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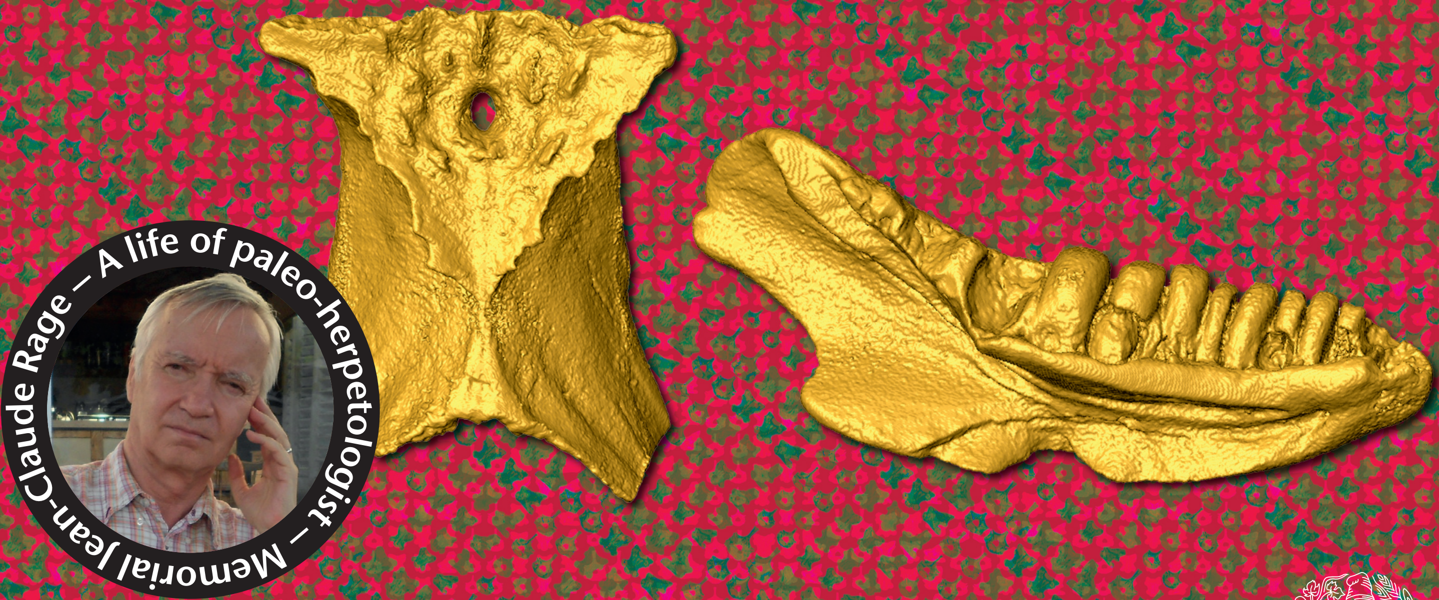

Memorial Jean-Claude Rage – A life of paleo-herpetologist –

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Osteological atlas of new lizards from the Phosphorites du Quercy (France), based on historical, forgotten, fossil material

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ABSTRACT

A long-forgotten, old collection of lizards from the Phosphorites du Quercy in southern France, housed in the Naturhistorisches Museum in Vienna (NHMW), is described in detail in this paper. The material, consisting of several almost complete cranial and postcranial disarticulated elements, originates from different, imprecisely known localities. Nevertheless, the completeness and exceptional preservation of many of these specimens permitted the identification of new taxa, as well as the recognition and better understanding of novel anatomical features of previously described forms. Among the specimens, the material described herein and referred to *Cadurcogekko* cf. *piveteaui* ranks among the most complete cranial remains of Paleogene gekkotans. A clarification about the type material of the previously described species *Cadurcogekko verus* Bolet, Daza, Augé & Bauer, 2015, is provided. A new species of lacertids is established, *Pseudeumeces kyrillomethodicus* n. sp. Additional, large lacertid material is referred to *Mediolacerta* Augé, 2005, representing also the largest one attributable to this genus. At least two glyptosaurine taxa are present in this collection, among which, the genus *Paraplacosauriops* Augé & Sullivan, 2006, is represented by exceptional cranial material, referred to *Paraplacosauriops quercyi* (Filhol, 1882). The completeness of the cranial material of *Paraplacosauriops* permits a more comprehensive understanding of its maxillary and mandibular anatomy. A detailed documentation of cranial and postcranial material for the genus *Palaeovaranus* Zittel, 1887-1890, is conducted. The new maxilla described herein allows a better understanding of the peculiar maxillary features of the genus *Palaeovaranus*. Emended diagnoses are provided for the genus *Palaeovaranus* and its type species *Palaeovaranus cayluxi* Zittel, 1887-1890. The parietal morphology of *Palaeovaranus* is analyzed in detail and intraspecific variation in this element is assessed. A new species of *Palaeovaranus* is established, *Palaeovaranus lismonimenos* n. sp., on the basis of an almost complete parietal that can be differentiated from that of *Palaeovaranus cayluxi* on the basis of a number of distinctive features. Additional, previously published specimens from Quercy are here referred to *Palaeovaranus lismonimenos* n. sp., representing younger individuals of this species, and photographs of this material is provided for the first time. The diversity of platynotans in the Paleogene of Europe is discussed and their distinction on the basis of parietal morphology is provided. According to the new emended diagnosis for *Palaeovaranus*, the genus *Melanosauroides* Kuhn, 1940, is revalidated herein to accommodate *Melanosauroides giganteus* Kuhn, 1940, from the late early or middle Eocene of Geiseltal, Germany. So far, *Melanosauroides giganteus* is solely known from its type area in Geiseltal, and all previously supposed occurrences of this taxon in Quercy are discarded. Abundant anguimorph vertebral material is referred to *Placosaurus* sp., Melanosaurini indet., Anguinae indet., *Palaeovaranus* sp., *Saniwa* sp., and Anguimorpha indet., although it is highlighted that certain of these referrals should be taken into consideration with caution. Especially, the problem of certain large isolated lizard vertebrae from Quercy is addressed; a tentative, potential distinction between vertebrae of the genera *Palaeovaranus* and *Placosaurus* Gervais, 1848-1852, is suggested, although admittedly only articulated skeletons of these genera may confirm or refute such taxonomic referrals. The importance of fossil squamates from the area of the Phosphorites du Quercy is highlighted. Detailed figuring of the specimens is provided through the means of both photography and micro-CT scanning, with 3D models of the most significant material also presented. This is the first time that micro-CT scanning is conducted on fossil squamates from Quercy. The many figures provided in this paper may serve as a pictorial key guide for fossil lizards from the Paleogene of Europe.

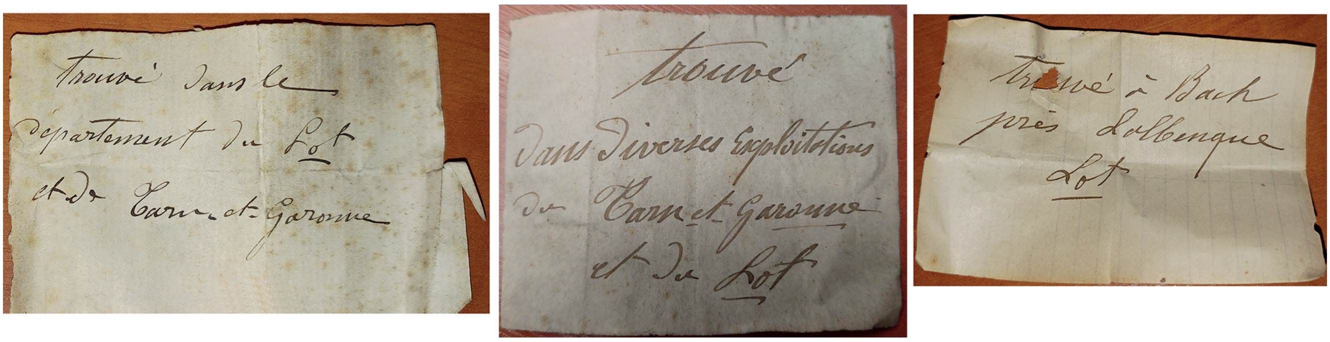
KEY WORDS
Squamata,
lizards,
Quercy,
Paleogene,
micro-CT scanning,
skeletal anatomy,
new species.

RÉSUMÉ

Atlas ostéologique de nouveaux lézards des Phosphorites du Quercy (France), basé sur des matériaux fossiles historiques et oubliés.

Cet article décrit une ancienne collection de lézards des Phosphorites du Quercy, région située dans le sud de la France, déposée au Naturhistorisches Museum de Vienne et tombée dans l'oubli. Les spécimens correspondent à plusieurs éléments désarticulés crâniens et postcraniens presque complets, et proviennent de différentes localités mal connues. Néanmoins, la complétude et la conservation exceptionnelle d'un grand nombre de spécimens permettent l'identification de nouveaux taxons, ainsi que la reconnaissance et une meilleure compréhension de nouvelles caractéristiques appartenant à des formes précédemment décrites. Le matériel décrit et référé à *Cadurcogekko* cf. *piveteaui* figure parmi les restes crâniens les plus complets de gekkos du Paléogène. Des éclaircissements sont donnés sur le matériel type de l'espèce *Cadurcogekko verus* Bolet, Daza, Augé & Bauer, 2015. Une nouvelle espèce de lacertidé est établie, *Pseudeumeces kyrillomethodicus* n. sp. De plus, du matériel d'un grand lacertidé est attribué à *Mediolacerta* Augé, 2005 – il s'agit du plus grand assemblage attribué à ce genre. Au moins deux taxons de glyptosaurines sont présents dans cette collection, comme le genre *Paraplacosauriops* Augé & Sullivan, 2006, représenté par un matériel crânien exceptionnel attribué à *Paraplacosauriops quercyi* (Filhol, 1882). La complétude du matériel crânien de *Paraplacosauriops* permet de mieux comprendre son anatomie maxillaire et mandibulaire. Une documentation détaillée du matériel crânien et post-crânien du genre *Palaeovaranus* Zittel, 1887-1890, est réalisée. Le nouveau maxillaire décrit ici permet de mieux comprendre l'anatomie particulière du genre *Palaeovaranus*. Des diagnoses émendées sont fournies pour le genre *Palaeovaranus* et son espèce type, *Palaeovaranus cayluxi* Zittel, 1887-1890. La morphologie du pariétal de *Palaeovaranus* est analysée en détail et sa variation intraspécifique évaluée. Une nouvelle espèce de *Palaeovaranus* est décrite, *Palaeovaranus lismonimenos* n. sp., d'après un pariétal presque complet qui se différencie de celui de *Palaeovaranus cayluxi* sur la base de caractéristiques distinctes. De plus, des spécimens précédemment publiés du Quercy sont attribués ici à *Palaeovaranus lismonimenos* n. sp. Ils représentent les plus jeunes individus de cette espèce. Des photographies de ce matériel sont fournies pour la première fois. La diversité des platynotes dans le Paléogène d'Europe est discutée et leur distinction fondée sur la morphologie du pariétal est donnée. D'après la diagnose émendée de *Palaeovaranus*, le genre *Melanosauroides* Kuhn, 1940, est revalidé et inclut *Melanosauroides giganteus* Kuhn, 1940, de l'Éocène moyen-supérieur à moyen du Geiseltal, en Allemagne. Jusqu'à maintenant, *Melanosauroides giganteus* était connu uniquement de la région-type du Geiseltal, et toutes ses occurrences précédentes dans le Quercy étaient rejetées. De nombreuses vertèbres anguimorphes sont attribuées à *Placosaurus* sp., Melanosaurini indet., Anguinae indet., *Palaeovaranus* sp., *Saniwa* sp., et Anguimorpha indet., bien que ces identifications doivent être prises avec précaution. Le problème de certaines grandes vertèbres isolées de lézards du Quercy est abordé ; une tentative de distinction entre les vertèbres des genres *Palaeovaranus* et *Placosaurus* Gervais, 1848-1852 est proposée car seuls des squelettes articulés de ces genres pourraient confirmer ou non ces références taxonomiques. L'importance des squamates fossiles de la région des Phosphorites du Quercy est soulignée. La représentation détaillée des spécimens est fournie à la fois par la photographie et la micro-tomographie, avec des modèles 3D du matériel le plus significatif. C'est la première fois qu'un CT-scan est réalisé sur des squamates fossiles du Quercy. Les nombreuses figures fournies dans cet article peuvent servir de guide pour les lézards fossiles du Paléogène d'Europe.

MOTS CLÉS
Squamata,
lézards,
Quercy,
Paléogène,
micro-CT,
anatomie squelettique,
espèces nouvelles.



trouvé dans le
département du Lot
et de Tarn-et-Garonne

trouvé
dans diverses exploitations
de Tarn-et-Garonne
et du Lot

trouvé à Bach
près Lalbenque
Lot

Fig. 1. — Old hand written labels accompanying part of the NHMW material.

INTRODUCTION

The Phosphorites du Quercy extend across a relatively large geographic area in southern France and are well known for their large number of vertebrate remains, offering a unique window into the Paleogene faunas of Europe (Bonis *et al.* 1973; Rage 1974, 2006; Crochet *et al.* 1981; Legendre *et al.* 1997; Sigé & Hugueney 2006). Fossils of lizards are known from the Phosphorites du Quercy since the second half of the 19th century, with descriptions of new and important finds taking place at that time (Filhol 1873, 1876, 1877a, b, c, 1882a, b; Gervais 1876; Zittel 1887-1890; Lydekker 1888a), even if sometimes misidentified as snakes (Rochebrune 1884) or even mammals (Filhol 1894)! New important finds were subsequently described in the first decades of the 20th century (De Stefano 1903, 1905; Leenhardt 1926; Fejérváry 1935; Kuhn 1940b; Hoffstetter 1944, 1946, 1957), including material originally misidentified as a frog (Piveteau 1927).

Unfortunately, the vast majority of these, so called "old collections" from Quercy that were amassed during the late 19th and the first half of the 20th centuries lack any kind of stratigraphic data or information about a precise locality. This is further hampered by the fact that at least 100 different fissure filling localities are known from the Phosphorites du Quercy, whereas others as well apparently have existed in the past decades but are not currently known or no longer accessible (Rage 2006). In any case, it was only during the past few decades that fieldwork in the area of the Phosphorites du Quercy recovered squamate remains that afforded well known stratigraphic and geographic data (e.g., Rage 1978, 1988b; Augé & Rage 1995; Augé 2005; Augé & Hervet 2009; Čerňanský *et al.* 2015a; Rage & Augé 2015; Augé & Brizuela 2020).

Nevertheless, some of the most impressive lizard fossil finds, including the earliest discoveries for several different groups, took place in the Phosphorites du Quercy. The "exotic nature" of most of these lizard finds sparkled the interest of early workers and made them envisage novel biogeographic patterns for European palaeoherpetofaunas (Filhol 1876, 1877a, b, c; De Stefano 1903). Many of these lizard taxa are still considered valid, representing an unparalleled means for comparisons with other subsequent finds. Additionally, many of them are known exclusively within the area of the Phosphorites du Quercy, representing potentially endemic forms. The importance of the Quercy fossil lizards is highlighted by the fact that several works since the second half of the past century focused on these, providing accounts of new remains and revisions of previously named taxa (Rage 1978, 1988a, 2013; Augé 1987a, b, 1988a, b, 1992, 2005, 2006, 2007, 2012; Augé & Rage 1995; Augé & Sullivan 2006; Sullivan & Augé 2006; Augé & Hervet 2009; Buffrénil *et al.* 2011; Augé & Pouit 2012; Čerňanský & Augé 2013; Bolet & Augé 2014; Bolet *et al.* 2015, 2017; Čerňanský *et al.* 2015a; Rage & Augé 2015; Georgalis 2017; Augé & Brizuela 2020).

Recently, one of us (GLG) located in the collections of Naturhistorisches Museum in Vienna (NHMW), inside the drawers with fossil mammals from Quercy, a large number of lizard cranial and postcranial remains. This almost "forgotten" fossil material, although housed apparently in the collections of NHMW since the 19th century, has never been mentioned in the literature. We here describe and figure in detail this material, establish two new taxa, document novel anatomical features for previously known forms, and assess intraspecific variability of certain fossil lizards from the Phosphorites du Quercy.

MATERIAL AND METHODS

The specimens described herein are part of the collections of NHMW. Judging from the hand writing style of old labels that accompanied several of these specimens, it can be deduced that they were acquired by NHMW somewhen during the second half of the 19th century (Fig. 1). Unfortunately, there are no precise records neither for the date(s) of acquisition of the material, nor for the persons who were involved in this / these acquisition(s). What is certain nevertheless, is that the material was collected during several different expeditions in the area of the Phosphorites du Quercy, as it is clearly mentioned in the label of some specimens ("Trouvé dans diverses exploitations du Tarn-et-Garonne et du Lot"). It is also worth noting that all these lizard fossils from NHMW are relatively large (most of them being more [or often much more] than 10 mm in absolute sizes), while certain cranial remains are rather complete. It appears thus that only the most "impressive" material was of interest, either to NHMW during the acquisition of this collection or either alternatively to the French collectors that found and prepared the specimens. Notably also, there are no osteoderms at all in this collection, although glyptosaurine cranial and vertebral material exists, pertaining to at least two different taxa.

In addition to the NHMW collection, five specimens from the collections of MNHN and UM, previously described by Augé (2005), were also used in this study in order to further highlight certain anatomical features and ontogenetic variation among taxa documented in our paper. Also, the holotype of a previously described gekkotan species from the collections of UM is discussed and figured.

Photographs of the NHMW material were taken with a Leica M205 C binocular microscope with an axially mounted DFC 290 HD camera; software: LAS (Leica Application Suite) 4.1.0 (build 1264). A GE Phoenix nanotom VR 180 X-ray tomography nano-CTVR system at the Slovak Academy of Sciences in Bratislava was used (Fairfield, CT) for µCT-scanning of the specimens. The CT data-sets were analyzed using Avizo 8.1. Note that for the gekkotan maxilla (NHMW 2019/0052/0001) further preparation was conducted after the micro-CT scanning.

Comparative fossil material of Paleogene lizards was studied at the collections of GMH, MNHN, NHMUK, PIMUZ, and SMF. Comparative skeletal material of extant lizards was studied at the collections of MDHC, NHMW, NMP, PRIF UK, UWr, and ZZSiD.

Institutional abbreviations

AMNH	American Museum of Natural History, New York;
GMH	Geiseltalmuseum of Martin-Luther Universität Halle-Wittenberg, now referred to as the Geiseltalsammlung, housed as part of the Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle;
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels;
MDHC	Massimo Delfino Herpetological Collection, University of Torino, Torino;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMUK	Natural History Museum, London;
NHMW	Naturhistorisches Museum Wien, Vienna;
NMP	Národní Muzeum Praha, Prague;
PIMUZ	Palaeontological Institute and Museum, University of Zurich, Zurich;
PRIF UK	Faculty of Natural Sciences, Comenius University, Bratislava, Slovakia; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main;
SU	Sorbonne Université, Paris;
UM	Université de Montpellier, Montpellier (formerly abbreviated as USTL);
UWr	University of Wrocław, Wrocław;
ZZSiD	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków.

GEOLOGICAL SETTINGS
AGE OF THE MATERIAL

As is the case with the majority of specimens that originate from the so called "old collections" ("anciennes collections") of the Phosphorites du Quercy, there are no precise locality data. The Phosphorites du Quercy span a significant time lapse, ranging from the early Eocene (MP 8+9) until the early Miocene (MN 3), however, the majority of the respective fossiliferous localities ranges between the late middle Eocene (MP 16) and the late Oligocene (MP 28) (Rage 2006; Sigé & Hugueney 2006; Georgalis 2017). Moreover, they encompass a large geographic area, extending over the current Departments of Lot, Tarn-et-Garonne, Tarn, and Aveyron, all in the administrative region of Occitanie, in southern France (Sigé & Hugueney 2006). For certain specimens from our collection, there were old labels indicating (in French) that they were found in the Departments of Lot and Tarn-et-Garonne (Fig. 1), but still this information is practically not informative at all, as these two Departments of France, in fact cover a considerable geographic range in the Phosphorites.

More specifically, for certain *Palaeovaranus* caudal vertebrae (NHMW 2019/0058/0041-NHMW 2019/0058/0046), it is clearly written in the associated old French label that they were found in several different expeditions ("Trouvé dans diverses exploitations du Tarn-et-Garonne et du Lot") (Fig. 1).

Several specimens (the gekkotan frontal [NHMW 2019/0052/0002], both parietals, the single maxilla, and two of the dentaries of *Palaeovaranus* [NHMW 2019/0047/0001, NHMW 2019/0048/0001, NHMW 2019/0048/0002, NHMW 2019/0058/0054, and NHMW 2019/0058/0055], all lacertids [NHMW 2019/0051/0001-NHMW 2019/0051/0005 and NHMW 2019/0050/0001]) were simply accompanied by an old French label written again the general information "Trouvés dans le Department du Lot et du Tarn-et-Garonne" (Fig. 1). But even for this material, however, we are almost certain that it was not collected in the same locality, as anatomical features suggest that most probably, lacertids are of Oligocene age, the gekkotan frontal of Eocene age, and the respective *Palaeovaranus* remains of Eocene or early Oligocene age.

The majority of the postcranial material (NHMW 2019/0046/0001-NHMW 2019/0046/0009; NHMW 2019/0094/0001-NHMW 2019/0094/0005; NHMW 2019/0093/0001; NHMW 2019/0058/0001-NHMW 2019/0058/0053; NHMW 2019/0065/0001-NHMW 2019/0065/0003; NHMW 2019/0095/0001) had no label at all apart from the basic information "Quercy". It is worth noting that the vast majority of lizard vertebral elements were alongside isolated vertebrae of the large snakes, such as *Palaeopython* Rochebrune, 1880, which are considered to have survived only up to the late Eocene (see Georgalis *et al.* in press for the description of the snakes of this collection).

For few specimens (the gekkotan maxilla [NHMW 2019/0052/0001], the smallest *Palaeovaranus* dentary [NHMW 2019/0058/0056], and all glyptosaurine cranial material [NHMW 2019/0049/0001-NHMW 2019/0049/0003]), there was an indication that they were found in "Bach prés Lalbenque" (i.e., Bach, near Lalbenque, Lot) (Fig. 1). The village Bach is rather close to the "middle" Oligocene (MP 26) locality Espeyrasse, which has yielded lizard and snake remains (Augé & Hervet 2009; Szyndlar & Rage 2003). On the other hand, however, Lalbenque is also rather close to the late

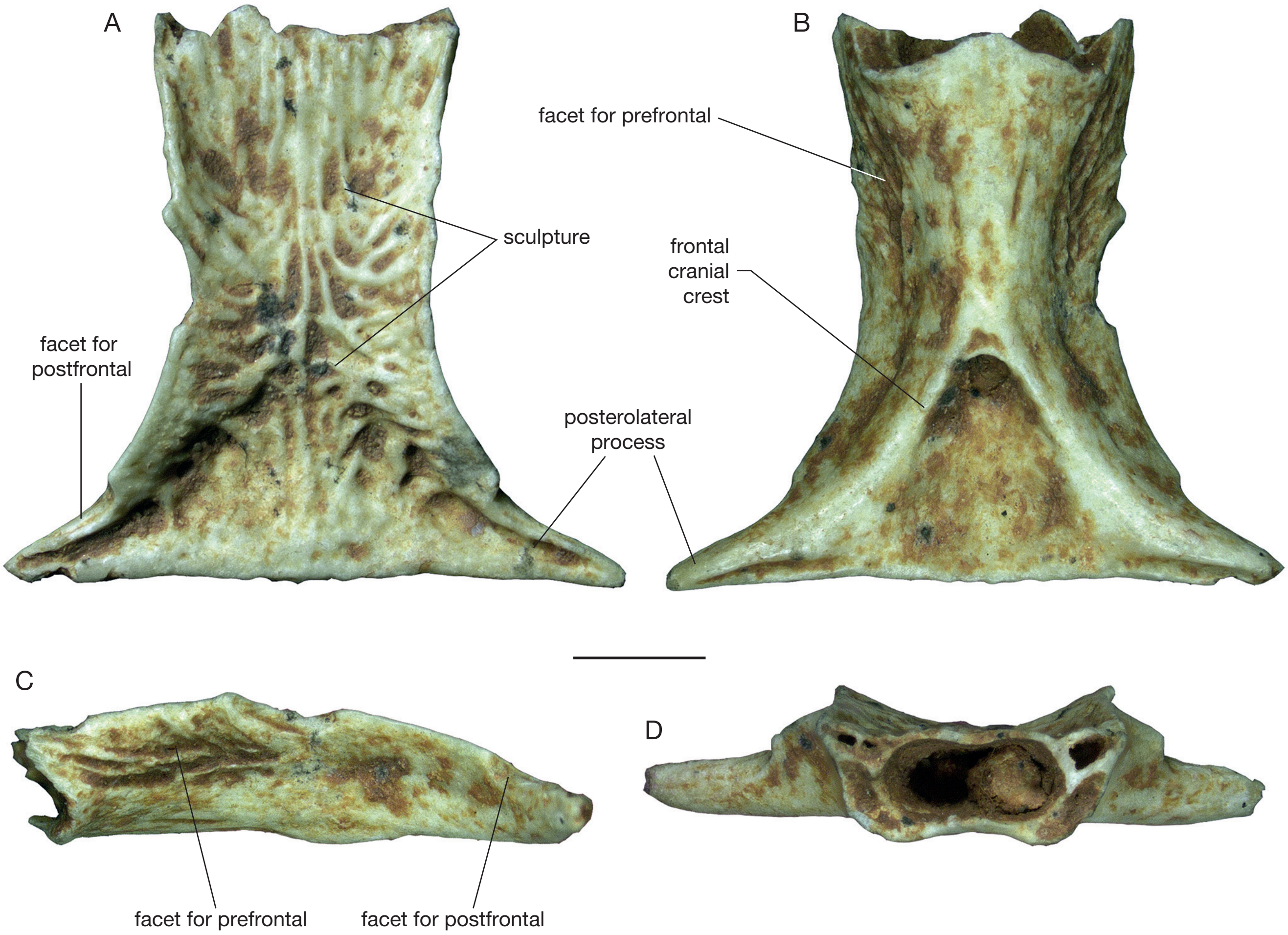


Fig. 2. — *Cadurcogekko* cf. *piveteaui*. Photographs of frontal NHMW 2019/0052/0002 in dorsal (**A**), ventral (**B**), left lateral (**C**), and anterior (**D**) views. Scale bar: 2 mm.

Eocene (MP 19) locality of Escamps, which has yielded several lizard remains (Augé 2005; Georgalis 2017). And notably, it is now known that the name of "Lalbenque" (misspelled also as "Labenque") has been mentioned in 19th century literature to denote fossil lizard specimens from Escamps (see Georgalis 2017). The material that was associated with this label fits indeed more with an Eocene age or at least early Oligocene one and certainly not with a "middle" or late Oligocene one.

A more precise geographic area can be provided for two vertebrae of *Palaeovaranus* (the presacral NHMW 2019/0067/0001 and the caudal NHMW 2019/0067/0001), which were, along with a large snake vertebra, accompanied by a label written "Mouilliac bei Caylux, Quercy". The commune of Mouillac (this is the current spelling, not Mouilliac) is located near the town of Caylus, in the Department of Tarn-et-Garonne. Although geographically this information is more precise than the above cases, from a stratigraphic point of view, however, it is still far from ideal, as there are several different Eocene and Oligocene fossiliferous localities nearby this village. Nevertheless, judging from the accompanied presence of the snake material, we tentatively treat these two lizard remains as of (probably late) Eocene age.

SYSTEMATIC PALAEONTOLOGY

SQUAMATA Oppel, 1811
GEKKOTA Cuvier, 1817
Family incertae sedis
Genus *Cadurcogekko* Hoffstetter, 1946

Type species. — *Cadurcogekko piveteaui* Hoffstetter, 1946 (type species by original designation; Hoffstetter 1946).

Cadurcogekko* cf. *piveteaui

(Figs 2-4)

Referred specimens. — A frontal (NHMW 2019/0052/0002); a left maxilla (NHMW 2019/0052/0001).

Description

Frontal NHMW 2019/0052/0002 (Fig. 2)

The left and right frontals are fused in this specimen, forming a single element, with a length of 8.1 mm (Fig. 2). It is almost completely preserved and only its anterior portion is damaged. It is rectangular, with a slight mid-constriction. Thus, the lateral margins are rather concave in dorsal aspect and fluently

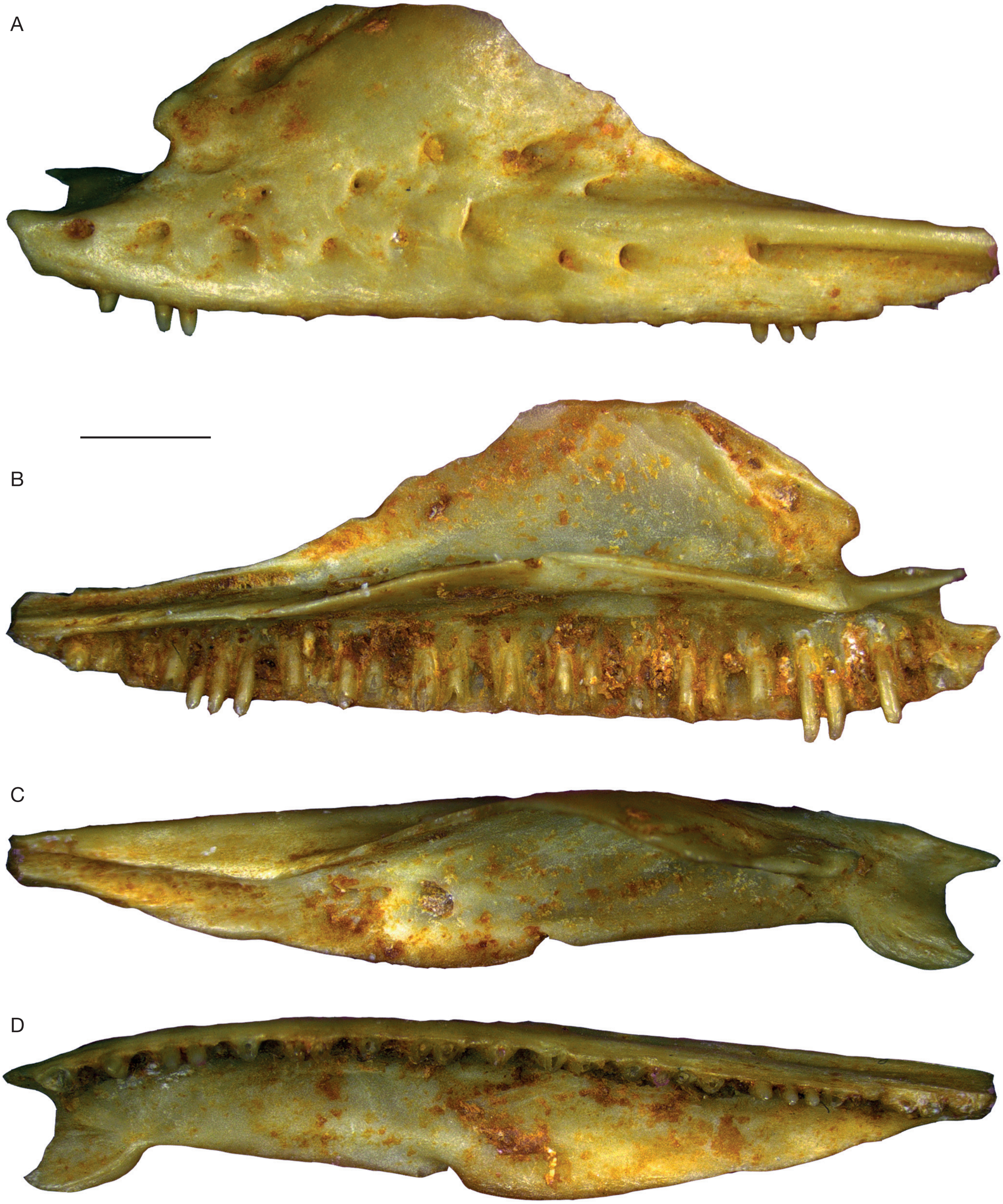


Fig. 3. — *Cadurcogekko* cf. *piveteaui*. Photographs of left maxilla NHMW 2019/0052/0001 in lateral (**A**), medial (**B**), dorsal (**C**), and ventral (**D**) views. Scale bar: 2 mm.

continue into well laterally expanded posterolateral processes. These processes form narrow triangles with pointed lateral terminations. The anterolateral margins of both processes are stepped due to a presence of short and narrow facets for the postfrontal. An additional step is present on both sides in the anterior region of the lateral margin of the frontal. There, the

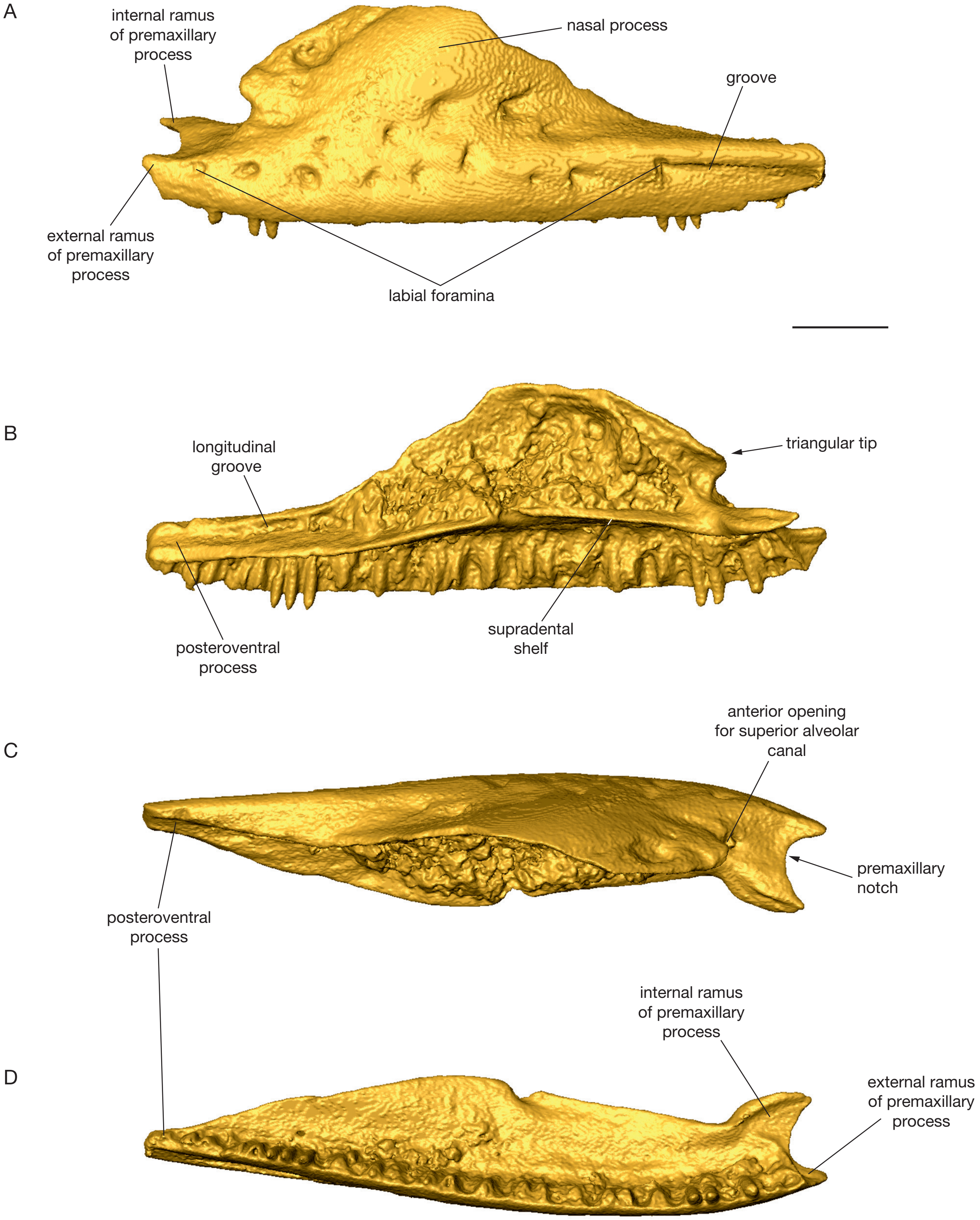


Fig. 4. — *Cadurcogekko* cf. *piveteaui*. Virtual 3D models of left maxilla NHMW 2019/0052/0001 in lateral (**A**), medial (**B**), dorsal (**C**), and ventral (**D**) views. Note that further preparation on this specimen was conducted after the micro-CT scanning. Scale bar: 2 mm.

large facet for prefrontal is located (Fig. 2B, C). It is mainly exposed in ventral aspect as a rough surface. It is wedge-shaped posteriorly, where its peak reaches posterior to the level of the step. The facet for prefrontal and postfrontal are not in contact, thus the frontal is not fully excluded from the orbit. In ventral view, the frontal cranial crests run medially from the posteroventral processes and merge together further anteriorly (Fig. 2B). They are completely fused to form a tunnel-like structure. The overall dorsal surface of the frontal, although slightly bulged in the central region, is slightly depressed, with dorsally inclined lateral portions. This external surface is sculptured, having a wrinkled appearance. The sculpturing pattern consists of ridges and pits (Fig. 2A). They are mainly developed in the mid-section and run to the periphery of the surface. A deep depression runs along the entire dorsal surface of both posterolateral processes. The posterior margin of the frontal is almost straight.

Maxilla NHMW 2019/0052/0001 (Figs 3; 4)
NHMW 2019/0052/0001 represents an almost complete left maxilla (Figs 3; 4). This element is elongate and lightly built, measuring 14.2 mm in length. It is straight with a small medial anterior curvature. A complete tooth row is preserved, bearing 37 tooth positions, of which six complete teeth are still attached. The premaxillary process is bifurcated. The external ramus of this process is short and blunt, whereas the internal ramus is more distinct and broader. The internal ramus is more medially oriented and more dorsally located relative to the external one. Between them, an oval and wide premaxillary notch is present. Dorsal to it, an anterior opening for the superior alveolar canal is located. The supradental shelf is thin. Its portion located in the anterior two thirds is slightly bent dorsally (convex) and expanded medially. In dorsal view, the medial margin of the supradental shelf is rounded, reaching the maximum of expansion at the level around of 18th tooth position (counted from anterior). This forms a palatine process. Slightly posteriorly to it, the rounded but flat superior alveolar foramen is located at the dorsal portion, at the level of the 21st tooth position (counted from anterior). The posterior ⅓ of the supradental shelf is more or less straight in medial aspect. In posterior direction, it is gradually less expanded medially. The anteroposterior length of the nasal process is greater than its dorsal height. The dorsal margin of the nasal process appears to be slightly worn, but in the case that it represents more or less the original shape, it shows a lack of a pronounced dorsal process. This configuration of the nasal process contrasts sharply with the prominent, often pointed process typical of many gekkotans and resembles that seen in *Euleptes* Fitzinger, 1843 (e.g., Bauer *et al.* 1997; Čerňanský *et al.* 2018; Villa *et al.* 2018). The nasal process is trapezoidal in shape, with the posterior margin being more ventrally slopped relative to the anterior one. The anterior margin possesses a free terminus. It forms a triangular tip (this feature can be seen in extant and extinct species of the genus *Euleptes* but also in the genera *Hemidactylus* Goldfuss, 1820, and *Tarentola* Gray, 1825; see e.g., Čerňanský *et al.* 2018; Villa *et al.* 2018), well delimited from the dental portion of the maxilla. In the anterior region of the nasal process, on the medial side there is a fine ridge that runs posterodorsally. This ridge originates from the supradental shelf at the level of the fifth tooth position. The internal side of the nasal process posterior to this ridge is excavated, forming a cavity. In dorsal aspect, the process has a rounded, laterally convex appearance. The posteroventral process of maxilla is moderately long. It possesses a longitudinal deep groove, which is roofed by a bent, dorsally depressed bony flange. This flange continues here from the dorsolateral side of the posteroventral process.

