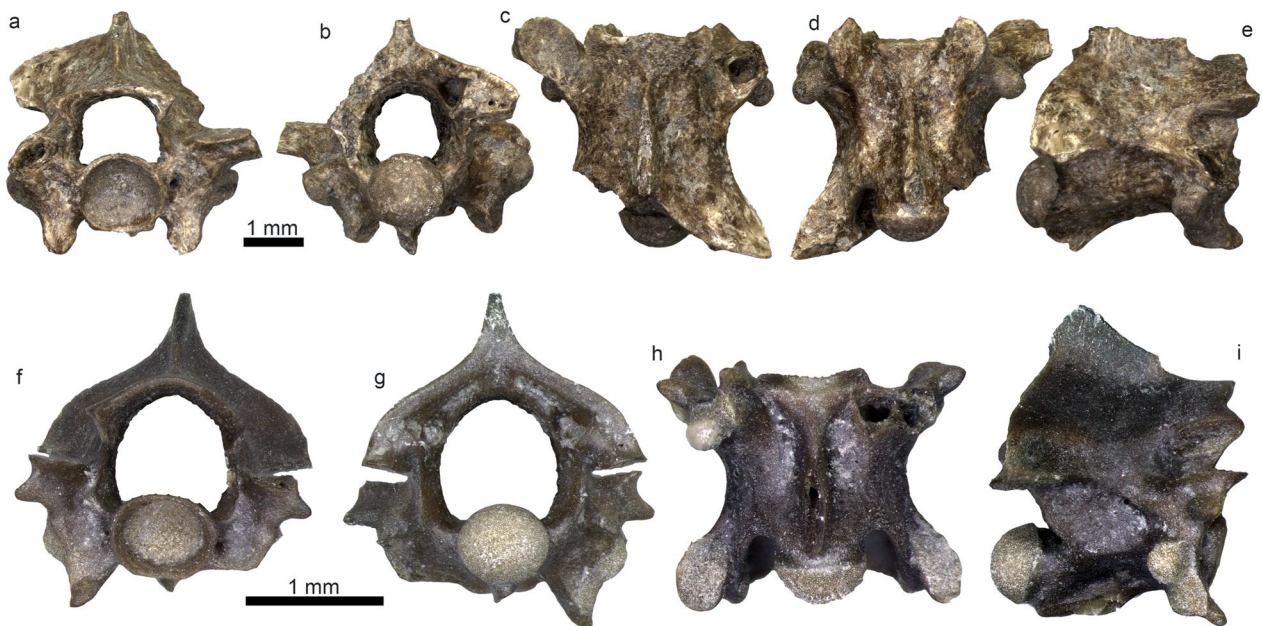


Fig. 58 Colubroidea indet. from Spilia 4. **a–e** Anterior trunk vertebra (UU SP4 507) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and right lateral (**e**) views; **f–i** trunk vertebra (UU SP4 618) in anterior (**f**), posterior (**g**), ventral (**h**), and right lateral (**i**) views

Description.

The mid-trunk vertebra (UU VE 602) from Vevi is a poorly preserved specimen that lacks the posterior part of the neural arch, including the postzygapophyses, as well as most of the neural spine, zygosphene, and paradiapophyses (Fig. 56). In lateral view (Fig. 56a, b), the interzygapophyseal ridges are strongly built. The rather large and dorsally faced lateral foramina are situated within wide and conspicuously deep depressions close below the interzygapophyseal ridges. The damaged parapophysis is well-separated from the diapophysis. Its partially eroded ventral margin reaches slightly below the ventral margin of the anterior keel of the hypapophysis (or haemal keel). The dorsally arched subcentral ridges are blunt and better developed in the anterior half of the centrum. The condyle is developed on a short neck. In dorsal view (Fig. 56c), the better preserved but strongly eroded left prezygapophyseal articular facet, with long axis directed anterolaterally, was probably large and widely oval or subtriangular shaped. The preserved basal portion of the left prezygapophyseal accessory process indicates that the process was most probably rather short reaching no more than one fourth of the length of the prezygapophyseal articular facet. The diapophysis is directed posterolaterally. In ventral view (Fig. 56d), the centrum is widely triangular with shallow subcentral grooves. Subcentral foramina are small situated roughly in the middle of the centrum length at the base of the hypapophysis/haemal keel. The posterior ventral margin of the latter structure is damaged and we cannot unambiguously confirm whether it is a haemal keel or a hypapophysis broken off close to its base. In anterior view (Fig. 56e), the prezygapophyses are horizontal. The neural canal is rounded with wide lateral sinuses. Paracotylar foramina are situated in markedly deep depressions on either side of the dorsoventrally depressed cotyle.

The two trunk vertebrae from Spilia 0 are fragmentary with neural spine and hypapophysis broken off close to their bases, damaged prezygapophyses with unpreserved prezygapophyseal processes, and mostly damaged neural arch (Fig. 57). In lateral view (Fig. 56a, b), the neural spine rises in the middle of the zygosphene length. The zygosphenal facets are oval. The interzygapophyseal ridges are sharp with lateral foramina situated close below them and within wide depressions. There is no distinct “paracentral ridge” (sensu Georgalis et al., 2019a) in the vertebrae. The diapophysis is well separated from the parapophysis. The dorsally arched subcentral ridges are rather blunt and better developed in the anterior half of vertebra. The relatively small condyle is developed on the short neck. In dorsal view (Fig. 57c), the zygosphene bears two distinct lateral lobes and a relatively incipient median one. In ventral view (Fig. 57d), the anterior keel of the hypapophyses

extends anteriorly but does not reach the ventral lip of the cotyle. In anterior view (Fig. 57e), the zygosphene is thin and almost straight, with its width being larger than that of the cotyle. The prezygapophyses are only slightly dorsally inclined. The cotyle is large and slightly elliptical. Prominent and large paracotylar foramina are situated on either side of the cotyle. In posterior view (Fig. 57f), the neural arch has a vaulting ratio (sensu Georgalis et al., 2021b) equal to 0.36.

The two vertebrae from Spilia 4 are also fragmentary (Fig. 58). UU SP4 507 probably represents an anterior trunk vertebra, judging from the presence of a hypapophysis and the relatively short anteroposteriorly centrum (Fig. 58a–e). However, most of the hypapophysis, the neural spine, the right prezygapophysis, and the whole left postzygapophysis are missing. The vertebra has paracotylar foramina (Fig. 58a), large (left) prezygapophyseal articular facet, and a trilobed zygosphene in dorsal view. One of the most characteristic features of this vertebra is the prominent paradiapophyses that are clearly divided into diapophyses and parapophyses, with the former being rather large and the latter being relatively elongated and facing anteroventrally in lateral view. The vaulting ratio (sensu Georgalis et al., 2021b) of this specimen equals to 0.32. The second vertebra from Spilia 4 (UU SP4 618) is considerably smaller and misses its left paradiapophysis and part of its neural spine (Fig. 58f–i). It possesses a thin and distinctly arched zygosphene in anterior view (Fig. 58f) and parapophyseal processes that are distinctly anteroventrally directed in lateral view (Fig. 58i). A striking feature of this small vertebra is its neural arch, which is strongly vaulted (Fig. 58g), with a vaulting ratio (sensu Georgalis et al., 2021b) equal to 0.70. The exact height and shape of the neural spine cannot be fully assessed but it seems that it was originally rather high. The prezygapophyses are almost horizontal to only slightly dorsally inclined in anterior view (Fig. 58f). The prezygapophyseal accessory processes are small and acute (Fig. 58h). It seems that UU SP4 618 pertains to a young individual, judging also from its very small size and the very large neural canal (see e.g., Georgalis & Scheyer, 2019; Szyndlar & Georgalis, 2023).

Remarks. The vertebra (UU VE 602) from Vevi is characterized by a vaulted neural arch, synapophyses well divided into diapophyses and parapophyses, and the presence of paracotylar foramina and prezygapophyseal accessory processes, which all clearly indicate assignment to Colubriiformes (e.g., Rage, 1984; Zaher et al., 2019). The probable absence of hypapophysis in this mid-trunk vertebra (UU VE 602) readily excludes Natricidae, Elapidae, and Viperidae (Szyndlar, 1991a, 1991b). Within the remaining colubriiforms that do not possess hypapophyses in their mid- and posterior trunk

vertebrae, psammophiid affinities seem to be unlikely, as the Vevi specimen possesses a relatively wide centrum (and not so elongated) (see Georgalis & Szyndlar, 2022). As such, it is most likely that this Vevi specimen pertains to Colubridae or (less likely) to Dipsadidae. The vertebra is indeed reminiscent of Colubridae. However, the combination of likely very short prezygapophyseal accessory processes in mid-trunk vertebrae and markedly large lateral foramina faced dorsally and situated in markedly deep depressions under the thick interzygapophyseal ridges are unusual in known extant Colubridae. The vertebra shares diameter and position of lateral foramina as well as the presence of the deep groove at the condylar base with *Paraxenophis spanios*, reported from the slightly older locality of Maramena, Greece (Georgalis et al., 2019b) and (tentatively) also from Spilia (see below). However, the haemal keel in the Vevi vertebra does not possess the lateral notches that are the most striking character of *Paraxenophis spanios*, whereas the prezygapophyseal accessory processes are short in the Vevi snake unlike in the latter taxon.

The vertebrae from Spilia 0 and Spilia 4 are much incomplete (Figs. 57, 58). Their elongated centrum, the presence of paracotylar foramina, the vaulted neural arch, the well developed prezygapophyseal accessory processes, the most probably short parapophyses, and the presence of a hypapophysis indicate that they belong to Colubroidea (e.g., Zaher et al., 2019). Although the hypapophyses, potentially distributed throughout the precloacal region, are reminiscent of Natricidae, the absence of epizygapophyseal spines, reported in small fossil natricids, as well as their insufficient preservation preclude any identification at the family level. Of special note is the small trunk vertebra UU SP4 618 from Spilia 4 (Fig. 58f–i), which with its strongly vaulted neural arch, the almost horizontal prezygapophyses, and the rather high neural spine, is indicative of affinities with Colubroidea. On the other hand, the strongly anteroventrally directed parapophyses of this specimen are somehow reminiscent of

viperids, but other features, especially its strongly vaulted neural arch, reject such referral.

Accordingly, we refer all these vertebrae from Vevi, Spilia 0, and Spilia 4, as Colubroidea indet.

Elapoidea Boié, 1827

Elapidae Boié, 1827

Elapidae gen. et sp. indet. (small form)

Figure 59

Material. *Spilia 4*: one trunk vertebra (UU SP4 537).

Description.

