

Roots of the European Cenozoic ecosystems: lizards from the Paleocene (~MP 5) of Walbeck in Germany

Andrej Čerňanský¹, Davit Vasilyan^{2,3}

¹ Department of Ecology, Laboratory of Evolutionary Biology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, Ilkovičova 6, 842 15 Bratislava, Slovakia

² JURASSICA Museum, Route de Fontenais 21, 2900 Porrentruy, Switzerland

³ Department of Geosciences, University of Fribourg, Chemin du musée 6, 1700, Fribourg, Switzerland

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Corresponding author: Andrej Čerňanský (cernansky.paleontology@gmail.com)

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Abstract

We studied at least part of Kuhn's original material of lizards from the Paleocene (~MP 5) of the Walbeck locality in Germany. The collection was considered to be lost but is consistently discussed in the literature due to its importance. We restudied the type material of aff. *Parasauromalus paleocenicus* and aff. *Glyptosaurus walbeckensis* described by Kuhn in 1940. The former was originally allocated to Iguania, the latter to Anguimorpha, though later on these identifications were questioned by several authors. We show such a classification of both cannot be upheld. *P. paleocenicus* resembles the morphology of lacertids showing their presence in Europe already around MP 5. We consider the name *P. paleocenicus* as a nomen dubium. The material of aff. *G. walbeckensis* was later suggested to belong to Lacertidae and also considered as a potential amphisbaenian. Although it differs from modern amphisbaenians, it shares features with one supposed polyodontobaenid – *Camptognathosaurus parisiensis*. The Walbeck form is identical to this species. Since the Walbeck taxon was described in 1940, the principle of priority makes *Camptognathosaurus parisiensis* a junior synonym of the species erected by Kuhn. We propose a new combined name for this form, *Camptognathosaurus walbeckensis* comb. nov. The specimen figured by Kuhn is currently lost, thus we designate a neotype from Walbeck. However, this taxon differs significantly from *Polyodontobaena* and new data doubt the attribution of *Camptognathosaurus* to Amphisbaenia. This taxon is tentatively assigned here to Lacertidae, as further confirmed by phylogenetic analyses. Material of Scincoidea is also described.

Key Words

early Paleogene, Europe, Lacertidae, Scincoidea, Squamata

Introduction

Palaeoherpetafaunas of the Paleocene are extremely rare in Europe and, thus, very little is known about squamates from this epoch. We here redescribed and revised lizards from the Paleocene of Walbeck fissure filling in Sachsen-Anhalt in Germany (Fig. 1). The mammalian fauna allowed to correlate the vertebrate assemblage likely to the middle Selandian age and probably corresponding to the European Paleogene mammalian reference interval MP 5 (De Bast et al. 2013; De Bast and Smith 2016). Walbeck is the only known Paleocene fossil site from

Germany and one of the few Paleocene localities known from Europe as a whole. Thus, this locality represents one of the unique and rare exceptions, serving as a window into the late Paleocene world. The fossiliferous sediments of Walbeck with Paleocene continental vertebrates were reworked by a transgressing Oligocene sea and deposited in protected fissures in Muschelkalk limestone (e.g., Storch 2008). Although a reworking of the sediments and fossils of the karstic pocket is present, all studies suggested that the continental vertebrates of Walbeck should have Paleocene age (Russell 1964). The fissure filling was excavated in 1939, and about fifteen tons

of sediment were processed (e.g., Weigelt 1939, 1940, 1942). As the pocket was fully excavated, it cannot be recollected. Dehm (1961) discussed Walbeck and noted how extensive it was: c. 15,000 specimens in a small pocket. The vertebrate fauna was studied already in early 20th century (e.g., Kuhn 1940a, b; Russell 1966; Weigelt 1942). Recently mammals and birds have been restudied, and their taxonomy has been revised (Mayr 2002, 2007; Storch 2008; Rose et al. 2015).

Here, we study a part of the original Kuhn's lizard material. In fact, since Kuhn did not use collection numbers, poorly figured only a few specimens, and provided limited descriptions, the recognition of number and allocation of old specimens studied by him is extremely limited. Besides lizards, Kuhn (1940a) also documented the earliest Cenozoic occurrence of Constrictores from Europe [this material is not included here, but Georgalis et al. (2021a) remarked on the size of these snakes]. In any case, the collection was considered to be lost for many years (Estes 1983; Rage and Augé 1993) but mentioned and discussed in the literature for decades due to its importance to our knowledge of the Paleocene (e.g., Estes 1983; Rage and Augé 1993; Augé 2005; Čerňanský and Augé 2013; Čerňanský et al. 2020a; Georgalis et al. 2021b). This material sheds new light on the early evolution of some lizard taxa and demonstrates the palaeodiversity of archaic members of lizard lineages in the late Paleocene of Europe.

Among squamates, for particular reasons, one of the groups one could expect in the Paleocene of Europe

are lacertids. They are the dominant reptilian group in Europe, where the origin of the clade has been also suggested (Arnold et al. 2007, and references therein). This hypothesis has been also supported by the fossil record (Borsuk-Bialynicka et al. 1999; Čerňanský and Augé 2013; Čerňanský and Smith 2018). Descendants of the basal-most divergence in crown Lacertidae, between Gallotiinae and Lacertinae, are also documented from Europe (the Oligocene *Pseudeumeces* and *Dracaenosaurus* and the Miocene *Janosikia*; see Čerňanský et al. 2016a, 2017). Based on molecular analyses, the Lacertidae clade has been estimated to diverge from its sister lineage before the Mesozoic-Cenozoic boundary (Vidal and Hedges 2009). According to Hipsley et al. (2009), modern lacertids arose shortly after the Cretaceous-Paleogene (K/P) transition. In a recent study, crown ages were recovered for Lacertidae in the Paleocene (Garcia-Porta et al. 2019). In any case, their fossil record is unknown in the Mesozoic. In the Paleocene, their fossils are extremely rare, sometimes even doubtful (Rage, 2013). A frontal tentatively allocated to Lacertidae was described from the upper Paleocene locality of Cernay (Čerňanský et al. 2020a; reference locality of MP 6, BiochroM 1997).

In regard to Walbeck, Kuhn (1940a) described isolated vertebra as *Saniwa* aff. *ensidens* and stated its similarity to this American varanoid. He also described an isolated dentary as “aff. *Parasauromalus paleocenicus* sp. nov.”, a new iguanian taxon. Kuhn also referred the species to *Iguanosaurus* (see Kuhn 1944) and to *Iguanosauriscus*



Figure 1. Location of Walbeck in Germany and other Paleocene localities of Northern France that yielded *Camptognathosaurus*.

(see Kuhn 1958; see also Estes 1983). Later, it was referred to Lacertidae by Estes (1983), who also tentatively reclassified it into *Plesiolacerta*. However, because the specimens were considered to be probably lost (see Estes 1983), the systematic position of the taxon has remained uncertain. Kuhn (1940a) also established the species aff. *Glyptosaurus walbeckensis*. Kuhn in 1940b better figured two specimens of this species (see Kuhn 1940b: tab II, fig. 4 and tab. III fig. 3). However, Estes (1983) rejected its glyptosaurine affinities and suggested that it was a lacertid as well and tentatively referred it to *Pseudeumeces*. Later, Augé (2005) suggested that it was a potential amphisbaenian and considered it a nomen dubium. Indeed, the Amphisbaenia clade is documented by a relatively rich fossil Paleocene record. Their fossils are known from America (Sullivan 1985; Longrich et al. 2015), Europe (Belgium and France, see Folie et al. 2013) and Africa (Augé and Rage 2006). These reptiles originated most likely in North America (Longrich et al. 2015). Later, they radiated and dispersed in the Paleogene following the Cretaceous-Paleogene (K-P) extinction. It seems that these events were somehow connected to the extinction, which has clearly an impact on squamate faunas as well (see Longrich et al. 2012, 2015).

The study of Walbeck lizards will help to resolve the allocation of the problematic Paleocene lizard taxa. Moreover, it can help better understand the Paleocene - the poorly known epoch which represents the beginning of the Cenozoic.

Institutional abbreviations

CR, Cernay-lès-Reims, collections at the Natural History Museum of Paris, France; **MLU**, the Institut für Geologische Wissenschaften und Geiseltalmuseum, Martin-Luther-Universität Halle-Wittenberg; **NHMW**, the Natural History Museum Vienna, Austria; **RIV PP**, Rivecourt-Petit Pâtis, collection houses at the Compiègne Museum, France; **SMF ME**, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany.

Materials and methods

Specimens examined, photography and terminology

All studied specimens are housed at the Institut für Geologische Wissenschaften und Geiseltalmuseum, Martin-Luther-Universität Halle-Wittenberg (MLU). The specimens were photographed using a Keyence VHX970 digital light microscope at the JURASSICA Museum (Porrentruy, Switzerland). The image processing program ImageJ (Schneider et al. 2012) was used for measurements. The terminology for teeth follows Richter (1994) and Kosma (2004). The terminology of the individual structures of the vertebrae are primarily from Hoffstetter

and Gasc (1969) and Tschopp (2016). Taxonomy follows Zheng and Wiens (2016) where the clade Lacertoidea includes Lacertidae, Amphisbaenia, Teiidae and Gymnophthalmidae (Laterata sensu Vidal & Hegdes, 2005; Burbrink et al. 2020) and, where Scincoidea consists of Xantusiidae, Gerrhosauridae, Cordylidae and Scincidae. However, others, such as Burbrink et al. (2020), use a different concept of Scincoidea that does not include cordyliforms. The authors unite the families Cordylidae and Gerrhosauridae into a clade Cordyloidea, which is a sister group to Xantusiidae.

The outline figure of the mandible of the holotype (SMF ME 2604) of *Cryptolacerta hassiaca* was redrawn from figures published by Müller et al. (2011: fig. 1). The left dentary of *C. hassiaca* found in the gut of *Paranecrosaurus feisti* was redrawn from figures published by Smith and Habersetzer (2021: fig. 26C-E). GE Phoenix nanotom VR 180 X-ray tomography nano-CTVR system at the Slovak Academy of Sciences in Bratislava was used (Fairfield, CT) for μ CT scanning of the holotype left dentary (NHMW 2019/0051/0001) of *Pseudeumeces kyrillomethodicus* (previously published and figured by Georgalis et al. 2021: figs 6, 7). The CT data was analyzed using Avizo 8.1.

Phylogenetic analysis

To test the relationships of *Camptognathosaurus* within Squamata, we added it to an updated version of the morphological dataset of Gauthier et al. (2012) that included K/Pg-boundary species from the Western Interior of North America assembled by Longrich et al. (2015) and recently published codings for four species in Pan-Lacertidae, three extinct (*Eolacerta robusta*, *Stefanikia siderea*, *Cryptolacerta hassiaca*) and one extant (*Gallotia galloti*) (see Longrich et al. 2015; Čerňanský et al. 2017; Čerňanský and Smith 2018). This morphological data matrix (see Suppl. material 1) was developed and modified using characters taken primarily from Brownstein (2022), in which several errors in the original Gauthier et al. (2012) matrix identified by Simões et al. (2015, 2017) were addressed. In matrix of Brownstein (2022), some species were deleted from this dataset for the purposes of their analysis, including fossorial species such as amphisbaenians. However, because *Camptognathosaurus* was proposed as an amphisbaenian, we returned this group to the matrix. The principal goal of this analysis is to understand the relationship of the Paleocene taxon among Squamata. The data matrix was analysed using maximum parsimony as an optimality criterion in the program TNT and the NT (New Technology) search (Goloboff et al. 2008; Goloboff and Catalano 2016). *Sphenodon punctatus* was specified as an outgroup. All characters were treated as unordered and were equally weighted. Support was estimated through Bremer support indices (Bremer 1994). Mesquite v.2.75 was used to visualize all trees (build 566; Maddison and Maddison 2011).

Data availability

All specimens from Walbeck are cataloged and accessible in the fossil collection of the Institut für Geologische Wissenschaften und Geiseltalmuseum, Martin-Luther-Universität Halle-Wittenberg (MLU), Germany. Digital surface model of the figured fossil specimen of *Pseudeumeces kyrillomethodicus* is available on Morphosource and Virtual Collections: NHMW 2019/0051/0001: <https://www.morphosource.org/concern/media/000610005?locale=en>.

Results

Systematic palaeontology

Squamata Opperl, 1811

Lacertoidea Opperl, 1811 (sensu Zheng & Wiens, 2016)

?Lacertidae Opperl, 1811

Camptognathosaurus Folie, Smith & Smith, 2013

Type species. *Camptognathosaurus parisiensis* Folie, Smith & Smith, 2013.

Camptognathosaurus walbeckensis (Kuhn, 1940a), comb. nov.

Figs 2–4

1940a (aff.) *Glyptosaurus walbeckensis*: Kuhn, p. 24, figs 4b, 5b.

1940b „*Glyptosaurus*“ *walbeckensis*: Kuhn, p. 482, tab. II fig. 4, tab. III fig. 3.

1983 *Pseudeumeces? walbeckensis*: Estes, p. 104.

2005 *Amphisbaenia incertae sedis*: Augé, p. 301

2013 *Camptognathosaurus parisiensis*: Folie, Smith & Smith, p. 229, fig. 3.

Neotype. MLU.GeoS.4045, almost complete left dentary.

Referred specimens. Germany (here): Two left maxillae MLU.GeoS.4048–4049; one right maxilla MLU.GeoS.4047; three left dentaries MLU.GeoS.4043–4045, MLU.GeoS.4055, MLU.GeoS.4038, 4039 and 4036; seven right dentaries MLU.GeoS.4051, 4040, 4053, 4037, 4041, 4042, and 4056.

France (see Folie et al. 2013): Two right dentaries RIV PP 413, RIV PP 414; left dentary RIV PP 415, MNHN CR 17420 about fifteen dentaries and maxillae, MNHN CR 17421, right dentary and MNHN CR 17425 left dentary.

Localities and horizons. The type locality of *Camptognathosaurus walbeckensis* (Kuhn 1940a), comb. nov. is Walbeck (~MP 5; Germany). This taxon is also known from France: Rivecourt-Petit Pâtis (MP 6b), Cernay-lès-Reims (MP 6a; both France) and, potentially, Montchenot (MP 6).

