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Original Article

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Timing of intercontinental faunal migrations: Anguimorph lizards from the earliest Eocene (MP 7) of Dormaal, Belgium

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ABSTRACT

Here we report on anguimorph lizards from the earliest Eocene (MP 7) of the Dormaal locality in Belgium, from the time of the warmest global climate of the past 66 million years. Several clades can be identified in this site: Glyptosauridae, Varanidae, and Palaeovaranidae. Our study focuses on glyptosaurid specimens previously reported from the site, some of which had been provisionally described as a new species, ?*Placosaurus ragei*, and some assigned to an unnamed *Placosauriops*-like 'melanosaurine'. Our study presents data on new material, including an almost complete glyptosaurine frontal that has enabled us to assign much of the previously described material to a single genus and species. The specimens that had been assigned to both ?*P ragei* and the 'melanosaurine' share apomorphies (flat osteoderms and chevron-shaped osteoderms) with *Gaultia*, a glyptosaurid previously known from the earliest Eocene of Wyoming, USA. The Dormaal material represents the first record of this genus outside North America. In fact, the only potential evidence of the occurrence of 'Melanosaurinae' in Dormaal might be a single isolated vertebra described here. Here we also describe previously unfigured material of *Saniwa* and palaeovaranids from Dormaal. The presence of previously reported helodermatids cannot be supported in this Belgian site.

Keywords: Squamata; Palaeogene; PETM; palaeobiogeography; Europe; North America

INTRODUCTION

The Eocene climate began with warming from the Palaeocene–Eocene Thermal Maximum, at 56 Mya. In fact, the warmest global climates of the past 66 Myr occurred during the Early Eocene epoch (about 56 to 48 Mya) and arguably represent the warmest time interval since the Permian–Triassic mass extinction and the Early Triassic (Cramwinckel *et al.* 2018). However, the data regarding the early Eocene squamates are unfortunately scant. In Europe, the locality of Dormaal in Belgium represents one rare exception, serving as a window into the earliest Eocene (MP 7 reference-level of the mammalian biochronological scale for the European Palaeogene; BiochroM'97, 1997) 'greenhouse world'. The site has already yielded numerous mammal taxa, including the earliest modern placental mammals of Europe (Smith *et al.* 2006, Solé *et al.* 2014; for the geological setting see: Smith and Smith 1996; Steurbaut *et al.* 1999). Lizards from Dormaal were only briefly discussed by Hecht and Hoffstetter (1962) and, moreover, the specimens were never figured by these authors. However, squamate specimens from Dormaal have been described and figured since the 1990s (Augé 1990, 1992, Augé and Smith 1997, 2002, Sullivan *et al.* 2012, Folie *et al.* 2013, Augé *et al.* 2022, Čerňanský *et al.* 2022a, 2023a).

Among these squamates are anguimorph lizards. Anguimorpha is a successful and diverse clade of limbed and limbless lizards (non-ophidian squamates), including clades such as Anguidae, Diploglossidae, Glyptosauridae [*sensu* Čerňanský *et al.* (2023b); note that most clades previously considered subfamilies of Anguidae *sensu* Camp (1923) are now considered taxa at the family level; see Čerňanský *et al.* (2023b)], Xenosauridae, Helodermatidae, Lanthanotidae, Palaeovaranidae (*sensu* Georgalis 2017), Varanidae, and Shinisauridae. The oldest widely accepted fossil record of the earliest anguimorph is represented by *Dorsetisaurus* Hoffstetter, 1967 from the Late Jurassic of Europe and North America (Estes 1983). The later fossil record of the clade Anguimorpha is well known from the Cretaceous (e.g. *Paraderma* Estes, 1964, *Gobiderma* Borsuk-Białynicka,

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1984, and *Estesia* Norell *et al.* 1992; see also: Pregill *et al.* 1986, Conrad *et al.* 2011), including amber fossil (*Barlochersaurus* Daza *et al.*, 2018) and its Cenozoic record is known from every continent except Antarctica (Estes 1983, Uetz *et al.* 2024). In Dormaal, several clades of anguimorphs have been reported—glyptosaurids (Augé 2005, Sullivan *et al.* 2012, Sullivan 2019), helodermatids (Augé 1995, 2003a), varanids with the first record of *Saniwa* outside North America (Dollo 1923, Hech and Hoffstettter 1962, Augé *et al.* 2022), and palaeovaranids (=Necrosauridae in: Augé 1990, 2003b, 2005; see: Georgalis 2017). Note that *Campinosaurus woutersi* Augé, 1992 was originally identified as a primitive anguimorph lizard (Augé 1992), but later was recognized as an amphisbaenian (see: Augé 2005).

Glyptosauridae (*sensu* Čerňanský *et al.* 2023b) are a particularly interesting clade of extinct anguimorphs. Glyptosauridae inhabited North America, Europe, and Asia, and are known from the Late Cretaceous to the Oligocene (Sullivan 1979, Rage and Augé 2003, Sullivan and Augé 2006, Conrad and Norell 2008, Keller 2009, Sullivan and Dong 2018, Čerňanský and Augé 2019, Georgalis *et al.* 2021, Čerňanský *et al.* 2023b). The clade is divided into Glyptosaurinae and the plesiomorphic ‘Melanosaurinae’ (Meszoely 1970, Sullivan 1979, 2019, Estes 1983, Augé and Sullivan 2006, Cicimurri *et al.* 2016, Čerňanský *et al.* 2023b). The latter is usually considered to form a paraphyletic group (Conrad 2008, Conrad and Norell 2008). Although both groups are well documented from the Early Eocene in North America, glyptosaurines are rare for most of the Early and Middle Eocene of Europe (see: Sullivan 2019, Čerňanský *et al.* 2023b). Among Glyptosaurinae, *Sullivanosaurus* Čerňanský *et al.*, 2023c (*Sullivania* in: Čerňanský *et al.* 2023b) from Cos in France and ?*Placosaurus ragei* Sullivan *et al.*, 2012 from Dormaal (see: Sullivan *et al.* 2012) are the only known taxa of the subfamily known from the Early Eocene of Europe, whereas only *Placosaurus* Gervais, 1848–52 is documented from the Late Eocene of France (some finds are also known from the Late Middle Eocene; Rage 1988, Augé 2005, Sullivan and Augé 2006, Sullivan 2019). The Dormaal ?*Placosaurus ragei* is based on the holotype dentary (Fig. 1) and a tentatively referred parietal and a cephalic osteoderm (Sullivan *et al.* 2012). The current taxonomy of *Placosaurus* species is based on the morphology of the frontal (Sullivan and Augé 2006), and the uncertainty of the generic allocation was expressed by Sullivan *et al.* (2012) by their use of the question mark. Besides this, a second glyptosaurid taxon, *Placosauriops*-like ‘melanosaurine’, was also reported from Dormaal (Sullivan 2019). Glyptosaurid palaeobiodiversity is very low in Europe relative to the numerous North American genera (Sullivan 1979, Smith 2009, 2011a). In Europe, this group disappeared at the Eocene–Oligocene boundary (e.g. Rage 2013).

Varanidae is a group of carnivorous and frugivorous lizards. Today, the genus *Varanus* Merrem, 1820 represents a clade of lizards that diversified into an exceptional range of body sizes, from the Komodo dragon (*Varanus komodoensis* Ouwens, 1912) to the pygmy monitors (*Varanus brevicauda* Boulenger, 1898 and *Varanus primordius* Mertens, 1942; see: Collar *et al.* 2011). Among the fossil taxa, *Saniwa* Leidy, 1870 is an Eocene varanid mainly known from North America. Outside of this continent, *Saniwa orsmaelensis* Dollo, 1923 was originally described by Dollo (1923), based on the material from the earliest Eocene of Dormaal, Belgium. More complete material was recently described by Augé *et al.* (2022). The Dormaal record represents stratigraphically the earliest occurrence of this taxon in Europe.

Here we report on new material from Dormaal, including frontal bones of glyptosaurids, which are crucial for the taxonomy of this clade. Other material belongs to palaeovaranids and also to *Saniwa*, showing the variability of this form in the Belgian locality.

MATERIALS AND METHODS

Specimens examined and terminology

The studied fossil material is housed in the Royal Belgian Institute of Natural Sciences in Brussels (Belgium), prefixed under individual IRSNB R numbers. The standard anatomical orientation system is used throughout this paper, and terminology describing individual bone structures is based on Evans (2008), Rage and Augé (2010), and Ledesma and Scarpetta (2018).

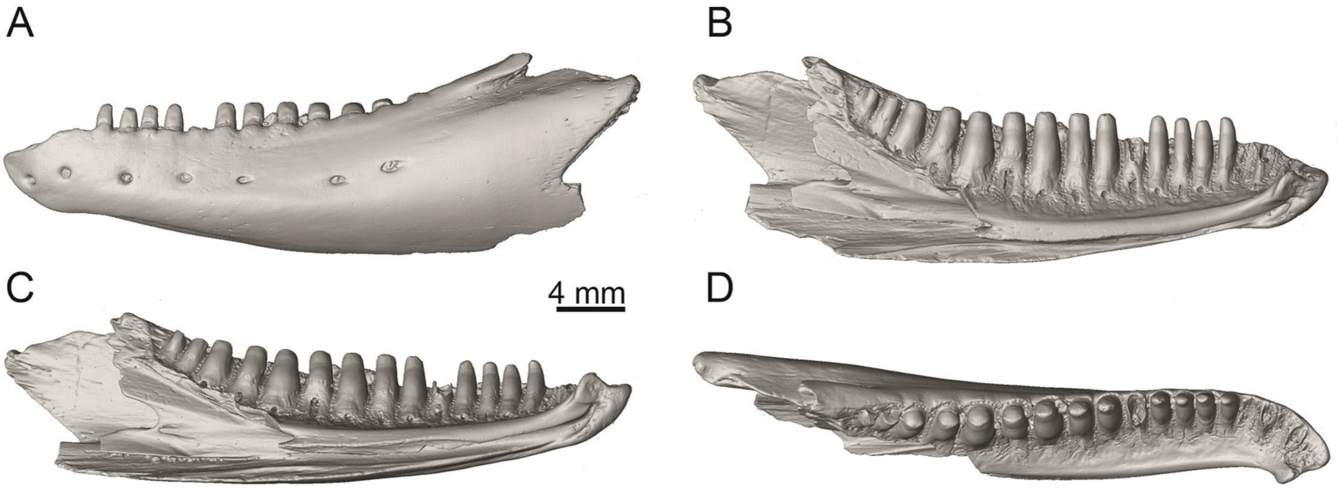

Figure 1. *Gaultia ragei* comb. nov. from the earliest Eocene of Dormaal. The holotypic left dentary IRSNB R 263 in A, lateral; B, medial; C, ventromedial; and D, dorsal views (all micro-CT visualizations).

Institutional abbreviation: IRSNB R, Institut royal des Sciences naturelles de Belgique, fossil reptile collection.

X-ray microtomography, three-dimensional visualization, photography, and measurements

Most of the fossil specimens were photographed using a VHX-7000 Series digital microscope and imaged on nano-computed tomography (CT) using the micro-CT facilities at the Slovak Academy of Sciences in Banská Bystrica, using a Phoenix mikro-CTv|tome|x L240. The specimen IRSNB R 263 was imaged on a RXSolutions EasyTom 150 at the Royal Belgian Institute of Natural Sciences. The CT datasets were analysed using VG Studio Max 3.1. and AVIZO 8.1.

RESULTS

Systematic palaeontology

Squamata Oppel, 1811

Anguimorpha Fürbringer, 1900

Glyptosauridae Marsh, 1872 (*sensu* Čerňanský *et al.* 2023b)
Glyptosaurinae Marsh, 1872

***Gaultia* Smith, 2009**

***Gaultia ragei* (Sullivan *et al.*, 2012) comb. nov.**

(Figs 1–6)

Zoobank LSID: urn:lsid:zoobank.org:act:DDA313D5-2D77-43B8-9896-C22E43FA7B32.

1962 Anguidae proche de *Melanosaurus*—Hecht and Hoffstetter: 6–8.
1978 cf. *Melanosaurus*—Godinot *et al.* 1978: 1273.
1983 *Melanosaurus*? sp.—Estes: 146.
1990 *Melanosaurini* indéterminé—Augé: 169, 170, fig. 6.
1990 Glyptosauriné indéterminé—Augé: 169.
2005 *Placosaurus* indét.—Augé: 203, figs 139, 142, 143.
2006 cf. *Paraplacosauriops quercyi*—Augé and Sullivan (in part): 135, fig. 4.
2012 ?*Placosaurus ragei*—Sullivan *et al.*: 630, figs 2, 3.

Holotype: IRSNB R 263 (formerly DO2 in Augé 2005), a nearly complete left dentary (Fig. 1; Sullivan *et al.* 2012: fig. 2).

Previously referred material: IRSNB R 112, incomplete left maxilla (Augé 1990: fig. 6); IRSNB R 264, incomplete parietal missing the left posterior corner and distal portions of the supratemporal processes (Sullivan *et al.* 2012: fig. 3); and IRSNB R 265, cephalic osteoderm (Sullivan *et al.* 2012: not figured).

Newly referred material: IRSNB R 478, IRSNB R 479, IRSNB R 480, three maxillae; IRSNB R 481, right frontal; IRSNB R 392, fused frontals; IRSNB R 266, medial part of a right frontal; IRSNB R 482, mid- and right portion of the parietal table; IRSNB R 483, left dentary without anterior end; IRSNB R 484, anterior portion of the left dentary; IRSNB R 485, posterior region of the left dentary.

Type locality and horizon: Dormaal, Flemish Brabant, eastern Belgium, Dormaal Member, Tienen Formation, Landen Group, earliest Eocene (MP 7).

Taxonomic comment: Since Hecht and Hoffstetter (1962), the Dormaal glytosaurid taxon has been questionably considered as *Melanosaurus* or *Placosaurus* based on a dentary and a parietal, and was eventually allocated to the new species ?*Placosaurus ragei* (Sullivan *et al.* 2012). However, the current taxonomy of species of *Placosaurus* is based on the morphology of the frontal. The newly referred frontal differs from that of the European *Placosaurus* (see: Sullivan and Augé 2006: figs 1, 3, Čerňanský *et al.* 2023b) and is similar to that of the North American *Gaultia* Smith, 2009 (Smith 2009: fig. 18D, E), sharing features such as apically flat osteoderms (not thick as in *Placosaurus*, and not bulbous as in, e.g. *Glyptosaurus*, *Helodermoides*, and *Stenoplacosaurus*) and presence of chevron-shaped osteoderms.

Revised diagnosis: A species of *Gaultia* that is similar to *Ga. silvaticus* but differs from it by (i) slightly laterally narrower frontal; (ii) presence of additional shields between the anterior one and chevron shields; and (iii) a different arrangement of shields in the posterior region—larger shields, less fragmented. It can be distinguished from *Sullivanosaurus gallicus* by the following combination of features: (i) frontal of *Ga. ragei* is narrower compared to *Su. gallicus*; (ii) frontal of *Ga. ragei* possesses fewer osteodermal shields in the posterior portion—three instead of four. The second row anterior to that possesses two osteoderms vs. three; (iii) the shape of osteoderms—the osteoderms of the first posterior row are hexagonal in *Ga. ragei* but distinctly elongate, roughly trapezoidal in *Su. gallicus*; (iv) the first anterior central shield in *Ga. ragei* reaches much further anteriorly vs. only slightly further anteriorly than the lateral shield; and (v) the first central shield in *Ga. ragei* is laterally larger than the lateral shield vs. a narrower central shield in *Su. gallicus*.