The vertebra (UU SP4 537) is small and incomplete, missing most of the right prezygapophysis and postzygapophysis and parts of the neural spine, the zygosphenes, and the left prezygapophyseal accessory process (Fig. 59). In anterior view (Fig. 59a), the zygosphenes are thin and moderately arched. The neural canal is large. The prezygapophyses are only slightly dorsally inclined. The cotyle is large; its precise outline cannot be assessed as it is damaged. A paracotylar foramen is visible next to the right side of the cotyle. In posterior view (Fig. 59b), the neural arch is depressed, with a vaulting ratio (sensu Georgalis et al., 2021b) equal to 0.25. The condyle is elliptical and slightly laterally compressed. In lateral view (Fig. 59c), the neural spine commences to rise in height slightly posterior to the zygosphenal facets. The neural spine is not well preserved and its original height cannot be precisely assessed; nevertheless, the thin base of the neural spine in dorsal view indicates that the neural spine was originally most probably very low in lateral view. The zygosphenal facets are narrowly elliptical. A large and deep lateral foramen is situated below the relatively straight interzygapophyseal ridge. The subcentral ridges are convex. The hypapophysis runs below most of the centrum but its height (slightly) augments only towards its posterior termination; its distal tip extends to the condylar base. Even at this maximum height, the hypapophysis is still rather short, still projecting more posteriorly than ventrally. In dorsal view (Fig. 59d), the neural spine is thin and runs throughout about 3/4 of the midline of the neural arch. The (sole

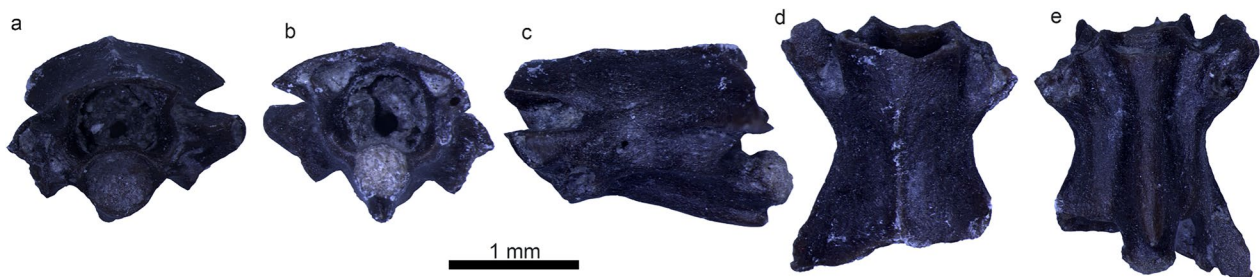


Fig. 59 Elapidae gen. et sp. indet. (small form) from Spilia 4. Trunk vertebra (UU SP4 537) in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views

preserved) left prezygapophysis is projecting anterolaterally. The interzygapophyseal constriction is deep. The posterior median notch of the neural arch is relatively deep. In ventral view (Fig. 59e), the centrum is elongated. The subcentral grooves are deep. The hypapophysis is thin, commencing anteriorly right below the ventral level of the cotyle and terminating posteriorly at the level of the condyle. The postzygapophyses extend posterolaterally. The postzygapophyseal articular facets are oval and elongated. A precondylar constriction is present, with the condyle developed at a distinct condylar neck.

Remarks. The trunk vertebra (UU SP4 537) can be attributed to a small-sized elapid (coral snakes) on the basis of its relatively small dimensions (centrum length), its elongated vertebral centrum, and the dorsoventrally short hypapophysis that is directed more posteriorly than ventrally (Ivanov, 2002; Zaher et al., 2019). It appears that there are some differences between the *Spilia* coral snake and *Micrurus* Wagler, 1824, which is also known from the Neogene of Europe (see Discussion below), as the latter is characterized by a longer hypapophysis and a low but well developed neural spine, compared to the Greek form (see figures in Camolez & Zaher, 2010; Escobar et al., 2024; Ivanov & Böhme, 2011; Onary et al., 2018; Rage & Holman, 1984; Zaher et al., 2019). In fact, the *Spilia* specimen appears to be overall similar to the small indeterminate Elapidae that has been described from Merkur-North, Czechia (Ivanov, 2002).

Viperoidea Opperl, 1811b

Viperidae Opperl, 1811b

Viperinae Opperl, 1811b

Viperinae (“Oriental Vipers”) indet.

Figure 60

Material. *Spilia* 3: one fang (UU SP3 601), two trunk vertebrae (UU SP3 674 and UU SP3 675), and six fragments of trunk vertebrae (UU SP3 676).

Description.

The isolated fang (UU SP3 601) from *Spilia* 3 is relatively complete (Fig. 60a–e). The specimen is relatively large. The apical termination is slightly curved, with a wide pulpal cavity and the venom canal situated anteriorly in central position. In dorsal view (Fig. 59e), the base of the entrance orifice, which is situated in the anteriormost proximal part of the element, is indicated by the separation of the dentine folds which form the anterior closure of the venom canal. In anterior view (Fig. 60c, d), there is a distinct suture close to the distal termination of the element. 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 preserved. A wide groove occurs on both lateral sides of the fang along its entire length.

The few available vertebrae from *Spilia* 3 are rather fragmentary, missing in fact, most parts of the vertebral body (Fig. 60f, g). Despite their fragmentary nature, they are characterized by a large overall size, massive cotyle and condyle, and the presence of hypapophysis.

Remarks. The fang can be referred to Viperidae based on the presence of a closed venom canal (Edmund, 1969; Kardong, 1979; Zahradnick et al., 2008). The large size of the fang suggests a probable referral to the “Oriental Vipers” complex. In fact, the fang looks very similar with the fang of “Oriental vipers” described by Georgalis et al. (2019b, fig. 38.6–10) from the nearby (and slightly older; MN 13/14) locality of Maramena. The fragmentary vertebrae can be referred to Viperidae based on their massive nature, the relatively short centrum, the presence of hypapophysis, and the dorsal inclination of the prezygapophyses in anterior view (Georgalis et al., 2016a; Szyndlar, 1984, 1991b; Zaher et al., 2019). Unfortunately, important viperid features, such as the anteroventral inclination of the parapophyses, the shape and inclination of the hypapophysis, the height of the neural spine, and the strongly depressed neural arch, are not preserved in the available vertebrae from *Spilia*, precluding thus a more precise identification. Nevertheless, as in the case of the fang above, the large size of the vertebrae suggests a probable referral to the “Oriental Vipers” complex.

Colubriformes incertae sedis

***Periergophis* Georgalis, Villa, Ivanov, Vasilyan & Delfino, 2019b**

***Periergophis micros* Georgalis, Villa, Ivanov, Vasilyan & Delfino, 2019b**

Figures 61, 62

Material. *Spilia* 1: one posterior mid- or posterior trunk vertebra (UU SP1 1011); *Spilia* 4: one anterior trunk vertebra (UU SP4 550), three trunk vertebrae (UU SP4 539, UU SP4 619, and UU SP4 623), and eight caudal vertebrae (UU SP4 542–UU SP4 545, UU SP4 547, UU SP4 548, UU SP4 620, and UU SP4 658).

Description.

A few trunk vertebrae were available in our sample from *Spilia* 1 and *Spilia* 4 (Fig. 61). UU SP4 550 is an anterior trunk vertebra, judging from the presence of a hypapophysis (Fig. 61a–c). The specimen has small dimensions, blunt subcentral ridges, and the anterior margin of the neural spine is inclined posteriorly. The zygosphenes in this specimen is distinctly trilobed and the posterior median notch of the neural arch is rather deep. The hypapophysis is not fully preserved, but it seems that it was somehow posteroventrally inclined in lateral view; in ventral view, this structure crosses the whole midline of the ventral surface of the centrum.



Fig. 60 Viperinae ("Oriental Vipers") indet. from Spilia 3. **a–e** Fang (UU SP3 601) in left lateral (**a**), right lateral (**b**), anterior (**c**), anterodorsal (**d**), and posterodorsal (**e**) views; **f** trunk vertebra (UU SP3 674) in ventral view; **g** trunk vertebra (UU SP3 675) in anterior view

The remaining trunk vertebrae from Spilia 4 (UU SP4 539, UU SP4 619, and UU SP4 623) and the single vertebra from Spilia 1 (UU SP1 1011) are all posterior mid- or posterior trunk vertebrae, judging from the wide haemal keel and the deep subcentral grooves (Fig. 61d–m). However, they all lack the characteristic haemal keel tubercles

that are known for the posterior trunk vertebrae of this species from the type locality of Maramena. In these small vertebrae, the haemal keel is considerably wide, running throughout the midline of the centrum. The haemal keel possesses a distinctive constriction, situated posteriorly from the level of the synapophyses; the degree



Fig. 61 *Periergophis micros* from Spilia 1 (SP1) and Spilia 4 (SP4), trunk vertebrae. **a–c** Anterior trunk vertebra (UU SP4 550) in left lateral (**a**), dorsal (**b**), and ventral (**c**) views; **d, e** mid-trunk vertebra (UU SP1 1011) in ventral (**d**) and right lateral (**e**) views; **f–i** posterior mid- or posterior trunk vertebra (UU SP4 539) in anterior (**f**), posterior (**g**), dorsal (**h**), and ventral (**i**) views; **j, k** posterior mid- or posterior trunk vertebra (UU SP4 619) in right lateral (**j**) and ventral (**k**) views; **l, m** posterior mid- or posterior trunk vertebra (UU SP4 623) in right lateral (**l**) and ventral (**m**) views

of this constriction varies, being apparently dependent on the vertebral position on the column, and is particularly prominent in UU SP4 619 (Fig. 61k). The neural spine is dorsoventrally short; when fully preserved, its anterior margin is straight to posteriorly inclined. The neural arch is much depressed, with a vaulting ratio sensu Georgalis et al. (2021b) ranging between 0.22 and 0.28. The zygosphene is trilobed, with the two lateral lobes being considerably prominent. The prezygapophyseal accessory processes are relatively long and acute. The synapophyses are clearly separated into diapophysis and parapophysis. Cotyles and condyles are small and almost circular.

All available caudal vertebrae from Spilia 4 are incomplete, with their haemapophyses being mostly damaged (Fig. 62). Because of this incompleteness, in most specimens it is not possible to assess whether or not the, presumably autapomorphic, haemapophyseal tubercles were indeed present in these vertebrae, as in the case of most caudal vertebrae from the type locality of Maramena. The only two caudal vertebrae that do possess more or less complete haemapophyses (Fig. 62h, n) do not show any evidence of haemapophyseal tubercles, but as it was already suggested by Georgalis et al. (2019b), this presence/absence across the column might be subjected to



Fig. 62 *Periergophis micros* from Spilia 4, caudal vertebrae. **a–e** Caudal vertebra (UU SP4 542) in anterior (**a**), posterior (**b**), left lateral (**c**), dorsal (**d**), and ventral (**e**) views; **f–i** caudal vertebra (UU SP4 543) in dorsal (**f**), ventral (**g**), right lateral (**h**), and anterior (**i**) views; **j–l** caudal vertebra (UU SP4 620) in anterior (**j**), right lateral (**k**), and ventral (**l**) views; **m** caudal vertebra (UU SP4 547) in right lateral view; **n** caudal vertebra (UU SP4 548) in right lateral view; **o, p** caudal vertebra (UU SP4 545) in dorsal (**o**) and ventral (**p**) views; **q, r** caudal vertebra (UU SP4 544) in dorsal (**q**) and right lateral (**r**) views

intracolumnar variation. The caudal vertebrae possess large subcentral foramina and unusual “lateral wings”, situated close to the base of the broken off pleurapophyses. These distinctive “lateral wings” are actually present in all available caudal vertebrae. The pleurapophyses are elongated, pointed, and face anteroventrally. The neural spine is dorsoventrally rather short; its posterior margin is either almost vertical or inclined anteriorly (Fig. 62h, k, m, n, r). Large lateral foramina are present below the interzygapophyseal ridges. Cotyles and condyles are small and almost circular. Paracotylar foramina are present. The more elongated vertebra UU SP4 543 represents a more posterior caudal vertebra than the other specimens (Fig. 62f–i).

Remarks. The material from Spilia 1 and Spilia 4 resembles *Periergophis micros*, otherwise known from the nearby Maramena, in regards to the following features: trunk vertebrae with anterior margin of the neural spine being posteriorly inclined, rather wide haemal keel with a constriction present posteriorly to the synapophyses, zygosphene with distinct lateral lobes, a depressed neural arch, large parapophyses, and a small size with an overall light structure (see Georgalis et al., 2019b). However, the most prominent diagnostic feature (the presumed autapomorphy) of this species is not evident in the Spilia sample: the distinct paired anteroventrally directed tubercles or short processes developed on the wide haemal keel of posterior mid- and posterior trunk vertebrae and the haemapophyseal tubercles separated from the remaining part of haemapophyses in caudal vertebrae, at least in a portion of the caudal series (Georgalis et al., 2019b). We here interpret this absence of this feature as:

- i) *intracolumnar variation*: the few available Spilia trunk vertebrae pertain to a part of the posterior mid- or anterior posterior trunk portion of the vertebral column that was genuinely not characterized by the presence of haemal keel tubercles. Similarly, the available caudal vertebrae from Spilia originate from a portion of the caudal vertebral column that was genuinely not characterized by the presence of haemapophyseal tubercles. As also suggested by Georgalis et al. (2019b, p. 45), “an alternative explanation would be that in some portion of the caudal series, the haemapophyseal tubercles are substituted by strongly ventrally exposed anterior thickenings of the haemapophyses”.
- ii) *chronospecific variation*: Spilia is younger than Maramena and eventually this structure disappeared from this lineage. In this case, perhaps the Spilia sample would pertain to a different species within the genus *Periergophis*.