Taxonomic comment. The newly referred dentaries show no evident differences relative to the type material of (aff.) *Glyptosaurus walbeckensis* described from the

same locality (Kuhn 1940a: figs 4b, 5b): in tooth count, tooth morphology, slightly arched ventral margin of the dentary and prominent, dorsally elevated coronoid process. This species has been considered a glyptosaurid (Glyptosauridae sensu Čerňanský et al. 2023a) by Kuhn (1940a). This assignment is untenable given the specimens studied here. Aff. *Glyptosaurus walbeckensis* lacks the following derived characters of Anguioidea (Estes et al. 1988; Gauthier et al. 2012): the splenial anterior inferior alveolar foramen is located between the splenial and the dentary (usually marked by the splenial spine) and the Meckelian canal opens ventrally in the anterior region (not medially for most of length). Moreover, the sulcus dentalis is present, whereas in anguimorphs, the dental crest is shallow and extends medioventrally. The material of aff. *G. walbeckensis* was later suggested to belong to Lacertidae (?*Pseudeumeces*; see Estes 1983). Augé (2005) suggested that it is a potential amphisbaenian and considered it a nomen dubium. In contrast, the new specimens share the following features of Paleocene *Camptognathosaurus parisiensis*: a long dentary bearing ten to twelve teeth, absence of an angle at the mandibular symphysis and robust amblyodont teeth decreasing the size towards the anterior end of the bone.

It should be noted that no holotype for aff. *Glyptosaurus walbeckensis* was explicitly assigned by Kuhn (1940a). He mentioned six dentaries as (aff.) *G. walbeckensis*, but he figured only one and provided a brief description of the dentary features of this taxon. Accordingly, following ICZN (1999: Article 73.2 and Recommendation 73F), all these six specimens mentioned by Kuhn (1940) (and not only the one he figured) are by definition considered as syntypes of the species. As such, the fact that these specimens cannot be adequately identified because they were not listed, figured, or described in detail does not affect their status as syntypes; in fact, a similar situation has been observed in other fossil Cenozoic reptiles as well, such as the constrictor snake *Palaeopython cadurcensis* (see Georgalis et al. 2021a: 22) and the testudinid turtle *Testudo marmorum* (see Vlachos et al. 2020: 3–4). It is difficult to identify the original syntype specimen figured by Kuhn (1940a: fig. 4b, 5b). In the available material studied here, no left dentary seems to be identical to the figured Kuhn's specimen. Unfortunately, the quality of the figure from the original publication is not sufficient to relocate the specimens. The overall shape and morphology of the figured syntype are very similar to MLU.GeoS.4045 (Fig. 3A–D), but a more detailed comparison, especially regarding the arrangement of preserved teeth, does not support the assignment. In Kuhn's (1940a) specimen, there is a small posterior tooth with empty tooth loci anterior to that and five teeth preserved in the row. In MLU.GeoS.4045, six teeth could be counted if we virtually complete the region between the first and last preserved teeth. Another explanation is that the current preservation of Kuhn's specimen is much worse than in 1940. This would make its identification challenging. In such a case, the specimen MLU.GeoS.4039 (Fig. 4F–H) with five

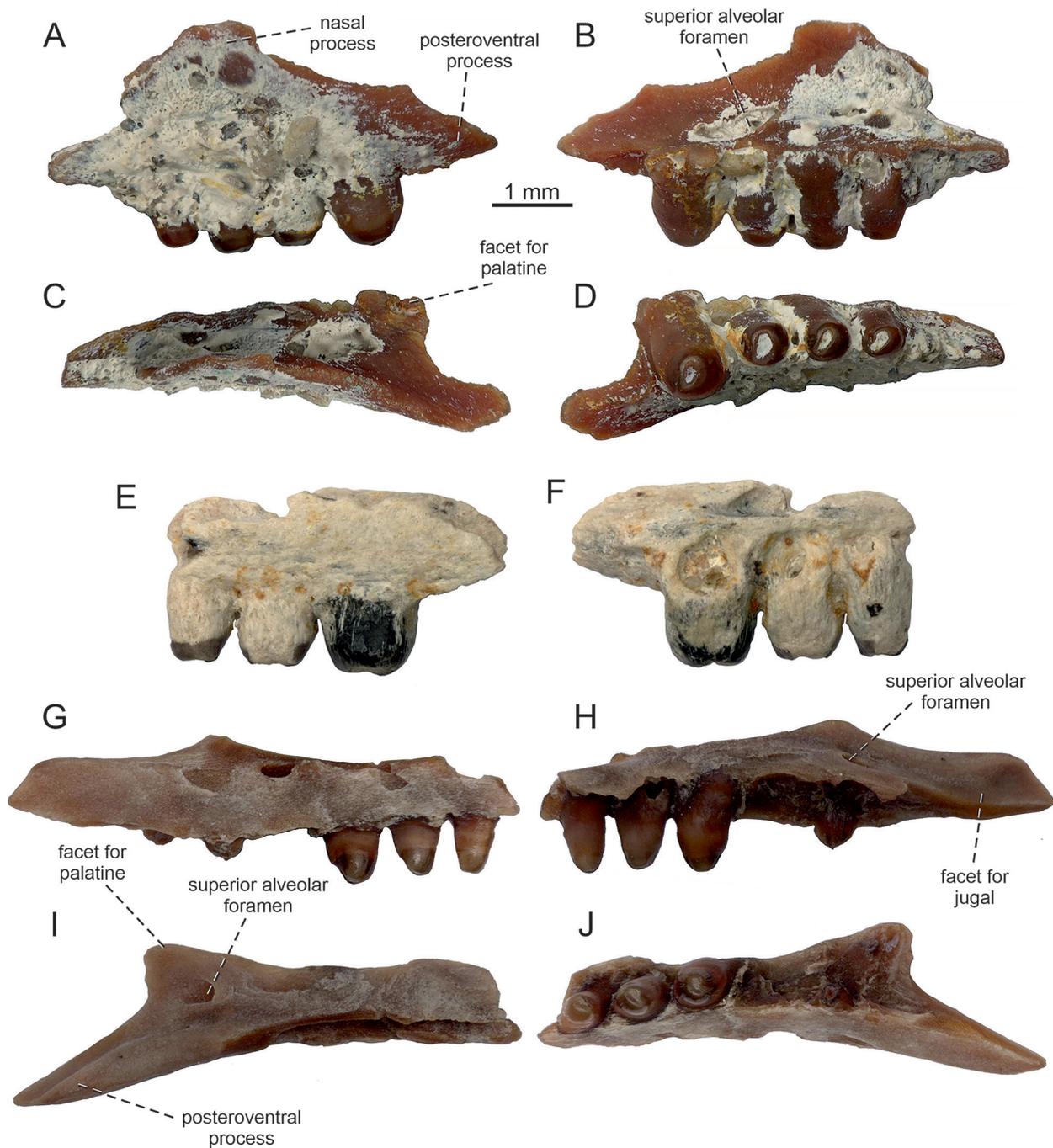


Figure 2. *Camptognathosaurus walbeckensis* comb. nov. from the Paleocene Walbeck locality. Two left maxillae MLU.GeoS.4048 (A–D) and MLU.GeoS.4049 (E, F) and right maxilla MLU.GeoS.4047 (G–J) in lateral (A, E, G); medial (B, E, H); dorsal (C, I); and ventral (D, J) views.

preserved teeth (and a total of eleven tooth positions) in a complete row would be a good candidate to represent the original Kuhn's (1940a) figured syntype specimen. In a closer look, however, the anterior portion of this dentary is not identical with the specimen of Kuhn (1940a) – the anterior portion of MLU.GeoS.4039 starts to rise dorsally at the level of the anteriormost preserved tooth (rather than in front of it), the dental crest is preserved in this anterior elevated portion, and the relative mutual size of teeth and their orientation do not match as well. For all these reasons, we cannot confidently exclude an option

that the syntype specimen figured by Kuhn (1940a: fig. 4b, 5b) has been lost.

Furthermore, in the same year, Kuhn (1940b) figured two additional specimens that he referred to aff. *Glyptosaurus walbeckensis*, i.e., a dentary (Kuhn 1940b:pl. II.4) and a maxilla (Kuhn 1940b: pl. III.3), which were both figured in much better quality than the figured syntype specimen in his 1940a publication. The same author further briefly described the maxilla (Kuhn 1940b: 482). However, Kuhn (1940b) did not mention anything that would imply that these two newly figured

specimens were part of the original type material of aff. *Glyptosaurus walbeckensis* that was established in Kuhn (1940a). The fact that Kuhn (1940a) did not mention anything about the existence of a maxilla for this species, renders us to safely regard that the maxilla is not a syntype. As for the dentary, it is impossible to know if this was a newly referred specimen or one of the six syntype dentaries. The same author, in his subsequent compendium of fossil lizards (Kuhn 1963), also did not specify any type material in the respective entry of this taxon. In the absence of any evidence, we have to treat it similarly to the maxilla, i.e., as a referred specimen. In any case, both these 1940b specimens should also be considered as lost: we have three maxillae in our sample but no one is, again, identical to his 1940b figured one, while the 1940b dentary is similar to the right dentary MLU.GeoS. 4042 described and figured herein (Fig. 4A), but a detailed comparison shows that this is not the same specimen.

Estes (1983: p.104) regarded the only figured specimen in Kuhn (1940a: fig. 4b, 5b) as the only type specimen. That action of Estes (1983) rendered him, in fact, as the designator of the lectotype, according to ICZN (1999: Article 74.5). By definition, the remaining five, non-figured, dentaries mentioned in Kuhn (1940a) represent paralectotypes of the species. As for two additional specimens figured by Kuhn (1940b), Estes (1983) regarded them as the “referred specimens” and “topotypic specimens”.

Taking into consideration the poorly figured lectotype of the aff. *Glyptosaurus walbeckensis* in Kuhn (1940a), coupled with the apparent loss of this material and the original brief description, we consider that it is most appropriate to designate a neotype that could render the taxon diagnostic and allow its anatomical features to be properly discerned. *Camptognathosaurus parisiensis* is a junior synonym of the new combination *Camptognathosaurus walbeckensis* and is a type species of the genus *Camptognathosaurus* (the type species of a genus can be a junior synonym of a valid species pertaining to the same genus, see ICZN 1999: Article 67.1.2; e.g., the case with the snake genus *Eryx* Daudin, 1803, but cannot be a non-diagnosable species, which cannot be diagnosed as a member of the genus). One option is to replace the lost one by the holotype of *Camptognathosaurus parisiensis* (RIV PP 413) in the new combination *Camptognathosaurus walbeckensis*. However, we think it is less dangerous to choose a neotype among the specimens from Walbeck (the type locality), some of which are not significantly less well-preserved than those from France. The reason for this is that there are more chances that the neotype we are choosing actually belongs to the same species erected by Kuhn, than if we chose it among specimens from a different region (with a slightly different age and which could ultimately be shown to represent a different species). Currently, only jaw elements are known and caution is needed.

Revised diagnosis. Small-sized lizard in regard to skull length (an anteroposterior maximum length of dentary around 10 mm). It differs from other members of Lacertoidea based on a unique combination of features: (1) pleurodont dentition (contra *Trogonophis*); (2) only moderately shortened dentary (as *Polyodontobaena*, *Pseudeumeces*, contra distinctly shortened in all modern amphisbaenians, contra markedly short in *Dracaenosaurus*, contra long in *Lacerta* and *Gallotia*); (3) absence of an angle at the symphysis (as lacertids, *Cryptolacerta*, contra *Cuvieribaena* and all modern amphisbaenians except *Amphisbaena ridleyi*); (4) rounded (arched) ventral margin of dentary (as lacertids, *Cryptolacerta*, contra *Polyodontobaena* and modern amphisbaenians); (5) higher number of labial foramina - around five or six (as *Lacerta*, *Pseudeumeces*, contra eight in *Gallotia*, contra four in *Polyodontobaena*, three in *Blanus* and *Rhineura*, two in *Cuvieribaena*); (6) opening of the alveolar canal beneath tooth row (as *Cryptolacerta*, *Polyodontobaena*, contra all modern amphisbaenians except *Rhineura*); (6) dentary tooth number 10–12 (as Pohl-Perner specimen of *Cryptolacerta* and *Polyodontobaena*; 12–14 in *Dracaena*, 12–17 in *Pseudeumeces*, contra higher tooth count in *Tupinambis* and extant lacertids; contra smaller number - seven or eight in *Dracaenosaurus* and in all modern amphisbaenians); (7) heterodont dentition, teeth increase their size posteriorly (the last tooth/teeth can be smaller) (as *Pseudeumeces*, *Janosikia*, *Polyodontobaena*, contra decreasing tooth size posteriorly in *Cuvieribaena* and usually in modern amphisbaenians – note that in *Blanus*, the third or fourth tooth is smaller); (8) teeth arranged in a single line along the tooth row (contra *Dracaena*); (9) robust, blunt teeth with constricted bases present in the posterior half of the tooth row (as *Dracaenosaurus*, *Pseudeumeces*, contra presence of robust and blunt teeth without constriction in the anterior region of the tooth row in *Cuvieribaena*); (10) absence of cementum deposits (contra teiids); (11) moderately low dental crest, teeth exceed the dental crest by more-or-less the half of the tooth length [as *Cryptolacerta*, contra high dental crest (most of the ventral tooth length laterally cover by the crest) in *Pseudeumeces*, *Dracaenosaurus*, *Janosikia* and *Lacerta*, contra low dental crest, shallowly pleurodont (most of the tooth length exposed laterally) in *Polyodontobaena* and most amphisbaenians]; (12) large, dorsally distinctly elevated coronoid process of dentary, which appears to cover, at least partly, the anterolateral part of the coronoid (as *Cryptolacerta* and many amphisbaenians, contra basal Rhineuridae); (13) open Meckelian canal (contra *Rhineura*); (14) fossa for adductor musculature well developed, extensive, running well below the dentary tooth row (as *Cryptolacerta*, ?*Cuvieribaena*, contra *Polyodontobaena* and extant amphisbaenians) and (15) posteroventral process of maxilla long (as lacertids, *Cryptolacerta*, contra derived state in modern amphisbaenians).

