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To cite this version:

Andrej Čerňanský, Rodolphe Tabuce, Dominique Vidalenc. Anguimorph lizards from the lower Eocene (MP 10–11) of the Cos locality, Phosphorites du Quercy, France, and the early evolution of Glyptosaurinae in Europe. Journal of Vertebrate Paleontology, 2023, 42 (5), 10.1080/02724634.2023.2211646 . hal-04295642

HAL Id: hal-04295642

https://hal.umontpellier.fr/hal-04295642v1

Submitted on 23 Nov 2023

ARTICLE

Anguimorph lizards from the early Eocene (MP 10–11) of the Cos locality, Phosphorites du Quercy, France and the early evolution of Glyptosaurinae in Europe

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ABSTRACT— Squamate faunas from the early Eocene of Europe are rare. A newly discovered early Eocene (MP 10–11) Cos locality in southwestern France has yielded an assemblage of anguimorph lizards that sheds light on the early evolution of this group. Among them is a new glyptosaurine lizard *Sullivania gallica* gen. et sp. nov., based on frontal material with a unique pattern and distribution of polygonal osteoderms that is distinct from that of the middle and late Eocene *Placosaurus* from France. It slightly resembles the stratigraphically older glyptosaurine *Gaultia silvaticus* from the earliest Eocene of North

America, but differs from it in several aspects. Although fossils of some members of Glyptosaurinae (sensu this paper; Glyptosaurini in previous taxonomies – Glyptosaurinae is returned to the family level originally proposed by Marsh) have been documented rarely from the middle and mainly from the late Eocene of Europe, they are virtually unknown from the early Eocene. One isolated osteoderm is referred only to Anguioidea indet. This specimen resembles osteoderms seen in Anguinae, provided that the absence of tuberclulate ornamentation is not caused by abrasion.

Varanoids are represented by an isolated frontal referred to Palaeovaranidae indet. It possesses a complex ornamentation composed of mounds on the dorsal surface. A maxilla is identified as an indeterminate varanoid based on the plicidentine infolding along the bases of the preserved teeth.

Although incomplete, this Cos lizard assemblage is an important and rare discovery that provides a glimpse into the ecosystems and paleobiodiversity of the early Eocene in western Europe.

LSID urn:lsid:zoobank.org:pub:5C6376A3-CC26-4CF1-BE56-E7279D508D5D

INTRODUCTION

The Cos fissure fill was the first “phosphatière” discovered in the Quercy by J. A. Poumarède in 1865 (Pulou, 1980), but one of us (DV) discovered vertebrate fossils in this locality only more recently. Cos constitutes the seventh pre-upper Eocene locality of Phosphorites du Quercy [for others see Astruc et al. (2003): Pasturat (MP 8+9), Viélase and Cazals (both MP 10–11), Cuzal, Parnac and Grélaou (all MP 13)]. Based on the studies of the primates (Godinot et al., 2021) and rodents (Vianey-Liaud et al., 2022), the vertebrate fauna of the Cos site has been dated as MP 10–11, a zone that spans the late Ypresian and early Lutetian.

Thus, it corresponds to the Early Eocene Climatic Optimum (EECO; see Inglis et al., 2020), which is dated as 53.3 to 49.1 Ma. EECO was a time of major climatic and environmental change caused by perturbations to the global carbon cycle (Hyland et al., 2017). This makes the Cos locality particularly important because the early Eocene terrestrial fossil record in Europe is poorly known.

There have been only a few early Eocene sites where assemblages of amphibians and reptiles have been described. These include: Dormaal (MP 7) in Belgium (Augé, 1990, 1992; Augé & Smith, 1997, 2002; Augé et al., 2022; Čerňanský et al., 2022; Folie et al., 2013; Hecht & Hoffstetter, 1962; Sullivan et al., 2012); Silveirinha (~MP 7) in Portugal (Rage & Augé, 2003); the early Eocene of (different localities in) Catalonia, Spain (Bolet, 2017); and some localities in France, notably Prémontré (~MP 10; Augé, 2003, 2005; Augé et al., 1997), Mutigny (MP 8–9; Čerňanský et al., 2020; Augé et al., 2022) and La Borie (MP 8–9) (Laurent et al., 2010). There are also some other famous early Eocene localities, which yielded snakes, turtles, and crocodiles, such as Monte Bolca, Italy (Seghetti et al., 2022) and the English localities in Isle of Sheppey, Bracklesham, and Kingston (Owen, 1841, 1850; Georgalis & Joyce, 2017; Smith & Georgalis, 2022). In contrast, such assemblages are relatively well-known for the middle and late Eocene in Europe, in part thanks to exceptional localities such as Geiseltal and Messel in Germany (Čerňanský & Smith, 2018, 2019 Keller, 2009; Smith et al., 2018; Sullivan et al., 1999; Villa et al., 2022) and in some of the localities of Phosphorites du Quercy in France (Augé, 2005; Čerňanský et al., 2015; Georgalis et al., 2021). Here we report on the fossil anguimorph lizards from the newly discovered Cos locality, on the southern Quercy limestone plateau, southern France.

Modern Anguimorpha includes Anguidae, Diploglossidae, Xenosauridae, Helodermatidae, Lanthanotidae, Varanidae and Shinisauridae. Anguidae represent a diversified and widely distributed group of reptiles of which Anguinae is the most derived clade (Augé, 2005; Uetz et al., 2023). Although there have been recent alterations to phylogenetical conceptions that have been stable for decades (e.g., Burbrink et al., 2020; Pyron et al., 2013) and the position of Diploglossidae is still debated (as a subclade of Anguidae, Conrad 2008; Gauthier et al., 2012; Pyron et al., 2013; as a distinct clade outside of Anguidae, Burbrink et al., 2020; Zheng & Wiens, 2016), aside from Anguinae three other extant clades were traditionally included in Anguidae. These are Gerrhonotinae, Anniellinae, and the extinct Glyptosaurinae (sensu McDowell & Bogert, 1954; see Gauthier et al., 2012; Georgalis et al., 2021; Sullivan, 1979, 2019; note, however, that if Diploglossidae is treated at the family level, then Glyptosaurinae must also be returned to the family level originally proposed by Marsh, 1872, as members of this clade are much morphologically distinct compared to Anguinae, see below). Glyptosaurinae (sensu McDowell & Bogert, 1954) inhabited North America, Europe, and Asia and are known from the Cretaceous to the late Paleogene-Oligocene (Čerňanský and Augé, 2019; Conrad & Norell, 2008; Keller, 2009; Sullivan, 1979, 2019). This clade was traditionally divided into the tribes Glyptosaurini and the paraphyletic "Melanosaurini" (Cicimurri et al., 2016; Estes, 1983; Sullivan, 1979, 2019). Among the former, *Placosaurus* Gervais, 1848–1852 is the only known member of the tribe in Europe (see Sullivan, 2019; Sullivan & Augé, 2006; Sullivan et al., 2012). It is represented by two currently valid species from the late Eocene of France (only the two species are definitely members of the genus, whereas the others are only questionably referred to *Placosaurus*), type of which are cranial remains. This is very low diversity compared to the North American glyptosaurine genera such as *Glyptosaurus* Marsh, 1871, *Paraglyptosaurus* Sullivan, 1979, *Helodermoides* Douglass, 1903 and *Gaultia* Smith, 2009 (Smith, 2009, 2011; Sullivan, 1979). Moreover, although members of the clade were well documented from the early Eocene in North America, glyptosaurines are largely unknown for most of the early and middle Eocene of Europe (Sullivan, 2019). In the early Eocene of Europe, the glyptosaurine taxon ?*Placosaurus ragei* Sullivan, Augé, Wille & Smith, 2012 and *Placosauriops*-like "melanosaurine" are known from Dormaal (MP 7). The Dormaal glyptosaurine ?*Placosaurus ragei* is known based on the holotype dentary and a referred parietal. However, the current taxonomy of species of *Placosaurus* is based on the morphology of the frontal (Sullivan & Augé, 2006), so its generic assignment is questionable (Sullivan et al., 2012). Indeterminate material (frontal and parietal) of glyptosaurines is also described from Silveirinha (~MP 7; Rage & Augé, 2003). In Asia, *Stenoplacosaurus mongoliensis* (Sullivan, 1979) was described from the middle Eocene of Mongolia (Sullivan & Dong, 2018; *Helodermoides mongoliensis* in Sullivan 1979; *Placosaurus mongoliensis* in Sullivan and Augé, 2006). This taxon is also based on the frontal morphology. Additionally, several isolated osteoderms of glyptosaurines, plausibly belonging to this early Eocene lineage, were described from the early Oligocene of Mongolia (Čerňanský & Augé, 2019). Thus, Glyptosaurinae has a continuous history in Asia at least until the Oligocene, although disappeared in Europe at the Eocene–Oligocene boundary (Rage, 2013). However, their early history in Europe remains largely unknown. All the specimens in this study are from the Cos fissure fill, Phosphorites du Quercy, 2.5 km southwest of Caylus, France.

Institutional Abbreviations— AMNH, American Museum of Natural History, New York; MNHN, Museum National d'Histoire Naturelle, Paris; UCMP, University of California Museum of Paleontology, Berkeley, USA; UM-COS, Université de Montpellier, France, Cos collection.

MATERIAL AND METHODS

Specimens examined and terminology

The studied material is housed at the University of Montpellier, cataloged under individual UM-COS-numbers. The standard anatomical orientation system is used throughout this paper, and terminology describing individual bone structures is based on Rage & Augé (2010).

X-ray Microtomography, Three-Dimensional Visualization, Photography and Reconstruction

The fossil specimens were imaged on micro-computed tomography (CT) at the micro-CT facility, Slovak Academy of Sciences in Banská Bystrica, Slovakia, using a Phoenix mikro-CTv|tome|x L240. The settings were as follows: VxSize = 0.01999999; Current = 150; Voltage = 130; Inttime = 20000; Average = 2; Steps = 1600; Steps360 = 2200; Filter = 0.1 mm Cu. The images were recorded over 360°. The CT data sets were analysed using VG Studio Max 3.1. and Avizo 8.1. The photographs of the UM-COS-1011 maxilla were taken with a Leica M205 C binocular microscope with an axially mounted DFC 290 HD camera; software: LAS (Leica Application Suite) 4.1.0 (build 1264). The image processing program ImageJ (Schneider et al., 2012) was used for measurements. For frontal reconstruction, the missing areas were restored by mirror imaging of the holotype and paratype, and estimation of the posterior portion is based on the preserved paratype. The holotype (UCMP 216000) and paratype (UCMP 150966) of *Gaultia silvaticus* were drawn from photographs published by Smith (2009: fig. 18). The holotype of *Stenoplacosaurus mongoliensis* (AMNH 6669 left frontal) was drawn based on photographs published by Sullivan & Dong (2018: fig. 1).

Geological Setting and Associated Fauna

Located in the southern part of the 'Causses du Quercy' plateau, the fissure fills of Cos lie within the Middle Jurassic (late Bajocian/Bathonian) marine limestones of the Cajarc

Formation (44°13'11.20"N, 1°44'58.21"E; Fig. 1). The site is a northwest-southeast trending large excavation (~80 m x 50 m), with the phosphate ore deposits nearly depleated. Positioned at the eastern end of the excavation, the fossiliferous fissure-fill at Cos is unlike those found in other localities of the Phosphorites du Quercy in that the strata that contain the fossiliferous unit are composed of small beds of granular and porous stratified limestones, alternating with red clays containing small pisolites. There are still uncertainties about geometric and stratigraphic relationships between the limestones and the interbedded red clays. There are few scattered vertebrate fossils through the entire section. The fauna recovered includes amphibians, squamates, crocodilians, birds, and more than twenty mammal species among which only primates and rodents have been studied (Godinot et al., 2021; Vianey-Liaud et al., 2022). All of the specimens described herein are from the Cos fissure fill of the Phosphorites du Quercy region and are early Eocene (MP 10–11 interval) in age.

SYSTEMATIC PALEONTOLOGY

Taxonomic note—If most clades previously considered subfamilies of Anguidae sensu Camp, 1923 – viz., Anguinae, Anniellinae and Diplglossinae – are now considered taxa at the family level, and there is no evidence that glyptosaurs are part of any of those radiations, then Glyptosaurinae sensu McDowell & Bogert, 1954 must also be returned to the family level originally proposed by Marsh (1872). Accordingly, we consider Glyptosauridae Marsh, 1872 to contain the subfamilies Melanosaurinae Sullivan, 1979, which is paraphyletic, and Glyptosaurinae Marsh, 1872, which correspond to the tribes Melanosaurini and Glyptosaurini of Sullivan (1979). The name “Placosauridae” (e.g., Cope, 1877; Kuhn, 1940) is a junior synonym of Glyptosauridae (Estes, 1983; McDowell & Bogert, 1954), so it does not affect our new status.

SQUAMATA Oppel, 1811

ANGUIMORPHA Fürbringer, 1900

ANGUIOIDEA Gray, 1825

GLYPTOSAURIDAE Marsh, 1872 (emended status)

GLYPTOSAURINAE Marsh, 1872 (sensu this paper)

SULLIVANIA gen. nov.

Type species— *Sullivania gallica* sp. nov.

Etymology—The genus is named in recognition of the American paleontologist Robert M. Sullivan for his valuable contributions to glyptosaurine morphology, paleobiogeography, and paleobiodiversity.

Diagnosis—As for *Sullivania gallica* sp. nov., the only known species.