Description of newly referred material

Maxilla: Three incomplete right maxillae were recovered. The specimen IRSNB R 478 (Fig. 2A–F) is better preserved, only its anterior portion forming the forked premaxillary process is broken off. Its maximum anteroposterior length is 23.7 mm. The specimen IRSNB R 480 (Fig. 2K, L) represents only the posterior region, whereas the specimen IRSNB R 479 (Fig. 2G–J) is a partly preserved mid-portion of the maxilla. IRSNB R 478 possesses 16 tooth positions (four teeth are still attached in the posterior region), IRSNB R 479 has nine (six teeth are preserved), and IRSNB R 480 has seven tooth positions (five and a half teeth are still preserved). The facial (nasal) process of the maxilla is fairly preserved in IRSNB R 478, forming a high, almost perpendicular wall to the subdental shelf (Fig. 2A–F). On its external surface, irregular osteoderms are preserved, the largest of which is the second one from the anterior tip of the bone (Fig. 2A). They are irregular in shape, some of them being roughly polygonal. They are sculptured with tubercles and divided by sulci. Ventrally, the labial face of the maxilla is pierced by eight supralabial foramina. They gradually increase in size posteriorly, where the posteriormost is located at the level of the sixth tooth position (counted from posterior). The facial process itself has an irregular shape. Its dorsal margin is wavy, roughly M-shaped. It has two peaks, of which the anterior one is smaller and slightly bent medially. The posterior peak of the facial process is larger, rising more-or-less straight dorsally. The posterior margin of this

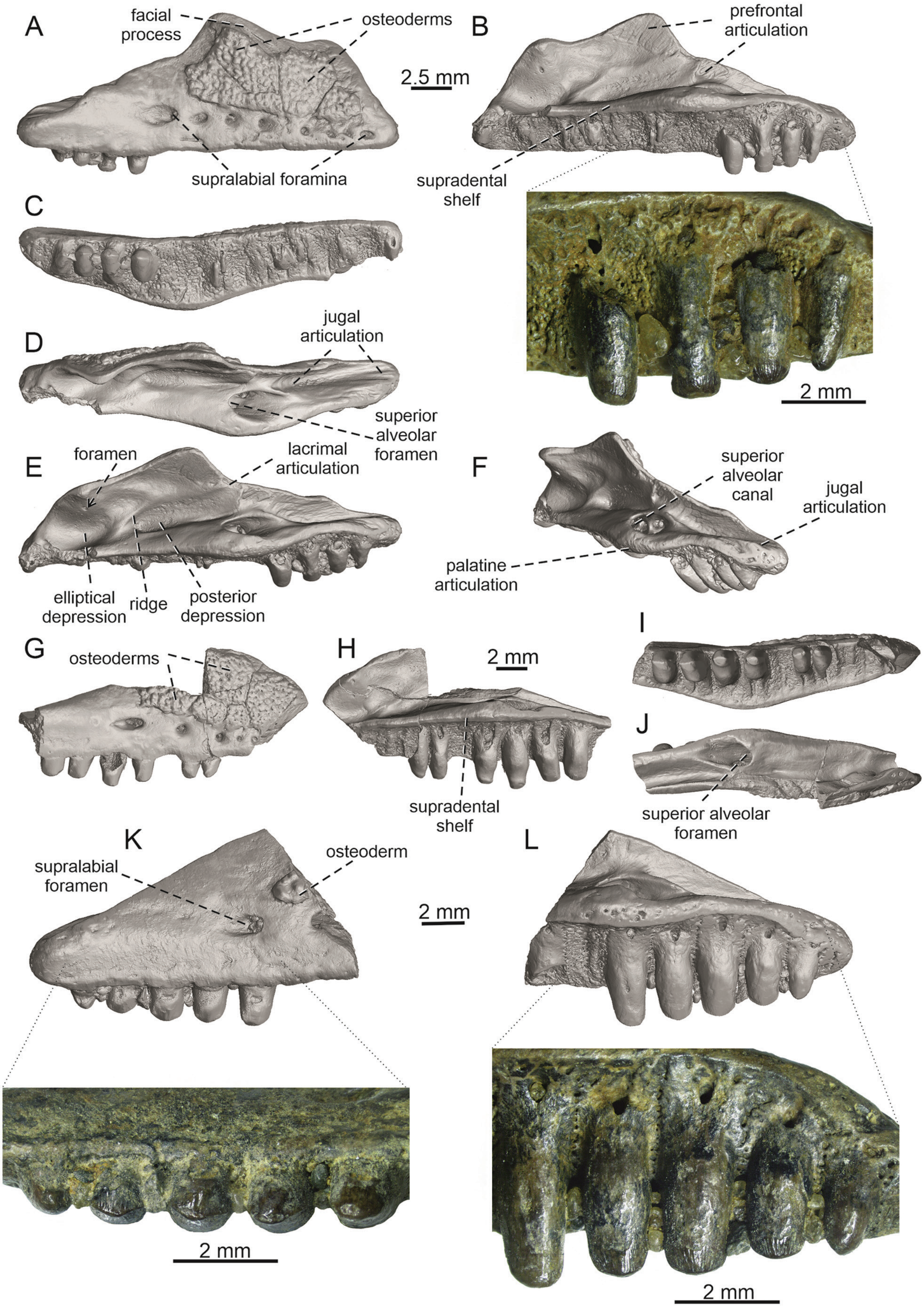

Figure 2. *Gaultia ragei* comb. nov. from the earliest Eocene of Dormaal. Right maxillae: IRSNB R 478 in A, lateral; B, medial with detail of teeth in ventromedial; C, ventral; D, dorsal; E, dorsomedial; and F, posterodorsomedial views. IRSNB R 479 in G, lateral; H, medial; I, ventral; and J, dorsal. IRSNB R 480 in K, lateral with detail of teeth in ventrolateral; L, medial with detail of teeth in ventromedial views (all micro-CT visualizations except of tooth details).

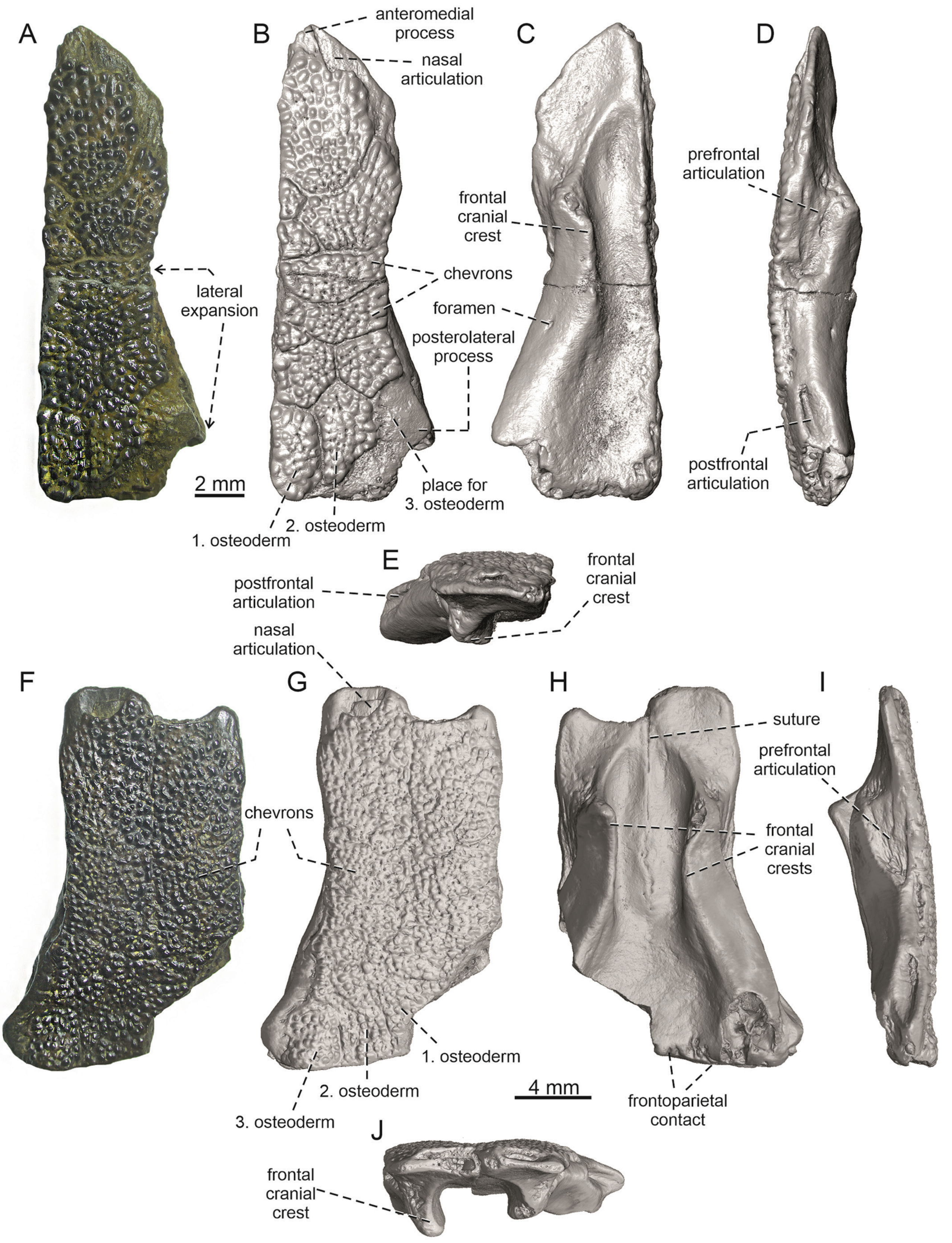

Figure 3. *Gaultia ragei* comb. nov. from the earliest Eocene of Dormaal. Right frontal IRSNB R 481 (A–E) and fused frontals IRSNB R 392 (F–J) in A, F, dorsal (photographs); B, G, dorsal; C, H, ventral; D, I, lateral; E, J, anterior views (all micro-CT visualizations, except A and F).

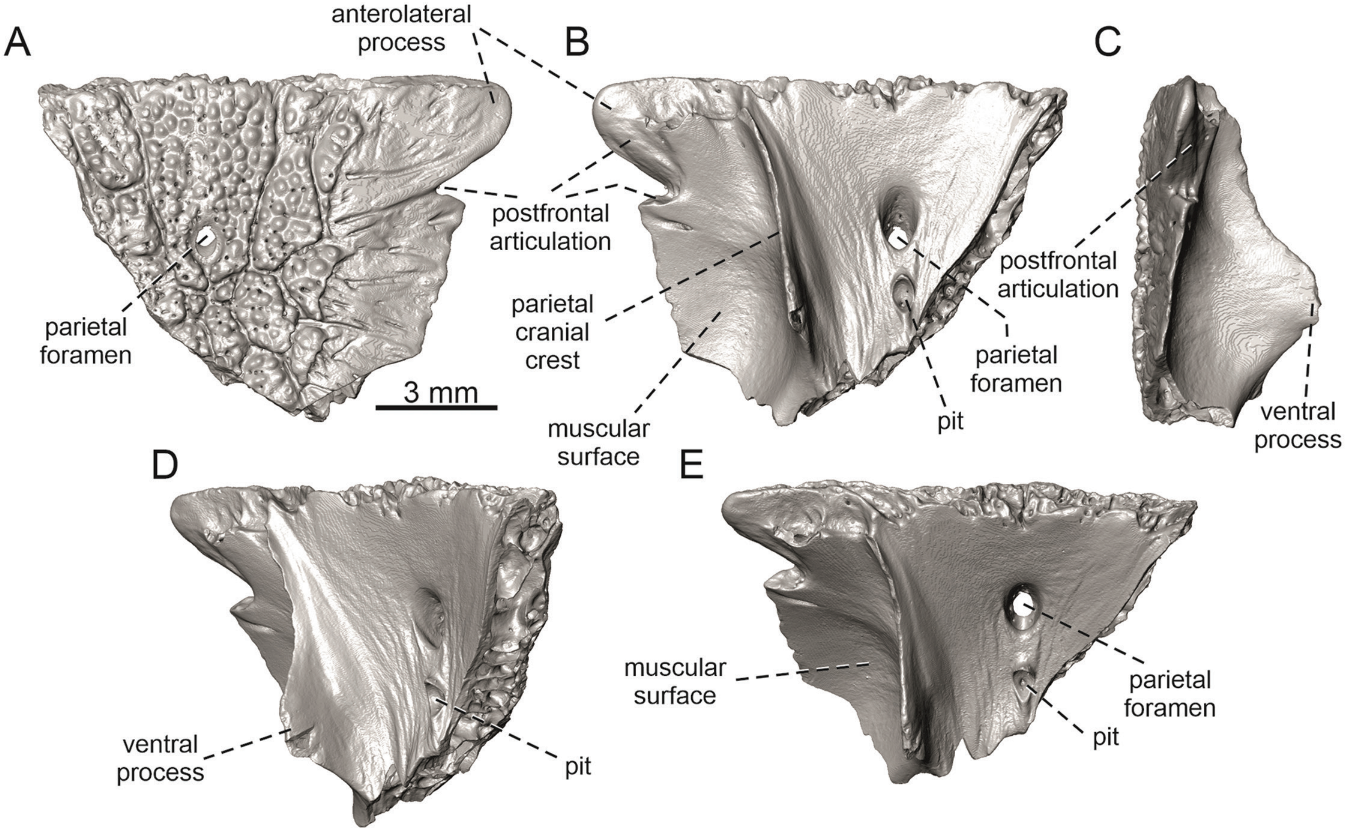

Figure 4. *Gaultia ragei* comb. nov. from the earliest Eocene of Dormaal. The parietal IRSNB R 482 in A, dorsal; B, ventral; C, lateral; D, anteroventrolateral; and E, anteroventral views (all micro-CT visualizations).

peak slopes distinctly ventrally and therefore gradually decreases in size posteriorly. Its end is stepped.

In medial view, the posterodorsal portion of the facial process (the posterior peak) broadly overlaps the prefrontal—the large and rough articulation surface is still clearly visible (Fig. 2B). In the posterior ventral corner, there is an articulation for the lacrimal (Fig. 2E). The smooth medial surface of the facial process bears two depressions: a large, elliptical one anteriorly [its dorsal portion bears a foramen–ethmoidal foramen *sensu* Conrad (2004); Fig. 2E] and a smaller, longitudinal one posteriorly [posterior depression *sensu* Evans (2008); the medial recess for the nasal sac *sensu* Ledesma and Scarpetta (2018)]. They are separated from each other by an anteroventrally to posterodorsally oriented ridge. The supradental shelf dorsal surface is straight (Fig. 2B), but its anterior section is broken off. The shelf itself expands medially, reaching its maximum at the level of the sixth tooth position (counted from posterior). Here, the contact with the palatine is present (Fig. 2F). All specimens bear the posterior opening of the superior alveolar canal (Fig. 2D–F, J, L). It is anteroposteriorly large, elliptical, and located at the level of the fifth tooth position (counted from posterior) in IRSNB R 480 and third tooth position in IRSNB R 479 (note, however, that the posterior portion in this specimen is broken off and the real number of the posterior teeth is unknown). The posterolateral margin of IRSNB R 478 (Fig. 2F) and IRSNB R 480 (Fig. 2L) is formed by a rounded lip of bone that, posteriorly, presents a deep facet for the jugal.