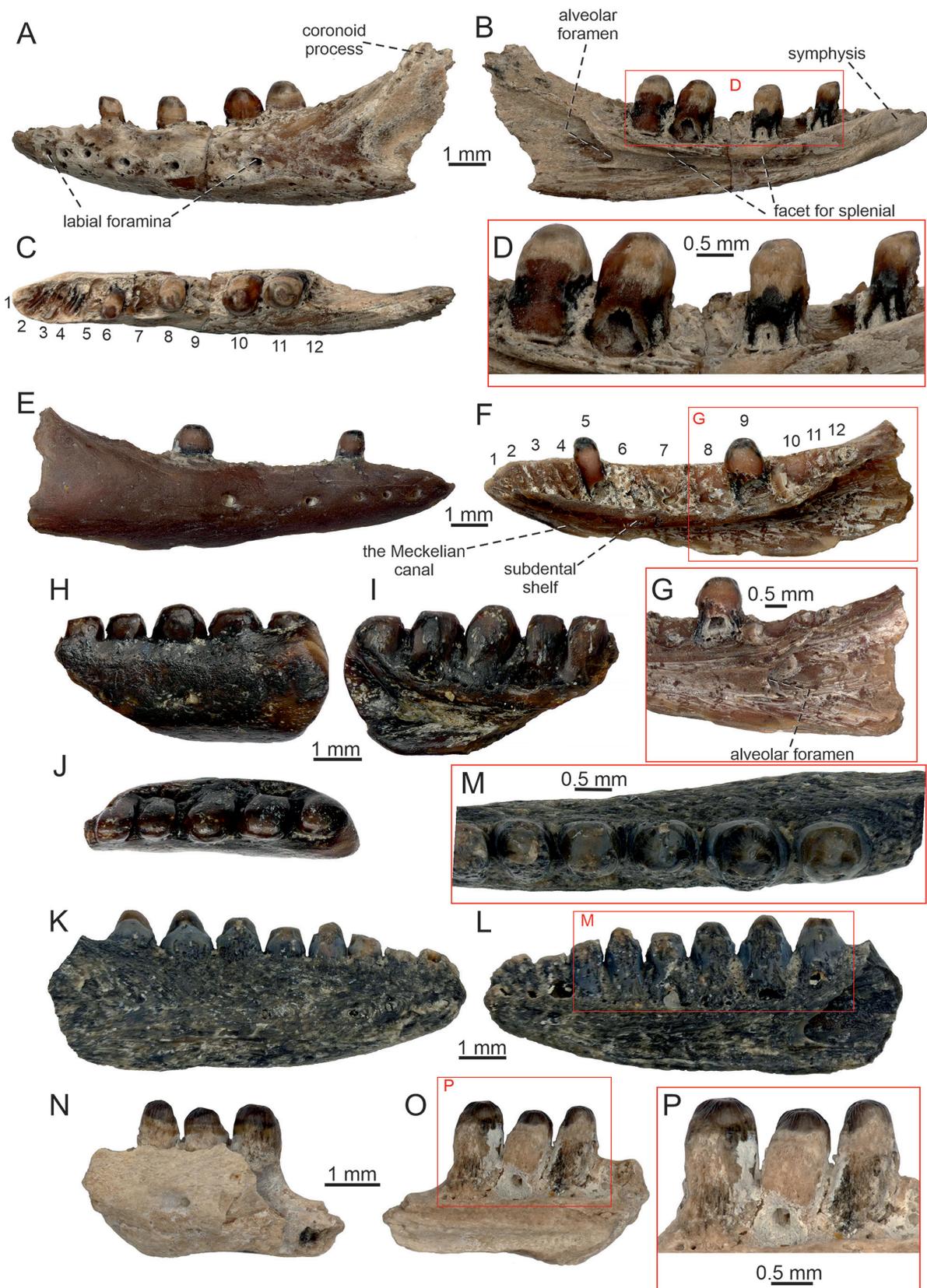


Figure 3. *Camptognathosaurus walbeckensis* comb. nov. from the Paleocene Walbeck locality. The neotypic left dentary MLU. GeoS.4045 in lateral (A), medial (B), dorsal (C) views; and tooth detail in medial (D) view. Right dentary MLU. GeoS.4051 in lateral (E) and medial (F) views; and detail of the area around the alveolar foramen in ventromedial (G) view. Left dentary MLU. GeoS.4055 in lateral (H), medial (I) and dorsal (J) views. Right dentary MLU. GeoS.4037 in lateral (K) and medial (L) views; and teeth in dorsal (M) view. Left dentary MLU. GeoS.4043 in lateral (N) and medial (O) views; and detail of teeth in medial (P) view.

Description. Maxilla. Three maxillae (two left, one right) are available in the material (Fig. 2A–F). The specimen MLU.GeoS.4048 is better preserved, whereas 4049 is represented only by a posterior fragment bearing three teeth. MLU.GeoS.4048 possesses six or seven tooth positions (see remarks) with four teeth still attached. The preserved portion of the maxilla appears to be antero-posteriorly short rather than long. Note, however, that it is incomplete and the true length of the element cannot be determined (but see remarks for Kuhn 1940b). It consists of two major portions: the dental portion bearing the marginal dentition and the dorsally extending nasal process (facial process sensu Evans 2008). In dorsal view, the bone gradually widens posteriorly except for the posteroventral process. A short process bearing a facet for the palatine extends posteromedially. Further posteriorly, the bone continues into the posteroventral process. The process is not pointed but forms a low perpendicular wall. The external side of the maxilla is slightly concave. In lateral view, the external surface of the bone is mostly covered by adhering sediment. The partly exposed areas are more-or-less smooth (the same is true for MLU.GeoS.4049 which, however, represents only a ventral portion of the maxilla, see below). The nasal process is small (note that the anterior part of the process is broken off) and slightly dorsally expanded. Its posterior portion is well demarcated from the further posterior portion of the maxilla by a recess.

Further posteriorly, the bone gradually decreases, but note that the dorsal margin of this part is slightly concave. The anterior region of the maxilla is damaged. In medial view, the partly damaged supradental shelf is well-developed and moderately expanded medially. Its maximum medial expansion, corresponding to the palatine process of the maxilla, can be seen at the level of the last posterior preserved tooth. The portion situated further posteriorly appears to be damaged. However, it can be assumed that the process did not protrude distinctly further posteriorly (Fig. 2C). The large posterior opening of the superior alveolar canal is located in the posterior region at the level of the fifth tooth position (counted from anterior).

The specimen MLU.GeoS.4047 represents a partly preserved right maxilla. It appears to be somewhat long (relative to amphisbaenians), but its dorsal portion, including the nasal process, is completely broken off. The anterior portion is missing as well. The preserved external surface of this specimen is smooth. Only a ventral half of one supralabial foramen is preserved. The bone extends posteriorly into the more-or-less long posteroventral process. The process is slightly inclined laterally relative to the anteriorly located portion of the maxilla (Fig. 2I, J; the same condition can be seen in MLU.GeoS.4049). The preserved maxilla bears six tooth positions where four teeth are still attached to the bone. The medial margin of the supradental shelf is damaged, although its sharp stepped end around the end of the tooth row is visible. It forms the medially expanded portion. In this area, the facet for the palatine is present. The posterior opening of

the superior alveolar canal is located at the level of the penultimate tooth position. The posteroventral process of maxilla is long rather than short. In lateral and medial views (Fig. 2G, H), its dorsal margin is concave and the posteroventral process forms a low perpendicular wall. The ventral margin of this wall reaches only slightly more posteriorly than its dorsal margin. From the level of the superior alveolar foramen, the posteroventral process is also slightly rotated ventrolaterally. Thus, its lateral surface is partly visible when the maxilla is observed in ventral view (Fig. 2J). The posterior region of the maxilla appears to bear a facet for jugal (Fig. 2H).

Remarks. All three maxillae, despite some small differences, are allocated to the same species. They share several features, such as robust teeth of which a robustness increases posteriorly; the location of the palatine process; and the presence of well-developed posteroventral process (in contrast to modern amphisbaenians). Identical dentition in this type of element helps to recognize that they most likely belong to the same taxon as dentaries described below. Moreover, they are comparable in size and come from the same locality. It seems to be unlikely that maxillae belong to a form for which dentaries have not been recorded in the locality. The small differences among maxillae are considered individual variability and/or may reflect ontogenetic differences (see Discussion). Therefore, until the intraspecific variability and ontogeny is better understood in this form, we prefer to provisionally refer the new maxillae to the species *Camptognathosaurus walbeckensis* comb. nov.

The tooth number in the tooth row is difficult to estimate because the region of the last posterior tooth in MLU.GeoS.4048 is damaged. It seems that there could be a place for one additional tooth. But in such case, this tooth, if present, would be much smaller than the last preserved (potentially penultimate) tooth. Actually, this would not be unusual and cannot be excluded (although nothing indicates such a condition in MLU.GeoS.4049). In such a case, the maxillary tooth number in a preserved (not complete) tooth row of this specimen is seven.

Besides these three specimens, there is an additional right maxilla figured by Kuhn (1940b: tab II fig. 4). This Kuhn's specimen is much more complete, but is not present in the material available to us (according to Estes 1983, it is lost). There are similarities with our material, such as an amblyodont dentition and a long posteroventral process with a concave dorsal margin, although it is difficult to be absolutely sure without proper study that this specimen represents the same taxon (*Camptognathosaurus*). Only its lateral aspect is figured and according to Kuhn (1940b), it has 11 mm in length (it is moderately long rather than short) and possesses seven teeth (the tooth count of a complete tooth row was ten). Its external surface (including the nasal process) is pierced by numerous small foramina. The posteriormost supralabial foramen is located at the level of the fourth tooth position. The nasal process is anteroposteriorly long but dorsally low. Its dorsal margin is rounded, whereas

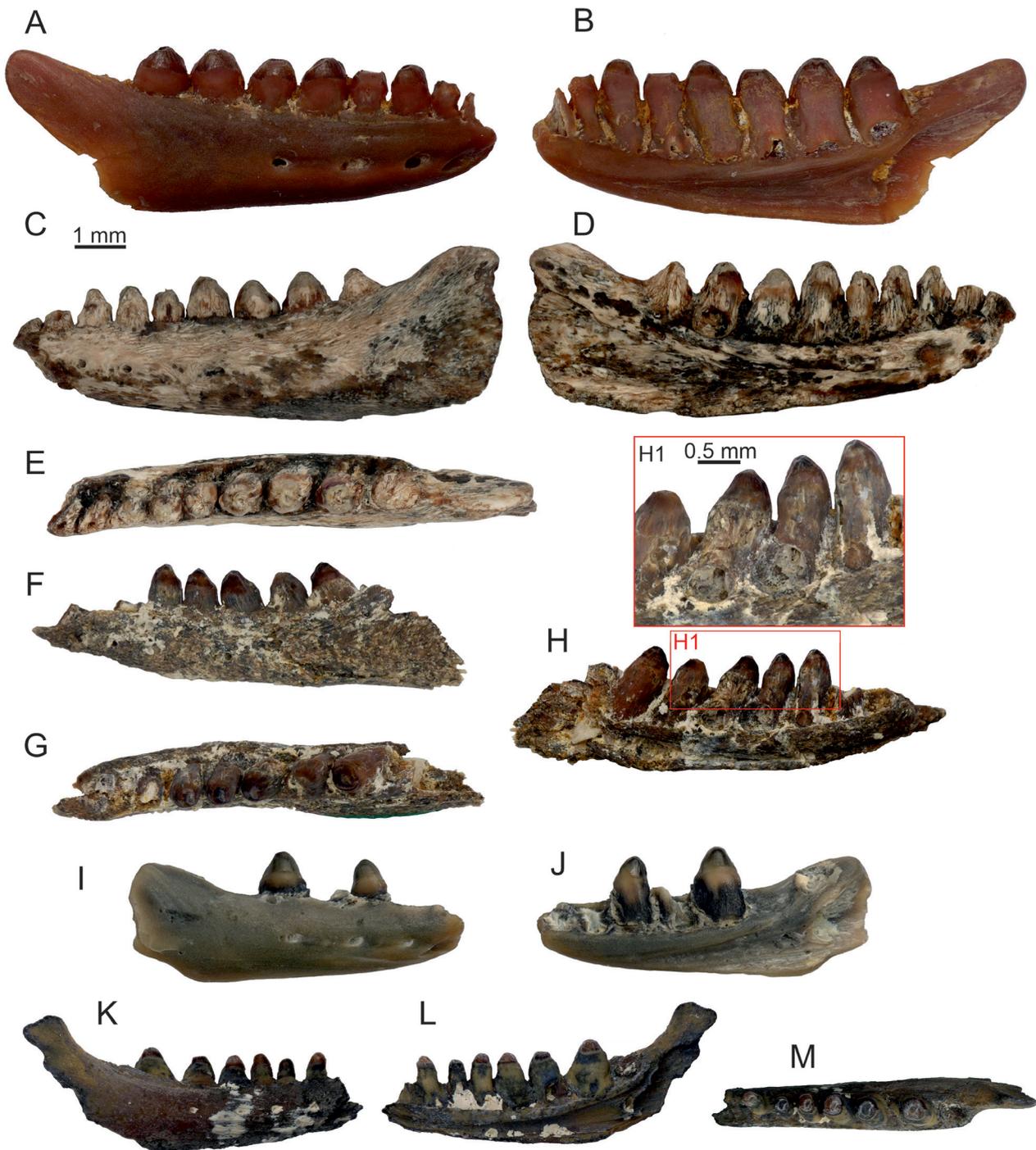


Figure 4. *Camptognathosaurus walbeckensis* comb. nov. from the Paleocene Walbeck locality. Right dentary MLU.GeoS. 4042 in lateral (A) and medial (B) views. Left dentary MLU.GeoS.4038 in lateral (C), medial (D) and dorsal (E) views. Left dentary MLU.GeoS. 4039 in lateral (F), dorsal (G) and medial (H) views and with detail of teeth (H1). Right dentary MLU.GeoS. 4056 in lateral (I) and medial (J) views. Right dentary MLU.GeoS. 4041 in lateral (K), medial (L), and dorsal (M) views.

its posterior portion slightly protrudes posteriorly. This portion is triangular, pointed and posteriorly directed. Estes (1983) stated that there is a weak sculpture reflecting osteodermal attachment on the nasal process.

Dentary. Several dentaries are preserved. Most of them are, however, only fragmentary (Figs 3, 4). The complete tooth row is preserved in the dentaries MLU.GeoS. 4045 (neotype) and 4051 (Fig. 3A–G). The specimens bear

twelve tooth positions (two teeth are still attached to the bone in 4051, see Fig. 3E, F; whereas four are preserved in 4045, see Fig. 3A–C). Some smaller dentaries bear eleven or perhaps ten tooth positions – this estimation is based on MLU.GeoS.4038, where only the anterior-most portion is broken off, but nine tooth positions are preserved (seven more-or-less complete teeth and half of two anteriormost ones are preserved in this specimen).

The otherwise smooth lateral surface is pierced by a single row of five (in MLU.GeoS.4051) to six (in 4045) labial foramina (in some cases four, e.g., MLU.GeoS.4042 – note, however, that these specimens are incomplete; Fig. 4A). The foramina are located in the mid-line of the bone and gradually increase in size posteriorly. The posteriormost foramen is located at the level of the fifth tooth position (counted from posterior) in MLU.GeoS.4051, but at the third in 4045 (note, however, that this is not a result of a different placement for the foramen in the dentary, but of the closely packed posteriormost teeth in 4051). In the posterior region of the dentary, there is a well-developed, wedge-shaped fossa for the adductor musculature. This structure is extensive, running well below the tooth row.