***Sullivania gallica* sp. nov.**

(Figs. 2, 3, 4A)

Etymology— The specific epithet *gallica* is based the Latin “gallicus” in reference to the country of France, where the fossils were found.

Holotype— UM-COS-1001, greater anterior portion of fused frontals.

Paratypes— UM-COS-1000, incomplete right frontal; and UM-COS-1003, posterior region of the right frontal.

Differential Diagnosis— Glyptosaurine differing from all other Glyptosauridae in having unique pattern of irregular cephalic osteoderms covering the frontal where the first two anterior central osteoderms straddle the midline, and are coalesced or fused, narrow, anteroposteriorly elongate, leaf-shaped, reaching only slightly further anteriorly than the much larger, anteroposteriorly elongated lateral osteoderm with rounded lateral margin. This is in a sharp contrast to several wide, chevron-shaped osteoderms in *Gaultia* (in *Sullivania*, only the second lateral left and right osteoderms appear expanded medially, having contact in the mid-line) and high and regular division of dermal armor into discrete hexagonal osteoderms in *Placosaurus*, *Stenoplacosaurus*, *Glyptosaurus*, *Paraglyptosaurus*, *Helodermoides*, and *Eoglyptosaurus*. It is further distinguished from all other glyptosaurines by the following combination of features of the frontal: (1) osteoderms are apically flat, as *Gaultia*, not thick as in *Placosaurus*, and not inflated (or bulbous) as in *Glyptosaurus*, *Eoglyptosaurus*, *Helodermoides* and *Stenoplacosaurus*; (2) generally rather fever osteoderms contra numerous in *Placosaurus* (especially *Placosaurus estesi*), *Glyptosaurus*, *Eoglyptosaurus* and *Helodermoides*; (3) concave lateral margins unlike in the North American *Helodermoides*; (4) posterolateral process not distinctly laterally expanded and expansion includes only the posterior 1/3 of the bone, unlike in *Placosaurus estesi* and *Stenoplacosaurus*, in which the lateral expansion starts at the posterior 2/3 of the bone; and (5) frontals fused only in the late ontogeny (fusion is present only in the larger, robust specimen). In *Stenoplacosaurus*, the frontals are unfused.

Type locality and horizon—Cos, fissure fill in the Quercy region (southwestern France); early Eocene (MP 10–11 interval); the species is so far known exclusively from the type locality.

Description

Frontal—The holotype (UM-COS 1001, Fig. 2) represents fused right and left frontals (although traces of fusion are still recognizable). Its lateral margin is slightly concave and gradually widens posteriorly. The dorsal area surrounding the mid-orbital margin slopes slightly toward the orbit. The posterior portion of the bone is missing due to breakage. Thus, only the anterior and mid-portions are preserved. The maximum width of the preserved frontal is 11.7 mm. The element is more robust than UM-COS-1000 and is inferred to be from a larger (older) individual. The external surface is largely covered by ornamented osteodermal shields of various irregular, polygonal to roughly ovoid outline. They are completely fused to the underlying bone and are separated one from another by sulci (note, however, that it is not clear whether the osteodermal boundaries coincide with the epidermal scale boundaries). The ornamentation is formed by small rounded discrete tubercles that are regularly and densely arranged. The exception is in its anterior section, where a broad semi-elliptical smooth surface is located. It forms the articular facet for nasal (which is preserved on the right side). Here, the bone expands into a prominent, pointed anteromedial (nasal) process. The process is triangular. The anterolateral process is only partly preserved on the right side, but this preserved portion extends much less anteriorly than the anteromedial one. Posterior to this, three osteodermal shields are present. The first one is an anterior central shield. Here, the left and right frontal are fused along the mid-line. Thus, the first two anterior osteoderms straddle the midline and are coalesced or fused into the one. The first central shield is narrow, anteroposteriorly elongate and more or less leaf-shaped. It extends only slighty more anteriorly than the lateral shields. The lateral osteodermal shields are large, much larger that the central one (completely preserved on the right side). The medial margin of the lateral shields is V- shaped, whereas the lateral margin is rounded. The medial peak of V-shaped medial margin indicates a mediolateral short sulcus, where the first anterior central shield ends. Posterior to the sulcus in the midline, there is a second central shield. The more posterior region bears several cracks and thus, it is difficult to properly identified the original borders of the osteodermal shields (Fig. 2A, B). However, it appears that the both second lateral shields are medially expanded (best visible on the left side). The left and right shields seem to have a short medial contact. If this is the case, these second lateral osteoderms are mediolaterally wide rather than anteroposteriorly long (in contrast to the first lateral shield). In this case, the second central osteodermal shield has truncated appearance of the posterior portion due to this contact and thus, being trapezoidal in shape.

In ventral view, a large and robust frontal cranial crest (crista cranii frontalis) is visible. Its anterior portion is expanded forming a well-defined and rounded prefrontal (=subolfactory) process. It is, however, only partly preserved (its end is damaged; Fig. 2C). The anteromedial margin of this crest is thin and sharp. Posteriorly, it widens, gradually diminishing dorsally. The anterior portion of the frontal crest, anterior to the subolfactory process, is less deep, forming a sharp, medially directed ridge. The right and left branches join together in the anterior mid-line, forming a sharp angle. Note, however, that there is the matrix that is still adhering to the ventral side of the frontal between the anterior portions of the left and right frontal cranial crests. It obscures much of the medial ventral surface of the frontal. In the anterior region, lateral to the frontal crest (including its lateral surface), a large facet for the prefrontal is located (the right one is preserved; Fig. 2D). Prefrontal and postfrontal are not in a contact, and did not exclude the frontal from the orbital border.

UM-COS-1000 and UM-COS-1003 (paratypes) —UM-COS-1000 (Fig. 3A-F) is a nearly complete right frontal, with only the anterior end broken. The maximum anteroposterior length of this incompletely preserved element is 15 mm. It is robust, although less than the holotype. UM-COS-1003 (Fig. 3G, H) represents the posterior portion of the right frontal and this specimen is much more robust than the UM-COS-1000. The posterolateral section of UM-COS-1000 protrudes into a short, but robust, posterolateral process (the expansion starts in the posterior 1/3 of the bone). Here, the bone is widest – the maximum mediolateral width of this part of the bone is 9.1 mm. Further anteriorly, the frontal narrows and the lateral margins are slightly concave. Thus, the bone appears to be narrowest at about mid-orbit (the minimum width of the single right frontal in this area is 5.9 mm). The external surfaces of both specimens are almost completely covered by tuberculated osteoderms of various irregular, polygonal (rhomboidal, hexagonal) to roughly ovoid outlines. The osteoderms are completely fused to the frontal and separated one from another by sulci. The ornamentation is formed by small rounded discrete tubercles that are regularly and densely arranged. The osteodermal shields on the posterior portion in UM-COS-1000, close to the more or less straight contact with the parietal, are weakly ornamented. Only few tubercles are present in this section on an otherwise smooth surface; however, the dorsal surface in this region seems to be slightly eroded. The posterolateral corner is smooth, although it appears that some partial covering was originally here but now is lost. The evidence of this is that a partly preserved medial margin of the shield still has several tubercles. Thus, the posterior portion of the right frontal possessed four osteodermal shields arranged in a mediolateral row. Thus, the frontal is relatively broad. These osteroderms are anteroposteriorly long, roughly trapezoidal except for the third one (Fig. 3B), which has a triangular end due to hexagonal shape of neighboring osteoderms in the second row. This second posterior row, located anterior to the first one (at the level of the anterior beginning of the postfrontal facet), possesses three osteoderms. They differ in shape from those forming the first posterior row, being polygonal (roughly hexagonal). The same condition is present in UM-COS-1003, although the ornamentation is strongly developed here. In the mid-region of UM-COS-1000, there is a shallow light groove close to the orbital margin. This groove extends almost parallel to this margin (Fig. 3B).

In ventral view, a frontal cranial crest can be observed in both specimens. Posteriorly, it widens, gradually diminishing dorsally. On the lateral side of the crest, a foramen is visible. The crest fades out at the beginning of the posterolateral process of the frontal (in both paratypes) and does not continue to the posterior end of the bone. Here, the large rugose facet for the postfrontal is clearly visible laterally. In UM-COS-1003, the wedge-shaped facet for parietal tab is visible dorsal to the frontoparietal suture. A facet for the prefrontal is preserved only in UM-COS-1000. The prefrontal and postfrontal are not in a contact, and thus did not exclude the frontal from the orbital border.

Virtual microanatomy and histology—The micro-CT scans of the frontals revealed a bone structure with a very similar internal microanatomy in terms of a vascular network and spongiosis (Fig. 2E, F; Fig. 3E, F). It revealed a large and complex meshwork of numerous cavities. They are irregular, bubble-shaped, and some are interconnected. Thus, the bone appears to be less compact in both axial and coronal sections. Note that the finer histological details such as growth marks and cell lacunae of the bone are not visible.

Remarks— UM-COS-1001 is designated as the holotype because it is from a more mature (adult) individual. The paratypes UM-COS-1000, the nearly complete right frontal, and UM-COS-10003, the posterior part of the right frontal, are nearly identical, although UM-COS-1003 is slightly more robust. UM-COS-1000 and UM-COS-10003 have the identical arrangement of osteoderms where they overlap the holotype UM-COS-1001. They can add to the diagnosis a unique character state for Glyptosaurinae - the osteoderms on the posteriormost portion of the frontal are anteroposteriorly elongate and roughly trapezoidal. Four osteoderms of equal size are arranged in a mediolateral row. The second posterior row (located anterior to the first row) possesses three osteoderms, which are roughly hexagonal. Although all frontals are incomplete, preservation of parts shared by all frontals permits for reconstruction of the missing areas based on mirror imaging of the right and left elements (UM-COS-1000). The anterior portion is reconstructed based on the UM-COS-1001 (Fig. 2A). The reconstructed image clearly shows that it is very different from the earliest Eocene North American glyptosaurine *Gaultia*, the late Eocene European *Placosaurus* and the middle Eocene Asian *Stenoplacosaurus* (Fig. 4).

With regard to the virtual microanatomy, microanatomical studies on fossil anguioids (i.g., anguids) have previously been conducted. These published works deal with parietals of *Ophisaurus holeci* (Georgalis & Scheyer, 2021), *Ophisaurus spinari* (Syromyatnikova et al., 2022), and *Pseudopus pannonicus* (Loréal et al., 2023).

Glyptosauridae indet.

(Figs. 5, 6A-J)

Referred Material—UM-COS-1002, medial portion of left maxilla; UM-COS-1011, posterior portion of right maxilla; UM-COS-1004 and 1005, cephalic osteoderms and UM-COS-1006 and 1007, dorsal trunk osteoderms.

Description

Maxilla—Two incomplete maxillae were recovered (Fig. 5), representing much of the posterior halves of the bone with the posterior ends broken on both specimens. The left maxilla (UM-COS-1002, Fig. 5A-D) has seven tooth positions with four-and-a-half teeth remaining in situ. The right maxilla (UM-COS-1011, Fig. 5E-H) has four posterior teeth and two broken teeth. The nasal process of the maxilla is partly preserved in both specimens, gradually decreasing in height posteriorly. Its external surface is ornamented with tubercles and is best preserved in UM-COS-1011. The extent of this tuberculated surface is not well delineated as the sulci are not recognizable (see Fig. 5A, E and remarks). The supralabial area, below the ornamented field, is pierced by supralabial foramina (two are preserved in UM-COS-1002 and one in 1011). In medial view, the supradental shelf is prominent. The shelf slopes slightly posteroventrally from the level of the third preserved tooth position (counted from posterior). The dorsal area of the shelf is concave, forming a longitudinal shallow depression for articulation with the jugal. The shelf itself expands medially, and this expansion (best preserved in UM-COS-1011) reaches its maximum at the level among third and fifth tooth positions (counted from the posterior end). Here, the contact with the palatine is present. UM-COS-1002 bears the posterior opening of the superior alveolar foramen (Fig. 5F, H). It is large, elliptical, and located at the level of the fifth tooth position (counted from posterior).

Dentition—The tooth implantation is pleurodont. The teeth are heterodont with the lingual sides of the teeth expanding medially and gradually increase in robustness posteriorly. The apices of posterior three teeth are blunt, mesiodistally robust, and possess distinct, well-defined, mesiodistally straight cutting edges. The lingual and labial surfaces of the tooth apices are distinctly striated. The first preserved anterior tooth is less robust and labiolingually compressed.

Remarks— The maxillae from the Cos site may belong to *Sullivania gallica*, but are here considered Glyptosauridae indet. owing to lack of definitive characters that would allow positive identification. The maxilla is similar to that of the late Eocene species *Paraplacosauriops quercyi* in the lateral ornamentation of the surface of the nasal process of maxilla and the presence of bulbous teeth (see Auge & Sullivan, 2006; Georgalis et al., 2021). The ornamentation lacks discrete hexagonal/polygonal osteoderms that would clearly indicate it was a glyptosaurine. Therefore, the maxilla may be from some unknown "melanosaurine" similar to *Paraplacosauriops*.