Remarks

The tuberculate sculpture of osteoderms (Fig. 2A, G) represents a synapomorphy of glyptosaurids (Camp 1923, Gilmore 1928, Sullivan 1979, 2019, Estes 1983, Gauthier *et al.* 2012, Čerňanský *et al.* 2023b). A division of osteodermal cover of the facial process indicates that the maxillae belong to Glyptosaurinae rather than 'Melanosaurinae' (although it lacks the well-defined hexagonal osteoderms, see below). Additional specimens are described here as *Gaultia ragei* on the basis of tooth morphology (including the holotype IRSNB R 263; Fig. 1, see: Sullivan *et al.* 2012: fig: 2) and size, all coming from the same locality of Dormaal, Belgium. Note that the osteodermal division on the lateral side of the maxilla is very atypical for Glyptosaurinae, lacking the well-defined hexagonal osteoderms. This might support the association of these elements with the frontal bones (Fig. 3) presenting also the same atypical osteodermal division (the pattern of osteoderm shapes; see below).

Frontal: The right frontal IRSNB R 481 is almost completely preserved, only the posterolateral corner is partly broken off (Fig. 3A–D). It is laterally narrow and robustly built. The bone is anteroposteriorly long (its maximum anteroposterior length is 19.7 mm), roughly triangular—the posterolateral corner expands into a short process. This lateral expansion starts at about the half length of the bone. At the posterior end, the bone is widest (the maximum width here is 6.9 mm; note, however, that as the posterolateral process is partly damaged, the original width of this region was slightly larger). The lateral margin of the bone is

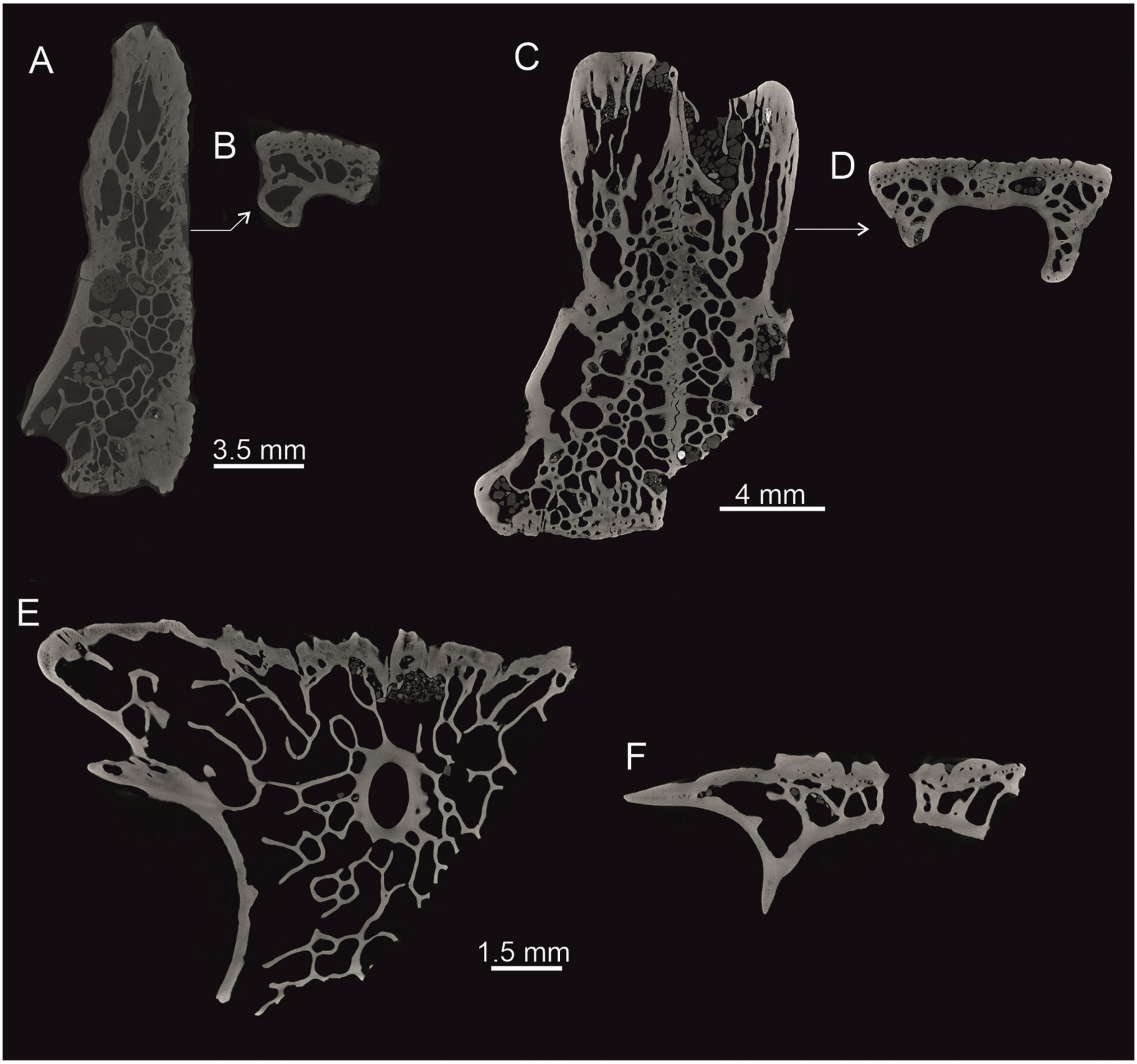

Figure 5. *Gaultia ragei* comb. nov. from the earliest Eocene of Dormaal. Axial section of right frontal IRSNB R 481 (A) and fused frontals IRSNB R 392 (C) and parietal IRSNB R 482 (E) at the mid-level of the dorsoventral thickness; B, D, coronal section at the level of the frontal cranial crests; F, coronal section at the level of the parietal foramen (all from the CT scans).

slightly concave medially, so the bone is the narrowest at around mid-orbit (the minimal width here is 4.4 mm). Anteriorly, the frontal extends into a long and pointed anteromedial (nasal) process. The dorsal surface of its anterolateral side is exposed, bearing weak longitudinal grooves and ridges forming the articulating surface for the nasal (Fig. 3A, B). The external surface of the frontal is almost fully covered by sculptured osteodermal shields. The sculpture is formed by small rounded discrete tubercles that are regularly and densely arranged. In the anterior section, tubercles are arranged in anteromedially to posterolaterally oriented parallel rows extending anteriorly from the centre. This most likely indicates an ossification centre. The osteodermal shields are of various irregular, polygonal (rhomboidal, pentagonal, hexagonal) to roughly oval or ovoid shape. In the anterior portion, there is a large, first anterior central shield that is ovoid in shape. Posterolaterally to this, a lateral shield is present. It is wing-shaped, with an anterolaterally protruding lateral section. However, it reaches anteriorly less than half of the first central shield. The posteromedial margin is V-shaped. Medially to this, two small second and third central shields are present. They probably continued to the left frontal. If so (estimating its mirror symmetry), they would be more-or-less hexagonal. Posteriorly, two single mediolaterally elongated and chevron-shaped shields are located in a row. They cover the mid-portion of the frontal (where the frontal is the narrowest) and expand medially, probably having contact in the midline with those on the left frontal.

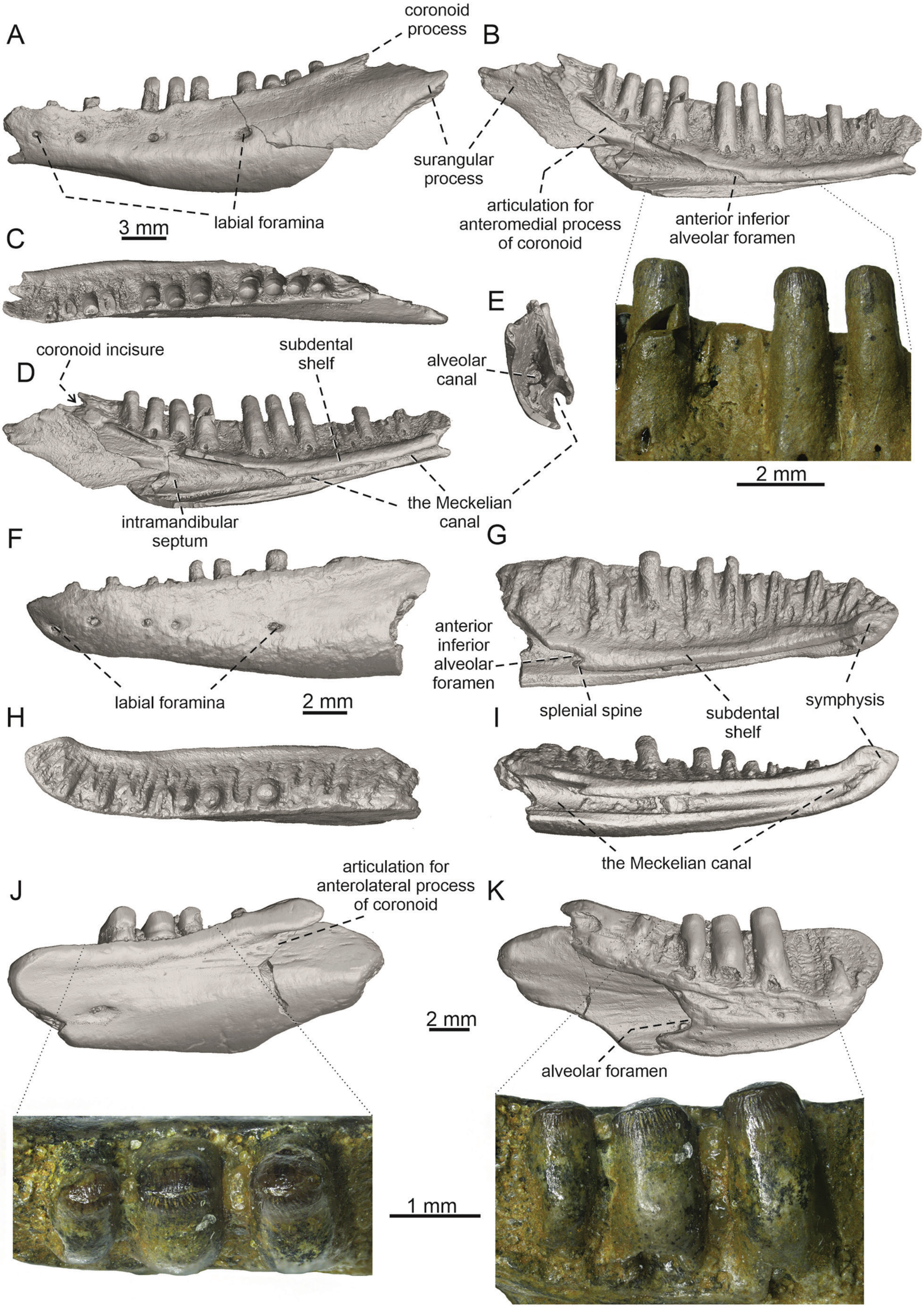

Figure 6. *Gaultia ragei* comb. nov. from the earliest Eocene of Dormaal. Left dentaries: IRSNB R 483 in A, lateral; B, medial with detail of teeth; C, dorsal; D, ventromedial and E, posterior views. IRSNB R 484 in F, lateral; G, medial H, dorsal; and I, ventromedial views. IRSNB R 485 in J, lateral with detail of teeth in dorsal; K, medial with detail of teeth in dorsomedial views (all micro-CT visualizations except of tooth details).

In the case of the second chevron shield (the most posterior one), however, one additional small triangular (if they continue to the left frontal, estimating its mirror symmetry, it was rhomboidal) shield is present posteriomedially to the second chevron one. Note, however, that it is not clear whether the groove separating it from the next posterior pentagonal osteoderm is a sulcus or a break (in such case, it would be a part of this pentagonal osteoderm). This posterior large pentagonal shield is one of two pentagonal shields that form a row posterior to the two chevron ones. In the posteriormost portion of the frontal, close to the straight contact with parietal, a row of three, anteroposteriorly slightly elongate, roughly hexagonal shields, is present (the lateral one is missing).

In lateral view (Fig. 3D), a large, wedge shaped and rugose facet for the prefrontal is located in the anterior region, laterally to the frontal cranial crest (Fig. 3C). On the lateral side of the posterolateral process, a slightly narrow facet for the postfrontal is clearly visible. Prefrontal and postfrontal were not in contact, so they did not fully exclude the frontal from the orbital border.

In ventral view (Fig. 3C), a large and robust frontal cranial crest can be observed. In its anterior portion, it extends ventrally into a rather well-defined and rounded prefrontal (=subolfactory) process (its end is slightly damaged) that achieves a maximum depth of 3.7 mm below the dorsal surface of the bone. The anterior portion of the frontal cranial crest, anterior to the subolfactory process, forms a sharp, medially directed ridge. The anteromedial margin of this crest is thin and sharp. Posteriorly, it widens, gradually diminishing dorsally and extending to the posterolateral process of the frontal. On the lateral side of the crest, a foramen is visible (Fig. 3C, D).

The nearly complete frontal IRSNB R 392 (Fig. 3F–J) is a large and unpaired element, missing only the anterior end and posterior corner, both on the right side. On the anterior edge of the dorsal surface, a small and clearly visible area is present for the articulation with the nasal (Fig. 3F, G). In the anterior and mid-section, the frontal bears traces of the original midline suture on both ventral and dorsal surfaces (more visible, however, in ventral view). The maximum anteroposterior length of the frontal is 20 mm. Overall, the bone is laterally wide, although a weak constriction can be seen in the mid-orbital region. At this level, the width of the bone is 9 mm. The lateral margins of the frontal are slightly concave medially and the whole bone gradually widens posteriorly. This lateral expansion starts at about the half length of the bone. The posterior region is expanded into short posterolateral processes (only the left one is preserved). The maximum width of the preserved element here is 12.8 mm. Note, however, that the right posterior portion of the bone is broken off and estimated width of the complete element in this region, based on the left half, was 16 mm. The external surface is covered by sculptured osteodermal shields that are completely fused to the underlying bone. The sculpture is formed by small, rounded, discrete tubercles. Although some divisions of the osteoderms are visible, they are not as clear as on the specimen IRSNB R 481. There is a hint of chevrons in the mid-region (Fig. 3F, G). In the posterior region, there are clear divisions of osteodermal armour to at least three osteoderms on the left side. The first two left (the two most lateral ones: osteoderms 2 and 3 on Fig. 3G) appear to be rectangular (or polygonal, their shape is unclear, especially at their anterior borders). Potentially, a hint of 'radiating' tubercles might be present, but overall, the division pattern is not recognizable.