- iii) *taphonomy*: these structures were originally present in (certain of) the Spilia specimens but have been eroded/faded out due to preservational/taphonomical issues.

Worth mentioning is that in our sample there are more available caudal vertebrae compared to trunk ones; Smith (2013) had proposed that in fossil localities, such high percentages of caudal versus trunk vertebrae could be indicative of snakes with long tails. However, based on such limited sample from Spilia, it is premature to assume anything about the tail proportions of the Spilia *Periergophis*. Moreover, the original material of *Periergophis micros* from the type locality of Maramena consisted of much more trunk vertebrae compared to caudal ones.

***Paraxenophis* Georgalis, Villa, Ivanov, Vasilyan & Delfino, 2019b**

***Paraxenophis spanios* Georgalis, Villa, Ivanov, Vasilyan & Delfino, 2019b**

?*Paraxenophis spanios*

Figure 63

Material. *Spilia 1*: three trunk vertebrae (UU SP1 1003, UU SP1 1009, and UU SP1 1010); *Spilia 4*: two anterior trunk vertebrae (UU SP4 562 and UU SP4 567).

Description.

Two anterior trunk vertebrae (UU SP4 562 and UU SP4 567) are present in the material from Spilia 4 (Fig. 63a–d). Both are characterized by the presence of hypapophysis instead of haemal keel and a more vaulted neural arch. Both anterior trunk vertebrae have their hypapophyses rather damaged and therefore the shape and size of this structure cannot be properly assessed. In UU SP4 567, there are distinct lateral notches running almost parallel to each side of the base of the hypapophysis (Fig. 63d). No mid-trunk vertebrae are known from Spilia and all the remaining vertebrae pertain to the posterior mid- and posterior trunk region of the column (Fig. 63e–k). All are characterized by a considerably wide and flattened haemal keel; it runs across most of the midline of the centrum, commencing at the level of the ventral lip of the cotyle and terminating well anterior to the level of the condyle. There are no signs of lateral notches of the haemal keel (a feature that is relatively prominent and diagnostic for the species in the material from Maramena; Georgalis et al., 2019b). The zygosphene is rather thin and wider than the cotyle in anterior view, whereas in dorsal view, it possesses two distinct lateral lobes, or in some specimens also an incipient median lobe (Fig. 63h). The prezygapophyses extend anterolaterally in dorsal view. The neural spine is incomplete in all specimens; its base runs much of the midline of the neural arch but commences well beyond the level of the zygosphene. The neural arch in these posterior mid- and

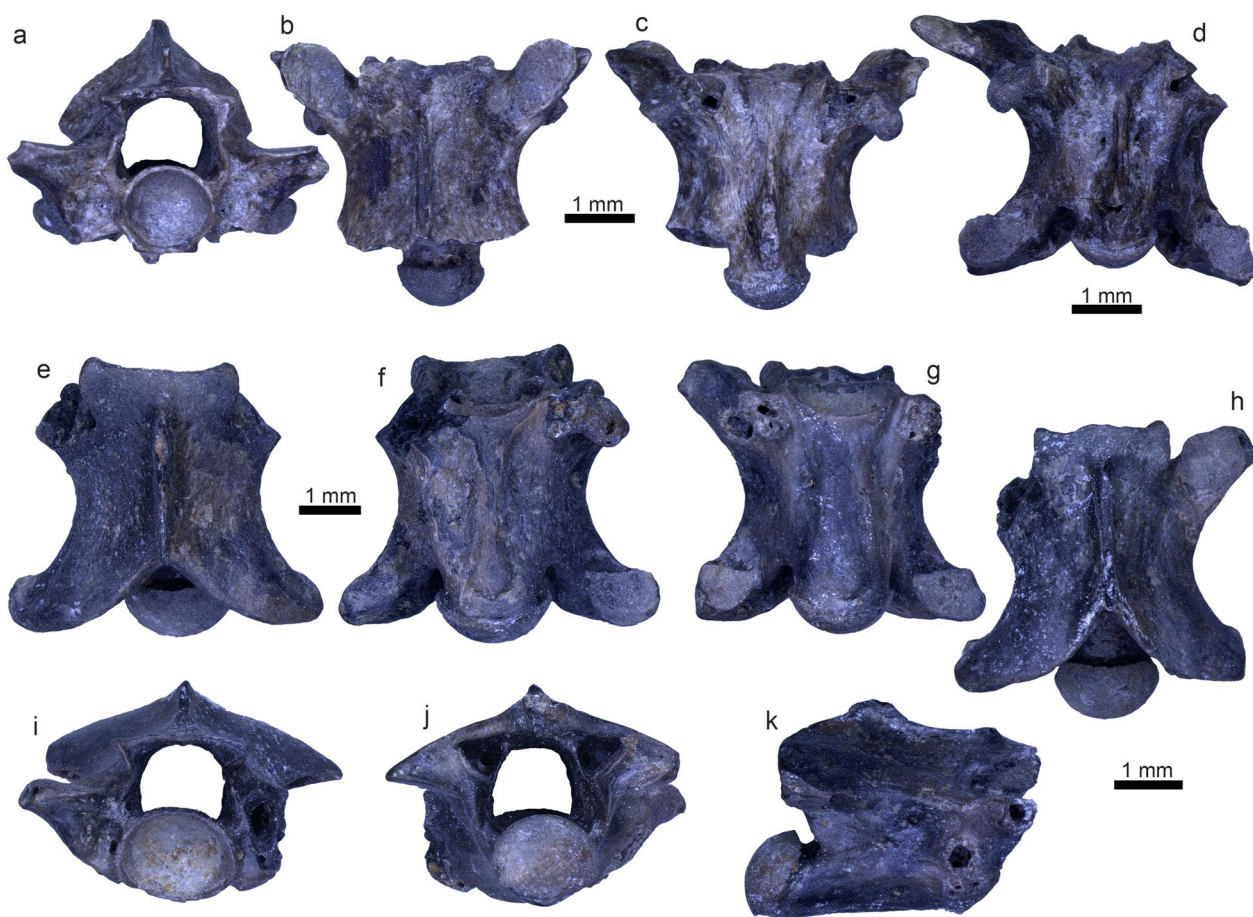


Fig. 63 *?Paraxenophis spanios* from Spilia 1 (SP1) and Spilia 4 (SP4). **a–c** anterior trunk vertebra (UU SP4 562) in anterior (**a**), dorsal (**b**), and ventral (**c**) views; **d** anterior trunk vertebra (UU SP4 567) in ventral view; **e, f** posterior mid-trunk vertebra (UU SP1 1010) in dorsal (**e**) and ventral (**f**) views; **g–k** posterior trunk vertebra (UU SP1 1003) in ventral (**g**), dorsal (**h**), anterior (**i**), posterior (**j**), and right lateral (**k**) views

posterior trunk vertebrae is depressed, reaching a vaulting ratio (sensu Georgalis et al., 2021b) as low as 0.3 in posterior trunk vertebrae. Cotyles and condyles are relatively large and slightly elliptical. Paracotylar foramina are present and can be occasionally considerably large (Fig. 63i). Lateral foramina are present. The posterior median notch of the neural arch is deep. The subcentral grooves are deep. Subcentral foramina are present.

Remarks. The material from Spilia 1 and Spilia 4 resembles *Paraxenophis spanios*, otherwise known from the nearby and slightly older locality of Maramena in: the wide haemal keel of posterior mid- and posterior trunk vertebrae, the blunt subcentral ridges, and the presence of large paracotylar foramina (Georgalis et al., 2019b). Moreover, the lateral notches of the hypapophysis observed in the anterior trunk vertebra UU SP4 567 match the pattern of the lateral notches of the haemal keel that is observed in mid- and posterior trunk vertebrae of this species in Maramena (Georgalis et al., 2019b). Nevertheless, it should be pointed out that six vertebrae from Maramena that were

described by Georgalis et. al. (2019b) as *?Paraxenophis spanios*, had much resemblance with that species but also did not possess the characteristic lateral notches of the haemal keel; these authors had interpreted such absence as either some ontogenetic variation (the six vertebrae without lateral notches of the haemal keel were relatively small and could eventually pertain to some subadult individual) or either that these vertebrae without lateral notches of the haemal keel simply represented some distinct taxon, other than *Paraxenophis spanios* (Georgalis et al., 2019b). With such a limited sample from Spilia, it is further difficult to speculate whether this absence in the new specimens is also indicative of some ontogenetic variation (the Spilia specimens are also relatively small) or represent some other taxon. For these reasons, we only questionably refer the Spilia material to *Paraxenophis spanios*.

Colubriformes “morphotype 1”

Figure 64

Material. *Vevi*: One mid-trunk vertebra (UU VE 629).

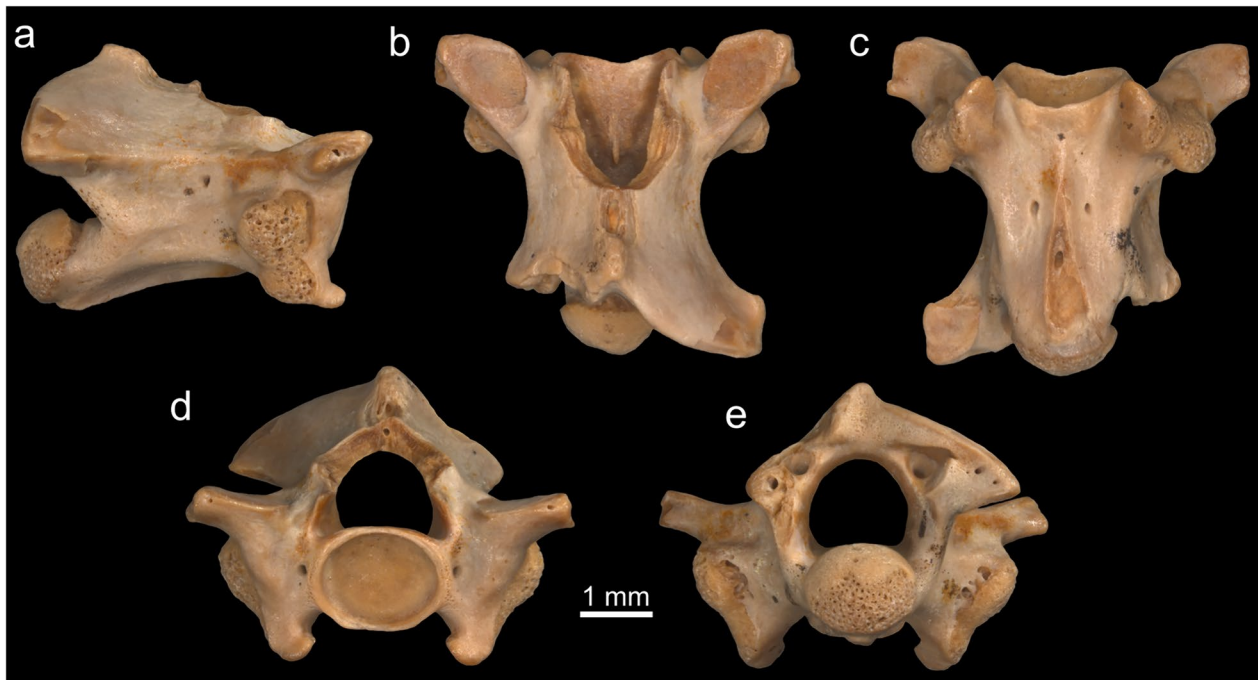


Fig. 64 Colubriformes "morphotype 1" from Vevi. Mid-trunk vertebra (UU VE 629) in right lateral (a), dorsal (b), ventral (c), anterior (d), and posterior (e) views

Description.