In medial view, the Meckelian canal is fully open, although narrow in the anterior region – the canal gradually widens posteriorly. The intramandibular septum, which separates the Meckelian canal from the alveolar canal, extends posteriorly almost to the end of the tooth row, but does not surpass it. The septum reaches the level of the third tooth position (counted from posterior) in MLU.GeoS.4051, whereas it reaches the level of the last tooth position in 4045 (this is likely related to the two additional posterior teeth in 4051, not a true shift in the structure position). The ventral margin of the septum forms a small and narrow crest (Fig. 3B). This crest is not free but is ventrolaterally fused to the bone (thus, this is not identical to a free posteroventral margin of the intramandibular septum sensu Gauthier 1982). Dorsally, the opening of the alveolar canal (i.e., alveolar foramen) is located. A subdental shelf roofs the Meckelian canal. Dorsally, the subdental shelf bears the sulcus dentalis (the sulcus becomes shallower posteriorly). The shelf is robust in the anterior section (Fig. 3B), but it distinctly narrows posteriorly due to the presence of the facets for the splenial and large facet for the coronoid on its ventromedial surface. The splenial facet is medially exposed and visible at the level of the third tooth position (counted from posterior; this condition is present in all specimens in which this feature can be observed). Then, it turns more ventrally and reaches far anteriorly, extending to the level of the sixth tooth position counted from posterior or the seventh tooth position if counted from anterior. The symphyseal region is preserved in MLU.GeoS.4045. It is slightly dorsally elevated relative to the mid-section of the shelf (the subdental shelf is slightly dorsally concave). The symphysis is small and rectangular in shape. The facet for the splenial is also present on the ventral margin, but the margin itself is weathered, worn or corroded in the specimens so it is difficult to estimate its anterior termination. The ventral margin of the bone is slightly arched. The posterior region of the bone (posterior to the end of the tooth row) distinctly rises dorsally to form a dorsally elevated and prominent coronoid process. It appears that it covered, at least partly, the anterolateral part of the coronoid. The coronoid itself is not preserved, so this cannot be fully

confirmed. The coronoid process of the dentary is fairly preserved in MLU.GeoS.4045. Only its dorsal portion is slightly damaged. The process reaches clearly higher than the level of the tooth apices of the largest teeth. The ventral posterior ends of all dentaries are damaged. At least a short angular process can be identified in MLU.GeoS.4045 (Fig. 3A, B). However, this appears to be only the base of the process, so its real length is unclear. The same is true for MLU.GeoS.4036, a left dentary without teeth.

Dentition. The tooth implantation is pleurodont. Teeth are tall (relative to the overall size of the jaw), over-arching the moderately low dental crest by more-or-less the half of the tooth length. Tooth size (robustness) in both maxilla and dentary gradually increases posteriorly. Note, however, that the last and/or penultimate tooth can be somewhat smaller again relative to the next anteriorly located tooth. The teeth are straight (not recurved) and slightly inclined anteriorly. In general, they are robust with blunt apices. The large teeth in the posterior region are extremely blunt, amblyodont and have rounded apical portions forming robust cylinders. Some specimens bear well-preserved fine radial striations of the crowns (Fig. 3M, O). The teeth are slightly constricted at their bases. Here, large circular resorption pits are located.

Although teeth are robust in some specimens, they have a slightly pointed appearance rather than being rounded and distinctly blunt. In some of these specimens, tooth crowns (however not all of them) have rounded mesial and slightly concave distal margins (Fig. 4H; note that this is also present in the penultimate preserved tooth of MLU.GeoS.4045, although in lesser form; see Fig. 3D). This feature (weak pointedness), however, can somehow vary among individuals and even in a single tooth row. Moreover, the conditions in the MLU.GeoS.4047 maxilla and 4042 dentary rather reflect an intermediate stage (Figs 2H, 4B; see remarks and Discussion).

Remarks. The material described here shares morphological features with the material of *Camptognathosaurus parisiensis* described by Folie et al. (2013: fig. 3) from France (MP 6b, Rivecourt-Petit Pâtis; MP 6a, Cernay-lès-Reims). The dentary RIV PP 413 (the holotype in Folie et al. 2013) is markedly similar to the specimen MLU.GeoS.4045 we describe here (Fig. 3A–D). All specimens from Germany and France (all localities are geographically relatively close to each other, see Fig. 1) share the following combination of features: (1) slightly rounded (arched) ventral margin of dentary; (2) number of labial foramina; (3) position of the alveolar foramen; (4) heterodont dentition in regard to size; (5) robust, blunt teeth with slightly constricted bases present in the posterior half of the tooth row (the last tooth/teeth can be smaller); (6) large, dorsally distinctly elevated coronoid process; and (7) similar tooth number – the specimen RIV PP 413, which is represented by a nearly complete right dentary from Rivecourt-Petit Pâtis, bears eleven tooth positions. Both paratypes CR 17420 and CR 17425 are, however, incomplete.

It should be noted that some dentaries described here show several small differences (or variation) among them: (1) size; (2) blunt tooth crown vs. slightly more pointed (although still robust); (3) slightly lower tooth number (twelve vs. eleven or ? ten tooth positions); and (4) potentially also the shape of the coronoid process. If the coronoid process is robust, dorsally rising in those dentaries with the well-preserved posterior portion (Fig. 3), the shape of this process is difficult to demonstrate clearly in some other dentaries. Namely, it is not markedly dorsally elevated in MLU.GeoS.4042 (Fig. 4A, B) and 4038 (Fig. 4C, D). It is clearly unrelated to the early ontogeny because the dorsally distinctly protruding process is observed in a small specimen MLU.GeoS.4041 (Fig. 4K, L). However, the left dentary MLU.GeoS.4038 is eroded. The relatively lower process in these two mentioned specimens seems to reflect only an artefact of preservation. All other differences seem to fall into the normal individual (and/or ontogenetic) variation; thus, all specimens studied here represent most likely a single taxon (see Discussion).

Lacertidae indet.

Figs 5, 6

1940a aff. *Parasauromalus paleocenicus*: Kuhn, p. 24, figs 4a, 5a nomen dubium.

1944 aff. *Iguanosaurus paleocenicus*: Kuhn, tab. 20, fig. 7 nomen dubium.

1958 *Iguanosauriscus paleocenicus*: Kuhn, p. 382 nomen dubium.

1983 *Plesiolacerta? paleocenica* new comb.: Estes, p 104 nomen dubium.

Material. One left dentary MLU.GeoS.4059; seven isolated dorsal vertebrae MLU.GeoS.4067, 4066, 4061–4064, 4068.

Description. *Dentary.* The specimen MLU.GeoS.4059 represents a left dentary (Fig. 5). It is in fair condition. Only the anterior region is missing. The smooth lateral surface of the bone is pierced by a line of labial foramina, four of which are preserved (Fig. 5A). In the anterior region, these foramina are located at mid-height on the dentary, but as the dentary deepens posteriorly, the last two foramina are located more-or-less in the dorsal one-third of the bone. The posteriormost foramen is located at the level of the eleventh tooth position (counted from posterior). The alveolar shelf supports 21 tooth positions. Seven complete teeth are still attached to the bone and eight teeth have partly preserved tooth bases. However, since its anterior region is missing, the total number of teeth is unknown, but it certainly would have been slightly higher. The Meckelian canal is fully open and exposed medially (Fig. 5B). It is narrow in the anterior region and widens slightly posteriorly. In the posterior region, it is only moderately broad. The alveolar canal (Fig. 5D) opens at the level of the seventh tooth position (counted from posterior). The intramandibular

septum forms the ventromedial wall, separating this canal from the Meckelian canal. The ventral margin of the bone is nearly straight. Note, however, that its posterior portion is damaged. The subdental shelf roofs the Meckelian canal (sensu Rage and Augé 2010), which is only slightly concave in medial view – the shelf is more-or-less straight in the anterior section, whereas it rises slightly dorsally from the ninth tooth position (counted from posterior). It gradually becomes thinner posteriorly due to the presence of the facet for the splenial on its ventromedial surface. This facet is present on the ventral margin as well. Unfortunately, the posterior section of the shelf is damaged. The sulcus dentalis is developed, mainly in the anterior region of the dorsal surface of the shelf. Posterior to the tooth row, the bone tapers into the narrow and pointed coronoid process, which rises slightly dorsally. On the dorsolateral surface of the posterior end, the articulation for the coronoid is preserved, showing that the coronoid overlapped the dentary dorsally.

Dentition. The tooth implantation is pleurodont. The teeth are tall and heterodont, ranging from monocuspid in the anterior region of the dentary to bicuspid with a dominant, triangular (pointed) and slightly recurved main cusp and an additional smaller, well-separated mesial cusp (Fig. 5D–F). The bicuspidity starts around the 14th tooth position (counted from posterior). Note, however, that only one tooth (14th) is preserved in this region, possessing an incipient mesial cusp. The tooth crowns are lingually slightly concave. Weak, delicate radial striations (converge at the tip of the main cusp) are present on the lingual side of, at least, some of the tooth crowns (well seen especially in the teeth located in the mid-portion of the dentary; see Fig. 5F). In some cases, two dominant striae form a slightly developed lingual cusp. The tooth neck is slightly swollen lingually. Small circular resorption pits are present on the lingual aspects of tooth bases in some teeth. The narrow inter-dental gaps of the preserved teeth indicate that the teeth were closely spaced.

Remarks. The specimen MLU.GeoS.4059 is identical to the left dentary on which Kuhn (1940a: figs 4a, 5a) established the new species aff. *Parasauromalus paleocenicus*, although one anterior tooth subsequently broke off. The specimen is undoubtedly the same one described by Kuhn. It was also figured by Kuhn in 1944 (see Kuhn 1944: tab. 20, fig. 7).

The specimen MLU.GeoS.4059 represents a lacertid since it exhibits the synapomorphies of the family (Estes et al. 1988; Gauthier et al. 2012), such as sulcus dentalis and lateral overlap of the posterodorsal margin of the dentary by the coronoid. The tooth morphology also indicates a lacertid rather than other groups: presence of bicuspid teeth, weak striations and sometimes a weakly-developed lingual cusp is common among members of Lacertidae, including *Lacerta* (see Kosma 2004; Čerňanský and Syromyatnikova 2019). Among scincoids, the lingual cusp is usually well separated. In scincids, the lingual cusp is usually framed by broadly mesially and distally running cristae lingualis anterior

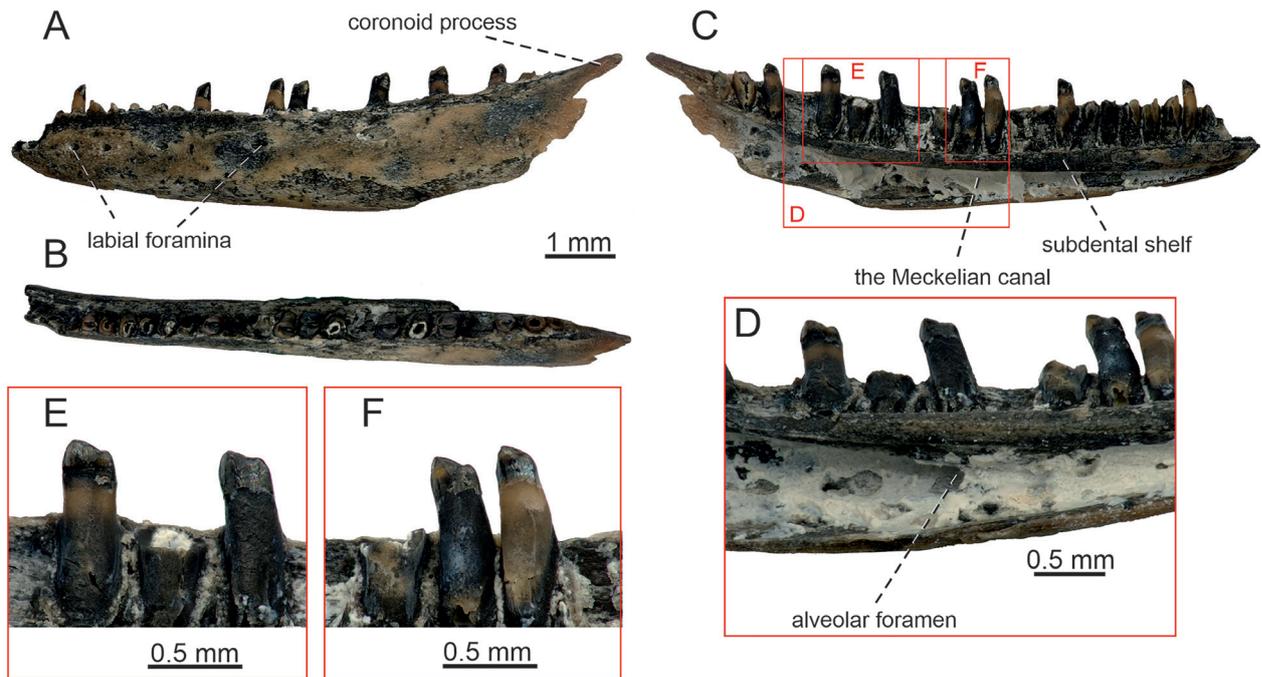


Figure 5. Lacertidae indet. from the Paleocene Walbeck locality. (A–F) Left dentary MLU.GeoS.4059 in lateral (A), medial (B) and dorsal (C) views. Detailed photographs of the area around the alveolar foramen in ventromedial (D) and detail of teeth in medial (E, F) views.

and posterior rather than more-or-less vertical striae dominans anterior and posterior (e.g., Caputo 2004; Kosma 2004; Čerňanský et al. 2020b; Čerňanský and Syromyatnikova 2021). Moreover, bicuspid teeth among scincoids are rare but present only in some cordyliformes (Estes, 1983) - bicuspid teeth are present in, e.g., *Gerrhosaurus flavigularis* and *Zonosaurus quadri-lineatus*, tricuspid teeth with dominant central cusp are present in, e.g., *Tracheloptychus*, and even multicusp teeth are present in a herbivorous gerrhosaurid - the posterior teeth of *Gerrhosaurus (Angolosaurus) skoogi* possess up to seven cusps Kosma 2004; Nance 2007). The presence of bicuspid and faintly tricuspid teeth is reported in a potential cordyliform *Deccansaurus* from the Deccan intertrappean strata (uppermost Cretaceous – lowermost Paleocene; Yadav et al. 2023). However, this taxon differs from the Walbeck lacertid by many aspects, e.g., the Meckelian canal is distinctly narrow (shallow) and exposed ventrally rather than medially, and a splenial is short. In teiids, the tricuspid teeth have extensive cementum depositions on tooth bases (Estes 1983).