The lateral surface of maxilla is pierced by nine labial foramina located in the ventral series, where the posteriormost one is located at the level of the 27th tooth position (Figs 3A; 4A). Posteriorly from this foramen, a well-developed groove runs along the entire portion of the posteroventral process. Dorsal to this series, the surface is pieced by additional five, irregularly arranged foramina. The rest of the lateral surface is rather rugose and irregularly pitted.

Remarks

The material can be referred to Gekkota on the basis of the following characters: 1) absence of osteoderms fused to the skull bones; 2) unpaired frontals; 3) fused subolfactory processes of frontal in the mid-line to form a tunnel like structure; and 4) the high number of conical, unicuspid pleurodont teeth (Estes 1983; Daza *et al.* 2014). The maxilla can be referred to the genus *Cadurcogekko* on the basis of the presence of rugose surface of the nasal process, an elongated groove associated with the most posterior neurovascular foramen, and a postnarial anterodorsal depression of the element (Augé 2005).

The genus *Cadurcogekko* is known exclusively from localities within the Phosphorites du Quercy. Two species of this genus are currently regarded as valid: the type species, *Cadurcogekko piveteaui* from the old collections of the Phosphorites du Quercy, and *Cadurcogekko verus* Bolet, Daza, Augé & Bauer, 2015, from the late Eocene (MP 17) of Les Pradigues, Quercy (see Bolet *et al.* 2015). Notably, the holotype dentary of the type species, *C. piveteaui*, was originally described as a frog by Piveteau (1927), until it was eventually demonstrated by Hoffstetter (1946) that it pertained instead to gekkotans. The two valid species of *Cadurcogekko* can be distinguished by: 1) different size of the available elements, with *Cadurcogekko verus* being smaller than *C. piveteaui*; 2) lower maxillary tooth number – according to Bolet *et al.* (2015), *C. verus* possesses 30 vs. 50 in *C. piveteaui*. The tooth row in the referred maxilla MNHN.F.QU17734 of *Cadurcogekko piveteaui* from the late Eocene (MP 17) of Perrière, Quercy, is incomplete, lacking its posterior portion; it has 38 tooth positions (Augé 2005: fig. 59). Daza *et al.* (2014) estimated the tooth number in a complete tooth row to be between 40 and 44, contrasting with only 27 tooth positions in *C. verus*; and 3) a coarser sculpture on the external surface of the maxilla and possibly the frontal in *C. verus*.

Note that a third named species of the genus, *Cadurcogekko rugosus* Augé, 2005, has recently been reidentified as a scincid and placed accordingly in its own genus, *Gekkomimus* Bolet, Daza, Augé & Bauer, 2015, by Bolet *et al.* (2015). Nevertheless, the figure of the type material of *Cadurcogekko verus* in Bolet *et al.* (2015: fig. 1) deserves a comment at this point. Bolet *et al.* (2015) established the species *Cadurcogekko verus* and they supposedly figured its holotype, the right maxilla UM PRA 9, in their fig. 1. That specimen, UM PRA 9, originated from the late Eocene (MP 17) of Les Pradigues, Quercy and was previously allocated to *C. rugosus* by Augé (2005). However, despite their figure caption which stated that UM PRA 9 was figured there, Bolet *et al.* (2015) did not figure at all this holotype, but instead their fig. 1 represents another specimen, the right maxilla MNHN.F.QU17734 of *C. piveteaui* originating from the late Eocene (MP 17) of Perrière, Quercy (see Augé 2005: fig. 59a-b [for MNHN.F.QU17734] vs. 64a-b [for UM PRA 9] and Daza *et al.* 2014: fig. 5a-b [for MNHN.F.QU17734]; this paper: Fig. 5 [for UM PRA 9]). In addition, Daza *et al.* (2014) mentioned in their text the maxilla UM PRA 9 (following the previously suggested referral by Augé [2005] to *C. rugosus*) and stated that they figured this specimen in their figure 5j-k. However, the photographs of the maxilla "UM PRA 9" figured by Daza *et al.* (2014: fig. 5j-k) represent a different specimen from the drawings of the maxilla "UM PRA 9" figured by Augé (2005: fig. 64a-b). Judging from newly furnished photographs of the specimen provided to us by UM, we here confirm that UM PRA 9 is the specimen figured by Augé (2005: fig. 64a-b) and not the one figured by Daza *et al.* (2014: fig. 5j-k). All these being said, despite the erroneous figure of Bolet *et al.* (2015), UM PRA 9 indeed represents the holotype of *Cadurcogekko verus*, as the diagnosis and description of this species is based on this specimen. We here provide photographs of this specimen, UM PRA 9, for the first time (Fig. 5).

The left maxilla NHMW 2019/0052/0001 described herein exhibits a complete tooth row, possessing 37 tooth positions. This seems to be an intermediate condition between *Cadurcogekko verus* and that what has been previously estimated for *Cadurcogekko piveteaui*. This brings several questions about this character state in these two currently valid species. The frontal NHMW 2019/0052/0002 is almost identical with specimen MNHN.F.QU17165, which has been referred to *C. piveteaui* (see Augé 2005: fig. 60; Daza *et al.* 2014: fig. 5h-i). However, the sculpturing pattern present on the dorsal surface of NHMW 2019/0052/0002 appears to be slightly more strongly developed relative to that of MNHN.F.QU17165. The frontal NHMW 2019/0052/0002, despite the fact that its anterior portion is damaged, currently represents the best preserved frontal of *Cadurcogekko*. In any case, the overall morphologies of the specimens NHMW 2019/0052/0001 and NHMW 2019/0052/0002 fit better to the diagnosis previously stated for *C. piveteaui*, although with some doubts. Therefore, we have decided to refer this gekkotan material to as *Cadurcogekko* cf. *piveteaui*.

LATERATA Vidal & Hedges, 2005
LACERTIFORMATA Vidal & Hedges, 2005
Family LACERTIDAE Oppel, 1811
Subfamily GALLOTIINAE Cano, Baez, López-Jurado & Ortega, 1984

Genus *Pseudeumeces* Hoffstetter, 1944

TYPE SPECIES. — *Plestiodon cadurcense* Filhol, 1877 (type species by original designation; Hoffstetter 1944).

FIG. 5. — *Cadurcogekko verus* Bolet, Daza, Augé & Bauer, 2015. Photographs of the holotype right maxilla UM PRA 9 in lateral (**A**) and medial (**B**) views. Scale bar: 2 mm.

Pseudeumeces kyrillomethodicus n. sp.
(Figs 6-14)

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HOLOTYPE. — A left dentary (NHMW 2019/0051/0001).

PARATYPE. — A right dentary (NHMW 2019/0051/0002).

ETYMOLOGY. — The new species epithet "*kyrillomethodicus*" honours Kyrillos (or Cyril; Greek: Κύριλλος) and Methodios (or Methodius; Greek: Μεθόδιος), the two Byzantine brothers from Thessaloniki that were sent by the Byzantine Emperor to the area of Bratislava (city of Dovina [currently Devin]) in 863 AD, where they created the first scripture for the people of Great Moravia. The name alludes to the fact that one of us (GLG) came from Thessaloniki to Bratislava (during which project also this paper was written) and generally to our nice collaboration among the three of us, Greek and Slovak scientists. Gender is masculine.

TYPE LOCALITY. — Imprecisely known locality, Phosphorites du Quercy, Department of Lot or Tarn-et-Garonne, Occitanie, southern France; probably Oligocene.

DIAGNOSIS. — A medium sized lacertid, morphologically similar to *Pseudeumeces cadurcensis*, but differing from it in the following combination of features: 1) the last posterior three or four dentary teeth are reduced (instead of only the last one or two posterior teeth being reduced); 2) the dentary is short and massive rather than anteroposteriorly long relative to its dorsoventral height (the overall morphology of dentary in *Pseudeumeces cadurcensis* has narrower appearance relative to that in *Pseudeumeces kyrillomethodicus* n. sp.); 3) the facet for the anterolateral process of the coronoid reaches around the level of the 4th tooth position (counted from posterior) rather than reaching the level of the posteriormost tooth position (in some cases, the level between the last and penultimate tooth positions); 4) the facet for anteromedial process of the coronoid reaches the level of the 3rd tooth position (counted from posterior) rather than only the level of the posteriormost tooth position; and 5) the dorsal elevation of the posterior section of the dentary is more pronounced.

DISTRIBUTION. — Oligocene, Phosphorites du Quercy, southern France.

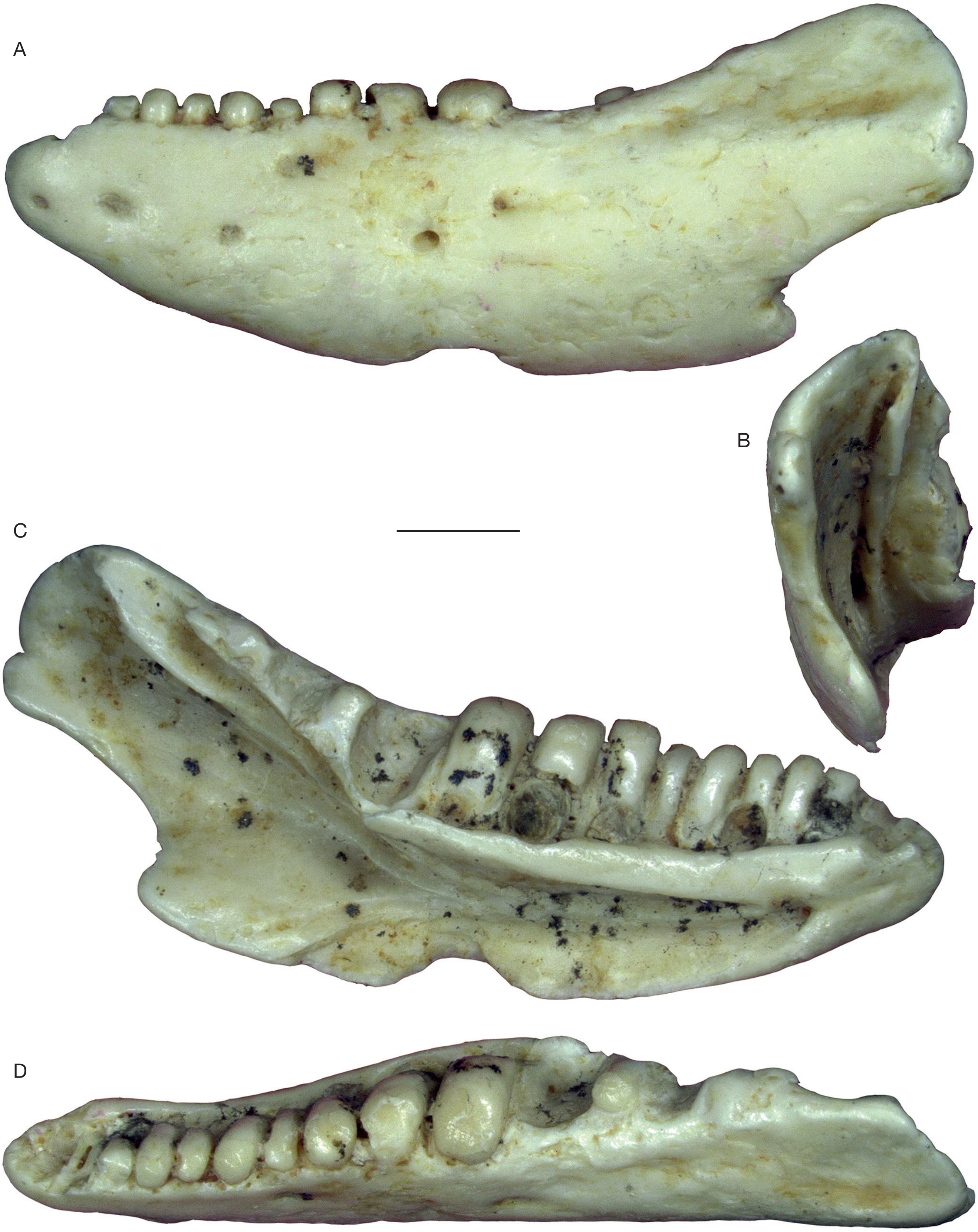

Fig. 6. — *Pseudeumeces kyrillomethodicus* n. sp. Photographs of the holotype left dentary NHMW 2019/0051/0001 in lateral (**A**), posterior (**B**), medial (**C**), and dorsal (**D**) views. Scale bar: 2 mm.

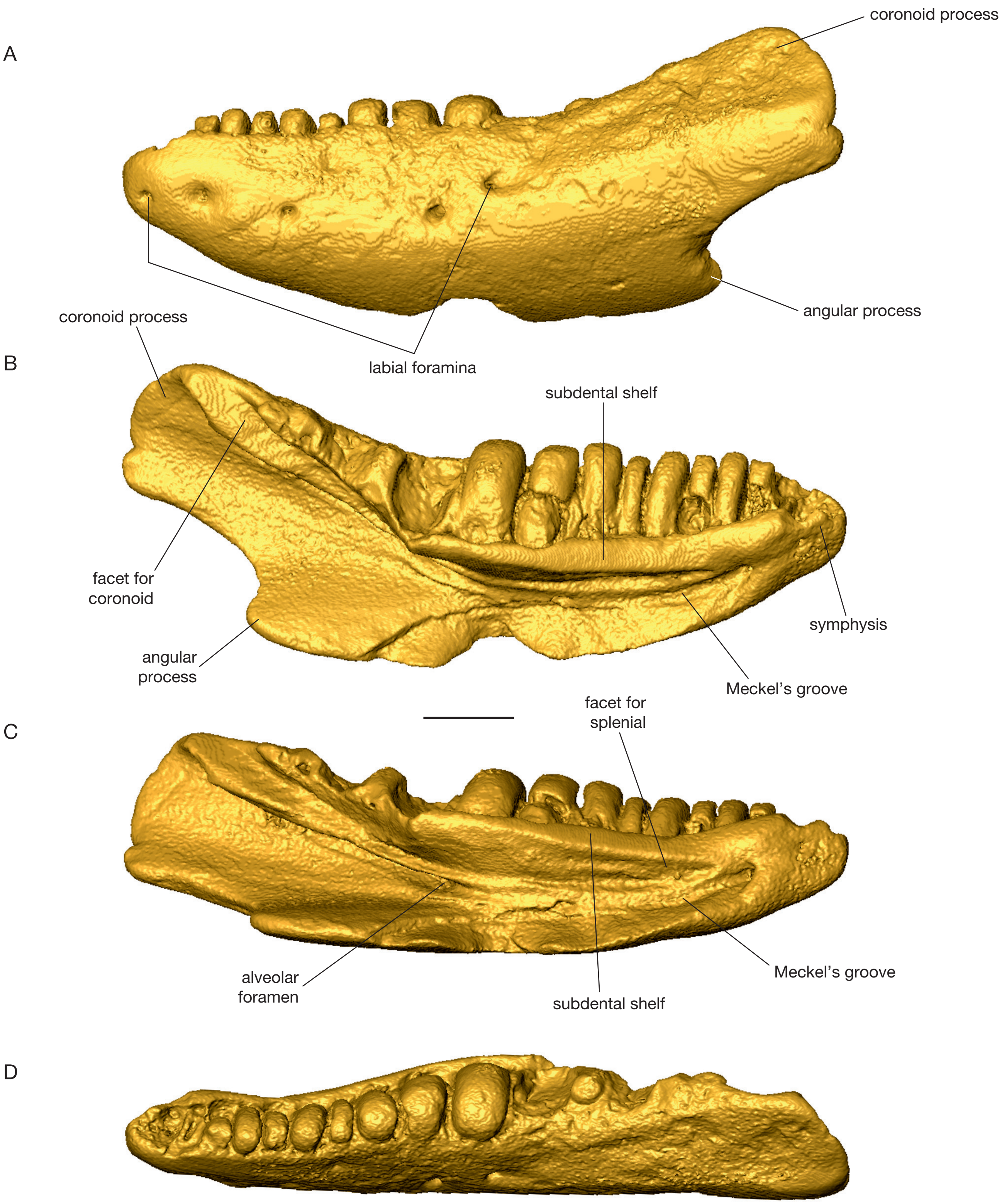

Fig. 7. — *Pseudeumeces kyrillomethodicus* n. sp. Virtual 3D models of the holotype left dentary NHMW 2019/0051/0001 in lateral (**A**), medial (**B**), ventromedial (**C**), and dorsal (**D**) views. Scale bar: 2 mm.

DESCRIPTION

Holotype NHMW 2019/0051/0001 (Figs 6-9)

The holotype left dentary NHMW 2019/0051/0001 is the most complete specimen (Figs 6-9). The specimen measures a total length of 16 mm. It is short, massively built, and ventrally deep. In cross-section, the dentary is C-shaped. In medial aspect, the dentary has a dorsally concave appearance and it gradually widens posteriorly. The CT scan reveals that

Fig. 8. — *Pseudeumeces kyrillomethodicus* n. sp. Close up photographs of posterior teeth of the holotype left dentary NHMW 2019/0051/0001 in medial (**A**) and dorsal (**B**) views. Scale bar: 1 mm.

the holotype dentary bears 15 tooth positions (see Fig. 9). On the medial side, the deep Meckel's groove is fully open and distinctly broad posteriorly. It gradually narrows anteriorly, but it is still relatively wide even in this region. It disappears posterior to the large symphyseal region. CT images show that it continues inside to the bone further anteriorly only as a small internal canal. The alveolar foramen is small, being located at the level between the 4th and 5th tooth positions (counting from the posterior tooth; in other words, at the level of 11th and 12th tooth position counted from anterior). Further anteriorly, the alveolar canal is separated from the Meckel's groove by the intramandibular septum, which is completely fused to the bone. Meckel's groove is roofed dorsally by the subdental shelf, which bears a facet for the splenial on its ventral side. This facet reaches the level of around the 5th tooth position (counted from anterior) and its anterior end is well stepped. Dorsally, the subdental shelf bears the sulcus dentalis. The whole shelf gradually narrows posteriorly in medial aspect. The posterodorsal portion of the dentary is inclined dorsally, being well elevated. This inclination starts at the level of the 4th tooth position (counted from posterior). Posterior to the tooth row, there is a long and robust coronoid process. It reaches highly above the level of the largest tooth crowns. On its dorsomedial side, it bears a facet for the anteromedial process of the coronoid. It reaches the level of the 3rd tooth position (counted from posterior). The posteroventral portion of the dentary is preserved. This region is slightly curved medially, forming a short angular process. Nevertheless, this region is also slightly weathered in this specimen.

The otherwise smooth lateral surface of the dentary is pierced by five labial foramina (Figs 6A; 7A). The posteriormost one is located at the level of around the 5th tooth position (counted

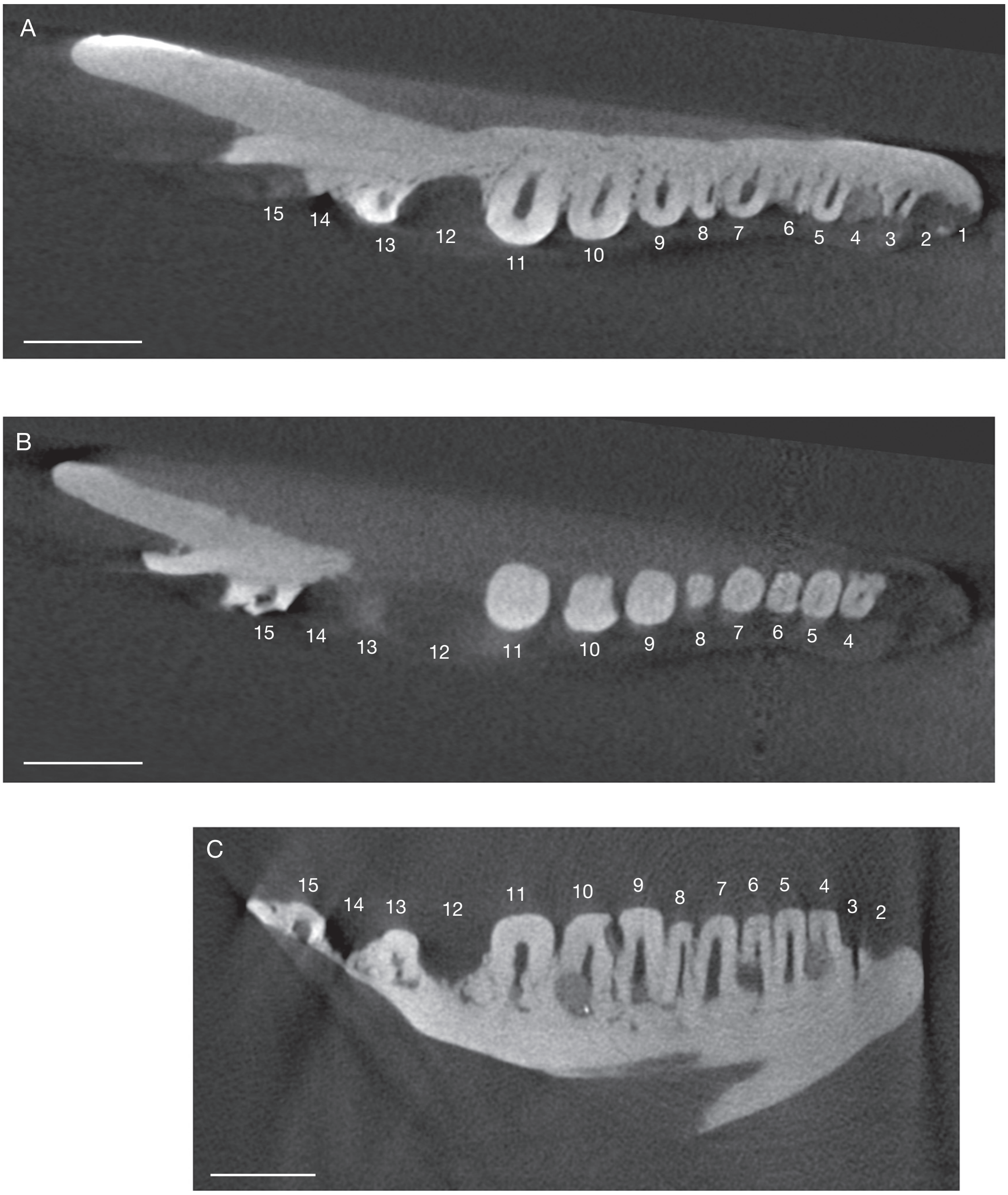

FIG. 9. — *Pseudeumeces kyrillomethodicus* n. sp. Virtual slices of the holotype left dentary NHMW 2019/0051/0001: horizontal, with a special emphasis on the anterior and mid-section of the tooth row (**A**), horizonal, upper-more section with a special emphasis on the mid- and posterior section of the tooth row (**B**), and sagittal (**C**). Note the preserved tooth position showing the tooth number of 15. Scale bars: 2 mm.

from posterior). In the posterodorsal region of the dentary, the wedge shaped facet for the anterolateral process of coronoid is present, being, however, very shallow. It appears to reach the level of the 4th tooth position (counted from posterior).

Paratype NHMW 2019/0051/0002 (Figs 10-14)
Besides the holotype described above, only a single other dentary, the paratype NHMW 2019/0051/0002, can be confidently referred to *Pseudeumeces kyrillomethodicus* n. sp. This is rather similar to the holotype. The paratype NHMW 2019/0051/0002 is larger and more robust than the holotype NHMW 2019/0051/0001 (Figs 10-14). The posteroventral portion of the dentary that is preserved in the holotype is not preserved here and only 12 tooth positions can be therefore observed in the paratype NHMW 2019/0051/0002 (see Fig. 14). The facet for coronoid on the lateral side is more developed in the paratype dentary if compared to the holotype. When the specimen NHMW 2019/0051/0002 was originally complete and in the case it possessed 15 tooth positions as the holotype, then the facet for the anterolateral process of the coronoid reached the level of the 5th tooth position (counted from posterior).

FIG. 10. — *Pseudeumeces kyrillomethodicus* n. sp. Photographs of the paratype right dentary NHMW 2019/0051/0002 in lateral (**A**), medial (**B**), ventromedial (**C**), and dorsal (**D**) views. Scale bar: 2 mm.

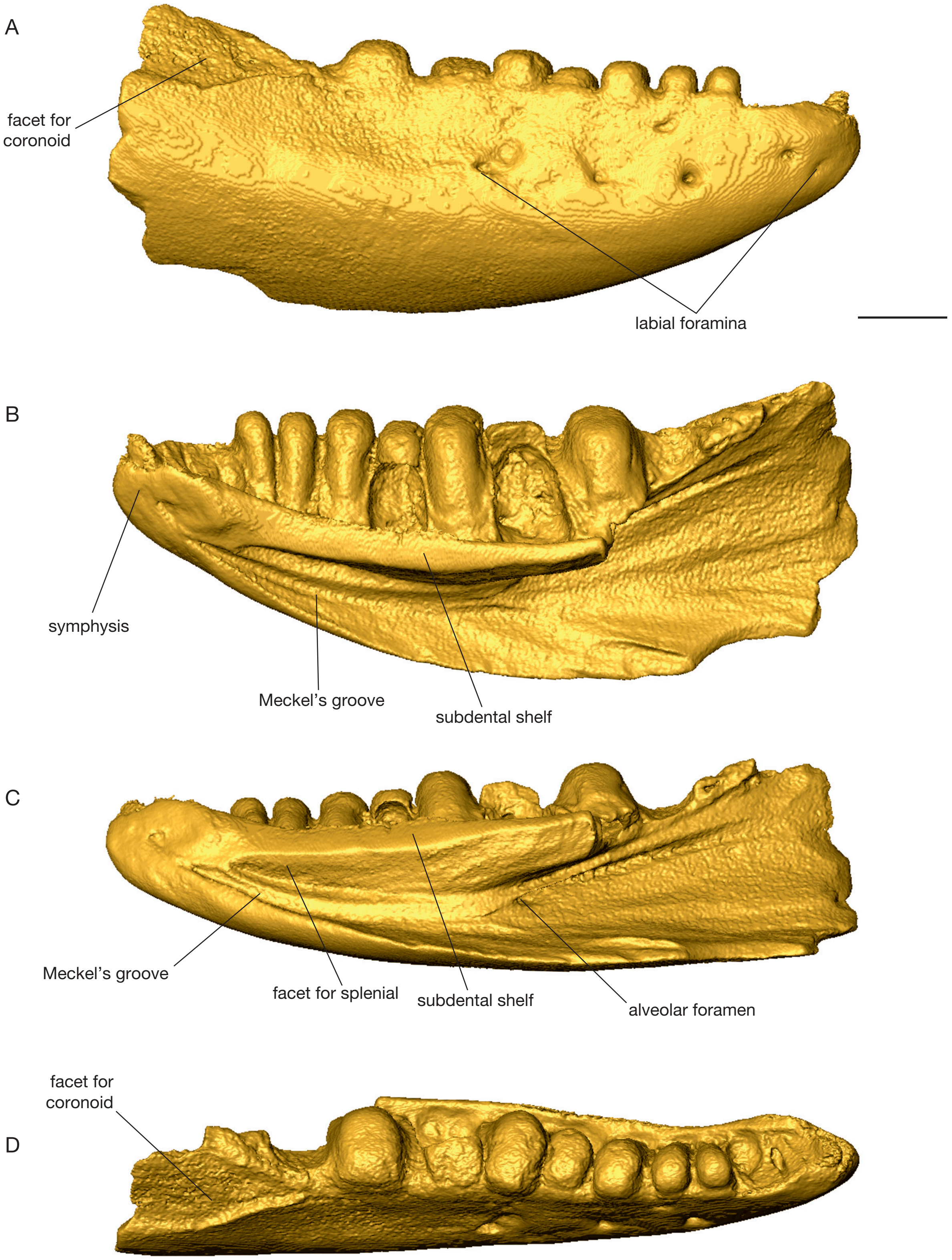

FIG. 11. — *Pseudeumeces kyrillomethodicus* n. sp. Virtual 3D models of the paratype right dentary NHMW 2019/0051/0002 in lateral (**A**), medial (**B**), ventromedial (**C**), and dorsal (**D**) views. Scale bar: 2 mm.

If the tooth count was only 14, the coronoid reached the level of the 4th tooth position, the condition being identical to the holotype. However, the difference between this specimen and the holotype is the position of the alveolar foramen, being located at the level of the 9th tooth position here (counted from anterior).

Fig. 12. — *Pseudeumeces kyrillomethodicus* n. sp. Close up photographs of posterior teeth of the paratype right dentary NHMW 2019/0051/0002 in medial (**A**) and dorsal (**B**) view. Scale bar: 1 mm.

Dentition

The dentition is pleurodont and strongly heterodont. The teeth are closely spaced. While the tooth size increases posteriorly (except for the last three or four teeth that are again small, reduced), the teeth in the anterior portion of the tooth row are small and slender. The teeth in the posterior region are robust, forming blunt cylinders (Figs 8; 12; 13). The teeth (especially those in the posterior half of the tooth row) are anteroposteriorly compressed. The tooth crowns bear delicate striations.

Remarks

Pseudeumeces cadurcensis was originally established by Filhol (1877a) as a scincid of the extant genus *Plestiodon* Duméril & Bibron, 1839. This taxonomic opinion was subsequently followed by others (e.g., Nopcsa 1908; Kuhn 1939), although affinities with the glyptosaurine *Placosaurus* also appeared in the literature (Lydekker 1888b; Leenhardt 1926). Hoffstetter (1944) was the first to realize its lacertid affinities and placed it into its own genus, *Pseudeumeces*. So far, *Pseudeumeces cadurcensis* represented the only currently recognized species of this genus, as other two species that have in the past been referred to *Pseudeumeces* are now known to pertain to other genera or represent indeterminate lizards (i.e., *Glyptosaurus walbeckensis* Kuhn, 1940, which was recombined into *Pseudeumeces* by Estes [1983], and *Pseudeumeces pouiti* Augé, 1993, which was subsequently recombined to its own genus *Ligerosaurus* Augé, Bailon & Malfay, 2003, as *Ligerosaurus pouiti* by Augé *et al.* [2003]).

We consider that the dentition and overall morphology of our new species *Pseudeumeces kyrillomethodicus* n. sp. appears to bear a resemblance with *Pseudeumeces cadurcensis*. Similarly to the case of our new taxon, the type material of *Pseudeumeces cadurcensis* also originates from an imprecise locality within the Phosphorites du Quercy (Filhol 1877a; for this taxon see also Augé 2005; Augé & Hervet 2009; Čerňanský & Augé 2012; Čerňanský *et al.* 2016a; Bolet *et al.* 2017). Nevertheless, the material described herein clearly exhibits several obvious differences relative to *Pseudeumeces cadurcensis* (see Diagnosis above). Besides the features stated in the diagnosis, there is one additional difference – the dentary tooth number in *Pseudeumeces cadurcensis* is usually 17 (note that the tooth number in that taxon can range from 15-17; the holotype of the species [the left dentary AMNH FARB 241A] is incomplete but the preserved portion bears seven teeth and at least five other empty tooth positions), whereas the dentary tooth number of *Pseudeumeces kyrillomethodicus* n. sp., based on material described here, is around 14-15. Although such small differences in tooth counts can be informative in some cases, it should be noted that the tooth number in lacertids (see e.g., Čerňanský & Syromyatnikova 2019), like virtually all lizards, should not be interpreted as absolute due to its variability. So, whether it seems that the tooth number of *Pseudeumeces cadurcensis* appears to be slightly higher than the new species, we cannot fully demonstrate it and we refrain from formally considering this feature as a diagnostic character.

Besides the resemblance with *Pseudeumeces cadurcensis* discussed above, it should be noted also that the dentaries of *Pseudeumeces kyrillomethodicus* n. sp. slightly resemble those of *Dracaenosaurus* Pomel, 1846, in the following features (see Müller 2004; Augé 2005; Čerňanský *et al.* 2016a, 2017): 1) dentary is a rather short, massive, and deep element; 2) the presence of a dorsally elevated posterior portion of the dentary; 3) the presence of the amblyodont dentition, where the posterior robust teeth are low and form blunt cylinders (this is more pronounced in *Dracaenosaurus*); and 4) the presence of striations on the tooth crown (note that the last two features are not unique to these two forms).

However, there are some important differences between these two forms, where *Pseudeumeces kyrillomethodicus* n. sp. can be differentiated from *Dracaenosaurus croizeti* Gervais, 1848-1852, by the following combination of features (for *Dracaenosaurus*, see Müller 2004; Augé 2005; Čerňanský *et al.* 2016a, 2017): 1) the dentary tooth number is around 14-15 rather than seven or eight; 2) the tooth size increases posteriorly, however, the largest tooth is the 4th or 5th one (counted from posterior), whereas the further posterior teeth decrease in size (to the contrary, the largest tooth in *D. croizeti* is usually the posteriormost one or sometimes the penultimate one); 3) the alveolar foramen, although its position can vary, is located further anteriorly (at the level between the 4th and 5th tooth positions in the holotype; counted from posterior) rather than at the level of the posteriormost tooth (or between last and penultimate tooth positions); 4) the facet for the anterolateral process of coronoid reaches around the level of the 4th tooth position (counted from posterior) rather than terminating posterior to the tooth row; and 5) teeth (especially those in the posterior half of the tooth row) are anteroposteriorly compressed rather than mediolateraly compressed.

Note that for *Dracaenosaurus* we follow recent workers and treat *Dracaenosaurus sauvagei* (Filhol, 1882) as a junior synonym of the type species *Dracaenosaurus croizeti* (see e.g., Augé 2005). In any case, the holotype dentary of *D. sauvagei* is different from that of *Pseudeumeces kyrillomethodicus* n. sp. and its tooth count is within the range of *D. croizeti*.

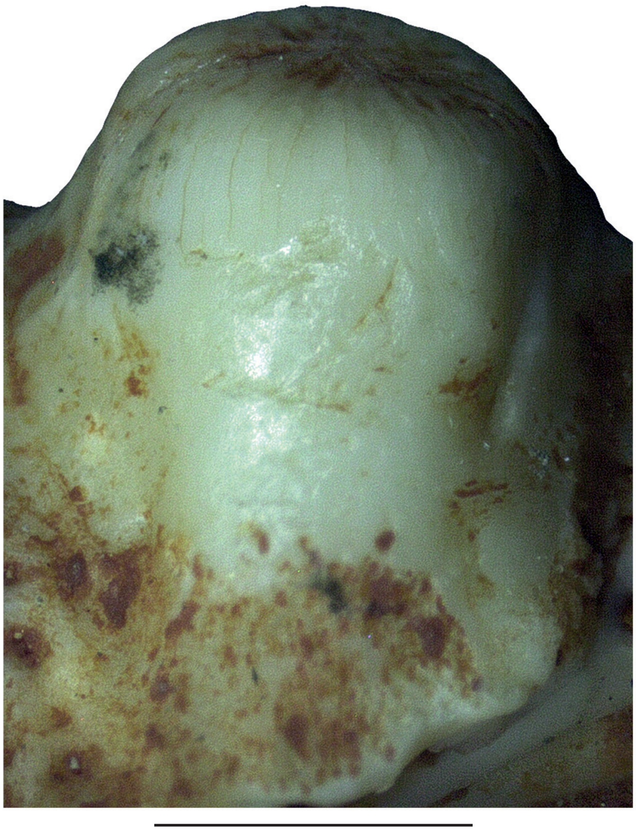

FIG. 13. — *Pseudeumeces kyrillomethodicus* n. sp. Close up photograph of the most robust tooth of the paratype right dentary NHMW 2019/0051/0002 in medial view. Note the prominent striations. Scale bar: 1 mm.

In regards to our material, the specimen MNHN.F.QU17169 (see Augé & Hervet 2009: fig. 1) deserves a comment. This specimen, which has been allocated to *Pseudeumeces cadurcensis* by Augé (2005) and Augé & Hervet (2009), has only 12 tooth positions instead of usual 16-17. Moreover, the dentary of this specimen appears to be robust rather than narrow. This would point to a huge level of variability. However, in MNHN.F.QU17169, only the last posterior tooth is reduced and the coronoid reaches the level of this last posterior tooth position on both sides as it is typical, indeed, for *Pseudeumeces cadurcensis* (in contrast to our material described herein).

In general, it can be expected stratigraphically that not identical but slightly similar forms of a lineage (the exact age of our material is unfortunately unknown, as is also that of the type material of *Pseudeumeces cadurcensis*) would exhibit a higher degree of morphological disparity reflecting the evolution through time than specimens collected from a single stratigraphic level. In those cases, it is of course difficult to add an exact border between such forms to distinguish taxa as units for science. However, we are convinced that all the above mentioned differences allow to erect a new taxon based on our type material. Even in

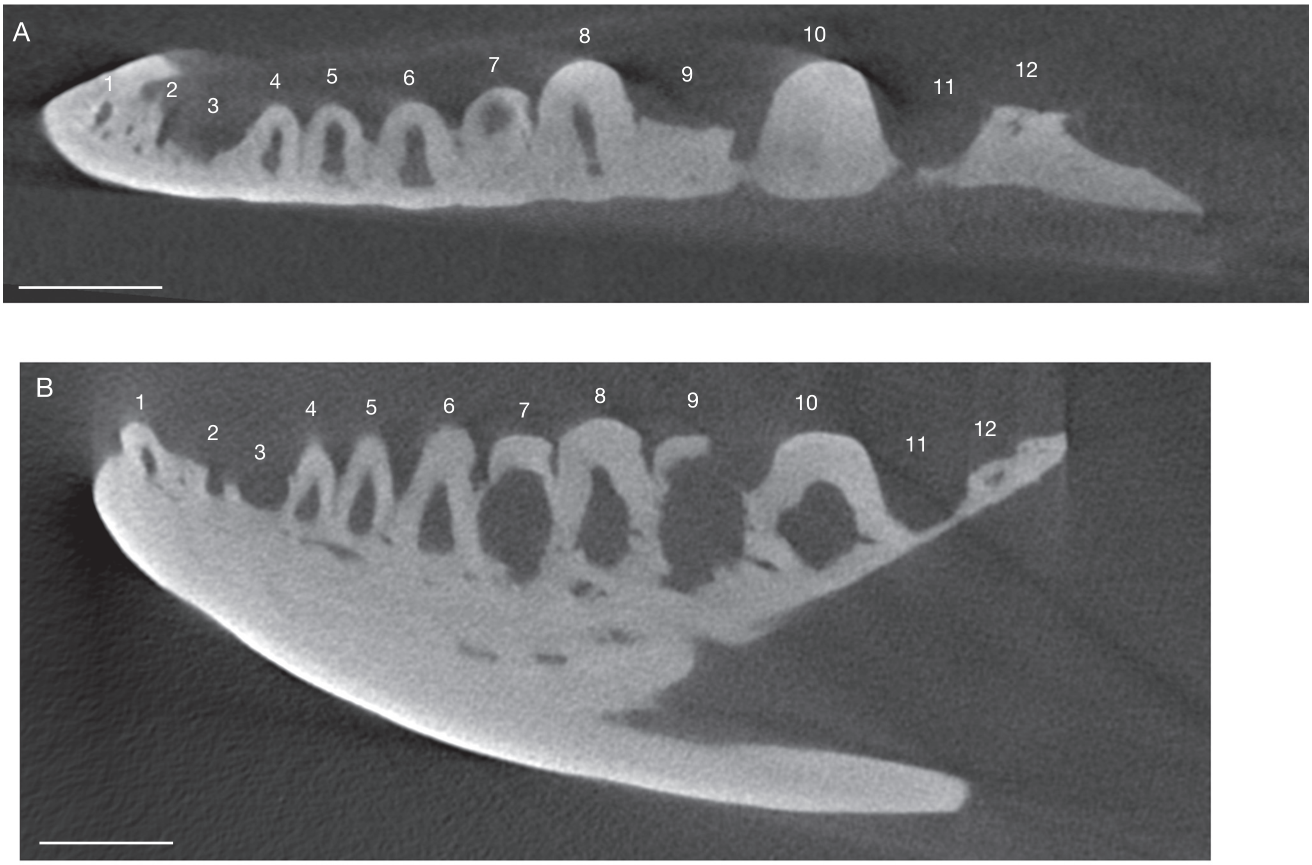

Fig. 14. — *Pseudeumeces kyrillomethodicus* n. sp. Virtual slices of the paratype right dentary NHMW 2019/0051/0002: horizontal (**A**) and sagittal (**B**). Note that the posterior section of the tooth row is missing. Scale bars: 2 mm.

extant herpetofaunas, lacertids include several morphologically cryptic species for which determination based on morphology can be even more difficult than the situation discussed here. Therefore, we consider the obvious differences in our material relative to the previously described forms as sufficient. Due to a high level of similarities of the currently known limited material with *Pseudeumeces cadurcensis*, we decided to allocate this new taxon *Pseudeumeces kyrillomethodicus* n. sp. to the same genus instead of erecting a new one.