This mid-trunk vertebra (UU VE 629) from Vevi is fragmentary, with broken off zygosphene, neural spine, prezygapophyseal processes, and the left postzygapophysis (Fig. 64). In lateral view (Fig. 64a), the interzygapophyseal ridges are sharp. The right lateral foramen is doubled and placed below the interzygapophyseal ridge. The preserved base of the prezygapophyseal accessory process is flat and posteroventrally inclined. The large diapophysis is of subtriangular outline and is about twice as large as the parapophysis. The parapophyseal process is thin and short, directed anteriorly rather than anteroventrally. The subcentral ridges are vaulted dorsally. In dorsal view (Fig. 64b), the long axis of the oval or rhomboid prezygapophyseal articular facets is directed anterolaterally. The diapophysis is situated on an unusually wide base forming a lamina between the diapophyseal facet and the centrum. The diapophyseal facet itself is directed posterolaterally. The posterior median notch of the neural arch reaches about one fourth of the vertebra length. In ventral view (Fig. 64c), the centrum is elongated anteroposteriorly. The subcentral ridges are roughly straight. The subcentral grooves are wide, with large subcentral foramina. The anterior keel of the hypapophysis is thin and diminishes close to the base of the cotylar rim. The small right postzygapophyseal articular facet is triangular in outline. In anterior view (Fig. 64d), the rounded neural canal has developed lateral sinuses with wide bases. The

prezygapophyses are tilted upwards. The small parapophyseal processes are inclined medially. Large paracotylar foramina are situated in shallow depressions on either side of the dorsoventrally depressed cotyle. In posterior view (Fig. 64e), the neural arch is moderately vaulted, with a vaulting ratio (sensu Georgalis et al., 2021b) equal to 0.32. The zygantral area is strongly built. There are two distinct parazygantral foramina and one small foramen on the posterior margin of the right postzygapophysis. The condyle is depressed dorsoventrally.

Remarks. The elongated centrum indicates that this hypapophysis-bearing vertebra from Vevi originates from the mid-trunk region of the vertebral column. The presence of hypapophysis in mid-trunk vertebrae is indicative of several snake lineages including Viperidae, the vast majority of Elapoidea, and among Colubroidea all Natricidae and several taxa of Dipsadidae (e.g., Szyndlar, 1984, 1991b; Szyndlar & Schleich, 1993; Zaher et al., 2019). Although prezygapophyses are tilted up dorsally and the diapophyses are developed on a wide base as in Viperidae, e.g., *Vipera berus* (Linnaeus, 1758) (e.g., specimen ISEZ R/22; see Szyndlar, 1984), the vertebra still differs from Viperidae by the vaulted neural arch, parapophyseal processes directed anteriorly rather than anteroventrally and in the thin anterior keel of the hypapophysis unlike wide and strongly built anterior keel of the hypapophysis extending as far as the cotylar rim in Viperidae. The Vevi vertebrae further differs from

small representatives of Elapidae (*Micrurus* and *Sinomicrurus* Slowinski et al., 2001; see Camolez & Zaher, 2010; Ivanov, 2002; Rage & Holman, 1984; Szyndlar & Schleich, 1993; Zaher et al., 2019) by the upswept prezygapophyses and diapophyses much larger than the parapophyses. We presuppose that the vertebra most likely belongs to a natricid-like Colubroidea despite the fact that the presence of epizygapophyseal spines, indicative of numerous Natricidae (e.g., Head, 2005; Ivanov, 2002; Szyndlar, 1984; Zaher et al., 2019), could not be verified in the damaged specimen. However, the vertebra, which we consider a distinct morphotype, differs from other Colubriformes by the unique combination of features: 1, the presence of hypapophysis in mid-trunk vertebrae; 2, the moderately vaulted neural arch; 3, the parapophyses upswept dorsally; 4, the diapophyses much larger than parapophyses; and 5, the diapophyseal facets situated on the markedly wide bases. However, the absence of several important structures such as the neural spine, zygosphene and hypapophysis as well as scarcity of the material precludes any more precise determination.

Colubriformes “morphotype 2”

Figure 65

Material. *Vevi*: two pathologically fused anterior trunk vertebrae (UU VE 630), four mid-trunk vertebrae (UU VE 631–UU VE 634), and three caudal vertebrae (UU VE 635–UU VE 637).

Description.

Only a few trunk vertebrae are available from *Vevi* (Fig. 65a–e). The two pathologically fused anterior trunk vertebrae (UU VE 630) are damaged with broken off neural spine, distal tip of hypapophysis and damaged paradiapophyses (Fig. 65a–e). The anterior half of the anteriorly placed vertebra is completely missing. In lateral view (Fig. 65a, b), the base of the neural spine rises close behind the posterior margin of the zygosphene. The interzygapophyseal ridges are short and sharp. The lateral foramina are situated in shallow depression close below the interzygapophyseal ridges. There is an indistinct “paracentral ridge” (sensu Georgalis et al., 2019a) developed above the blunt and dorsally arched subcentral ridge on either side of both vertebrae. Both vertebrae indicate a distinct sign of

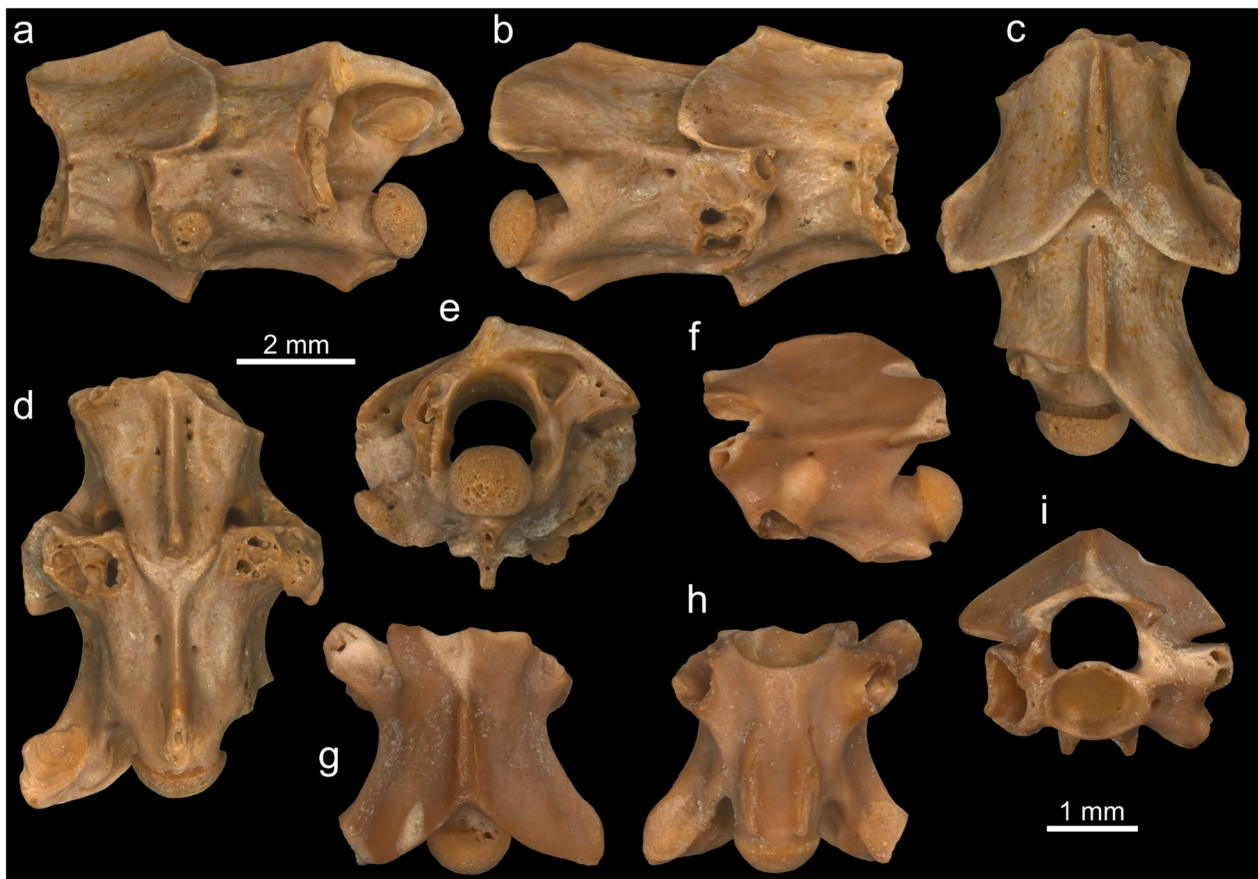


Fig. 65 Colubriformes “morphotype 2” from *Vevi*. **a–e** Two fused anterior trunk vertebrae (UU VE 630) in left lateral (**a**), right lateral (**b**), dorsal (**c**), ventral (**d**), and posterior (**e**) views; **f–i** anterior caudal vertebra (UU VE 635) in left lateral (**f**), dorsal (**g**), ventral (**h**), and anterior (**i**) views

a pathological development in the zygosphene-zygantral articulation with prezygapophyses and postzygapophyses completely fused in the two successive vertebrae. In dorsal view (Fig. 65c), the visible posterior margin of the zygosphene is wide in the posteriorly placed vertebra and the posterior median notch of the neural arch is deep, reaching about one third of the vertebral length. The condylar base is separated from the centrum by a distinct groove. In ventral view (Fig. 65d), the roughly parallel subcentral ridges are wide and better developed in the anterior half of the vertebra. The subcentral grooves are narrow with large subcentral foramina situated in the middle of the centrum length. The hypapophysis is narrow along its entire length reaching the pathologically developed condylar-cotylar connection. The distal tip of the hypapophysis was directed posteriorly. The only preserved left diapophysis is directed posterolaterally and it is well divided from the strongly damaged parapophysis. The right postzygapophyseal articular facet is subtriangular in outline. In posterior view (Fig. 65e), the neural arch is moderately vaulted, with a vaulting ratio (sensu Georgalis et al., 2021b) equal to 0.33. The zygantrum is wide; there are two parazygantral foramina in the caudal margin of the only preserved right postzygapophysis of the posteriorly placed vertebra. The remaining trunk vertebrae from Vevi pertain to the mid-trunk region, however, they are rather incomplete.

The best-preserved caudal vertebra is the anterior caudal vertebra (UU VE 635), which is still fragmentary with broken off neural spine, pleurapophyses, and haemapophyses, completely missing right and damaged left prezygapophyses (Fig. 65f–i). In lateral view (Fig. 65f), the neural spine rises at the level of the posterior margin of the oval zygosphenal facet. The interzygapophyseal ridges are sharp and the lateral foramina are situated close below them. The bases of haemapophyses indicate their likely posteroventral direction but the distal tips of both haemapophyses are unpreserved. In dorsal view (Fig. 65g), the prezygapophyseal articular facets are large and oval-shaped. The interzygapophyseal constriction is deep, as well as deep is the posterior median notch of the neural arch. In ventral view (Fig. 65h), the postzygapophyseal articular facets are large and elongated. In anterior view (Fig. 65i), the neural arch is vaulted. The zygosphene is arched dorsally. The neural canal is rounded with wide lateral sinuses. The cotyle is depressed dorsoventrally. Paracotylar foramina are present.

Remarks. Although the pathological development of the zygosphene-zygantrum connection precludes a detailed morphological evaluation of these anatomical structures, the anterior trunk vertebrae share the following combination of characters with non-hypapophyses bearing Colubriformes: 1, gracile structure; 2, vaulted neural arch; 3, absence of epizygapophyseal spines; 4, parapophyses well-divided from diapophyses; 5, the presence of

likely originally well developed (now broken off close to their base) prezygapophyseal accessory processes. The centrum is relatively short and wide, with blunt subcentral ridges, which indicates an anterior position within the trunk section of the vertebral column. The narrow subcentral grooves and the presence of moderately developed “paracentral ridges” (sensu Georgalis et al., 2019a) are reminiscent of the poorly preserved trunk vertebrae of “Colubridae” indet. from the Greek Early Miocene (MN 4) locality of Karydia 2 (see Georgalis et al., 2019a, fig. 9). Although the vertebrae most likely pertain to Colubridae (based on the widely triangular centrum with distinct blunt subcentral ridges, thin hypapophysis without distinct triangular anterior keel extending as far as the cotylar rim), we avoid a family-level identification, as the presence of haemal keel in mid-trunk vertebrae cannot be verified. The anterior caudal vertebra with lateral foramina situated close below the sharp interzygapophyseal ridges, the neural spine rising roughly at the level of the posterior margin of zygosphenal facets, and the wide zygosphene in dorsal view, indicate a possible assignment also of this specimen to the same taxon as the above-mentioned anterior trunk vertebrae. The material is different than the Colubriformes “morphotype 1”, also from Vevi, therefore it is assigned here as Colubriformes “morphotype 2”.