Vertebrae. Seven vertebrae are available in the material (three of them are figured, see Fig. 6). The neural spine is moderately high (MLU.GeoS.4067; the short vertebrae with tall neural spines tend to be cervicals and thoracics) or rather low (MLU.GeoS.6066, 4061 and 4063) (Fig. 6) and slightly inclined posteriorly. It originates on the anterior border of the neural arch, forming a median ridge here (prespinal lamina sensu Tschopp 2016). It rises progressively posteriorly, and its top is slightly rounded. This part is wider and drop-shaped in dorsal view. The neural canal is large and pentagonal in outline.

The well-developed prezygapophyses are distinctly inclined dorsally, having well-defined, roughly elliptical articulation surfaces at the level of which the vertebra reaches its greater width. The postzygapophyses are oval in shape. Both pre- and postzygapophyses are slightly elongated and oriented obliquely but more anteroposteriorly than mediolaterally. The vertebrae are only slightly constricted between the pre- and postzygapophyses and consequently, they are relatively broad in dorsal view. In lateral view, the interzygapophyseal ridge (postzygoprezygapophyseal lamina sensu Tschopp 2016) is visible as a sharp ridge, connecting both pre- and postzygapophyses laterally. The synapophyses are well-developed, being located in the anterior region. The centrum gradually narrows posteriorly. In ventral view, it has a triangular shape. Its relative length varies among vertebrae, being short in MLU.GeoS.4067 and 4068, but rather long in MLU.GeoS.4066 and 4061. The ventral margin of the centrum is concave in lateral view. In ventral view, the centrum is pierced by two small foramina in its anterior third. The cotyle and condyle are mainly preserved in MLU.GeoS.4067 and 4066. They are moderately large, being rounded in MLU.GeoS.4067, but slightly depressed in 4066. The condyle is well demarcated from the centrum - the condyle (especially where the cartilage has been stripped from it) is narrower than the centrum. Note, however, that the true precondylar constriction seen in varanids (the width of the condyle is greater than the width of the centrum immediately anterior to it, e.g., Rieppel 1980; Estes 1983; Smith et al. 2008; Holmes et al. 2010; Čerňanský et al. 2022a) is absent in the herein described material.

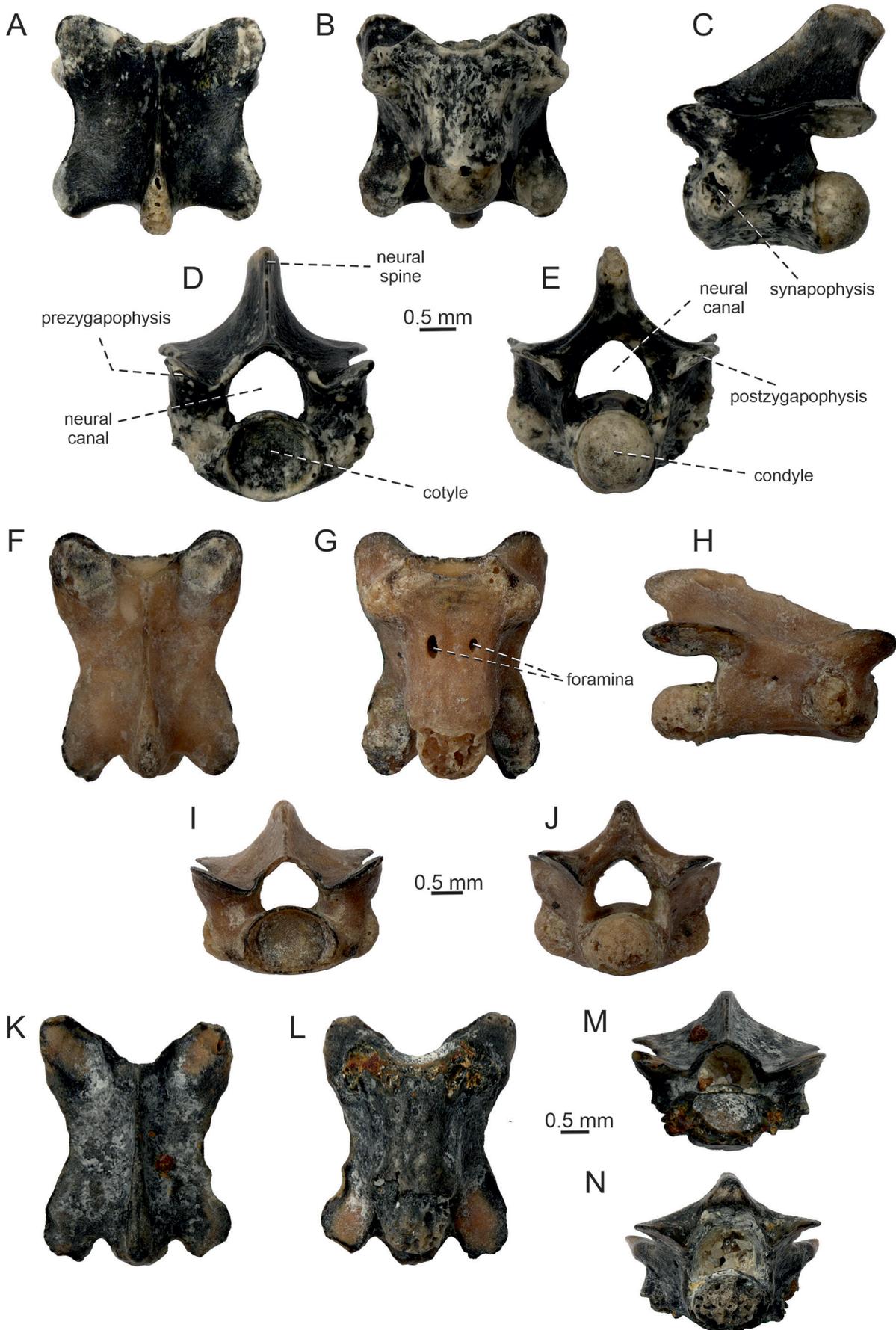


Figure 6. Lacertidae indet. from the Paleocene Walbeck locality. Isolated dorsal vertebrae MLU.GeoS.4067 (A–E), MLU.GeoS.4066 (F–J), MLU.GeoS.4061 (K–N) in dorsal (A, F, K), ventral (B, G, L), lateral (C, H), anterior (D, I, M) and posterior (E, J, N) views.

Remarks. Kuhn (1940a) originally described an isolated dorsal vertebra as *Saniwa* aff. *ensidens*, although stated that the specimen is by two-thirds smaller than a vertebra of this American varanoid. The vertebra described and figured by Kuhn (1940a: fig. 3) is identical to the material we describe here, although one cannot be sure if one of the vertebrae represents the same specimen Kuhn described. Thus, the oldest occurrence of *Saniwa* in Europe should be considered to be younger, namely from the earliest Eocene age locality Dormaal (Augé et al. 2022). For the identification of the vertebrae described here, see Discussion.

Scincoidea Oppel, 1811 (sensu Zheng & Wiens, 2016)

Fig. 7

? Scincoidea indet.

Material. One right maxilla MLU.GeoS.4057, one left maxilla MLU.GeoS.4058.

Description. Maxilla. Two maxillae are preserved. The specimen MLU.GeoS.4057 is larger and represents a fragment of the right maxilla around the superior alveolar foramen (Fig. 7A, B). The anterior and posterior portions are broken off. The specimen possesses nine-and-a-half tooth positions (eight teeth are still attached). The lateral surface is eroded, but it can be estimated that the preserved portion was smooth. It is pierced by three supralabial foramina. The nasal process of the maxilla forms an almost perpendicular wall, although note that it is only partly preserved. It expands almost to the posterior end of the preserved portion of the bone. This posterior margin appears not to be stepped but gradually decreases posteriorly. In medial view, the supradental shelf is almost straight, only slightly expanded medially – however, it is heavily damaged. The superior alveolar opening is at the level of the sixth tooth position (counted from posterior). However, the exact number of teeth is unknown in this specimen due to the missing portions. Posterior to the opening, the bony dorsolateral wall is damaged, and thus, the area ventral to it, is exposed.

The specimen MLU.GeoS.4058 is smaller and slightly in overall better condition than 4057. It represents the left maxilla (Fig. 7C–H) around the region of the superior alveolar foramen, but here, the posterior region is preserved. The lateral surface is smooth. It is pierced by three supralabial foramina: the first anterior is located at the level of the seventh tooth position; the second is at the level of the sixth tooth position and the last posterior one lies at the level of the third tooth position (all counted from posterior). The first two are moderately large, whereas the posterior one is smaller. The dental crest is well-developed, reaching more-or-less the half the tooth height. Nine tooth positions are preserved (six teeth are still attached). The supradental shelf is only partly preserved, especially in the posterior section of the bone. The opening of the superior alveolar canal is

located at the level of the sixth tooth position (counted from posterior). However, the anterodorsal margin of the bone, which demarcates the opening, appears to be partially damaged. Due to this, the original opening might be slightly more posteriorly located, approximately at the level between the fifth and sixth tooth positions. The further posterior region is well-excavated, forming a longitudinal depression. The nasal process is partly preserved. Only its ventral portion remained intact. Its posterior margin appears to be stepped, but this region is partly broken off. Thus, an actual outline is unknown. The posterior portion protrudes into a short and narrow posteroventral process. It is bluntly ended.

Dentition. The tooth implantation is pleurodont. The teeth are tall, although the posterior last ones are slightly smaller (the last and penultimate teeth in MLU.GeoS.4058). The teeth are robust; the robustness increases posteriorly. They are slightly inclined posteriorly, being closely spaced with small interdental gaps. The apices are more-or-less rounded and blunt rather than having a sharp and pointed appearance (although it should be noted that the sixth tooth in MLU.GeoS.4058 has a roughly triangular appearance). The tooth crowns in MLU.GeoS.4057 are eroded, and some preservational artefact makes crowns look more rounded (plausibly because of digestion). The tooth crowns in MLU.GeoS.4058 are fairly preserved. In this specimen, the lingual surface of the crown in these teeth is concave, being curved inwards, whereas the labial one is distinctly convex. The lingual aspect of the crown is bordered by the culmen lateris anterior and culmen lateris posterior. No apicobasal crown striation can be recognized. The tooth crowns possess labial and lingual cusps, being transversally bicuspid. Note that this morphology is less noticeable, possibly due to preservation (the enamel appears to be slightly eroded – as occurs, for example, when teeth pass through stomach acid). However, further structures on enamel, such as striae, would be also affected (see Smith et al. 2021). The labial cusps form a somewhat rounded labial edge. For this reason, the overall appearance of these teeth is blunt. These labial cusps are slightly bent inwards – lingually, which is well-visible mainly in the tooth at the sixth tooth position (counted from posterior). Most tooth crowns show some longitudinal asymmetry (the mesial portion is longer than the distal one). The lingual cusps are small and hardly recognizable. They appear to be framed by short, mesially and distally running cristae lingualis dominans anterior and posterior. The tooth bases are well-expanded medially relative to the rest of the tooth shafts. The bases are pierced by oval resorption pits. A few teeth have huge pits, reaching almost over the half of their length. This feature is probably related to an artefact of preservation.

Remarks. The material resembles mostly scincid, where the lingual cusp is usually framed by the broadly mesially and distally running cristae lingualis anterior and posterior rather than more-or-less vertical striae dominans anterior and posterior (e.g., Kosma 2004) – the

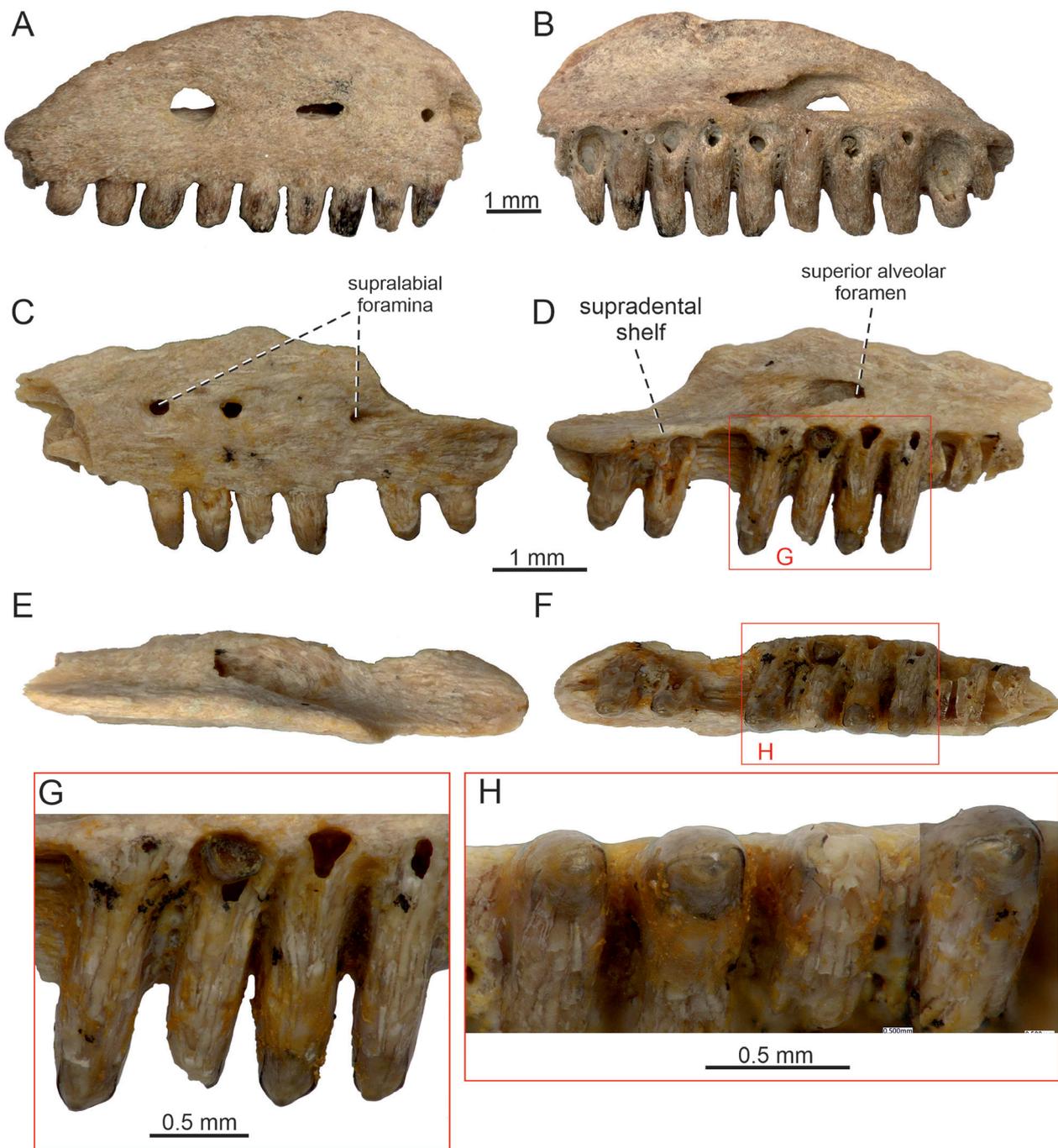


Figure 7. ?*Scincoidea* indet. from the Paleocene Walbeck locality. Right maxilla MLU.GeoS.4057 (A, B) and left maxilla MLU.GeoS.4058 (C–H) in lateral (A, C), medial (B, D), dorsal (E) and ventral (F) views. Detail of teeth of MLU.GeoS.4058 in medial (G) and ventromedial (H) views.

presence of the lingual, well-separated cusp is more common among the cordylids than the scincids (Folie et al. 2005). Transversely bicuspid teeth can be present in some gekkotans, e.g., eublepharids (Sumida and Murphy 1987). In contrast to the robust Walbeck specimens, gekkotans have lightly built skeletons, which reflects their rarity in the fossil record (Evans 2003, 2008). Transversely bicuspid teeth can be also present in teiids (in members of this group; in contrast to the Walbeck material, the teeth have extensive cementum depositions

at tooth bases, see Estes 1983) and polyglyphanodontids, but the lingual cusp is much better developed in these taxa than the small cusp of the Walbeck material and scincoideans (see Nydam 1999). In lacertids, the lingual cusp, if present, is only weakly developed. Moreover, crown lacertids usually have bi- and tricuspid tooth crowns (Čerňanský and Syromyatnikova 2019).