Osteoderms—Four tuberculated osteoderms were recovered from the Cos site (Fig. 6A-J). Two are hexagonal/polygonal in shape (Fig. 6A-E) and two are rectangular/rhombic (Fig. 6F-M). The former are from the skull and the latter are from the body. The tubercles are prominent on the cephalic osteoderms and less so on the body osteoderms but this may be an artifact of preservation. The keel and the smooth overlap surface are absent on the first type of osteoderms. These osteoderms are also slightly thicker than the second (rectangular) type. The internal surfaces of the cephalic osteoderms are pierced by numerous foramina along with several grooves and ridges that extend anteroposterly. The rectangular body osteoderms (Fig. 6F-J) are distinguished by a prominent contact surface that is nearly one-third the anteroposterior length. It is slightly higher than the posterior ornamented portion, from which it is separated by a transverse groove. The latter is covered by discrete tubercles of various sizes. A blunt, weak and slightly oblique keel is present midway along the posterior margin of the osteoderm. The internal surface is pierced by three foramina located in the central region.

Remarks—Taxonomic assignment of isolated osteoderms below Glyptosauridae is not possible (de Buffrénil et al., 2010; Estes, 1983; Gauthier et al., 2012; Rage, 1978; Sullivan, 1979, 2019). Although differences in general shape and absence/presence of the overlap surface clearly exist among these osteoderms, their positions on the body plays more likely a major role in this case. Although it seems to be unlikely that these osteoderms belong to a form for which no other elements have not been recorded in the locality, we do not necessarily associate them with the frontals described above and identify them only as Glyptosauridae indet. The hexagonal/polygonal osteoderms strongly suggest that they are cranial. In the case of their cranial placement, they belong to Glyptosaurinae. However, the fact that they may pertain to the cheek region of a “melanosaurine” cannot be ruled out. The rectangular body (trunk) osteoderms could also be equally be attributed to a “melanosaurine.”

Anguioidea indet.

(Fig. 6K-M)

Referred Material —One isolated osteoderm UM-COS-1008

Description

Osteoderm— UM-COS-1008, a single isolated rectangular osteoderm (Fig. 6K-M) is thin rather than thick (although slightly thicker than the body osteoderms described above), with a low medial ridge (which is slightly more pronounced in the posterior section) extending along the entire central region, being restricted to the sculptured region. The anterior overlap surface is well defined. It occupies about one quarter of the external surface. The lateral bevel is narrow and the lateral imbrication is weak but present. The posterior portion of the external surface is weakly ornamented. The ornamentation is formed by pits and hardly distinguishable ridges diverging from the central region – pits are transformed into short grooves at the periphery. The internal surface is pierced by several foramina (at least two of which are visible). Besides these, few short grooves are ridges are located on the periphery in the mid-section of the osteoderm, but only on one side.

Remarks—The osteoderm UM-COS 1008 appears to differ from osteoderms of Glyptosauridae described above by its shape, thickness, length of overlap surface, presence of lateral bevel, and the apparent absence of typical discrete tubercles forming the external ornamentation. This specimen resembles osteoderms present in members of Anguinae (Čerňanský & Klembara, 2017; Estes, 1983; Georgalis et al., 2019; Hoffstetter, 1962; Williams et al., 2022), provided that the absence of tuberclulate ornamentation is not caused by abrasion or corrosion. The osteoderm appears to be slightly water-worn. The fact that this osteoderm is thicker might also support glyptosaurid affinity.

Varanoidea Gray, 1827 (sensu Estes et al., 1988).

Palaeovaranidae Georgalis, 2017

Palaeovaranidae indet.

(Fig. 7)

Referred Material — UM-COS-1009, nearly complete frontal.

Description

Frontal— The nearly complete frontal (Fig. 7) is an unpaired element, missing only the anterior end and the left posterolateral corner. In the posterior section, the frontal bears traces of the original midline suture on both ventral and dorsal surfaces (Fig. 7A, B). It is narrow anteroposteriorly and flares outward posterolaterally on the right side. The frontal is small, measuring only 4.6 mm along the mid-line, but was slightly longer in life as the anterior portion is broken off. The lateral margin of the frontal is concave, with the narrowest part anterior to the mid-orbit region. Although the anterior portion is missing, the frontal widens anteriorly, based on the lateral flaring of the crista cranii frontalis on the ventral side (Fig. 7B).

The dorsal surface of the frontal is ornamented with irregular small, distinct mounds. Their structures are complex, having a shrunken (or rumpled) appearance with several longitudinal crests, whereas others are pointed, forming several small spike-like structures (they are of high relief). The posterior margin, which contacts the parietal, is anteriorly concave, giving it a slight irregular or wavy appearance in dorsal view (Fig. 7A, B).

On the ventral side, the frontal cranial crests are well-developed, forming a prominent orbital rim. The cranial crests are slightly deeper ventrally in the anterior region where the ventral margins are distinct. The crests extend to the posterolateral end of the frontal where they are slightly wider and blunt. They are pierced by three foramina on each side. The left lateral side preserves a wedge-shaped facet for the prefrontal at the anterior end (Fig. 7C). The right lateral side a bears a distinct facet at the posterior for the reception of the postfrontal (Fig. 7D). These articular surfaces are separated by a large portion of the orbital margin.

Varanoidea indet.

(Fig. 8)

Referred Material—UM-COS-1010, greater portion of left maxilla.

Description

Maxilla— The nearly complete left maxilla is preserved in matrix, with the lateral side visible (Fig. 8A). The anterior portion is broken. The preserved portion has a maximum anteroposterior length of 10.2 mm and a maximum height of 4.6 mm, measured from the ventral edge of the maxilla to the uppermost extent of the nasal process. The nasal process of the maxilla is rather thin and has a slightly concave smooth surface with a few fractures along the anterior half of the process due to crushing. The posterior margin of the nasal process slopes posteroventrally at an angle of 28° where it ends near a small slit at the level of the last preserved tooth. The external surface of the process is pierced by a series of four large supralabial foramina along the external labial margin of the tooth row. In addition, there are several smaller foramina located anterodorsally to the anteriormost preserved tooth. The maxilla bears five complete teeth and has positions for four others. Posterior to the last labial foramen, four tooth positions are present. The supradental shelf is relative thin, but widens anteriorly (Fig. 8B). It protrudes medially, reaching its maximum at the level between the fourth and fifth tooth position (counted from posterior) because of its contact with palatine. The posterior opening of the superior alveolar canal is large and located at the level of the sixth tooth position (counted from posterior). The medial surface of the preserved portion of nasal process of maxilla is smooth and no nasal crest on the dorsomedial surface can be observed; however, the dorsal portion of the maxilla is fractured.

Dentition—The dentition is subpleurodont (sensu Hoffstetter 1954, 1955), the maxilla parapet is low, and the bases of the teeth are attached to a sloping, concave surface. The teeth are pointed, tall, and recurved distally and slightly lingually. The mesial and distal cutting edges are sharp. Serrations appear to be absent. Based on the CT images, the tooth bases are mesiodistally broad and bear well preserved typical basal striae (i.e., plicidentine; Fig. 8F), which is typical for both Varanidae and Palaeovaranidae (Kearney & Rieppel, 2006; Georgalis & Scheyer, 2019).

DISCUSSION

The Cos locality is as a unique window into the early Eocene "greenhouse world" in Europe, providing a glimpse into the paleobiodiversity of anguimorphs during this geological time. The anguimorphs from this locality include a new glyptosaurine, an indeterminate anguioid (potentially an anguine but its glyptosaurid affinity cannot be ruled out), and varanoids. Although the Cos lizard fauna is important for our understanding of the Eocene ecosystems, many aspects can be fully resolved only by future systematic research and studies of new material from Europe.

Glyptosauridae

The tuberculated cranial material and osteoderms from Cos present an autapomorphy of glyptosaurids, i.g., tuberculate ornamentation (Camp, 1923; Gilmore, 1928; Estes, 1983; Gauthier et al., 2012; Sullivan, 1979, 2019). Thus, this material clearly belongs to this clade. In Glyptosaurinae (sensu this paper), subhexagonal (or polygonal) osteoderms are present on the skull whereas they have rectangular osteoderms on the most of the dorsal and ventral portions body (Sullivan, 1979). Members of the paraphyletic “Melanosaurinae“ (sensu this paper) are characterized by irregular plate-like osteoderms that cover the skull roof (Sullivan, 1979, 2019). Thus, isolated glyptosaurine frontals (and parietals) can be identified based on the presence of hexagonal/polygonal tuberculate osteoderms covering the skull roof. For this reason, the Cos frontal specimens clearly represents a member of Glyptosaurinae.

Until now the only glyptosaurine known from Europe has been *Placosaurus* from the Eocene (Depéret, 1917; Gervais, 1848-52; Sullivan, 1979; Sullivan & Augé, 2006). Today, it comprises four species: *Placosaurus rugosus* Gervais, 1848–1852, *Placosaurus estesi* Sullivan & Augé, 2006, "*Placosaurus*" *europaeus* (Filhol, 1876; based on a dentary with teeth, so its generic assignment is equivocal; Sullivan & Augé, 2006), and ?*Placosaurus ragei* Sullivan et al., 2012 (based on a dentary and a referred parietal). Most finds are from the late Eocene (except for ?*P. ragei*), while some are also known from the late middle Eocene (Lavergne and Le Bretou, Quercy; Rage 1988 and Augé 2005, Sullivan & Augé, 2006). *Placosaurus* can be distinguished from the North American glyptosaurine genera *Glyptosaurus*, *Paraglyptosaurus*, *Proglyptosaurus*, and *Helodermoides* by the following combination of features on frontal (Sullivan & Augé, 2006): (1) frontals are fused and (2) slightly arched; and (3) cephalic osteoderms usually form one or two complete rows of hexagonal osteoderms over each orbit. However, the Cos frontals have a unique distribution of skull ostoderms and therefore cannot be referred to this taxon or any of the other taxa (Fig. 4).

The early Eocene glyptosaurines compared to post-early Eocene glyptosaurines in Europe—All glyptosaurine frontals from Cos described here most likely belong to the same taxon as they have the same flat osteoderm morphology and display similar distribution pattern on the frontal where they correspond and are similar size. Moreover, they are comparable in size and come from the same locality. These frontals are markedly different from *Placosaurus* (Sullivan & Augé, 2006; see Diagnosis and descriptions here). For this reason, we proposed a new genus and species for the Cos taxon, *Sullivania gallica*.

Sullivania cannot be compared with the stratigraphically older ?*Placosaurus ragei*, from the earliest Eocene (MP 7) from Dormaal, because it is based on an isolated dentary and a parietal. For this reason, Sullivan et al. (2012) questionably assigned it to *Placosaurus*. New glyptosaurine lizard material from Dormaal, including a frontal that is different from both *Placosaurus* and *Sullivania*, is currently under study of one of us (AČ).

The frontals described by Rage & Augé (2003:fig. 3A) from Silveirinha (~MP 7, Portugal) as indeterminate "Glyptosaurini" (Glyptosaurinae sensu this paper) are also different from *Sullivania* in the following features: (1) the dorsal surface is covered with hexagonal osteoderms; (2) one osteoderm is located in the anterior central region, whereas posterior large ones are arranged in two rows; and (3) the frontal is robust and fused, although it is much smaller than the specimens from Cos (the minimum width of the paratypic right frontal of *Sullivania* is 5.9 mm, whereas the width of the fused paired frontals from Silveirinha is 4.5 mm).

European *Sullivania* compared to North American *Gaultia*—The clade Glyptosauridae first appears in the early Eocene of Europe (Rage, 2013; Sullivan, 2019). The earliest European record of glyptosaurid lizards is from MP 7 at Silveirinha and Dormaal (Rage and Augé, 2003; Sullivan, 2019; Sullivan et al., 2012). Thus, the presence of glyptosaurids is another taxon between Europe and North America during the Eocene (e.g., the lizard *Saniwa*: Augé et al., 2022; the questionable iguanian *Tinosaurus*: Čerňanský et al., 2023; the turtle *Axestemys*: Georgalis & Joyce, 2017; many other non-congeneric but related taxa on both continents, notably charinaine snakes; Smith & Scanferla, 2021). These imply faunal exchange between North America and Europe during the late Paleocene to early Eocene. Several episodes of faunal exchange occurred between Europe and North America before and after the Palaeocene–Eocene Thermal Maximum PETM, based on mammals (DeBast & Smith, 2017; Smith & Smith, 2013; Solé et al., 2016), but known coeval Asian fossil lizard record is too poor to draw any definite conclusions regarding faunal exchanges. Interestingly, the frontal of *Sullivania gallica* from France resembles *Gaultia silvaticus* from the earliest Eocene (biozone Wa-0, Willwood Formation) of Wyoming (Smith, 2009).

The holotype of *Gaultia silvaticus* is an incomplete fused frontal (although no evidence of a suture is apparent on the ventral surface and most of the right half of the bone is broken away, Smith, 2009: fig. 18D, Fig. 4B) diagnosed by: (1) apically flat osteodermal shields covering the frontal and (2) different division of osteodermal cover relative to the typical hexagonal one in other glyptosaurines. However, several differences are notable, especially in the distribution of osteodermal shields and their shapes; in the anterior portion, osteodermal shields are wide in *Gaultia*, mediolaterally elongated and chevron-shaped. They form several lines, with two prominent rows of osteoderms extending along the mediolateral width of the frontal. In contrast, most frontal osteoderms in *Sullivania* are anteroposteriorly elongate rather than wide and, moreover, there is the presence of leaf-shaped first central osteoderm. However, the second lateral left osteoderm crosses over the entire mediolateral width of the frontal in *Sullivania*, having contact with the right one along the mid-line, similar to that seen in *Gaultia*. The overall shape of these lateral osteoderms is different compared to the shevron-shaped osteoderms in *Gaultia*; posteriorly, the osteodermal shields in *Gaultia* are divided into convex polygons that are smaller than the chevrons. However, there is no indication of the presence of anteroposteriorly elongated, roughly trapezoidal osteoderms in the posterior region of both paratype frontals of *Sullivania*.