It should be further noted that the extinct genera *Pseudeumeces*, *Dracaenosaurus*, and *Janosikia* Čerňanský, Klembara, & Smith, 2016, have been recovered as sister taxa to the extant *Gallotia* Boulenger, 1916, from the Canary Islands, and all these taxa together with *Psammodromus* Fitzinger, 1826, form the clade Gallotiinae. This was firstly observed by Čerňanský *et al.* (2016b, 2017), who also applied this revelation on the principles of the island rules, and later supported by Garcia-Porta *et al.* (2019) by their analyses based on a supermatrix relying on novel phylogenomic datasets. Therefore, we allocate *Pseudeumeces kyrillomethodicus* n. sp., as a member of *Pseudeumeces*, to the Gallotiinae as well.

Recently described fossil material from the early Eocene (MP 8-9) French locality of Mutigny (Paris Basin) indicates that not only stem but also morphologically modern-like (potentially crown or close to crown) lacertids were present on the European continent already in the early Eocene (Čerňanský *et al.* 2020). And later, lacertids were a rather diverse group during the Paleogene. The new taxon described herein, *Pseudeumeces kyrillomethodicus* n. sp., fully supports this high diversity and abundance of European Paleogene lacertids.

Pseudeumeces sp.
(Figs 15-17)

Referred specimens. — A left maxilla (NHMW 2019/0051/0004); a left dentary (NHMW 2019/0051/0003); a right dentary (NHMW 2019/0051/0005).

Description

Maxilla NHMW 2019/0051/0004 (Fig. 15)

Only one such element is available in our collection, the left maxilla NHMW 2019/0051/0004 (Fig. 15). This specimen is almost completely preserved. In medial view, the supradental shelf is well medially expanded, having rounded (dorsally convex) course (Fig. 15B). The maxilla bears 11 tooth positions (10 teeth are still attached). However, the premaxillary process is broken off and only its posterior root portion is preserved. Thus, it can be estimated that the

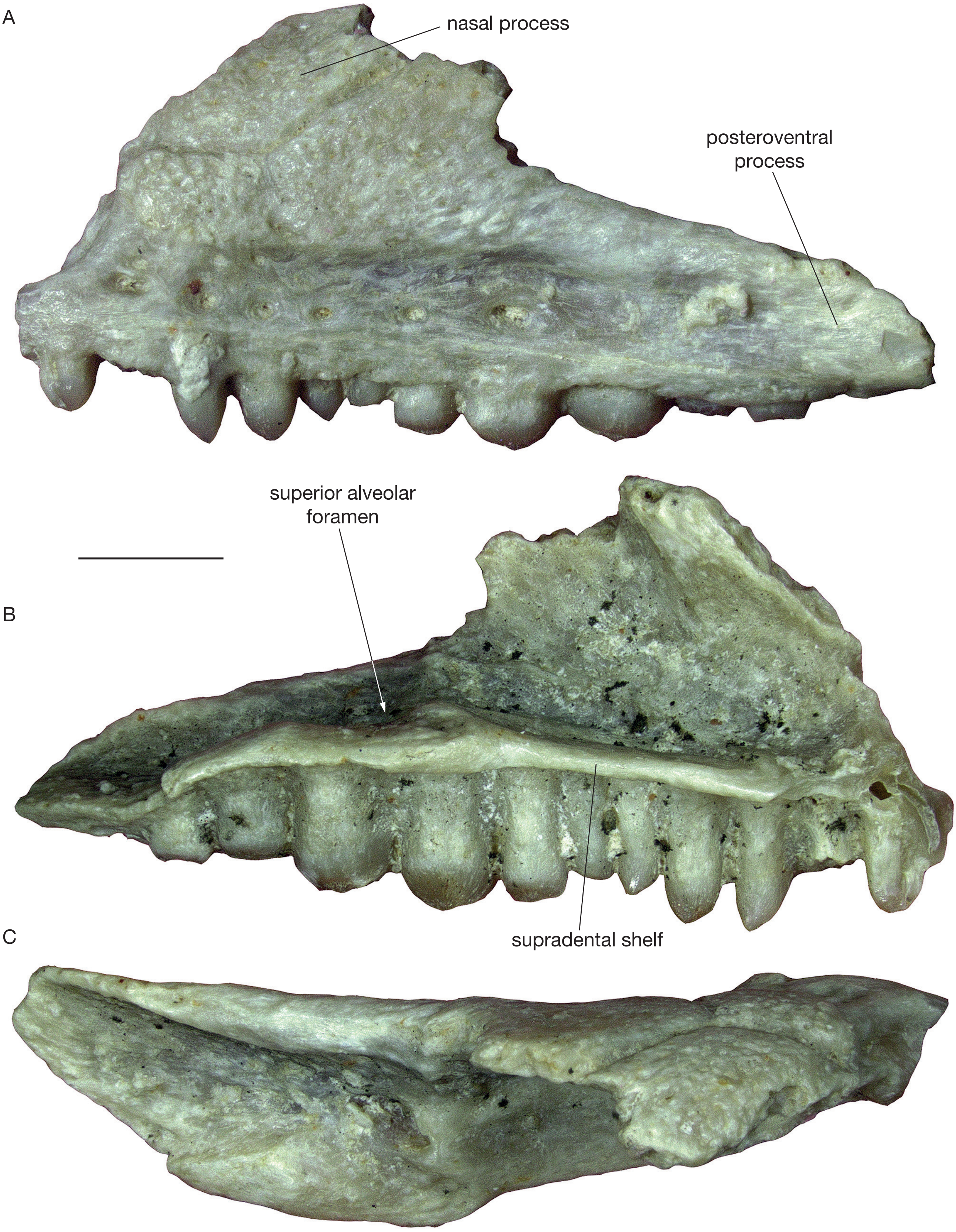

Fig. 15. — *Pseudeumeces* sp. Photographs of left maxilla NHMW 2019/0051/0004 in lateral (**A**), medial (**B**), and dorsal (**C**) views. Scale bar: 2 mm.

Fig. 16. — *Pseudeumeces* sp. Photographs of right dentary NHMW 2019/0051/0005 in lateral (**A**), medial (**B**), and dorsal (**C**) views. Scale bar: 2 mm.

tooth number in a complete tooth row was around 12. The superior alveolar foramen is located at the level between the 3rd and 4th tooth positions (counted from posterior). Posterior to this, the maxilla protrudes into the posteroventral process, having a facet for jugal on its dorsal internal side. A facet for the palatine is positioned medial to the superior alveolar foramen. The posteroventral process of the maxilla slightly narrows posteriorly, although its termination is not pointed, but rather stepped. This posteriormost portion does not bear dentition. In the anterior half of the bone, the nasal process is well dorsally elevated, being high. Its dorsal end slightly bents medially. However, the posterodorsal tip, which forms the contact with the frontal, is broken off. On the medial side of the nasal process, the carina maxillaris starts to rise dorsally at the level of the 3rd preserved tooth (counted from anterior). Further, it is inclined posteriorly and thus it does not reach a high level dorsally. In the dorsal portion of the process, a facet for the prefrontal is present.

In lateral view, the ventral region of the maxilla is pierced by six labial foramina of various sizes (Fig. 15A). The posteriormost one is located at the level of the 4th tooth position (counted from posterior). The dorsally located nasal process is completely covered by three osteoderms. These are clearly demarked by sulci. The sulci meet all together at the level of the 4th tooth position (counted from ante-

Fig. 17. — *Pseudeumeces* sp. Photographs of left dentary NHMW 2019/0051/0003 in lateral (**A**), medial (**B**), and dorsal (**C**) views. Scale bar: 2 mm.

rior), forming a Y-shaped structure. The anteroventral osteoderm is the smallest one, whereas the largest is the posterior osteoderm. All three osteoderms are sculptured. The sculpture consists of densely arranged pits and ridges running to the periphery. The posteroventral process, posterior to the level of osteoderm, has bulged dorsal margin.

Dentaries NHMW 2019/0051/0003 and NHMW 2019/0051/0005 (Figs 16; 17)

Specimen NHMW 2019/0051/0005 is small in size and slightly damaged, whereas NHMW 2019/0051/0003 represents only fragment of the posterior portion of the dentary. NHMW 2019/0051/0005 possesses 15 tooth positions, with seven teeth being still attached (Fig. 16). The dorsal crest is high and the teeth only slightly exceed it dorsally. Meckel`s groove is fully open, but the ventral portion of the dentary is broken off. In any case, the dentary is narrow rather than robust. Its lateral surface is pierced by five labial foramina. In the posterodorsal region of the dentary, the wedge shaped, well defined facet for the anterolateral process of coronoid is present. It reaches the level of the penultimate tooth position. NHMW 2019/0051/0003 possesses only six tooth positions, with five teeth preserved (Fig. 17); its further anterior region is broken off and missing. The facet for the anteromedial process of the coronoid reaches the level of the last posterior tooth. On lateral side, the facet for the anterolateral process of coronoid is well defined, reaching the level between the last and penultimate tooth position.

Dentition

The dentition is pleurodont and amblyodont. The teeth are closely spaced. The tooth crowns bear delicate striations on both maxillary and dentary teeth. The maxillary tooth length varies, resulting in a sinuous occlusal surface. Here, the teeth in the posterior section are more robust except for the last two. The teeth in the anterior portion of the tooth row are slightly pointed and curved posterolingually. On some of those maxillary teeth, there is a very small indication of an indistinct, incipient mesial cusp.

Remarks

The maxilla NHMW 2019/0051/0004 bears 12 tooth positions, whereas 15 are present in that of *Pseudeumeces cadurcensis* (see Augé 2005; Augé & Hervet 2009). For this reason, the maxilla NHMW 2019/0051/0004 potentially pertains to the above described species *Pseudeumeces kyrillomethodicus* n. sp. However, as there is a lack of a strong support for such association based on the available material, we decided to allocate this maxilla only as *Pseudeumeces* sp. Small differences in the anterior maxillary teeth of NHMW 2019/0051/0004 and the dentary teeth of *Pseudeumeces kyrillomethodicus* n. sp. can be explained by an ontogenetic change. Judging from the smaller size of the maxilla NHMW 2019/0051/0004 relative to dentaries, the former specimen most likely represents a late juvenile (or subadult) individual. Similar changes have been observed in both extant and extinct lacertids. For example, in the early Miocene *Janosikia ulmensis* (Gerhardt, 1903), vestiges of mesial cusps are present on some anterior maxillary teeth in a juvenile specimen (see Čerňanský *et al.* 2016b). Additionally, the ontogenetic change in the tooth morphology is sometimes observed in the extant *Gallotia stehlini* (Schenkel, 1901) as well, where the juvenile tricuspid teeth are replaced by multicuspid ones in adult individuals (Barahona *et al.* 2000).

The maxilla NHMW 2019/0051/0004 further differs from that of *Dracaenosaurus* in the following features: 1) maxillary tooth number is ~12 rather than 7; 2) the posteroventral process of the maxilla is not markedly high as it is in *D. croizeti*; and 3) the presence of three well developed osteoderms attached to the nasal process of maxilla.

Two dentaries are also referred to *Pseudeumeces* sp. The specimen NHMW 2019/0051/0005 represents the smallest lacertid dentary in our sample. It is very likely that it represents a juvenile (or subadult) ontogenetic stage, that could potentially pertain to the above described *Pseudeumeces kyrillomethodicus* n. sp. Nevertheless, in comparison with that taxon, NHMW 2019/0051/0005 does not appear to be so robust and the facet for the anterolateral process of coronoid reaches at the level of the penultimate tooth position. In the other specimen, the fragment of left dentary (NHMW 2019/0051/0003), this facet reaches the level between the last and penultimate tooth. Moreover, only the last posterior tooth was reduced (it is absent, but its size can be estimated based on its tooth loci). These characters are in a sharp contrast with the type material of *Pseudeumeces kyrillomethodicus* n. sp. Therefore, we cannot exclude that this material does not pertain to *Pseudeumeces cadurcensis*, which also occurs in the Oligocene of the Phosphorites du Quercy and shares these features (e.g., Augé & Hervet 2009). The proper taxonomic allocation of fragmentary material needs always to be met with caution. This is especially true for similar forms such as those discussed herein.

Family LACERTIDAE incertae sedis

Genus *Mediolacerta* Augé, 2005

TYPE SPECIES. — *Mediolacerta roceki* Augé, 2005 (type species by original designation; Augé 2005).

Mediolacerta sp.
(Fig. 18)

REFERRED SPECIMEN. — A left dentary (NHMW 2019/0050/0001).

Description

The only available specimen, the left dentary NHMW 2019/0050/0001, is almost completely preserved, with only the half posterior ventral portion being broken off and missing (Fig. 18). It is an anteroposteriorly long and massive element, with a slight medial curvature at its anterior end. The tooth row is completely preserved and the alveolar crest supports 23 tooth positions (17 teeth still attached). Meckel's groove is fully open along its entire length, although it is narrow in the anterior region (Fig. 18B). The alveolar foramen is located at the level of the 6th tooth position (counted from posterior). The intramandibular septum is fused to the bone, being almost horizontal in this section. Meckel's groove is roofed by a more or less straight subdental shelf (only its posterior portion is arched). The shelf is somewhat broad only in the anterior section, but it narrows posteriorly and thus is rather

Fig. 18. — *Mediolacerta* sp. Photographs of left dentary NHMW 2019/0050/0001 in lateral (**A**), medial (**B**), and dorsal (**C**) views. Scale bar: 2 mm.

thin. This is mainly caused by the presence of the facet for the splenial, situated on its ventral margin. This facet reaches the level of the 8th tooth position (counted from anterior). Anteriorly, the shelf continues to the small rectangular symphysis. Posteriorly, the dentary protrudes into a short and low coronoid process, which bears a facet for the coronoid.

The otherwise smooth lateral surface of the bone is pierced by six labial foramina (Fig. 18A). They are arranged in a single row, located in the dorsal half of the dentary. The posteriormost foramen is located at the level of the 6th tooth position (counted from posterior). A facet for the coronoid is present on the dorsolateral surface of the bone.

Dentition

The dentition is pleurodont and heterodont (Fig. 18). The tooth size gradually increases posteriorly (although it should be noted that the last posterior tooth is slightly smaller than the penultimate one). The teeth in the anterior section of the tooth row are small, slender, and somewhat pointed, with the tooth crowns slightly curved posterolingually. Posteriorly located teeth (from the 13th one if counted from the anterior) are markedly robust and blunt in comparison to those from the anterior region. The tooth apices of several teeth are worn (or weathered), but those which are complete show bicuspidity, with an incipient small mesial cusp being present.

REMARKS

The dentary NHMW 2019/0050/0001 described herein represents the largest lacertid from this collection. The anterior teeth are pointed, whereas those located further posteriorly are robust and blunt, but with some of them bearing mesial cusp - this character fits to the diagnosis of *Mediolacerta* and its so far sole named species, *Mediolacerta roceki*, also from the Phosphorites du Quercy (stratigraphic occurrence MP23-MP30; see Augé 2005). As such, in respect of these features, NHMW 2019/0050/0001 can be differentiated from both *Pseudeumeces* and *Dracaenosaurus*. Besides the dentition, NHMW 2019/0050/0001 also shares several other features with *Mediolacerta*: 1) rather thin subdental shelf; 2) small rectangular symphysis; and 3) the position of the alveolar foramen at the level of the 6th tooth position, counted from posterior.

Nevertheless, there appear also to be differences among NHMW 2019/0050/0001 and other known specimens of *Mediolacerta*. Most principally, the tooth number of the holo-

Fig. 19. — *Placosaurus* sp. Photographs of cervical vertebra NHMW 2019/0046/0002 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and right lateral (**E**) views. Scale bar: 2 mm.

type dentary (MNHN.F.PFR11006) of *Mediolacerta roceki* is 19, whereas this number is 23 in NHMW 2019/0050/0001. Dentaries of the same taxon have been also described from the late Oligocene of Germany (*Mediolacerta* cf. *roceki* of Čerňanský *et al.* 2016a); the complete tooth row of the German material bears 18 tooth positions. However, it should be noted that tooth number in lacertids, like virtually most lizards, might be variable and also likely to be size related (the anteroposterior length of the dentary NHMW 2019/0050/0001 is 23.7 mm, thus this dentary is larger than the holotype of *Mediolacerta roceki* and the German material. These numbers should not be interpreted as absolutes. However, because the differences in the overall size and the dentary tooth count objectively exist, we decided to allocate NHMW 2019/0050/0001 only to the genus level, as *Mediolacerta* sp.

ANGUIMORPHA Fürbringer, 1900
Family ANGUIDAE Gray, 1825
Subfamily GLYPTOSAURINAE Marsh, 1872

Genus *Placosaurus* Gervais, 1848-1852

TYPE SPECIES. — *Placosaurus rugosus* Gervais, 1848-1852 (type species by original designation; Gervais 1848-1852).

Placosaurus sp.
(Figs 19-22)

REFERRED SPECIMENS. — Three presacral vertebrae (NHMW 2019/0046/0001, NHMW 2019/0046/0002, and possibly also NHMW 2019/0046/0008); one caudal vertebra (NHMW 2019/0046/0009).

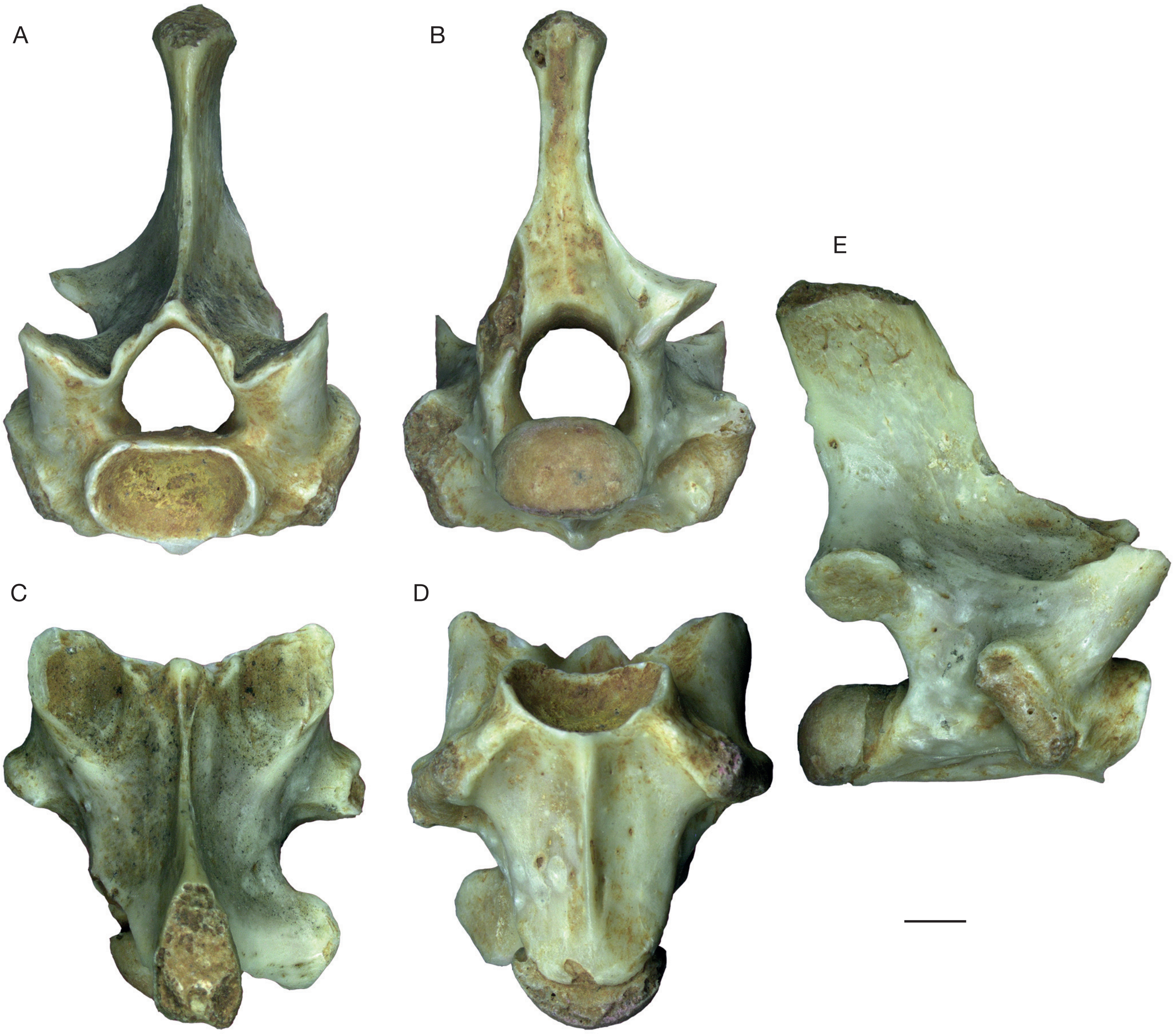

Fig. 20. — *Placosaurus* sp. Photographs of presacral vertebra NHMW 2019/0046/0001 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and right lateral (**E**) views. Scale bar: 2 mm.

Description

Presacral vertebrae (Figs 19-21)

The vertebra NHMW 2019/0046/0001 is relatively large (centrum length = 9.8 mm) (Figs 20; 21), while the cervical vertebra (NHMW 2019/0046/0002) is also large, with a centrum length of 8.5 mm (Fig. 19) (Appendix 1). NHMW 2019/0046/0001 is primarily characterized by the presence of a median ridge running throughout the ventral surface of the centrum (Figs 20; 21). This median ridge is prominent and sharp, being slightly thicker at its anteriormost portion. Nevertheless, in the single known, cervical vertebra (NHMW 2019/0046/0002), this median ridge is substituted by a thick hypapophysis (Fig. 19). The base of the hypapophysis in this specimen is broad and extends throughout the entire midline surface of the centrum. In this cervical vertebra, the neural spine is relatively thick in dorsal view, while in lateral view it is inclined much posteriorly and develops in height mostly in the posterior portion of the neural arch. In NHMW 2019/0046/0001, the neural spine is rather high in lateral view, whereas in anterior view, it possesses a distinctive dorsal thickening. The neural spine augments in height only at the posterior half of the neural arch, but its base extends, in the shape of a longitudinal ridge, much anteriorly, reaching the anteriormost edge of the neural arch. The prezygapophyses are much dorsally inclined. The postzygapophyses are small. The synapophyses are massive and elongated. The cotyle and the condyle are dorsoventrally depressed. Similarly to the vertebrae of *Palaeovaranus* described below, the cotyle is rather anteroventrally directed, so that its dorsal level can be observed even in ventral view of the specimens. Unlike the melanosaurine and palaeovaranid presacral vertebrae

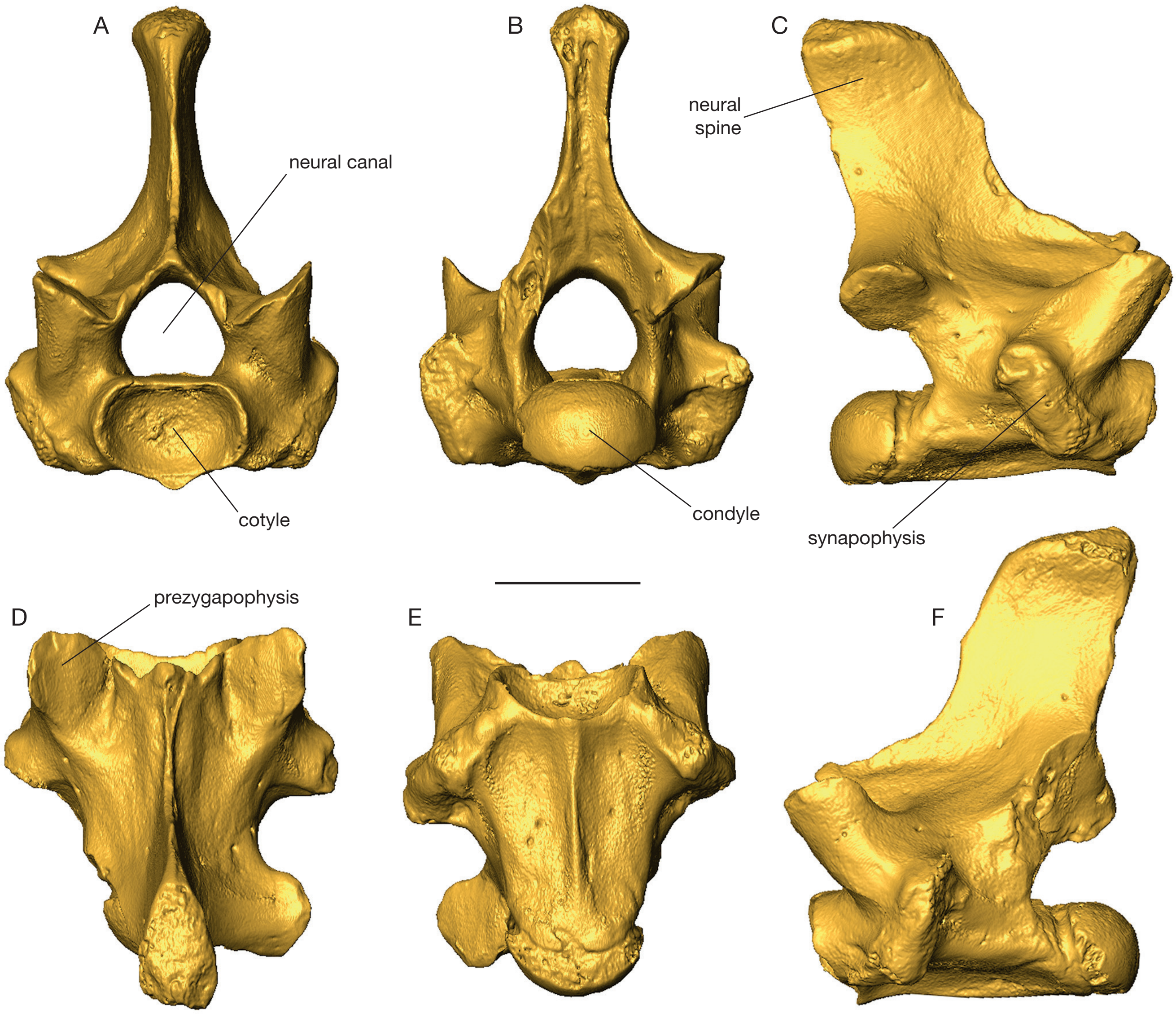

FIG. 21. — *Placosaurus* sp. Virtual 3D models of presacral vertebra NHMW 2019/0046/0001 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), ventral (**E**), and left lateral (**F**) views. Scale bar: 5 mm.

described below, there are no anocotylar foramina (i.e., foramina above the cotyle). NHMW 2019/0046/0008 is a rather fragmentary specimen and its size cannot be fully evaluated, though it is certainly a much smaller specimen than the other two. The median ridge in this specimen is in fact a much wide surface and not sharp; the fact that the posterior portion of the ventral surface of the centrum is totally missing does not even permit to identify this specimen as a cervical or post-cervical vertebra. The referral of NHMW 2019/0046/0008 to *Placosaurus* should be considered as rather tentative.

Caudal vertebra (Fig. 22)

The single available caudal vertebra NHMW 2019/0046/0009 is relatively large in size, with a centrum length of 9.5, but its outline is rather slender (Fig. 22). The transverse processes extend laterally in dorsal view. The neural spine is much broken but seems to have been developed only at the posterior half of the neural arch, although, similarly to the presacral vertebrae, its base was extending also anteriorly until the anteriormost edge of the neural arch, in the shape of a thin longitudinal ridge. The prezygapophyses are strongly dorsally inclined in anterior view. Both cotyle and condyle are dorsoventrally depressed. The haemapophyses are not fused to each other and appear almost parallel in ventral and posterior views; they are situated rather near the level of the condyle. The autotomic septum is evident in the anterior portion of the ventral surface of the centrum, at the level of the transverse processes.

REMARKS

The main distinction of the (post-cervical) presacral vertebrae of *Placosaurus* from those of *Palaeovaranus* appears to be the presence of a median ridge in the ventral surface of

FIG. 22. — *Placosaurus* sp. Photographs of caudal vertebra NHMW 2019/0046/0009 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and right lateral (**E**) views. Scale bar: 2 mm.

the centrum of the former genus (Rage 1978; see Discussion below). We accordingly refer this material to *Placosaurus*, highlighting the overall resemblance it shares with similar vertebrae described and figured by Rage (1978) from the late Eocene of Sainte Néboule, also in Quercy. The cervical vertebra NHMW 2019/0046/0002 possesses a rather thick hypapophysis. Such thick hypapophyses are present also in cervical vertebrae of *Palaeovaranus* (see Rage 1978: fig. 4), however, the latter specimens are slenderer and more elongated in dorsal view, while their hypapophyses do not extend throughout the centrum and are not so broad. Additionally, the single caudal vertebra described herein is strongly reminiscent to the one described and figured also by Rage (1978: fig. 2B) from the late Eocene of Sainte Néboule.

As it is also highlighted in the Discussion below, an identification of isolated vertebrae to the genus *Placosaurus* should be considered as tentative and is apparently primarily based on the existing figures and documentation of that genus in the literature (Rage 1978). Frustratingly, there is no associated articulated cranial material or osteoderms of *Placosaurus* in this (or any other) collection that would enable a more confident identification. Moreover, the types of all known species of *Placosaurus* (i.e, the type species *Placosaurus rugosus*, as well as *Placosaurus estesi* Sullivan & Augé, 2006, "*Placosaurus*" *europaeus* [Filhol, 1876], and ?*Placosaurus ragei* Sullivan, Augé, Wille & Smith, 2012) are cranial remains. Note that other species that have originally established as species of *Placosaurus*, are now considered to belong to different genera. These are: *Placosaurus leenhardti* Leenhardt, 1926 (currently considered a junior synonym of *Paraplacosauriops quercyi*), *Placosaurus lugdunensis* Depéret, 1917 (never figured), and *Placosaurus waltheri* Weigelt, 1929 (a *nomen dubium*). In any case, these are also typified by cranial material, with the exception of the latter taxon which is based on isolated osteoderms. Nevertheless, these glyptosaurine vertebrae from the NHMW collection appear to be much distinct from the below described melanosaurine ones.

Tribe MELANOSAURINI Sullivan, 1979

Genus *Paraplacosauriops* Augé & Sullivan, 2006

TYPE SPECIES. — *Plestiodon quercyi* Filhol, 1882 (type species by original designation; Augé & Sullivan 2006).

Paraplacosauriops quercyi (Filhol, 1882)
(Figs 23-29)

REFERRED SPECIMENS. — An incomplete left maxilla (NHMW 2019/0049/0003); a right dentary (NHMW 2019/0049/0001); a left dentary (NHMW 2019/0049/0002).

DESCRIPTION

Maxilla (Figs 23; 24)

About the anterior half of the maxilla is preserved, however, its anteriormost portion is missing (Figs 23; 24). The external wall of the maxilla consists of two complete and three incomplete ornamented shields divided by more or less distinct grooves (Figs 23A; 24A). One of the shields lying between the two anterior and two posterior shields is the largest and is of pentagonal shape. The ornamentation consists of small tubercles (Fig. 23E). The ornamented surface is ventrally delimited by a shallow and narrow, anteroposteriorly running groove. Immediately ventral to the groove, the surface of the maxilla is smooth and four labial foramina are present there (Figs 23A; 24A).

The smooth medial surface bears two depressions; a large one anteriorly (lacrimal recess) and a smaller one posteriorly (Figs 23B; 24B). The supradental shelf is straight and the bone immediately laterally to the posterior portion of the shelf is burrowed by the superior alveolar canal. The teeth are mesiodistally narrow and the apex is pointed.

Dentaries (Figs 25-29)

The right dentary NHMW 2019/0049/0001 is almost completely preserved, with only several pieces of the posteriormost portion are missing (Figs 25-28), while the left dentary NHMW 2019/0049/0002 is much more incomplete, missing both anterior and posterior portions (Fig. 29). Accordingly, we base our description on the almost complete right dentary NHMW 2019/0049/0001. The dentary is massively built. Its external surface is smooth. A distinct groove runs immediately anteroventrally to the root portion of the coronoid process (Figs 25-28). From there, a shallow sulcus runs anteriorly along the dorsal crest of the dentary. Ventrally to this sulcus, five labial foramina are present. The coronoid process is small and short. The posteriormost portion of the dentary has an almost perpendicular margin and represents a surangular process (Figs 26C, D; 28A).

The most distinctive feature of the dentary is a huge alveolar canal (Figs 25-28). The intramandibular septum runs in dorsolateral-ventromedial direction and, in the place of the alveolar foramen, it is distinctly embayed anteriorly. The ventral margin of the intramandibular septum is divided from the wall of the dentary by a distinct groove (Figs 25-28). The posteroventral margin of the intramandibular septum extends to a distinct posterior spine (Figs 25-28). The dental crest extends medioventrally. The Meckel's groove opens medioventrally.

There are 22 tooth positions, while at least 10 teeth are rather well preserved (Figs 25-27). The teeth are dorsoventrally straight and they increase in size mesiodistally (Figs 25-28). The most robust are the 3rd and 4th teeth from posterior. The lingual walls of the teeth are medially bulged. The apices become mesiodistally gradually more robust and bear distinct mesiodistally straight cutting edges (Figs 25-28). The lingual and labial surfaces of the apices are distinctly striated.

REMARKS

The almost complete dentary NHMW 2019/0049/0001 bears strong resemblance with the neotype dentary of *Para-*

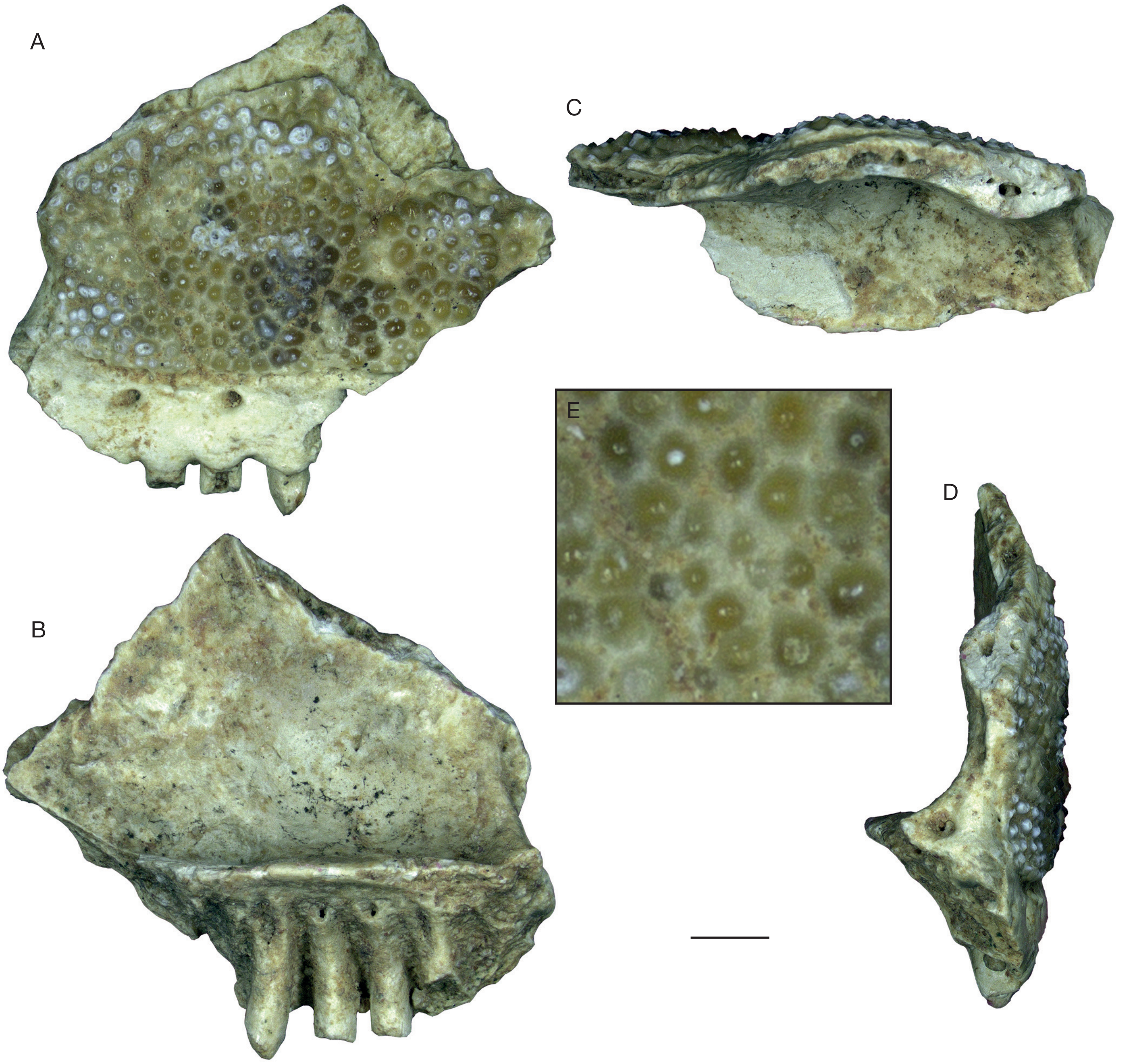

Fig. 23. — *Paraplacosauriops quercyi* (Filhol, 1882). **A**-**D**, photographs of left maxilla NHMW 2019/0049/0003 in lateral (**A**), medial (**B**), dorsal (**C**), and anterior (**D**) views; **E**, close up photograph of the sculpturing pattern of the same specimen. Scale bar: A-D, 2 mm.

placosauriops quercyi (MNHN.F.QU16569). Most characteristically, both specimens share the strongly heterodont dentition, with the anterior teeth being much slender and the posterior ones robust, a developed intramandibular septum, with its ventral margin fused to the floor of the Meckel's groove (Augé & Sullivan 2006). The fragmentary dentary NHMW 2019/0049/0002, although much incomplete, seems to possess also this dental morphology. The general morphology of the preserved portion of the maxilla and the type of ornamentation correspond to those described by Augé & Sullivan (2006).

The specimen NHMW 2019/0049/0001 represents the most complete dentary assigned to *Paraplacosauriops quercyi* and thus, enhances our understanding of this element in this melanosaurine taxon. We agree with recent authors that the species *Diploglossus cadurcensis* De Stefano, 1903, and *Placosaurus leenhardti* Leenhardt, 1926 (both from the old collections of the Phosphorites du Quercy) are junior synonyms of *Paraplacosauriops quercyi* (e.g., Augé 2005), although we have to highlight that the completeness of the holotype of *Placosaurus leenhardti* is remarkable and this taxon is certainly worth of a comprehensive redescription.