In ventral view (Fig. 3H), large and robust frontal cranial crests are visible. Their anterior portions are ventrally expanded forming well-defined and rounded prefrontal (=subolfactory) processes—the end of the left one is slightly damaged. The anteromedial margins of the crests are thin and sharp, whereas they are wide posteriorly. The anterior portion of the frontal crest, anterior to the subolfactory process, is less deep, forming a well-visible, medially directed ridge. The right and left branches gradually diminish anteriorly, although they appear to join in the anterior mid-line.

In lateral view (Fig. 3I), in the anterior region, lateral to the frontal crest (including its lateral surface), a large wedge-shaped facet for the prefrontal is located. In the posterior region, there is a narrower facet for the postfrontal. Prefrontal and postfrontal were probably not in contact, and did not exclude the frontal from the orbital border. The posterior margin forms a contact with the parietal.

Remarks

This frontal was briefly described by Hecht and Hoffstetter (1962) but never figured. Recently, it was figured and discussed by Sullivan (2019: fig. 2) and identified as indeterminate 'melanosaurine'. According to Sullivan (2019), this specimen bears the frontoparietal scale impression typically present in 'melanosaurines' and appears to be similar to that of *Placosauriops* Kuhn, 1940a. This frontal is, however, problematic, because the exact division pattern of osteodermal cover is difficult to define. Moreover, when studied in detail, the osteoderm morphology differs from that of *Placosauriops* (see: Meszoley *et al.* 1978, Smith *et al.* 2018): there is a complex division of osteodermal cover in the posterior region and traces of chevrons, and maybe a hint of 'radiating' tubercles, indicate typical features of *Gaultia*. So both frontals IRSNB R 392 and R 481 share an apomorphy (chevrons). The unclear division deserves a comment here. As documented in extant *Pseudopus* Merrem, 1820, sulci separating osteodermal cover are difficult to observe in large adults due to stronger ossification (Klembera *et al.* 2017: fig. 17C). This is probably the case of the frontal IRSNB R 392, which is almost completely fused (note that traces of the fusion are still visible). We regard IRSNB R 392 and R 481 as both belonging to *Gaultia ragei*, the differences in size, shape, and degree of fusion all being attributable to the greater maturity of R 392. In both specimens, the lateral expansion (posterolateral process) starts at about the half length of the bone. A fusion of the frontals in mature adult individuals is also documented in *Gaultia* (Smith 2009), as well as in *Sullivanosaurus* (Čerňanský *et al.* 2023b) and other glyptosaurids in which either fused or separate frontals can be found (Sullivan 1979). This can be seen in anguids as well. In adult specimens of extant *Pseudopus*, the frontal shields may fuse together (Klembera *et al.* 2017) and in extinct *Pseudopus pannonicus* (Kormos 1911), the frontals are firmly coalesced (Roček 2019). Another interesting feature is an orbital margin, which can be slightly different between younger and mature individuals. In *P. apodus*, it is markedly concave in juvenile specimens in contrast to an almost convex margin in adults (Klembara *et al.* 2017: fig. 31A, B). The more convex orbital margin is present also in a single left frontal of *Gaultia silvaticus* if compared to fused, larger frontals of this species (Smith 2009: fig. 18D, E). The same appears to be true for *Sullivanosaurus* (Čerňanský *et al.* 2023b: figs 2A, 3A). This is probably related to the presence of larger eyes (and thus larger orbits) in juvenile lizards relative to the skull size, as it is also observed in, e.g. lacertids (Čerňanský and Syromyatnikova 2019: fig. 31J).

Finally, it is worth mentioning that the Indeterminate 'Melanosaurini' IRSNB R 266, also from Dormaal and representing the medial part of a right frontal described by Sullivan *et al.* (2012: fig. 4), appears to share similar morphology to the specimen describe here as well. Therefore this specimen could potentially be also included in the material attributed to *Gaultia ragei*.

Parietal: The parietal IRSNB R 482 is incomplete—the anterior, mostly central and right sides are preserved (Fig. 4). The left part is only partly preserved, whereas the posterior portion, including supratemporal processes, is completely broken off. A network of sulci marks the boundaries of osteodermal shields that cover the dorsal surface of the bone. The largest is the interparietal one, which is trapezoidal in shape. In the posterior section of the shield, the bone is pierced by the parietal foramen. Other osteoderms are smaller and of various size and shape, generally being more rounded than those of the frontal (Fig. 3). The lateral portion of the bone is smooth, lacks osteodermal covering, and some lateral osteoderms are partly peeled off. This surface is pierced by small foramina accompanied by anterolaterally (in the anterior portion) or posterolaterally (in the posterior portion) running grooves. The anterolateral process is robust and well expanded laterally. Its end is rounded and blunt. Ventrally, at the base of the process, a wedge cut from the anterolateral margin of the parietal is present and forms the articulation facet with the postfrontal. The facet is mainly visible in lateral and ventral views (Fig. 4B, C). In ventral view, it forms a triangular blunt imprint on the anterolateral process. In this view, a strongly developed sharp parietal cranial crest is developed. It separates the supratemporal fossa (containing a muscular surface) from the cranial vault. The crest is low at the level between the frontoparietal suture and the parietal foramen. Posteriorly, it grows markedly in depth and further forms a large (although not distinctly ventrally protruding), mediolaterally compressed ventral process. Its end is blunt and well preserved (only the posterior small portion is partly damaged—note, however, that the preservation of this process is exceptional since the process is broken in most specimens of glyptosaurine isolated parietals). The muscular surface in the supratemporal fossa is broad. Its mediolateral width is slightly larger than the width between the cranial crest and the median line of the parietal at the level of the parietal foramen. The parietal foramen is clearly visible, having a dorsoposterior-anteroventral orientation. The elliptical secondary pit is located posteriorly to the foramen (its presence is caused by the 'pineal-related cartilage' immediately underlying the bone; see: Smith *et al.* 2018). It is lens-shaped, anteroposteriorly elongated, and mediolaterally compressed. It is bordered by a sharp bony lamina. Its anterior tip is well ventrally protruded to form a lip of bone. The posterior tip is connected to a ridge that shortly diminishes in height posteriorly. The frontoparietal suture is more-or-less straight, only slightly interdigitated.

Remarks

The parietal is associated on the basis of size and osteoderm morphology. Indeed, the size of the parietal IRSNB R 482 matches very well with the frontal IRSNB R 392 (Fig. 3A, B). In both cases, the osteoderms also appear to match.

Virtual microanatomy and histology

The micro-CT scans of the frontals and parietal revealed a very similar pattern of the internal microanatomy in terms of a vascular network and spongiosis (Fig. 5). There is a large and complex meshwork of numerous cavities. They are irregular, bubble-shaped, and some are interconnected. The bone appears to be less compact in both axial and coronal sections [in comparison to *Ophisaurus holeci* (Georgalis and Scheyer 2021), *Ophisaurus spinari* (Syromyatnikova *et al.* 2022), and *Pseudopus pannonicus* (Loréal *et al.* 2023)] and slightly resembles another European glyptosaurid *Sullivanosaurus* (Čerňanský *et al.* 2023b: fig. 3E). In the IRSNB R 392 frontal, traces of a complex firm suture can be visible (Fig. 5C). Note that the finer histological details, such as growth marks and cell lacunae of the bone, are not visible.

Dentary: Three left dentaries are preserved. The best preserved one, IRSNB R 483, is only missing the anteriormost end with the symphysis and most of the angular process (Fig. 6A–E). The maximum anteroposterior length of the preserved portion is 30.2 mm. It bears 15 tooth positions (seven teeth and half of two others are still attached to the bone). The bone gradually widens posteriorly in lateral and medial views. The lateral surface of the dentary is laterally convex, except at the anterior region. In dorsal view (Fig. 6C), from the level of the 10th tooth position (counted from posterior), the bone is slightly rotated dorsolaterally. Thus, its lateral surface is partly visible when the dentary is viewed in dorsal view. The lateral surface of the bone is smooth, being pierced in the mid-region by four labial foramina (Fig. 6A). The last posterior foramen is located at the level of the fourth tooth position (counted from posterior). In the dorsal posterior region of the bone, there is a wedge-shaped depression forming the articulation surface for the anterolateral process of the coronoid. The dentary is slender rather than robust, being straight in dorsal view, except the anteriormost section, which appears to be slightly bent medially (note that only the beginning of the anterior portion is preserved, and the anterior end is broken off). The dentary has a slightly dorsally concave appearance in medial view, although the ventral margin of the bone seems to be fairly straight (Fig. 6D). This latter margin bears a facet for the splenial reaching the level of the ninth tooth position anteriorly. The Meckelian canal is fully open, although narrow in the anterior and mid-section, being exposed ventrally rather than medially. Posteriorly, the Meckelian canal gradually widens, being open medially. The alveolar canal is large, ventromedially oriented, and separated from the Meckelian canal by the intramandibular septum (Fig. 6E). The posteroventral margin of the intramandibular septum extends to a distinct posterior spine that does not fuse to the internal surface of the dentary and is divided from the wall of the dentary by a distinct groove. The Meckelian canal is roofed by a distinctly dorsally convex subdental shelf [dental crest *sensu* Georgalis *et al.* (2021)], which is reduced to a smooth sloping, slightly rounded border. Its ventral section slightly expands into a lip of bone that partly overlaps the dorsal portion of the Meckelian canal. On the dorsal section, there is no dental sulcus. In the posterior region, the shelf is interrupted by a notch—it forms the dorsal and anterior border of the anterior inferior alveolar foramen. In IRSNB R 484, the splenial spine is preserved (Fig. 6G). The foramen is located at the level of the sixth tooth position (its anterior margin is located at the level between the sixth and seventh tooth position, counted posteriorly). Further posteriorly, the subdental shelf (or crest) is dorsally elevated (Fig. 6B, D). It distinctly narrows to form a thin, sharp crest. Note, however, that it is partly damaged. Posteroventrally to this crest, an articulation for the anteromedial process of the coronoid is located, reaching the level of the fourth tooth position (counted from posterior). The bone ends posteriorly in three processes. The coronoid process is short, forming only a small projection (Fig. 6A, B, D). It is well defined, separated by a coronoid incisure. The surangular process is large and roughly triangular in shape. It is well projected posteriorly. Only the root portion of the angular process is preserved, but the rest is broken off.

The anterior portion of the dentary, including a symphyseal region, is preserved in the specimen IRSNB R 484 (Fig. 6F–I). This dentary narrows anteriorly in medial view. Its anterior end is distinctly bent medially in dorsal view (Fig. 6H). The symphysis is well developed, being rectangular in shape. This region is slightly elevated relative to the shelf. The ventral section of the symphysis is pierced by the Meckelian canal. The specimen IRSNB R 485 represents the posterior region of the dentary. It bears seven tooth positions (three and half teeth are still attached).

All these characters are also present on the holotype, the left dentary IRSNB R 263 (Fig. 1; Sullivan *et al.* 2012: fig. 2), which is nearly complete.

Dentition: The tooth implantation is pleurodont. Teeth are not tightly packed—large gaps are present between them. The teeth are heterodont—in the anterior section of the tooth row, they are smaller and obtusely pointed. More posteriorly, the teeth become gradually anteroposteriorly larger and blunter. The tooth crowns of the posteriormost teeth have a square appearance in lingual view (Fig. 6B, J, K). The mesiodistal cutting edges are present (although less distinct than in the jaws of Glyptosauridae indet. from the French Early Eocene Cos locality; see: Čerňanský *et al.* 2023b: fig. 5). The apicobasal striations are well developed on the lingual side, being restricted on the tooth crown. The labial sides of the tooth crowns are more-or-less smooth. Note, however, that striations can be present on the labial side in some individual teeth, although such striae are not as pronounced as those on the lingual side. Nonetheless, it cannot be excluded that the smooth surface of most of the teeth is caused by poor preservation. In anterior or posterior view, the tooth necks are slightly swollen lingually. The tooth bases are pierced by small elliptical resorption pits.

Remarks

The Glyptosauridae described here from Dormaal, Belgium strongly resembles that of the earliest Eocene North American *Gaultia silvaticus* Smith, 2009 (biozone Wa-0, Willwood Formation in Wyoming; Smith 2009: fig. 18). Both share apomorphies (flat osteoderms and chevron-shaped osteoderms). Moreover, tubercles are arranged in anteromedially to posterolaterally oriented parallel rows, extending anteriorly from the centre; the dentitions of both American and European forms are also very similar. This is not surprising. In fact, half of the North American mammal taxa are close to Dormaal mammals (Gingerich and Smith 2006; see Discussion).

Glyptosauridae indet.

(Figs 7, 8)

Material examined: IRSNB R 486, IRSNB R 487, two premaxillae; IRSNB R 488, right nasal; IRSNB R 489, supraocular; IRSNB R 490, R 491, R 492 and R 493, osteoderms; IRSNB R 494, one dorsal vertebra.

Locality and horizon: Dormaal, Flemish Brabant, eastern Belgium, Dormaal Member, Tienen Formation, Landen Group, earliest Eocene (MP 7).

Description

Premaxilla: Two premaxillae are preserved. This bone is a triradiate, T-shaped element. The larger specimen IRSNB R 486 represents a ventral portion of the premaxilla with nine tooth positions—although the first left one is partly damaged (two teeth are still preserved, their crowns are, however, weathered; Fig. 7A–E). The anterior face of this premaxilla is smooth and broadly arched. It is pierced by a pair of anterior premaxillary foramina (ethmoidal foramina). They form the openings of the canals. These canals are not closed inside the bone, and their dorsal portions are open. This open area is large on the right side, whereas there is a tendency of its closing (or, in fact, most likely initial opening) on the left side, although a notch is still present. Thus, the connection posteriorly with the posterior premaxillary foramen and a canal running ventrally are exposed on both sides in dorsal view. Lateral to that, the wedge-shaped facet for the maxilla is present on the dorsolateral surface of the maxillary process of the premaxilla (Fig. 7C, D). The maxillary processes are slightly reduced, although well defined. They form posterolaterally running triangles in anterior view (Fig. 7A). In this view, the ventral margin of the bone is straight. In posterior view, the supradental shelf is well posteriorly expanded, having a slightly wavy appearance (Fig. 7B). Its median portion extends ventrally into a bilobed incisive process. A short median fissure is present only in the posterior section between both incisive processes (Fig. 7E). Dorsally, a vomerine process is preserved (Fig. 7B). It is triangular in shape in dorsal view, gradually narrowing posteriorly. Only the base of the broad nasal process is preserved.