A close relationship between *Gaultia* and *Sullivania* than to *Placosaurus* and *Glyptosaurus* cannot be ruled out. Assuming that they are closely related, *Sullivania* seems to retain some characteristics from its North American ancestor. It worth noting that half of the mammal taxa from the early Eocene of North America are closely related to the mammalian taxa known from Dormaal (Gingerich & Smith, 2006). The breakup of plate-like osteoderms into smaller polygonal/hexagonal osteoderms on the skull roof is likely a derived feature among glyptosaurines, in contrast to plesiomorphic type of the large dermal plates covering the skull roof (Sullivan, 1979). The Late Cretaceous *Odaxosaurus piger* retains the plate-like osteoderm pattern seen in many anguids (Meszoely, 1970; Klembara et al., 2019) and "proto-glyptosaurines" (Sullivan, 2019). The fragmentation of cephalic osteoderms seen in the early Eocene *Sullivania* and *Gaultia* may represent an intermediate stage. *Gaultia*, like *Sullivania*, has its frontal roof armor divided into heterogenous plates as in *Arpadosaurus* (see Meszoely, 1970), not into discrete subequal hexagonal osteoderms as in *Glyptosaurus*, *Paraglyptosaurus*, *Placosaurus*, and other taxa (Sullivan, 1979; Sullivan & Augé, 2006). Sullivan (2019:754) considered *Gaultia* a sister taxon to Glyptosaurinae (sensu this paper, "Glyptosaurini" sensu Sullivan, 1979). Ultimately, it is a question of how Glyptosaurinae is circumscribed. At present, no phylogenetic definition of Glyptosaurinae has been put forward. There is no apparent disagreement about the intermediate morphology of *Gaultia* and its close relationship with Glyptosaurinae as circumscribed by Sullivan (1979). Sullivan (1979:15) gave "hexagonal osteoderms that cover the entire skull" as a defining feature, and since such osteoderms are only present on the parietal, not the frontal, of *Gaultia*, it would support Sullivan´s (1979) position. However, *Gaultia* clearly does not fit the definition of "Melanosaurinae" (sensu this paper, "Melanosaurini" sensu Sullivan, 1979) either. For this reason, given the close relationship between *Gaultia* and accepted members of Glyptosaurinae, we continue to follow Smith´s 2009 assignment ("Glyptosaurini" in Smith, 2009). We envision a time when a robust phylogenetic hypothesis of glyptosaurine relationships exists and clade names can be redefined on that basis.

Hypothetically, this might raise a question whether *Sullivania* is referable to Glyptosaurinae or is a sister taxon to this clade. Again, however, the phylogenetic topology of these taxa within Glyptosauridae can be resolved only based on phylogenetic analyses. For now, we decided to tentatively assign *Sullivania* to Glyptosaurinae. The phylogenetic relationships of *Sullivania* and *Placosaurus* are unknown. Taking account that the taxonomy is based on the frontal bone, *Stenoplacosaurus* from presumably the late-middle Eocene of Mongolia is morphologically more similar to *Placosaurus* (previously, it was even placed to *Placosaurus* [Sullivan & Augé, 2006] and later placed to its own genus [Sullivan & Dong, 2018]) than to *Sullivania* gen. nov. Thus, an Asian origin of *Placosaurus* cannot be excluded. Owing to an incomplete glyptosaurine fossil record between the early and late Eocene in Europe, their evolution and distribution patterns between these distant regions remain largely unresolved.

Varanoidea

UM-COS 1009 represents a "miniature" palaeovaranid. It differs from currently known genera by the following combination of features: (1) overall small size; the frontals of *Paranecrosaurus feisti* (Stritzke, 1983), which is known only from the early–middle Eocene of Messel in Germany, are much larger (18.2 mm in the holotype and even 30.8 in the paratype; see Smith & Habersetzer, 2021); (2) the non-paired (fused) narrow frontal, as in *Palaeovaranus* Zittel, 1887–1890 (Georgalis et al., 2021) and *Paranecrosaurus feisti* (Stritzke, 1983) (Smith & Habersetzer, 2021), unlike the paired frontals in *Eosaniwa* Haubold, 1977 (Rieppel et al., 2007); (3) the type of an ornamentation. Its ornamentation, which consists of small, densely arranged mounds, slightly resembles that of *Palaeovaranus lismonimenos* Georgalis, Čerňanský & Klembara, 2021 (Georgalis et al., 2021). *Palaeovaranus lismonimenos* was previously reported from the late Eocene (~ MP 17, see Georgalis et al., 2021), whereas the Cos frontal is much older. However, the detailed surface texture is different – the ornamentation of the Cos specimen is more complex, having also several spikes forming each mound (rather than possessing more-or-less simple mounds). The ornamentation of UM-COS 1009 differs from the distinct sculpturing pattern observed on the frontal of the holotype of *Melanosauroides giganteus* Kuhn, 1940 from Geiseltal. The dorsal surface of the frontal of *M. giganteus* possesses broad, apically flat, rugose patches that appear to be fused broad (not distinctly keeled) osteoderms (Georgalis, 2017; Smith & Habersetzer, 2021). The dorsal surface of the frontal of *Paranecrosaurus* Smith & Habersetzer, 2021 frontal is also different (Smith & Habersetzer, 2021); and (4) the long posterolateral process relative to the the overall size of the frontal, as *Paranecrosaurus* (Smith & Habersetzer, 2021), and unlike the short process in *Palaeovaranus* (Georgalis et al., 2021) and *Eosaniwa* (Rieppel et al., 2007).

UM-COS 1009 represents most likely a new taxon, but the taxonomy of palaeovaranids is now mainly based on the parietal morphology (Georgalis et al., 2021). For this reason, we identified this frontal only as Palaeovaranidae indet.

It is unclear whether the maxilla (UM-COS 1010) and the frontal (UM-COS 1009) represent a single taxon, although they are comparable in size and come from the same locality. The overall morphology and plicidentine support allocation of the maxilla to a varanoid (Kearney and Rieppel, 2006; Georgalis & Scheyer, 2019). It cannot be referred to Shinisauridae, a group of anguimorph presence that is well-documente from the Eocene of Europe (Smith, 2017; Smith et al., 2018). The maxilla has several teeth posterior to the last labial foramen where at least four tooth positions are preserved. This condition resembles *Saniwa orsmaelensis* Dollo, 1923, which is known from Dormaal (Augé et al., 2022). Indeed, the teeth and the concave lateral surface (the posterior portion of the maxilla is slightly bent laterally) of the Cos specimen resemble the condition in this taxon (Augé et al., 2022: fig. 2). The geological age of the maxilla would also be consistent with the presence of *Saniwa* in Cos. However, several tooth positions posterior to the last labial foramen are also present in *Paranecrosaurus feisti* (Smith & Habersetzer, 2021). The diagnostic parts of palaeovaranid maxillae, however, are mainly found in medial view. The presence of a distinctly developed nasal crest on the dorsomedial surface of the nasal process is a distinguishing feature of *Palaeovaranus* (Georgalis et al., 2021) and *Paranecrosaurus* (nasolacrimal ridge sensu Smith & Habersetzer, 2021). Unfortunately, this portion in the Cos maxilla is heavily damaged and there is no indication of its presence. The teeth and the overall shape of the Cos specimen are also similar to *Melanosauroides* Kuhn, 1940 (see Georgalis, 2017: fig. 4B). For all these reasons, caution is needed and we decided to identify this maxilla only as Varanoidea indet. (although we cannot be sure if palaeovaranids are indeed varanoids). More complete material from Cos will shed light on the diversity of the varanoids here.

ACKNOWLEDGMENTS

For access to this fossil material and help, we thank Mehdi Mouana (Institut des Sciences de l'Evolution de Montpellier, France). For English correction and helpful advice, we are indebted to Robert M. Sullivan (New Mexico Museum of Natural History and Science, USA) and Hans-Dieter Sues (Editor). For advice, we thank Georgios Georgalis (Polish Academy of Sciences), Krister Smith (Senckenberg Research Institute, Frankfurt am Main), Thierry Smith and Annelise Folie (both Royal Belgian Institute of Natural Sciences, Brusssels). We thank Nour-Eddine Jalile (MNHN) for permissions and sending us additional photographs of specimens under their care. The photographs were taken by Philippe Loubry. For critically reading the manuscript, we thank Hans-Dieter Sues (Editor), Georgios Georgalis (Polish Academy of Sciences, Poland) and one anonymous reviewer. This work was supported by the Scientific Grant Agency of the Ministry of Education of Slovak Republic and Slovak Academy of Sciences, Grant Nr. 1/0191/21 (to A. Č).

AVAILABILITY OF MATERIALS AND DATA

All specimens are catalogued and accessible in the fossil reptile collection of the University of Montpellier in France. Digital surface models of the figured fossil specimens are available on Morphosource and Virtual Collections:

UM-COS-1001: https://www.morphosource.org/concern/parent/000514175/media/000514178
UM-COS-1000: https://www.morphosource.org/concern/media/000514185?locale=en
UM-COS-1003: https://www.morphosource.org/concern/media/000514194?locale=en
UM-COS-1002: https://www.morphosource.org/concern/media/000514200?locale=en
UM-COS-1004: https://www.morphosource.org/concern/media/000514206?locale=en
UM-COS-1005: https://www.morphosource.org/concern/media/000514212?locale=en
UM-COS-1006: https://www.morphosource.org/concern/media/000514218?locale=en
UM-COS-1007: https://www.morphosource.org/concern/media/000514224?locale=en
UM-COS-1008: https://www.morphosource.org/concern/media/000514230?locale=en
UM-COS-1009: https://www.morphosource.org/concern/media/000514236?locale=en
UM-COS-1010: https://www.morphosource.org/concern/media/000514242?locale=en

LITERATURE CITED

Astruc, J. G., Hugueney, M., Escarguel, G., Legendre, S., Rage, J.-C., Coinçon, R. S., Sudre, J., & Sigé, B. (2003). Puycelci, nouveau site à vertébrés de la série molassique d’Aquitaine. Densité et continuité biochronologique dans la zone Quercy et bassins périphériques au Paléogène. *Geobios*, *36*, 629–648.

Augé, M. L. (1990). La faune de lézards et d’amphisbènes (Reptilia, Squamata) du gisement de Dormaal (Belgique, Eocène inférieur). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, *60*, 161–173.

Augé, M. L. (1992). *Campinosaurus woutersi* n.g. n.sp., Anguimorphe nouveau (Lacertilia) de l'Éocène inférieur de Dormaal (Belgique). Une relique éocène des Dorsetisauridae du Jurassique terminal/Crétacé basal? *Comptes rendus de l'Académie des Sciences*, *315*, 885–889.

Augé, M. L. (2003). La faune de Lacertilia (Reptilia, Squamata) de l'Éocène inférieur de Prémontré (Bassin de Paris, France). *Geodiversitas*, *25*, 539–574.

Augé, M. (2005). Evolution des lézards du Paléogène en Europe. *Mémoires du Muséum national d'Histoire naturelle, Paris*, 192, 1–369.

Augé, M. L., Duffaud, S., Lapparent de Broin, F., Rage, J.-C., & Vasse, D. (1997). Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin parisien): une herpétofaune de référence pour l'Eocène inférieur. *Géologie de la France*, *1*, 23–33.

Augé, M. L., Folie, A., Smith, R., Phélizon, A., Gigase, P., & Smith, T. (2022). Revision of the oldest varanid, *Saniwa orsmaelensis* Dollo, 1923, from the earliest Eocene of northwest Europe. *Comptes Rendus Palevol*, *21*, 511–529.

Augé, M. L., & Smith, R. (1997). Les Agamidae (Reptilia, Squamata) du Paléogène d'Europe occidentale. *Belgian Journal of Zoology*, *127*, 123–138.

Augé, M. L., & Smith, R. (2002). Nouveaux Lacertidae (Reptilia, Squamata) de l'Eocène inférieur européen. *Belgian Journal of Zoology*, *131*, 3–15.

Augé, M. L., & Sullivan, R. M. (2006). A new genus, *Paraplacosauriops* (Squamata, Anguidae, Glyptosaurinae) from the Eocene of France. *Journal of Vertebrate Paleontology*, *26*, 133–137.

Bolet, A. (2017). First early Eocene lizards from Spain and a study of the compositional changes between late Mesozoic and early Cenozoic Iberian lizard assemblages. *Palaeontologia Electronica*, *20.2.20A*, 1–22.

Burbrink, F.T., Grazziotin, F.G., Pyron, A.R., Cundall, D., Donnellan, S., Irish, F., Keogh, S.J., Kraus, F., Murphy, R.W., Noonan, B., & Raxworthy, C. J. (2020). Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology*, *69*, 502–520.

Camp, C. L. (1923). Classification of the lizards. *Bulletin of the American Museum of Natural History*, *48*, 289–481.

Čerňanský, A., & Augé, M. L. (2019). The Oligocene and Miocene fossil lizards (Reptilia, Squamata) of Central Mongolia. *Geodiversitas*, *41*, 811–839.

Čerňanský, A., Augé, M. L., & Phelizon, A. (2020). Dawn of lacertids (Squamata, Lacertidae): new finds from the upper Paleocene and the lower Eocene. *Journal of Vertebrate Paleontology*, e1768539.