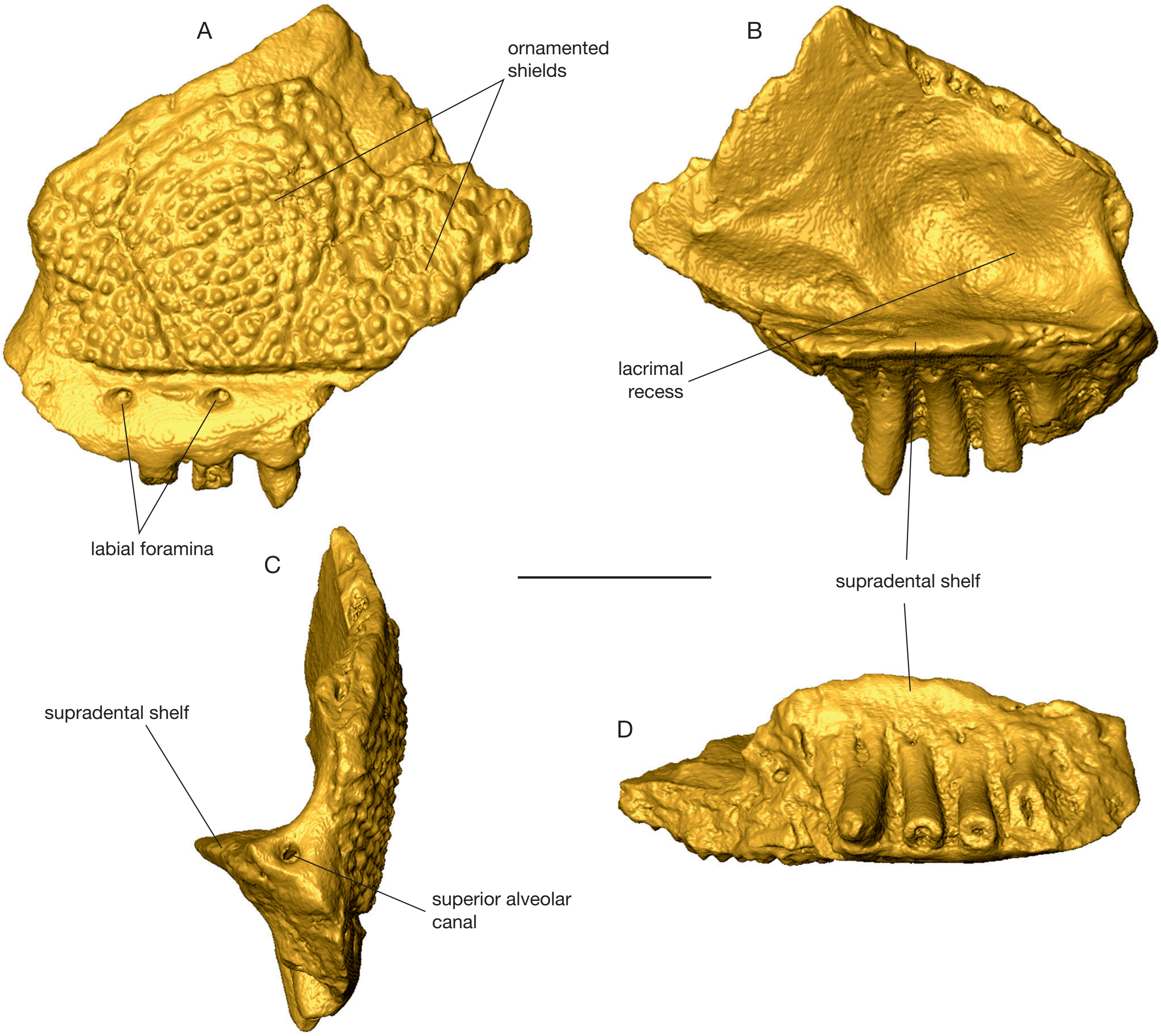

FIG. 24. — *Paraplacosauriops quercyi* (Filhol, 1882). Virtual 3D models of left maxilla NHMW 2019/0049/0003 in lateral (**A**), medial (**B**), anterior (**C**), and ventral (**D**) views. Scale bar: 5 mm.

Melanosaurini indet.
(Figs 30-32)

REFERRED SPECIMENS. — Four presacral vertebrae (NHMW 2019/0094/0001- NHMW 2019/0094/0003 and NHMW 2019/0094/0005); one sacral vertebra (NHMW 2019/0094/0004).

DESCRIPTION

Presacral vertebrae (Figs 30; 31)

In all specimens, the centrum is significantly anteriorly widened (Figs 30; 31). Their size varies, with centrum lengths ranging between 6 and 9.4 mm (Appendix 1). There is a distinct and rather wide groove in the ventral surface of the centrum, originating anteriorly almost at the level of the cotyle and terminating posteriorly at around the level of the condyle, being almost uniform in wideness across its length. The prezygapophyses are strongly dorsally inclined in anterior view. Both cotyle and condyle are strongly dorsoventrally compressed. The neural spine, when preserved, develops mostly at the posterior half of the neural arch, however, its base extends anteriorly in the shape of a narrow longitudinal ridge until the anterior most edge of the neural arch. The height of the neural spine varies, being either high (NHMW 2019/0094/0002) or rather short (NHMW 2019/0094/0001). In one specimen (NHMW 2019/0094/0001), the posterior edge of the neural spine (as seen in dorsal view) is bifurcated. The postzygapophyses are large and extend much laterally in dorsal view. The neural canal is relatively large and triangular in shape. The shape of the neural arch in posterior view varies, apparently depending on the exact position of the vertebra in the column; as such it can be either depressed (e.g., NHMW 2019/0094/0005 and NHMW 2019/0094/0003) or relatively vaulted (e.g., NHMW 2019/0094/0002).

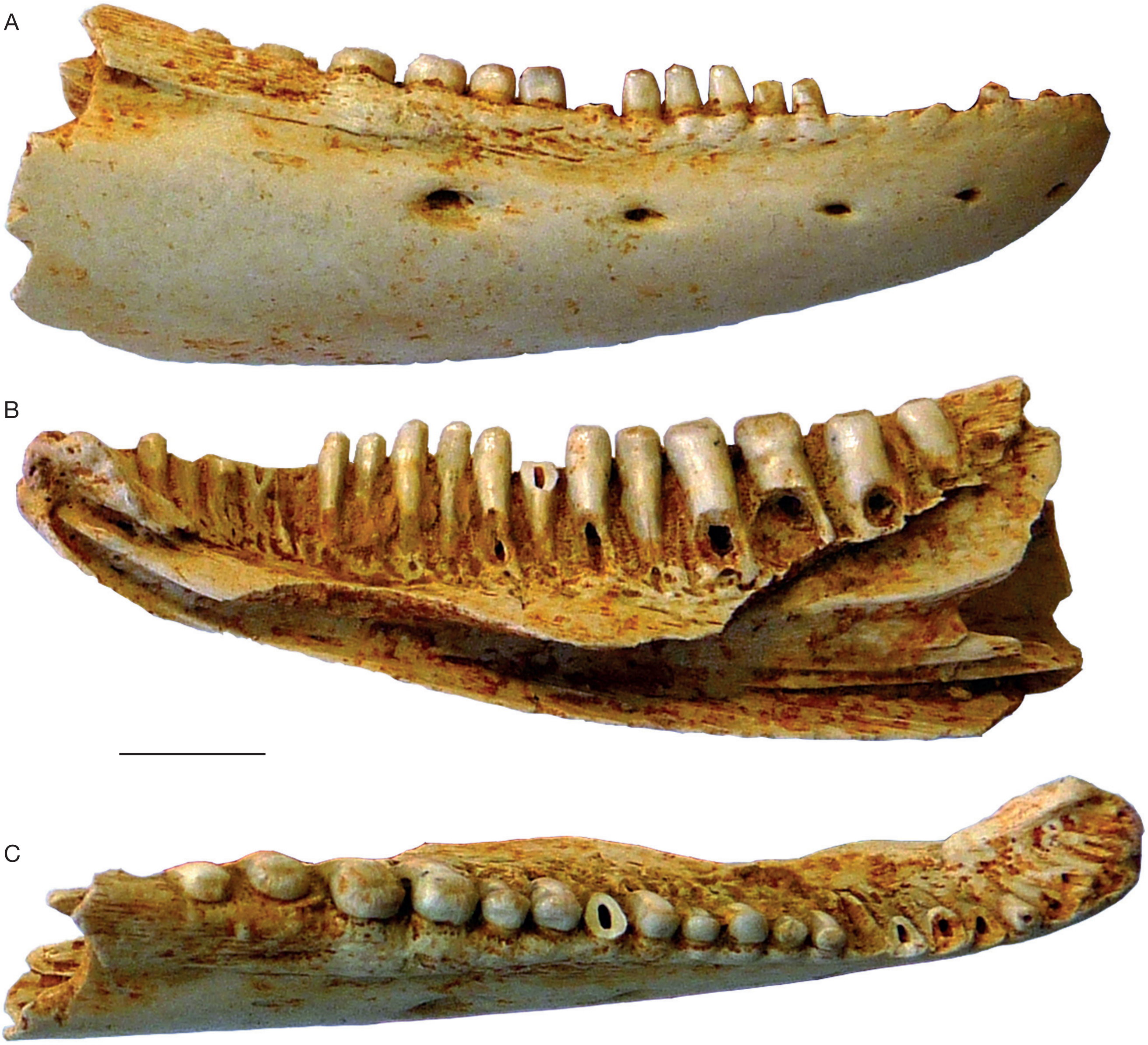

FIG. 25. — *Paraplacosauriops quercyi* (Filhol, 1882). Photographs of right dentary NHMW 2019/0049/0001 in lateral (**A**), medial (**B**), and dorsal (**C**) views. Scale bar: 5 mm.

Sacral vertebra NHMW 2019/0094/0004 (Fig. 32)

The sacral vertebra NHMW 2019/0094/0004 is rather similar to the above described presacral ones, especially at the degree of the anterior widening of its centrum, the dorsally inclined prezygapophyses, and the much dorsoventrally compressed cotyle and condyle (Fig. 32). The prezygapophyses are robust. The postzygapophyses are short and do not extend significantly laterally. The neural spine is high, and is mostly developed and augmenting in height in the posterior half of the neural arch. The neural arch is moderately vaulted in posterior view. Subcentral foramina are present. Two distinct foramina, each situated between each prezygapophysis, are present above the cotyle, a structure herein defined as "ano-cotylar" foramina (see Remarks below). Interestingly also, this specimen is pierced by distinct foramina in the dorsal surface of its neural arch.

REMARKS

The referral of this vertebral material to Melanosaurini is made primarily on the basis of the much anteriorly widened centrum than in 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 (see figures in Gilmore 1928 and Augé 2003, 2005). One other important difference between NHMW 2019/0094/0001 (but not the other melanosaurine vertebrae from our collection) and the above ones referred to *Placosaurus* is that the former possess much more massive postzygapophyses that extend more prominently laterally in dorsal view.

A plausible taxonomic scenario could be that these specimens pertain to *Paraplacosauriops quercyi* described above from cranial material, however, on the absence of articulated specimens and the imprecisely known locality

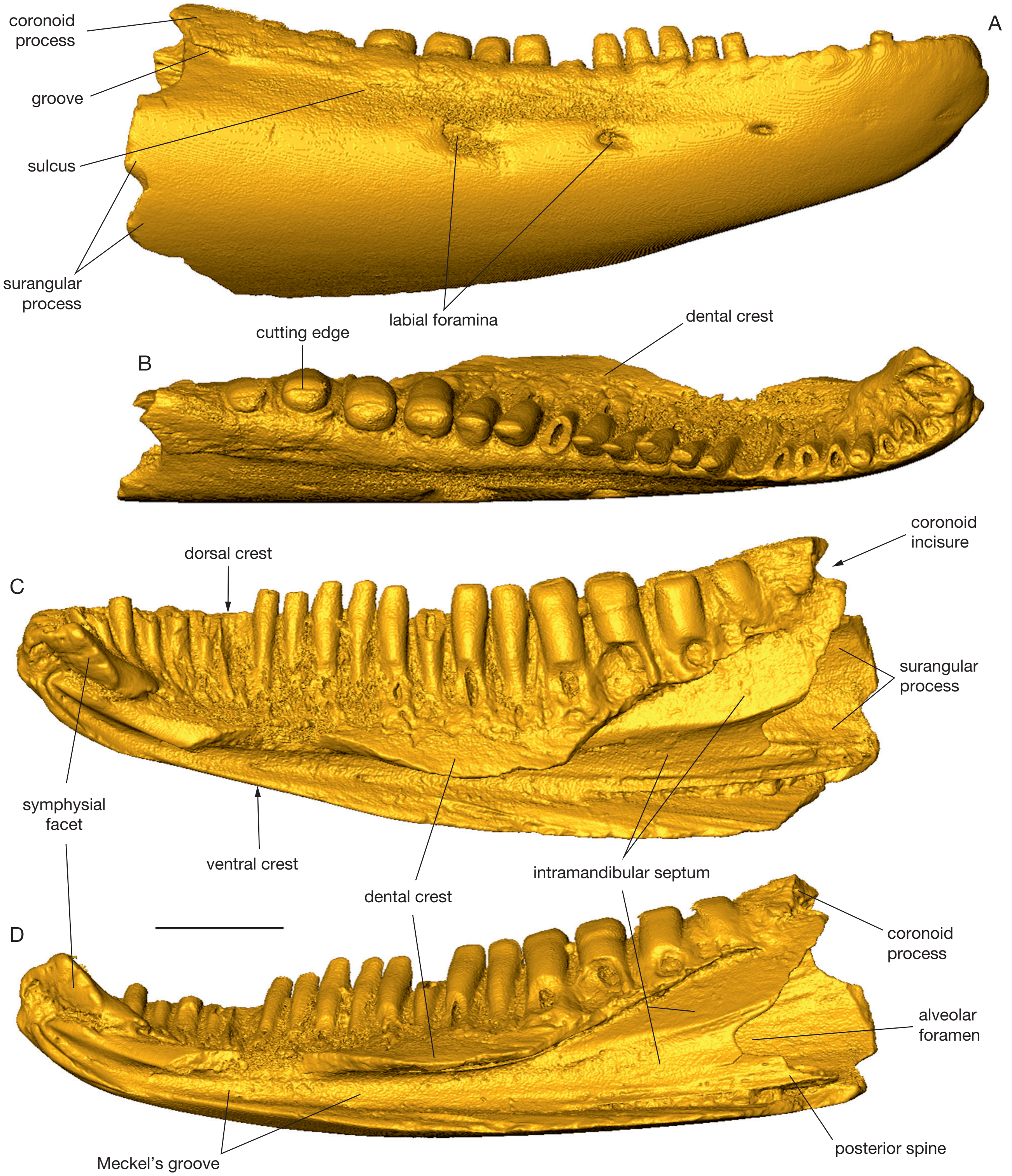

FIG. 26. — *Paraplacosauriops quercyi* (Filhol, 1882). Virtual 3D models of right dentary NHMW 2019/0049/0001 in lateral (**A**), dorsal (**B**), medial (**C**), and ventromedial (**D**) views. Scale bar: 5 mm.

data (including the fact that the material was probably collected from different localities), we refrain from referring them to the same taxon.

The presence of two distinct foramina above the cotyle of the sacral vertebra, a feature also prominent in several presacral vertebrae of *Palaeovaranus* (see below), is interesting. We acknowledge the presence of these structures in large-sized vertebrae of extant specimens of the anguid *Pseudopus* Merrem, 1820, and the varanid *Varanus* Merrem, 1820. We consider that their presence is widespread

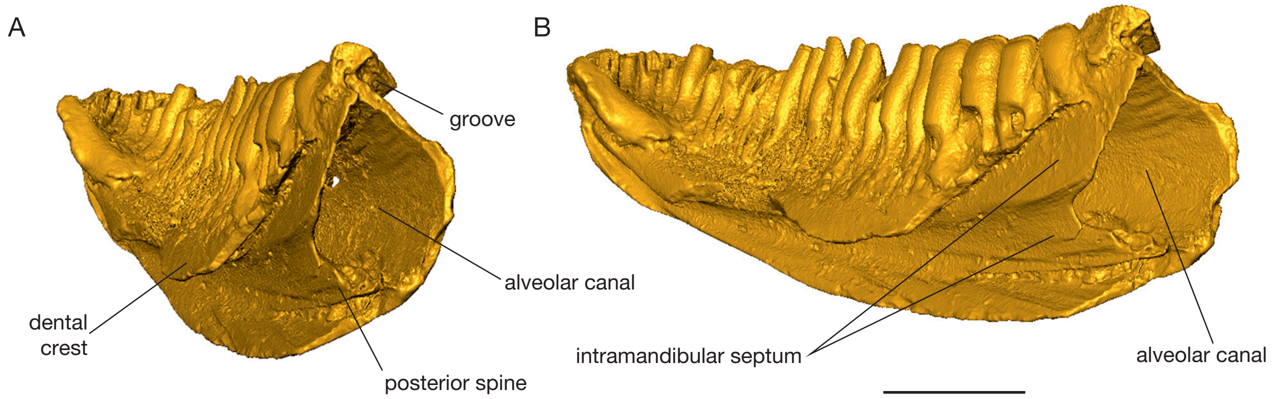

Fig. 27. — *Paraplacosauriops quercyi* (Filhol, 1882). Virtual 3D models of right dentary NHMW 2019/0049/0001 in posterior and slightly medial (**A**) and postero-medial (**B**) views. Scale bar: 5 mm.

in large-sized anguimorphs and is apparently correlated with large size; we define these structures as "anocotylar foramina", from the Greek words "ἄνω" ("ano"), meaning "above" and "κότυλος" ("cotylos"), meaning "cup", in a similar trend of the term "paracotylar foramina", which applies in snake vertebrae terminology. The potential taxonomic utility of anocotylar foramina needs to be further investigated in the light of detailed quantitative analyses on extant forms, as well as articulated fossil specimens.

Subfamily ANGUINAE Gray, 1825

Anguinae indet.
(Fig. 33)

REFERRED SPECIMENS. — Two presacral vertebrae (NHMW 2019/0093/0001 and NHMW 2019/0093/0002).

DESCRIPTION

The presacral vertebrae NHMW 2019/0093/0001 and NHMW 2019/0093/0002 are almost totally complete (Fig. 33). They are relatively large, both having a centrum length of 8.4 mm. In anterior view (Fig. 33A, G), the prezygapophyses are dorsolaterally inclined. The neural canal is triangular in shape. The cotyle is exceedingly depressed. In posterior view (Fig. 33B, H), the neural arch is moderately vaulted. The condyle is rather depressed, with its ventral level being flattened. In dorsal view (Fig. 33D, G), the neural spine extends across the whole midline of the neural arch. The neural spine is relatively thickened in its posterior portion, while it is much thinner throughout its middle and anterior portions, where it takes the shape of a sharp, longitudinal ridge. The prezygapophyseal articular facets are enlarged. In ventral view (Fig. 33E, K), the centrum is widened anteriorly; its surface is flattened, with only a slight median ridge running throughout its midline. The subcentral ridges are straight; they are not parallel. Two prominent subcentral foramina pierce the centrum of NHMW 2019/0093/0001, while in the other specimen (NHMW 2019/0093/0002) these are smaller. In lateral view (Fig. 33C, F, I), the neural spine is rather short. It augments in height gradually towards the posterior portion of the neural arch, reaching its maximum height at its posteriormost portion. Its dorsal surface is straight, with its posterodorsal edge being slightly inclined posteriorly. The synapophyses are large and elongated.

REMARKS

These two vertebrae are strongly resembling to the ones of the genus *Pseudopus* on the basis of their wide centrum, being wider anteriorly, straight subcentral ridges in ventral view, and their neural spine slightly inclined posteriorly (Klembara 1979, 1981; Klembara & Rummel 2018; Čerňanský *et al.* 2019). Such resemblance is also supported by a biogeographic and stratigraphic rationale, as material assigned (or tentatively assigned) to *Pseudopus* is known in the Oligocene of Western Europe (Boettger 1875). However, it is known that at least other three non-glyptosaurine anguid genera were present in the Paleogene of Western and Central Europe, i.e., *Helvetisaurus* Augé, 2005, *Ophisauromimus* Čerňanský, Klembara & Müller, 2016, and *Ophisauriscus* Kuhn, 1940 (Augé 2005; Čerňanský *et al.* 2016a). Considering that the vertebral morphology of *Ophisauromimus* is currently unknown, we refrain from further assigning these two NHMW vertebrae to *Pseudopus*, although their overall large size, may suggest that such taxonomic referral may be most plausible.

Family PALAEOVARANIDAE Georgalis, 2017

Genus *Palaeovaranus* Zittel, 1887-1890

TYPE SPECIES. — *Palaeovaranus cayluxi* Zittel, 1887-1890 (type species by subsequent designation; Georgalis 2017).

EMENDED GENERIC DIAGNOSIS. — 1) Presence of a distinctly developed nasal crest on the dorsomedial surface of the nasal process of maxilla; and 2) the dorsolateral crests on the dorsal surface of the parietal meeting in the median plane to form a median crest in adult specimens.

FIG. 28. — *Paraplacosauriops quercyi* (Filhol, 1882). **A**, close up photograph of the posterior portion of right dentary NHMW 2019/0049/0001 in medial view; **B**, close up photograph of the posterior teeth in medial view; **C**, close up photograph of a posterior tooth in dorsal view. Scale bars: A, 5 mm; B, 2 mm; C, 0.5 mm.

Palaeovaranus cayluxi Zittel, 1887-1890
(Figs 34-36; 37A, C; 41A)

EMENDED DIFFERENTIAL DIAGNOSIS. — The parietal of *Palaeovaranus cayluxi* differs from that of the sole other recognized species of the genus, *Palaeovaranus lismonimenos* n. sp., described below, in the following distinguished characters and the combination of features: 1) presence of a long median crest (longer than the length of the median triangular field measured in the median plane); 2) dorsolateral crests are low and without crenulations; 3) anterior end of the dorsolateral crests disappears on the dorsal surface of the root of the anterolateral process; 4) the ornamentation is weakly developed consisting of only several low ridges of various lengths running medially to the medial margins of the dorsolateral crests, as well as small mounds; and 5) the anterior margin of the parietal fossa lies at or posterior to the level of the junctions of the anterolateral margins of the supratemporal processes with the parietal plate.

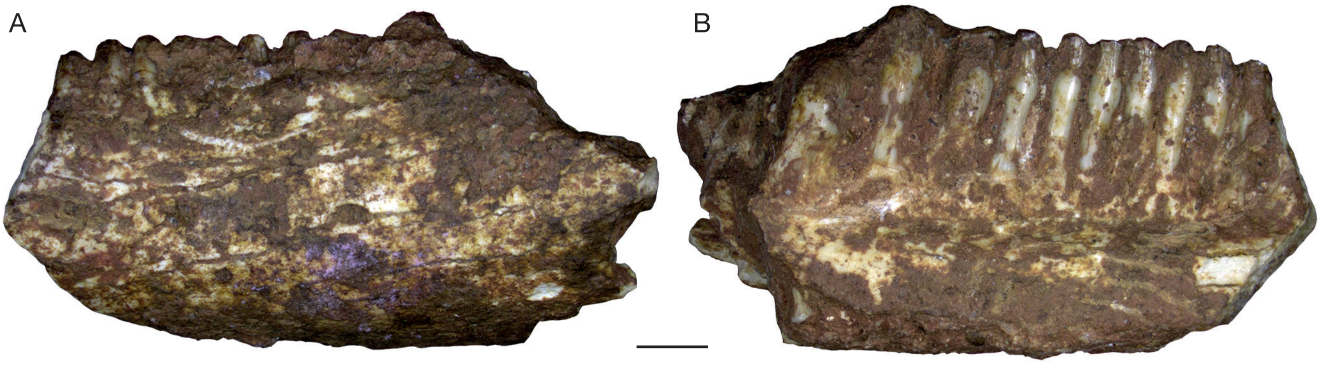

Fig. 29. — *Paraplacosauriops quercyi* (Filhol, 1882). Photographs of left dentary NHMW 2019/0049/0002 in lateral (**A**) and medial (**B**) views. Scale bar: 2 mm.

Referred specimens. — Two almost complete parietals (NHMW 2019/0048/0001 and MNHN.F.QU17176).

Description

The parietal plate is rectangular; only the basis of the supratemporal processes is preserved in both parietals (Figs 34-36). The anterolateral process is slender. The parietal foramen lies in about the mid-length of the anterior half of the parietal plate. The most distinctive feature of the dorsal surface of the parietal are two dorsolateral crests. The crests run in anterolateral-posteromedial direction. The anterior end of each crest gradually diminishes and terminates on the dorsal surface of the anterolateral process. The posterior ends of the dorsolateral crests meet in the median plane. The crests, together with the anterior margin of the parietal, limit a triangular field containing the parietal foramen. The surface bears several low mounds and more or less long ridges running along the medial margins of the dorsolateral crests. From the junction of the dorsolateral crests, a median crest extends posteriorly. The length of the crest increases with the size of the parietal and it seems that this increase in length comes to the negative expense of the midline length of the anterior triangular surface, which gradually throughout ontogeny becomes proportionally shorter. This can be demonstrated by comparing the largest known parietal of this species (the one figured by Rage 1978) relative to the two ones described in our paper. From the posterior end of the median crest, a median triangular field is located. The triangular field is a space between the posteriormost portions of the dorsolateral crests. The triangular field achieves its largest width posteriorly; its posterior end is the posteromedian margin of the parietal table (Figs 34-36). The supratemporal fossa is mediolaterally broad indicating a strongly developed adductor musculature.

The ventral surface of the parietal is smooth (Figs 34B; 36B; 37C). The anterior margin of the parietal fossa lies at the level (or posterior to the level in large specimens) of the junctions of the anterolateral margins of the supratemporal processes with the parietal table. The ventral cranial crest is low and runs immediately medially to the lateral margin of the parietal. Its posterior end is turned posteromedially. The length of the juxtaotic and postfoveal crests is about the same. The posterior portion of the postfoveal crest runs immediately laterally to the medial margin of the basal portion of the supratemporal process.

Remarks

Although we acknowledge that the holotype of *Palaeovaranus cayluxi* is a maxilla (see Georgalis 2017 for details), we assign these parietals to the same species on the basis of the referral of a parietal by Rage (1978) to the same species (see Discussion below for details). The so far three known parietals of this species (the two ones documented herein plus the one described by Rage [1978]) enhance our understanding of the parietal morphology and variation in this species and allow a confident distinguishment from its new congeneric species described below.

Palaeovaranus lismonimenos n. sp.

(Figs 37B, D; 38-40; 41B; 42; 43)

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Holotype. — An almost complete parietal (NHMW 2019/0047/0001).

Etymology. — The new name originates from the Greek word “λησμονημένος” (“lismonimenos”) meaning “forgotten”, alluding to the fact that the holotype specimen was forgotten and unnoticed inside a museum drawer for more than a century.

Type locality. — Imprecisely known locality, Phosphorites du Quercy, Department of Lot or Tarn-et-Garonne, Occitanie, southern France; probably late Eocene, around MP 17 (see Distribution below).

Diagnosis. — The parietal of *Palaeovaranus lismonimenos* n. sp. differs from that of *Palaeovaranus cayluxi* by the following distinguished features and the combination of features: 1) the dorsolateral crests are rather distinct, extending posterolaterally and dorsally, and their margins are distinctly crenulated; 2) the median crest is short (shorter than the length of the median triangular field measured in the median plane) and its posterior tip fits between the anterolateral processes of the triangular median field; 3) the anterior ends of the dorsolateral crests extend to the tips of the anterolateral processes; 4) the ornamentation of the parietal consists of small, more or less densely arranged mounds having more or less distinctly developed crest; and 5) the anterior margin of the parietal fossa lies anterior to the level of the junctions of the anterolateral margins of the supratemporal processes with the parietal plate.

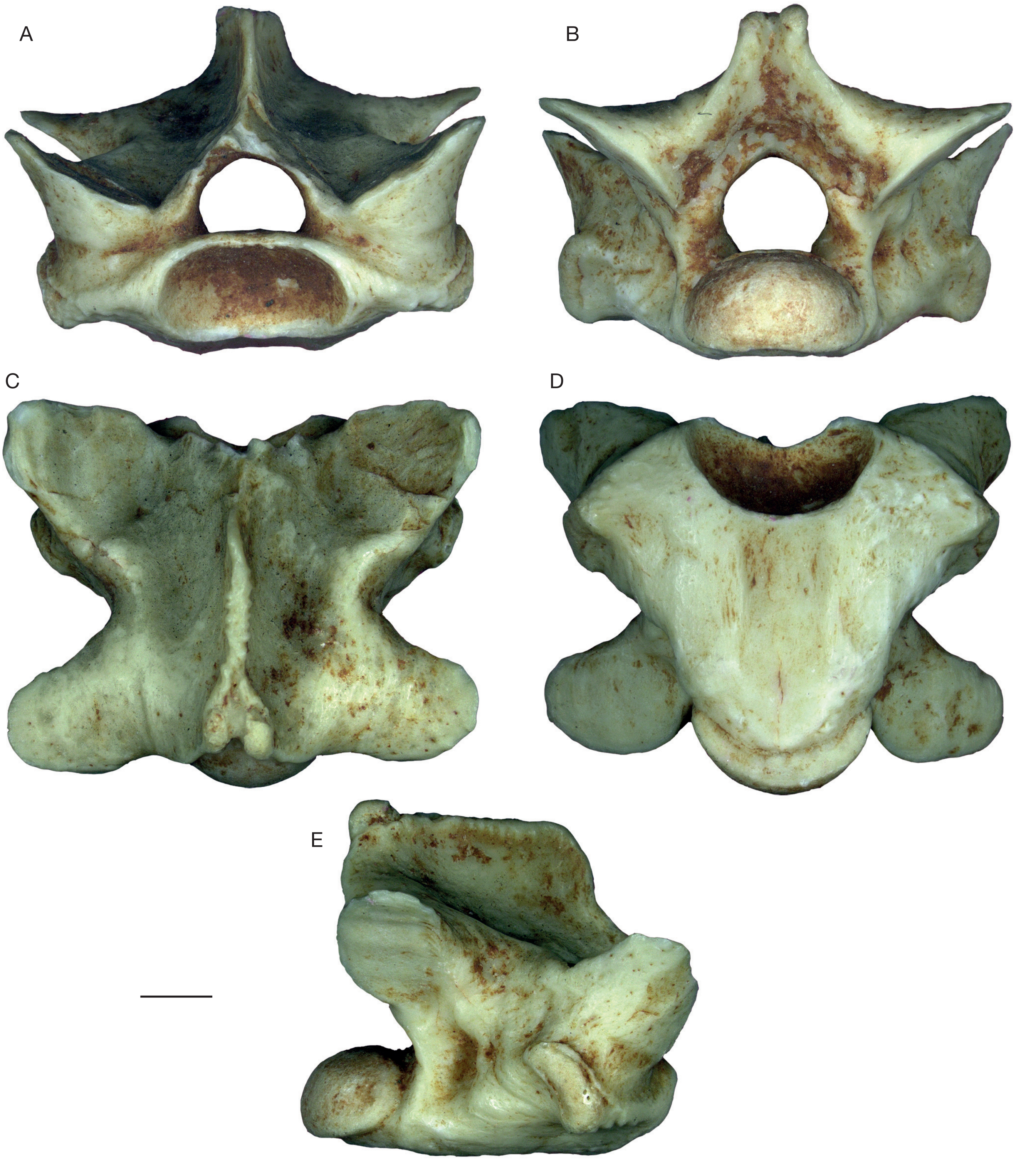

FIG. 30. — Melanosaurini indet. Photographs of presacral vertebra NHMW 2019/0094/0001 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and right lateral (**E**) views. Scale bar: 2 mm.

REFERRED SPECIMENS. — A complete parietal (MNHN.F.QU17177) and a partial parietal (UM BFI 1873), both from juvenile individuals. Tentatively also, two frontals (MNHN.F.QU17175 and UM PRA 8).

DISTRIBUTION. — The holotype parietal NHMW 2019/0047/0001, the referred parietal MNHN.F.QU17177, and the tentatively referred frontal MNHN.F.QU17175, all originate from imprecisely known localities in the Department of Lot or that of Tarn-et-Garonne, within the Phosphorites du Quercy. The referred parietal UM BFI 1873 originates from the late Eocene (MP 17) of Bouffie (= La Bouffie), Quercy (Department of Lot), while the tentatively referred frontal UM PRA 8 originates from the coeval, late Eocene (MP 17) locality of Les Pradigues, also in Quercy (but in the Department of Tarn-et-Garonne). Accordingly, we here sug-

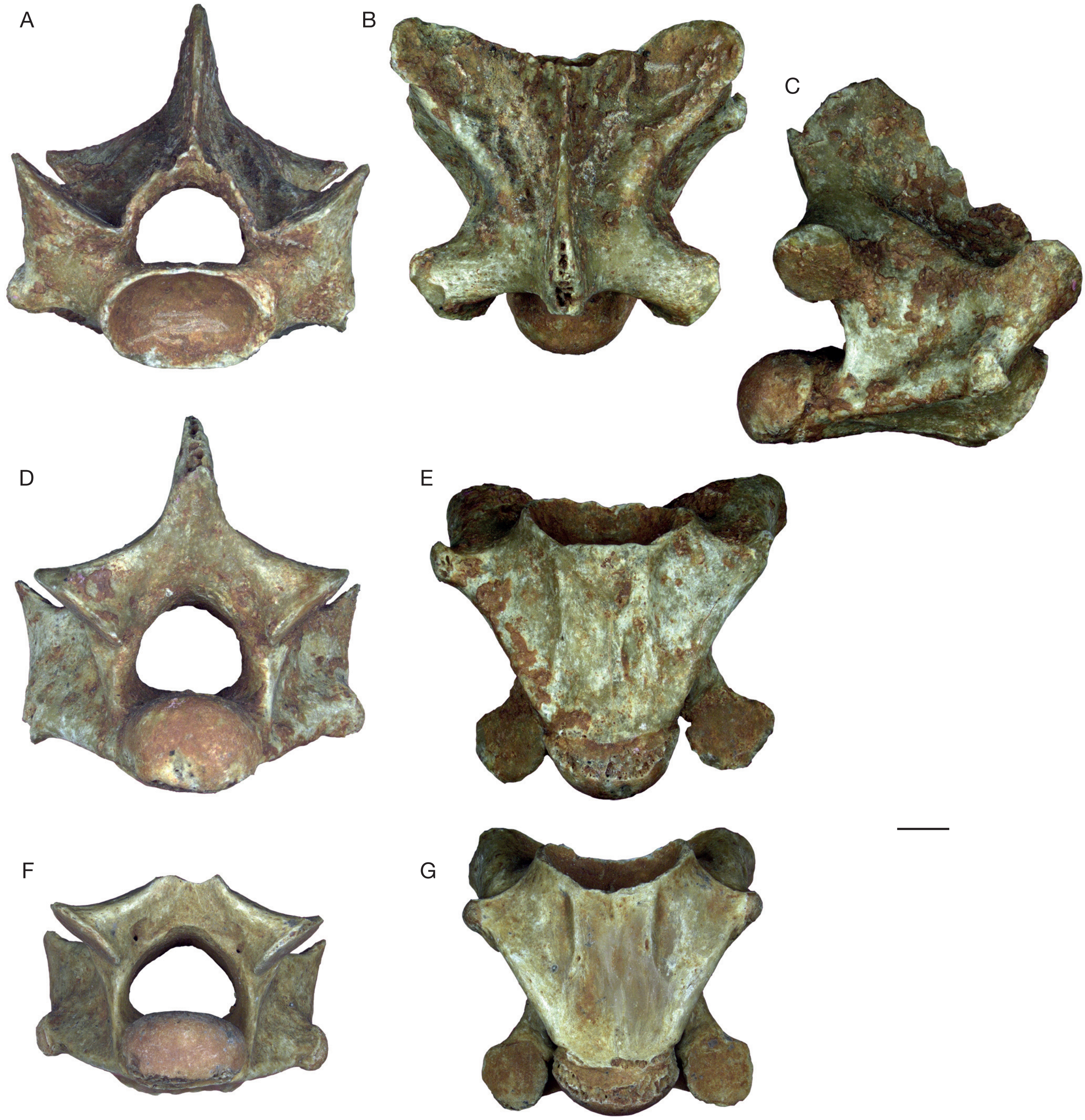

FIG. 31. — Melanosaurini indet. **A**-**E**, photographs of presacral vertebra NHMW 2019/0094/0002 in anterior (**A**), dorsal (**B**), right lateral (**C**), posterior (**D**), and ventral (**E**) views; **F**, **G**, photographs of presacral vertebra NHMW 2019/0094/0003 in posterior (**F**) and ventral (**G**) views. Scale bar: 2 mm.

gest that the specimens with imprecise locality date (including the holotype), originate also from late Eocene locality(ies), potentially also around the MP 17 stage.

DESCRIPTION

Holotype NHMW 2019/0047/0001 (Figs 37B, D; 38-40; 41B)

The holotype NHMW 2019/0047/0001 has a length of its parietal table 14.5 mm (measured in mid-line). The parietal table is anteroposteriorly elongate (Figs 37B; 38B; 39A). The anterolateral process is slender. The dorsolateral crest is distinctly developed. It extends posterolaterally and dorsally. Its margin is distinctly crenulated. The crenulation consists of several more or less shallow and long notches. The anterior end of the dorsolateral crest reaches the tip of the anterolateral process. The dorsolateral crests and the anterior margin of the parietal limit a triangular field. Its deepest portion is pierced by the parietal foramen. The foramen lies in about the mid-length of the anterior half of the parietal table. The surface of the triangular field is covered by small, but distinct mounds, most of them bearing the longitudinal crests on their surfaces.