The smaller specimen IRSNB R 487 represents an element with probably nine tooth positions—note that the left corner is broken off and the internal surface is partly weathered (two worn teeth are still attached to the left side). Its anterior face is smooth and arched (although less than in IRSNB R 486). It is pierced by a pair of anterior premaxillary foramina, but these are completely enclosed in the bone. Note, however, that the bony tissue of the dorsal side of the left foramen is distinctly narrowed. Close to the posterior opening, there are some additional small foramina located medially on each side (the same is true for the

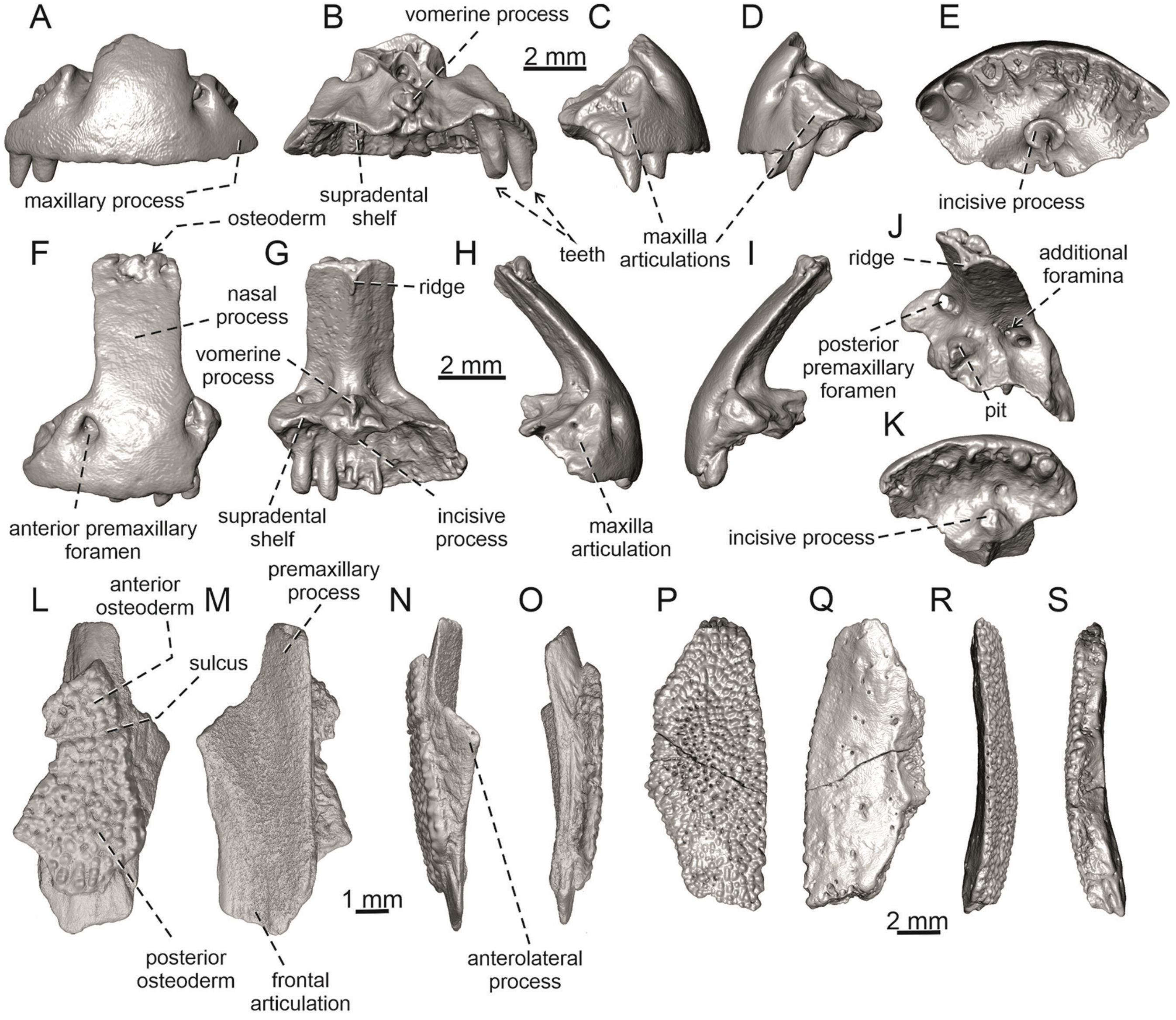

Figure 7. Glyptosauridae indet. from the earliest Eocene of Dormaal. Premaxillae IRSNB R 486 (A–E) and IRSNB R 487 (F–K) in A, F, anterior; B, G, posterior; C, H, lateral right; D, I, lateral left; J, dorsolateral; and E, K, ventral views. Right nasal IRSNB R 488 in L, dorsal; M, ventral; N, lateral; and O, medial views. Supraocular IRSNB R 489 in P, dorsal; Q, ventral; R, lateral; and S, medial views (all micro-CT visualizations).

premaxilla IRSNB R 486; Fig. 7J). The vomerine process is well preserved, identical as on the larger specimen, IRSNB R 486. In both, a pit is located on the dorsal side and one additional smaller one is located anterior to the vomerine process. In IRSNB R 487, the nasal process is preserved, although its posterodorsal end is broken off. It is laterally broad, running distally with more-or-less the same width along the preserved portion. The external surface of the process is flat and an osteoderm is attached to it in the dorsal section. It is partly preserved and the tuberculate sculpture is still visible. On the internal surface, there is a low ridge running across the midline of the nasal process, being sharper in the dorsal region, giving to the process section a triangular shape.

Remarks

A premaxilla has been indeed described in the North American taxon *Gaultia silvaticus*, although being highly worn (Smith 2009: fig. 18A) and resembling the premaxillae here described from Dormaal (Fig. 7A–K). However, the nasal process of the *Gaultia silvaticus* premaxilla is broad basally and tapers distally (see: Smith 2009). This is not a similar feature to the Dormaal specimens, which have the width almost equal along the preserved portion of the nasal process. Moreover, the tooth crowns of both premaxillae are more-or-less worn. Thus, the allocation of the premaxillae IRSNB R 486 and IRSNB R 487, even to the genus *Gaultia*, cannot be supported without doubts.

Nasal: The right nasal IRSNB R 488 is preserved (Fig. 7L–O). It is an elongated plate-like bone. It extends anteriorly into a broad premaxillary process—its anterior end is, however, broken off. The median suture of the nasal is straight, whereas the lateral portion slightly expands ventrally into an anterolateral process. The process is flexed ventrolaterally. The bone thus slightly widens anteriorly (expect of the premaxillary process).

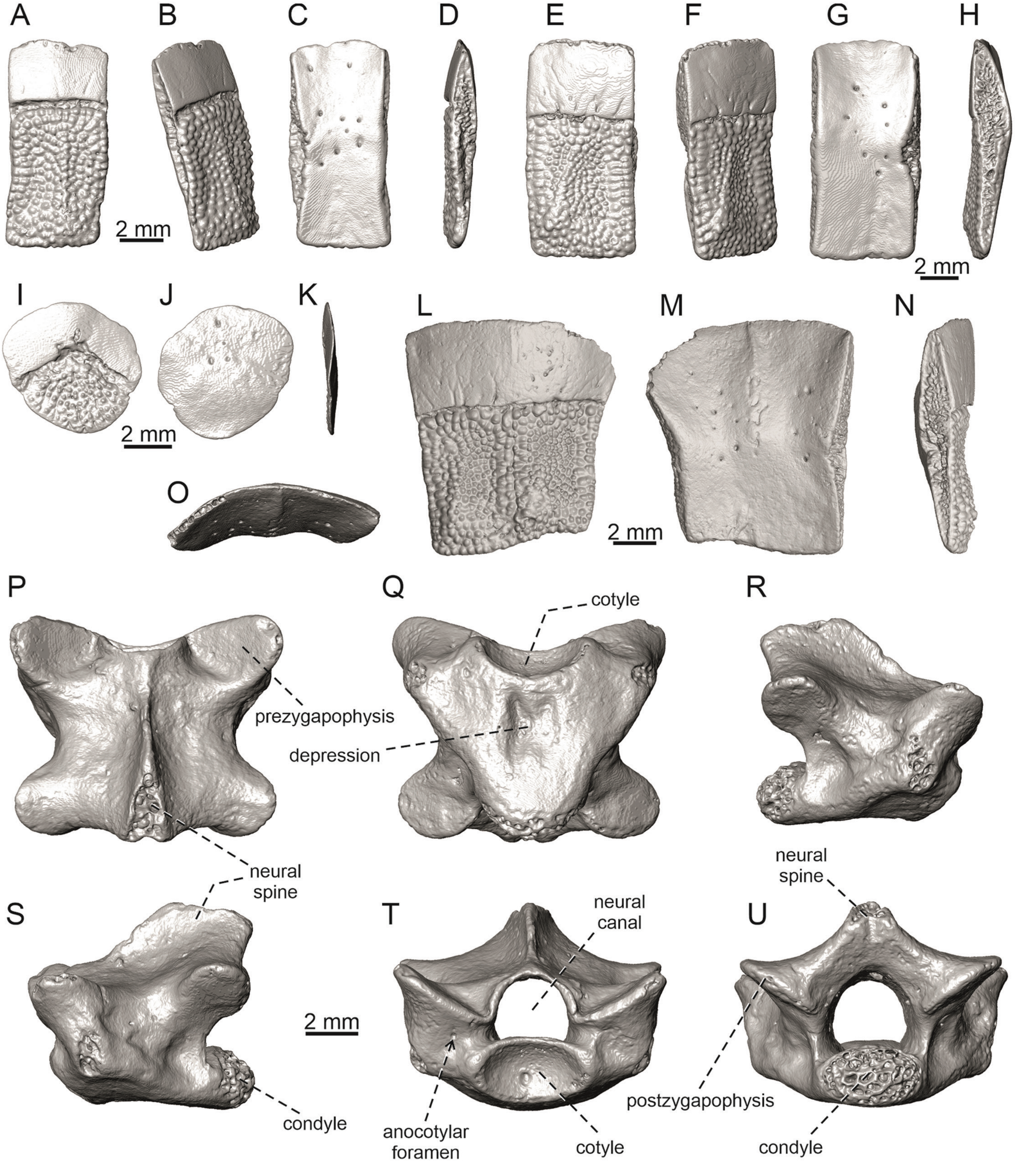

Figure 8. Glyptosauridae indet. from the earliest Eocene of Dormaal. Osteoderms: IRSNB R 490 in A, external; B, lateroexternal; C, internal; and D, lateral views. IRSNB R 491 in E, external; F, lateroexternal; G, internal; and H, lateral views. IRSNB R 492 in I, external; J, internal; and K, lateral views. IRSNB R 493 in L, external; M, internal; N, lateral; and O, anterointernal views. Dorsal vertebra IRSNB R 494 in P, dorsal; Q, ventral; R, lateral right; S, lateral left; T, anterior; and U, posterior views (all micro-CT visualizations).

The dorsal surface of this nasal is covered with two sculptured shields separated by a slightly anterolaterally directed sulcus. The anterior sculptured shield is much smaller than the posterior one. The former one is anteroposteriorly elongated, slightly widens posteriorly and its posteriormost end forms a narrow expansion. The sculpture consists of small, rounded, discrete tubercles. The ventral surface of the nasals is finely weathered. It is not flat, but due to ventrolateral flection, there is a longitudinal shallow depression. The posterior end bears a frontal articulation.

Remarks

In glyptosaurine taxa, hexagonal osteoderms cover the entire skull (Sullivan 1979). This does not appear to be the case on the right nasal IRSNB R 488 (Fig. 7L–O) where osteoderms are more irregular in shape. The division of osteodermal cover (the pattern of osteoderm shapes) might indicate a member of 'Melanosaurinae', but it is also possible that it belongs to *Gaultia*.

Supraocular: The supraocular IRSNB R 489 is anteroposteriorly elongated (Fig. 7P–S). In cross-section it narrows laterally. Its lateral margin is only slightly rounded, almost straight in dorsal view. The medial portion is trapezoidal. The whole external surface is sculptured by numerous small, discrete tubercles radiating from the ossification centre.

Remarks

The sculpture of this specimen is typical for glyptosaurids in general. However, the tubercles are smaller and more densely distributed in this supraocular than in the frontal and parietal of *Gaultia*. Therefore, we refer it to Glyptosauridae indet..

Osteoderms: Several tuberculated osteoderms are described. Most are isolated and rectangular/rhombic in shape. The tubercles are prominent. A keel appears to be absent or is only weakly developed as a tiny line in the middle of some osteoderms (e.g. IRSNB R 490; Fig. 8A). In one osteoderm, IRSNB R 491 (Fig. 8E, F), in contrast, there is a small depression in the central region. Osteoderms have a prominent and smooth overlap surface running on nearly one-third of the anteroposterior length. It is slightly higher than the posterior sculptured portion, from which it is separated by a transverse groove. The sculptured portion is covered by discrete tubercles of various sizes. The internal surface is smooth and pierced by several foramina located along the central region and, in some cases, also in the anterior region. One osteoderm (IRSNB R 492; Fig. 8I–K) is of irregular or roughly rounded shape. It is also slightly smaller than the other osteoderms. The overlap surface of this osteoderm is large (compared to sculptured surface) and is a somewhat reversed V-shape. There is also one specimen (IRSNB R 493) that represents two fused osteoderms, although traces of fusion are still visible (Fig. 8L–O). In anterior view, its lateral sides are bent, so it has a slightly rounded appearance (Fig. 8O).

Remarks

Taxonomic assignment of isolated osteoderms below Glyptosauridae is not possible without doubts (Rage 1978, Sullivan 1979, 2019, Estes 1983, Gauthier *et al.* 2012, Čerňanský *et al.* 2023b). Although differences in general shape exist among these osteoderms, their positions on the body probably play a more major role in this case.

Dorsal vertebra: One large dorsal vertebra, IRSNB R 494, is available (Fig. 8P–U). In ventral view, the centrum is significantly anteriorly widened. The maximum anteroposterior length of the centrum is 8 mm, whereas its maximum width is 9.6 mm. In lateral view, the neural spine is robust and inclined posteriorly but its dorsal margin is damaged. It starts to rise dorsally in the first anterior third of the anteroposterior length of the neural arch. In anterior and posterior views, the neural canal is large and slightly oval in shape (higher than wide). In dorsal and ventral views, the pre- and postzygapophyses are large and extend more laterally. There is a slight interzygapophyseal constriction, but overall, the vertebra has a distinctly wide appearance. The neural arch has no anterior notch, thus only a dorsal rim of the cotyle is visible in dorsal view. Both cotyle and condyle are strongly dorsoventrally depressed. Note, however, that the surface of the condyle is damaged and the spongy bone is exposed. In lateral view, the cotyle is inclined anterodorsally–posteroventrally. For this reason, its ventral rim is located more posteriorly than the dorsal one and a small dorsal portion of the cotyle is clearly visible in ventral view. The anocotylar foramina (*sensu* Georgalis *et al.* 2021) appear to be present—at least the right one is visible (CT-scan reveals that it continues further inside the vertebra as a canal). The centrum is almost triangular in ventral view. Its anterior portion expands laterally into synapophyses (their extremities are, however, damaged on both sides). The subcentral ridges are more-or-less straight in ventral view, except near the condyle, where a small concavity is present. A distinct and wide depression is present on the ventral surface of the centrum, being located slightly anterior from the mid-section.