Čerňanský, A., Augé, M., & Rage, J.C. (2015). A complete mandible of a new amphisbaenian reptile (Squamata, Amphisbaenia) from the late Middle Eocene (Bartonian, MP 16) of France. *Journal of Vertebrate Paleontology*, *35*, e902379.

Čerňanský, A., Daza, J. D., Smith, R., Bauer, A. M., Smith, T., & Folie, A. (2022). A new gecko from the earliest Eocene of Dormaal, Belgium - a thermophilic element of the "greenhouse world". *Royal Society Open Science*, *9*, 220429.

Čerňanský, A., & Klembara, J. (2017). A skeleton of *Ophisaurus* (Squamata: Anguidae) from the middle Miocene of Germany, with a revision of the partly articulated postcranial material from Slovakia using microcomputed tomography. *Journal of Vertebrate Paleontolology*, e1333515.

Čerňanský, A., & Smith, K.T. (2018). Eolacertidae: a new extinct clade of lizards from the Palaeogene; with comments on the origin of the dominant European reptile group – Lacertidae. *Historical Biology*, *30*, 994–1014.

Čerňanský, A., & Smith, K.T. (2019). The first juvenile specimen of *Eolacerta* (Squamata: Eolacertidae) from the early–middle Eocene of the Messel Pit (Germany). *Comptes Rendus Palevol*, *18*, 735–745.

Čerňanský, A., Smith, R., Smith, T., & Folie, A. (2023). Iguanian lizards (Acrodonta and Pleurodonta) from the earliest Eocene (MP 7) of Dormaal, Belgium: the first stages of these iconic reptiles in Europe. *Journal of Vertebrate Paleontology*, e2184696. https://doi.org/10.1080/02724634.2023.2184696.

Cicimurri, D. J., Knight, J. L., Self-Trail, J. M., & Ebersole, S. M. (2016). Late Paleocene glyptosaur (Reptilia: Anguidae) osteoderms from South Carolina, USA. *Journal of Paleontology*, *90*, 147–153.

Conrad, J. L. (2008). Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History*, *2008*, 1–182.

Conrad, J. L., & Norell, M. A. (2008). The braincases of two glyptosaurines (Anguidae, Squamata) and anguid phylogeny. American Museum Novitates, *3613*, 1–24.

Cope, E. D. (1877). Report on extinct vertebrates obtained in New Mexico by parties of the expedition of 1874. United States. *Geographical Surveys West of the 100th Meridian, Wheeler*, *4*, 1–370.

De Bast E., & Smith T. (2017) The oldest Cenozoic mammal fauna of Europe: implication of the Hainin reference fauna for mammalian evolution and dispersals during the Paleocene. *Journal of Systematic Palaeontology*, *15*, 741–785.

De Buffrénil, V., Sire, J.-Y., & Rage, J.-C. (2010). The histological structure of glyptosaurine osteoderms (Squamata: Anguidae), and the problem of osteoderm development in squamates. *Journal of Morphology*, *271*, 729–737.

Depéret, C. (1917). Monographie de la faune de mammifères fossiles du Ludien inférieur d’Euzet-les-Bains (Gard). *Annales de l’Université de Lyon, Nouvelle Série*, *40*, 288 p.

Dollo, L. (1923). *Saniwa orsmaelensis*, Varanide nouveau du Landénien supérieur d’Orsmael (Brabant). *Bulletin de la Société belge de géologie, de paléontologie et d’hydrologie*, *33*, 76–82.

Douglass, E. (1903). New vertebrates from the Montana Tertiary. *Annals of the Carnegie Museum*, *2*, 145–199.

Estes, R. (1983). Sauria Terrestria, Amphisbaenia. In P. Wellnhofer (Ed.), *Encyclopedia of Paleoherpetology, Part 10a*. Gustav Fischer Verlag, Stuttgart and New York, 249 pp.

Estes, R., de Queiroz, K., & Gauthier, J. A. (1988). Phylogenetic relationships within Squamata. In R. Estes, & G. K. Pregill (Eds.), *Phylogenetic Relationships of the Lizard Families*. Stanford University Press, Stanford, pp. 119–281.

Filhol, H. (1876). Sur les reptiles fossiles des phosphorites du Quercy. *Bulletin de la Société Philomathique de Paris*, *6*, 27–28.

Folie, A., Smith, R., & Smith, T. (2013). New amphisbaenian lizards from the Early Paleogene of Europe and their implications for the early evolution of modern amphisbaenians. *Geologica Belgica*, *16*, 227–235.

Fürbringer, M. (1900). Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Zeitschrift für Naturwissenschaften*, *34*, 215–718.

Gauthier, J. A., Kearney, M., Maisano, J. A., Rieppel, O., & Behlke, A. D. (2012). Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History*, *53*, 3–308.

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

Georgalis, G. L., Čerňanský, A., & Klembara, J. (2021). Osteological atlas of new lizards from the Phosphorites du Quercy (France), based on historical, forgotten, fossil material. In Steyer, J.-S., Augé, M. L. & Métais, G. (Eds.), *Memorial Jean-Claude Rage: A life of paleo-herpetologist*. *Geodiversitas*, *43*, 219–293.

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

Georgalis, G. L., & Scheyer T. M. (2021). Lizards and snakes from the earliest Miocene of Saint-Gérand-le-Puy, France: an anatomical and histological approach of some of the oldest Neogene squamates from Europe. *BMC Ecology and Evolution*, *21*, 144.

Georgalis, G. L., Villa, A., Ivanov, M., Vasilyan, D., & Delfino M. (2019). Fossil amphibians and reptiles from the Neogene locality of Maramena (Greece), the most diverse European herpetofauna at the Miocene/Pliocene transition boundary. *Palaeontologia Electronica*, *22.3.68*, 1–99.

Gervais, P. (1848-1852). *Zoologie et Paléontologie françaises (animaux vertébrés): ou nouvelles recherches sur les animaux vivants et fossiles de la France*. Arthus Bertrand, Paris, 271 pp.

Gilmore, C. W. (1928). The fossil lizards of North America. *Memoirs of the National Academy of Sciences*, *11*, 1–197.

Gingerich, P. D., & Smith, T. (2006). Paleocene-Eocene land mammals from three new latest Clarkforkian and earliest Wasatchian wash sites at Polecat Bench in the Northern

Bighorn Basin, Wyoming. *Contributions from the Museum of Paleontology*. *The University of Michigan*, *31*, 245–302.

Godinot, M., Blondel, C., Escarguel, G., Lézin, C., Pélissié, T., Tabuce, R., Vidalenc, D., (2021). Primates and Plesiadapiformes from Cos (Eocene; Quercy, France). *Geobios*, doi: https://doi.org/10.1016/j.geobios.2021.03.004

Gray, J. E. (1825). A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. *Annals of Philosophy*, *Series 2*, *10*, 193–217.

Gray, J. E. (1827). A synopsis of the genera of saurian reptiles, in which some new genera are indicated, and the others reviewed by actual examination. *The Philosophical Magazine, or Annals of Chemistry, Mathematics, Astronomy, Natural History, and General Science*, *2*, 54–58.

Haubold, H. (1977). Zur Kenntnis der Sauria (Lacertilia) aus dem Eozän des Geiseltales. In H. W. Matthes, & B. Thaler (Eds.), *Eozäne Wirbeltiere des Geiseltales*.Vol. 2. Wissenschaftliche Beiträge, Wittenberg, pp. 107–122.

Hecht, M. K., & Hoffstetter, R. (1962). Note préliminaire sur les Amphibiens et les Squamates du Landénien supérieur et du Tongrien de Belgique. *Bulletin de l 'Institut royal des Sciences naturelles de Belgique*, *38*, 1–30.

Hoffstetter, R. (1954). Sur la position systématique de *Necrosaurus*: saurien de l'Éocène européen. *Comptes Rendus de la Société géologique de France*, *1954*, 422–424.

Hoffstetter, R. (1955). Squamates de type moderne. In Piveteau J. (Ed.), *Traité de Paléontologie*. Volume 5. Masson et Compagnie, Paris, 606–662.

Hoffstetter, R. (1962). Observations sur les ostéodermes et la classification des anguides actuels et fossiles (Reptiles, Sauriens). *Bulletin du Muséum national d'Histoire naturelle*, *34*, 149–157.

Hyland, E.G., Sheldon, N. D., Cotton, J. M. (2017). Constraining the early Eocene climatic optimum: A terrestrial interhemispheric comparison. *GSA Bulletin*, *129*, 244–252

Inglis, G. N., Bragg, F., Burls, N. J., Cramwinckel, M. J., Evans, D., Foster, G. L., Huber, M., Lunt, D. J., Siler, N., Steinig, S., Tierney, J. E., Wilkinson, R., Anagnostou, E., de Boer, A. M., Dunkley Jones, T., Edgar, K. M., Hollis, C. J., Hutchinson, D. K., and Pancost, R. D. (2020). Global mean surface temperature and climate sensitivity of the early Eocene Climatic Optimum (EECO), Paleocene–Eocene Thermal Maximum (PETM), and latest Paleocene. *Climate of the Past*, *16*, 1953–1968

Kearney, M., & Rieppel, O. (2006). An investigation into the occurrence of plicidentine in the teeth of squamate reptiles. *Copeia*, 2006, 337–350.

Keller, T. (2009). Beiträge zur Kenntnis von *Placosauriops abderhaldeni* Kuhn, 1940 (Anguidae, Glyptosaurinae March, 1872) aus dem Mitteleozän der Grube Messel – Skelettanatomie, Taphonomie und Biomechanik. *Kaupia*, *16*, 3–145.

Klembara, J., Hain, M., & Čerňanský, A. (2019). The first record of anguine lizards (Anguimorpha, Anguidae) from the early Miocene locality Ulm – Westtangente in Germany. *Historical Biology*, *31*, 1016–1027.

Kuhn, O. (1940). Die Placosauriden und Anguiden aus dem Mittleren Eozän des Geiseltales. *Nova Acta Academia Leopoldina, Carolinska*, *53*, 461–486.

Laurent, Y., Adnet, S., Bourdon, E., Corbalan, D., Danilo, L., Duffaud, S., Fleury, G., Garcia, G., Godinot, M., Le Roux, G., Maisonnave, C., Métais, G., Mourer-Chauviré, C., Presseq, B., Sigé, B, & Solé, F. (2010). La Borie (Saint-Papoul, Aude): un gisement exceptionnel dans l'Éocène basal du Sud de la France. *Bulletin de la Société d'histoire naturelle de Toulouse*, *146*, 89–103.

Loréal, E., Syromyatnikova, E. V., Danilov, I. G., & Čerňanský, A. (2023). The easternmost record of the largest anguine lizard that has ever lived – *Pseudopus pannonicus*

(Squamata, Anguidae): new fossils from the late Neogene of Eastern Europe. *Fossil Record*, *26*, 51–84.

Marsh, O. C. (1871). Notice of some new fossil reptiles from the Cretaceous and Tertiary formations. *American Journal of Science*, *3(6)*, 447–459.

Marsh, O. C. (1872). Preliminary description of new Tertiary reptiles. Parts I and II. *American Journal of Science*, *4(3)*, 298–309.

McDowell, S. B., & Bogert, C. M. (1954). The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. *Bulletin of the American Museum of Natural History*, *105*, 1–142.

Meszoely, Ch. A. M. (1970). North American fossil anguid lizards. *Bulletin of the Museum of Comparative Zoology at Harvard College*, *139*, 87–149.

Oppel, M. (1811). *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. Joseph Lindauer, Munich, 87 p.

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

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

Pulou, R. (1980). Jean-André Poumarède et l’industrie des phosphates du Quercy au XIXe siècle. *Mémoires de l’Académie des Sciences, Inscriptions et Belles Lettres de Toulouse*, *16*, 83–92.

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

Rage, J.-C. (1978). 5. Squamates. In B. Geze, J.-C. Rage, F. Vergnaud-Grazzini, F. de Broin, E. Buffetaut, C. Mourier-Chauvire, J.-Y. Crochet, B. Sigé, J. Sudre, A. Remy, L. Langebadre, L., de Bonis, J. L. Hartenberger, & M. Vianey-Liaud (Eds.), La poche à Phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérior. *Palaeovertebrata*, *8*, 201–215.

Rage, J.-C. (1988). Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Éocène supérieur. I Amphibiens et Reptiles. *Palaeontographica Abteilung A*, *205*, 3–27.

Rage, J.-C. (2013). Mesozoic and Cenozoic squamates of Europe. In J. D. Gardner, & R. L. Nydam (Eds.), *Mesozoic and Cenozoic lissamphibian and squamate assemblages of Laurasia*. *Palaeobiodiversity and Palaeoenvironments*, *93*, 517–534.

Rage, J.-C., & Augé, M. L. (2003). Amphibians and squamate reptiles from the lower Eocene of Silveirinha (Portugal). *Ciências da Terra (UNL)*, *15*, 103–116.

Rage, J.-C., & Augé M. L. (2010). Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. *Geobios*, *43*, 253–268.

Rieppel, O., Conrad, J. L., & Maisano, J. A. (2007). New morphological data for *Eosaniwa koehni* Haubold, 1977 and a revised phylogenetic analysis. *Journal of Paleontology*, *81*, 760-769.