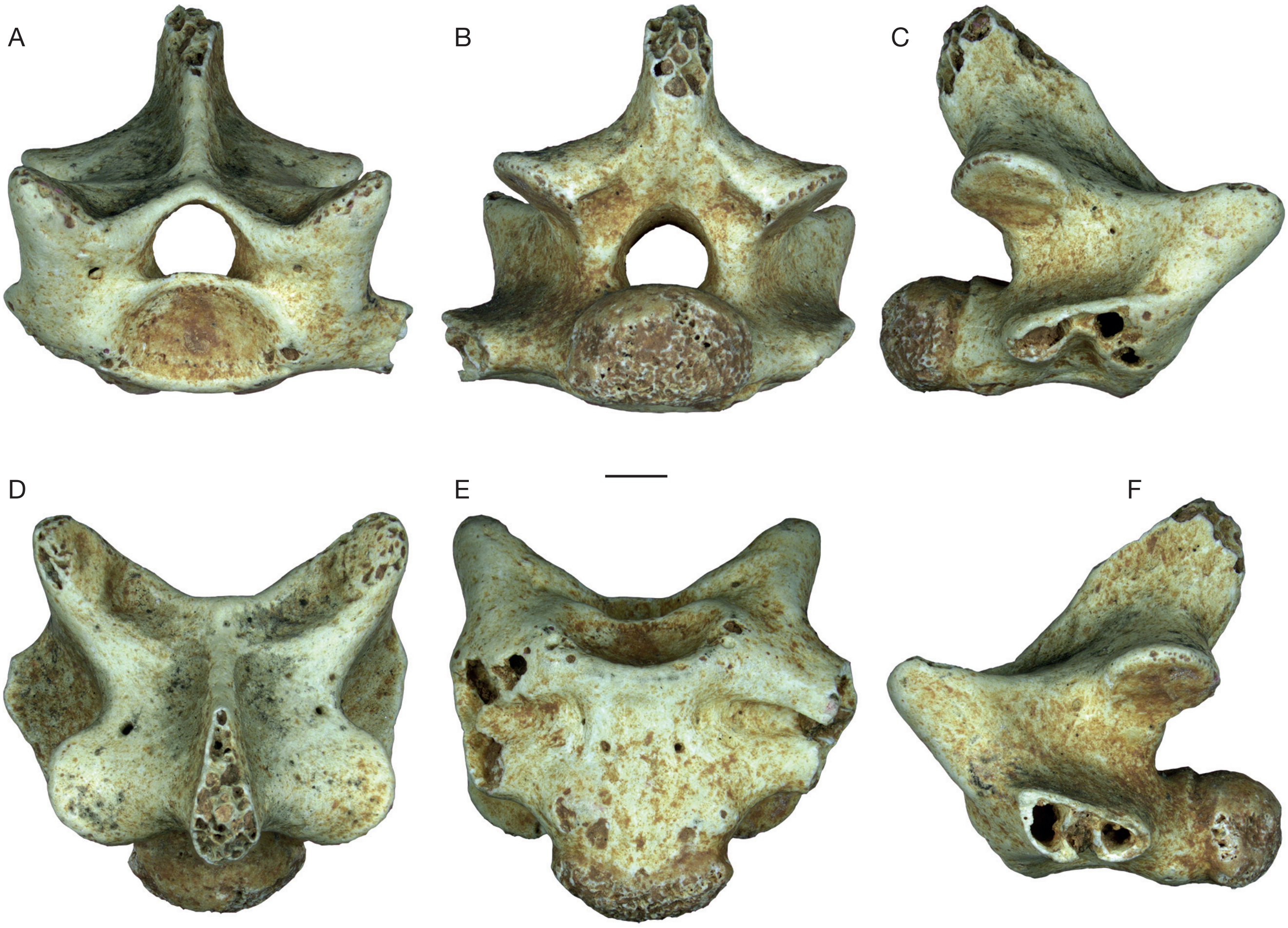

Fig. 32. — Melanosaurini indet. Photographs of sacral vertebra NHMW 2019/0094/0004 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), ventral (**E**), and left lateral (**F**) views. Scale bar: 2 mm.

The median crest is short and its posterior pointed portion fits between the two anteriorly pointed anterolateral processes of the triangular median field (Fig. 39A). The supratemporal fossa is large and is inclined ventrolaterally.

The ventral surface is smooth (Figs 37D; 38A; 39B). The anterior margin of the parietal fossa lies anterior to the level of the junctions of the anterolateral margins of the supratemporal processes with the parietal plate. The ventral cranial crest is rather low and runs closely medially to the lateral margin of the parietal table. The postfoveal crest passes along the medial margin of the root portion of the supratemporal process (Fig. 38A).

Remarks

The two smaller specimens MNHN.F.QU17177 and UM BFI 1873 (Fig. 42), which we herein assign to *Palaeovaranus lismonimenos* n. sp. were originally described by Augé (2005) who also provided drawings of both (his Figs 194 and 195 respectively) and referred them to as "*Necrosaurus eucarinatus*" (see Discussion below about the status of this name). MNHN.F.QU17177 has a length of the parietal table 11.5 mm (measured in the mid-line) (Fig. 42A, B); thus, it is smaller than the holotype parietal NHMW 2019/0047/0001 (14.5 mm). The right supratemporal process is completely preserved in MNHN.F.QU17177; it extends posterolaterally (Fig. 42A, B). The dorsolateral crests of the specimen MNHN.F.QU17177 bear slightly developed crenulations and do not meet in the mid-line, as is also the case in the still smaller specimen UM BFI 1873 (Fig. 42C, D). In this smallest specimen UM BFI 1873, the ornamentation is weakly developed and the dorsolateral crests are still more distantly placed one to another than in MNHN.F.QU17177. We may interpret this here by the hypothesis that during ontogenetic growth, the dorsolateral crests move one to another and finally fuse together in about their posterior portions to form a median crest. As a consequence, large anterior and small posterior median triangular fields are produced (Fig. 42). If so, the anatomy of three different size stages presented and discussed herein represent the first evidence of the medial movement of the dorsolateral crests to their final fusion in the median plane in adult specimens. We suppose the same process of the origin of the similar morphology of the dorsal surface of parietal in *Palaeovaranus cayluxi*.

Although there is no palaeovaranid frontal material in the NHMW collection, there have been previously described such elements from the Phosphorites du Quercy (Fig. 43).

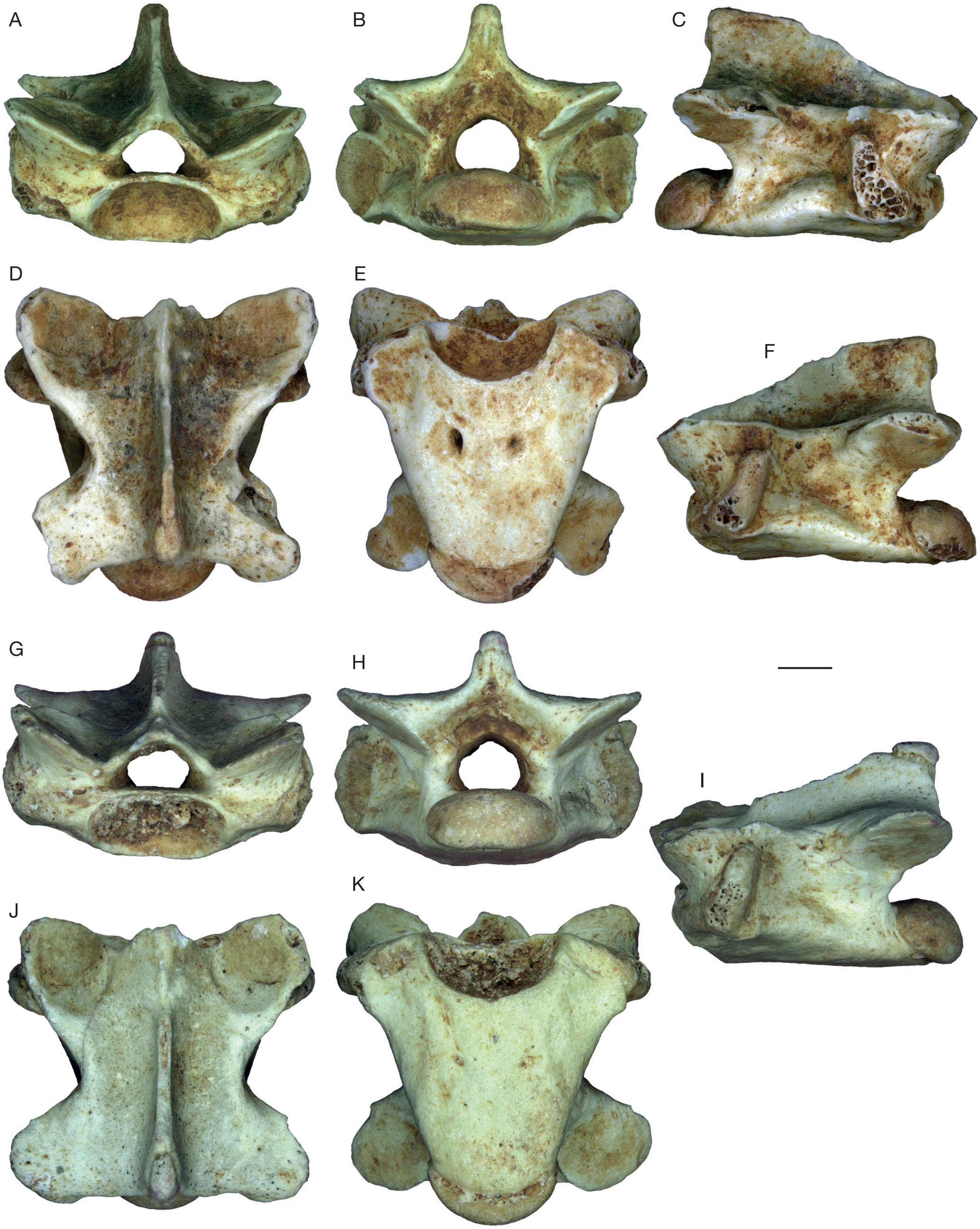

FIG. 33. — Anguinae indet. **A**-**F**, photographs of presacral vertebra NHMW 2019/0093/0001 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), ventral (**E**), and left lateral (**F**) views; **G**-**K**, photographs of presacral vertebra NHMW 2019/0093/0002 in anterior (**G**), posterior (**H**), left lateral (**I**), dorsal (**J**), and ventral (**K**) views. Scale bar: 2 mm.

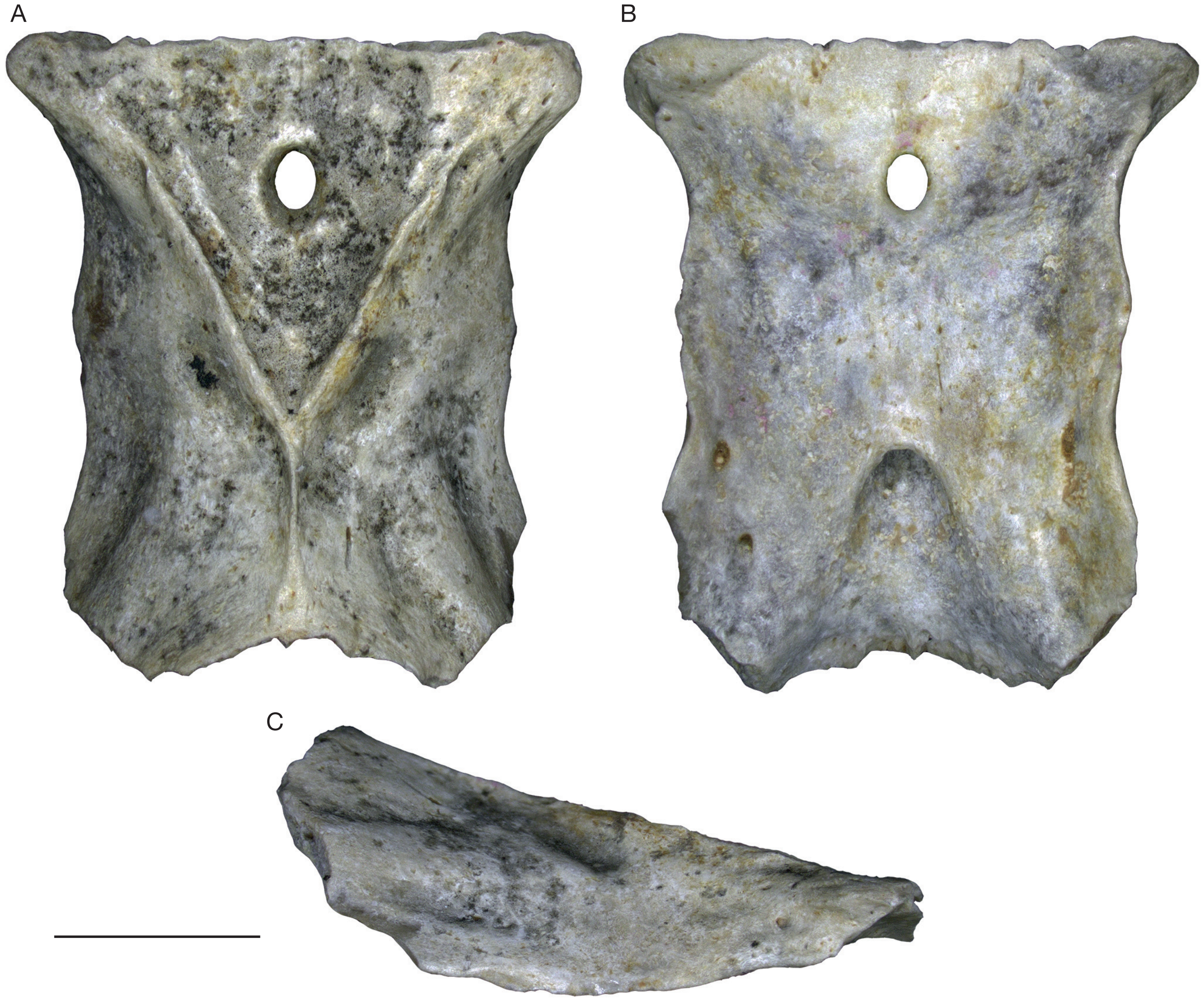

Fig. 34. — *Palaeovaranus cayluxi* Zittel, 1887-1890. Photographs of parietal NHMW 2019/0048/0001 in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. Scale bar: 5 mm.

Augé (2005) described the frontal MNHN.F.QU17175 as belonging to "*Necrosaurus cayluxi*" and that of the specimen UM PRA 8 as "*Necrosaurus eucarinatus*". In contrast to *Palaeovaranus cayluxi*, however, both these frontals have the same type of mounds as those present in the dorsal surface of the parietals of *Palaeovaranus lismonimenos* n. sp. (Fig. 43). To the contrary, the dorsal surfaces of all three known parietals of *Palaeovaranus cayluxi* have no such type of ornamentation, as that exhibited in *Palaeovaranus lismonimenos* n. sp. Thus, it is highly probable that these two frontals belong to *Palaeovaranus lismonimenos* n. sp. and we accordingly, tentatively assign them to our new species.

Palaeovaranus sp.
(Figs 44-58)

Referred specimens. — A left maxilla (NHMW 2019/0048/0002); a left dentary (NHMW 2019/0058/0054); two right dentaries (NHMW 2019/0058/0055 and NHMW 2019/0058/0056); 35 presacral vertebrae (NHMW 2019/0058/0001-NHMW 2019/0058/0009, NHMW 2019/0058/0011-NHMW 2019/0058/0027, NHMW 2019/0058/0030, NHMW 2019/0058/0041-NHMW 2019/0058/0046, NHMW 2019/0058/0051, and NHMW 2019/0067/0001); two articulated sacral vertebrae (NHMW 2019/0058/0028); two sacral vertebrae (NHMW 2019/0058/0029 and NHMW 2019/0058/0047); 16 caudal vertebrae (NHMW 2019/0058/0031-NHMW 2019/0058/0040, NHMW 2019/0058/0048-NHMW 2019/0058/0050, NHMW 2019/0058/0052, NHMW 2019/0058/0053, and NHMW 2019/0067/0002).

Description

Maxilla NHMW 2019/0048/0002 (Figs 44; 45)

The left maxilla NHMW 2019/0048/0002 is not fully preserved; its anterior half is well preserved, however, the anteriormost and the posterior portions are missing (Figs 44; 45). The external surface of the maxilla consists of large and low mounds divided by narrow grooves. Between the dorsal and ventral margins, the wall of the maxilla is distinctly concave. Immediately dorsal to the ventral maxilla

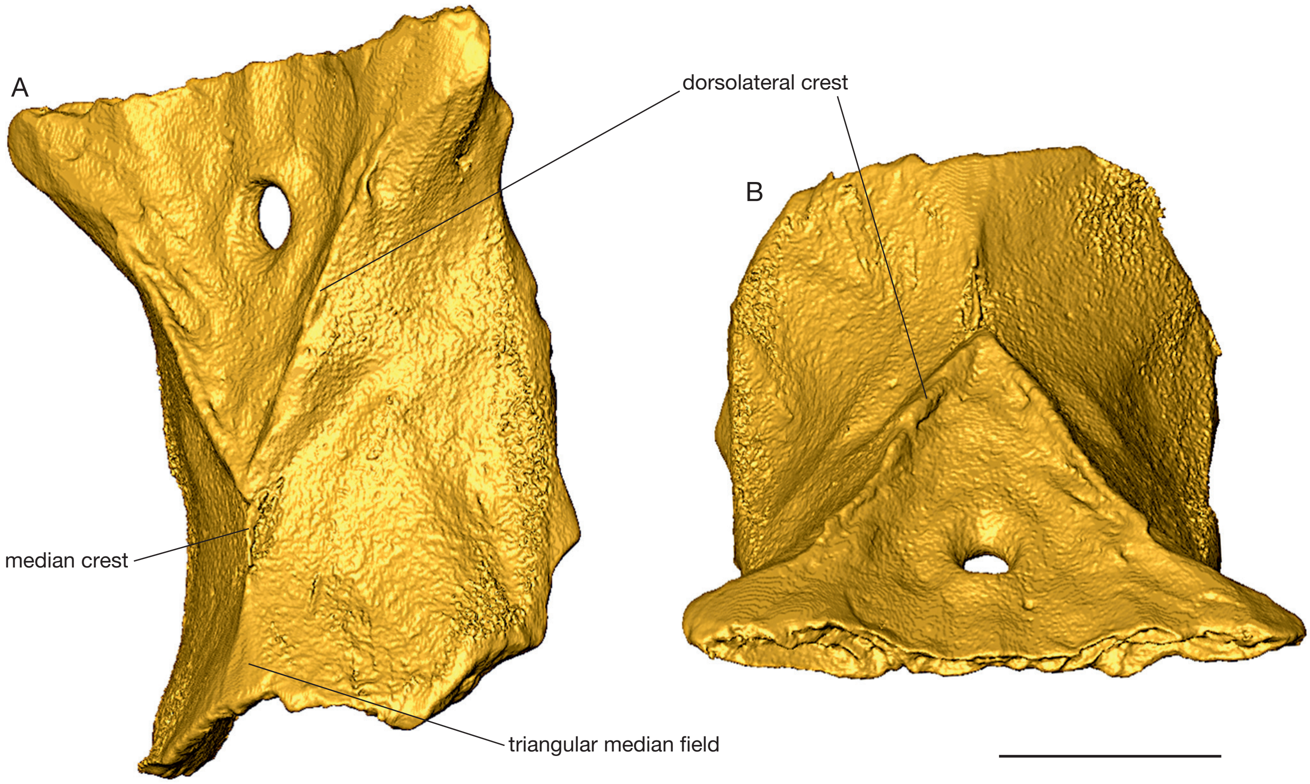

FIG. 35. — *Palaeovaranus cayluxi* Zittel, 1887-1890. Virtual 3D models of parietal NHMW 2019/0048/0001 in dorsolateral (**A**) and anterior (**B**) views. Scale bar: 5 mm.

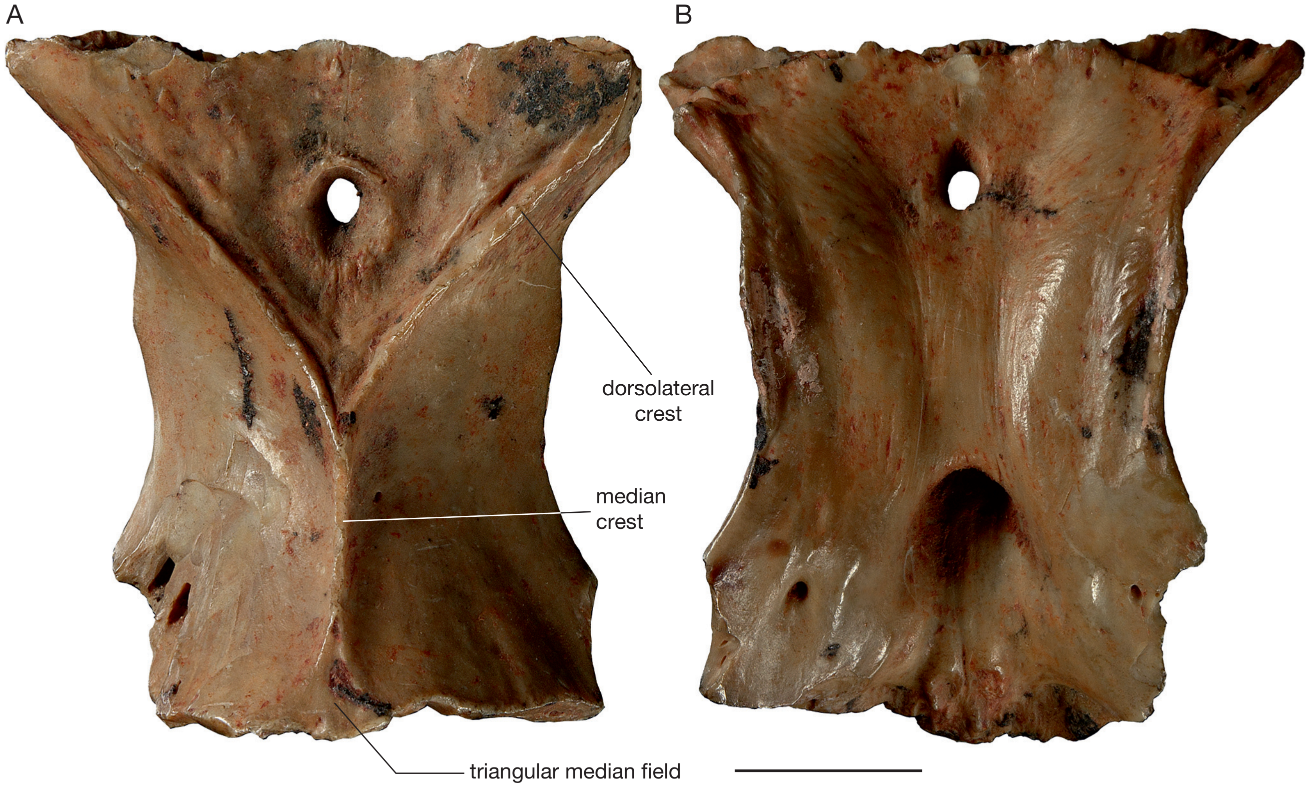

FIG. 36. — *Palaeovaranus cayluxi* Zittel, 1887-1890. Photographs of parietal MNHN.F.QU17176 in dorsal (**A**) and ventral (**B**) views. This specimen originally appeared as drawings in Augé (2005: fig. 188). Scale bar: 5 mm.

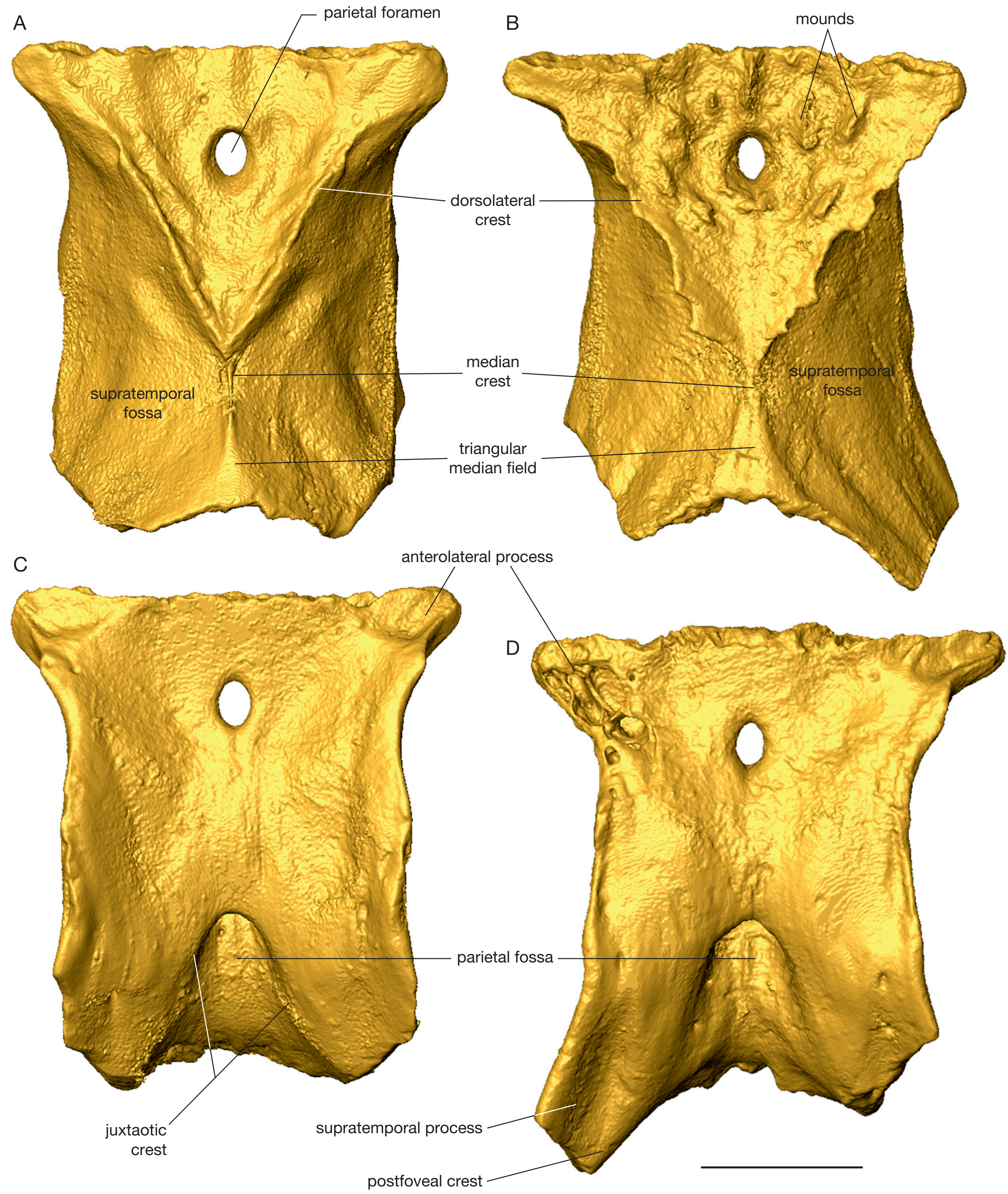

Fig. 37. — *Palaeovaranus cayluxi* Zittel, 1887-1890 and *Palaeovaranus lismonimenos* n. sp. **A**, **C**, virtual 3D models of parietal NHMW 2019/0048/0001 of *Palaeovaranus cayluxi* in dorsal (**A**) and ventral (**C**) views; **B**, **D**, virtual 3D models of the holotype parietal NHMW 2019/0047/0001 of *Palaeovaranus lismonimenos* n. sp. in dorsal (**B**) and ventral (**D**) views. Scale bar: 5 mm.

margin, five labial foramina are preserved. The most distinguished feature of the dorsomedial surface of the nasal process (prefrontal process sensu Fejérváry 1935) of the maxilla is a shelf extending medially and running some distance ventral to the dorsal margin of the nasal process of the maxilla (Fig. 45B, D, F). This shelf is the nasal crest

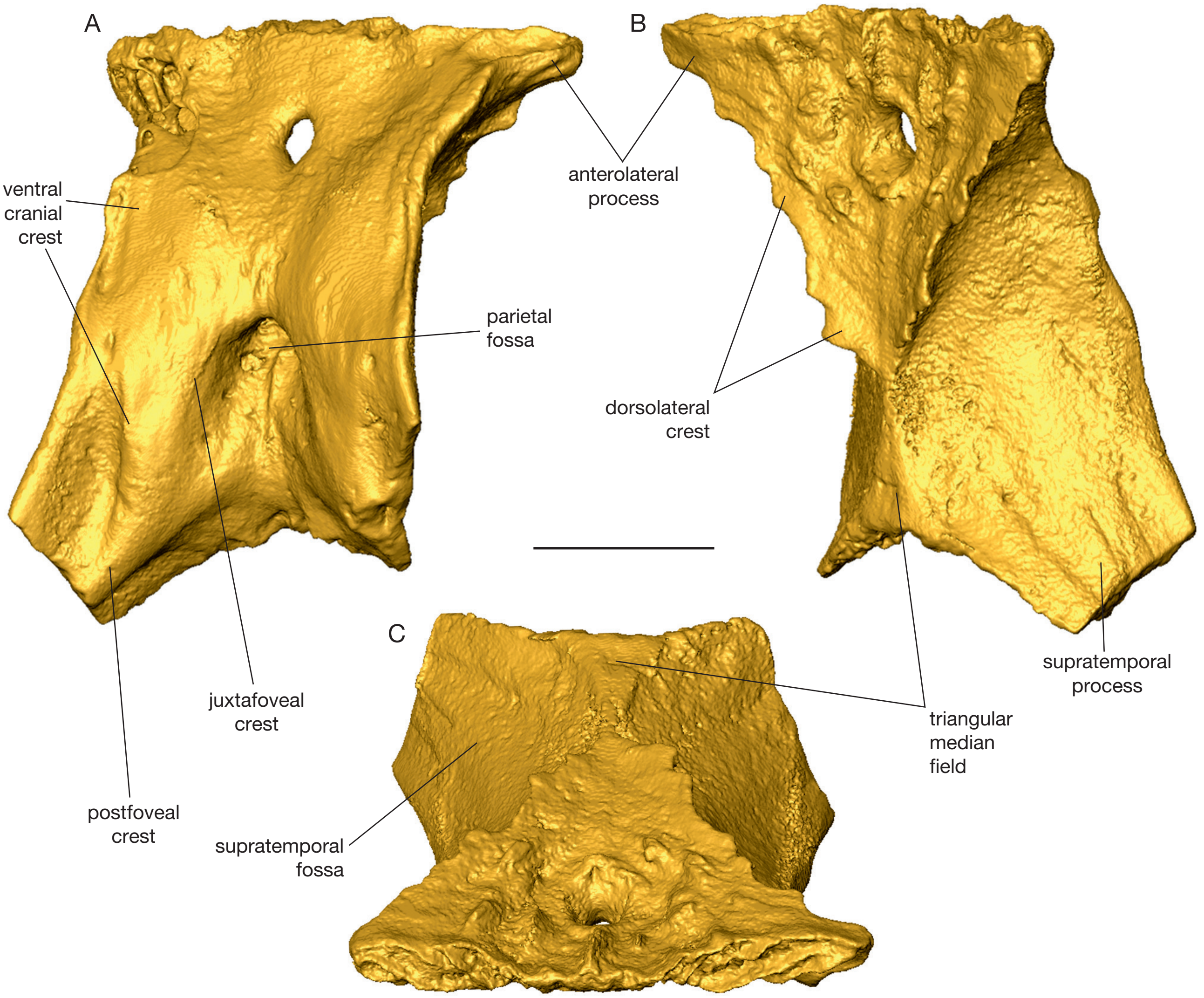

Fig. 38. — *Palaeovaranus lismonimenos* n. sp. Virtual 3D models of the holotype parietal NHMW 2019/0047/0001 of *Palaeovaranus lismonimenos* n. sp. in posteroventral (**A**), dorsolateral (**B**), and anterodorsal (**C**) views. Scale bar: 5 mm.

which articulated with the nasal (a distinguished feature for *Palaeovaranus*). There is a deep sulcus between the medial margin of the nasal crest and the dorsal margin of the nasal process of the maxilla; the sulcus represents an articulating surface for the maxillary crest of the nasal. Immediately ventral to the mid-length of the nasal crest lies a semilunar impression in the medial surface of the nasal process of the maxilla; this is the articulating surface for the maxillary lamina of the prefrontal. Anteroventrally and anteriorly to the nasal crest, the medial surface of the maxilla is massively constructed; Fejérváry (1935) called this structure the basal torus (Fig. 45B). Ventral to the semilunar impression and dorsal to the supradental shelf lies a large, elliptical depression in the medial wall of the nasal representing a lacrimal recess. Its anteriormost portion bears a foramen (Fig. 45C). The supradental shelf is straight. Its dorsal surface bears a distinct sulcus for the nasolacrimal duct (Fig. 45E). The anterior portion of the supradental shelf bears an elliptical and slightly dorsomedially inclined surface, an oblique internasal lamella (Fig. 45B). The maxilla immediately laterally to the supradental shelf is burrowed by the superior alveolar canal; its anterior and posterior openings are well preserved (Fig. 45D, F). The bases of three teeth of the maxilla are well preserved. The bases are mesiodistally broad and bear well preserved basal striae, i.e., plicidentine (Fig. 44B, D). The teeth are strongly curved distally and slightly lingually. The distal cutting edges are well developed.

Dentaries (Figs 46-49)

All three dentaries are incomplete, missing the anteriormost and posteriormost edges. The specimens NHMW 2019/0058/0054 and NHMW 2019/0058/0055 are relatively large and robust, with preserved maximum lengths 27.6 and 21 mm, while NHMW 2019/0058/0056 is smaller and slenderer, with a maximum preserved length of 18 mm. In all three dentaries, the maximum height is achieved at their posterior portions. NHMW 2019/0058/0054 bears four preserved teeth, one more tooth base, and three other empty tooth positions

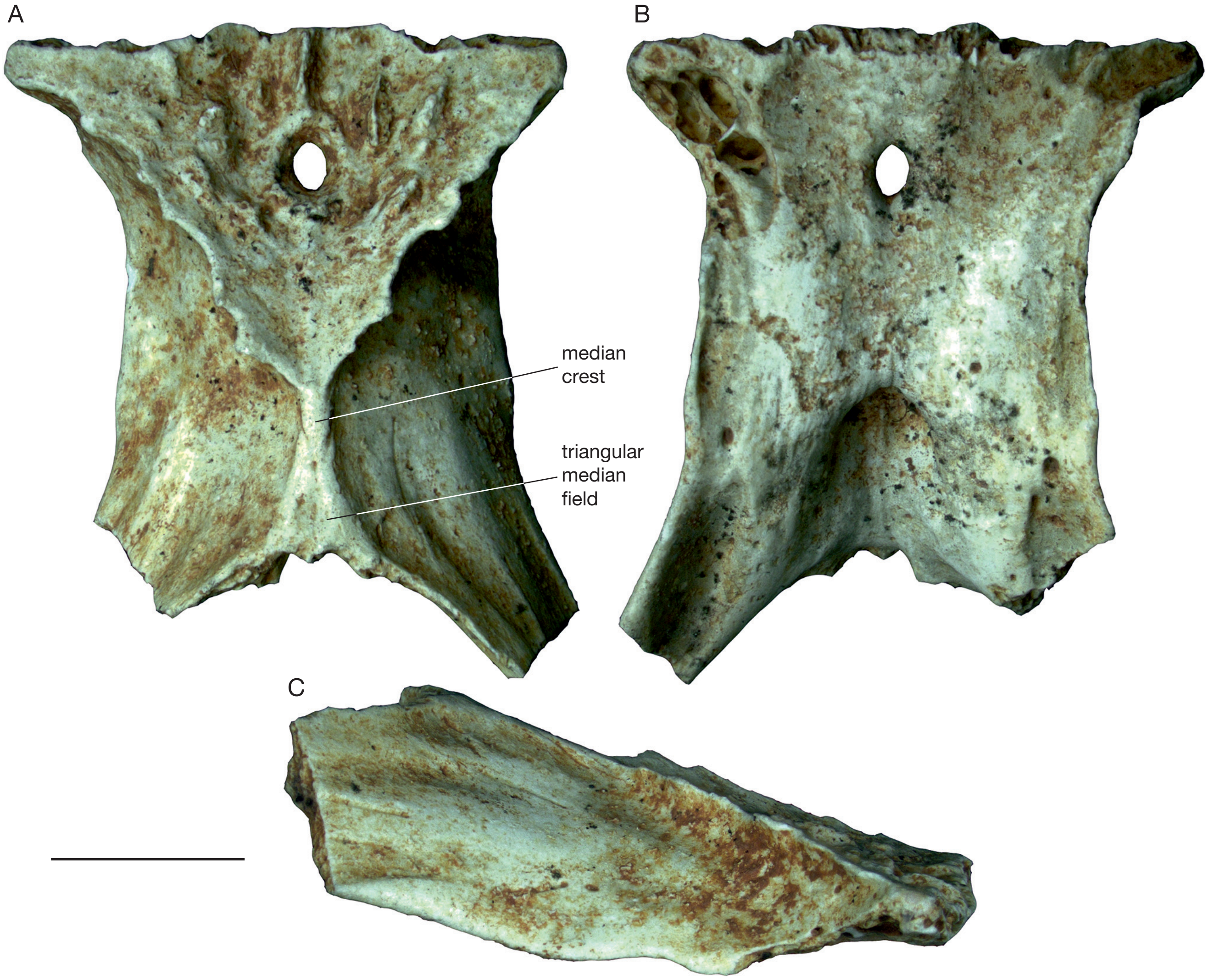

FIG. 39. — *Palaeovaranus lismonimenos* n. sp. Photographs of the holotype parietal NHMW 2019/0047/0001 in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. Scale bar: 5 mm.

(Figs 46; 47), NHMW 2019/0058/0055 bears six preserved teeth and two other empty tooth positions (Figs 48A, B; 49A-D), and NHMW 2019/0058/0056 bears two preserved teeth, fragments of two other teeth, and two other empty tooth positions (Figs 48C-E; 49E, F). All teeth are subpleurodont, recurved, and rather pointed. Their bases are broad and are marked by the distinct presence of plicidentine. The latter feature is significantly most prominent in the anteriormost tooth of NHMW 2019/0058/0056 (Fig. 48E). Teeth possess cutting edges, with this serration being most prominent in NHMW 2019/0058/0056. In the largest specimen (NHMW 2019/0058/0054), remains of the coronoid process are visible (Fig. 47A). The coronoid articulation facet is preserved in NHMW 2019/0058/0054 (Fig. 47D). Splenial articulation facets are visible in all specimens. The Meckel's groove is open throughout the preserved lengths of all specimens. This structure becomes much widened posteriorly in all three dentaries, whereas in the anterior half of these specimens it is partially "blanketed" (but not closed) by the dental crest. In the posterior portion of the two largest dentaries, the characteristic alveolar canal (foramen dentale pro introitu partis alveolaris inferioris nervi mandibularis sensu Fejérváry 1935) is prominent, delimiting a large longitudinal groove, which in NHMW 2019/0058/0055 extends and is visible also in its anterior edge. The posterior spine is thin, with its termination being acute. The intramandibular septum is wide (Fig. 47C).

In lateral view, several dorsoventrally elongated labial foramina pierce the dentaries' surfaces, situated across irregular intervals, but otherwise these surfaces are relatively smooth (Figs 46A; 47A; 48A, C; 49A).

Presacral vertebrae (Figs 50-53)

The size of the presacral vertebrae varies, with centrum lengths ranging between 7.0 and 10.8 mm (Appendix 1). There are usually two distinct ridges in the ventral surface of the centrum that commence at around the level of the cotyle and terminate slightly prior to the condyle (Figs 50-53). In

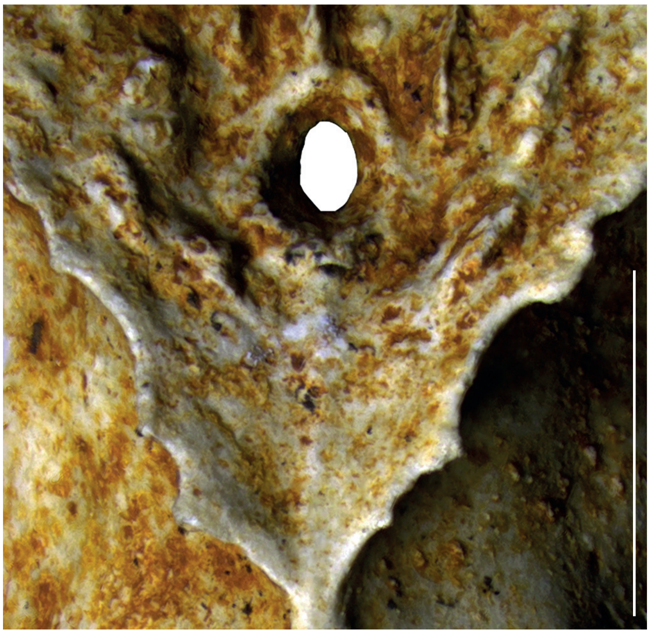

FIG. 40. — *Palaeovaranus lismonimenos* n. sp. Close up photograph of the sculpturing pattern of the holotype parietal NHMW 2019/0047/0001 and the crenulation of its dorsolateral crests in dorsal view. Scale bar: 5 mm.