Remarks

This dorsal vertebra has the anterior centrum markedly widened compared to other glyptosaurines, similar to that observed for the North American *Melanosaurus maximus* Gilmore, 1928, and, to a lesser degree, *Paraplacosauriops* from the Eocene of Europe (Gilmore 1928, Augé 2003a, 2005). The laterally expanded postzygapophyses also suggest an allocation to 'Melanosaurinae'. Moreover, a median ridge in the ventral surface of the centrum, typical of the European glyptosaurine *Placosaurus*, is absent and the anocotylar foramina are present unlike *Placosaurus* (see: Georgalis *et al.* 2021). However, the vertebral morphology of *Gaultia* is unknown and Smith (2009: 343) indicated that '*Gaultia silvaticus* is intermediate in character between typical "melanosaurines" and glyptosaurines'. We, therefore, decided here to allocate this vertebra to Glyptosauridae indet. Nevertheless, if the allocation to 'Melanosaurinae' is correct, this vertebra represents the only evidence of this subfamily in Dormaal.

Varanoidea Gray, 1827
Varanidae Gray, 1827

Saniwa Leidy, 1870

Type species: Saniwa ensidens Leidy, 1870 by original designation.

Saniwa orsmaelensis Dollo, 1923

(Fig. 9)

New referred material: IRSNB R 495, left dentary; IRSNB R 496, IRSNB R 497, two presacral vertebrae; IRSNB R 498, distal portion of humerus.

Locality and horizon: Dormaal, Flemish Brabant, eastern Belgium, Dormaal Member, Tienen Formation, Landen Group, earliest Eocene (MP 7).

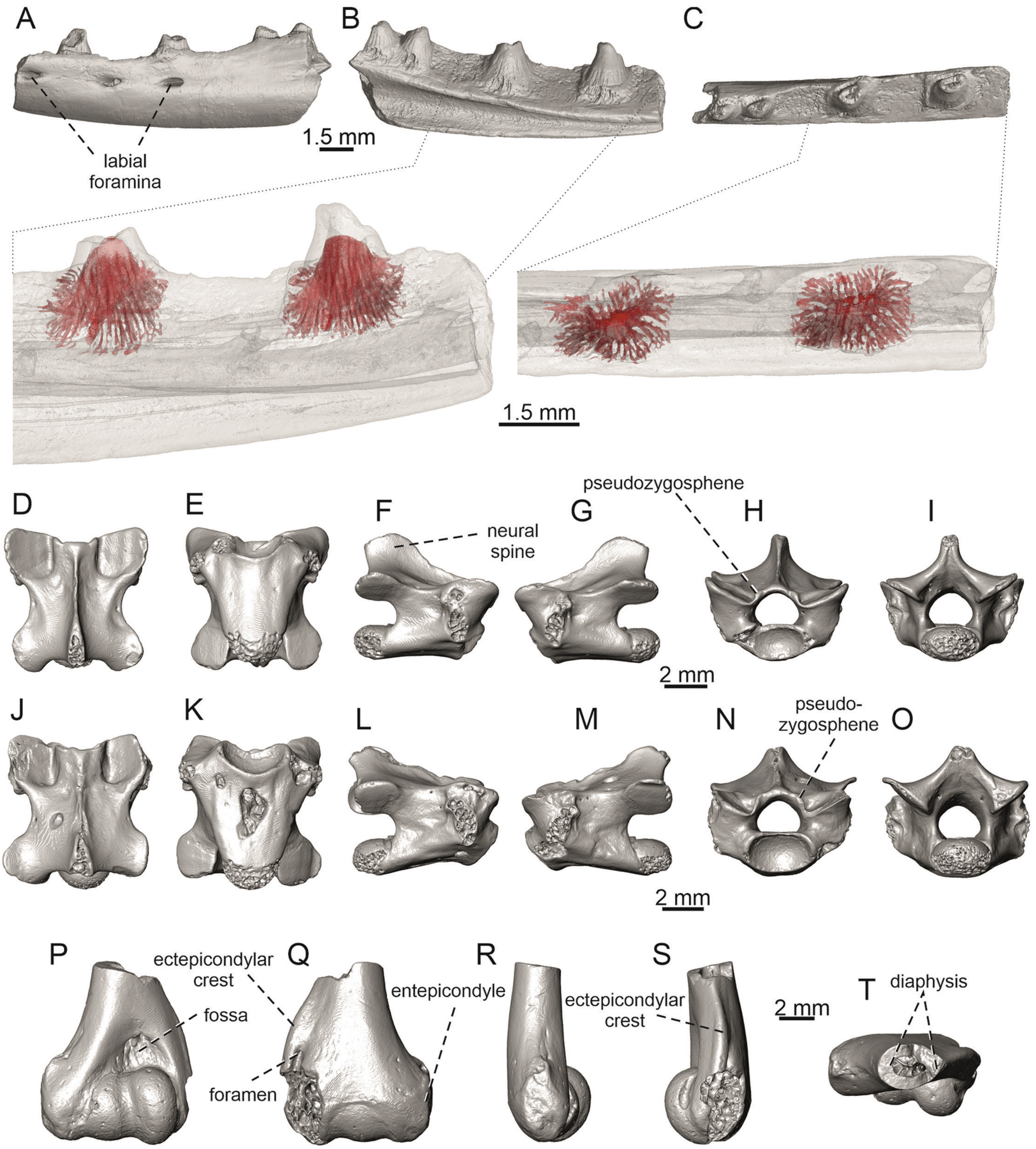

Figure 9. *Saniwa orsmaelensis* from the earliest Eocene of Dormaal. Left dentary IRSNB R 495 in A, lateral; B, medial (with virtually segmented pulp cavities of the anterior teeth); and C, dorsal (with virtually segmented pulp cavities of the anterior teeth) views. Dorsal vertebrae IRSNB R 496 (I–N) and IRSNB R 497 (O–T) in I, O, dorsal; J, P, ventral; K, Q, lateral right; L, R, lateral left; M, S, anterior; and N, T, posterior views. Left humerus IRSNB R 498 in U, ventral; V, dorsal; W, posterior; X, anterior; and Y, medial views (all micro-CT visualizations).

Description

Dentary: A mid-section of a left dentary, IRSNB R 495, is preserved (Fig. 9A–C). It bears six and half tooth positions (only four teeth are mostly preserved). The bone is anteroposteriorly elongated, having a slightly concave appearance. In the posterior preserved section, it widens dorsoventrally, being slightly dorsally elevated. The lateral surface of the bone is smooth, except for three large elliptical labial foramina located more-or-less in the dorsal anterior third of the lateral wall. In medial view, the Meckelian canal is fully open, although narrow. It gradually dorsoventrally widens posteriorly. The subdental shelf is thin and only weakly medially expanded.

Dentition: The dentition is subpleurodont (*sensu* Hoffstetter 1954, 1955), the jaw parapet is low and the bases of the teeth are attached to a sloping, concave surface, without any angle between two different planes (Fig. 9A–C). The tooth bases are mesiodistally broad and bear well-preserved typical basal striae, i.e. plicidentine is present (the infolding of dentine in the pulp cavity; Kearney and Rieppel 2006). It is complex and dense, as many closely spaced basal infoldings are present. All tooth tips are broken off. However, the labiolingual tooth crown compression is visible in broken teeth and partly, to a small extent, in the virtual 3D model of a pulp cavity (Fig. 9C).

Remarks

The overall morphology and plicidentine support allocation of the dentary to a varanoid (Kearney and Rieppel 2006, Georgalis and Scheyer 2019). Unfortunately, the Dormaal dentary is only partly preserved. In fact, the preserved portion of this dentary is very similar to that of *Saniwa orsmaelensis* described by Augé *et al.* (2022) from the same locality by having many closely spaced basal infoldings present on tooth bases—in contrast to *Palaeovaranus* Zittel, 1887–90, which has more widely spaced infoldings (Georgalis and Scheyer 2019). The presence of a labiolingual tooth crown compression, with mesial and distal carinae, is considered a synapomorphy of the varanoid genera *Lanthanotus* Steindachner, 1878 and *Varanus*; in *Varanus* this compression extends to the tooth base and is visible in the pulp cavity (Georgalis *et al.* 2023). Although some degree of the labiolingual compression of the pulp cavities is visible in IRSNB R 495 (Fig. 9C), this compression is markedly smaller (not highly compressed) in comparison to extant *Varanus* (see: Georgalis *et al.* 2023: fig. 3D, F).

Dorsal vertebra: Two varanoid dorsal vertebrae are available in the material (Fig. 9D–O). They are medium-sized, with centra that widen anteriorly, being almost triangular in ventral view. The maximum anteroposterior length is 5.7 mm in IRSNB R 496 and 7 mm in IRSNB R 497. The subcentral ridges are more-or-less straight in ventral view. The neural spine is well developed, starting its rise dorsally approximately in the half of the anteroposterior length the neural arch (Fig. 9F). It is trapezoidal in shape; however, its distal tip is broken off in both specimens. Its dorsal posterior portion is narrow, being drop shaped in cross-section (Fig. 9D, J). This portion occupies the posterior third of the anteroposterior length of the neural arch. Anteriorly, there is a median ridge that continues almost until the anterior end of the neural arch. The neural canal is large, pentagonal in shape. It is vaulted in posterior view (Fig. 9I, O). The prezygapophyseal articular facets are large and broad in dorsal view. The postzygapophyseal articular facets are also large. There is a slight constriction between pre- and postzygapophyses. In this region, a small foramen is located on the lateral side near the constriction on each side in dorsal aspect (Fig. 9G–M). Overall, the vertebrae are wide in dorsal view. A pseudozygosphene and a pseudozygantrum are present [this would correspond to character state 468: 1 in Gauthier *et al.* (2012)]. The synapophyses are damaged. The cotyle and the condyle are dorsoventrally depressed. In lateral view, the cotyle is distinctly inclined—its ventral rim is located more posteriorly than the dorsal one. Thus, the dorsal portion of the cotyle is clearly visible in ventral view (Fig. 9E–K). The condyle is well exposed from both dorsal and ventral views. The ventral surface of the centrum is slightly ventrally concave in lateral view. Small subcentral foramina are visible on the ventral side of the centrum.

Remarks

The pseudozygosphene–pseudozygantrum are very prominent in these specimens (Fig. 9H, I, N, O). This favours their assignment to the genus *Saniwa* (Gilmore 1922, Rage and Augé 2003, Augé 2005, Georgalis *et al.* 2021). The precondylar constriction appears to be practically absent here, but this could be due to bad preservation (the condyles are eroded on these two vertebrae) and (to a degree) variable through ontogeny. Moreover, *Saniwa* does not have very prominent precondylar constriction in any case (relative to *Varanus*, e.g. Rieppel 1980, Estes 1983, Smith *et al.* 2008, Holmes *et al.* 2010, Čerňanský *et al.* 2022b). Vertebrae of *Saniwa orsmaelensis* from Dormaal were previously described by Dollo (1923), Hoffstetter (1969), and Augé *et al.* (2022: fig. 5A–F).

Humerus: Only the distal portion of the left humerus, IRSNB R 498 is preserved (Fig. 9P–T). It is robust and large. The maximum width of the preserved specimen is 8.6 mm. The preserved portion of the diaphysis is elliptical in cross-section (Fig. 9T). The entepicondyle is well developed, being set off from the posterior margin of the diaphysis. An entepicondylar foramen is absent. The distal portion of the ectepicondyle is damaged and partly broken off, but the ectepicondylar ridge is well developed. This region is pierced by an ectepicondylar foramen (Fig. 9Q). The ulnar and radial condyles are large, proximally accompanied by a fossa.

Remarks

The humerus is also allocated to the genus *Saniwa* based on the following features (see: Rieppel and Grande 2007, Augé *et al.* 2022): (i) an entepicondylar foramen is absent and (ii) the entepicondyle is set off from the posterior margin of the diaphysis of the humerus (although not in such degree present in humerus of *Saniwa ensidens*).

Palaeovaranidae Georgalis, 2017
Palaeovaranidae indet.

(Fig. 10)

1962 *Necrosaurus*—Hecht and Hoffstetter: 11.
1990 *Necrosaurus* sp.—Augé: 166–167.
2003 cf. *Necrosaurus*–Augé: 443, fig. 1I.
2005 *Necrosaurus* sp.—Augé: 287.

Referred material: IRSNB R 499, right maxilla, IRSNB R 500, osteoderm.

Locality and horizon: Dormaal, Flemish Brabant, eastern Belgium, Dormaal Member, Tienen Formation, Landen Group, earliest Eocene (MP 7).

Description

Maxilla: Only a fragment of the right maxilla is preserved (IRSNB R 499; Fig. 10A–E). It possesses nine tooth positions (three and

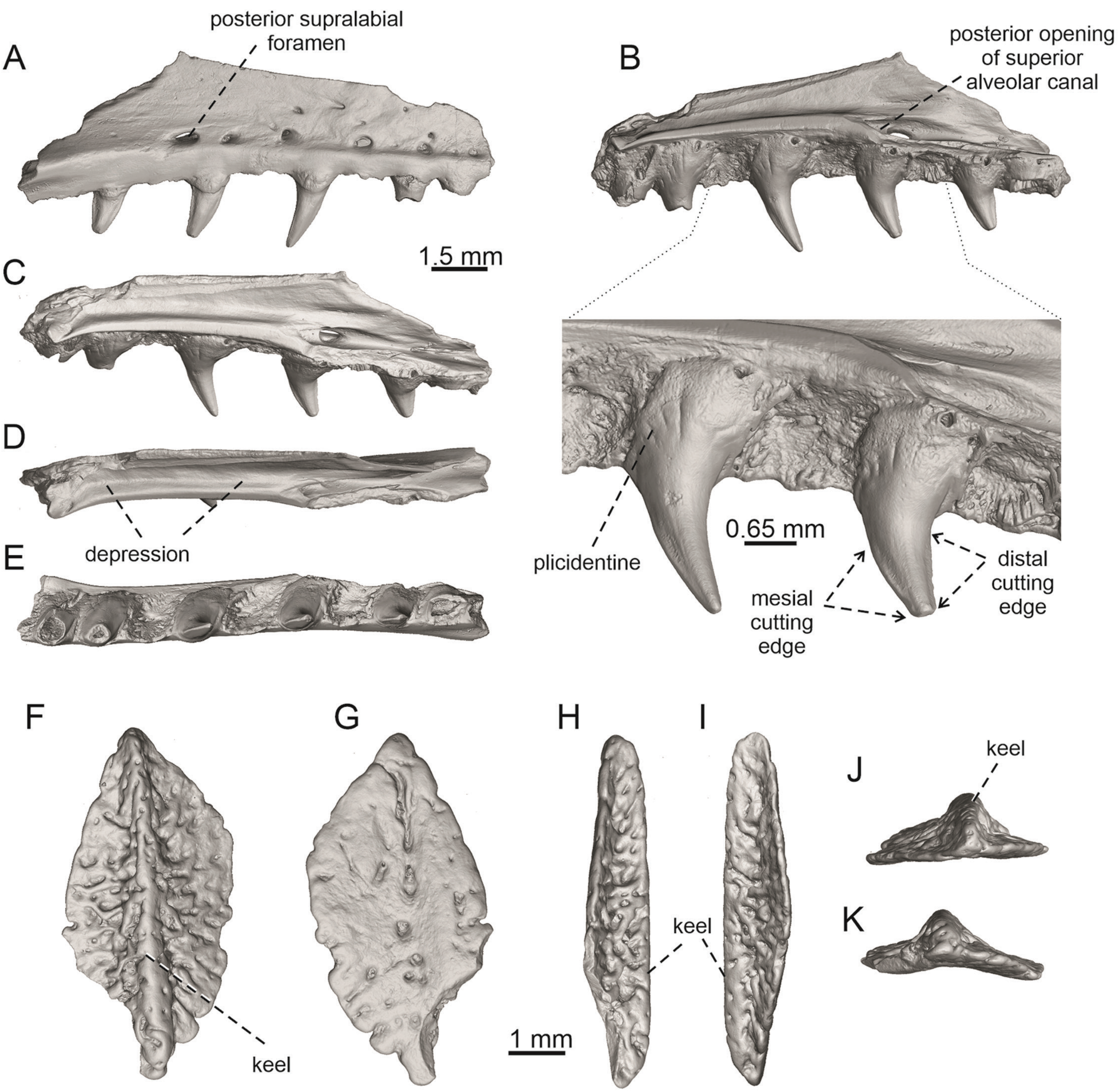

Figure 10. Palaeovaranidae indet. from the earliest Eocene of Dormaal. Right maxilla IRSNB R 499 in A, lateral; B, medial with detail of teeth; C, dorsomedial; D, dorsal; and E, ventral views. Osteoderm IRSNB R 500 in F, external; G, internal; H, right side of the osteoderm; I, left side of the osteoderm; J, anterior; and K, posterior views (all micro-CT visualizations).