Seghetti, S. M., Georgalis G. L., Tschopp, E., & Delfino, M. (2022). A historical overview of the reptile fauna from the Eocene Bolca Fossil-Lagerstätte (Italy). *Bollettino della Società Paleontologica Italiana*, *61*, 119–143.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675.

Solé, F., Smith, T., De Bast, E., Codrea, V., & Gheerbrant, E. (2016). New carnivoraform latest Paleocene of Europe and their bearing on the origin and radiation of

Carnivoraformes (Carnivoramorpha, Mammalia). *Journal of Vertebrate Paleontology*, el082480.

Smith, K. T. (2009). A new lizard assemblage from the earliest Eocene (zone Wa0) of the Bighorn Basin, Wyoming, USA: biogeography during the warmest interval of the Cenozoic. *Journal of Systematic Palaeontology*, *7*, 299–358.

Smith, K. T. (2011). The long-term history of dispersal among lizards in the early Eocene: New evidence from a microvertebrate assemblage in the Bighorn Basin of Wyoming, USA. *Palaeontology*, *54*, 1243–1270.

Smith, K. T. (2017). First crocodile-tailed lizard (Squamata: Pan- *Shinisaurus*) from the Paleogene of Europe. *Journal of Vertebrate Paleontology*, e1313743.

Smith, K. T., Čerňanský, A., Scanferla, A., & Schaal, S. (2018). Lizards and snakes: warmth-loving sunbathers. In K. T, Smith, S. F. K. Schaal, & J. Habersetzer (Eds.), *Messel, An Ancient Greenhouse Ecosystem*. Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, pp. 122–147.

Smith, K.T., & Georgalis G. L. (2022). The diversity and distribution of Palaeogene snakes - a review, with comments on vertebral sufficiency. In D. Gower, & H. Zaher (Eds.), *The Origin and Early Evolution of Snakes*. Cambridge: Cambridge University Press, pp. 55–84.

Smith, K. T., & Habersetzer, J. (2021). The anatomy, phylogenetic relationships, and autecology of the carnivorous lizard "*Saniwa*" *feisti* Stritzke, 1983 from the Eocene of Messel, Germany. In A. Folie, E. Buffetaut, N. Bardet, A. Houssaye, E. Gheerbrant, & M. Laurin (Eds), *Palaeobiology and palaeobiogeography of amphibians and reptiles: An homage to Jean-Claude Rage*. *Comptes Rendus Palevol*, *20 (23)*, 441–506.

Smith, K. T., & Scanferla, A. (2021). A nearly complete skeleton of the oldest definitive erycine boid (Messel, Germany). *Geodiversitas*, *43*, 1–24.

Smith, T., & Smith, R. (2013). A land micro-mammal fauna from the Early Eocene marine Egem deposits (NP12, Belgium) and the first occurrence of the peradectid marsupial *Armintodelphys* outside North America. *Geologica Belgica*, *16*, 302–310.

Stritzke, R. (1983). *Saniwa feisti* n. sp., ein Varanide (Lacertilia, Reptilia) aus dem Mittel-Eozän von Messel bei Darmstadt. *Senckenbergiana Lethaea*, *64*, 497–508.

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

Sullivan, R. M. (2019). The taxonomy, chronostratigraphy and paleobiogeography of glyptosaurine lizards (Glyptosaurinae, Anguidae). *Comptes Rendus Palevol*, *18*, 747–763.

Sullivan, R. M., & Augé, M. L. (2006). Redescription of the holotype of *Placosaurus rugosus* Gervais 1848-1852 (Squamata, Anguidae, Glyptosaurinae) from the Eocene of France and a revision of the genus. *Journal of Vertebrate Paleontology*, *26*, 127–132.

Sullivan, R. M., Augé, M. L., Wille, E., & Smith, R. (2012). A new glyptosaurine lizard from the earliest Eocene of Dormaal, Belgium. *Bulletin de la Société géologique de France*, *183*, 629–635.

Sullivan, R. M., & Dong, L. (2018). *Stenoplacosaurus mongoliensis*, a new generic name for *Placosaurus mongoliensis* (Anguidae, Glyptosaurinae) from the Shara Murun Formation, Nei Mongol (Inner Mongolia), China. In S. G. Lucas & R. M. Sullivan (Eds.), *Fossil Record 6. New Mexico Museum of Natural History and Science Bulletin*, *79*, 691–694.

Sullivan, R. M., Keller T., & Habersetzer, J. 1999. Middle Eocene (Geiseltalian) anguid lizards from Geiseltal and Messel, Germany. I. *Ophisauriscus quadrupes* Kuhn 1940. *Courier Forschungsinstitut Senckenberg*, *216*, 97–129.

Syromyatnikova, E. V., Klembara, J., & Redkozubov, O. (2022). The Pliocene *Ophisaurus* (Anguidae) from Eastern Europe: new records and additions to the history of the genus and its palaeoenvironment. *Palaeobiodiversity and Palaeoenvironments*. https://doi.org/10.1007/s12549-022-00556-w.

Uetz, P., Freed, P., & Hošek, J. (2023). *The Reptile Database*. http://www.reptile-database.org. [accessed February 2023]

Vianey-Liaud, M., Vidalenc, D., Orliac M. J., Maugoust, J., Lézin, C., & Pélissié, T. (2022). Rongeurs de la localité éocène de Cos (Tarn-et-Garonne, Quercy, France). Comparaison avec les rongeurs de localités de la transition Éocène inférieur/Éocène moyen. *Geodiversita*s, *44*, 753–800.

Villa, A., Wings, O., & Rabi, M. (2022). A new gecko (Squamata, Gekkota) from the Eocene of Geiseltal (Germany) implies long-term persistence of European Sphaerodactylidae. *Papers in Palaeontology*, *8*, 1434.

Williams, C., Kirby, A., Marghoub, A., Kéver, L., Ostashevskaya-Gohstand, S., Bertazzo, S., Moazen, M., Abzhanov, A., Herrel, A., Evans, S. E., & Vickaryous, M. K. (2022). Review of the osteoderms of lizards (Reptilia: Squamata). *Biological Reviews*, *97*, 1–19.

Zheng, Y., & Wiens, J. J. (2016). Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution*, *94*, 537–547.

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

Figure legend

FIGURE 1. Location of the Cos locality in France. [planned for 2/3 of full-page width]

FIGURE 2. *Sullivania gallica* gen. et sp. nov. from the early Eocene Cos locality of France. UM-COS-1001 (holotype) anterior portion of fused frontals: in **A**, dorsal; **B**, outline drawing showing the armour division pattern; **C**, ventral; and **D**, lateral views (all micro-CT visualizations). **E**, axial section at the mid-level of the dorsoventral thickness; and **F**, coronal section at the level of the frontal cranial crests. [planned for page width]

FIGURE 3. *Sullivania gallica* gen. et sp. nov. from the early Eocene Cos locality of France. UM-COS-1000 (paratype), nearly complete right frontal: in **A**, dorsal; **B**, photograph with line drawing indicating the interpretation of osteoderm distribution; **C**, ventral; and **D**, lateral views (micro-CT visualizations). **E**, Axial section at the mid-level of the dorsoventral thickness; and **F**, coronal section at the level of the frontal cranial crests. UM-COS-1003 (paratype), posterior portion of right frontal: in **G**, dorsal; and **H**, ventral views (all micro-CT visualizations). [planned for page width]

FIGURE 4. The reconstruction of complete frontal of *Sullivania gallica* gen. et sp. nov. comparing it to frontals of *Gaultia silvaticus,* from the earliest Eocene of Wyoming, USA; *Placosaurus estesi* and *P. rugosus*, from the middle and late Eocene of France; and *Stenoplacosaurus mongoliensis* from the late-middle Eocene of Mongolia (all are dorsal views, except G, which is left lateral view). **A**, *Sullivania gallica*, reconstruction based on

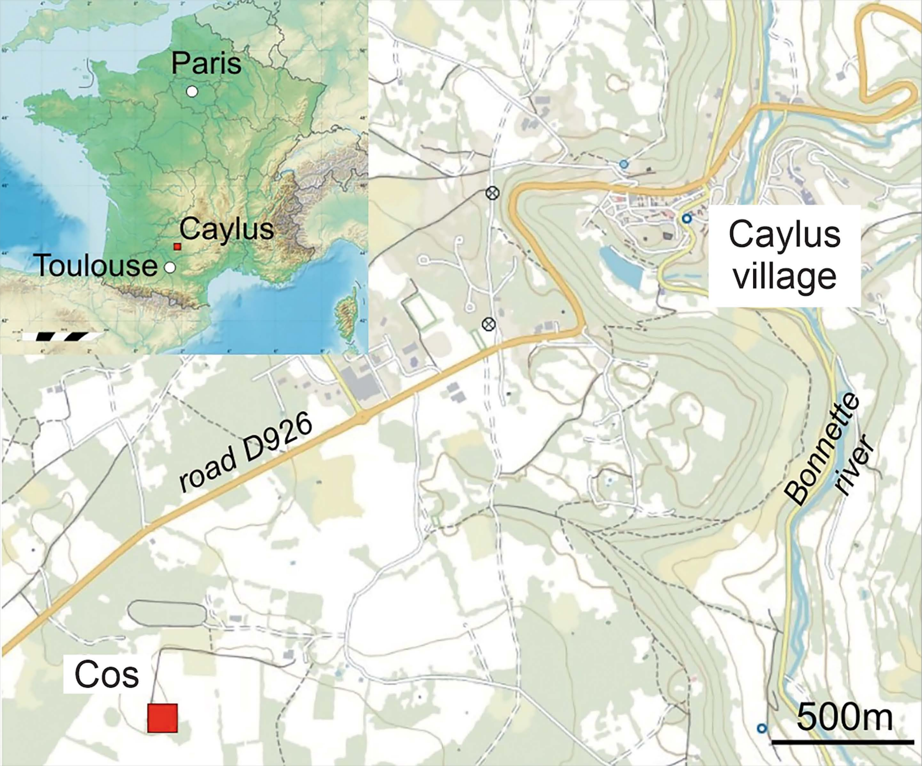
UM-COS-1000 and 01; **B**, *Gaultia silvaticus* UCMP 216000, (holotype) middle portion of frontal and **C**, UCMP 150966 (paratype) partial left frontal (modified from Smith, 2009); **D**, *Placosaurus estesi* (MNHN QU-17735, holotype) nearly complete frontal; **E**, *P. rugosus* (MNHN 1906-25, holotype) nearly complete frontal and left prefrontal; and **F**, **G**, *Stenoplacosaurus mongoliensis* (AMNH 6669, holotype), left frontal (modified from Sullivan & Dong, 2018). The arrow in *Gaultia* (**B**) indicates the position of the mid-line between the left and right frontals (see Smith, 2009). The dotted line in *P. rugosus* (**E**) indicates the frontal – prefrontal contact. [planned for page width]

FIGURE 5. Glyptosauridae indeterminate from the early Eocene Cos locality of France. UM-COS-1002 left maxilla. **A**, left lateral view; **B**, medial (lingual) view; **C**, occlusal (ventral) view; and **D**, dorsal view. **A**-**D** are micro-CT visualizations; UM-COS-1011, right maxilla. **E**, right lateral view, F, medial (lingual) view, **G**, occlusal (ventral) view (with close-up of teeth in ventromedial view); and **H**, dorsal view. [planned for page width]

FIGURE 6. Glyptosauridae indeterminate (**A**-**J**) and Anguioidea indet. (**K**-**M**) from the early Eocene Cos locality of France. Isolated cephalic osteoderms. UM-COS-1004, hexagonal osteoderm: **A**, dorsal; **B**, ventral; and **C**, lateral views. UM-COS-1005, polygonal osteoderm: **D**, external and **E**, internal views. Isolated body osteoderms. UM-COS-1006: **F**, external; **G**, internal and **H**, lateral views. UM-COS-1007: **I**, external; and **J**, internal views. UM-COS-1008; **K**, external; **L**, internal; and **M**, oblique lateral views. All images are micro-CT visualizations. [planned for page width]

FIGURE 7. Palaeovaranidae indeterminate from the early Eocene Cos locality of France. UM-COS- 1009, nearly complete frontal. **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, right lateral; and **E**, anterodorsal views. All images are micro-CT visualizations. [planned for page width]