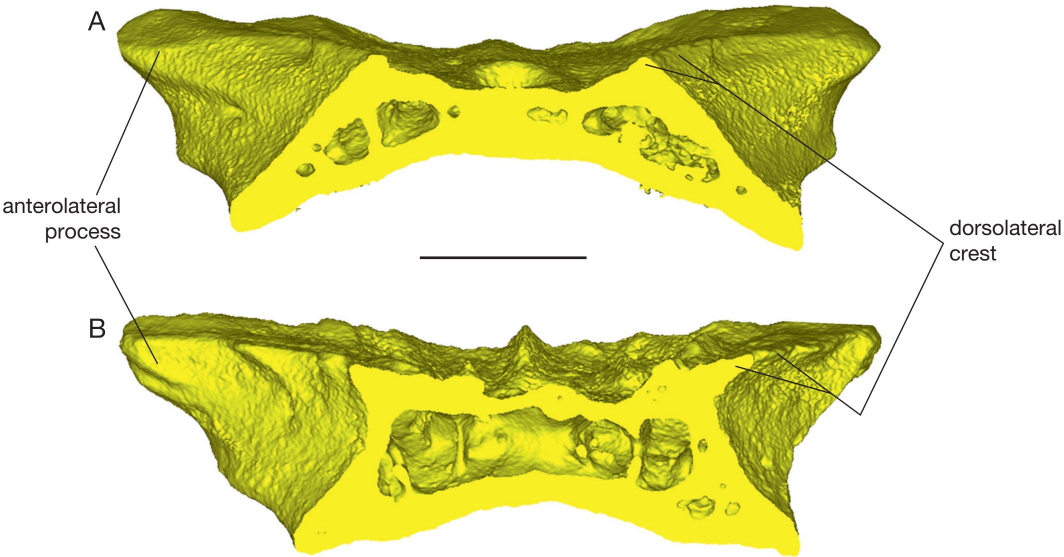

FIG. 41. — *Palaeovaranus cayluxi* Zittel, 1887-1890 and *Palaeovaranus lismonimenos* n. sp. Transverse sections of 3D models of parietals. **A**, parietal NHMW 2019/0048/0001 of *Palaeovaranus cayluxi*; **B**, holotype parietal NHMW 2019/0047/0001 of *Palaeovaranus lismonimenos* n. sp. Scale bar: 3 mm.

certain large specimens (e.g., NHMW 2019/0058/0005) a distinct deep groove is clearly delimited between these two ridges. Subcentral foramina are usually present and can be, at certain specimens, rather prominent (e.g., NHMW 2019/0058/0001; Figs 50-53). The neural spine is high in lateral view and is posteriorly inclined. The neural spine mostly develops and augments in height in the posterior half of the neural arch, but nevertheless, its base crosses, in all specimens, the entire midline of the neural arch, in the shape of longitudinal ridge. In certain large specimens, a distinct dorsal thickening of the neural spine is obvious (e.g., NHMW 2019/0058/0001; NHMW 2019/0058/0003; NHMW 2019/0067/0001). The neural arch is vaulted (or at least moderately vaulted) in all specimens. Foramina on the neural spine can be present (e.g., NHMW 2019/0058/0001). The cotyle is rather depressed; in fact, it appears to be exceedingly depressed in certain small-sized specimens (e.g., NHMW 2019/0058/0002; Fig. 52A) but also in certain rather large ones (e.g., NHMW 2019/0058/0003; Fig. 53A). In certain specimens, the cotyle is rather anteroventrally directed, so that its dorsal level can be observed even in ventral view of the vertebra (e.g., NHMW 2019/0058/0005; NHMW

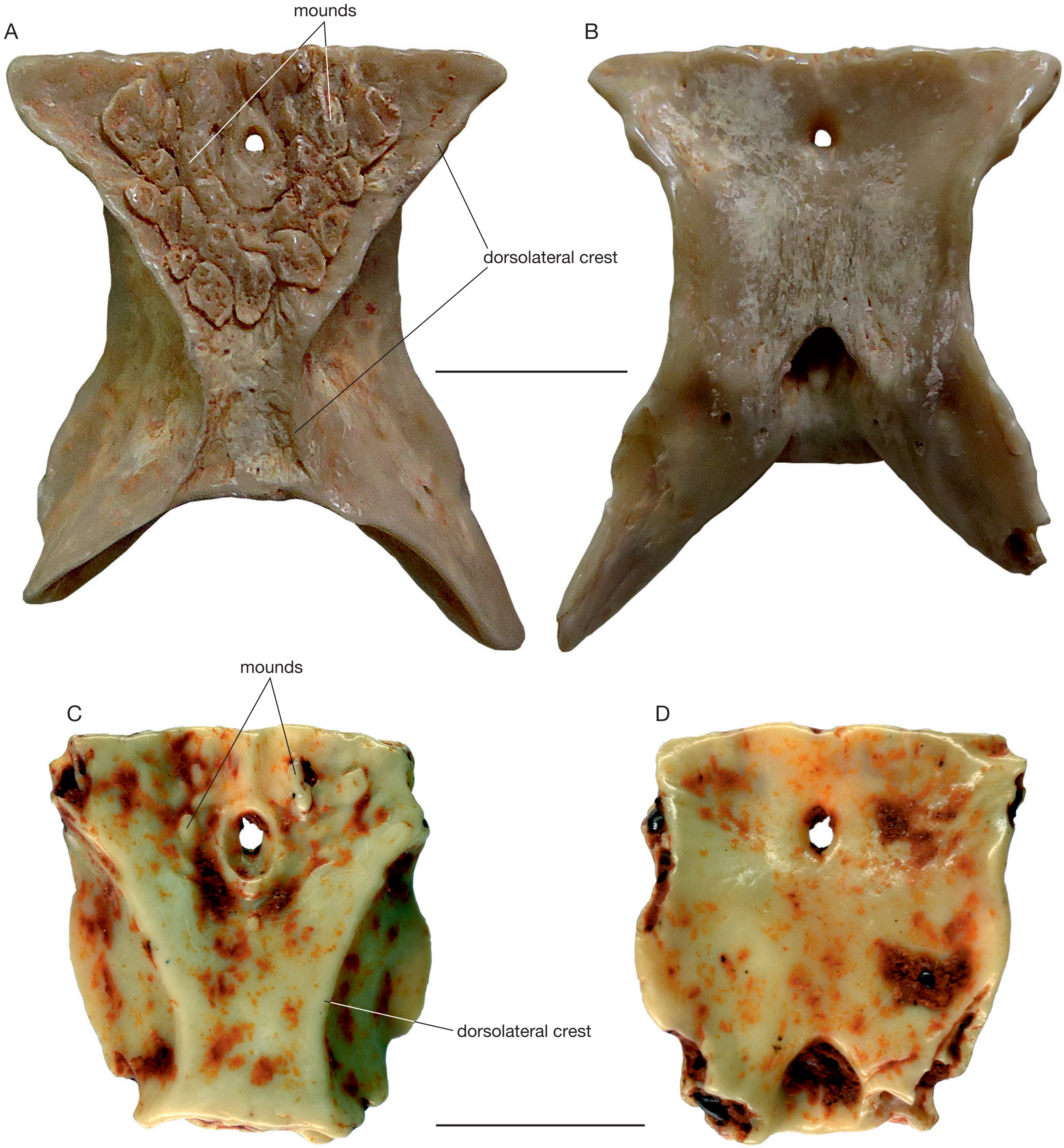

FIG. 42. — *Palaeovaranus lismonimenos* n. sp. Parietals of juvenile individuals. **A**, **B**, photographs of parietal MNHN.F.QU17177 in dorsal (**A**) and ventral (**B**) views; **C**, **D**, photographs of parietal UM BFI 1873 in dorsal (**C**) and ventral (**D**) views. Both these specimens originally appeared as drawings in Augé (2005: Figs 194 and 195 respectively). Scale bars: 5 mm.

2019/0058/0006), a condition reminiscent of varanids. In certain specimens (NHMW 2019/0058/0001; NHMW 2019/0058/0005), distinct anocotylar foramina are present above the cotyle. The synapophyses are massive and elongated.

Sacral vertebrae (Figs 54-56)

Two of these specimens (one isolated [NHMW 2019/0058/0029] and two articulated sacral vertebrae [NHMW 2019/0058/0028]) are rather large in size (Figs 54; 55; 56A-F), especially the latter one, which exceeds in centrum length all the above described presacral vertebrae (see Appendix 1). The much smaller specimen NHMW 2019/0058/0047 is almost identical with the two other specimens, with their only major difference being this size contrast (Fig. 56G-J); apparently it pertains to a much smaller (?younger) individual, however, any taxonomic

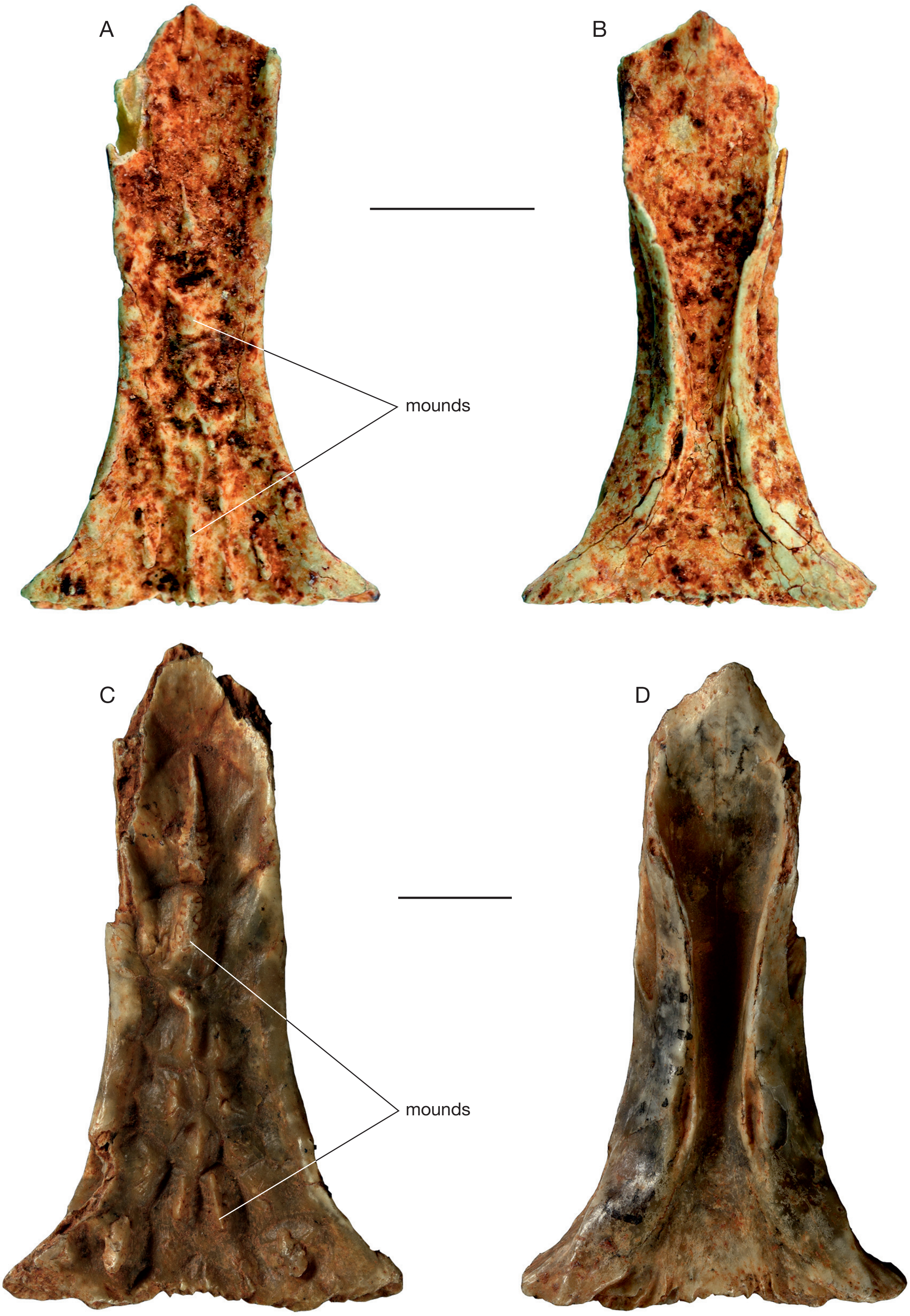

FIG. 43. — *Palaeovaranus lismonimenos* n. sp. frontals: **A**, **B**, photographs of frontal UM PRA 8 in dorsal (**A**) and ventral (**B**) views; **C**, **D**, photographs of frontal MNHN.F.QU17175 in dorsal (**C**) and ventral (**D**) views. Both these specimens originally appeared as drawings in Augé (2005: figs 196 and 189 respectively). Scale bars: 5 mm.

implication for this size deviation cannot be excluded. Similarly to the presacral vertebrae, there are also in these specimens two distinct ridges in the ventral surface of the centrum, that commence at around the level of the cotyle and terminate slightly prior to the condyle. The centrum is convex in lateral view, with the ventral levels of both cotyle and condyle situated below the level of the ventral surface of the centrum. The neural arch is relatively vaulted.

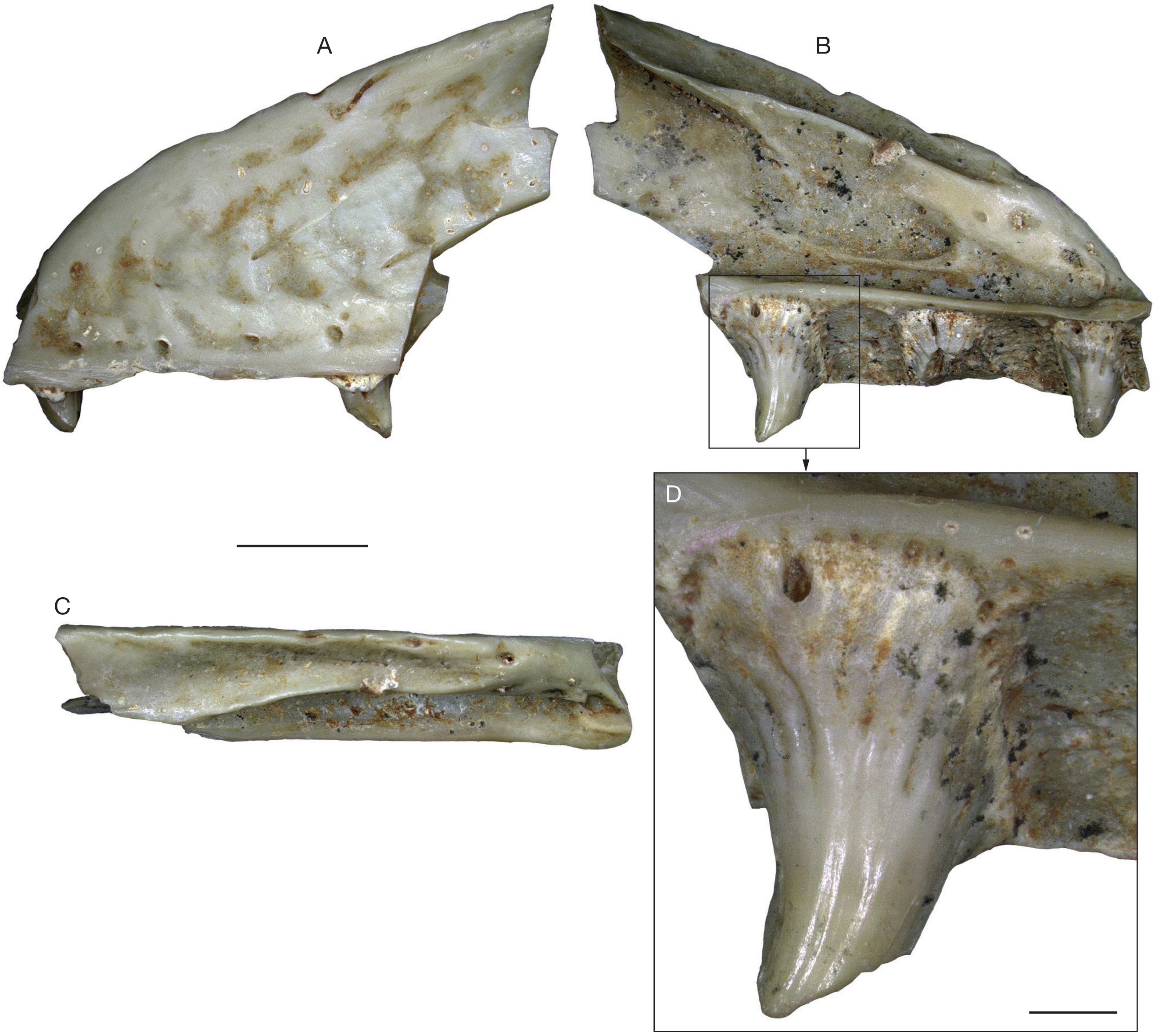

Fig. 44. — *Palaeovaranus* sp. **A**-**C**, photographs of left maxilla NHMW 2019/0048/0002 in lateral (**A**), medial (**B**), and dorsal (**C**) views; D, close up of the posteriormost preserved tooth of the same specimen. Scale bars: A-C, 5 mm; D, 1 mm.

The neural spine develops mostly at the posterior half of the neural arch. The cotyle and condyle are depressed. "Pseudozygosphenes" and "pseudozygantra" are visible. The pleurapophyses extend much laterally and their distal termination is rather broad, so that in the two large articulated vertebrae (NHMW 2019/0058/0028), these elements from both vertebrae are united to each other (Fig. 55D-F). A large fenestra is being formed by the unification of pleurapophyses of succeeding vertebrae. Also in this larger specimen, two distinct foramina are present below the neural arch in posterior view, inside the "pseudozygantrum" (Fig. 55B).

Caudal vertebrae (Figs 57; 58)

These are extremely elongated and rather slender (Figs 57; 58), with the elongation becoming more prominent in the slenderer specimens (e.g., NHMW 2019/0058/0031; NHMW 2019/0058/0033), whereas the more robust ones tend to have a smaller centrum length but nevertheless wider vertebral centra (NHMW 2019/0058/0035; NHMW 2019/0058/0036; NHMW 2019/0058/0048). Their centrum lengths vary between 8.9 and 15.9 mm (see Appendix 1). The neural spine, when preserved, is rather high in lateral view, it augments in height rapidly but only at the posterior portion of the neural arch, and is inclined posteriorly (e.g., NHMW 2019/0058/0035; NHMW 2019/0058/0036). Nevertheless, the base of the neural spine extends much anteriorly in dorsal view, in the shape of a thin longitudinal ridge. The cotyle is large and elliptical. The prezygapophyses are dorsally inclined. The postzygapophyses are rather small. The pedicles for articulation with the chevrons are rather thick in the robust

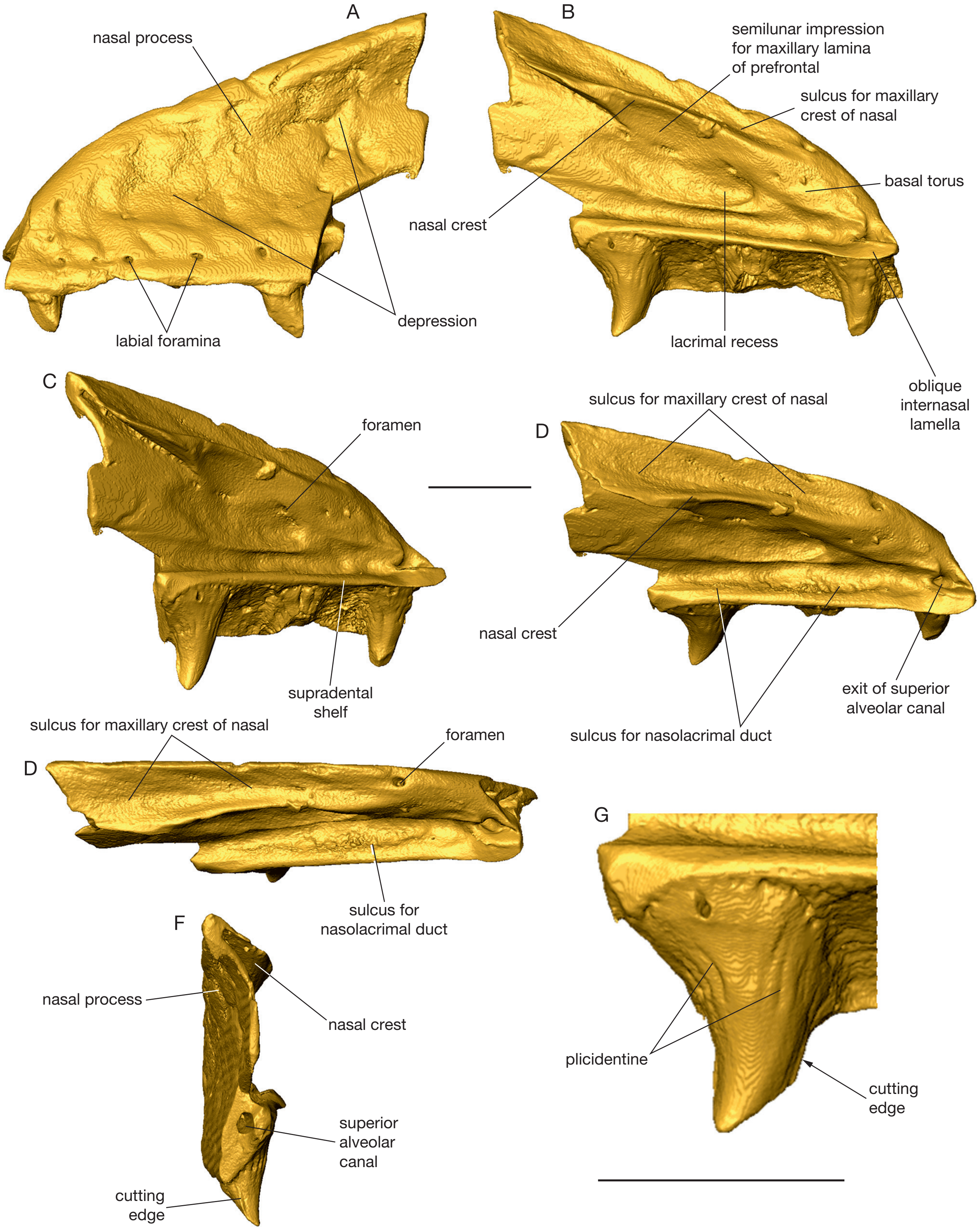

FIG. 45. — *Palaeovaranus* sp. **A**-**G**, virtual 3D models of left maxilla NHMW 2019/0048/0002 in lateral (**A**), medial (**B**), posteromedial (**C**), dorsomedial (**D**), dorsal (**E**) and posterior (**F**) views; **G**, close up view of posteriormost preserved tooth of the same specimen. Scale bars: 5 mm.

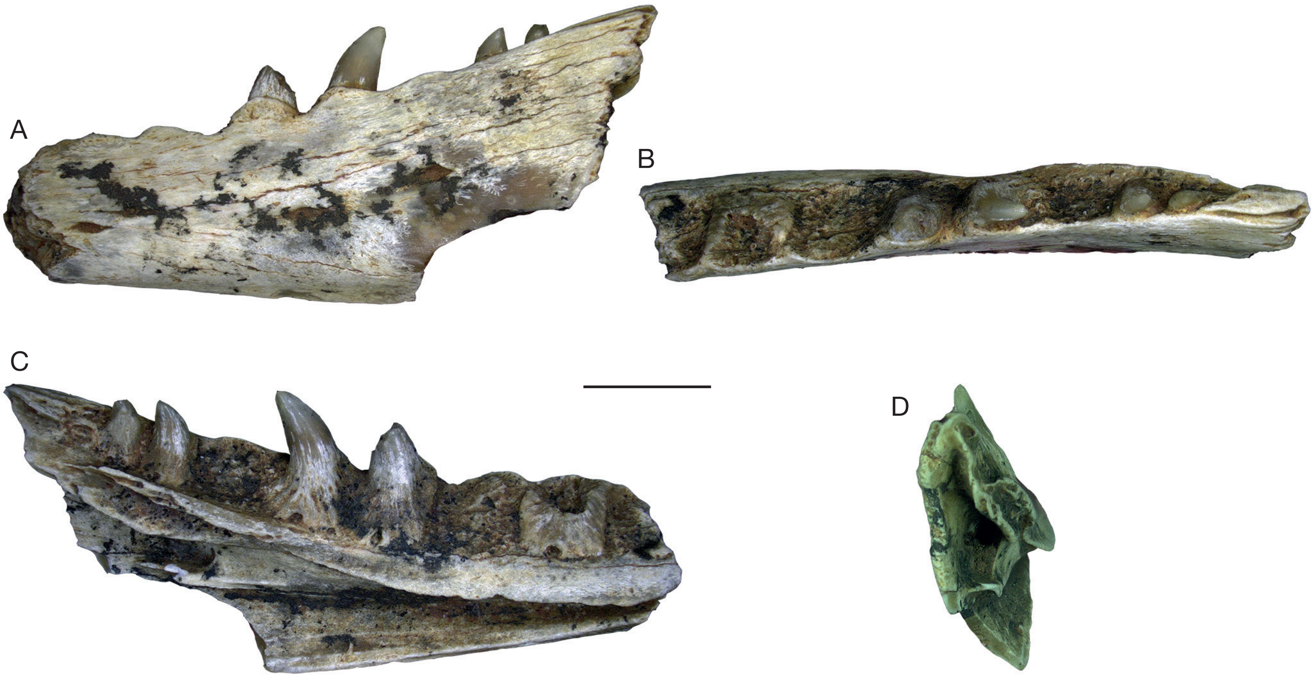

Fig. 46. — *Palaeovaranus* sp. Photographs of left dentary NHMW 2019/0058/0054 in lateral (**A**), dorsal (**B**), medial (**C**), and posterior (**D**) views. Scale bar: 5 mm.

vertebrae and are located rather close to the condyle. A longitudinal groove runs throughout the centrum, originating posteriorly between the two pedicles and reaching anteriorly prior to the level of the cotyle. In the most robust specimens, this groove becomes rather thin in the anterior half of the centrum, while it is almost constantly wide in the slender, elongated specimens. There are no signs of autotomic septa. The transverse processes differ in size. In the most robust specimens, they occupy a larger surface at the lateral sides of the centrum, whereas in the more slender ones, they are rather thin. They extend laterally. In several specimens, there are "pseudozygosphenes" and "pseudozygantra" (sensu Hoffstetter 1969).

Remarks

The distinctly developed nasal crest on the dorsomedial surface of the nasal process of maxilla represents the most distinctive maxillary structure of *Palaeovaranus*. This crest was not mentioned by Zittel (1887-1890) in the original, brief description of the holotype maxilla of *Palaeovaranus cayluxi*, but it was extensively described and discussed for the same specimen by Fejérváry (1935), and we here use mostly his terminology. Fejérváry (1935) was able to confirm the morphology of its medial wall and the presence of this nasal crest and continuously highlighted this feature as principally differentiating this genus from *Varanus*. This crest is also present in the referred maxilla of *Palaeovaranus cayluxi* from Sainte Néboule, Quercy, described and figured by Rage (1978). With the new photographs and the 3D models we provided above, this maxillary feature is evident and this enhances our understanding of this peculiar feature in *Palaeovaranus*.

The fact that the external side of the maxilla is not smooth but rather appears to bear some kind of ornamentation could hint for a referral of this maxilla to *Palaeovaranus lismonimenos* n. sp., the holotype parietal of which is characterized by more prominent sculpturing in comparison with that of *Palaeovaranus cayluxi* described above. Furthermore, the holotype maxilla of *Palaeovaranus cayluxi* does not bear any kind of ornamentation as it can be judged by Fejérváry's (1935) photographs and especially from his extremely detailed and careful descriptions of this specimen. Neither also exists any kind of ornamentation in the referred maxillary material from Sainte Néboule described and figured by Rage (1978). Nevertheless, we avoid of formally assigning this maxilla to *Palaeovaranus lismonimenos* n. sp., preferring the most conservative approach and determining the specimen solely to the genus level.

The dentaries of *Palaeovaranus* described herein show an array of sizes, general morphologies, and tooth shapes. They also seem different and more robust that other *Palaeovaranus* dentaries described from Quercy (De Stefano 1903; Augé 2005) and Dielsdorf, Switzerland (Georgalis & Scheyer 2019). Whether such differences in robustness reflect some kind of taxonomic or simply intraspecific variation, cannot be evaluated on the basis of this material and our current knowledge of *Palaeovaranus* mandibular variability.

While the cranial material of palaeovaranids resembles in many respects that of varanids, the vertebral morphology of the two groups is relatively distinct, with the former lacking a precondylar constriction and having a relatively more straight centrum, not so widened anteriorly as in the latter group (Rage 1978). Nevertheless, cervical and caudal vertebrae of both palaeovaranids and varanids bear strong resemblance. The two

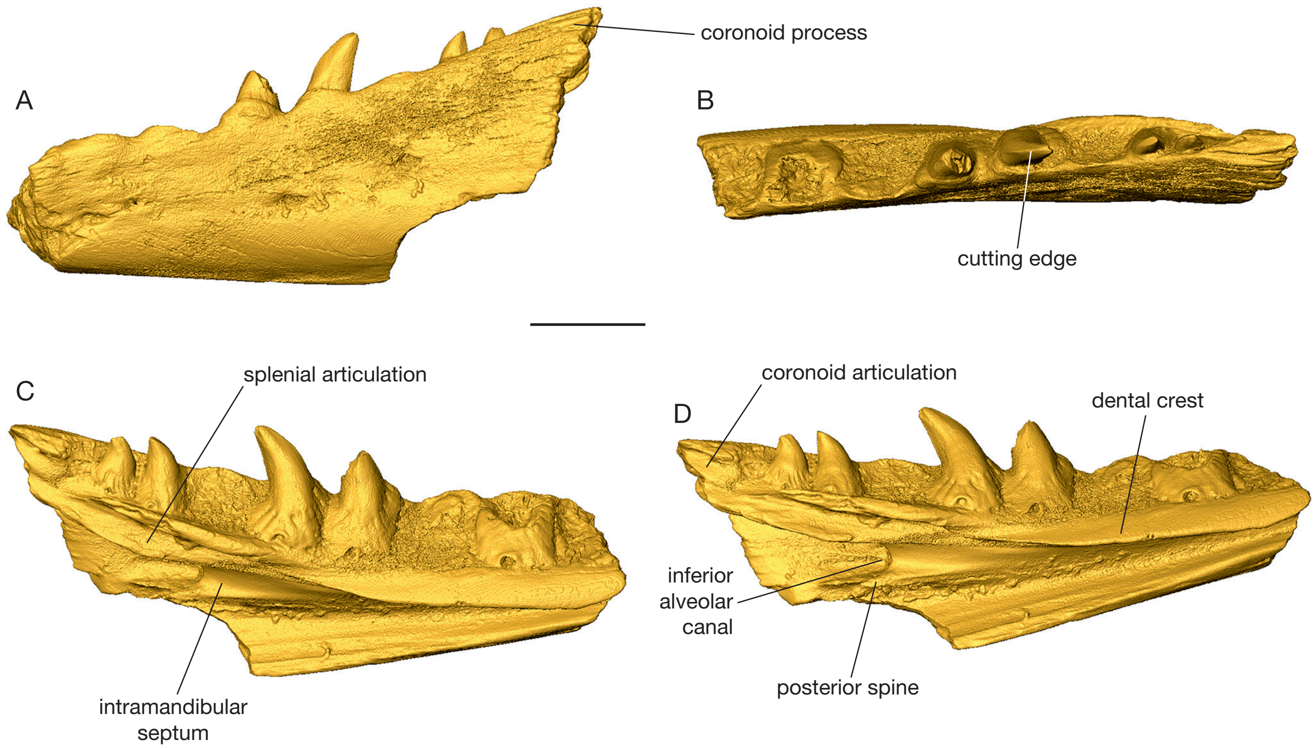

Fig. 47. — *Palaeovaranus* sp. Virtual 3D models of left dentary NHMW 2019/0058/0054 in lateral (**A**), dorsal (**B**), medial (**C**), and ventromedial (**D**) views. Scale bar: 5 mm.

articulated sacral vertebrae resemble much the specimen figured by De Stefano (1903: pl. X, fig. 3). Note that due to the fact that vertebrae of certain varanoids, especially varanids (but also observable in our material), possess an anteroventrally directed cotyle, two different centrum lengths can be obtained; we here consider as centrum length the so-called "minimum centrum length" of Bailon & Rage (1994), i.e., the length between the tip of the condyle and the ventral margin of the cotyle (Bailon & Rage 1994; Georgalis *et al.* 2018). For a further, detailed discussion about the resemblance and identification of *Palaeovaranus* and *Placosaurus* vertebrae, see Discussion below.

Family VARANIDAE Gray, 1827 (*sensu* Estes *et al.* 1988)

Genus *Saniwa* Leidy, 1870

Type species. — *Saniwa ensidens* Leidy, 1870 (type species by original designation; Leidy 1870).

Saniwa sp.
(Figs 59-61)

Referred specimens. — Three presacral vertebrae (NHMW 2019/0065/0001-NHMW 2019/0065/0003).

Description

Presacral vertebrae (Figs 59-61)

The three vertebrae are large (Figs 59-61), with centrum lengths ranging from about 8.8 to 9.6 mm (see Appendix 1). The centrum is almost triangular in ventral view and widens anteriorly (though not to that extent as in melanosaurine vertebrae described above). The subcentral ridges are straight in ventral view. The prezygapophyses are either much dorsally tilted (NHMW 2019/0065/0003) or only slightly so (in the other two specimens). The prezygapophyseal articular facets are massive and broad in dorsal view. The postzygapophyseal articular facets are also massive. The neural spine develops in height mostly in the posterior half of the neural arch. The neural arch is vaulted in posterior view. There are slight signs of "pseudozygosphene" and "pseudozygantrum" (sensu Hoffstetter 1969). The cotyle and the condyle are strongly depressed. The centrum appear more convex in lateral view is NHMW 2019/0065/0001 and NHMW 2019/0065/0002, while it is more straight in NHMW 2019/0065/0003. In all specimens though, the dorsal level of the cotyle can be clearly visible in ventral view of the specimen. Precondylar constriction can be observed (even slightly though) in NHMW 2019/0065/0001, as the respective portion of the centrum is eroded in the other two specimens. Anocotylar foramina are present and are most prominent in the largest vertebra NHMW 2019/0065/0001 (Fig. 59A).

Remarks

These three vertebrae can be referred to *Saniwa* on the basis of their triangular centrum that widens anteriorly and the slight presence of "pseudozygosphene" and "pseudozygantrum" (Gilmore 1922; Rage & Augé 2003; Augé 2005). See Discussion below for further information on European material of *Saniwa*.

FIG. 48. — *Palaeovaranus* sp. **A**, **B**, photographs of right dentary NHMW 2019/0058/0055 in lateral (**A**) and medial (**B**) views; **C**, **D**, photographs of right dentary NHMW 2019/0058/0056 in lateral (**C**) and medial (**D**) views; E, close up photograph of a tooth of right dentary NHMW 2019/0058/0056, showing the presence of plicidentine. Scale bars: A-D, 5 mm; E, 1 mm.

Anguimorpha indet.
(Figs 61; 62)

REFERRED SPECIMENS. — Five presacral vertebrae (NHMW 2019/0046/0003- NHMW 2019/0046/0007); a partial pectoral girdle (NHMW 2019/0095/0001).

DESCRIPTION AND REMARKS

Presacral vertebrae (Fig. 61)

These vertebrae are relatively large (Fig. 61), with centrum lengths ranging between 6.9 and 9.3 mm (see Appendix 1). The vertebrae demonstrate a mix of several features present in the above described specimens of *Placosaurus*, Anguinae indet., and *Palaeovaranus*. They have high neural spines, depressed cotyle and condyle, while the ventral surface of their centra is crossed by a wide surface or groove that is unlike the conditions seen above for the other taxa (Fig. 61). Considering the high intracolumnar variation observed in the vertebrae of extant lizards (e.g., *Pseudopus*), we are reluctant in assigning these specimens in a more precise taxonomic rank and we cannot even exclude that they (or part of them) pertain to some of the above described taxa.

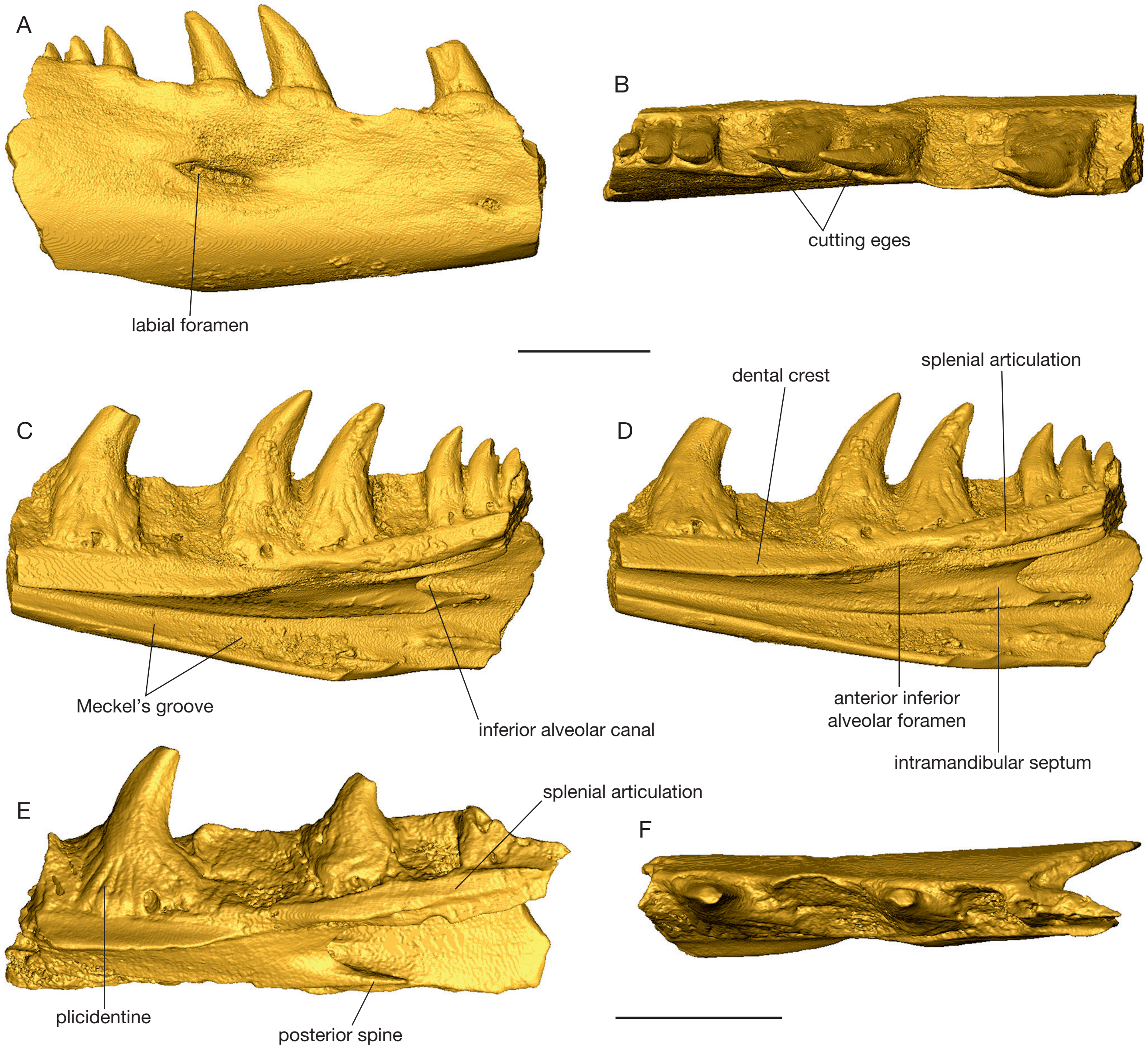

Fig. 49. — *Palaeovaranus* sp. **A**-**D**, virtual 3D models of right dentary NHMW 2019/0058/0055 in lateral (**A**), dorsal (**B**), medial (**C**), and ventromedial (**D**) views; **E**, **F**, virtual 3D models of right dentary NHMW 2019/0058/0056 in medial (**E**) and dorsal (**F**) views. Scale bars: 5 mm.

