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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

ANDREJ ČERNANSKÝ[1 *], RODOLPHE TABUCE[2], AND DOMINIQUE VIDALENC[3]

[1]Department of Ecology, Laboratory of Evolutionary Biology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, 84215, Bratislava, Slovakia, cernansky.paleontology@gmail.com;

[2]ISEM, Université de Montpellier, CNRS, IRD, EPHE, Cc 064, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France;

[3]103 Avenue François Mitterand, 31800 Saint-Gaudens, France

*corresponding author: Andrej Čerňanský, cernansky.paleontology@gmail.com

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.

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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

123 The studied material is housed at the University of Montpellier, cataloged under
124 individual UM-COS-numbers. The standard anatomical orientation system is used throughout
125 this paper, and terminology describing individual bone structures is based on Rage & Augé
126 (2010).
127
128 **X-ray Microtomography, Three-Dimensional Visualization, Photography and**
129 **Reconstruction**
130 The fossil specimens were imaged on micro-computed tomography (CT) at the micro-
131 CT facility, Slovak Academy of Sciences in Banská Bystrica, Slovakia, using a Phoenix mikro-
132 CTv|tome|x L240. The settings were as follows: VxSize = 0.01999999; Current = 150; Voltage
133 = 130; Inttime = 20000; Average = 2; Steps = 1600; Steps360 = 2200; Filter = 0.1 mm Cu. The
134 images were recorded over 360°. The CT data sets were analysed using VG Studio Max 3.1.
135 and Avizo 8.1. The photographs of the UM-COS-1011 maxilla were taken with a Leica M205
136 C binocular microscope with an axially mounted DFC 290 HD camera; software: LAS (Leica
137 Application Suite) 4.1.0 (build 1264). The image processing program ImageJ (Schneider et al.,
138 2012) was used for measurements. For frontal reconstruction, the missing areas were restored
139 by mirror imaging of the holotype and paratype, and estimation of the posterior portion is based
140 on the preserved paratype. The holotype (UCMP 216000) and paratype (UCMP 150966) of
141 *Gaultia silvaticus* were drawn from photographs published by Smith (2009: fig. 18). The
142 holotype of *Stenoplacosaurus mongoliensis* (AMNH 6669 left frontal) was drawn based on
143 photographs published by Sullivan & Dong (2018: fig. 1).
144
145 **Geological Setting and Associated Fauna**
146 Located in the southern part of the ‘Causses du Quercy’ plateau, the fissure fills of Cos
147 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

273 at about mid-orbit (the minimum width of the single right frontal in this area is 5.9 mm). The
274 external surfaces of both specimens are almost completely covered by tuberculated
275 osteoderms of various irregular, polygonal (rhomboidal, hexagonal) to roughly ovoid outlines.
276 The osteoderms are completely fused to the frontal and separated one from another by sulci.
277 The ornamentation is formed by small rounded discrete tubercles that are regularly and
278 densely arranged. The osteodermal shields on the posterior portion in UM-COS-1000, close to
279 the more or less straight contact with the parietal, are weakly ornamented. Only few tubercles
280 are present in this section on an otherwise smooth surface; however, the dorsal surface in this
281 region seems to be slightly eroded. The posterolateral corner is smooth, although it appears
282 that some partial covering was originally here but now is lost. The evidence of this is that a
283 partly preserved medial margin of the shield still has several tubercles. Thus, the posterior
284 portion of the right frontal possessed four osteodermal shields arranged in a mediolateral row.
285 Thus, the frontal is relatively broad. These osteroderms are anteroposteriorly long, roughly
286 trapezoidal except for the third one (Fig. 3B), which has a triangular end due to hexagonal
287 shape of neighboring osteoderms in the second row. This second posterior row, located
288 anterior to the first one (at the level of the anterior beginning of the postfrontal facet),
289 possesses three osteoderms. They differ in shape from those forming the first posterior row,
290 being polygonal (roughly hexagonal). The same condition is present in UM-COS-1003,
291 although the ornamentation is strongly developed here. In the mid-region of UM-COS-1000,
292 there is a shallow light groove close to the orbital margin. This groove extends almost parallel
293 to this margin (Fig. 3B).
294 In ventral view, a frontal cranial crest can be observed in both specimens. Posteriorly,
295 it widens, gradually diminishing dorsally. On the lateral side of the crest, a foramen is visible.
296 The crest fades out at the beginning of the posterolateral process of the frontal (in both
297 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.e., 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.

448

449 **Varanoidea indet.**

450 (Fig. 8)

451

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

453

454 **Description**

455 **Maxilla—** The nearly complete left maxilla is preserved in matrix, with the lateral
456 side visible (Fig. 8A). The anterior portion is broken. The preserved portion has a maximum
457 anteroposterior length of 10.2 mm and a maximum height of 4.6 mm, measured from the
458 ventral edge of the maxilla to the uppermost extent of the nasal process. The nasal process of
459 the maxilla is rather thin and has a slightly concave smooth surface with a few fractures along
460 the anterior half of the process due to crushing. The posterior margin of the nasal process
461 slopes posteroventrally at an angle of 28° where it ends near a small slit at the level of the last
462 preserved tooth. The external surface of the process is pierced by a series of four large
463 supralabial foramina along the external labial margin of the tooth row. In addition, there are
464 several smaller foramina located anterodorsally to the anteriormost preserved tooth. The
465 maxilla bears five complete teeth and has positions for four others. Posterior to the last labial
466 foramen, four tooth positions are present. The supradental shelf is relative thin, but widens
467 anteriorly (Fig. 8B). It protrudes medially, reaching its maximum at the level between the
468 fourth and fifth tooth position (counted from posterior) because of its contact with palatine.
469 The posterior opening of the superior alveolar canal is large and located at the level of the
470 sixth tooth position (counted from posterior). The medial surface of the preserved portion of
471 nasal process of maxilla is smooth and no nasal crest on the dorsomedial surface can be
472 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

498 characterized by irregular plate-like osteoderms that cover the skull roof (Sullivan, 1979, 2019).
499 Thus, isolated glyptosaurine frontals (and parietals) can be identified based on the presence of
500 hexagonal/polygonal tuberculate osteoderms covering the skull roof. For this reason, the Cos
501 frontal specimens clearly represents a member of Glyptosaurinae.