FIGURE 8. Varanoidea indeterminate from the early Eocene Cos locality of France. UM-COS-1010, left maxilla. **A**, lateral; **B**, medial; **C**, dorsomedial; **D**, dorsal; and **E**, ventral views (A-E are micro-CT visualizations); and **F**, μCT slice of tooth bases showing the presence of plicidentine. [planned for page width]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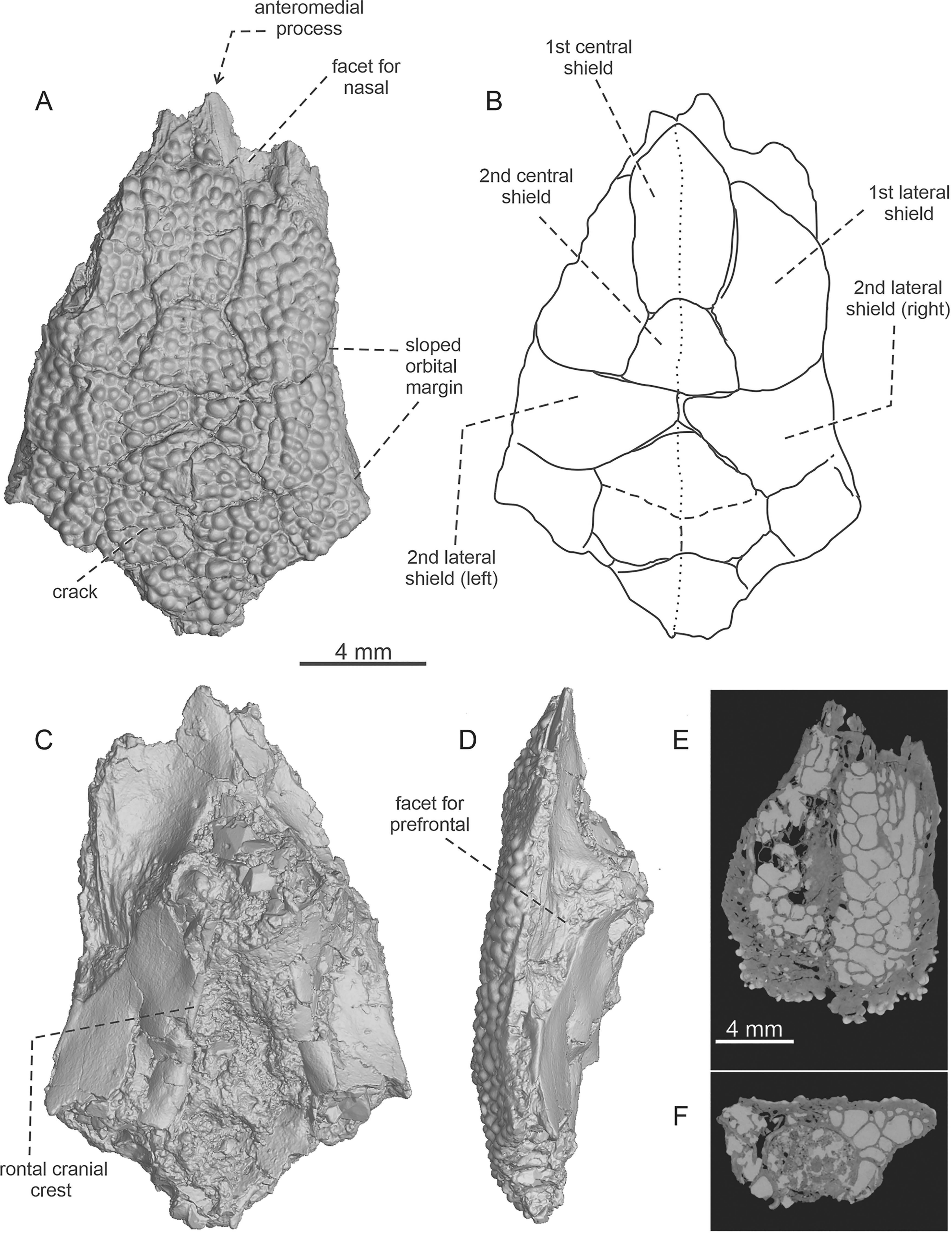
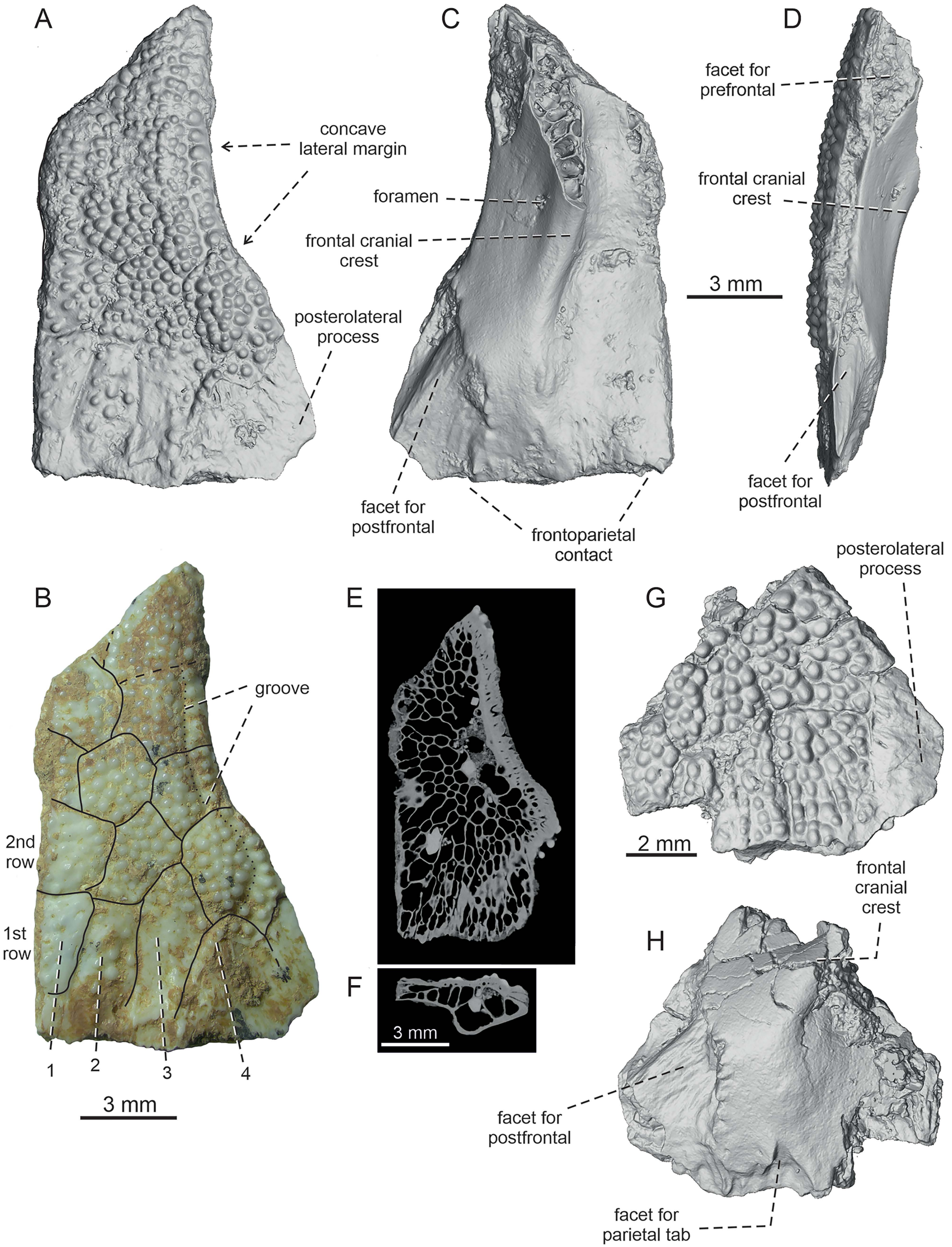

anteromedial process
facet for nasal
A
B
1st central shield
2nd central shield
1st lateral shield
2nd lateral shield (right)
sloped orbital margin
2nd lateral shield (left)
crack
4 mm
C
D
E
F
facet for prefrontal
frontal cranial crest
4 mm


A
concave
lateral margin
posterolateral
process
C
foramen
frontal cranial
crest
facet for
postfrontal
frontoparietal
contact
D
facet for
prefrontal
frontal cranial
crest
3 mm
facet for
postfrontal
B
groove
2nd
row
1st
row
1
2
3
4
3 mm
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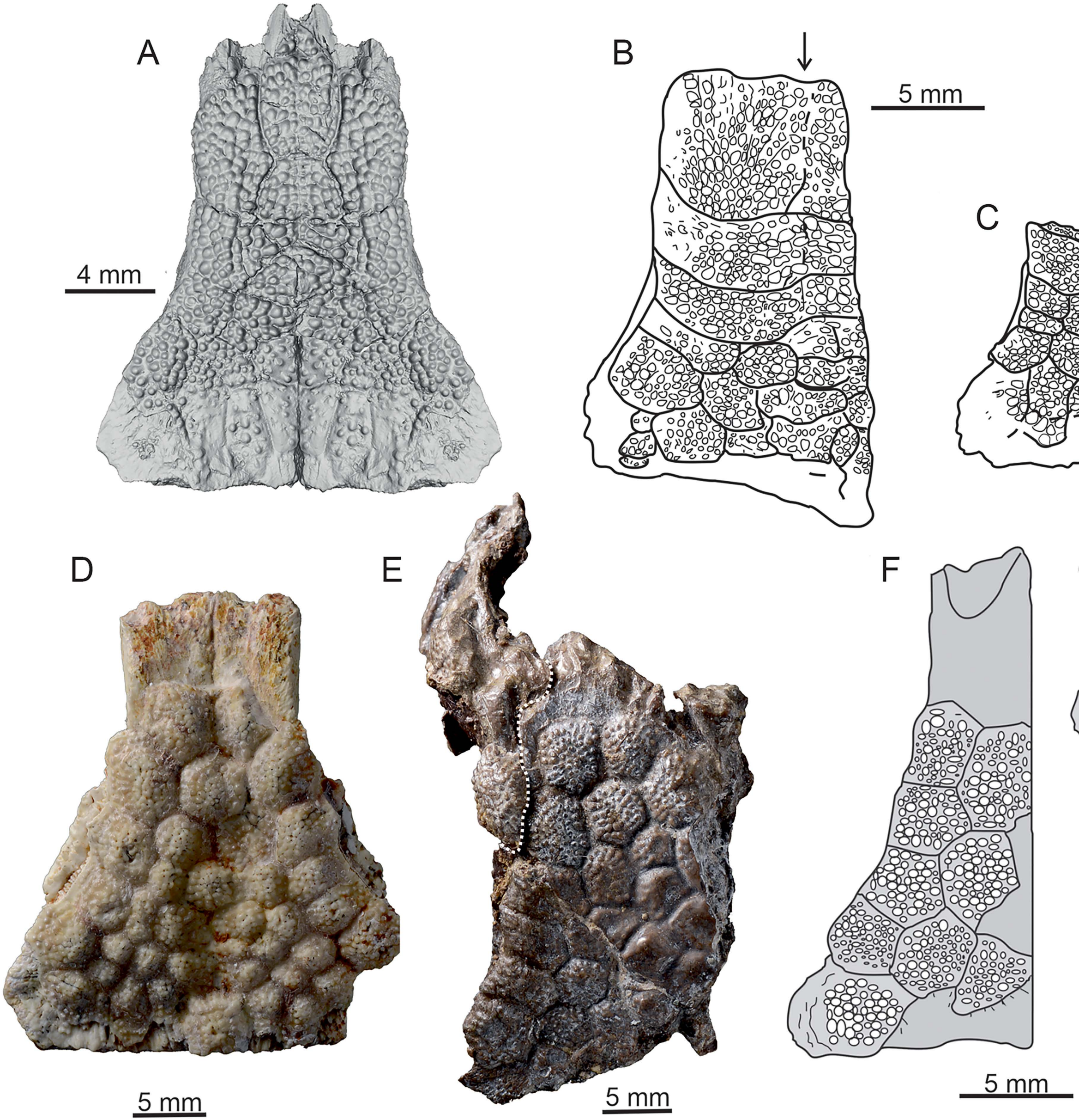
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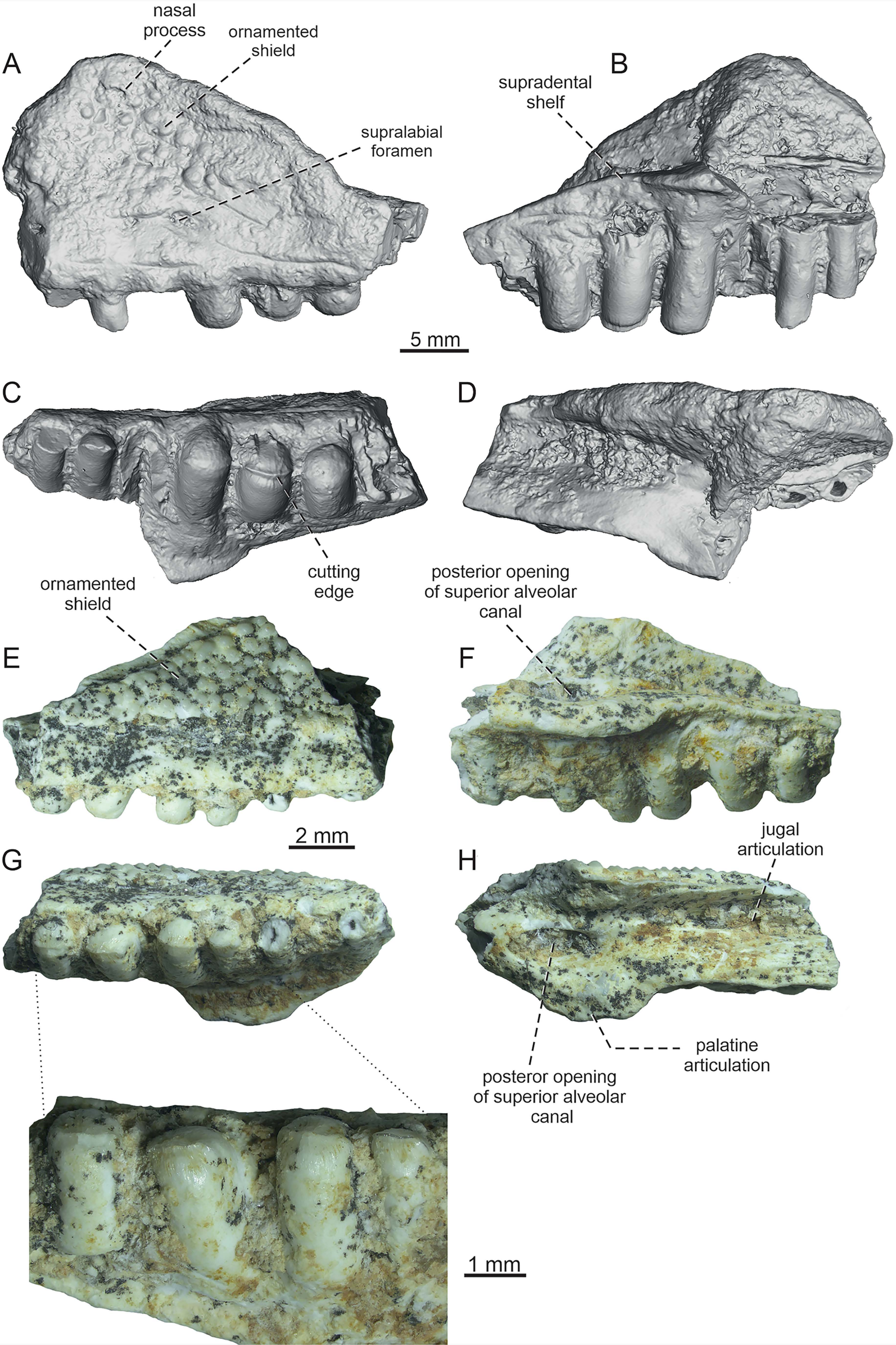
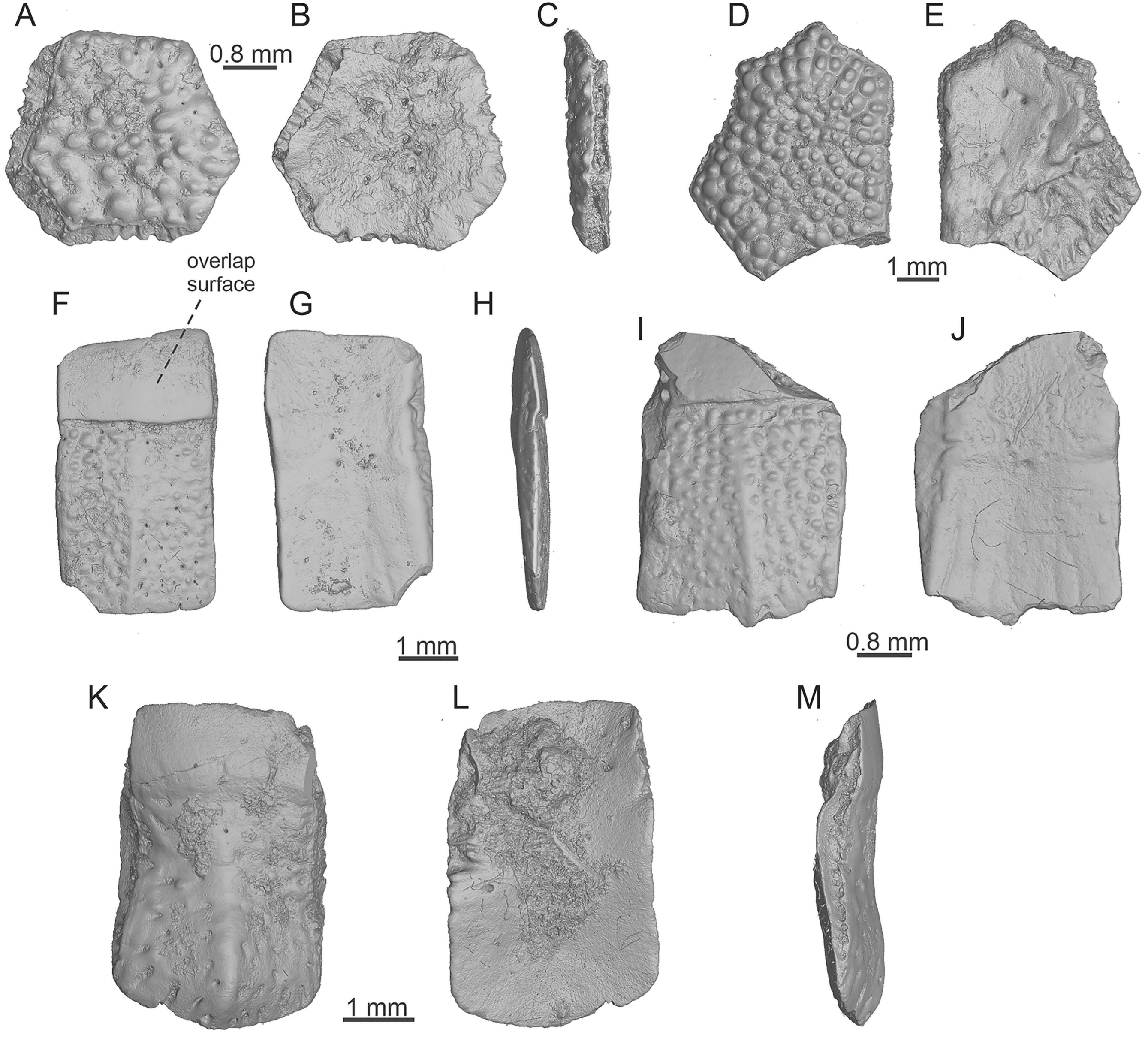