We cannot be certain whether both Walbeck specimens belong to the same taxon (because true crown morphology is only known for the well-preserved one

–MLU.GeoS.4058). In fact, some features do not support an allocation to a single taxon (the supralabial foramina appear to be much larger in the poorly preserved specimen MLU.GeoS.4057, teeth look a little bit more robust). However, these differences can be related to the level of preservation, ontogenetic and/or individual variability. In any case, we provisionally allocated both specimens together as ? *Scincoidea* indet.

Phylogenetic analysis of *Camptognathosaurus walbeckensis*

The phylogenetic tree presented here is based on limited fossil material – the jaws, and thus more complete fossil specimens of this taxon are needed to draw more robust conclusions. The results of the phylogenetic showed that *Camptognathosaurus* was consistently recovered as a lacertid lizard. A New Technology (NT) search in TNT produced two equally parsimonious trees (for a consensus tree, see Fig. 8). *Camptognathosaurus walbeckensis* was placed as sister to *Gallotia atlantica* (Bremer value 1, relative Bremer 25; see Suppl. material 2). The sister group relationship between *C. walbeckensis* and *G. atlantica* was supported by 4 characters (present unambiguously in all trees, namely: characters 356, 417, 419, and 420). They together are sister to the clade [[*Cryptolacerta hassiaca* + *Lacerta viridis*] + *Takydromus ocellatus*], forming all together the clade Lacertidae (Bremer value 1, relative Bremer 33). Eolacertidae are recovered as being sister to Lacertidae. Interestingly, *Cryptolacerta* is recovered as sister to *Lacerta* (Bremer value 1, relative Bremer 25); in contrast to results of Brownstein et al. (2022), where *Cryptolacerta* was placed as sister to *Gallotia* [the phylogenies of Brownstein et al. 2022: figs S9–11 differ somewhat in the topology of Lacertidae (fig. S9–10 a polytomy, but S11 with *Gallotia* and *Takydromus* as sister-taxa, which contravenes the assumption that Gallotiinae and Lacertinae are the basal divergence].

Overall, although this may be true or not, the support for the clade is very low and thus, the interpretation of the *Camptognathosaurus* relationship among Lacertidae needs to be met with caution (*Camptognathosaurus* is represented by a very limited fossil material). In the event that future studies based on more complete material of *Camptognathosaurus* would support its closer relationship to members of Gallotiinae, this would show the presence of this lineage already in the Paleocene. In our analysis, in any case, this Paleocene taxon was never recovered as an amphisbaenian. According to morphological data, many studies show them grouping with snakes and other limbless squamates (e.g., Rage 1982; Estes et al. 1988; Conrad 2008; Gauthier et al. 2012). However, recent molecular analyses using DNA sequencing suggest that amphisbaenians is the sister group to Lacertidae (e.g., Townsend et al. 2004; Vidal and Hedges 2005; Pyron et al. 2013; Reeder et al. 2015; Zheng and Wiens 2016; Burbrink et al. 2020).

Discussion

Although Walbeck fossil lizards are represented only by isolated elements (this is the case of most Paleogene assemblages in Europe, except of, e.g., Messel), they form an important dataset on the evolution of terrestrial herpetofauna in Europe during the late Paleocene. The paleodiversity of squamates from this locality is low. Regarding the number of specimens, this seems to be not a result of sampling or taphonomic bias. Lizards are represented only by small forms with some unusual features (*Camptognathosaurus*, for its revision, see chapter below), and some, in contrast, have very modern appearances (MLU.GeoS.4059 – Lacertidae indet).

The fauna is different in many aspects (diversity, types, etc.) relative to the faunas described from slightly younger, earliest Eocene localities, such as Dormaal in Belgium (Augé 1990, 1992; Augé and Smith 1997, 2002; Sullivan et al. 2012; Folie et al. 2013; Čerňanský et al. 2022b, 2023b; Augé et al. 2022), Cos in France (Čerňanský et al. 2023a, c) and localities in Spain (Bolet 2017).

Overall, this is consistent with the previous statement of Rage (2013) that squamates were rare and poorly diverse during the Paleocene. This is true at least according to the few known localities. However, our knowledge about this geological epoch is limited. It is worth considering a possibility that there is a bias towards selected groups, and that other faunas that were present are not recorded. However, records are still too sketchy to allow much speculation regarding the reasons for the missing groups. The Walbeck fossils provide us with the rare opportunity to observe, although only partly, the composition of herpetofaunas during this crucial interval in Europe.

In any case, a few taxa can be identified in Walbeck – Lacertidae, *Camptognathosaurus* (a lacertoid that forms the dominant group of lizards in regard to the number of elements), and (provisionally) *Scincoidea*. However, immigrants that occurred later in Europe are absent. This is in sharp contradiction with an original statement of Kuhn (1940a) that the Walbeck lizards show very close relationships with North American faunas. Although this herpetofauna of Walbeck is limited, it forms one of the few initial discoveries for our understanding of the Paleocene and the roots of the European Cenozoic ecosystems. Nevertheless, many aspects can be resolved only by future systematic research on new localities and studies of further new material from this part of the Earth history.

Camptognathosaurus

Although Lacertoidea (the clade Lacertoidea includes Lacertidae, Amphisbaenia, Teiidae and Gymnophthalmidae, see Zheng and Wiens 2016; Laterata sensu Vidal & Hedges, 2005; Burbrink et al. 2020) have a well-documented Eocene record in Europe (e.g., Augé 2005, 2012; Folie et al. 2013; Čerňanský et al. 2015b;

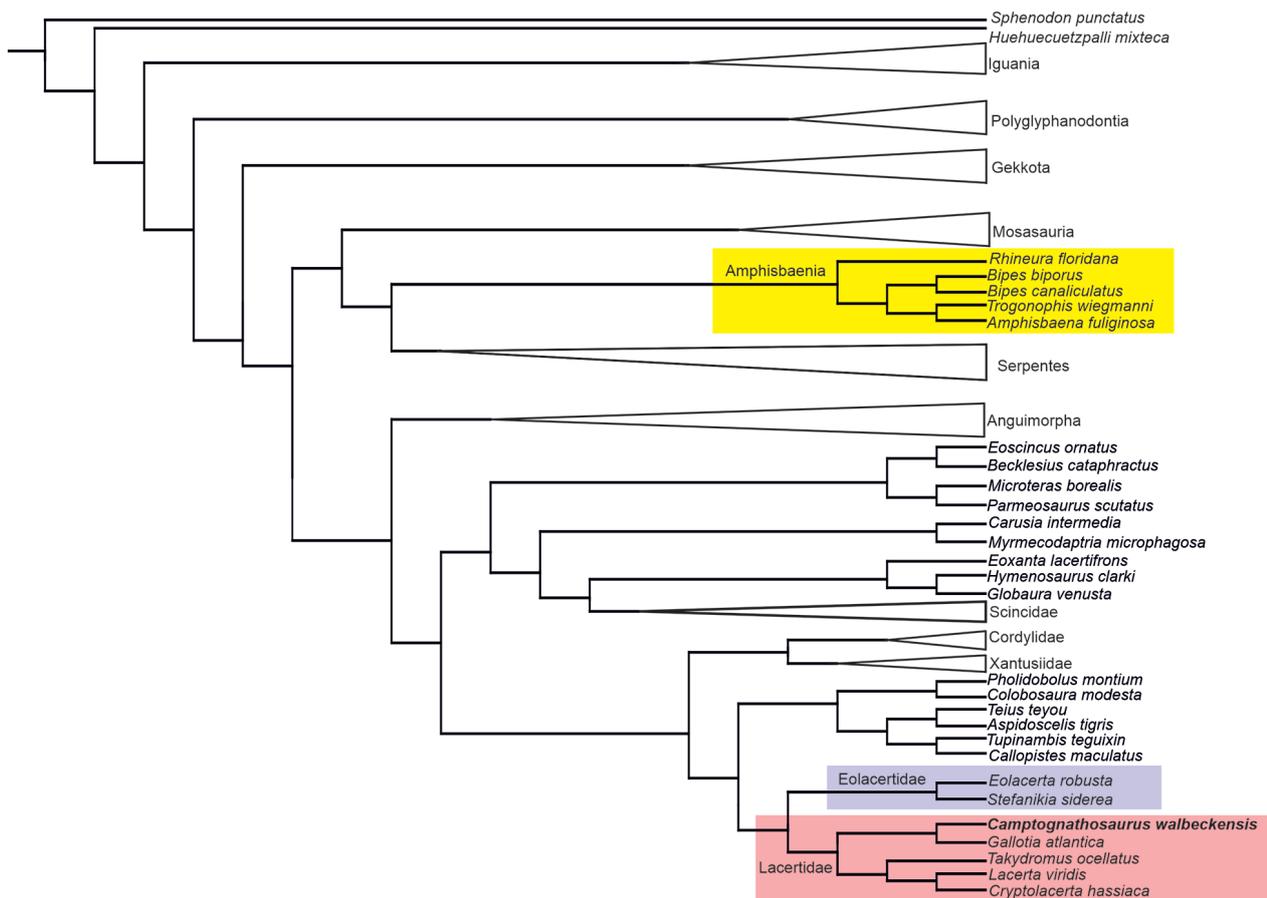


Figure 8. Parsimony phylogenetic analysis of *Camptognathosaurus*. Strict consensus topology generated in parsimony analysis of dataset in TNT v. 1.5. showing the potential position of the Paleocene species within Lacertidae.

Rage and Augé 2015; Čerňanský and Smith 2018), they have only rarely been reported from Paleocene deposits (Augé 2005; Folie et al. 2013; Čerňanský et al. 2020a). In regards to quantity, as previously mentioned, *Camptognathosaurus* forms a dominant component of the late Paleocene lizard fossils in Walbeck assemblage. However, in contrast to that, species diversity appears to be low – only one taxon is identified. A huge amount of individuals in the record might point to a very successful population (considering that this is not caused simply by the fact that the jaws of this taxon are more robust than those of other lizards and, therefore, more resistant to destructive processes related to fossilization processes, as also reflected in their resistance to destruction by digestion of predators). Low diversity of fauna might eventually cause less competition for a species in regard of its particular lifestyle. In any case, this potentially shows that lacertids (pan-lacertids sensu Čerňanský and Smith 2018), not amphisbaenians (see below), formed likely a dominant group of the Paleocene lizard fauna in Europe.

Revision of *Camptognathosaurus*

In regard to aff. *Glyptosaurus walbeckensis* described by Kuhn (1940a), Estes (1983) rejected its glyptosaurid affinities and suggested that it was a lacertid and

tentatively referred it to *Pseudeumeces*. Later, Augé (2005) suggested it was a potential amphisbaenian and considered it a nomen dubium. Indeed, it could appear to be a polyodontobaenid based on the combination of the following features (see diagnosis in Folie et al. 2013:227): (1) the tooth number (10–12); (2) an absence of an angle at the symphysis (the presence of this feature is related to fossoriality, see Gans 1974); and (3) teeth increase in size posteriorly. Thus, the posterior teeth are robust and massively built. The first is, however, a plesiomorphy. The second is also a plesiomorphy that is not shared with *Polyodontobaena* – one of the important features included by Longrich et al. (2015) in their study was the “kink” in the ventral margin of the dentary associated with the expansion of the symphysis below the Meckelian canal. Such a morphology is seen in *Polyodontobaena*, but not in *Camptognathosaurus*. The third is important but hardly determinative, as such dentition has arisen numerous times in Squamata. It evolved independently in various lineages such as Lacertidae, Amphisbaenia, Iguanidae, Teiidae, Scincidae, Xantusiidae, Anguidae, Varanidae and Mosasauridae (Estes and Williams 1984). Polyodontobaenidae deserves a comment here. Although Folie et al. (2013) mentioned the presumed archaic features of polyodontobaenids („primitive amphisbaenians“), the fact is that in the most extensive phylogenetic analysis of

amphisbaenians (Longrich et al. 2015) *Polyodontobaena* is sister to the clade Blanidae, more derived than rhineurids. Thus, “a primitive morphology” in *Polyodontobaena* can be seen only in regard to crown members of Blanidae.

The stratigraphically older species *Polyodontobaena belgica* from the early Paleocene of Belgium (MP 1–5, Hainin) is, however, very different from *Camptognathosaurus* by the following features: (1) pointed tooth crowns are present (Folie et al. 2013); (2) the dentition is shallowly pleurodont (most of the tooth length is exposed from the lateral side as well – the condition seen in amphisbaenians); (3) the dentary of the Belgian taxon is slender and its ventral dentary margin is straight (except for the kink); (4) the Meckelian canal is narrow; (5) the intramandibular septum reaches the level of the last tooth position posteriorly; (6) the fossa for the adductor musculature is located behind the tooth row; (7) lower number of labial foramina.