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

516 **The early Eocene glyptosaurines compared to post-early Eocene glyptosaurines**
517 **in Europe—**All glyptosaurine frontals from Cos described here most likely belong to the
518 same taxon as they have the same flat osteoderm morphology and display similar distribution
519 pattern on the frontal where they correspond and are similar size. Moreover, they are
520 comparable in size and come from the same locality. These frontals are markedly different
521 from *Placosaurus* (Sullivan & Augé, 2006; see Diagnosis and descriptions here). For this
522 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

548 fossil lizard record is too poor to draw any definite conclusions regarding faunal exchanges.
549 Interestingly, the frontal of *Sullivania gallica* from France resembles *Gaultia silvaticus* from
550 the earliest Eocene (biozone Wa-0, Willwood Formation) of Wyoming (Smith, 2009).
551 The holotype of *Gaultia silvaticus* is an incomplete fused frontal (although no
552 evidence of a suture is apparent on the ventral surface and most of the right half of the bone is
553 broken away, Smith, 2009: fig. 18D, Fig. 4B) diagnosed by: (1) apically flat osteodermal
554 shields covering the frontal and (2) different division of osteodermal cover relative to the
555 typical hexagonal one in other glyptosaurines. However, several differences are notable,
556 especially in the distribution of osteodermal shields and their shapes; in the anterior portion,
557 osteodermal shields are wide in *Gaultia*, mediolaterally elongated and chevron-shaped. They
558 form several lines, with two prominent rows of osteoderms extending along the mediolateral
559 width of the frontal. In contrast, most frontal osteoderms in *Sullivania* are anteroposteriorly
560 elongate rather than wide and, moreover, there is the presence of leaf-shaped first central
561 osteoderm. However, the second lateral left osteoderm crosses over the entire mediolateral
562 width of the frontal in *Sullivania*, having contact with the right one along the mid-line, similar
563 to that seen in *Gaultia*. The overall shape of these lateral osteoderms is different compared to
564 the shevron-shaped osteoderms in *Gaultia*; posteriorly, the osteodermal shields in *Gaultia* are
565 divided into convex polygons that are smaller than the chevrons. However, there is no
566 indication of the presence of anteroposteriorly elongated, roughly trapezoidal osteoderms in
567 the posterior region of both paratype frontals of *Sullivania*.
568 A close relationship between *Gaultia* and *Sullivania* than to *Placosaurus* and
569 *Glyptosaurus* cannot be ruled out. Assuming that they are closely related, *Sullivania* seems to
570 retain some characteristics from its North American ancestor. It worth noting that half of the
571 mammal taxa from the early Eocene of North America are closely related to the mammalian
572 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

598 now, we decided to tentatively assign *Sullivania* to Glyptosaurinae. The phylogenetic
599 relationships of *Sullivania* and *Placosaurus* are unknown. Taking account that the taxonomy
600 is based on the frontal bone, *Stenoplacosaurus* from presumably the late-middle Eocene of
601 Mongolia is morphologically more similar to *Placosaurus* (previously, it was even placed to
602 *Placosaurus* [Sullivan & Augé, 2006] and later placed to its own genus [Sullivan & Dong,
603 2018]) than to *Sullivania* gen. nov. Thus, an Asian origin of *Placosaurus* cannot be excluded.
604 Owing to an incomplete glyptosaurine fossil record between the early and late Eocene in
605 Europe, their evolution and distribution patterns between these distant regions remain largely
606 unresolved.
607
608 **Varanoidea**
609 UM-COS 1009 represents a "miniature" palaeovaranid. It differs from currently
610 known genera by the following combination of features: (1) overall small size; the frontals of
611 *Paranecrosaurus feisti* (Stritzke, 1983), which is known only from the early–middle Eocene
612 of Messel in Germany, are much larger (18.2 mm in the holotype and even 30.8 in the
613 paratype; see Smith & Habersetzer, 2021); (2) the non-paired (fused) narrow frontal, as in
614 *Palaeovaranus* Zittel, 1887–1890 (Georgalis et al., 2021) and *Paranecrosaurus feisti*
615 (Stritzke, 1983) (Smith & Habersetzer, 2021), unlike the paired frontals in *Eosaniwa*
616 Haubold, 1977 (Rieppel et al., 2007); (3) the type of an ornamentation. Its ornamentation,
617 which consists of small, densely arranged mounds, slightly resembles that of *Palaeovaranus*
618 *lismonimenos* Georgalis, Čerňanský & Klembara, 2021 (Georgalis et al., 2021).
619 *Palaeovaranus lismonimenos* was previously reported from the late Eocene (~ MP 17, see
620 Georgalis et al., 2021), whereas the Cos frontal is much older. However, the detailed surface
621 texture is different – the ornamentation of the Cos specimen is more complex, having also
622 several spikes forming each mound (rather than possessing more-or-less simple mounds). The