Colubriformes indet.

Figures 66, 67

Material. *Chalicorrema*: three trunk vertebrae (UU RA 411–UU RA 413); *Spilia 1*: seven trunk vertebrae (UU SP1 1004–UU SP1 1008, UU SP1 1013, and UU SP1 1016), three fragments of trunk vertebrae (UU SP1 1014), and one caudal vertebra (UU SP1 1015); *Spilia 3*: three trunk vertebrae (UU SP3 612, UU SP3 613, and UU SP3 617) and one caudal vertebra (UU SP3 611); *Spilia 4*: one fang (UU SP4 660), 13 trunk vertebrae (UU SP4 534–UU SP4 536, UU SP4 538, UU SP4 540, UU SP4 541, UU SP4 552–UU SP4 554, UU SP4 557, UU SP4 559, UU SP4 560, UU SP4 561, and UU SP4 629), one cloacal vertebra (UU SP4 622), and nine caudal vertebrae (UU SP4 508, UU SP4 546, UU SP4 549, UU SP4 551, UU SP4 555, UU SP4 556, UU SP4 558, UU SP4 563, and UU SP4 564); *Vevi*: three trunk vertebrae (UU VE 638–UU VE 640).

Description and remarks.

The isolated fang (UU SP4 660) is incomplete, missing its distal termination (Fig. 66a–c). It is rather curved and possesses a wide pulpal cavity. In anterior view, a narrow groove is present in the dorsal surface of the fang (Fig. 66a). There are no grooves on the lateral side of the fang (Fig. 66b). The specimen resembles elapoid fangs that possess such kind of a groove on their anterior side but not on their lateral ones, however, it could also be the case that it pertains to some juvenile or subadult viperid (Bogert,



Fig. 66 Colubriformes indet. from Spilia. **a–c** Fang (UU SP4 660) in anterior (**a**), left lateral (**b**), and posterodorsal (**c**) views; **d, e** trunk vertebra (UU SP1 1006) in anterior (**d**) and ventral (**e**) views; **f** trunk vertebra (UU SP1 1007) in ventral view; **g** trunk vertebra (UU SP3 613) in ventral view; **h–k** trunk vertebra (UU SP3 612) in anterior (**h**), posterior (**i**), left lateral (**j**), and ventral (**k**) views; **l–p** trunk vertebra (UU SP4 534) in anterior (**l**), posterior (**m**), right lateral (**n**), dorsal (**o**), and ventral (**p**) views; **q–u** trunk vertebra (UU SP4 536) in anterior (**q**), posterior (**r**), left lateral (**s**), dorsal (**t**), and ventral (**u**) views; **v–y** trunk vertebra (UU SP4 538) in anterior (**v**), right lateral (**w**), dorsal (**x**), and ventral (**y**) views; **z–za** cloacal vertebra (UU SP4 622) in dorsal (**z**) and anterior (**za**) views; **zb–zf** caudal vertebra (UU SP3 611) in anterior (**zb**), posterior (**zc**), right lateral (**zd**), dorsal (**ze**), and ventral (**zf**) views; **zg, zh** posterior caudal vertebra (UU SP1 1015) in ventral (**zg**) and left lateral (**zh**) views

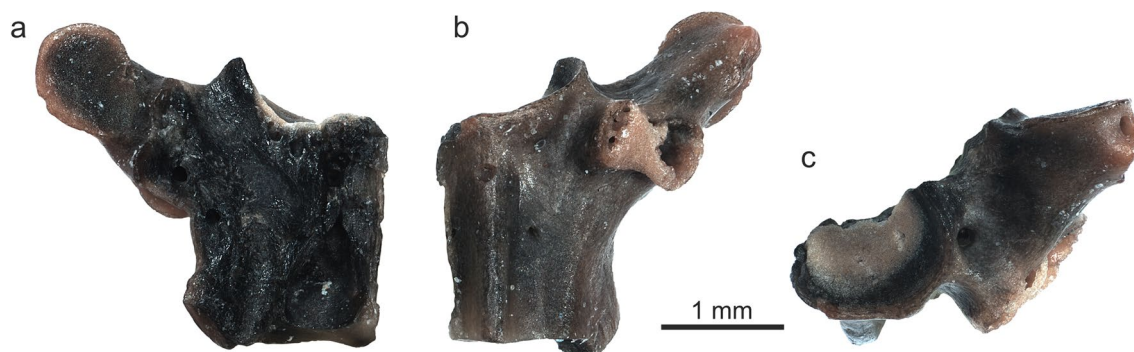


Fig. 67 Colubriformes indet. from Chalicorrema. Fragmentary trunk vertebra (UU RA 411) in dorsal (a), ventral (b), and anterior (c) views

1943; Georgalis et al., 2019b; Kuch et al., 2006; Syromyatnikova & Lopatin, 2024; Zahradnicek et al., 2008).

Trunk vertebrae from Spilia (Fig. 66d–y) include both forms without hypapophyses as well as forms with hypapophyses, however, these are all damaged/eroded and thus, their shape, size, and direction cannot be fully assessed. It could also be that some of the small vertebrae from Spilia 4 pertain to *Periergophis micros* described above, however, their incompleteness does not afford some secure taxonomic determination.

The three trunk vertebrae from Chalicorrema are rather poorly preserved (Fig. 67). The only preserved left prezygapophysis of the most complete fragment (UU RA 411) is not upswept dorsally (Fig. 67c). The prezygapophyseal articular facet is drop-like in outline (Fig. 67a). Although the distal termination of the prezygapophyseal accessory process is missing, that process was most probably rather short. The distally damaged diapophysis is well-divided from the short parapophysis. The ventral parapophyseal margin reached below the ventral margin of the cotylar rim (Fig. 67c). The blunt subcentral ridge is moderately developed. The preserved portion of the haemal keel is thin in ventral aspect but its posterior termination might have originally slightly expanded laterally (Fig. 67b). The only preserved left paracotylar foramen is large and situated within a wide depression (Fig. 67c). The three vertebrae from Vevi are rather incomplete.

All in all, these fragmentary trunk vertebrae are only poorly preserved and so even identification at the family level is problematic. The presence of haemal keel in some of these mid- and posterior trunk vertebrae, as well as the presence of paracotylar foramina, indicate that these vertebrae might belong to Colubridae but a referral to some other Colubriformes lineages, excluding Viperidae and Natricidae, is also possible (e.g., Psammophiidae, Dipsadidae). Similarly, for the hypapophyses-bearing trunk vertebrae, it cannot be ascertained whether they pertain to natricids, viperids, or elapids, or even they are simply cervical vertebrae of colubrids.

The single cloacal vertebra (UU SP4 622) from Spilia is incomplete, missing much of the left lymphapophysis and the left postzygapophysis (Fig. 66z–za). It bears two distinct haemapophyses.

Several caudal vertebrae are known from Spilia (Fig. 66zb–zh). UU SP4 556 is an anterior caudal vertebra that is clearly different than *Periergophis*. The same for UU SP4 563 and UU SP4 564, which apparently belong to relatively large-sized taxa. The single caudal vertebra from Spilia 1 (UU SP1 1015; Fig. 66zb–zf) bears some resemblance to those of natricids, especially in the shape of its neural spine that is rather high and strongly inclined anteriorly and the presence of short but distinct epizygapophyseal ridges. The caudal vertebra from Spilia 3 (UU SP3 611; Fig. 66zg, zh) could be a posterior caudal of *Paraxenophis* but its preservation state does not allow some precise determination.

Serpentes indet.

Figure 68

Material. *Chalicorrema*: a fragment of a vertebra (UU RA 406); *Spilia* 3: two fragments of vertebrae (UU SP3 614 and UU SP3 615); *Spilia* 4: one right maxilla (UU SP4 606), one right quadrate (UU SP4 615), two trunk vertebrae (UU SP4 654 and UU SP4 657), one cloacal or anterior caudal vertebra (UU SP4 655), two vertebral fragments (UU SP4 509), and several vertebral fragments and ribs (UU SP4 630 and UU SP4 659).

Description and remarks.

The cranial bone (UU SP4 606) from Spilia 4 represents the posterior portion of a right maxilla, with partially preserved the ectopterygoid process and 3–4 tooth positions posterior to this process (Fig. 68a, b). The right quadrate (UU SP4 615) from Spilia 4 is also incomplete, preserving only the ventral half of the bone (Fig. 68c). The trochlea quadrati is much convex, reminiscent of certain colubrids. Both these cranial elements are too incomplete for a more precise taxonomic identification within snakes.

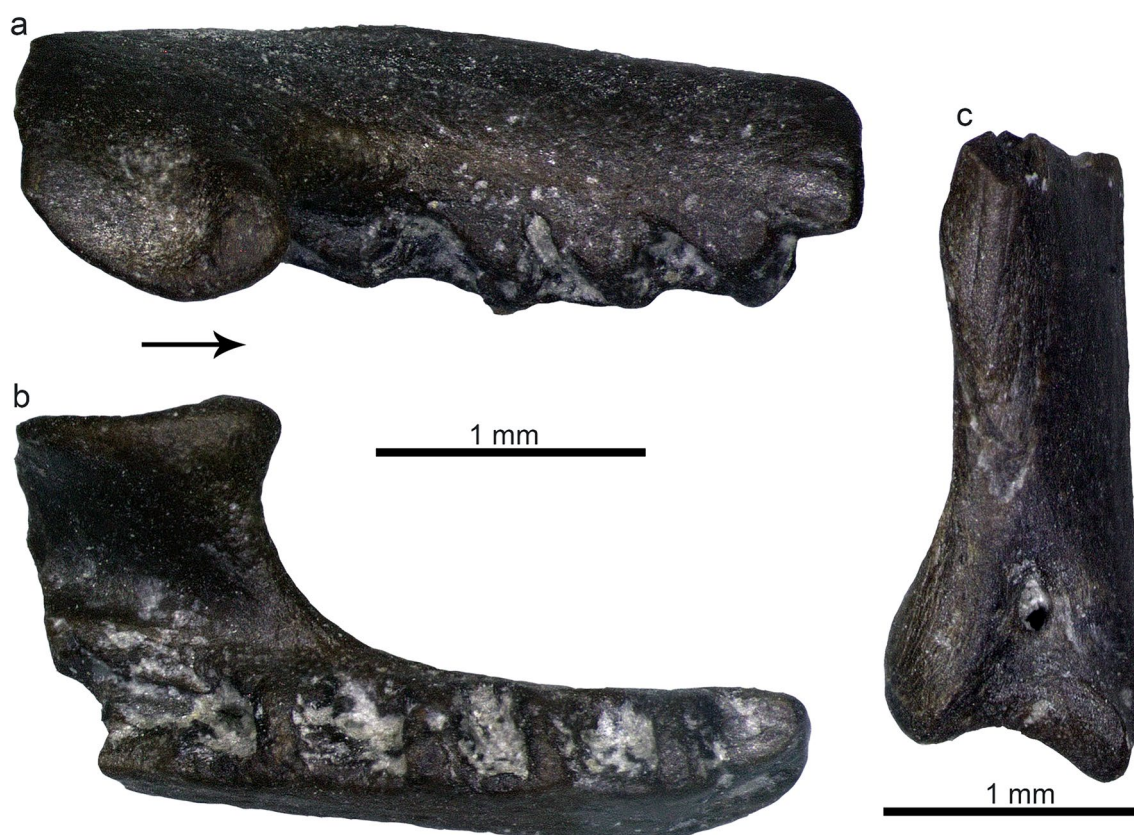


Fig. 68 Serpentes indet. from Spilia 4. **a, b** Posterior portion of a right maxilla (UU SP4 606) in medial (**a**) and ventral (**b**) views; **c** right quadrate (UU SP4 615) in posterior view. Arrow indicates the posterior direction

Certain vertebrae and vertebral fragments from Spilia 3 and Spilia 4 cannot be more precisely identified. Similarly, the sole specimen from Chalicorrema, UU RA 406, is a fragment of a snake vertebra, preserving the right anterolateral side (with the paradiapophyses, part of the anterior cotyle, the prezygapophyses, and part of the prezygapophyseal accessory process); this too can only be identified as Serpentes indet.