Pectoral girdle NHMW 2019/0095/0001 (Fig. 62)

This specimen is incomplete, though preserving in relatively good state the right scapulocoracoid. The glenoid fossa is visible, well demarking the point of attachment with the humerus. Anteriorly to the glenoid fossa, lies the coracoid foramen. Dorsally to the foramen, the scapulocoracoid is of rectangular shape and is dorsoventrally elongated. The ventral portion of the element is anteroposteriorly elongated.

It is readily obvious that this specimen apparently pertains to a rather large-sized lizard. Considering our currently inadequate state of knowledge of the appendicular skeleton of Paleogene European lizards, it is impossible to associate it with any of the above described glyptosaurines, palaeovaranids, and varanids, all of which could attain a considerably large size.

Squamata indet.

Referred specimen. — A ?sacral vertebra (NHMW 2019/0095/0002).

Description and remarks.

This vertebra is incomplete and not informative.

DISCUSSION

The diversity of large Platynotans in the Paleogene of Europe

The identification and description of relatively large, *Varanus*-like lizards in the Paleogene fossil record of Europe, was already made by the second half of the 19th century (Filhol 1873,

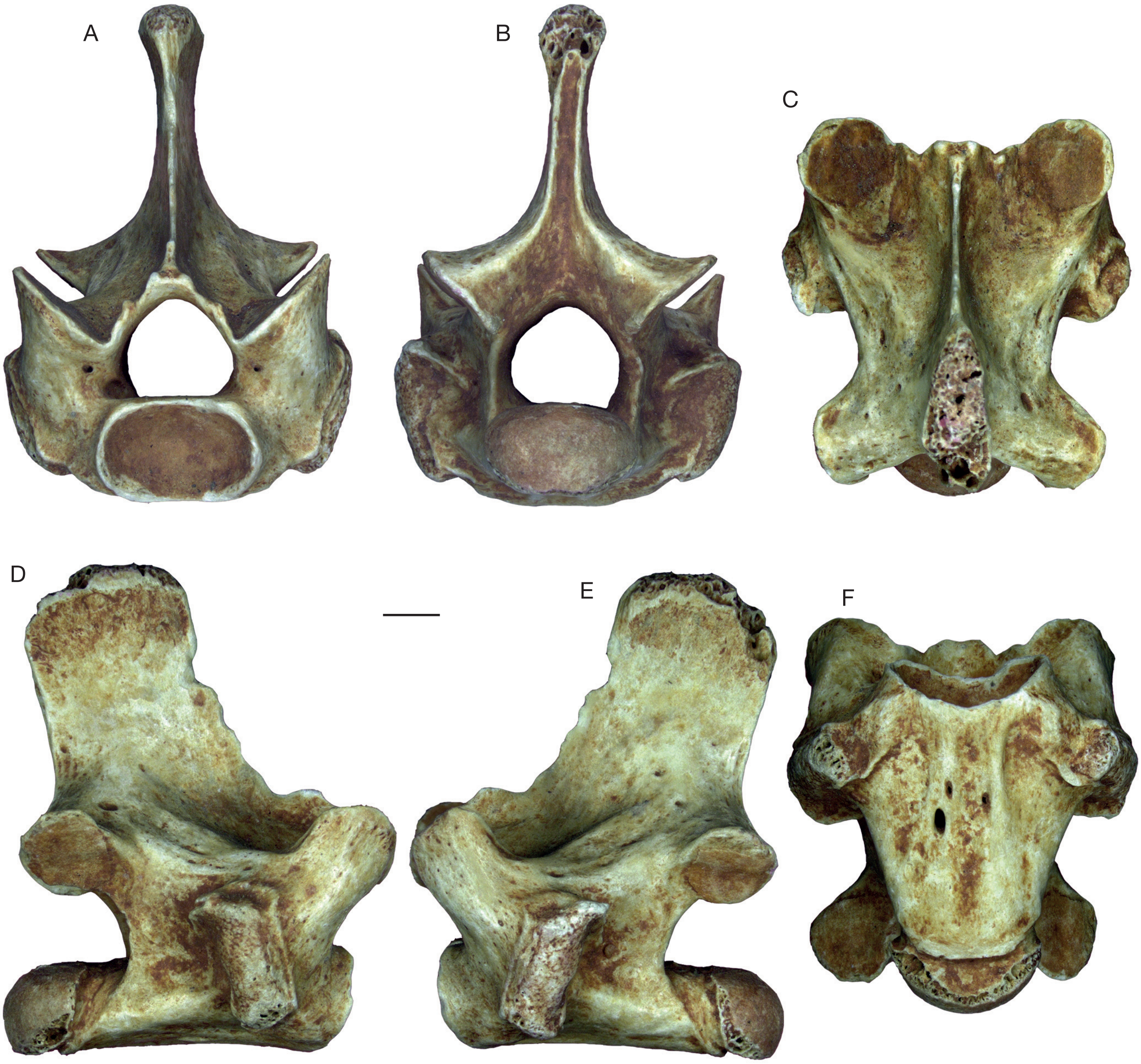

Fig. 50. — *Palaeovaranus* sp. Photographs of presacral vertebra NHMW 2019/0058/0001 in anterior (**A**), posterior (**B**), dorsal (**C**), right lateral (**D**), left lateral (**E**), and ventral (**F**) views. Scale bar: 2 mm.

1876, 1877a, b, c; Zittel 1887-1890) even if in few cases misidentified as snakes (type of *Odontomophis atavus* Rochebrune, 1884; paralectotype of *Pylmophis gracilis* Rochebrune, 1884). Ironically, the only find that was originally referred to the genus *Varanus*, i.e., *Varanus margariticeps* Gervais, 1876, has proven to be in fact a glyptosaurine and thus not a platynotan at all (Estes 1983; Augé 2005). It is worth noting that for the Neogene of Europe instead, such varanid discoveries had been made much earlier, with *Varanus* identified in the Miocene of Greece already during the 1860's (Gaudry 1862a, b, 1862-1867; see discussion in Georgalis 2019). The Phosphorites du Quercy played the most pivotal role in these Paleogene platynotan discoveries, as all these first finds, but also all subsequent fossil remains during the next several decades, were recovered from that area (Filhol 1873, 1876, 1877a, b, c; Zittel 1887-1890; De Stefano 1903; Fejérváry 1935; Kuhn 1940b; Hoffstetter 1957). Approximately at the same time, reports of Paleogene large lizards were made from the Paris Basin (Lemoine 1878-1879), however, these were not accompanied by any kind of description or figure. Further, sporadic descriptions of isolated remains were subsequently made during the 20th century from Belgium (Dollo 1923) and Germany (Kuhn 1940a). Only later though, discoveries of complete articulated skeletons of platynotan lizard remains would take place in the famous Lagerstätte Eocene localities of Geiseltal and Messel in Germany (Kuhn 1940b; Haubold 1977; Stritzke 1983; Keller & Schaal 1988; Smith 2017; Smith *et al.* 2018b). Additionally, in the past few decades,

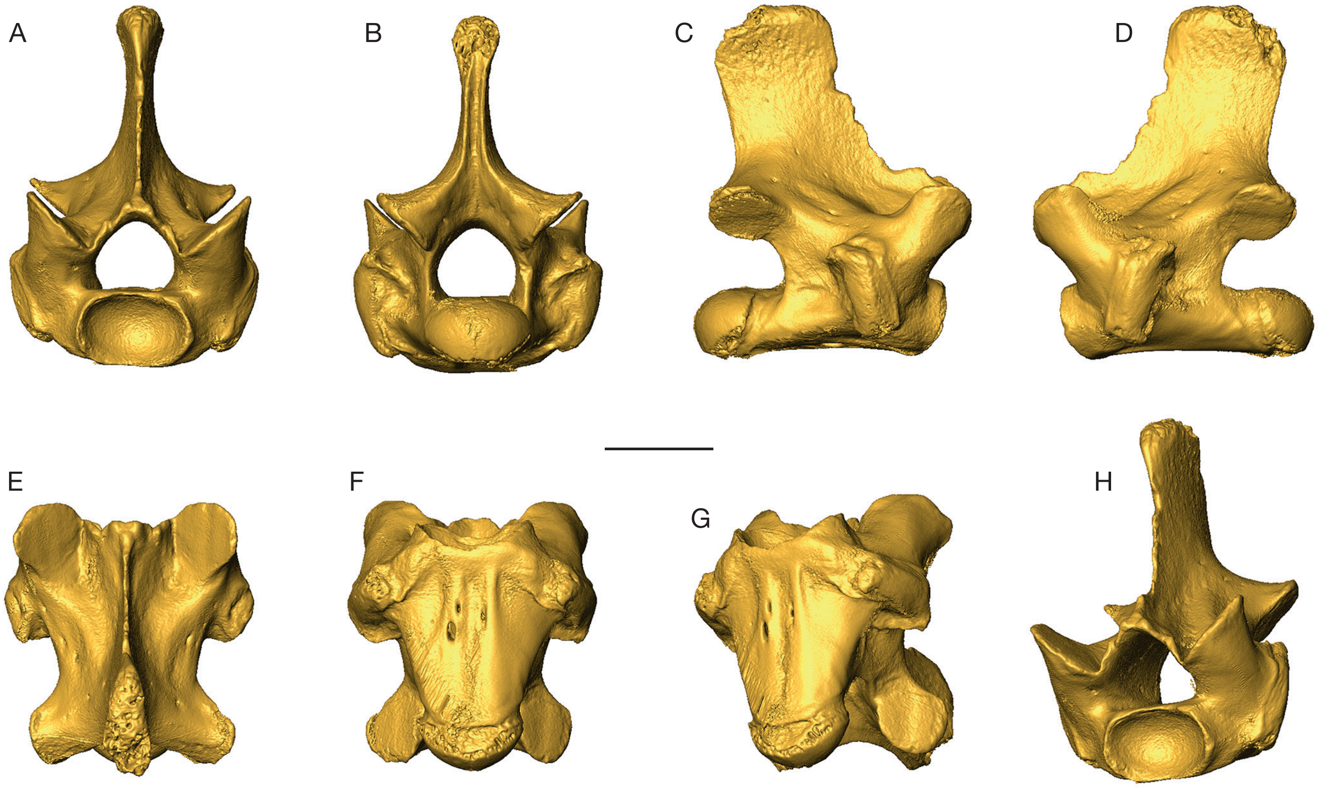

Fig. 51. — *Palaeovaranus* sp. Virtual 3D models of presacral vertebra NHMW 2019/0058/0001 in anterior (**A**), posterior (**B**), right lateral (**C**), left lateral (**D**), dorsal (**E**), ventral (**F**), ventrolateral (**G**), and anterolateral (**H**) views. Scale bar: 5 mm.

the recent, well stratigraphically constrained excavations in the Phosphorites du Quercy, this time bearing precise locality data, yielded also platynotan remains (Rage 1978, 1988a, 2013; Augé 2005; Rage & Augé 2015), while similar finds from other parts of France have also been described (Duffaud & Rage 1997; Augé 1990a, b, 2003, 2005; Laurent *et al.* 2010; Rage & Augé 2010; Smith *et al.* 2011). Additionally, these large lizards have been further identified in the Paleogene of Belgium (Hecht & Hoffstetter 1962; Augé 1990b, 1995, 2005; Augé & Smith 2009), the United Kingdom (Rage & Ford 1980; Klembara & Green 2010), Portugal (Rage & Augé 2003), Spain (Bolet 2017), and Switzerland (Hünermann 1978; Georgalis & Scheyer 2019). But the major question is: how many and which taxa were present?

Palaeovaranus cayluxi Zittel, 1887-1890, was the first formally established platynotan taxon from the Paleogene of Europe (Zittel 1887-1890). This species has suffered from a rather perplexing taxonomic history; it was variously attributed the invalid name *Necrosaurus cayluxi*, the authorship was erroneously attributed to Filhol (1877a), and even the nature of its type material was not properly identified. Nevertheless, Georgalis (2017), recently clarified thoroughly this perplexing taxonomic history, demonstrated that the appropriate genus name is *Palaeovaranus*, attributed authorship of the taxon to Zittel 1887-1890), recognized Escamps (late Eocene, MP 19) in Quercy as the exact type locality, and identified the maxilla that had been described and figured by Zittel (1887-1890) as the holotype of the species. This holotype maxilla, currently unfortunately lost, was extensively described by Fejérváry (1935), who provided also photographs of this specimen for the first time. Fejérváry (1935) pointed out distinctive maxillary features that could readily distinguish *Palaeovaranus cayluxi* from extant and extinct *Varanus* spp., characters that were subsequently followed by other workers (Hoffstetter 1943; Estes 1983; Augé 2005; Georgalis 2017). Hoffstetter (1943), on the basis of disarticulated remains from Quercy, recognized further the arched and rather short nasal process of the premaxilla, the fused frontals with their descending processes that do not meet below on the midline, and the oval osteoderms ornamented with a median keel, as important diagnostic features that could suit to this taxon. The same author also stated that the parietal morphology of this taxon bears some resemblance to that of *Varanus* but has also some unique features; however, he never explained which are these features, neither figured any of this material (Hoffstetter 1943). Kuhn (1940b) figured additional fragmentary cranial material of *Palaeovaranus cayluxi* from the Phosphorites du Quercy. New cranial and vertebral material was subsequently referred from the late Eocene (MP 18) locality of Sainte Néboule in Quercy by Rage (1978), who was also the first to formally describe and figure a parietal referable to *Palaeovaranus cayluxi*. Additional cranial material of *Palaeovaranus cayluxi* was described by Augé (2005), originating from both the old and new collections of the Phosphorites du Quercy.

A number of specimens (including maxillae, dentaries, but also parietals and frontals) from the Phosphorites du Quercy

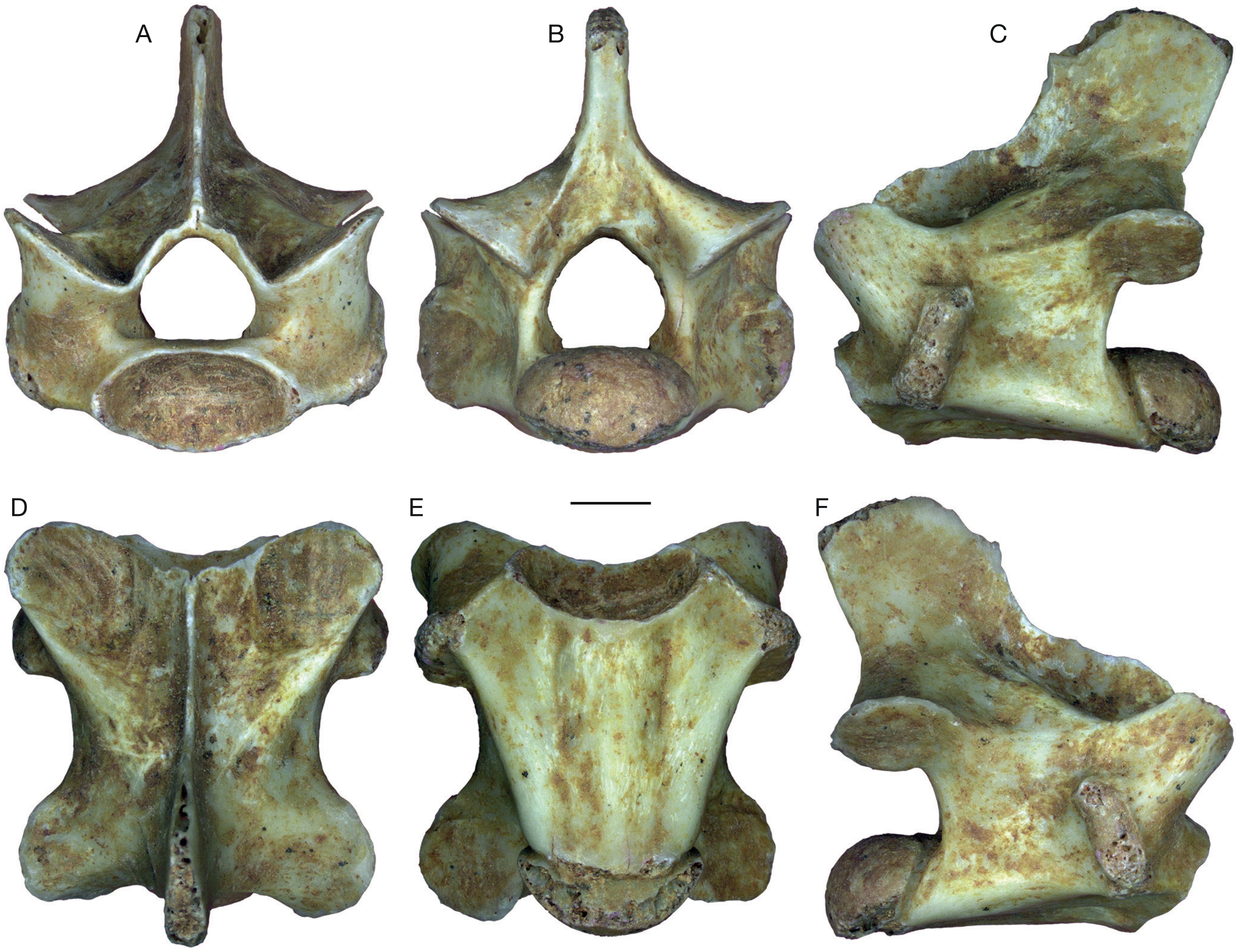

Fig. 52. — *Palaeovaranus* sp. Photographs of presacral vertebra NHMW 2019/0058/0002 in anterior (**A**), posterior (**B**), left lateral (**C**), dorsal (**D**), ventral (**E**), and right lateral (**F**) views. Scale bar: 2 mm.

has been variously attributed to "*Necrosaurus eucarinatus*" (Augé 2005), a taxon originally established from Geiseltal, Germany, as *Ophisauriscus eucarinatus* Kuhn, 1940. As it was recently shown, however, the holotype of *Ophisauriscus eucarinatus* was not diagnostic at the species level (see also below), and so these supposedly referred specimens from Quercy were tentatively assigned to *Palaeovaranus giganteus* (Georgalis 2017).

Other specimens from the old collections of the Phosphorites du Quercy have been referred to palaeovaranids but are currently considered as non-diagnostic to the species level. These are: *Palaeovaranus filholi* De Stefano, 1903, *Odontomophis atavus* Rochebrune, 1884, and *Pylmophis gracilis* Rochebrune, 1884. *Palaeovaranus filholi* De Stefano, 1903, was the second named species of the genus *Palaeovaranus*, and was established upon multiple specimens (a maxilla, dentaries, several vertebrae, and appendicular remains). Nevertheless, the validity of this taxon has been strongly questioned (e.g., Nopcsa 1908; Fejérváry 1918; Augé 2005) and the taxon is currently considered an indeterminate palaeovaranid (Georgalis 2017). *Odontomophis atavus* and *Pylmophis gracilis* were initially identified as snakes (Rochebrune 1884). *Odontomophis atavus* was established upon a dentary (Rochebrune 1884); *Pylmophis gracilis* was established upon two snake vertebrae, a snake "mummified" specimen, and a dentary (Rochebrune 1884), of which the former specimen was later designated as the lectotype of the species (Rage 1984). In any case, both these dentaries (holotype of *Odontomophis atavus* and paralectotype of *Pylmophis gracilis*) are currently considered to pertain to indeterminate palaeovaranids (see Georgalis 2017).

The Phosphorites du Quercy have also yielded helodermatids: *Eurheloderma gallicum* Hoffstetter, 1957, from the (probably) Eocene of the old collections of the Phosphorites du Quercy, was the first helodermatid described from Europe (Hoffstetter 1957). It remains the only so far named helodermatid taxon from the continent, as this group seems to be represented by rather infrequent finds in the European fossil record, mostly based on fragmentary and isolated cranial and postcranial remains (Augé 1995, 2003, 2005). Nevertheless, an astonishingly preserved, probably congeneric with *Eurheloderma*, specimen from Messel has been recently figured by Smith

Fig. 53. — *Palaeovaranus* sp. **A**-**E**, photographs of presacral vertebra NHMW 2019/0058/0003 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and right lateral (**E**) views; **F**-**J**, photographs of presacral vertebra NHMW 2019/0058/0014 in anterior (**F**), posterior (**G**), dorsal (**H**), ventral (**I**), and left lateral (**J**) views; **K**-**O**, photographs of presacral vertebra NHMW 2019/0058/0045 in anterior (**K**), posterior (**L**), dorsal (**M**), ventral (**N**), and left lateral (**O**) views; **P**-**T**, photographs of presacral vertebra NHMW 2019/0058/0004 in anterior (**P**), posterior (**Q**), dorsal (**R**), ventral (**S**), and left lateral (**T**) views; **U**-**Y**, photographs of presacral vertebra NHMW 2019/0058/0020 in anterior (**U**), posterior (**V**), dorsal (**W**), ventral (**X**), and right lateral (**Y**) views; **Z**-**D'**, photographs of presacral vertebra NHMW 2019/0058/0012 in anterior (**Z**), posterior (**A'**), dorsal (**B'**), ventral (**C'**), and left lateral (**D'**) views. Scale bar: 2 mm.

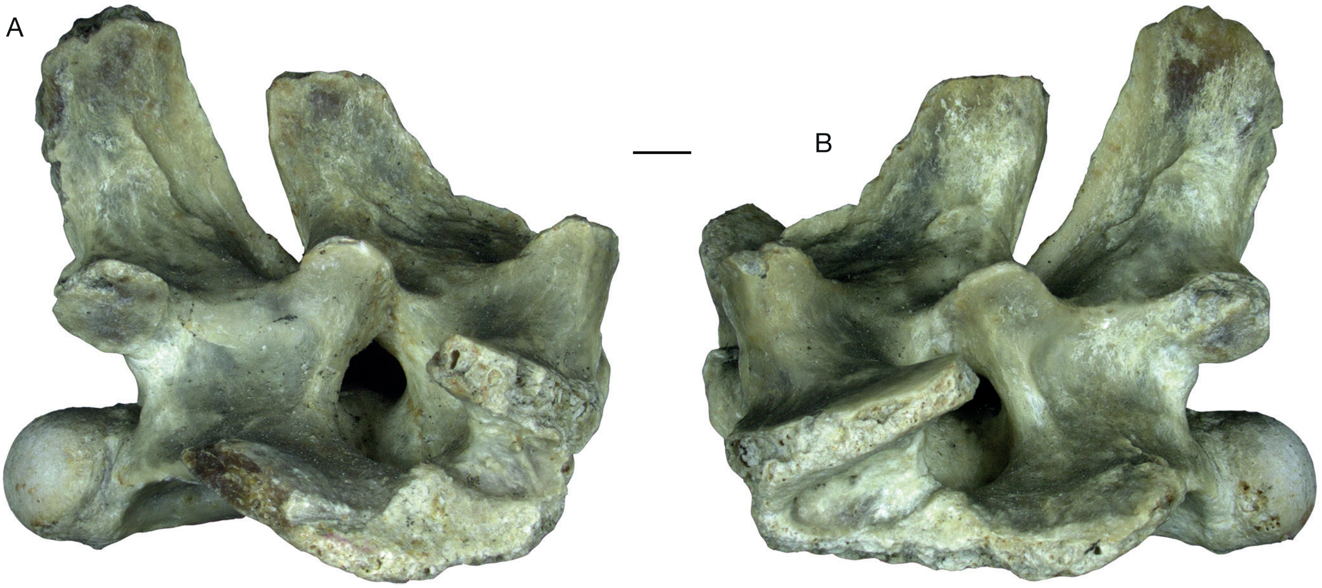

Fig. 54. — *Palaeovaranus* sp. Photographs of two articulated sacral vertebrae NHMW 2019/0058/0028 in right (**A**) and left lateral (**B**) views. Scale bar: 2 mm.

et al. (2018b), demonstrating that this lizard group was more widespread than what was previously thought.

Outside the area of the Phosphorites du Quercy, other named species of large platynotans from the Paleogene of Europe have been established from the early Eocene (MP 7) of Dormaal, Belgium, the early-middle Eocene (MP 11) of Messel, Germany, and the late early or middle Eocene of Geiseltal, Germany. These are *Saniwa orsmaelensis* Dollo, 1923, from Dormaal, "*Saniwa*" *feisti* Stritzke, 1983 from Messel, and *Eosaniwa koehni* Haubold, 1977, *Melanosauroides giganteus* Kuhn, 1940, and *Ophisauriscus eucarinatus* Kuhn, 1940, from Geiseltal.

Saniwa orsmaelensis represents so far the only "true" varanid named species from the Paleogene of Europe. Established on the basis of a maxilla, two vertebrae, and a femur (Dollo 1923), of which, however, only one trunk vertebra (IRSNB IG 8737) has been later figured (Hoffstetter 1969) and the same specimen has been subsequently treated as the lectotype (Estes 1983), while additional vertebral material has been described from the Eocene of Belgium and France (Augé 1990a, b, 2005). Nevertheless, *Saniwa* is a North American typified genus, known from there by rather complete material (Gilmore 1922, 1928; Rieppel & Grande 2007; Smith *et al.* 2018a); as the cranial material of the European species has not been figured, its congeneric affinities with the American species of *Saniwa* cannot be confirmed with certainty, although vertebral anatomy hints indeed towards a true resemblance among all these taxa (Gilmore 1922; Hoffstetter 1969; Estes 1983; Augé 2005; Rieppel & Grande 2007; Smith & Gauthier 2013). Pending that, for the time being, we here accept the inclusion of *S. orsmaelensis* into *Saniwa*, although we have to highlight the fact that its lectotype being a vertebra instead of a cranial element (see Estes 1983) is not an ideal case for varanids, as vertebrae of this group are subjected to variability and possess few or none diagnostic elements for distinction to the species level (see Delfino *et al.* 2013 and Georgalis *et al.* 2018). The redescription and figuring of the paralectotype maxilla of *S. orsmaelensis* is certainly much anticipated. "*Saniwa*" *feisti* is represented by several almost complete articulated skeletons with skulls, known exclusively from Messel (Stritzke 1983; Smith *et al.* 2018b). It was soon realized that it does not pertain to the varanid genus *Saniwa* but in fact probably belongs to palaeovaranids (Augé 1990b, 2005). Smith (2017) referred it as "*Necrosaurus feisti*" a name that appeared also in Smith *et al.* (2018b). Kuhn (1940b) established two large platynotan taxa from Geiseltal: *Melanosauroides giganteus* and *Ophisauriscus eucarinatus*. *Melanosauroides giganteus* was established upon a beautiful disarticulated skeleton with skull (GMH Ce III-4139-1933) which was later considered to have shinisaurian affinities (McDowell & Bogert 1954). On the other hand, the holotype of *Ophisauriscus eucarinatus*, is a much more incomplete specimen, being solely a hind limb with osteoderms (GMH Ce IV-4021-1933). Despite this incompleteness, Estes (1983), who considered both *Melanosauroides giganteus* and *Ophisauriscus eucarinatus* as conspecific, treated the latter as a senior synonym. This synonymy was widely accepted, with specimens even from Quercy attributed to this species, under the combination "*Necrosaurus eucarinatus*" (Augé 2005). Nevertheless, Georgalis (2017) demonstrated that the holotype of *Ophisauriscus eucarinatus* is not diagnostic at the species level and has to be considered a nomen dubium, with the material representing an indeterminate palaeovaranid, and of course having no actual relationship with the type species of that genus, the anguid *Ophisauriscus quadrupes* Kuhn, 1940, also from Geiseltal. A third platynotan taxon was subsequently named from Geiseltal by Haubold (1977): *Eosaniwa koehni*. This form was based on a single, articulated skeleton with a partial skull (Haubold 1977). *Eosaniwa koehni* was redescribed by Rieppel *et al.* (2007), who, in their phylogenetic analysis, confirmed also its platynotan affinities.

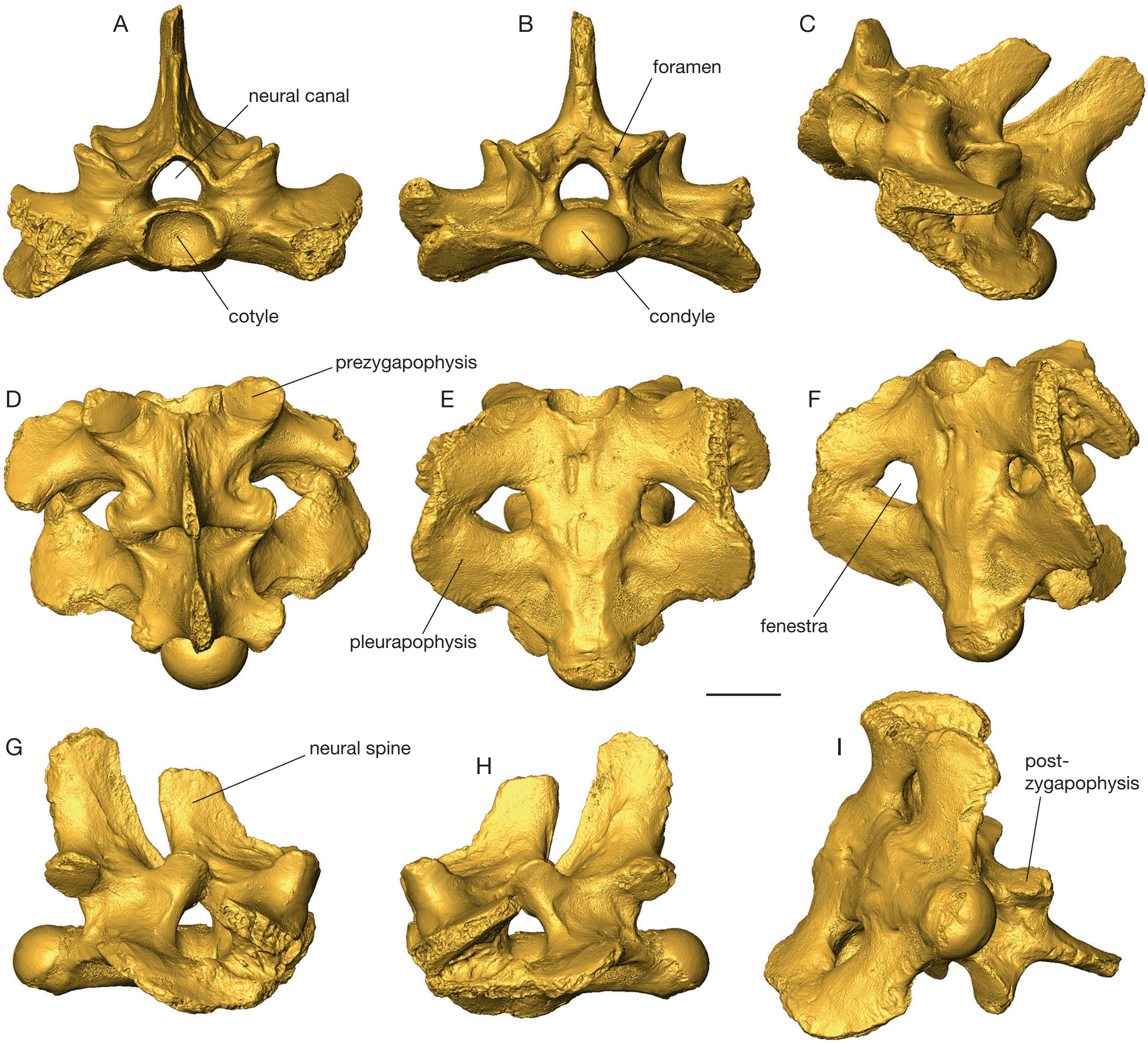

Fig. 55. — *Palaeovaranus* sp. Virtual 3D models of two articulated sacral vertebrae NHMW 2019/0058/0028 in anterior (**A**), posterior (**B**), anterolateral (**C**), dorsal (**D**), ventral (**E**), ventrolateral (**F**), right lateral (**G**), left lateral (**H**), and posteroventral (**I**) views. Scale bar: 5 mm.

Beyond all these named taxa, there is indication of even higher platynotan diversity: shinisaurians are present, though rather poorly represented in the Paleogene of Europe, known exclusively from three only occurrences, i.e., a well preserved tail from Messel (Smith 2017) as well as limited fragmentary cranial material from the late Oligocene of southern France (Vianey-Liaud *et al.* 2014) and southern Germany (Böhme 2008). Finally, a further, unnamed platynotan seems to have existed in the middle Eocene (MP 14) of Lissieu, France (Augé 2005; Rage & Augé 2010). The drawing of the single known parietal of this form (Augé 2005: fig. 201; Rage & Augé 2010: fig. 2.1) seems to denote a distinct form, characterized by the absence of dorsolateral crests in this element.

Parietals consist among the most diagnostic elements in anguimorph lizards (Klembara & Rummel 2018). This has been repeatedly demonstrated particularly for anguines, in which the majority of fossil forms are well defined on the basis of their parietal features (Klembara 1979, 1981, 2012, 2015; Klembara & Green 2010; Klembara & Rummel 2018). Parietals have also been shown to possess unique diagnostic features for other anguimorphs, such as lanthanotids (McDowell & Bogert 1954), shinisaurians (e.g., Klembara 2008; Smith & Gauthier 2013), helodermatids (e.g., Hoffstetter 1957; Augé 2005), and varanids (e.g., Ivanov *et al.* 2018). This taxonomic importance of parietals apparently applies also to the diverse Paleogene European platynotans. The case of *Palaeovaranus*, however, poses a relative taxonomic obstacle in this respect, as the holotype of its type species, *Palaeovaranus cayluxi*, is a maxilla and thus cannot afford any direct clue about the parietal morphology of this specimen. Nevertheless, we may

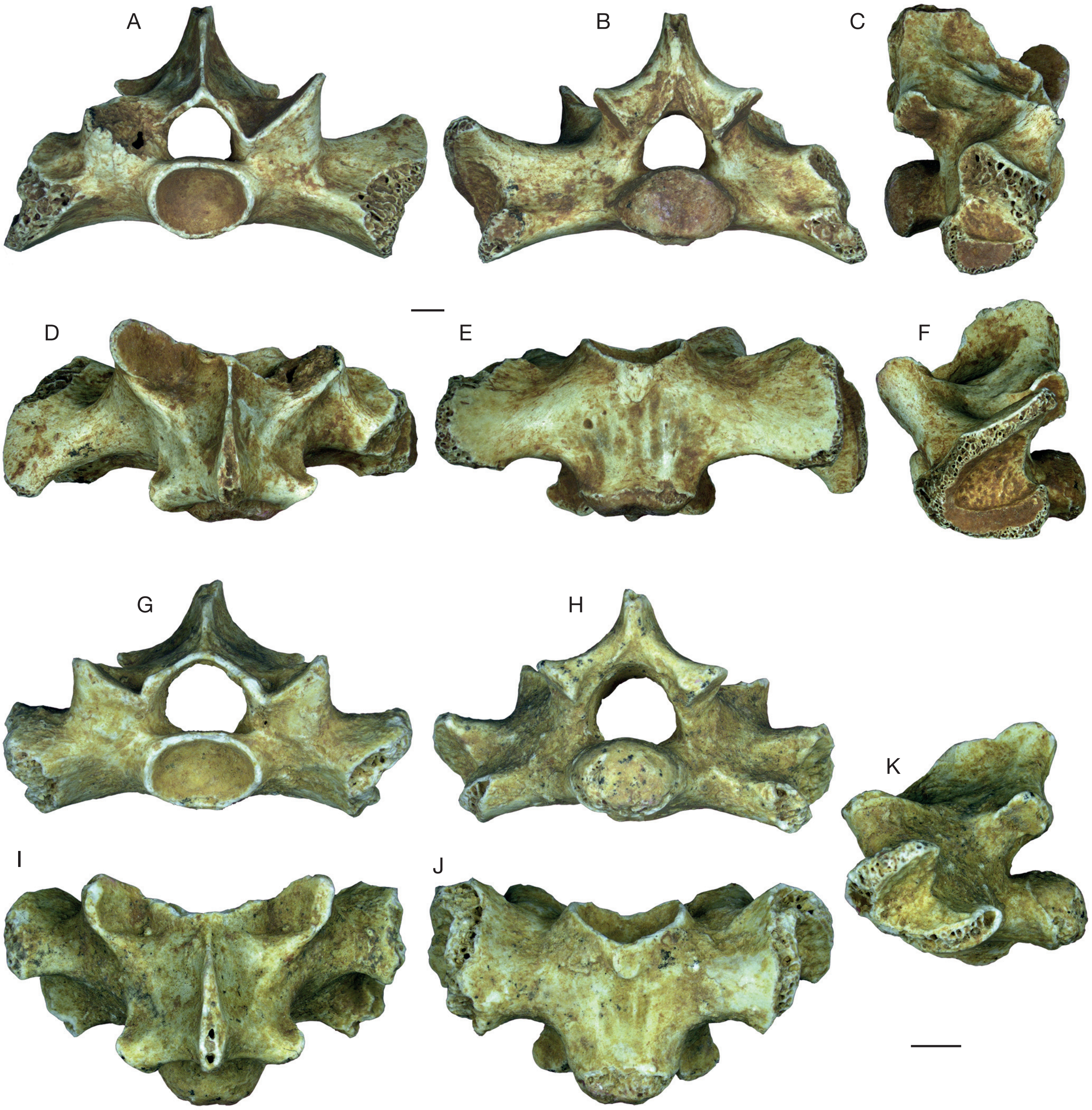

Fig. 56. — *Palaeovaranus* sp. **A**-**F**, photographs of sacral vertebra NHMW 2019/0058/0029 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), ventral (**E**), and left lateral (**F**) views; **G**-**K**, photographs of sacral vertebra NHMW 2019/0058/0047 in anterior (**G**), posterior (**H**), dorsal (**I**), ventral (**J**), and left lateral (**K**) views. Scale bars: 2 mm.

get information on the parietal morphology of *Palaeovaranus cayluxi*, on the basis of a referred parietal (SU.PAL.SNB 1006) from the late Eocene (MP 18) locality of Sainte Néboule in Quercy, described and figured by Rage (1978: fig. 3A). This element was found isolated and not in articulation with any maxillary material that would permit a direct comparison with the holotype of *Palaeovaranus cayluxi*. Nevertheless, Sainte Néboule has yielded also remains of maxillae, described and figured in the same paper by Rage (1978: fig. 3B), which are rather reminiscent of the holotype of *Palaeovaranus cayluxi*. Accordingly, Rage (1978) assigned both the parietal and the maxillary material to the same species. Of course, we have to admit that this situation is not ideal and it cannot be excluded the possibility that these two elements pertained to two distinct large platynotans. On the total lack, however, of any articulated cranium of *Palaeovaranus cayluxi* from the Phosphorites du Quercy, that would only then allow a confident referral of such isolated remains, and taking also into consideration the strong resemblance among the holotype maxilla of *Palaeovaranus cayluxi* and the referred maxillary

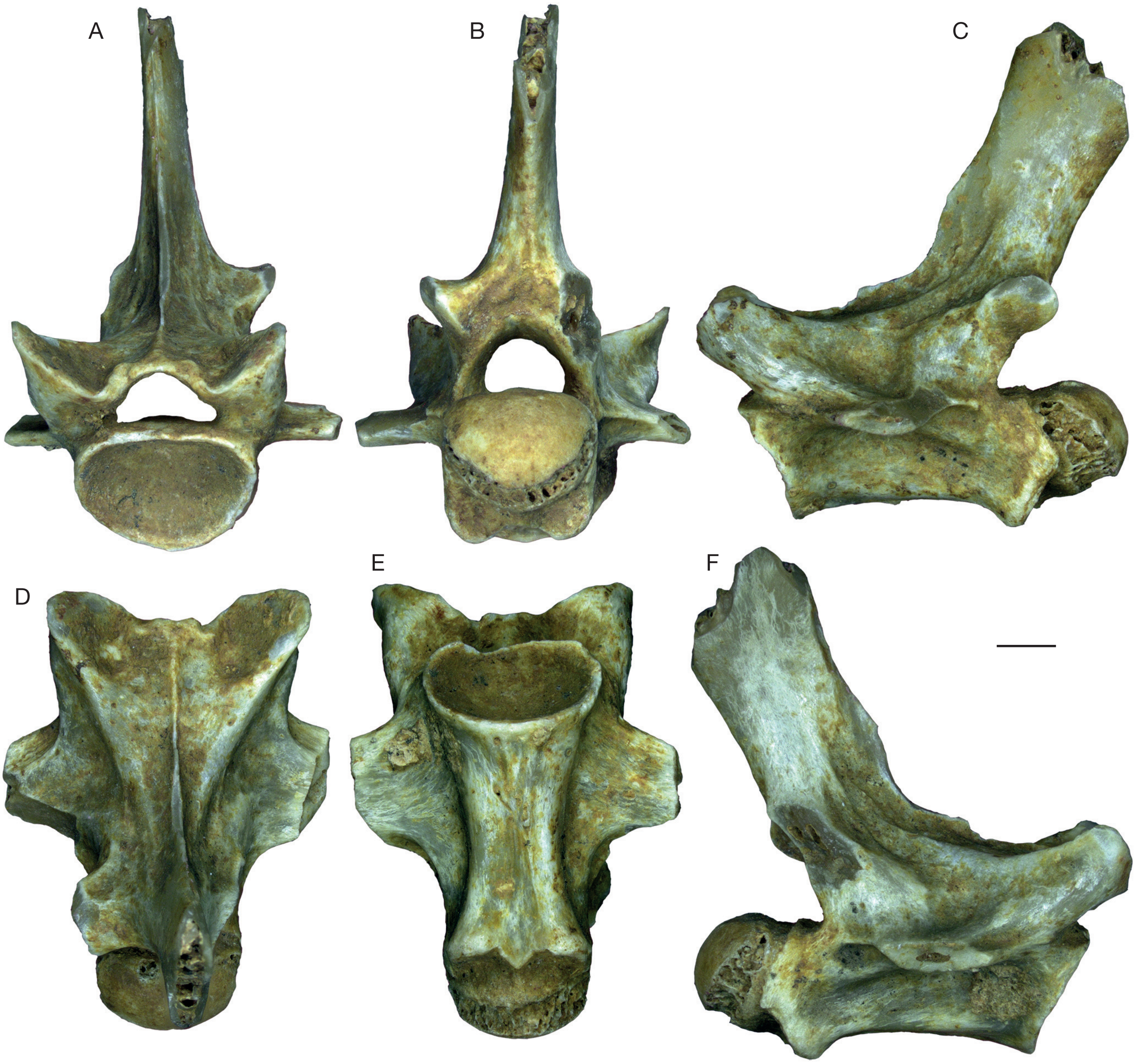

Fig. 57. — *Palaeovaranus* sp. Photographs of caudal vertebra NHMW 2019/0058/0035 in anterior (**A**), posterior (**B**), left lateral (**C**), dorsal (**D**), ventral (**E**), and right lateral (**F**), views. Scale bar: 2 mm.

material from Sainte Néboule, as well as the geographic and stratigraphic proximity of the type locality Escamps (MP 19) and Sainte Néboule (MP 18), we here have to follow Rage's (1978) opinion and consider that this parietal from Sainte Néboule pertains to *Palaeovaranus cayluxi*, allowing thus to understand the parietal morphology of this species. Note that this situation is relatively similar to the North American fossil platynotan *Provaranosaurus* Gilmore, 1942, the type species of which, *Provaranosaurus acutus* Gilmore, 1942, from the Paleocene of USA, is typified by a maxilla (Gilmore 1942), while a second referred species, *Provaranosaurus fatuus* Smith & Gauthier, 2013, from the early Eocene of United States, was typified by a dentary (Smith & Gauthier 2013). In any case, following Rage's (1978) suggested parietal morphology, Augé (2005: fig. 188) subsequently assigned another parietal (MNHN.F.QU17776), originating from the old collections of the Phosphorites du Quercy, to *Palaeovaranus cayluxi*. We also agree with the latter referral, and above provided photographs of this specimen for the first time (see Fig. 36). These being said, adding also our new parietal (NHMW 2019/0048/0001), *Palaeovaranus cayluxi* is currently known by three parietals. The different sizes of these three specimens, as well as the different ratios of median crest/midline of the triangular surface between the dorsolateral crests, allow a better, even if tentative, evaluation of intraspecific (or ontogenetic) variation in the parietal morphology of this species.