623 ornamentation of UM-COS 1009 differs from the distinct sculpturing pattern observed on the
624 frontal of the holotype of *Melanosauroides giganteus* Kuhn, 1940 from Geiseltal. The dorsal
625 surface of the frontal of *M. giganteus* possesses broad, apically flat, rugose patches that
626 appear to be fused broad (not distinctly keeled) osteoderms (Georgalis, 2017; Smith &
627 Habersetzer, 2021). The dorsal surface of the frontal of *Paranecrosaurus* Smith &
628 Habersetzer, 2021 frontal is also different (Smith & Habersetzer, 2021); and (4) the long
629 posterolateral process relative to the the overall size of the frontal, as *Paranecrosaurus* (Smith
630 & Habersetzer, 2021), and unlike the short process in *Palaeovaranus* (Georgalis et al., 2021)
631 and *Eosaniwa* (Rieppel et al., 2007).
632 UM-COS 1009 represents most likely a new taxon, but the taxonomy of
633 palaeovaranids is now mainly based on the parietal morphology (Georgalis et al., 2021). For
634 this reason, we identified this frontal only as Palaeovaranidae indet.
635 It is unclear whether the maxilla (UM-COS 1010) and the frontal (UM-COS 1009)
636 represent a single taxon, although they are comparable in size and come from the same
637 locality. The overall morphology and plicidentine support allocation of the maxilla to a
638 varanoid (Kearney and Rieppel, 2006; Georgalis & Scheyer, 2019). It cannot be referred to
639 Shinisauridae, a group of anguimorph presence that is well-documente from the Eocene of
640 Europe (Smith, 2017; Smith et al., 2018). The maxilla has several teeth posterior to the last
641 labial foramen where at least four tooth positions are preserved. This condition resembles
642 *Saniwa orsmaelensis* Dollo, 1923, which is known from Dormaal (Augé et al., 2022). Indeed,
643 the teeth and the concave lateral surface (the posterior portion of the maxilla is slightly bent
644 laterally) of the Cos specimen resemble the condition in this taxon (Augé et al., 2022: fig. 2).
645 The geological age of the maxilla would also be consistent with the presence of *Saniwa* in
646 Cos. However, several tooth positions posterior to the last labial foramen are also present in
647 *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.

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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

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989 **Figure legend**

990

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

992

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

998

999 FIGURE 3. *Sullivania gallica* gen. et sp. nov. from the early Eocene Cos locality of France.
1000 UM-COS-1000 (paratype), nearly complete right frontal: in **A**, dorsal; **B**, photograph with
1001 line drawing indicating the interpretation of osteoderm distribution; **C**, ventral; and **D**, lateral
1002 views (micro-CT visualizations). **E**, Axial section at the mid-level of the dorsoventral
1003 thickness; and **F**, coronal section at the level of the frontal cranial crests. UM-COS-1003
1004 (paratype), posterior portion of right frontal: in **G**, dorsal; and **H**, ventral views (all micro-CT
1005 visualizations). [planned for page width]

1006

1007 FIGURE 4. The reconstruction of complete frontal of *Sullivania gallica* gen. et sp. nov.
1008 comparing it to frontals of *Gaultia silvaticus,* from the earliest Eocene of Wyoming, USA;
1009 *Placosaurus estesi* and *P. rugosus*, from the middle and late Eocene of France; and
1010 *Stenoplacosaurus mongoliensis* from the late-middle Eocene of Mongolia (all are dorsal
1011 views, except G, which is left lateral view). **A**, *Sullivania gallica*, reconstruction based on

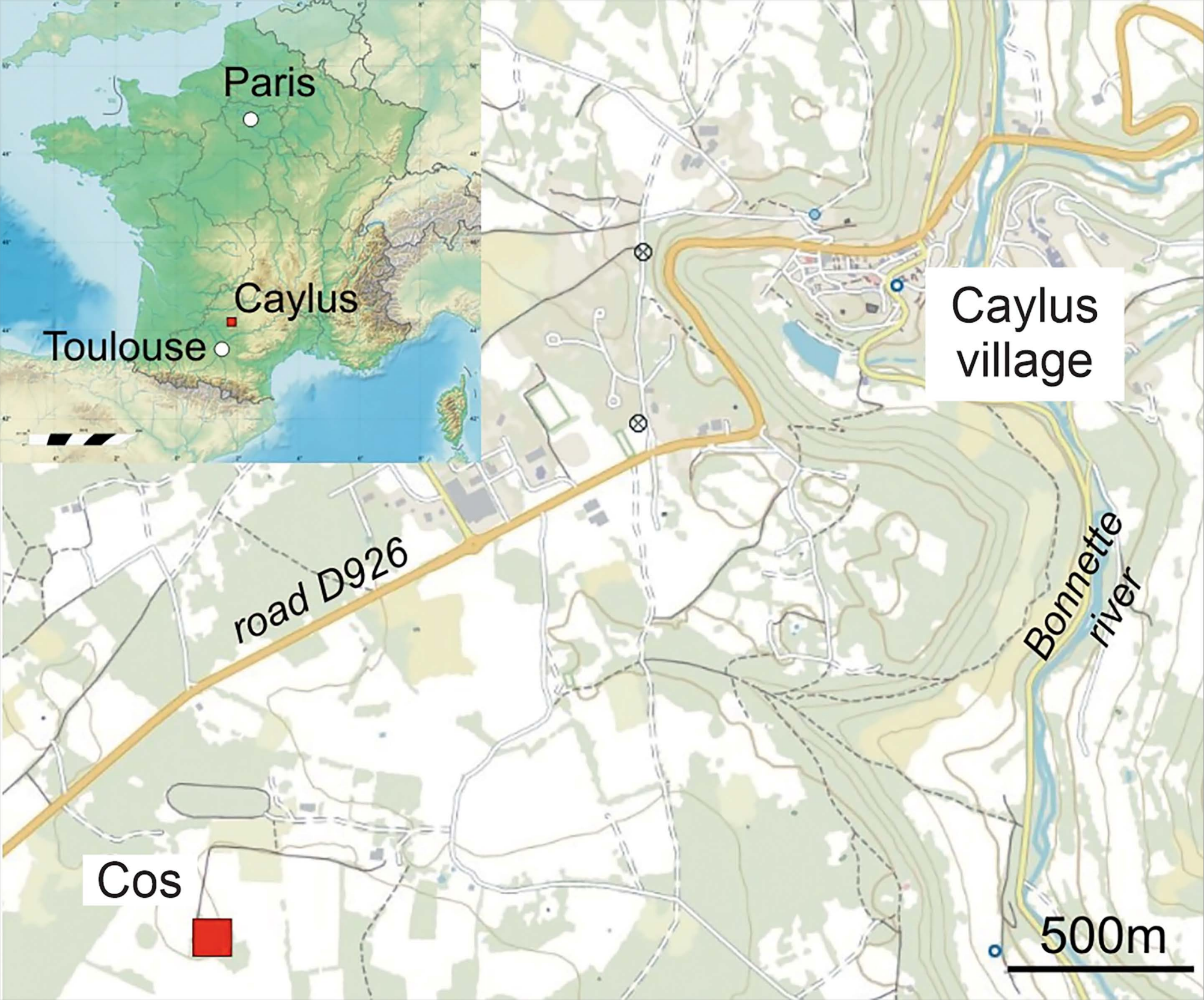
UM-COS-1000 and 01; **B**, *Gaultia silvaticus* UCMP 216000, (holotype) middle portion of frontal and **C**, UCMP 150966 (paratype) partial left frontal (modified from Smith, 2009); **D**, *Placosaurus estesi* (MNHN QU-17735, holotype) nearly complete frontal; **E**, *P. rugosus* (MNHN 1906-25, holotype) 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]