half teeth are still preserved). The bone is lightly built and rather thin. In lateral view, between the dorsal and ventral margins, the wall of the maxilla is distinctly concave. The facial process is only partly dorsally preserved, being lateromedially thin. The external surface of the bone is smooth. It is pierced by a series of large labial foramina (six are present in the preserved portion) located in a row on the ventral section of the bone surface. Posterior to the last labial foramen, several teeth are present (at least three are preserved). Besides labial foramina, several small foramina are present, being located more dorsally (Fig. 10A). In medial view, there is a thin supradental shelf that slightly widens posteriorly. It is not markedly medially expanded. Laterally, in the dorsal portion of the shelf (between the shelf and the facial process), there is a narrow longitudinal depression—the sulcus for the nasolacrimal duct. The maxilla immediately laterally to the supradental shelf is burrowed by the superior alveolar canal. Its posterior opening, the superior alveolar foramen, is located in the posterior section, being large and anteroposteriorly elongated. It is located at the level of the sixth preserved tooth position (counted from anterior). The foramen is dorsolaterally bordered by a lip of bone.

Dentition: The dentition is subpleurodont (*sensu* Hoffstetter 1954, 1955), the jaw parapet is low and the bases of the teeth are attached to a sloping, concave surface, without any angle between two different planes (Fig. 10A–E). The tooth bases are mesiodistally broad and bear well-preserved typical basal striae, i.e. plicidentine. These basal infoldings are widely spaced. The tooth tips are pointed, tall, and strongly curved distally and slightly lingually. The mesial and distal cutting edges are well developed. Although the mesial one is more distinct in the anterior preserved tooth, both mesial and distal cutting edges are more-or-less equal in the posterior teeth.

Osteoderm: The osteoderm IRSNB R 500 (Fig. 10F–K) is oval in shape with an external medial high keel running through the entire length of the osteoderm. It is sculptured by pits and ridges. The internal surface is slightly concave with small foramina [neurovascular foramina *sensu* Smith and Gauthier (2013)].

Remarks

The overall morphology and plicidentine support allocation of the maxilla to a varanoid (Kearney and Rieppel 2006, Georgalis and Scheyer 2019). Although preserved diagnostic features are limited, the maxilla can be distinguished from *Varanus* and *Saniwa ensidens* in having at least three tooth positions posterior to the last supralabial foramen. In *Saniwa orsmaelensis*, which was previously known from Dormaal (there is only one species of *Saniwa* in Dormaal for the moment; see: Augé *et al.* 2022), four teeth are present posterior to the last supralabial foramen. It should be noted, however, that several tooth positions posterior to the last labial foramen are also present in *Paranecrosaurus feisti* (Stritzke, 1983), which is known only from the Early–Middle Eocene of Messel in Germany (Smith and Habersetzer 2021; previously this taxon was regarded as *Saniwa feisti*, see: Stritzke 1983). 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* (previously mentioned in the literature with the name *Necrosaurus*; see: Georgalis 2017) and *Paranecrosaurus* [nasolacrimal ridge *sensu* Smith and Habersetzer (2021)]. Unfortunately, this portion in the Dormaal maxilla is heavily damaged and there is no indication of its presence. However, this jaw fragment is characterized by an alternate tooth replacement (teeth are widely spaced), which is diagnostic for *Palaeovaranus* (Augé and Smith 2009). Moreover, it seems that the prominence of the plicidentine is not as prominent as in *Saniwa*; it is represented by plicidentine with widely spaced striations, which is more typical for *Palaeovaranus* (Georgalis and Scheyer 2019, Georgalis *et al.* 2021). The mesial and distal cutting edges on tooth tips are present, but this feature can also be find in *Palaeovaranus* [*Necrosaurus* in Augé and Smith (2009: fig. 7)], *Paranecrosaurus* (Smith and Habersetzer 2021), and *Saniwa* (Rieppel and Grande 2007). Finally, if we compare the specimen IRSNB R 499 (Fig. 10B) with the specimen attributed to '*Necrosaurus*' sp. from the Oligocene of Boutersem, also in Belgium (see: Augé and Smith 2009: fig. 7), we can observe several similarities, such as the general shape of the teeth, space between the infoldings, curvature of the tooth crowns, and presence of mesial and distal cutting edges on the tooth crowns.

Anguimorpha indet.

(Fig. 11A–F)

Referred material: IRSNB R 501, one dorsal vertebra.

Type locality and horizon: Dormaal, Flemish Brabant, eastern Belgium, Dormaal Member, Tienen Formation, Landen Group, earliest Eocene (MP 7).

Description

Dorsal vertebra: The single indeterminate anguimorphan dorsal vertebra in the sample (Fig. 11A–F) is large—the maximum anteroposterior length of the centrum is 9.4 mm, whereas its maximum width is 9 mm. The neural spine is low and robust. It starts to rise gradually, dorsally from slightly behind the anterior margin of the neural arch. This anterior portion of the spine is dorsally inclined in an angle of 37° from the horizontal. However, the dorsal margin of the neural spine is damaged. The neural canal is large and oval (Fig. 11E, F). The pre- and postzygapophyses are large, being oriented anterolaterally and posterolaterally in dorsal and ventral views (Fig. 11A, B). In dorsal view, the prezygapophyses markedly overreach the anterior margin of the neural arch, which is located almost at the level of the posterior border of the prezygapophyseal articular surfaces. Due to the presence of this wide notch (pars tectiformis of the neural arch between prezygapophyses), the dorsal surface of the centrum, posterior to the cotyle, is exposed in this view. The mid-region of the neural arch is slightly expanded anteriorly, having a small medial notch. Posterolaterally from this region, a shallow but wide depression is present on the dorsolateral wall on both sides of the neural arch. These depressions form slopes running from the anterolateral side of the neural spine to the posterior end of the prezygapophyseal articular surfaces. In contrast, the other area of the neural arch has a slightly swollen appearance. In posterior view, the neural arch is moderately vaulted and its roof-like posterior portion rises dorsally to the posterior base of the neural spine and gradually connects it with the postzygapophyses (Fig. 11F). Synapophyses are present, being laterally expanded. Their ends, however, are more-or-less damaged. Both cotyle and condyle are strongly dorsoventrally depressed. In lateral view, the cotyle is slightly inclined—its ventral rim is located more posteriorly than the dorsal one. Thus, the small dorsal portion of the cotyle is clearly visible in ventral view. In the condyle, the articular surface is developed mainly on the dorsal side rather than on the ventral side. Thus, the condyle is only slightly exposed in ventral view. In ventral view, the centrum is anteriorly widened, being almost triangular (Fig. 11B). The subcentral ridges are more-or-less straight, except at the condyle level, where a weak precondylar constriction is present (the width of the condyle is slightly larger than the width of the centrum immediately anterior to it). The small subcentral foramina are located in the anterior region of the centrum.

Remarks

Although the precondylar constriction might indicate the allocation of this dorsal vertebra IRSNB R 501, to *Saniwa*, the constriction is much more visible and forms a slightly more pronounced hook in *Saniwa orsmaelensis* from Dormaal (see: Augé *et al.* 2022: fig. 5C, F, I). However, the intracolumnar variation of *Saniwa* is unknown. The vertebra IRSNB R 501 is a posterior presacral and in some varanids, these are also wide but not to the extent as seen in *Saniwa*, as we can see in IRSNB R 501. A pseudozygosphene and pseudozygantrum are absent and the postzygapophyses are laterally expanded, which would indicate

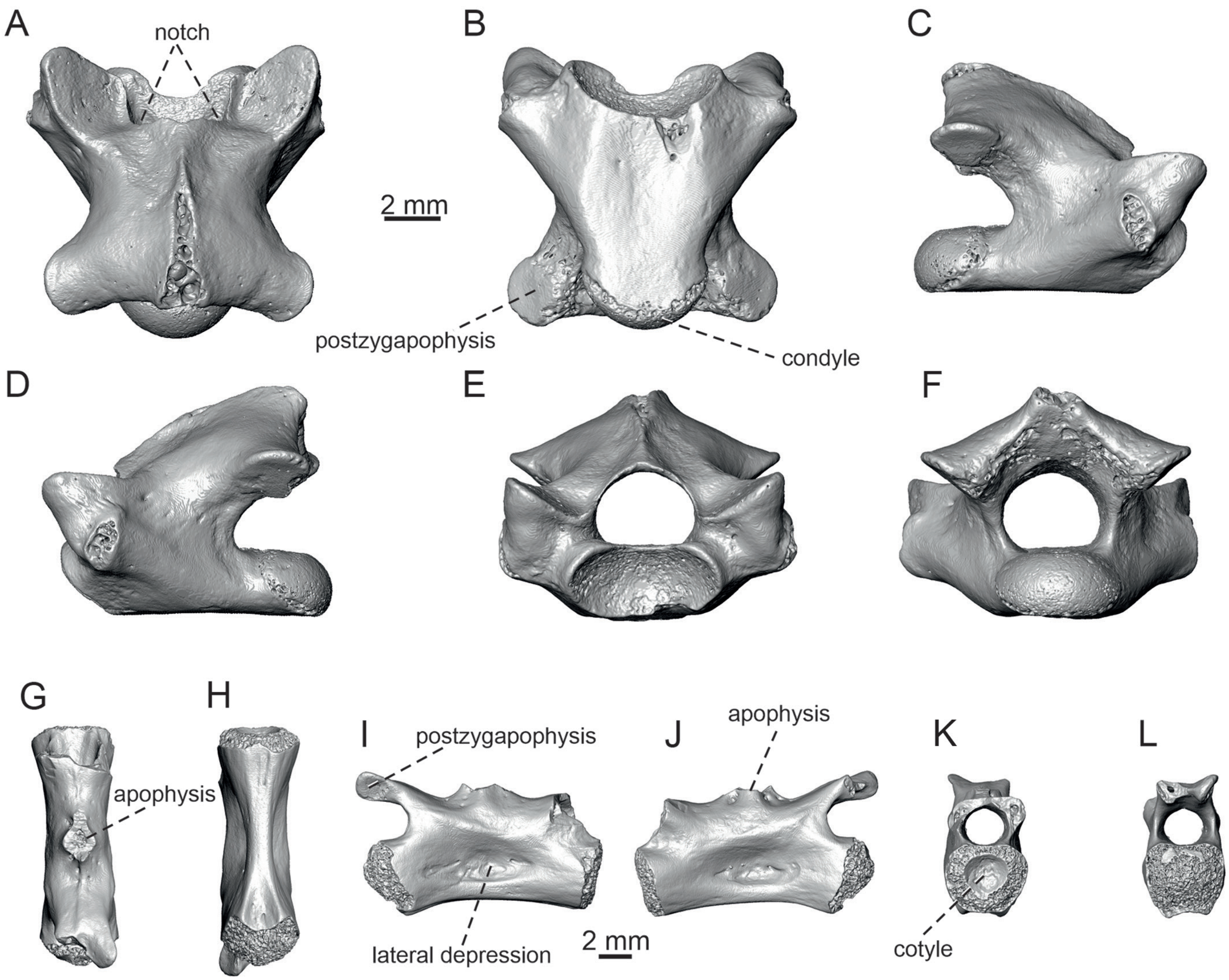

Figure 11. Anguimorpha indet. 1 (A–F) and Squamata indet. (G–L) from the earliest Eocene of Dormaal. Dorsal vertebra IRSNB R 501 in: A, dorsal; B, ventral; C, lateral right; D, lateral left; E, anterior; and F, posterior views. Caudal vertebra IRSNB R 502 in G, dorsal; H, ventral; I, lateral right; J, lateral left; K, anterior; and L, posterior views (all micro-CT visualizations) (all micro-CT visualizations).

an attribution to Glyptosauridae (plausibly to 'melanosaurines' rather than glyptosaurines; see: Georgalis *et al.* 2021).

Squamata indet.

(Fig. 11G–L)

Referred material: IRSNB R 502, one caudal vertebra.

Locality and horizon: Dormaal, Flemish Brabant, eastern Belgium, Dormaal Member, Tienen Formation, Landen Group, earliest Eocene (MP 7).

Description

Caudal vertebra: Only one caudal vertebra, IRSNB R 502, is preserved (Fig. 11G–L). It is large, with the maximum anteroposterior length of the centrum being 14.1 mm (taking into account its damaged condyle, the real length was slightly larger). The vertebra is extremely elongated and rather slender. The neural spine is reduced to a tiny crest on the neural arch and diminishes posteriorly. Anterior to this, approximately in the mid-portion of the vertebra, a large apophysis is located on the dorsal side of the neural arch (Fig. 11G). In lateral view, it seems to form a triangular structure, but its dorsal portion is, however, broken off (Fig. 11I, J). Both prezygapophyses are broken off. In anterior and posterior views, the neural canal is small (Fig. 11K, L). Only the right postzygapophysis is preserved. Its articular surface faces lateroventrally, with the pronounced dorsal inclination. The long centrum is laterally compressed, bearing a fossa on each side. Thus, the ventral portion has an hour-glass shape in ventral view (Fig. 11H). The condyle is damaged, whereas a rounded cotyle is partly preserved.