The dentaries of *Camptognathosaurus* clearly possess several interesting features that are in contrast to members of Amphisbaenia: (1) absence of an angle at the symphysis (an angle is present at the symphysis of the dentary in most amphisbaenians, e.g., Gans 1974; Gans and Montero 2008); (2) high number of teeth (the presence of ten or fewer teeth is synapomorphic of Amphisbaenia, see Smith 2009; although not unique to them among squamates. The amphisbaenian skull is short and robustly built, and the reduced dentary of modern forms bears five to nine teeth, see Kearney 2003); (3) moderately low dental crest [teeth exceed the dental crest by more-or-less the half of their length in contrast to amphisbaenians, in which the tooth implantation is shallowly pleurodont (acrodont in Trogonophiidae) - the dental crest is markedly low]; (4) sulcus dentalis is well developed (in amphisbaenians, it is usually only slightly developed; see, e.g., Bolet et al. 2014); (5) splenial reaches the anterior section of the dentary (among amphisbaenians, the presence of a splenial is restricted to members of Blanidae – the splenial in the extant *Blanus* is a tiny splint of bone, partly covering the Meckelian canal medially and barely leaves an imprint on the medial side of the subdental shelf, see Gans and Montero 2008; Bolet et al. 2014; Villa et al. 2019; although note that the splenial is relatively large in the Eocene *Cuvieribaena*, see Čerňanský et al. 2015b); (6) intramandibular septum does not reach the end of the tooth row posteriorly (the intramandibular septum extends along the entire tooth row in amphisbaenians, except of *Rhineura*, see Smith 2009; Čerňanský 2019); (7) wedge-shaped fossa for the adductor musculature is extensive, running well below the tooth row (although this can be simply connected to a stronger bite force connected to amblyodont teeth; in *Polyodontobaena* and extant Amphisbaenia, it is usually behind the tooth row); (8) high number of labial foramina (five or six instead of usually three in amphisbaenians, see Gans and Montero 2008; Čerňanský 2019; Villa et al. 2019) and (9) the largest amblyodont teeth in Walbeck specimens are present in the posterior section of the

jawbone. This is in sharp contrast to stratigraphically younger amphisbaenians with amblyodont dentition, in which the largest teeth are in the anterior region (see Čerňanský et al. 2015b; Čerňanský 2023). Thus, by having robust teeth in the posterior rather than anterior region of the tooth row, these Paleocene forms resemble members of the clade Lacertidae (see, e.g., Čerňanský et al. 2016a,b, 2017). If *Camptognathosaurus* would be an amphisbaenian, then this would be a plesiomorphic condition for Amphisbaenia. The position of the largest teeth in a tooth row is not random but reflects the lever mechanism of the mandible to be more effective. The postdentary position of the articulation area of the mandible with the quadrate is directly determined by the length and the orientation of the posterior region of the mandible, which influences the tooth row and mandibular geometry and mechanics. The lever mechanism in a typical amphisbaenian mandible is more effective when the larger teeth are in the anterior region rather than posteriorly (Čerňanský et al. 2015b; note that the condition in amphisbaenians represents rather a novel adaptation among lacertoids). Overall, it seems likely that the mandibular mechanism of *Camptognathosaurus* was more similar to lacertids rather than to amphisbaenians (in regard, see *Cuvieribaena* from the Eocene of France described by Čerňanský et al. 2015b). Note, however, that the largest teeth in the posterior section of the tooth row are also present in the extant *Amphisbaena ridleyi* (see Pregill 1984: fig. 1A). The mandible of this species is rather atypical for amphisbaenians. The whole mandible of *A. ridleyi* is concave dorsally, and the typical feature of most amphisbaenian dentaries - an angle at the symphysis (e.g., Gans 1974; Gans and Montero 2008; Longrich et al. 2015), is absent. In fact, however, the condition in lacertids such as *Pseudeumeces cadurcensis*, *Dracaenosaurus croizeti*, *Janosikia ulmensis*, *Maioricalacerta rafelinensis*, is also common in other lizards – amblyodont teeth in most durophagous lizards are in the posterior or mid-posterior region of the dentary, as in, e.g., *Dracaena guianensis*, *Tiliqua scincoides*, *Eumeces schneideri*, *Paraplocosauriops quercyi*, *Pseudopus apodus*, and *Varanus niloticus* (Dalrymple 1979; Rieppel and Labhardt 1979; Pregill 1984; Augé 2005; Bailon et al. 2014; Klembara et al. 2014; Čerňanský et al. 2016a, b, 2017; Čerňanský and Syromyatnikova 2021; Georgalis et al. 2021b).

Both maxillae MLU.GeoS.4047 and 4048 possess some very interesting features. In all modern amphisbaenians (including Miocene forms), the posteroventral process is reduced, whereas the posterior section is formed by the posteriorly distinctly protruded ectopterygoid process (sensu Bolet et al. 2014) of the maxilla (see Gans and Montero 2008; Bolet et al. 2014; Čerňanský 2019; Villa et al. 2019). This is an opposite condition to the Walbeck maxillae. Moreover, the delicate, well-developed, pre-terminal palatine process is not known in any crown amphisbaenian, and the flaring of the maxilla posteriorly is also unknown (except in *Trogonophis*). One

feature deserves a comment: the posterior region of the maxilla implies the presence of a jugal. If this is correct, a jugal is present in known crown amphisbaenians only in Rhineuridae (Gans and Montero 2008). Moreover, Estes (1983) stated that there is a weak sculpture reflecting osteodermal attachment on the nasal process of the specimen figured by Kuhn (1940b: tab. II fig. 4), although this specimen cannot be allocated to *Camptognathosaurus* without doubts, since it is figured only in lateral view.

Thus, while this seemed possible based on the holotype dentary from France, the detailed study of the Walbeck dentary and especially maxillae reveals a stunningly primitive morphology for anything but a hypothetically basal-most stem amphisbaenian. Although *Polyodontobaena* appears to belong to Amphisbaenia, possibly representing a stem blanid (it is recovered as the sister taxon to Blanidae, see Longrich et al. 2015), there are serious doubts that the same is true for *Camptognathosaurus*. Indeed, the latter one resembles more, in some features, the Eocene *Cryptolacerta* from the classic Messel locality in Germany. *Cryptolacerta* was considered as being closest to the amphisbaenian ancestor (Müller et al. 2011), but this was put in doubt in several studies and the phylogenetic analyses placed it with Lacertidae (Longrich et al. 2015; Tałanda 2016; Brownstein et al. 2022). *Camptognathosaurus* shares the following features with *Cryptolacerta* (see Müller et al. 2011; Smith and Habersetzer 2021; Fig. 9A–C here): (1) the large coronoid process that, at least partly, might cover the anterolateral part of the coronoid; (2) the slightly arched ventral margin; (3) the rounded subdental shelf; (4) the absence of an angle at the mandibular symphysis; (5) the Meckelian canal is fully open and exposed medially, being narrow in the anterior region and widens slightly posteriorly; (6) the position of the alveolar foramen relative to the tooth row; (7) the around five labial foramina; (8) the well-developed, wedge-shaped fossa for the adductor musculature; (9) the moderately low dental crest; (10) the heterodont dentition; (11) the short tooth row (fourteen tooth positions are present in the holotype, but only eleven in the second specimen; Müller et al. 2011; Smith and Habersetzer 2021); (12) the enlarged posterior teeth; (13) the posteroventral process of maxilla long rather than short; (14) the maxillary tooth row does not reach the posterior end of the bone but leaves a small posterior toothless portion; and (15) the presence of jugal. There are, however, important differences as well, such as the presence of bicuspid tooth crowns in *Cryptolacerta*. In fact, most of these character states suggest lacertid affinities in general or, among them, of durophagous lacertids (most of them are widespread among lacertids, particularly amblyodont lacertids like *Dracaenosaurus* and *Pseudeumeces*). Interestingly, however, the first character state (the large coronoid process that, at least partly, might cover the anterolateral part of the coronoid) is absent in crown lacertids, in which a lateral overlap of the posterodorsal margin of the dentary by the coronoid is present. The condition in *Cryptolacerta* and

Camptognathosaurus is rather typical of amphisbaenians (not in *Rhineura*, see Gans and Montero 2008; Čerňanský 2019). However, this feature is not restricted to them and is also present in, e.g., dibamids (Čerňanský 2019) and in skinks, such as *Acontias*, *Ophiomorus*, *Heremites*, *Tiliqua* and *Eumeces* (Čerňanský 2019; Čerňanský et al. 2020b; Čerňanský and Syromyatnikova 2021). The last two taxa also have amblyodont dentition, although *Tiliqua* has a closed Meckelian canal. In fact, the tendency toward closure of the Meckelian canal is a characteristic of many scincid lizards (Greer 1970, 1974; Rieppel 1981; Estes 1983; Evans 2008; Augé and Smith 2009; Hutchinson and Scanlon 2009; Gauthier et al. 2012; Čerňanský et al. 2020b; Čerňanský and Syromyatnikova 2021). Although members of *Eumeces* have an open Meckelian canal in dentary and amblyodont teeth, they differ from *Camptognathosaurus* in many aspects (see Čerňanský et al. 2020b), e.g., (1) higher tooth number (around 18); (2) higher dental crest relative to the tooth size; (3) although splenial is well developed, its dorsal portion attached to the subdental shelf reaches only to the half of the tooth row; and (4) the maxillary tooth row reaches almost the posterior end of maxilla. So the conclusion is that although *Camptognathosaurus* has amblyodont teeth, it does not seem to have any characteristics that would indicate its allocation to skinks.

Thus, in general, all the new data bring serious concerns about the attribution of *Camptognathosaurus* to Amphisbaenia. It seems much reasonable to suggest its relationship being closer to lacertids, e.g., to forms such as *Pseudeumeces* or *Cryptolacerta*. Unfortunately, *Cryptolacerta* requires a detailed revision of its anatomy and phylogenetic relationship. As mentioned above, its current status is considered to be a lacertid (Longrich et al. 2015; Tałanda 2016; Brownstein et al. 2022). It may be a specialized lacertid with burrowing adaptations (see, e.g., Tałanda 2016). Based on current data, we can suggest the hypothetical possibility that *Camptognathosaurus* is related to *Cryptolacerta* rather than to *Blanus*, and that both these early Paleogene taxa might be lacertids (at least pan-lacertids). *Camptognathosaurus* is too incomplete, but can be assigned to clade Lacertoidea without doubt. Based on the overall bone morphology, *Camptognathosaurus* is provisionally assigned here to the total clade Lacertidae. It shares the following combination of features with Lacertidae (see Estes et al. 1988; Čerňanský and Syromyatnikova 2019; Villa and Delfino 2019): (1) well-developed sulcus dentalis; (2) subdental shelf of the dentary (without splenial spine) is well protruded medially; (3) wide medially open Meckelian canal (restricted in eolacertids, see Čerňanský and Smith 2018, 2019); (4) an arched dentary, with concave tooth row, subdental shelf, and ventral edge; (5) pleurodont implantation and replacement areas located at the center of the tooth bases; (6) dentary tooth number 10–12; the number spans well among the number of the amblyodont lacertids such as the Paleogene *Pseudeumeces* and *Dracaenosaurus*; (7) well-developed and continuous

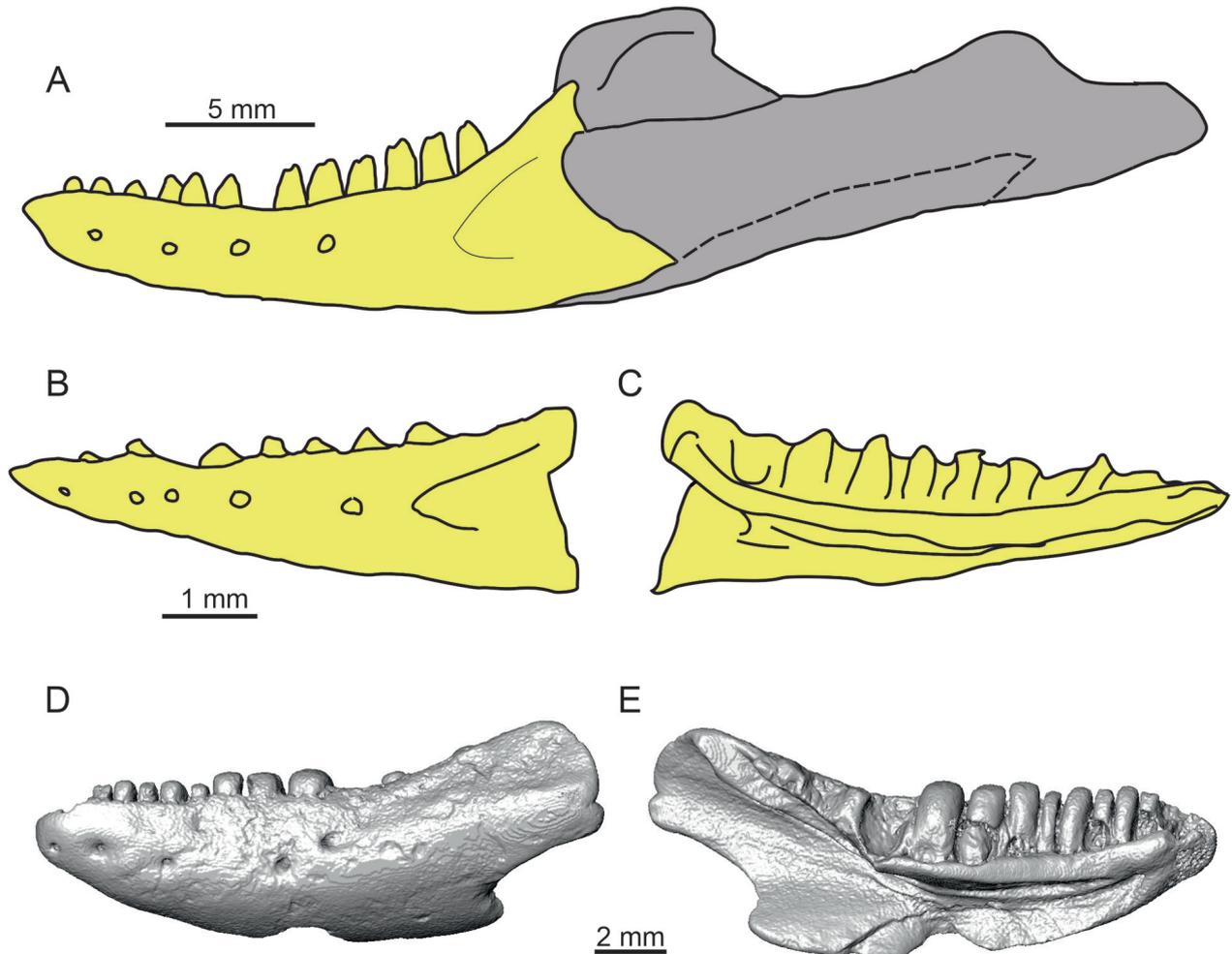


Figure 9. Paleogene lacertoids – the Eocene *Cryptolacerta hassiaca* (A–C) from Messel and the Oligocene *Pseudeumeces kyrillo-methodicus* from Quercy (D, E). Left mandible of the holotype SMF ME 2604 in lateral (A) view (modified from Müller et al. 2011); left dentary of the specimen found in the gut of *Paraneocrocodon feisti* in lateral (B) and ventral (C) views (modified from Smith and Habersetzer 2021). Virtual 3D models of the holotype left dentary NHMW 2019/0051/0001 in lateral (D) and medial (E) views.

splenic facet on the medioventral edge of the subdental shelf; (8) splenic is large and long, reaching the anterior region of dentary; (9) the maxillary tooth row does not reach the posterior end of the bone but leaves a small posterior toothless portion (contra, e.g., teiids and skinks) and, (10) potentially, assumed presence of osteoderms fused to the lateral side of the facial process of maxilla (suggested by Estes 1983). The presence of all these features indicates lacertid lizards rather than members of other groups. Note, however, that there are some differences between this Paleocene form and crown lacertids such as a large coronoid process of the dentary mentioned above. On the other hand, although this condition is not the same, a large and slightly dorsally elevated coronoid process is also present in crown lacertids with amblyodont dentition such as *Pseudeumeces* (Fig. 9D, E), *Dracaenosaurus* and *Janosikia* (all members of Gallotiinae; see Čerňanský et al. 2016a, b, 2017; Georgalis et al. 2021b). Thus, in fact, this might be potentially related to the amblyodont dentition, rather than being a character suggesting this form is out of the crown. In any case, this hypothesis about the

relationship of *Camptognathosaurus* to lacertids needs to be met with caution and should be tested by future studies of new, more complete fossil record of this taxon.