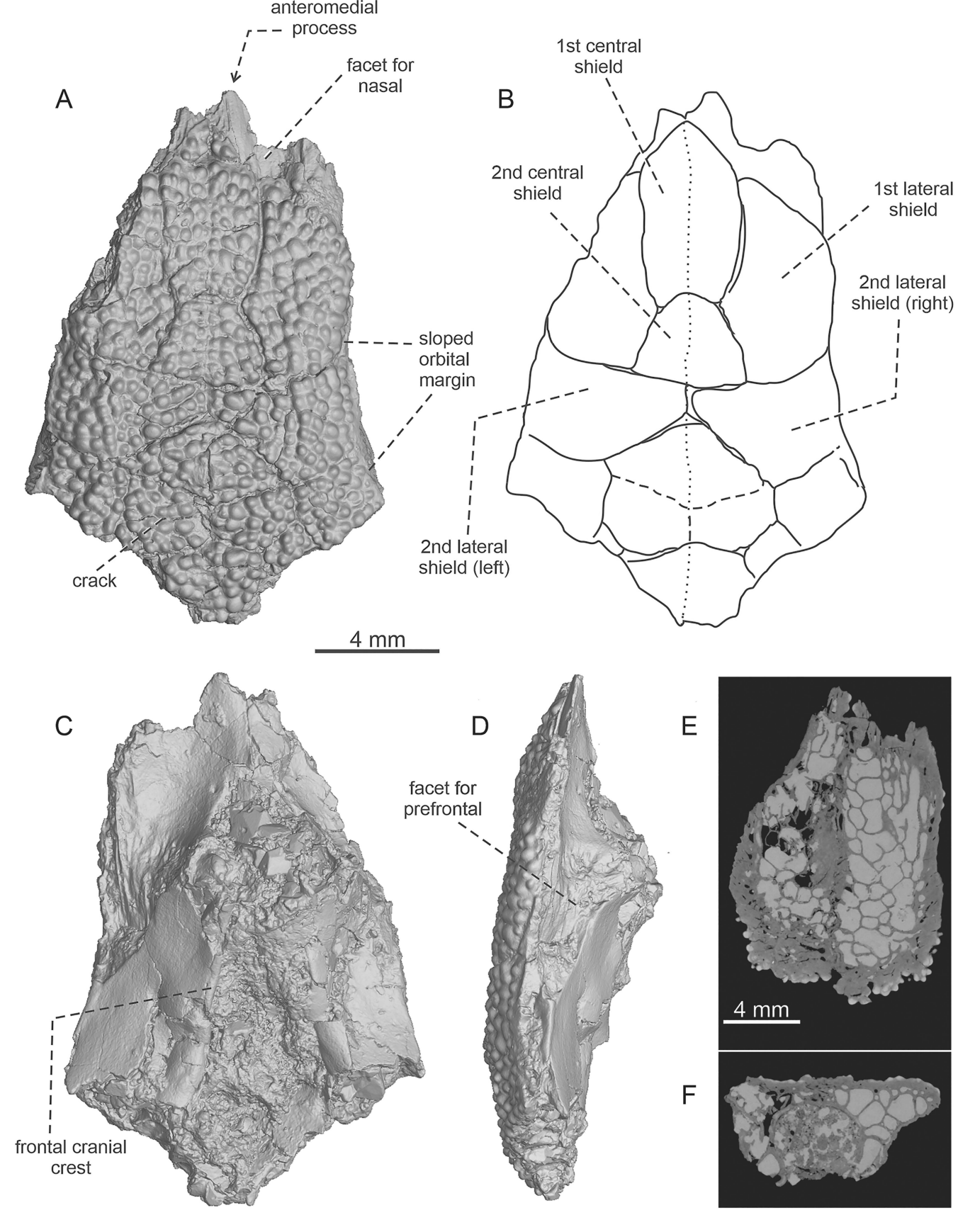
FIGURE 5. Glyptosauridae indeterminate from the early Eocene Cos locality of France. UM-COS-1002 left maxilla. **A**, left lateral view; **B**, medial (lingual) view; **C**, occlusal (ventral) view; and **D**, dorsal view. **A**-**D** are micro-CT visualizations; UM-COS-1011, right maxilla. **E**, right 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]