Discussion

The new material described herein from the late Neogene localities of Spilia (MN 14 and MN 15), Vevi (MN 15), Chalicorrema (Late Miocene or Pliocene), and Rema Marmara (Late Miocene or Pliocene) documents a rich herpetofauna from northern Greece. New occurrences of taxa are recorded, which, on several occasions extend their known distribution in Greece and the broader area or even represent first occurrences for the Greek fossil record. This adds substantially to the Pliocene herpetofaunas of the county, which have been otherwise scarce and inadequately known (e.g., Delfino & Georgalis, 2022; Georgalis & Delfino, 2022b; Georgalis & Kear, 2013; Georgalis et al., 2016a; Vlachos, 2022).

Salamanders are represented in the new material exclusively by specimens from Spilia 1 and 4, and pertain to the salamandrid genera *Ommatotriton* and *Ichthyosaura*, plus certain finds that cannot be precisely assigned to the genus level. The genus *Ommatotriton* is currently distributed in the Middle East, Anatolia and the Caucasus (van Riemsdijk et al., 2021). The fossil record of *Ommatotriton* is extremely scarce, being so far represented solely by vertebral and appendicular material from the locality of Maramena (Georgalis et al., 2019b), which is only a few kilometers away (and slightly older, MN 13/14) from Spilia (though see Macaluso et al., 2022, for an alternative attribution of that Maramena material as Pleurodelinae indet.), plus two vertebrae from the Pleistocene of the Levant (Lev et al., 2023). Therefore, the new material described herein from Spilia 4 that is tentatively referred to this genus, represents only the third occurrence of *Ommatotriton* in the fossil record and further suggests that the genus was present across different (even if nearby) localities across the Miocene/Pliocene boundary of the southern Balkans, well outside its extant geographic range. *Ichthyosaura* is present in extant herpetofaunas of Greece (Sparreboom, 2014), however, there

was as far no fossil record documented from the country (Delfino & Georgalis, 2022). The remains of *Ichthyosaura* from Spilia 4 therefore represent the first occurrence of this genus in the fossil record of Greece and demonstrate that it was present in the area at least since the Early Pliocene (MN 15).

Frogs are abundant in all the studied localities of Spilia, Vevi, Chalicorrema, and Rema Marmara, being represented by at least seven different taxa. The identification of the bombinatorid *Bombina* in the Late Miocene or Pliocene of Chalicorrema marks the first known occurrence of this genus in Greece. This is of particular importance, taking into consideration that *Bombina* is currently present in Greece and represented by two different species, *Bombina bombina* (Linnaeus, 1761) and *Bombina variegata* (Linnaeus, 1758) (Speybroeck et al., 2020).

Discoglossids are herein described from Spilia, Vevi, and Chalicorrema. The latter are very fragmentary and only referred to as Discoglossidae indet., whereas the Spilia and Vevi remains are by far more complete and can be securely referred to the genus *Latonia*. More specifically, the Spilia specimens bear much resemblance with *Latonia ragei*, otherwise known from the Early Miocene of Western Europe (Hossini, 1993; Roček, 1994) and are here tentatively referred to the same species as *Latonia* cf. *ragei*. The material from Vevi is relatively less complete and can only be referred as *Latonia* sp. In any case, the new remains of *Latonia* from Spilia and Vevi add to the known fossil record of the genus from Greece, which had so far been described from the Early Miocene (MN 4) of Aliveri and Karydia and the latest Miocene/Early Pliocene of Maramena and the Ptolemais area (see Delfino & Georgalis, 2022). Moreover, the Spilia specimens afford the second identification of *Latonia* to the species level from Greece, the other being *Latonia* cf. *gigantea* from the Early Miocene (MN 4) of Karydia, described by Georgalis et al. (2019a). Syromyatnikova et al. (2019b) recently proposed the interpretation of *Latonia gigantea* as a junior synonym of *Latonia seyfriedi*, and thus, the occurrence from Karydia may be revised here as *Latonia* cf. *seyfriedi*.

The pelobatid genus *Pelobates* has been previously mentioned from various Neogene and Quaternary fossil localities in Greece, however, none of these has been formally described or figured, with the sole exception being the material described by Sanchíz (1984) as *Pelobates* cf. *syriacus* from the Quaternary of Kos Island (see Delfino & Georgalis, 2022). Accordingly, the new remains described herein from the Late Miocene or Pliocene of Chalicorrema and the Early Pliocene of Spilia represent the oldest documented occurrences of the genus in the Greek fossil record. Pelobatidae are currently represented in the extant Greek herpetofauna by two species,

Pelobates balcanicus Karaman, 1928 and *Pelobates syriacus* (see Dufresnes et al., 2019b). Interestingly though, the material from Spilia does not seem to belong to either of the two extant species but instead likely pertains to an extinct taxon, *Pelobates* aff. *preafuscus*, which is otherwise known from the Late Miocene of the Caucasus (Syromyatnikova, 2019). The Chalicorrema specimens cannot be more precisely identified beyond the genus level. The new material further adds to the fossil record of pelobatids from the southern Balkans, which although being extremely scarce, goes back to the Oligocene of the region (MP 26/27; Georgalis et al., 2021a).

Ranids are represented in the new material by at least two genera, *Pelophylax* and *Rana*, the former from the Spilia sites and the latter from both Spilia and Vevi. Both *Pelophylax* and *Rana* are currently present in the herpetofauna of Greece (Dufresnes et al., 2024; Jablonski et al., 2021; Papežik et al., 2023). *Pelophylax* has been so far known in the Greek fossil record from a few Quaternary localities plus the latest Miocene/earliest Pliocene (MN 13/14) of Maramena (see Delfino & Georgalis, 2022). *Rana* has been so far known in the Greek fossil record only from a few Pliocene and Quaternary localities (see Delfino & Georgalis, 2022). In particular, for the single ilium from Spilia 4 that we described above as *Rana* cf. *dalmatina*, this is of importance as it corresponds to the only documented occurrence of this extant taxon in the Greek fossil record—otherwise, this taxon has been so far known only from a simple mention (without any description or figure) from the Quaternary of Attica (see Delfino & Georgalis, 2022). Nevertheless, as we highlighted above, this taxonomic identification should be treated with caution, considering that the skeletal anatomy of many *Rana* spp., including the Greek endemic *Rana graeca*, remains largely unknown.

Hylids are represented in the new material by several postcranial specimens from Spilia 1, Spilia 3, and Spilia 4, referred to the *Hyla arborea* species complex. This complex is represented in the extant herpetofauna of Greece by two species, *Hyla arborea* and *Hyla orientalis* Bedriaga, 1890 (see Stöck et al., 2008; Speybroeck et al., 2020; Birbele et al., 2023). However, the fossil record of *Hyla* in the country is rather limited: beyond simple mentions of its occurrence across several localities (Sanchíz, 1998), the genus has been formally described only from the latest Miocene/earliest Pliocene of Maramena (*Hyla* sp. of Georgalis et al., 2019b) and the Early Pleistocene of Kaiafas, Peloponnese (*Hyla* gr. *arborea* of Villa et al., 2020).

Bufonids are represented in the new material by several postcranial specimens from Spilia 1, Spilia 3, and Spilia 4, that are referred to *Bufo* gr. *viridis*. Other, indeterminate, bufonids are also described from Spilia 1, Spilia

3, Spilia 4, and Chalicorrema, however, their incompleteness prevents any genus level placement. *Bufotes viridis* has been frequently mentioned in the Greek fossil record; however, these are all exclusively mentions, without any kind of description or illustration (Delfino & Georgalis, 2022). Therefore, the new record from Spilia represents the sole documented occurrence of the taxon, extending with certainty its presence in the early Neogene. The *Bufotes viridis* complex is still present in the extant herpetofaunas of Greece, represented by *Bufotes viridis* in the mainland and *Bufotes sitibundus* (Pallas, 1771) in some Aegean Islands (Dufresnes et al., 2019a).

Turtles are represented in Vevi by two taxa, the emydid *Emys* gr. *orbicularis* and an indeterminate geoemydid. The find of an emydid at the Early Pliocene of Vevi is of particular importance, as emydids had been so far described from the Greek fossil record exclusively from a few Quaternary localities in Peloponnese and Central Macedonia, all attributed to the extant species *Emys orbicularis* (Athanassiou et al., 2018; Vlachos, 2022; Vlachos & Delfino, 2016; Vlachos et al., in press). It has been further suggested that 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 & Delfino, 2016). The herein identification of a much older (Early Pliocene; MN 15) emydid from northern Greece that is reminiscent in morphology to *E. orbicularis* pushes back the known stratigraphic range of the group in the country. What is, however, even more interesting, is that the age of the Vevi material ranks it as one of the oldest members of *Emys* known from Europe in general and one of only a few Neogene records from the continent (Chkhikvadze, 1980, 1983; Danilov et al., 2017; Khosatzky, 1956; Khosatzky & Redkozubov, 1989; Młynarski, 1956; Młynarski et al., 1984). As a matter of fact, *Emys* first appears in the European fossil record only during the Late Miocene of Eastern Europe (Chkhikvadze, 1980, 1983; Yanenko & Kovalchuk, 2023). The taxonomy of the late Neogene emydids from Europe is at state of a taxonomic flux, as the boundaries between the named taxa are vague, whereas most of the original material has not been adequately revised for decades or has only been briefly redescribed (e.g., Danilov et al., 2017). In particular, four, supposedly valid, taxa of *Emys* are recognized from the Neogene of Europe: *Emys tarashchuki* (Chkhikvadze, 1980), from the Late Miocene (MN 11) of Ukraine and Georgia (Chkhikvadze, 1980, 1983), *Emys sukhanovi* Chkhikvadze, 1983, from the Late Miocene (MN 12) of Ukraine and western Russia (Chkhikvadze, 1983), *Emys wermuthi* Młynarski, 1956, from the Early Pliocene (MN 15b/16a) of Poland (Młynarski, 1956), and *Emys orbicularis antiqua* Khosatzky, 1956, from the Early

and Late Pliocene of Russia, Ukraine, Moldova, Poland, and Slovakia (Chkhikvadze, 1983; Khosatzky, 1956; Khosatzky & Redkozubov, 1989; Młynarski et al., 1984). In addition, indeterminate remains of *Emys* or even tentatively attributed to *E. orbicularis* are also known from the Late Miocene of Ukraine (Yanenko & Kovalchuk, 2023) and the Pliocene of Italy (Kotsakis, 1980; Portis, 1890), Poland (Młynarski, 1964), Slovakia (Młynarski, 1963), and Romania (Szalai, 1934). Considering the perplexing taxonomy of the few known European Neogene emydids, the Vevi material cannot be precisely identified to the species level, though its resemblance with the extant species that currently inhabits the area permits us to tentatively refer it to as *Emys* gr. *orbicularis*. In any case, considering the scarcity of Neogene emydids from the continent, it adds substantially to their fossil record both regionally and at a European level, demonstrating a wider distribution of *Emys* at that time, encompassing also the southern Balkans.