Remarks

Isolated caudal vertebrae are usually difficult to confidently identify. The vertebra has no sign of a fracture plane, which helps in assigning it to a varanoid lizard. The tail of *Saniwa ensidens* is markedly long (68% of the total length of the specimen; see: Rieppel and Grande 2007). Extremely elongated and rather slender caudal vertebrae are present in the distal section of the tail. However, at present no vertebra so distal has been described yet for *Saniwa orsmaelensis*. The origin of this vertebra from the caudal region is supported by the reduction of the neural spine and dorsal inclination of postzygapophyses (Rieppel and Grande 2007). Its large size indicates that it belonged to a large lizard. Thus, *Saniwa* might be a good candidate. However, caution is needed, and we have decided to allocate this vertebra only as non-ophidian squamate.

DISCUSSION

Several clades of Anguimorpha can be identified in Dormaal—Glyptosauridae, Varanidae, and Palaeovaranidae studied here. At least some of these clades probably first appeared in Europe in the earliest Eocene (MP 7) and represent immigrants in Dormaal (Sullivan *et al.* 2012, Augé *et al.* 2022). Besides these, Augé (1995) mentioned four vertebrae, including two that are described and drawn, which he referred to Helodermatidae based on the morphology of the ventral view. However, these vertebrae present a rather general anguimorph morphology and one is reminiscent of an amphisbaenian vertebra (Augé 1995: fig. 2; one of these previously figured vertebrae is tentatively referred to ?Amphisbaenia) by the neural arch that is constricted at midlength, its U-shaped anterior border, the prezygapophyses distinct from the neural arch, and subcentral foramina situated in the anterior part of the centrum (Folie *et al.* 2013, Georgalis *et al.* 2018, Čerňanský 2023). They do not present characters allowing an attribution to the family Helodermatidae and the presence of this family in the earliest Eocene of Dormaal is not confirmed.

Glyptosaurinae

Previously, a glyptosaurine taxon, ?*Placosaurus ragei*, was described from Dormaal by Sullivan *et al.* (2012). The original type material of ?*P. ragei* is represented only by an isolated dentary (Fig. 1; IRSNB R 263; Sullivan *et al.* 2012: fig. 2), while a parietal (IRSNB R 264; Sullivan *et al.* 2012: fig. 3) and a cephalic osteoderm had also been referred to this taxon. However, the current taxonomy of *Placosaurus* species is based on the morphology of the frontal (Sullivan and Augé 2006). Thus, the generic assignment of the Dormaal taxon was questionable (see: Sullivan *et al.* 2012). The Dormaal material described here includes various types of bones, including the frontal of a glyptosaurine lizard. This sheds a new light on this Dormaal taxon. Indeed, the Early Eocene glyptosaurines in Europe are different from the post-Early Eocene *Placosaurus* (Čerňanský *et al.* 2023b) and the same is true for the Dormaal taxon. Interestingly, ?*Placosaurus ragei* strongly resembles the earliest Eocene North American *Gaultia silvaticus* Smith, 2009 (biozone Wa-0, Willwood Formation, Wyoming, USA) by the following features [which are diagnostic to *Gaultia* based on Smith (2009)]: (i) having wide, chevron-shaped osteoderms (or shields) on anterior end of frontal; (ii) flat osteoderms over most of the skull roof; and (iii) a ray arrangement of the tubercles. Thus, the Dormaal material is here attributed to the genus *Gaultia* as the new combination *Gaultia ragei* and represents the first record of this genus outside North America. Note that the glyptosaurine from Silveirinha (see: Rage and Augé 2003), however, is a different taxon and cannot be allocated to *Sullivanosaurus* (see comparison in: Čerňanský *et al.* 2023b) or to *Gaultia*.

Sullivan (2019: 754) considered *Gaultia* a sister-taxon to Glyptosaurinae. However, Čerňanský *et al.* (2023b) indicate that the fragmentation of cephalic osteoderms seen in the Early Eocene *Sullivanosaurus* and *Gaultia* may represent an intermediate stage between typical (plesiomorphic) division and derived fragmented hexagonal osteoderms of glyptosaurines such as *Glyptosaurus* and *Placosaurus*.

'Melanosaurinae'—were they present in the Dormaal earliest Eocene ecosystem?

A *Placosauriops*-like 'melanosaurine' has been previously described from Dormaal based on a mid-portion of a right frontal (IRSNB R 266; Sullivan *et al.* 2012: fig. 4) and fused frontals (IRSNB R 392; Sullivan 2019: fig. 2) described here and previously discussed by other authors (Hecht and Hoffstetter 1962, Sullivan 2019). However, these frontals bear traces of chevrons very similar to *Gaultia* (see Description above) and we, therefore, here attribute them to *Gaultia ragei*.

The occurrence of 'Melanosaurinae' in Dormaal, therefore, could be hypothetically supported only by isolated the dorsal vertebrae (IRSNB R 494 and potentially 501) described here (Figs 8P–U, 11A–F). In the dorsal vertebra IRSNB R 501 (Anguimorpha indet.; Fig. 11A–F), the prezygapophyses markedly overreach the anterior margin of the neural arch in dorsal view and a wide notch is present (pars tectiformis of the neural arch between prezygapophyses). Thus, the dorsal surface of the centrum, posterior to the cotyle, is exposed in this view. This is not present in IRSNB R 494 (Fig. 8P–U) mentioned above. Moreover, the lateral orientation of the prezygapophyses is not so pronounced relative to that in IRSNB R 494. In the case that IRSNB R 501 is also a glyptosaurid, these differences might indicate the presence of (at least) two glyptosaurid taxa in Dormaal. However, ontogenetic and individual variabilities of glyptosaurid vertebrae are unknown. Based on current knowledge and the absence of well-identified vertebrae of *Gaultia*, we have decided here to allocate these vertebrae only to Glyptosauridae indet. and Anguimorpha indet. (we cannot be sure which morphotype of these vertebrae, if any, might belong to *Gaultia*). Overall, these vertebrae cannot be taken as strong evidence of the occurrence of 'Melanosaurinae' in Dormaal.

Varanidae

Only *Saniwa orsmaelensis* is reported from Dormaal (Dollo 1923, Augé *et al.* 2022). This varanid appeared in Europe during MP 7 and appears to be an immigrant (Augé *et al.* 2022). Our material described here adds to the material already known as a base for observing the variability of the Dormaal *Saniwa*. There is one feature in regard to new specimens that deserve a comment here: the entepicondyle of humerus IRSNB R 498 (Fig. 9P–T) is set off from the posterior margin of the diaphysis, but not in such degree as it is present in the North American *Saniwa ensidens* (Rieppel and Grande 2007).

Palaeovaranidae

Hecht and Hoffstetter were the first to indicate the presence of *Palaeovaranus* in Dormaal (Hecht and Hoffstetter 1962: 11), represented by one osteoderm and some caudal vertebrae characterized by transverse processes less anteriorly placed and transversely oriented, and articulation processes with the chevron bones that are against the condyle. Later, Augé mentioned one osteoderm and two caudal vertebrae (General Inventory number 23197; Augé 1990: 166–167). In 2005, the same author added to this taxon two slender and gracile dentaries (from collection Coupatez–Wouters) presenting posterolingually curved teeth with mesial and distal cutting edges (Augé 2005: 287).

Although the allocation of the maxilla to palaeovaranids might be questionable due to a limitation of its preservation, the isolated osteoderm IRSNB R 500 described here and referred to Palaeovaranidae indet. confirms the presence of this clade in Dormaal. An oval and high-keeled osteoderm is part of the diagnosis for palaeovaranids (Hoffstetter 1943, Georgalis 2017). Although palaeovaranid osteoderms have a tall keel similar to that of shinisaurids (Smith 2017), some differences are present. In cross-section, the keel appears as a lamina perpendicular to the plate as in shinisaurs, whereas the palaeovaranid keel arises progressively from the plate with a cross-sectional triangular shape (Čerňanský *et al.* 2015), as it is in the Dormaal osteoderm.

Palaeovaranus is known in Europe from the Palaeocene of Cernay (MP6, France) to the Oligocene of the Quercy (MP23, France; Hecht and Hoffstetter 1962, Augé 2003b, 2005, Rage 2012). It is, therefore, not surprising to confirm its presence in the Eocene of Dormaal (Belgium).

However, similarities have been underlined between palaeovaranids and shinisaurids, such as the shape of the osteoderms and dentition (Kuhn 1940a, Hoffstetter 1943) and even the basal infoldings on teeth could be shared by both families instead of being characteristic of only palaeovaranids (Smith and Gauthier 2013). Following Smith and Gauthier (2013), some palaeovaranid specimens could, in fact, be shinisaurids. Shinisaurids were certainly present in Europe during the Eocene (Smith 2017).

Migrations during the Early Eocene

An important faunal reorganization occurred near the Palaeocene/Eocene boundary and represents immigration during an interval of global warmth that enabled the dispersal of many taxa between the continents of the northern hemisphere (Bowen *et al.* 2002, Smith *et al.* 2006, Smith 2011b). Occurrence of the genus *Gaultia* in Belgium, previously documented only from the earliest Eocene of North America, is not surprising. Indeed, half of the mammal taxa from that age in North America are closely related to Dormaal mammals (Smith 2000, Gingerich and Smith 2006, Smith *et al.* 2006), while at least one turtle genus is common in both Dormaal and North America, i.e. the trionychid *Axestemys* (Georgalis and Joyce 2017, Pérez-García and Smith 2021). The clade Glyptosauridae represents a newcomer in the Early Eocene of Europe (Rage 2013), precisely showing North American relationships (Sullivan *et al.* 2012). Thanks to the important richness, high species' diversity, and good preservation of the Dormaal vertebrate fauna, we can see which exact genus of glyptosaurids arrived in Europe. Therefore, after the revision of the Dormaal material, we can conclude that no record of *Placosaurus* is documented in the Early Eocene of Europe (see also: Čerňanský *et al.* 2023b). Instead of *Placosaurus*, *Gaultia* represents another shared faunal element between Europe and North America. As for other lizards, several cases are already documented, including the varanid *Saniwa* (Augé *et al.* 2022) and, potentially, the iguanian *Tinosaurus* (see: Čerňanský *et al.* 2023a). Note that *Saniwa* was also reported by Kuhn (1940b) from the Middle Palaeocene Walbeck locality in Germany, but this material is not a varanid (Čerňanský and Vasilyan 2024). Moreover, there are coeval snake genera in the Eocene of North America and Europe (see: Smith and Georgalis 2022). *Scincoideus* Folie *et al.*, 2005, which is known from the Mid-Palaeocene of Belgium (the continental Hainin Formation; Folie *et al.* 2005), occurred in North America during the Early Eocene, documenting intercontinental dispersal to North America (Smith 2011b). These imply faunal exchanges between North America and Europe during the Late Palaeocene to Early Eocene (in regard to mammals, there are indeed several episodes of faunal exchanges between Europe and North America before, during, and after the Palaeocene–Eocene Thermal Maximum (PETM; see, e.g. Smith *et al.* 2006, Smith and Smith 2013, Solé *et al.* 2016, De Bast and Smith 2017), but nevertheless the coeval Asian reptile fossil record is still rather poor to afford definite conclusions. For example, the omomyid haplorhine primate *Teilhardina* is suggested to have an Asian origin, and a westward Asia-to-Europe-to-North America dispersal for this taxon is proposed (Smith *et al.* 2006). Note, however, that *Archaeovaranus* from the Early Eocene of China has been suggested to be sister to genus *Varanus*, whereas *Saniwa* is sister to (*Archaeovaranus* + *Varanus*) (Dong *et al.* 2022). Dong *et al.* (2022) suggest that the transition from Cretaceous varaniform lizards to *Varanus* occurred in East Asia before the origin and dispersal of *Varanus* to other regions.

The North Atlantic Land Bridge has been suggested as one potential route (the Thulean route) for faunal dispersals (McKenna 1975). It was a land bridge, now submerged beneath the Atlantic Ocean, that connected the British Isles to central Greenland (Brikiatis 2014). Organisms could migrate throughout Greenland, Faeroes, and Great Britain. The land bridge appeared during the Late Palaeocene and disappeared during the Early Eocene, although the timing of its end has been debated (Denk *et al.* 2011). Indeed, the data indicate that the Eocene Greenland and even Spitzbergen climate was generally warm (Eldret *et al.* 2009, Greenwood *et al.* 2010). Moreover, land bridges and on-land migrations are not the only way organisms get to new territories. Dispersal over sea is not uncommon for lizards (e.g. Losos 2009, Čerňanský *et al.* 2020). It should be noted, however, that one can suggest different alternative scenarios. The presence of these taxa (at least some of them) in both North America and Europe might just be potentially an indication of a widespread distribution of the ancestral stock in Laurasia, and the breakup of this landmass led to a lineage separation. This scenario has, however, two main issues: (i) it works with a very long geological time (the initial breakup is dated to the Jurassic, 190–170 Mya, e.g. Labails *et al.* 2010), whereas the evolution of closely related allopatric species of one genus in general requires a relatively short time (Yang *et al.* 2021, Enriquez-Urzelai *et al.* 2022). It can be expected that the long time of separation (time of the split over 100 Myr) would lead to an accumulation of many significant differences among lineages; (ii) the current, although limited data suggest that the palaeodiversity of squamates from Palaeocene localities, such as Walbeck in Germany, is low (Folie *et al.* 2013, Rage 2013, Augé *et al.* 2021, Čerňanský and Vasilyan

2024). The Palaeocene faunas are different in many aspects (diversity, types, etc.) relative to the faunas described from slightly younger, earliest Eocene localities, such as Dormaal, Cos (Čerňanský *et al.* 2023a, b), and localities in Spain (Bolet 2017). Many lineages, such as glyptosaurids and varanids that occurred later in Europe are absent in the Palaeocene.

For this reason, it is more reasonable (at least based on current knowledge) to regard many of these lineages as immigrants in Europe. The congeneric relationship of *Gaultia silvaticus* and *G. ragei* is supported by morphological analysis and detailed comparison. Based on that it seems to be highly probable that both taxa represent closely related species (markedly different from *Glyptosaurus* and *Placosaurus*), although having a distribution on two continents (North America and Europe; for intercontinental distributions of one genus in modern nature, e.g. a skink *Trachylepis* Fitzinger, 1843 (Carranza and Arnold 2003). Although this model is the most parsimonious based on current data, new light to this issue can be shed by future phylogenetic analyses of glyptosaurids based on more complete material.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

All specimens are catalogued and accessible in the fossil reptile collection of the Institut royal des Sciences naturelles de Belgique, Brussels. Digital surface models of the figured fossil specimens are available on Morphosource and Virtual Collections:

IRSNB R 263: https://www.morphosource.org/concern/media/000636005?locale=en
IRSNB R 478: https://www.morphosource.org/concern/media/000603030?locale=en
IRSNB R 479: https://www.morphosource.org/concern/media/000603036?locale=en
IRSNB R 480: https://www.morphosource.org/concern/media/000603041?locale=en
IRSNB R 481: https://www.morphosource.org/concern/media/000603130?locale=en
IRSNB R 482: https://www.morphosource.org/concern/media/000603124?locale=en
IRSNB R 483: https://www.morphosource.org/concern/media/000603136?locale=en
IRSNB R 484: https://www.morphosource.org/concern/media/000603141?locale=en
IRSNB R 485: https://www.morphosource.org/concern/media/000603146?locale=en
IRSNB R 486: https://www.morphosource.org/concern/media/000603308?locale=en
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