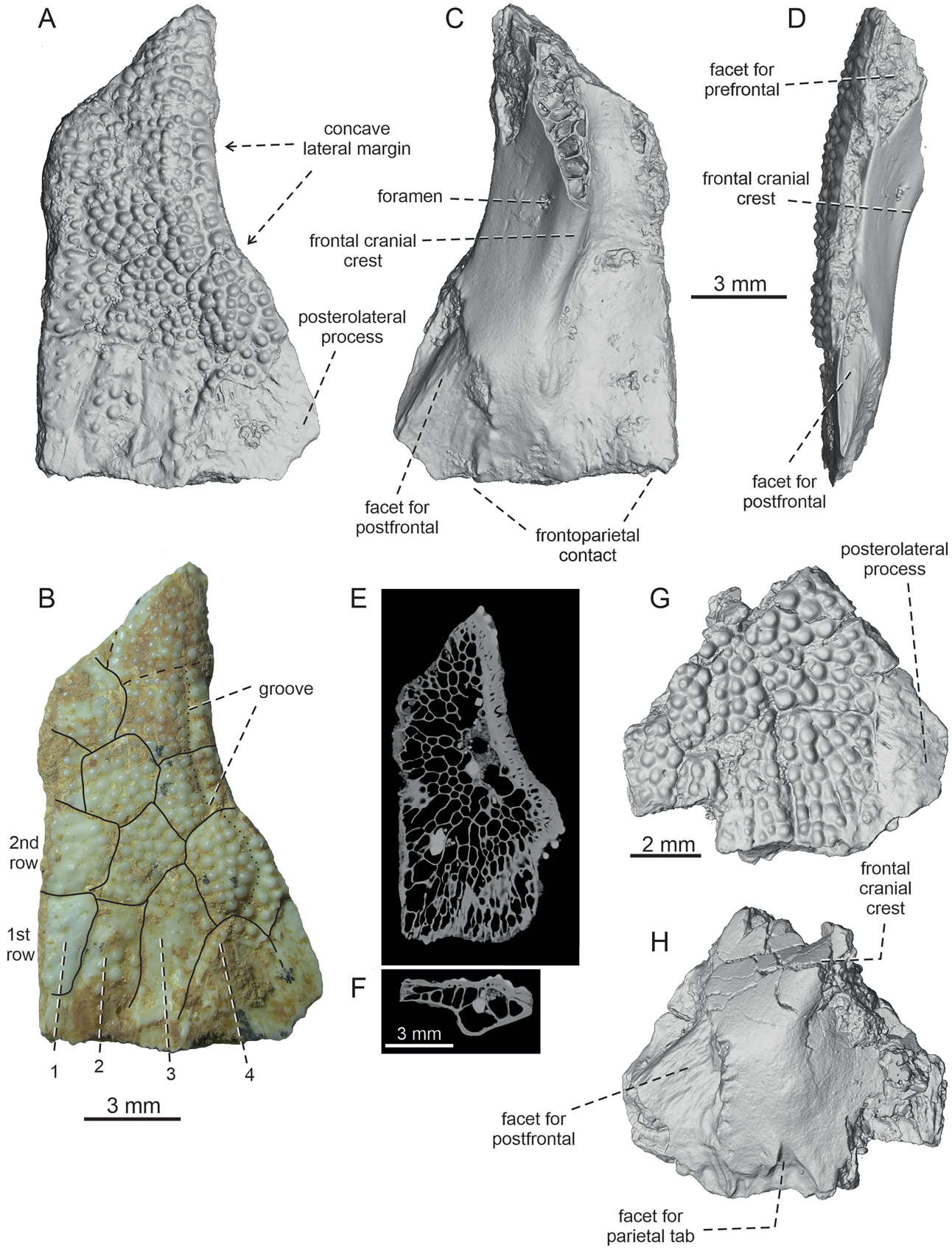
FIGURE 6. Glyptosauridae indeterminate (**A**-**J**) and Anguioidea indet. (**K**-**M**) from the early Eocene Cos locality of France. Isolated cephalic osteoderms. UM-COS-1004, hexagonal osteoderm: **A**, dorsal; **B**, ventral; and **C**, lateral views. UM-COS-1005, polygonal osteoderm: **D**, external 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]

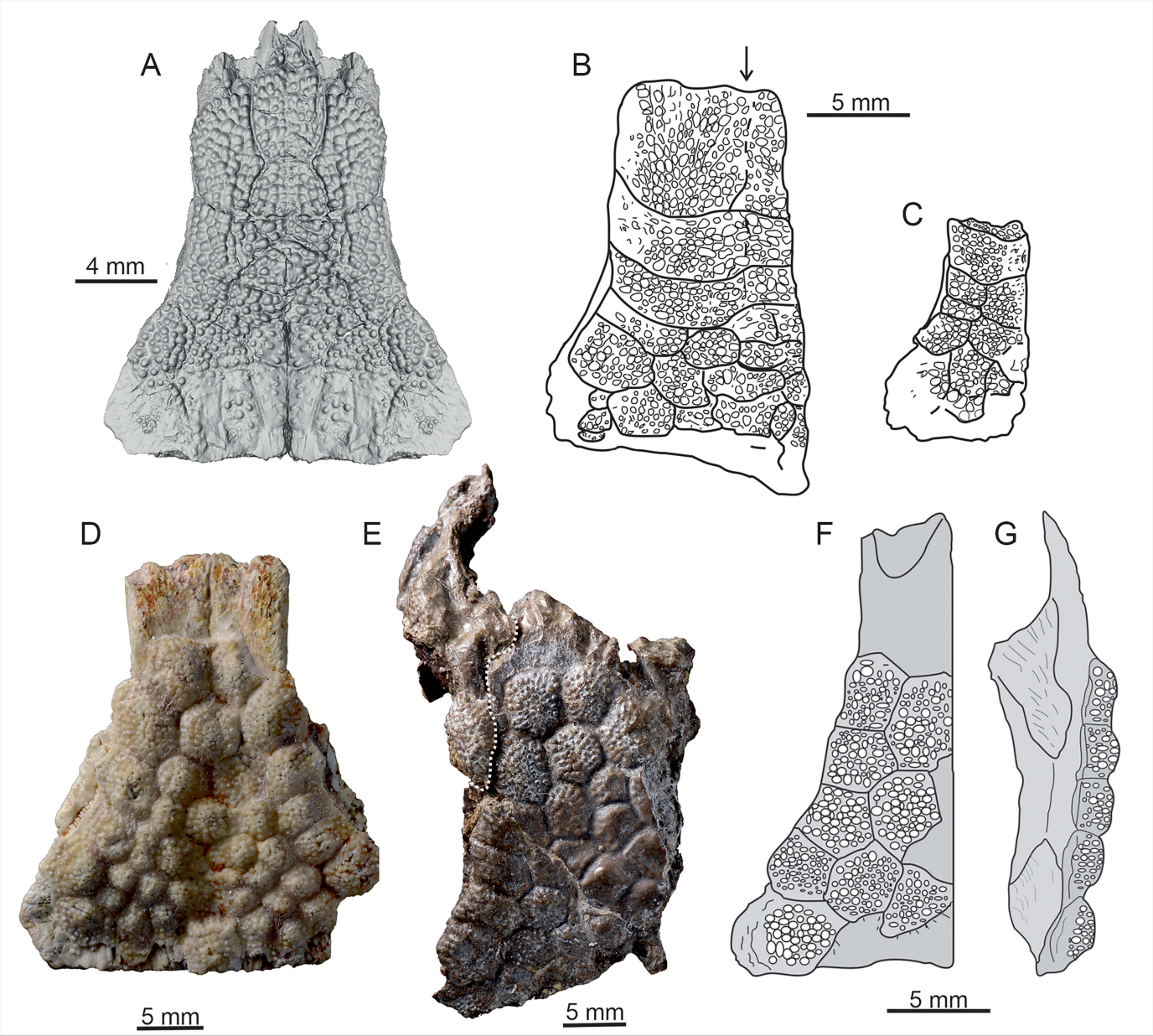
FIGURE 7. Palaeovaranidae indeterminate from the early Eocene Cos locality of France. UM-COS- 1009, nearly complete frontal. **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, right lateral; and **E**, anterodorsal views. All images are micro-CT visualizations. [planned for page width]