Geoemydids represent the most abundant aquatic turtle group in the Greek fossil record, all pertaining to a single genus, *Mauremys*, with a stratigraphic distribution spanning from the Late Miocene (MN 9) up to today (Georgalis & Kear, 2013; Georgalis et al., 2016b; Vlachos, 2022; Vlachos et al., 2019). Most fossil geoemydids from Greece have been either tentatively referred to the extant species that inhabits the country, *Mauremys rivulata* (Valenciennes in Bory de Saint-Vincent, 1833) or as indeterminate occurrences of the genus (Georgalis & Kear, 2013; Georgalis et al., 2016b; Vlachos, 2022; Vlachos & Delfino, 2016), but also an extinct species, *Mauremys aristotelica* Vlachos et al., 2019, characterized by rather wide vertebral scutes, has been described from the latest Miocene–Early Pliocene of northern Greece (Georgalis et al., 2019b; Vlachos et al., 2019). The new occurrence of an indeterminate geoemydid from Vevi provides limited information for a more precise, genus level identification; based on a biogeographic rationale it is likely that this too pertains to *Mauremys*, however, other geoemydid genera have been also recognized from Eastern Europe (see Danilov et al., 2017). Turtle remains from Spilia and Rema Marmara are very fragmentary and cannot be referred beyond Testudinoidea indet.

Squamates from our fossil material are very diverse, pertaining to at least seven lizard and eight snake taxa. Of particular importance is the identification of the scincid *Ophiomorus* in Spilia 4, known from several cranial and postcranial remains. This represents the fourth only known fossil occurrence of this diminutive, extant genus, the others being a single dentary from the Early Pleistocene of Kaiafas in southern Greece that was recently described by Villa et al. (2020), a single presacral vertebra from the Pleistocene of the Levant described by Lev

et. al. (2023), plus three dentaries from the Late Miocene of Mongolia that were tentatively referred to the genus by Daxner-Höck et. al. (2022). *Ophiomorus* has a wide distribution in Western Asia and reaches also the south-eastern margins of Europe (i.e., Greece) (Kornilios et al., 2018). In the latter region, this is represented by two, geographically disjunct, species: *Ophiomorus punctatissimus* from southern mainland Greece and Kythera Island and, at the other side of the Aegean Sea, *Ophiomorus kardesi* Kornilios et al., 2018, that inhabits Kastellorizon Island (Dodecanese) and southwestern Anatolia (Kornilios et al., 2018). Molecular divergence date estimates suggested that the lineages of these two extant species have split already prior to the formation of the Mid-Aegean Trench in the Late Miocene (Kornilios et al., 2018). The identification of the Spilia *Ophiomorus* documents the existence of the genus far outside its extant geographic range. As highlighted above, the Spilia form could potentially represent a species different from *O. punctatissimus*, however, on the absence of more complete fossil material and the current limited knowledge of the skeletal anatomy of most extant *Ophiomorus* spp., it is hard to make a secure species level assignment for the Spilia fossil material. In any case, with an Early Pliocene (MN 15) age, the new *Ophiomorus* material from Spilia 4 represents one of the oldest fossil occurrences of the genus globally, and potentially even the oldest, taking into consideration that the Late Miocene Mongolian material described by Daxner-Höck et. al. (2022) was only tentatively referred to *Ophiomorus*.

Lacertids are represented in our sample by at least two different species. The largest among them, recovered from the Early Pliocene of Spilia 1 (MN 14) and Spilia 3 (MN 15), seems to pertain to the extant genus *Lacerta*, though such genus level assignment should be better considered as tentative. If correct though, such identification of the Spilia specimens would mark the first known occurrence of *Lacerta* in the Greek fossil record, denoting the presence of the genus since at least the Early Pliocene. This would be in concordance with molecular data which have suggested that the extant species groups of *Lacerta* already appeared in the Greek area since the Middle Miocene (Sagonas et al., 2014). As a matter of fact, lacertids are the most diverse reptiles in the extant herpetofauna of Greece (Arnold et al., 2007; Kornilios et al., 2020; Lymberakis et al., 2008; Psonis et al., 2017; Sagonas et al., 2014; Speybroeck et al., 2020; Strachinis et al., 2021) and have a considerably rich fossil record across the country, spanning from the Early Miocene up to the Holocene (see Georgalis & Delfino, 2022b). Nevertheless, practically all fossil lacertid specimens from the country have not been identified beyond the family level (Georgalis & Delfino, 2022b), with the sole exception

material from the Late Pleistocene of Crete that was described by Kotsakis (1977) as *Podarcis* cf. *erhardii*, however, the latter referral should also be considered with caution because was likely based more on biogeography than diagnostic morphological characters. The current identification of a second, smaller lacertid taxon in Spilia, matches well with this high diversity pattern of this group in the area. Unfortunately, as is the case with most Greek fossil lacertid remains, the remaining lacertid material from Spilia, as well as the lacertid material from the Late Miocene or Pliocene of Rema Marmara, cannot be identified beyond the family level; this is obviously affected by the incompleteness of the fossil remains but is also tremendously hindered by our currently limited knowledge of the skeletal anatomy of extant Greek lacertids, despite recent essential advances in this matter (e.g., Čerňanský & Syromyatnikova, 2019; Villa & Delfino, 2019a).

Amphisbaenians are currently present in Greece, solely in a few islands in the eastern and southeastern Aegean Sea, represented by a single species, the blandid *Blanus strauchi* (Bedriaga, 1884) (Sindaco et al., 2014). Their scarce fossil record nevertheless attests for a broader past distribution in the Greek area, encompassing also the Late Miocene (MN 9) of Crete (Georgalis et al., 2016b) and the Early Pliocene (MN 15) of Central Macedonia (Georgalis et al., 2018c). In fact, the latter record was a single vertebra that originated from the site of Spilia 4 and represented the youngest record of amphisbaenians from continental Eastern Europe (Georgalis et al., 2018c). The new vertebral material from Spilia 4 further adds to this essential fossil occurrence, with its abundance also providing some insights on the intracolumnar variation. It seems entirely possible that all these Greek amphisbaenian fossil remains pertain as well to the genus *Blanus* Wagler, 1830, especially when taken into consideration the extant distribution of the genus in the area (Sindaco et al., 2014) but also its confirmed presence in the Neogene fossil record of nearby Anatolia (Georgalis et al., 2018a). However, the total absence of cranial elements from all Greek fossil localities hinders any definite genus level conclusion, particularly because only skull elements possess such diagnostic features (Čerňanský, 2023; Georgalis et al., 2018a; Syromyatnikova et al., 2021; Villa et al., 2019).

Agamids are present in extant herpetofaunas of Greece, represented by a single species, the agamine *Stellagama stellio*, which achieves a disjunct distribution in some islands and a few spots in the continental area of the country (Karameta et al., 2022). Molecular evidence has recently suggested that the lineage of the extant *S. stellio* originated already in the Middle Miocene and then further diversified during the Late Pliocene (Karameta et al., 2022). Nevertheless, the agamid fossil record in Greece is rather patchy, limited to a few cranial and vertebral finds,

exclusively from the latest Miocene/earliest Pliocene (MN 13/14) of Maramena, pertaining to indeterminate agamids (Georgalis et al., 2019b). The herein description of additional fossil agamid remains from the Late Miocene or Pliocene of Chalicorrema and the Early Pliocene (MN 15) of Vevi add thus substantially to the existing fossil record of agamids in Greece, but generally also to their Neogene European one, which is also considerably limited (Delfino et al., 2008; Villa & Delfino, 2019b).

Anguids are represented in our sample by *Pseudopus* from Spilia 4 and indeterminate anguine(s) from Chalicorrema and Spilia 4. Anguids have a rather rich fossil record in Greece, spanning from the Early Miocene (MN 4) up to the Quaternary (see Georgalis & Delfino, 2022b), but the group represents also a prominent part of the extant Greek herpetofaunas, comprising four extant species: *Anguis cephallonica* Werner, 1894, *Anguis fragilis* Linnaeus, 1758, *Anguis graeca* Bedriaga, 1881, and the largest extant European lizard, *Pseudopus apodus* (Pallas, 1775) (see Gvoždík et al., 2023). The identification of *Pseudopus* from Spilia 4 is rather important, as it represents only the third documented fossil occurrence of this genus from Greece, adding to the previous known records from the latest Miocene/earliest Pliocene (MN 13/14) of Maramena (Georgalis et al., 2019b) and the Early Pleistocene of Kaiafas (Villa et al., 2020). Interestingly, the Maramena material was suggested by Georgalis et al. (2019b) to bear some resemblance with the extinct taxon *Pseudopus pannonicus* (Kormos, 1911), the largest known anguine, which achieved a wide distribution during the Neogene and early Quaternary of Europe (Loréal et al., 2023, 2024). Such opinion was subsequently tentatively followed by Georgalis and Delfino (2022b) and Loréal et al. (2023), with Loréal et al. (2024) even formally referring the Maramena material to *P. pannonicus*. Being very geographically proximate and only slightly younger than Maramena, the new material of *Pseudopus* from Spilia 4 could eventually pertain to the same taxon as that from the former locality. Nevertheless, more complete remains from Spilia are necessary in order to decipher whether this form represents an extinct Neogene taxon or pertains to the extant *Pseudopus apodus*. What is further noticeable is the absence of the genus *Ophisaurus*, from our anguid sample; of course, though, such absence should not be taken for granted, as there are indeterminate anguines from both Spilia 4 and Chalicorrema, which certainly do not pertain to the genus *Anguis* and therefore could either represent *Pseudopus* or *Ophisaurus*, but nevertheless cannot be precisely assigned to the genus level. *Ophisaurus* is relatively widespread in the Miocene of northeastern Mediterranean (Čerňanský et al., 2017; Syromyatnikova et al., 2019a; Villa & Delfino, 2019b) and has a presence

in Eastern Europe since at least the “middle” Oligocene (MP 25; Georgalis et al., 2021a). In Greece, *Ophisaurus* has been recorded from the Early Miocene (MN 4) of Karydia (Georgalis et al., 2019a), the Late Miocene (MN 13) of Ano Metochi (Georgalis et al., 2017a), and its last known occurrence in the area is documented in the latest Miocene/earliest Pliocene (MN 13/14) of Maramena (Georgalis et al., 2019b). Interestingly, in the latter locality, *Ophisaurus* is known with five different morphotypes, though it is not certain whether they represented distinct species or their anatomical differences could be merely attributed to some intraspecific or ontogenetic variation, or even tooth wearing (Georgalis et al., 2019b). The Maramena occurrence represents the last occurrence of *Ophisaurus* in the region (Georgalis et al., 2019b) but also one of the last in Eastern Europe (see Syromyatnikova et al., 2023 for even younger remains). This is in further concordance with the general post-Miocene demise of that genus in Europe (Blain & Bailon, 2019; Georgalis et al., 2017a; Klembara & Rummel, 2018; Macaluso et al., 2023a; Rage, 2013; Syromyatnikova et al., 2023).

A single tooth from the Early Pliocene (MN 15) of Spilia 4 is tentatively assigned to varanids, adding to the virtually absent Pliocene record of this group from Greece. Varanids have been known in continental Greece from Late Miocene localities across the country (Georgalis, 2019; Georgalis & Delfino, 2022b; Georgalis et al., 2018b; Villa et al., 2018; Weithofer, 1888), a single Pliocene occurrence from the Thessaloniki area (Drakopoulou et al., 2022), and then from the Middle Pleistocene of Athens area, the latter coinciding with the youngest occurrence of the group in Europe (Georgalis et al., 2017b). The sole other occurrence from the country coeval with the Spilia fossil consists of nicely preserved, but so far only briefly presented, material from the Early Pliocene (MN 15) of Megalo Emvolon, near Thessaloniki (Drakopoulou et al., 2022). The species level taxonomy of most Greek varanid fossil specimens remains though at a state of a flux, as they are usually represented by isolated vertebrae or teeth (Georgalis, 2019; Georgalis et al., 2018b, 2019b). As a matter of fact, it is generally impossible to assess whether these belong to *Varanus marathoniensis* Weithofer, 1888, which has been established upon cranial material from the Late Miocene (MN 11–13) of Pikermi, near Athens (de Fejérváry, 1935; Weithofer, 1888; Villa et al., 2018) and had a wide distribution in the Miocene of Europe (Villa et al., 2018), or whether they belong to a distinct species. One further interesting point of the Spilia varanid is the presence of tooth serration in both its margins. Ivanov et al. (2018) considered the smooth cutting edges as a plesiomorphic state for varanids. Nevertheless, tooth serration in extant varanids is widespread across an array of different species (see

Georgalis et al., 2023b), however, in the European fossil record only a few varanid occurrences are known to possess serration on their teeth (Georgalis et al., 2019b, 2023b). Among these, fossil serrated teeth are also documented for the Maramena varanids described by Georgalis et al. (2019b), with four different kinds of serration potentially observed (either completely serrated, both mesially and distally; either completely non-serrated; either serrated mesially but not distally; and either serrated distally but not mesially). However, it is not clear if these differences can be attributed to some intraspecific variation, ontogeny, taphonomy, or whether they can even have taxonomic significance.