The parietal of *Palaeovaranus lismonimenos* n. sp. described in detail above offers a glimpse in an unexpected diversity of

Fig. 58. — *Palaeovaranus* sp. **A**-**E**, photographs of caudal vertebra NHMW 2019/0058/0036 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and left lateral (**E**) views; **F**-**J**, photographs of caudal vertebra NHMW 2019/0058/0037 in anterior (**F**), posterior (**G**), dorsal (**H**), ventral (**I**), and right lateral (**J**) views; **K**-**O**, photographs of caudal vertebra NHMW 2019/0058/0048 in anterior (**K**), posterior (**L**), dorsal (**M**), ventral (**N**), and left lateral (**O**) views; **P**-**T**, photographs of caudal vertebra NHMW 2019/0058/0049 in anterior (**P**), posterior (**Q**), dorsal (**R**), ventral (**S**), and left lateral (**T**) views. Scale bar: 2 mm.

FIG. 59. — *Saniwa* sp. Photographs of presacral vertebra NHMW 2019/0065/0001 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and left lateral (**E**) views. Scale bar: 2 mm.

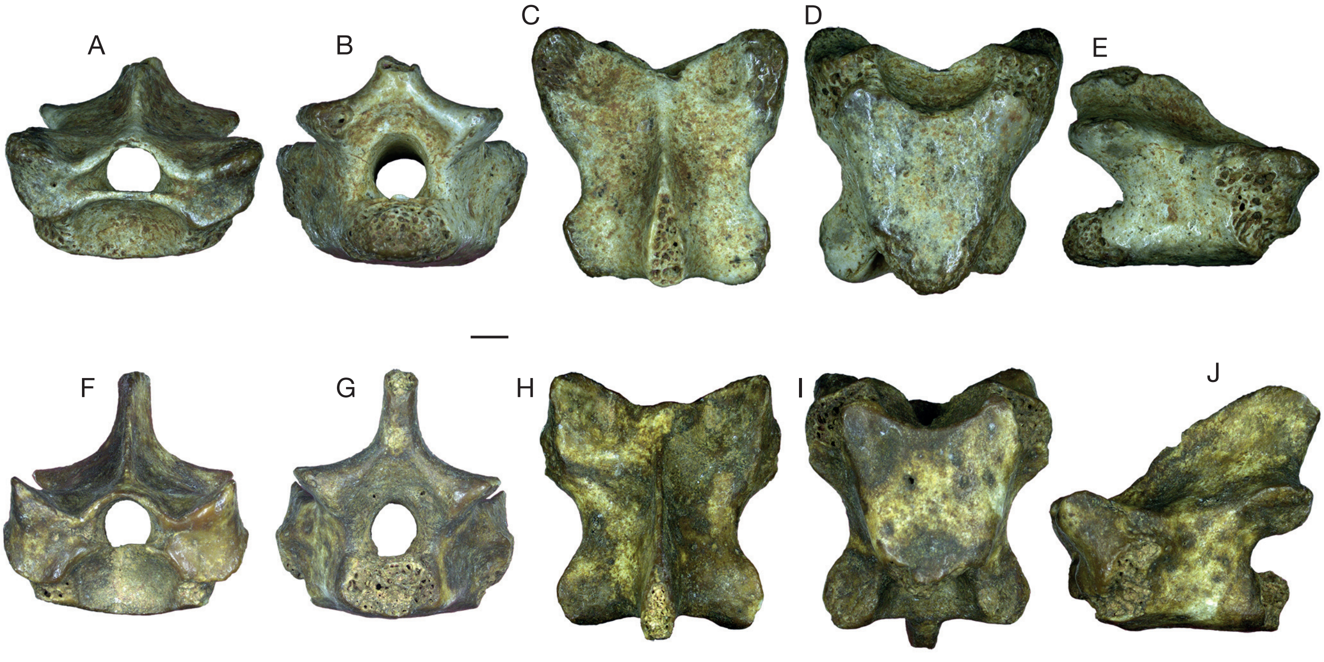

Fig. 60. — *Saniwa* sp. **A**-**E**, photographs of presacral vertebra NHMW 2019/0065/0002 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and right lateral (**E**) views; **F**-**J**, photographs of presacral vertebra NHMW 2019/0065/0003 in anterior (**F**), posterior (**G**), dorsal (**H**), ventral (**I**), and left lateral (**J**) views. Scale bar: 2 mm.

parietal structures and morphology in these Quercy platynotans. Furthermore, the referral of two previously described parietals of young individuals to the same species, offers the opportunity to assess ontogenetic variation in these lizards. The prominent ontogenetic parietal feature in *Palaeovaranus lismonimenos* n. sp. seems to be the fact that the dorsolateral crests do not coincide in early ontogenetic stages and seem to eventually approach and finally meet in adult individuals. Whether this feature is characteristic also in early ontogenetic stages of its congeneric species *Palaeovaranus cayluxi*, cannot be assessed with certainty, as juvenile parietals of that species are so far unknown.

The parietal of the holotype and only known specimen (GMH Ce III-4139-1933) of *Melanosauroides giganteus* from Geiseltal possesses a contrasting morphology with that of *Palaeovaranus* spp. This is obvious principally on the basis of its dorsolateral crests not meeting and the overall elongated shape of the element (see Georgalis 2017: fig. 4C). Taking into consideration that the feature of the dorsolateral crests inclining and forming a single median ridge in adults is regarded herein a defining feature in the emended diagnosis of the genus *Palaeovaranus*, the Geiseltal form has thus to be excluded from that genus. This is further supported by the distinct sculpturing pattern observed in the frontal of the holotype of *Melanosauroides giganteus*, as well as the much slender dentition of the German form in comparison with *Palaeovaranus* spp. Accordingly, we herein revalidate the genus *Melanosauroides* Kuhn, 1940, to accommodate this species. That being said, available data suggest that *Melanosauroides giganteus* is confined only to Geiseltal, with all the previously supposed conspecific forms from Quercy, pertaining to different forms (e.g., parietals and frontals now referred to *Palaeovaranus lismonimenos* n. sp.).

The parietal of the other so far valid species from Geiseltal, *Eosaniwa koehni*, is not preserved (Haubold 1977; Rieppel *et al.* 2007). The sculpturing pattern of its frontal, however, denotes that the condition is rather distinct from that of *Palaeovaranus* spp. Whether and how *Eosaniwa koehni* is related to its sympatric *Melanosauroides giganteus*, remains only to be answered when the holotype skeleton of the latter species will be comprehensively redescribed via CT scanning.

As was stated above, *Saniwa orsmaelensis* from Belgium and northern France, is so far poorly documented and no parietal is known for this species. Nevertheless, if its generic placement is correct, then it should have distinctive parietal morphology, judging from parietals known from congeneric specimens from North America, especially those of the genotype *Saniwa ensidens*, which was recently shown to possess a rather unique structure among all vertebrates, i.e., a pineal eye behind the third eye (Smith *et al.* 2018a). The general morphology of *Saniwa* parietals includes dorsolateral crests never meeting in the midline even throughout ontogeny (e.g., Gilmore 1922, 1928; Rieppel & Grande 2007; Smith *et al.* 2018a), so this genus is readily distinguished from *Palaeovaranus*.

Despite its completeness, and the relative abundance of complete specimens, the parietal of "*Saniwa*" *feisti* from Messel, has not yet been described in detail and adequately figured. Judging from newly furnished photographs of the holotype cast and other referred specimens (K. Smith, pers. communication, May 2019), it seems that the parietal morphology is much distinct than *Saniwa*, possessing a characteristic ornamentation. On the basis of its maxillary shape, we agree that it approaches more the condition of *Palaeovaranus*. Nevertheless, the overall shape of the parietal and the fact that the dorsolateral crests do not meet can readily

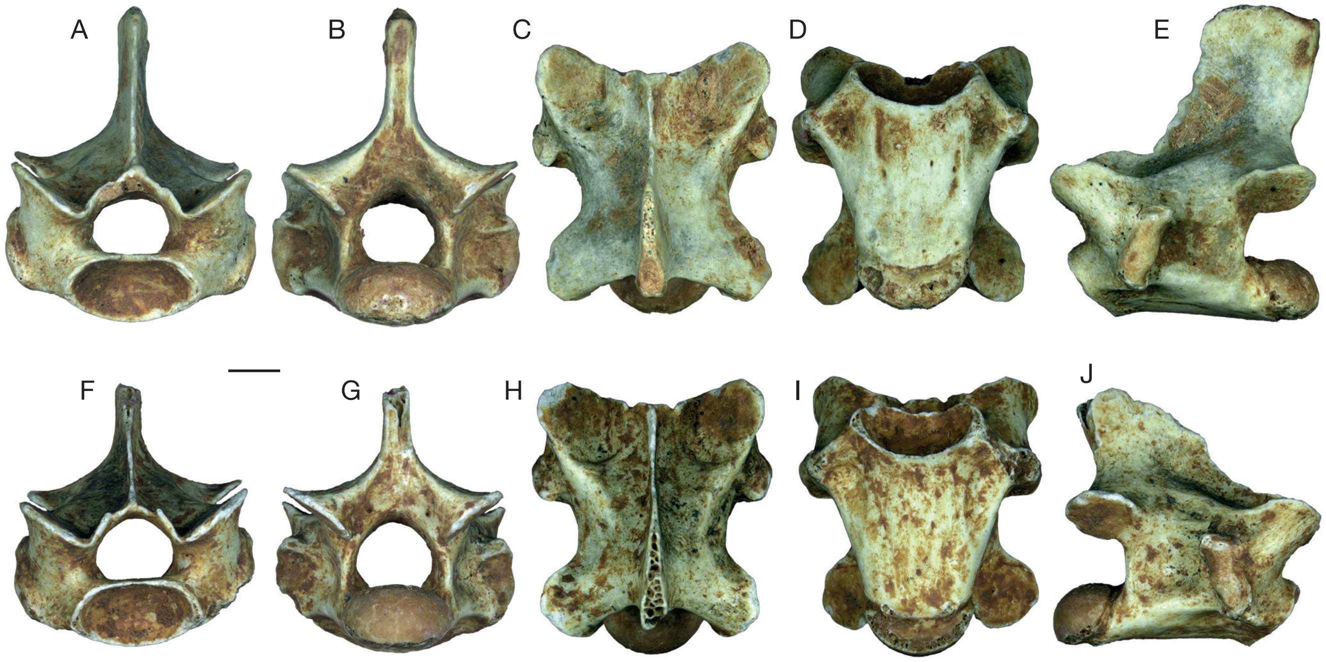

Fig. 61. — Anguimorpha indet. **A**-**E**, photographs of presacral vertebra NHMW 2019/0046/0005 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), and left lateral (**E**) views; **F**-**J**, photographs of presacral vertebra 2019/0046/0004 in anterior (**F**), posterior (**G**), dorsal (**H**), ventral (**I**), and right lateral (**J**) views. Scale bar: 2 mm.

differentiate it from *Palaeovaranus* spp. We tentatively suggest that a frontal (IRSNB R 249) from the early Oligocene of Boutersem, Belgium, described by Augé & Smith (2009: fig. 8) possesses a characteristic sculpturing pattern that is reminiscent of "*Saniwa*" *feisti.* It is of course beyond the scope of this paper to assess the taxonomic affinities of "*Saniwa*" *feisti* and we consider that a comprehensive redescription of the nicely preserved skeletons from Messel will shed light in its exact phylogenetic relationships.

Helodermatids possess a rather distinct parietal morphology; judging from our first hand observation of the type material of *Eurheloderma gallicum*, we can confirm that its parietal morphology is clearly distinct from *Palaeovaranus* spp. and other Paleogene platynotans. Lastly, there are no parietals preserved among the few known specimens of European Paleogene shinisaurians – nevertheless, their youngest Paleogene European occurrence (late Oligocene [MP 30] of Oberleichtersbach, southern Germany) was referred to *Merkurosaurus* Klembara, 2008, by Böhme (2008), a genus of which the parietal morphology is well known for younger, early Miocene specimens (Klembara 2008), and which is distinct from *Palaeovaranus* spp.

It is thus evident that European platynotans during the Paleogene, and especially during the Eocene, enjoyed a large taxonomic diversity, with an array of distinct genera and species characterized by unique parietal, frontal, maxillary, and dental morphologies. Nevertheless, it seems that the heyday of European platynotans did not continue into the Neogene, as only the varanid *Varanus* is known from the continent in the period (see Georgalis *et al.* 2018), with the sole exception of the much rarer shinisaurian *Merkurosaurus*, which has been recovered from the early Miocene of the Czech Republic and Germany (Klembara 2008; Čerňanský *et al.* 2015b). Platynotans totally vanished from Europe during the Quaternary, with their youngest record known from the Middle Pleistocene of Athens area in Greece (Georgalis *et al.* 2017).

PLACOSAURUS OR *PALAEOVARANUS*? THE TAXONOMIC CHALLENGE OF QUERCY LARGE LIZARD VERTEBRAE

As it is a common problem with disarticulated remains, the large anguimorph vertebrae that were frequently found in Quercy have been subjected to numerous different taxonomic referrals (Zittel 1887-1890; Lydekker 1888a; De Stefano 1903; Hoffstetter 1943; Rage 1978; Augé 2003, 2005). Especially, presacral vertebrae of *Placosaurus* and *Palaeovaranus*, pose a real taxonomic problem that has puzzled squamate researchers for several decades, due to the fact that they have a similar general absolute appearance and a comparable size range. This striking resemblance has lead to several misidentifications in the past, with palaeovaranid vertebrae being referred to glyptosaurines and vice versa, while apparently supporting the misconception about the purported synonymy of *Palaeovaranus* with *Placosaurus* followed by certain early workers, being especially advertised by Lydekker (1888a, b). This synonymy is now universally rejected, as cranial material has clearly demonstrated the much distant relationship of these two genera (Fejérváry 1935; Estes 1983; Augé 2005; Sullivan & Augé 2006; Georgalis 2017).

Hoffstetter (1943), after his study of the collections at the MNHN, suggested that palaeovaranid vertebrae had a distinct morphology that nevertheless deviated from the so called

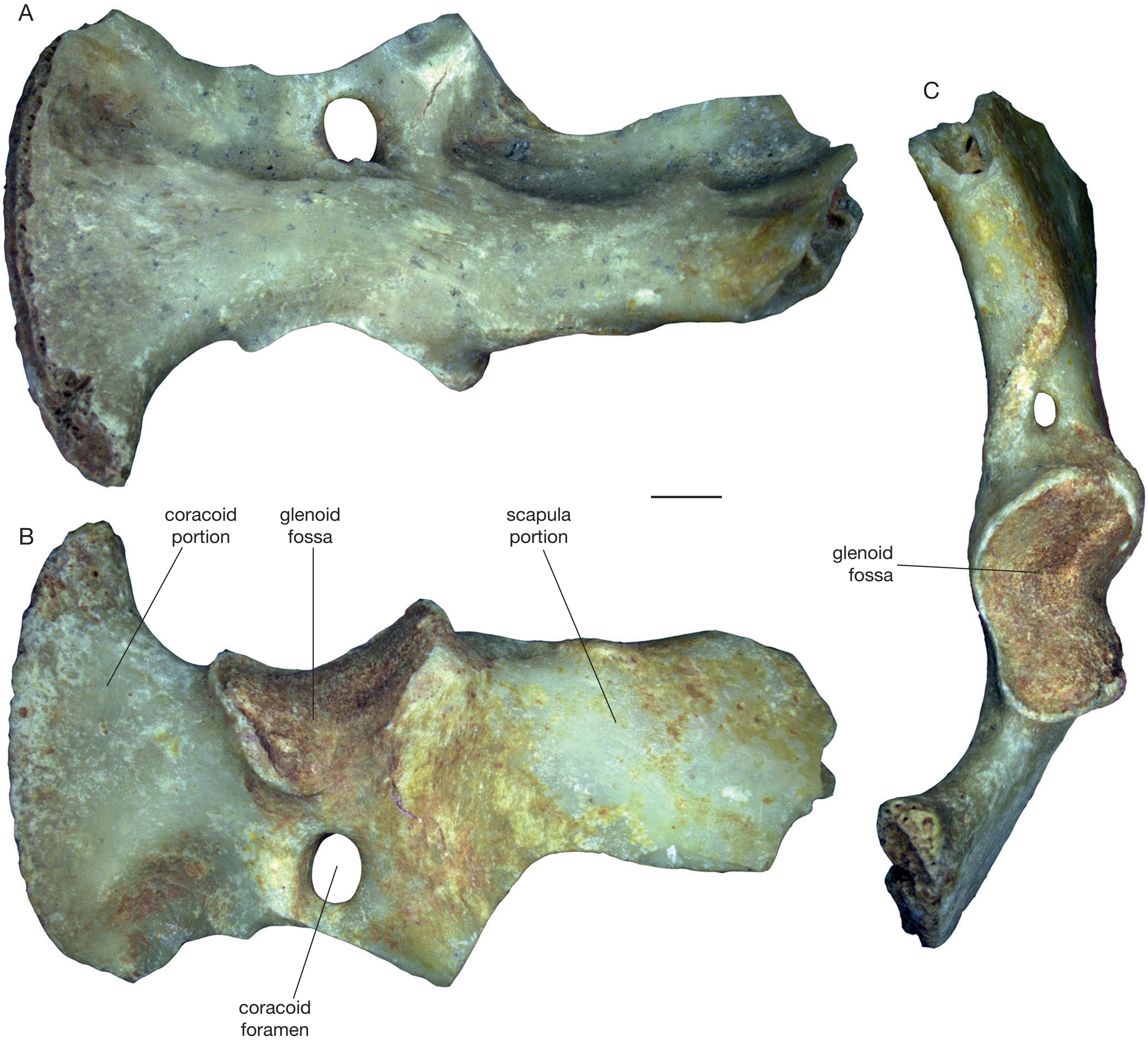

FIG. 62. — Anguimorpha indet. Photographs of pectoral girdle NHMW 2019/0095/0001 in dorsal (**A**), ventral (**B**), and posterolateral (**C**) views. Scale bar: 2 mm.

"varanian" style. According to the same author, the presacral vertebrae of palaeovaranids possess a more elongate centrum, which is much less convex in lateral view than in *Varanus*, their condyle is not enlarged transversely, and there is no strong precondylar constriction (Hoffstetter 1943). Nevertheless, Hoffstetter (1943) admitted that the palaeovaranid cervical and caudal vertebrae had much stronger resemblance with extant *Varanus* spp., with the former elements sharing "epiphyseal hypapophyses" and the latter ones sharing the presence of articulated chevron bones. The same author further referred to palaeovaranids previously figured vertebrae by Lydekker (1888a), Zittel 1887-1890), and De Stefano (1903). Subsequently, Hoffstetter (1954) and Hecht & Hoffstetter (1962) continued to address the similarities but also the differences among palaeovaranid, varanid, and anguid vertebrae, but still did not provide any figure.

Rage (1978) proposed differentiating characters to distinguish vertebrae of *Placosaurus* and *Palaeovaranus*, including the degree of convexity of the centrum, fusion of hypapophyses and haemapophyses to the centrum (also present in diploglossines and anguines, but not in *Palaeovaranus*), and differing degrees of dorsoventral compression between the three groups. On the basis of respective material from the late Eocene of Sainte Néboule, Quercy, the same author illustrated selected presacral and caudal vertebrae of both *Placosaurus* and *Palaeovaranus*, depicting the characteristic vertebral morphology of each genus (Rage 1978). It should be nevertheless noted that Rage (1978) made this referral of the vertebral material to *Placosaurus* and *Palaeovaranus* on the basis of the presence of isolated cephalic and trunk osteoderms of the former genus and maxillary remains of the latter one from the same locality; hence, it has to be noted that these vertebrae were not found in articulation with "diagnostic" cranial elements of the respective genera.

In any case, judging from his pictorial key, we can deduce that the main distinction of *Placosaurus* and *Palaeovaranus* presacral vertebrae is the presence of a median ridge in the ventral surface of the centrum of the former group (Rage 1978: fig. 2A; Fig. 21E), while in the latter group, the major difference is the presence of two distinct ridges running throughout the ventral surface of the centrum, interspaced by a shallow groove (Rage 1978: fig. 5A; Fig. 51F-G). The latter Rage's (1978) figure also depicts a distinct dorsal thickening of the neural spine of *Palaeovaranus* (Rage 1978: fig. 5A), however, it should be noted that such dorsal thickening is herein identified also in *Placosaurus* vertebrae from our collection, so this character is apparently much more widespread in large-sized lizards. Later on, however, in an almost contradictory way, Rage & Ford (1980: 51) described a seemingly similar median ridge that "constitutes a haemal keel" in a palaeovaranid vertebra from the late Eocene of the United Kingdom. With that specimen never figured, it is difficult to assess that claim and we thus prefer to maintain the presence of a median ridge in the ventral surface of the centrum as a characteristic of *Placosaurus* and not *Palaeovaranus*, as was figured by Rage (1978). In support of this, we confirm that vertebrae pertaining to articulated skeletons with skulls of large platynotans from the late early or middle Eocene of Geiseltal also possess these characteristic two distinct ridges in the ventral surface of their centra (e.g., holotype of *Melanosauroides giganteus* [GMH Ce III-4139-1933]; holotype of *Eosaniwa koehni* [GMH XXXVIII-57-1964]). Other features that have been used in the literature to distinguish (post-cervical) presacral vertebrae of *Palaeovaranus* and *Placosaurus* are that the former are generally higher and possess a deeper interzygapophyseal constriction (Hecht & Hoffstetter 1962; Augé 1990a).

Caudal vertebrae afford a clearer and more confident taxonomic referral. Indeed, caudal vertebrae of *Placosaurus* possess a characteristic shape of the chevron bones, which are attached to the centrum, being parallel and in certain distance one from each other and the presence and the position of the autotomic septum (Rage 1978). On the other hand, caudal vertebrae of *Palaeovaranus* are characterized by an elongated centrum, the lack of fused haemapophyses, the presence of two facets for the articulation with the chevrons, the neural spine developing in the posterior portion of the neural arch, and absence of an autotomic septum (Hecht & Hoffstetter 1962; Rage 1978; Rage & Ford 1980; Georgalis & Scheyer 2019). Furthermore, our material confirms that several caudal vertebrae of *Palaeovaranus* possess "pseudozygosphenes" and "pseudozygantra", an otherwise typical feature of the varanid *Saniwa*, which has anyway, however, been also reported in the literature for palaeovaranid caudal vertebrae (Augé 1990a).

It is worth noting, however, that the well documented glyptosaurine *Helodermoides tuberculatus* Douglass, 1903, known from several complete articulated and disarticulated skeletons from the Oligocene of North America has a caudal vertebral morphology that seems to approach much that of European palaeovaranids, at least judging from an autotomic caudal figured by Sullivan (1979a: figs 2-3). This morphology is strongly similar especially in the pedicles for the articulation for the chevron bones, the shape of the neural spine, the dorsal inclination of the prezygapophyses, and the overall size, however, the caudal vertebra of *Helodermoides* Douglass, 1903, figured in Sullivan (1979a) bears an autotomic septum, a feature that is totally absent in European palaeovaranids. Nevertheless, non-autotomic vertebrae (even if only few) are known in *Helodermoides* skeletons, but still, caudal vertebrae with autotomy planes are much more abundant, as is the case with all anguids (Sullivan 1979a).

The relatively easy distinguishment of caudal vertebrae of *Palaeovaranus*, has enabled their identification since the late 19th century, in several localities, not only in the area of the Phosphorites du Quercy (Zittel 1887-1890; De Stefano 1903; Rage 1978; Rage & Augé 2015), but also in other European regions (Rage & Ford 1980; Georgalis & Scheyer 2019). To the contrary, caudal vertebrae of *Placosaurus* are still apparently rare, with the only figure that was so far provided being that of Rage (1978) from the locality of Sainte Néboule. Note, however, that a relatively similar caudal vertebra has been described and figured by Hoffstetter (1962: fig. 2) from the late Eocene of Mormont, Switzerland, with that author questionably referring it to the anguid genus *Paraxestops* Hoffstetter, 1962. Whether this Swiss specimen belongs also (or not) to *Placosaurus*, a genus that is anyway present in the area of Mormont (Pictet *et al.* 1855-1857), remains to be confirmed only in the light of more complete finds and more abundant material.

THE SIGNIFICANCE OF THE QUERCY SQUAMATE COLLECTIONS

The new "old material" of lizards from Quercy described herein provides an important insight about the diversity of the squamate faunas of this area. Both old and recent collections of lizards and snakes from the Phosphorites du Quercy reveal a large diversity of taxa, unparalleled by any other area in the Paleogene of Europe, with a huge array of morphotypes, bauplans, sizes, and ecological and locomotory adaptations. Especially for the recent collections that contain well stratigraphically constrained data, such fossils from Quercy offer a unique opportunity to assess biogeographic patterns, dispersal scenarios, faunal turnovers, and extinction events. Notably, the succession of latest Eocene and earliest Oligocene localities in the area of the Phosphorites du Quercy can afford quantitative studies on the effect of squamate faunal turnover during the Grande Coupure, one of the most significant extinction events that took place in Europe during the Cenozoic.

The new species established in this paper reveal that we still have to learn much more about the lizard faunas from the Phosphorites du Quercy, which certainly offer a unique window in our understanding of the evolution of squamate faunas in the Paleogene of Europe. Admittedly, the non-precise age and unknown exact type localities does not represent an ideal case, but nevertheless, this is often the situation for many other extinct squamates from the Phosphorites du Quercy that are currently considered as valid. Such cases are the lacertid *Pseudeumeces cadurcensis* (Filhol, 1877), the glyptosaurines *Placosaurus europaeus* (Filhol, 1876) and *Paraplacosauriops quercyi* (Filhol, 1882), the agamids *Quercygama galliae* (Filhol, 1877) and *Uromastyx europaeus* (De Stefano, 1903), the iguanids *Geiseltaliellus lamandini* (Filhol, 1877) and *Pseudolacerta mucronata* (Filhol, 1877), the helodermatid *Eurheloderma gallicum* Hoffstetter, 1957, the gekkotan *Cadurcogekko piveteaui* Hoffstetter, 1946, the constrictor (sensu Georgalis & Smith 2020) snakes *Palaeopython cadurcensis* (Filhol, 1877), "*Palaeopython*" *filholii* Rochebrune, 1880, "*Palaeopython*" *neglectus* Rochebrune, 1884, *Plesiotortrix edwardsi* Rochebrune, 1884, and *Rageophis lafonti* (Filhol, 1877), but also taxa established much more recently as well, such as the "erycine" *Cadurceryx filholi* Hoffstetter & Rage, 1972, the colubriform *Natrix mlynarskii* Rage, 1988, the teiid *Brevisaurus smithi* Augé, 2005, and the scincid *Ayalasaurus tenuis* Augé, 2005. Therefore, to these 18 Quercy valid taxa with non-precisely known type localities, we now add the two new species described herein, *Pseudeumeces kyrillomethodicus* n. sp. and *Palaeovaranus lismonimenos* n. sp., highlighting that distinctive anatomical features must always be valued over good stratigraphic data, when the latter are not adequately available.

Acknowledgements

We are rather pleased to participate in this volume dedicated to the memory of our dear colleague Jean-Claude Rage. The squamates of the Phosphorites du Quercy were always a main interest for Jean-Claude, whose work revitalized and advanced to a large extent the knowledge of these faunas. The legacy he left on fossil squamate taxonomy, evolution, and palaeobiogeography is invaluable.

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APPENDIX 1. — Centrum lengths of all lizard vertebrae from the NHMW Quercy collection.

Specimen	**Taxon**	**Type of vertebra**	**centrum length (mm)**
Placosaurus sp.			
NHMW 2019/0046/0001	*Placosaurus* sp.	presacral vertebra	9.8
NHMW 2019/0046/0002	*Placosaurus* sp.	presacral vertebra (cervical)	8.5
NHMW 2019/0046/0008	*Placosaurus* sp.	presacral vertebra	?
NHMW 2019/0046/0009	*Placosaurus* sp.	caudal vertebra	9.5
Melanosaurini indet.			
NHMW 2019/0094/0002	Melanosaurini indet.	presacral vertebra	9.4
NHMW 2019/0094/0003	Melanosaurini indet.	presacral vertebra	8.4
NHMW 2019/0094/0001	Melanosaurini indet.	presacral vertebra	8.0
NHMW 2019/0094/0005	Melanosaurini indet.	presacral vertebra	*c.* 6.0
NHMW 2019/0094/0004	Melanosaurini indet.	?sacral vertebra	8.0
Anguinae indet.			
NHMW 2019/0093/0001	Anguinae indet.	presacral vertebra	8.4
NHMW 2019/0093/0002	Anguinae indet.	presacral vertebra	8.4
Palaeovaranus sp.			
NHMW 2019/0058/0003	*Palaeovaranus* sp.	presacral vertebra	10.8
NHMW 2019/0058/0005	*Palaeovaranus* sp.	presacral vertebra	10.8
NHMW 2019/0058/0001	*Palaeovaranus* sp.	presacral vertebra	10.2
NHMW 2019/0058/0013	*Palaeovaranus* sp.	presacral vertebra	10.1
NHMW 2019/0058/0030	*Palaeovaranus* sp.	presacral vertebra	10.1
NHMW 2019/0058/0014	*Palaeovaranus* sp.	presacral vertebra	10.0
NHMW 2019/0058/0017	*Palaeovaranus* sp.	presacral vertebra	10.0
NHMW 2019/0058/0006	*Palaeovaranus* sp.	presacral vertebra	9.8
NHMW 2019/0058/0007	*Palaeovaranus* sp.	presacral vertebra	9.6
NHMW 2019/0058/0025	*Palaeovaranus* sp.	presacral vertebra	9.5
NHMW 2019/0058/0008	*Palaeovaranus* sp.	presacral vertebra	9.3
NHMW 2019/0058/0009	*Palaeovaranus* sp.	presacral vertebra	9.3
NHMW 2019/0058/0011	*Palaeovaranus* sp.	presacral vertebra	9.3
NHMW 2019/0058/0019	*Palaeovaranus* sp.	presacral vertebra	9.3
NHMW 2019/0058/0045	*Palaeovaranus* sp.	presacral vertebra	9.3
NHMW 2019/0058/0041	*Palaeovaranus* sp.	presacral vertebra	9.0
NHMW 2019/0058/0023	*Palaeovaranus* sp.	presacral vertebra	8.8
NHMW 2019/0058/0021	*Palaeovaranus* sp.	presacral vertebra	8.6
NHMW 2019/0058/0004	*Palaeovaranus* sp.	presacral vertebra	8.4
NHMW 2019/0058/0044	*Palaeovaranus* sp.	presacral vertebra	8.3
NHMW 2019/0058/0020	*Palaeovaranus* sp.	presacral vertebra	8.2
NHMW 2019/0058/0022	*Palaeovaranus* sp.	presacral vertebra	8.2
NHMW 2019/0058/0043	*Palaeovaranus* sp.	presacral vertebra	8.1
NHMW 2019/0058/0015	*Palaeovaranus* sp.	presacral vertebra	7.9
NHMW 2019/0058/0046	*Palaeovaranus* sp.	presacral vertebra	7.9
NHMW 2019/0058/0012	*Palaeovaranus* sp.	presacral vertebra	7.6
NHMW 2019/0058/0016	*Palaeovaranus* sp.	presacral vertebra	7.6
NHMW 2019/0058/0002	*Palaeovaranus* sp.	presacral vertebra	7.4
NHMW 2019/0058/0024	*Palaeovaranus* sp.	presacral vertebra	7.4
NHMW 2019/0058/0042	*Palaeovaranus* sp.	presacral vertebra	7.3
NHMW 2019/0058/0027	*Palaeovaranus* sp.	presacral vertebra	7.0
NHMW 2019/0058/0018	*Palaeovaranus* sp.	presacral vertebra	?
NHMW 2019/0058/0026	*Palaeovaranus* sp.	presacral vertebra	?
NHMW 2019/0058/0051	*Palaeovaranus* sp.	presacral vertebra	?
NHMW 2019/0067/0001	*Palaeovaranus* sp.	presacral vertebra	?
NHMW 2019/0058/0028	*Palaeovaranus* sp.	(two articulated) sacral vertebrae	*c.* 11.5 (the second)
NHMW 2019/0058/0029	*Palaeovaranus* sp.	sacral vertebra	8.3
NHMW 2019/0058/0047	*Palaeovaranus* sp.	sacral vertebra	6.0
NHMW 2019/0058/0037	*Palaeovaranus* sp.	caudal vertebra	15.9
NHMW 2019/0058/0049	*Palaeovaranus* sp.	caudal vertebra	15.4
NHMW 2019/0058/0031	*Palaeovaranus* sp.	caudal vertebra	14.0
NHMW 2019/0058/0033	*Palaeovaranus* sp.	caudal vertebra	14.9
NHMW 2019/0058/0034	*Palaeovaranus* sp.	caudal vertebra	14.5
NHMW 2019/0058/0036	*Palaeovaranus* sp.	caudal vertebra	14.3
NHMW 2019/0058/0038	*Palaeovaranus* sp.	caudal vertebra	13.8
NHMW 2019/0067/0002	*Palaeovaranus* sp.	caudal vertebra	12.9
NHMW 2019/0058/0040	*Palaeovaranus* sp.	caudal vertebra	12.8
NHMW 2019/0058/0050	*Palaeovaranus* sp.	caudal vertebra	11.8
NHMW 2019/0058/0035	*Palaeovaranus* sp.	caudal vertebra	11.7
NHMW 2019/0058/0039	*Palaeovaranus* sp.	caudal vertebra	11.3
NHMW 2019/0058/0048	*Palaeovaranus* sp.	caudal vertebra	10.4
NHMW 2019/0058/0052	*Palaeovaranus* sp.	caudal vertebra	10.4
NHMW 2019/0058/0053	*Palaeovaranus* sp.	caudal vertebra	10.1
NHMW 2019/0058/0032	*Palaeovaranus* sp.	caudal vertebra	8.9

Appendix 1. — Continuation.

Specimen	Taxon	Type of vertebra	centrum length (mm)
Saniwa sp.			
NHMW 2019/0065/0001	*Saniwa* sp.	presacral vertebra	9.6
NHMW 2019/0065/0002	*Saniwa* sp.	presacral vertebra	9.2
NHMW 2019/0065/0003	*Saniwa* sp.	presacral vertebra	*c.* 8.8
Anguimorpha indet.			
NHMW 2019/0046/0003	Anguimorpha indet.	presacral vertebra	9.3
NHMW 2019/0046/0006	Anguimorpha indet.	presacral vertebra	8.7
NHMW 2019/0046/0005	Anguimorpha indet.	presacral vertebra	7.9
NHMW 2019/0046/0004	Anguimorpha indet.	presacral vertebra	7.8
NHMW 2019/0046/0007	Anguimorpha indet.	presacral vertebra	6.9
Squamata indet.			
NHMW 2019/0095/0002	Squamata indet.	?sacral vertebra	7.7