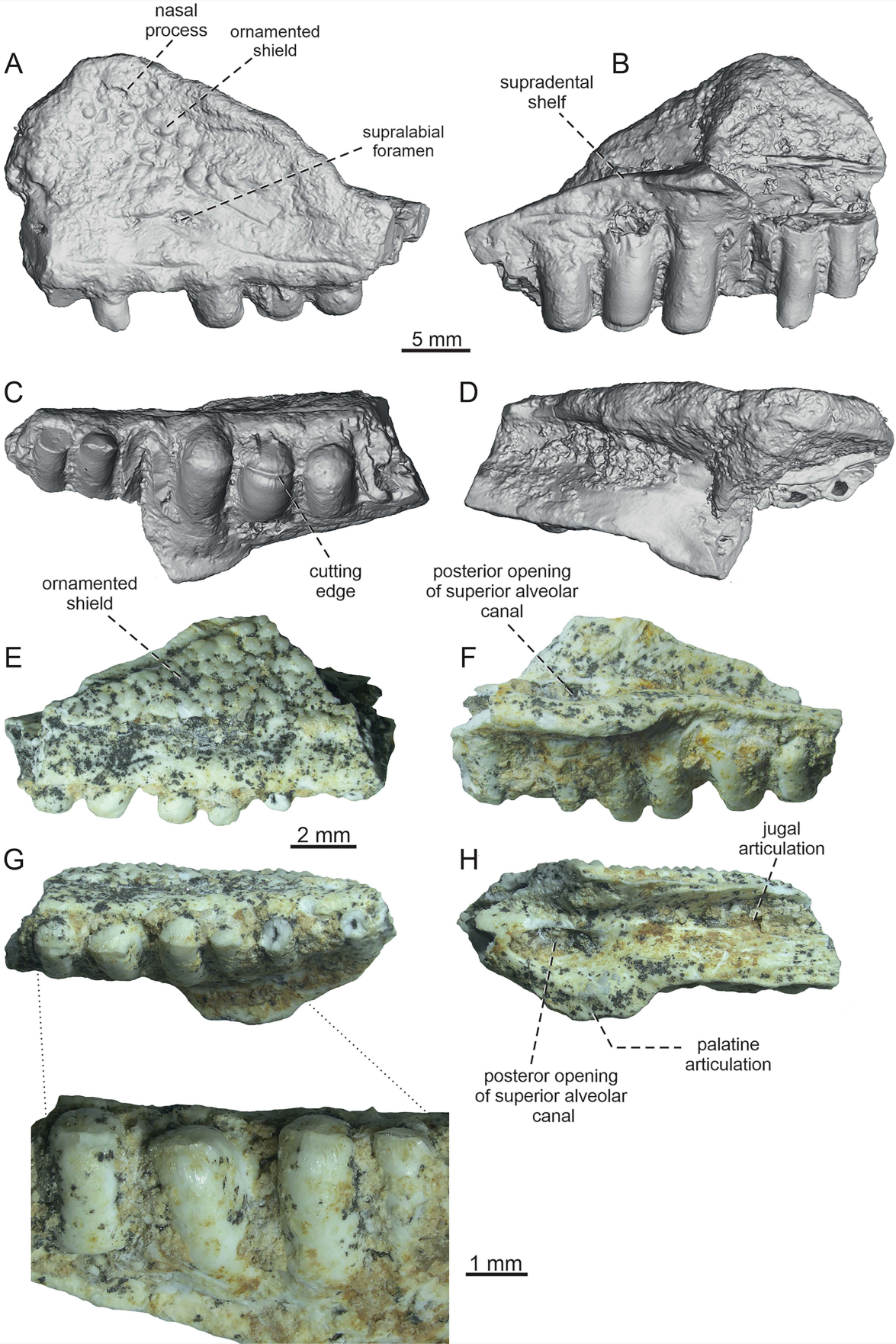
FIGURE 8. Varanoidea indeterminate from the early Eocene Cos locality of France. UM-COS-1010, left maxilla. **A**, lateral; **B**, medial; **C**, dorsomedial; **D**, dorsal; and **E**, ventral views (A-E are micro-CT visualizations); and **F**, μCT slice of tooth bases showing the presence of plicidentine.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