Snakes are represented in our new sample by at least eight different taxa, all of which pertaining to caenophidians, with the sole exception of the constrictor *Eryx*. The latter genus is here tentatively identified on the basis of a single trunk vertebra from the Early Pliocene (MN 15) of Spilia 4. Nevertheless, unlike many other snakes, the most important diagnostic features in the erycid postcranial skeleton lie within their caudal vertebral region, where these vertebrae are characterized by a highly complex morphology with additional apophyses (see Szyndlar & Georgalis, 2023). For this reason, the available trunk vertebra from Spilia cannot be assigned with confidence to the genus level. *Eryx* is nevertheless present in the extant herpetofauna of Greece, represented by the species *Eryx jaculus* (Linnaeus, 1758) (Speybroeck et al., 2020; Wallach et al., 2014). The erycid fossil record in the county is rather scarce: a potential erycid has been described upon a single trunk vertebra from the Late Miocene of Pikermi, however, as with the case of the vertebra from Spilia 4, on the absence of caudal vertebrae, such referral should be also considered as tentative (Georgalis, 2019). Otherwise, more confident occurrences of *Eryx*, based on caudal vertebrae, are known from the Early Pliocene (MN 14) of Rhodes Island plus those of the extant species *E. jaculus* from the Quaternary of Kos and Chios Islands (see Georgalis & Delfino, 2022b).

Natricids are the most abundant snake remains in our sample. Beyond a few indeterminate potential natricids from Chalicorrema, Spilia 0, and Vevi, the remaining among our new material, which originated from Vevi, Spilia 0, and Spilia 4, is referred to *Natrix* aff. *rudabanyaensis*. The species *Natrix rudabanyaensis* was previously known solely from the Late Miocene (MN 9) of its type area, Rudabánya, Hungary (Szyndlar, 2005), and tentatively also from the Middle and Late Miocene (MN 7/8 and MN 9) of Felsőtárkány-Felnémet Basin, Hungary (*Natrix* cf. *rudabanyaensis* of Venczel, 2011 and Venczel & Hír, 2013) and the Middle Miocene (MN 7/8) of Tauț, Romania (*Natrix* cf. *rudabanyaensis* of Venczel & Știucă, 2008 and Venczel, 2011). Material from the slightly older

(latest Miocene/earliest Pliocene, MN 13/14) locality of Maramena (located only a few kilometers from the Spilia sites) was recently described and also identified as *Natrix* aff. *rudabanyaensis* by Georgalis et al. (2019b). We nevertheless consider that such taxonomic referral of these Late Miocene and Early Pliocene natricids from northern Greece (Maramena, Spilia 0, Spilia 4, and Vevi) should be handled with high cautiousness, as the species boundaries among most of the Neogene European species of *Natrix* are not well defined, because their intracolumnar variation is much inadequately known and certain of their diagnostic vertebral features appear in fact to be more widespread among natricid snakes. What seems somehow clear though is that this Greek fossil material pertains anyway to an extinct natricid species and not to any of the two species that currently inhabit the country, i.e., *Natrix natrix* (Linnaeus, 1758) and *Natrix tessellata* (Laurenti, 1768). Besides this material tentatively referred to *Natrix* aff. *rudabanyaensis*, the Greek fossil record comprises mostly occurrences of indeterminate members of *Natrix* from a few Late Miocene and Pliocene localities in the northern part of the country (Georgalis et al., 2017a, 2019b; Loréal et al., 2020), remains of *N. tessellata*, tentatively identified from the Pleistocene of Crete (Szyndlar, 1991b), as well as indeterminate potential natricids from older Early (?MN 3) and Late Miocene (MN 9) localities in Lesbos and Crete Islands (Georgalis et al., 2016b; Vasileiadou et al., 2017).

Besides *Natrix*, the Early Pliocene (MN 15) of Vevi also yielded as many as three other different colubri-form snakes. One of them (Colubroidea indet.) seems to belong to either colubrids or (less likely) to dipsadids and is therefore more precisely placed within Colubroidea. The other two cannot be placed more safely within any of the colubri-form subgroups and they are therefore only tentatively referred as Colubri-formes indet. “morphotype 1” and “morphotype 2”. Nevertheless, despite its incompleteness, this Vevi material attests for a high diversity of colubri-form snakes in the Early Pliocene of the area.

A small elapid (coral snake) is also potentially present in Spilia 4. Among coral snakes, the extant American genus *Micrurus* has been previously recorded from a few Early and Middle Miocene localities in Europe (Augé & Rage, 2000; Ivanov, 2000; Ivanov & Böhme, 2011; Rage & Bailon, 2005; Rage & Holman, 1984; Szyndlar & Schleich, 1993), including a named extinct species, *Micrurus gallicus* Rage & Holman, 1984, from the Middle Miocene of France (Augé & Rage, 2000; Rage & Holman, 1984); in addition, a vertebra from the latest Miocene/earliest Pliocene (MN 13/14) of Maramena, Greece has been also tentatively referred to this genus (Georgalis et al., 2019b). However, it should be noted that such genus level identification of the European finds as congeneric with the American extant

genus *Micrurus* should be considered as tentative, owing to the presence of other genera of coral snakes in both America (*Micruroides* Schmidt, 1928) and Asia (*Calliophis* Gray, 1835 in Gray & Hardwicke, 1830–1835, *Hemibungarus* Peters, 1862, and *Sinomicrurus*), which have also a relatively similar vertebral morphology (Nakamura et al., 2013; Zaher et al., 2019), an opinion that has already appeared as a concern in recent literature (e.g., Augé & Rage, 2000; Head et al., 2016; Ivanov, 2022; Kelly et al., 2009; Rage & Bailon, 2005; Szyndlar & Schleich, 1993; Zaher et al., 2019, 2021). Molecular evidence has recently shown that *Micrurus* split from other coral snakes already by the Early Miocene [20 Ma (Zaher et al., 2021) or 18 Ma (Jowers et al., 2023)] or even in much older times, at around the late Oligocene (28 Ma; Lee et al., 2016). The small coral snake from Spilia 4 seems to share much resemblance with the, older, small elapid described by Ivanov (2002) from the Early Miocene (MN 3) of Merkur-North, Czechia, which seems to be different than *Micrurus*. A comprehensive investigation of the vertebral morphology and variation of the extant coral snakes from both the Americas and Asia is required in order to properly assess the genus placement of the European fossil finds. Whatever the case, if our identification is correct, the Spilia 4 specimen represents the youngest record of a coral snake from Europe, extending their range up to the late Early Pliocene (MN 15).

Viperids are represented in our sample by limited fragmentary vertebral material and one fang from the Early Pliocene (MN 15) of Spilia 3. The overall size of these specimens supports a tentative attribution to the so called “Oriental vipers” complex. This complex of large viperids is represented in extant herpetofaunas of Greece by the genera *Macrovipera* Reuss, 1927, and *Montivipera* Nilsson, Tuniyev, Andrés, Orlov, Joger & Herrmann, 1999 (see Wallach et al., 2014). Nevertheless, distinction among the two genera is mainly based on external morphology and molecular evidence (Nilsson et al., 1999; Wüster et al., 2008), hence, in the fossil record, their remains are usually solely identified as an indeterminate member of the “Oriental vipers” (see Szyndlar & Rage, 1999, 2002; but see also Codrea et al., 2017, for an alternative taxonomic approach). It is further worth noting, that during exactly the same time (Early Pliocene, MN 15), the geographically very proximate Thessaloniki area in northern Greece hosted the largest viperid snake of all time, the giant and enigmatic *Laophis crotaloides* Owen, 1857 (see Georgalis et al., 2016a).

The bizarre snakes *Periergophis* and *Paraxenophis* have been so far known exclusively from the latest Miocene/earliest Pliocene (MN 13/14) locality of Maramena (Georgalis et al., 2019b), in just a few kilometers distance from the slightly younger Spilia localities. The new, but admittedly limited, material of *Periergophis* and *Paraxenophis* from Spilia tentatively enables the identification

of an additional occurrence for the two taxa. As highlighted above though, important differences among the Spilia and the Maramena (abundant) material do exist for both the cases of *Periergophis* and *Paraxenophis*. It is unclear whether such differences could be attributed to some degree of (so far) unknown intracolumnar or ontogenetic variation, or taphonomy/preservation, or different chronospecies/chronomorphotypes across two chronologically successive localities, or even if the Spilia material does not, in fact, pertain to these two taxa. Accordingly, the Spilia specimens shed no further light on the mystery surrounding the exact taxonomic affinities of *Periergophis* and *Paraxenophis* within Caenophidia.

The late Neogene (Late Miocene and Pliocene) is characterized by major climatic, environmental, and palaeogeographic alterations and perturbations that affected tremendously European faunas (Koufos & Vasileiadou, 2015; Koufos et al., 2005; Minwer-Barakat et al., 2018; Rögl, 1999; Rook et al., 2006), with a particular impact on the herpetofaunas of the continent (Delfino et al., 2003; Georgalis & Szyndlar, 2022; Georgalis et al., 2019b; Ivanov, 2022; Macaluso et al., 2023a; Rage, 2013; Rage & Roček, 2003; Roček, 2013; Villa & Delfino, 2019b; Villa et al., 2024a, 2024b). The area of Greece, situated at the southern tip of the Balkan Peninsula and at the margins of the European continent with Asia, has witnessed major faunal turnovers during the late Neogene, as it is exemplified by its rich fossil mammal assemblages (e.g., Koufos & Vasileiadou, 2015; Koufos et al., 2005); however, the herpetofauna turnovers have not been well documented (Georgalis et al., 2019b; Macaluso et al., 2023a), especially when considering the scarcity of Pliocene amphibian and reptile fossil remains from the area (Delfino & Georgalis, 2022; Georgalis & Delfino, 2022b). All in all, the herein described material from the Early Pliocene of Spilia (MN 14 and 15), the Early Pliocene (MN 15) of Vevi, and the Late Miocene or Pliocene of Chalicorrema and Rema Marmara witnesses a high diversity of amphibians and reptiles in the late Neogene of Greece. Most importantly, the identification of the first fossil occurrences in the area for certain taxa enables a better understanding of their overall evolution and palaeobiogeography. The new material comprises forms that are now extinct (e.g., *Periergophis* and *Paraxenophis*) or extirpated from Europe (e.g., *Latonia*, Varanidae, Elapidae) but at the same time also attests the emergence of extant taxa that dominate the extant herpetofaunas of Greece (the newt *Ichthyosaura*, the anurans *Bombina*, *Pelobates*, *Pelophylax*, *Rana*, *Hyla*, and *Bufo*, the turtle *Emys*, the lizards *Ophiomorus*, *Lacerta*, and *Pseudopus*, and the snakes *Eryx* and *Natrix*), for certain of which their fossil record is documented here for the first time in the area.

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Author contributions

GLG, AV, MI, and MD wrote the manuscript text; GLG, AV, and MI took the photographs and prepared the Figures. All authors read and approved the final manuscript.

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Availability of data and materials

All fossil specimens described herein are permanently curated in the collections of the Department of Earth Sciences, University of Utrecht, Utrecht, Netherlands. No datasets were generated or analysed during the current study.

Declarations

Competing interests

The authors declare no competing interests.

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