nasal process
ornamented shield
supralabial foramen
A
B
supradental shelf
5 mm
C
D
cutting edge
ornamented shield
posterior opening of superior alveolar canal
E
F
2 mm
G
H
jugal articulation
palatine articulation
posteror opening of superior alveolar canal
1 mm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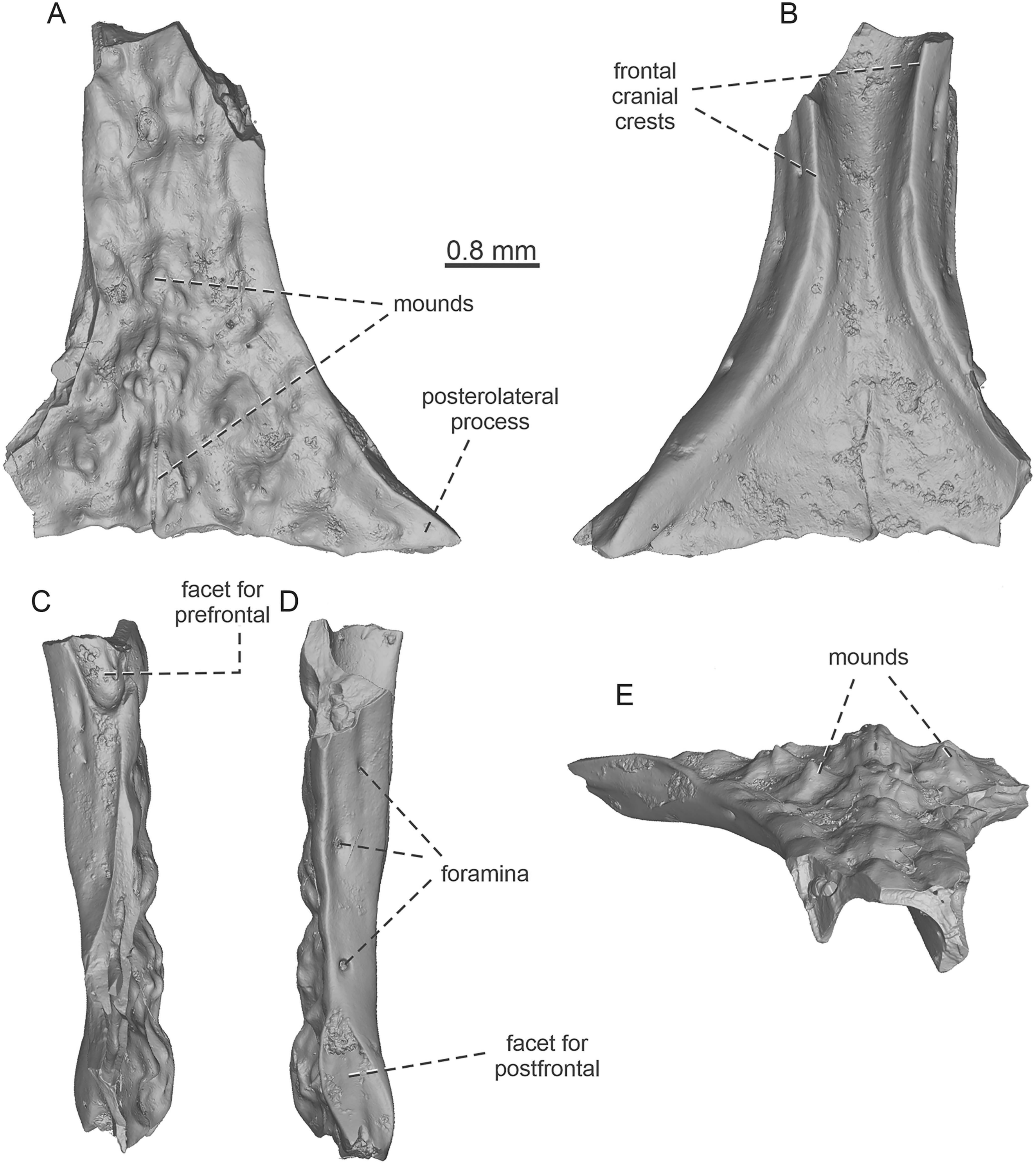
K
L
M
1 mm


A
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frontal
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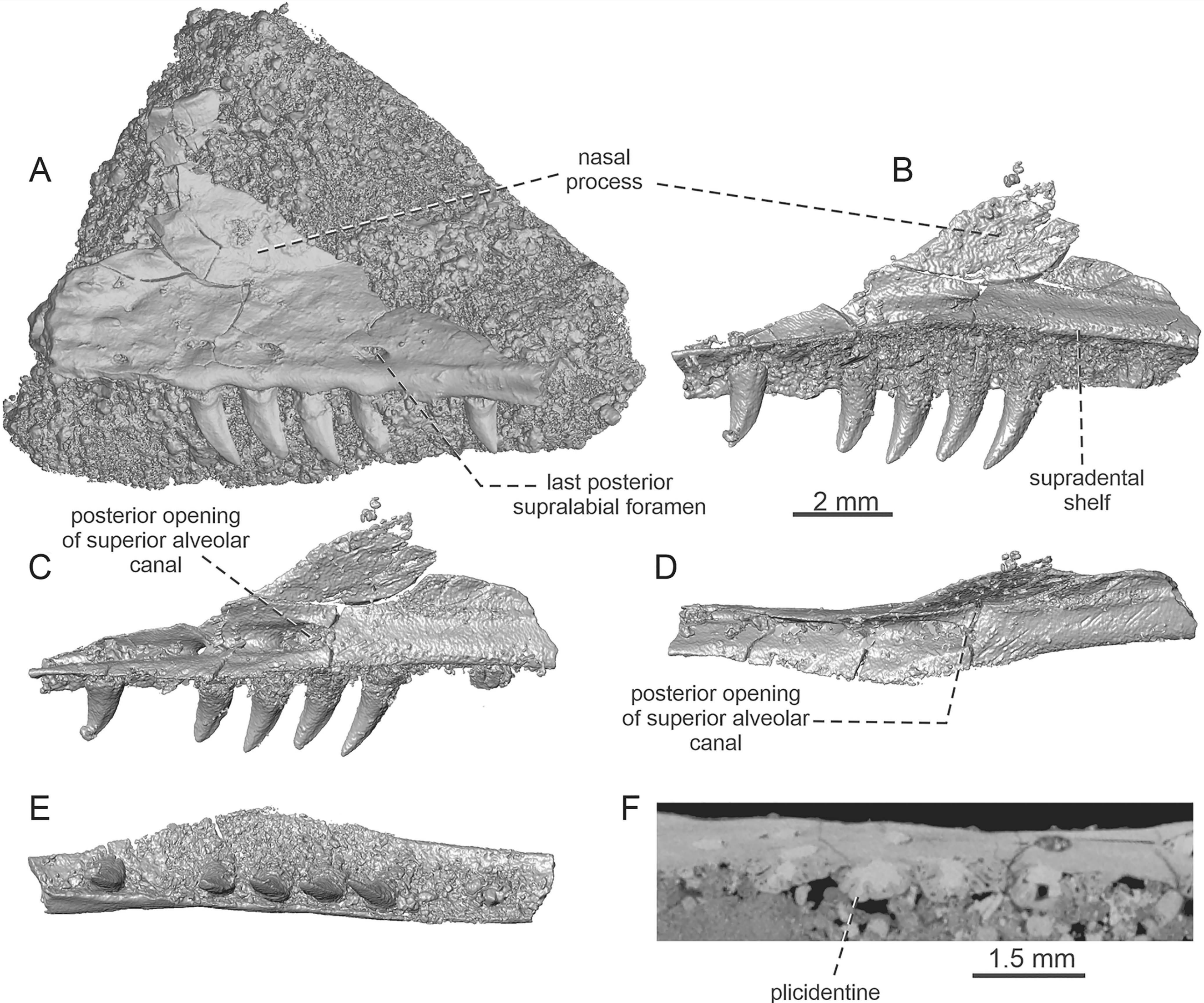
facet for
postfrontal


A
nasal process
B
last posterior supralabial foramen
2 mm
supradental shelf
posterior opening of superior alveolar canal
C
D
posterior opening of superior alveolar canal
E
F
1.5 mm
plicidentine