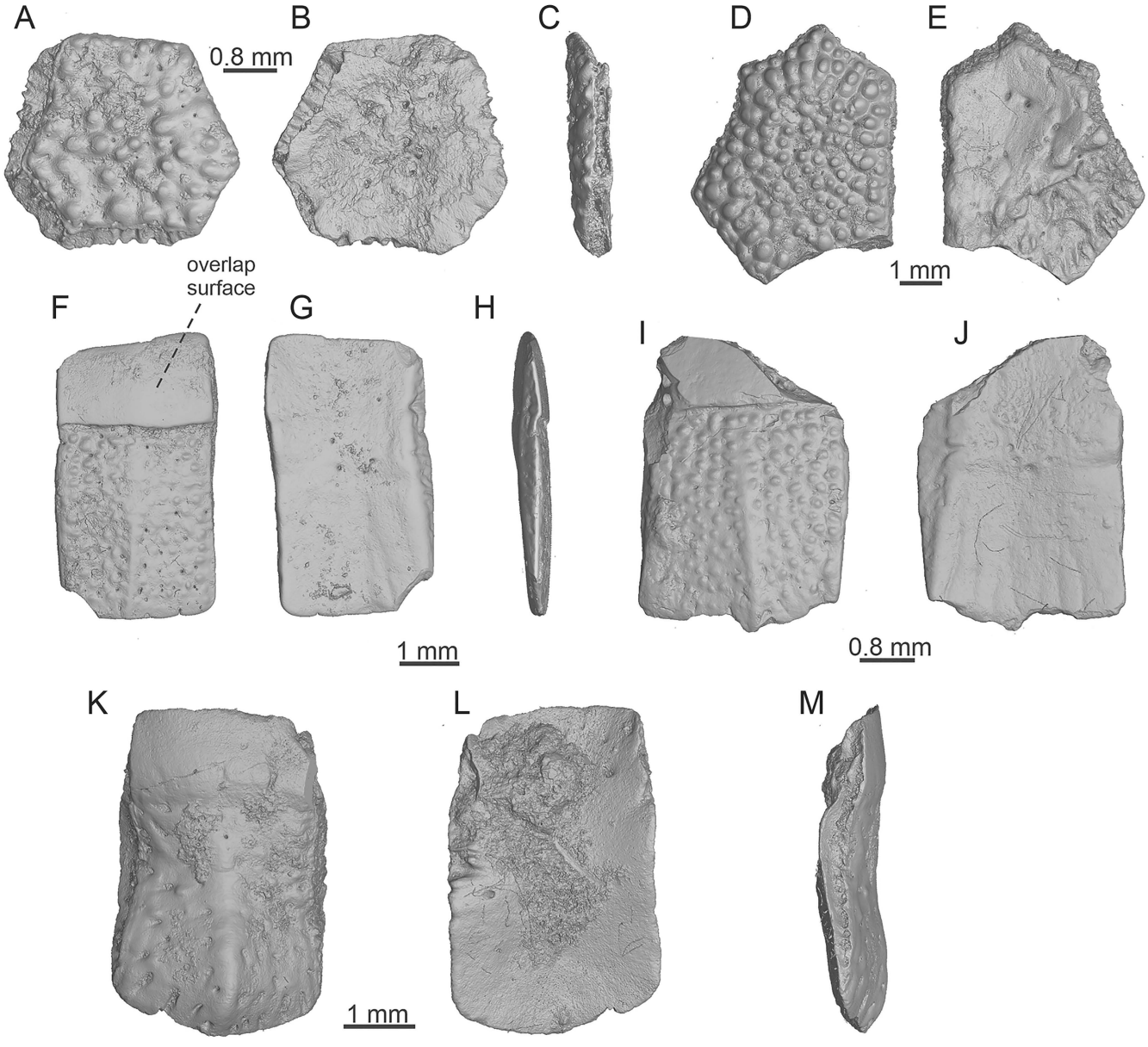

Paris
Caylus
Toulouse
Caylus village
road D926
Bonnette river
Cos
500m

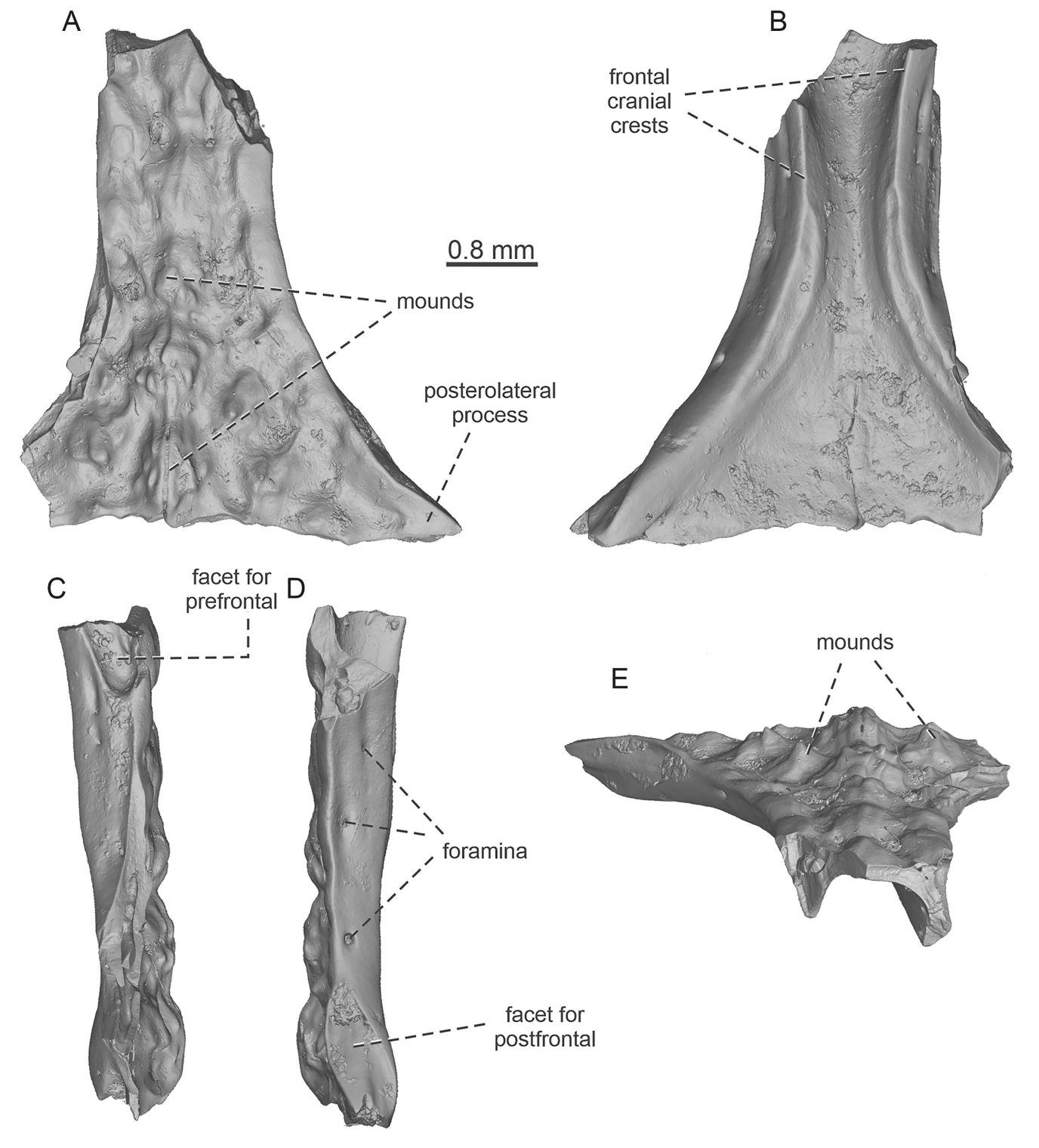

A
anteromedial process
facet for nasal
sloped orbital margin
crack
B
1st central shield
2nd central shield
1st lateral shield
2nd lateral shield (right)
2nd lateral shield (left)
4 mm
C
frontal cranial crest
D
facet for prefrontal
E
4 mm
F

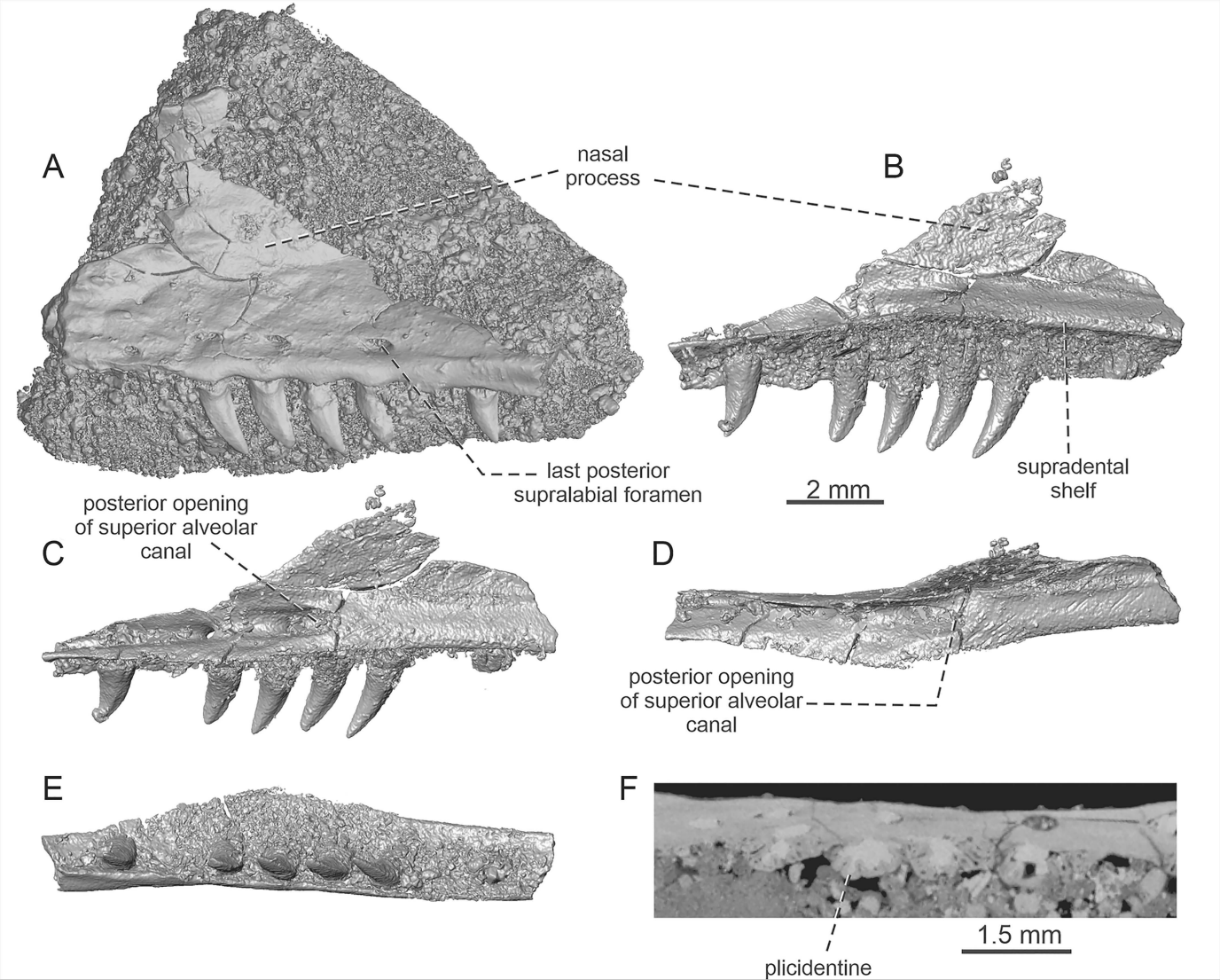

A
concave
lateral margin
posterolateral
process
C
foramen
frontal cranial
crest
facet for
postfrontal
frontoparietal
contact
D
facet for
prefrontal
frontal cranial
crest
3 mm
facet for
postfrontal
B
groove
2nd
row
1st
row
1
2
3
4
3 mm
E
F
3 mm
G
posterolateral
process
2 mm
H
frontal
cranial
crest
facet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


A
4 mm
B
5 mm
C
D
5 mm
E
5 mm
F
G
5 mm


A
nasal process
ornamented shield
supralabial foramen
B
supradental shelf
5 mm
C
cutting edge
D
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


A
B
C
D
E
0.8 mm
1 mm
overlap
surface
F
G
H
I
J
1 mm
0.8 mm
K
L
M
1 mm


A
0.8 mm
mounds
posterolateral process
B
frontal cranial crests
C
facet for prefrontal
D
foramina
facet for postfrontal
E
mounds


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