In general, our hypothesis would support the model proposed by Čerňanský and Smith (2018) about the origin and early history of Lacertidae that the Paleogene of Europe, rather than being dominated by archaic forms only distantly related to Lacertidae (e.g., Mayer and Benyr 1994; Müller et al. 2011), in fact, hosted large radiation of pan-lacertids - the total clade including Lacertidae [Pan-Lacertidae sensu Čerňanský and Smith 2018, the stem-based clade. Note that this name was originally used in Čerňanský and Smith (2018), later in Čerňanský et al. (2020a) and Brownstein et al. (2022), however, has never been officially erected. It should include extant Lacertidae and all extinct taxa descended from its last common ancestor, as well as stem lacertids that diverged prior to the origin of the crown. *Camptognathosaurus walbeckensis* is only questionably referred here to lacertids based on its morphology (as further confirmed by phylogenetic analyses) and also overall similarity to forms such

as *Pseudeumeces* and *Cryptolacerta*, following studies of the latter taxon (Longrich et al. 2015; Tałanda 2016; Brownstein et al. 2022), in which, *Cryptolacerta* is a crown lacertid]. In other words, the Paleogene of Europe does not only contain members of the stem, but a mixture of members of the stem (*Eolacerta*, *Stefanikia*), and crown groups (see Čerňanský and Augé 2013; Čerňanský et al. 2016a, 2017; Čerňanský and Smith 2018). Note that the position of *Cryptolacerta* and *Camptognathosaurus* is uncertain. They could, hypothetically, represent stem members (more closely related to the crown than to eolacertids), but as mentioned above, in regard to *Cryptolacerta*, the Brownstein et al. (2022) reference phylogenies all find it as a sister-taxon to *Gallotia atlantica*, i.e., in crown Lacertidae. Longrich et al. (2015) do not necessarily contradict this assignment, because they did not include any extant member of Gallotiinae. In our analysis, *Cryptolacerta* is sister to *Lacerta* and *Camptognathosaurus* is sister to *Gallotia* (Fig. 8). So as far as the current reference phylogenies are concerned, both *Cryptolacerta* and *Camptognathosaurus* appear to be crown Lacertidae. But again, this Messel taxon requires a detailed revision to resolve its exact phylogenetic position and more complete fossil specimens of *Camptognathosaurus* are needed to draw more robust conclusions.

Kuhn's „*Glyptosaurus walbeckensis*“ vs. „*Camptognathosaurus parisiensis*“

Kuhn (1940a) diagnosed „(aff.) *Glyptosaurus walbeckensis*“ as:

1. having a maximum of ten tooth positions. Although it is possible since some dentaries from Walbeck could possess ten tooth positions, we can doubt it based on Kuhn's figures. It seems to be more likely (based on comparison with herein studied specimens) that his specimen has eleven tooth positions (the teeth in the anterior region are much smaller). Based on the figures of Kuhn (1940a, b), Estes (1983) also regarded the number of teeth as 10–12.
2. the amblyodont dentition, the last teeth gradually decrease in size.
3. the strongly elevated “coronoid” (Kuhn used the term coronoid, but because the coronoid bone is not preserved in the material, we suggest that he probably thought the coronoid process of dentary), i.g., the same as the form described here as *Camptognathosaurus*.

The specimen figured by Kuhn (1940a: fig. 4b, 5b) is very similar to the specimen RIV PP 413 selected by Folie et al. (2013: fig. 3A) as the holotype of *Camptognathosaurus parisiensis* from the French localities. Moreover, the dentary RIV PP 413 shares the same features with the Walbeck specimen MLU.GeoS.4045 described here (Fig. 3A–D; see remarks

above). The principle of priority regarding the scientific name of the International Code of Zoological Nomenclature ICZN (1999) makes *Camptognathosaurus parisiensis* a junior synonym of the species described by Kuhn (1940a). Thus, this taxon gets a combined name, *Camptognathosaurus walbeckensis* comb. nov., because Kuhn used *Glyptosaurus* as a generic name. It does not matter if the older type species is a junior synonym – it is clear in ICZN (Article 67.1.2: “The name of a type species remains unchanged even when it is a junior synonym or homonym, or a suppressed name”).

Problem of morphotypes in Walbeck

Paleocene lizards from Europe are described based only on the isolated jaws, whereas more complete specimens, which would shed more light on their morphology and taxonomy, are currently unknown. Potentially, one could suggest that two morphotypes can be identified in Walbeck. They can be distinguished by a slightly different tooth count and tooth crown morphology. Regarding the second character, we prefer not to describe two forms based on minor differences (see argumentations below). We suggest two hypothetical explanations:

1. the jaws with slightly more pointed teeth represent different taxon.
2. more probably – the Walbeck material with slightly more pointed teeth represents younger, juvenile ontogenetic stages (at least some of them, e.g., MLU.GeoS.4041; see Fig. 4K–M) of *Camptognathosaurus walbeckensis* comb. nov. (e.g., Fig. 3A–D). Some minor differences can be also caused by individual variability and taphonomic alteration. In any case, all differences in tooth crown morphology can be explained. It is important to note that specimens with intermediate conditions are present in the material, and no strict border clearly separating two morphotypes could be found:
 - a. pointedness: this feature varies among individuals and even in a single tooth row. There are many intermediate stages, for example, the robust teeth in MLU.GeoS.4042 (Fig. 4A, B). Moreover, the concave distal margin of the tooth crown is also present in the penultimate preserved tooth of MLU.GeoS.4045, although less pronounced (see Fig. 3D). The same condition can be seen in the type material of *Camptognathosaurus parisiensis* described by Folie et al. (2013: fig. 3). The change in tooth crown morphology during ontogeny is well documented for many lizards, even in a much higher degree. For example, dental complexity decreases during ontogeny in *Ctenosaura* (*C. pectinata* and *C. similis*), which is generally insectivorous as a juvenile and herbivorous as an adult (Christensen and Melstrom 2021). Among anguines, the apices

of teeth are more-or-less pointed in juveniles of *Pseudopus* (both extant *P. apodus*, see Klembara et al. 2014 and fossil *P. pannonicus*, see Loréal et al. 2023), whereas adults have robust amblyodont teeth. In extant lacertids, an ontogenetic change in the tooth morphology is sometimes observed, as in *Gallotia stehlini*, where the juvenile tricuspid teeth are replaced by multicusp teeth in the adult (Barahona et al. 2000). Among fossil lacertids, this was observed in the Early Miocene *Janosikia* – although amblyodont dentition is present in the juvenile specimen (as in adults), vestiges of mesial cusps are present on some anterior maxillary teeth (see Čerňanský et al. 2016a).

- b. tooth count: note that the original holotype of *Camptognathosaurus parisiensis*, RIV PP 413, has eleven tooth positions (Folie et al. 2013). This observation falls within the variability range of the Walbeck specimens. Moreover, the number of teeth and labial foramina in all lizards is variable and in general size-related, so these numbers should not be regarded as absolute differentiation.

In any case, all differences are too small to be considered as distinguishing features.

For all these reasons, we regard them to be intraspecific and/or ontogenetic variations, some of them are caused by poor preservation and, thus, should represent the same taxon. It should be noted, however, that the biological (not just taxonomic) conspecificity of two populations – based on fragmentary dentaries – is not 100% secure.

Paleoecology

Nowadays, true feeding specialists among lizards are rare. The problem is also that although squamates seem to be ideal subjects for investigating relationships between diet and dental patterns, studies exploring patterns between tooth shape and diet are remarkably rare for squamates (Christensen and Melstrom 2021). The dentition of *Camptognathosaurus* indicates durophagous specialist. Although it may have preferred to eat hard-shelled invertebrates, as is generally the case in amblyodont lizards (Dalrymple 1979; Rieppel and Labhardt 1979; Estes and Willams 1984), the presence of amblyodont teeth does not demonstrate that *Camptognathosaurus* fed solely on shelled invertebrates, because durophagy is not restricted to such prey. Most fossil taxa with amblyodont dentition (except of, e.g., *Dracaenosaurus* with its extremely durophagous specialization, see Čerňanský et al. 2017) were probably faunivorous (or even more likely omnivorous, as it is seen in the extant scincid *Tiliqua*, see, e.g., Christian et al. 2003; Shea 2006). In fact, only a few durophagous specialists exist worldwide nowadays. Among Tupinambinae, for example, only *Dracaena* is a truly durophagous form, whereas other teiids with

amblyodont teeth are omnivorous (Mercolli and Yanosky 1994; Kiefer and Sazima 2002).

Interestingly, snails are highly unusual in the diets of modern amphisbaenian species and have been reported as the main prey for only two species: *Amphisbaena ridleyi* (Pregill 1984), which has robust, but still somewhat pointed teeth and *Trogonophis wiegmanni* (Gans 1960; Martín et al. 2013), which has robust, blunt teeth, with acrodont implantation. Teeth indicative of durophagy have been observed in the Eocene amphisbaenians *Cuvieribaena* from France (Čerňanský et al. 2015b) and the North American *Oligodontosaurus wyomingensis* (Estes 1975; although in this latter species the teeth are somewhat pointed). On the other hand, amblyodont teeth repeatedly occur among lacertid members during different periods of the European Cenozoic (Augé 2005; Bailon et al. 2014; Čerňanský et al. 2016a, b, 2017). Amblyodonty is certainly adaptive and can respond to several environmental cues and climate change might be one of them. Paleogene terrestrial ecosystems faced significant changes and reorganisations. If *Camptognathosaurus* is a lacertid, then this type of ecology shows a tendency in members of the clade already in the Paleocene. This is interesting because present-day lacertids are more uniform (no lacertid species with amblyodont dentition is known to exist today). The interpretation of *Cryptolacerta* as a member of the total clade of Lacertidae (Longrich et al. 2015; Tałanda 2016; Brownstein et al. 2022) suggests that members of the clade was also able to evolve modifications such as partially reduced both fore- and hindlimbs (Tałanda 2016). It seems that lacertids were able to respond to changes by evolving different types of adaptations which allowed them to occupy different ecological niches (much broader than seen in present-day members of this lineage). As already stated by Čerňanský and Smith (2018), the ecological breadth of pan-lacertids is amply demonstrated by the differences in size and body form (e.g. small semifossorial forms like *Cryptolacerta*, mid-sized and large terrestrial forms like *Stefanikia* and *Eolacerta*). Some of these (*Succinilacerta*, *Plesiolacerta*) were more closely related to crown Lacertidae than others, and even crown representatives may have been present (Borsuk-Bialynicka et al. 1999; Čerňanský and Augé 2013; Čerňanský et al. 2016a). Most of these lineages became extinct until only members of the crown remained. Meanwhile, one lineage (Lacertinae) radiated magnificently in the Neogene, uplifting Lacertidae as the dominating group of reptiles in present day Europe (Čerňanský and Smith 2018).

“aff. *Parasauromalus paleocenicus*” as Lacertidae

As mentioned in the Introduction, Kuhn (1940a) established the species “aff. *Parasauromalus paleocenicus*” based on an isolated left dentary. This dentary has been identified among the material studied herein (Fig. 5).

However, the left dentary MLU.GeoS.4059 clearly does not correspond to an iguanian (for *Parasauromalus* see Smith and Gauthier 2013: fig. 8C). The same is true for isolated vertebrae, which do not belong to either an iguanian or a varanoid. Indeed, as Estes (1983) suggested, the dentary can be allocated to Lacertidae. However, its reclassification to *Plesiolacerta*, questionably suggested by Estes (1983), cannot be supported. That Eocene taxon is characterized (see Čerňanský and Augé 2013; Čerňanský and Syromyatnikova 2019) by: (1) heterodont dentition, including mono-, bi- and tricuspid teeth; (2) dentary with an overall prominently arched shape; and (3) widely open and large Meckelian groove. If lacertid vertebrae (at least some of them) belong to the same taxon as the dentary, then their morphology could be a further argument against its allocation to *Plesiolacerta*, in which the vertebrae are characterized by a strongly-developed zygosphene and zygantrium (Čerňanský and Augé 2013). The dentary morphology resembles the one present in typical crown insectivorous lacertids (see, e.g., Čerňanský et al. 2015a: fig. 3a,b; Čerňanský and Syromyatnikova 2019, although it cannot be fully excluded that this dentary belonged to a taxon which is on the stem of Lacertidae, just closer than other forms described so far from the Paleocene). Therefore, the name „*aff. Parasauromalus paleocenicus*“ should be considered as a nomen dubium. In any case, this record forms an important evidence because it strongly supports the presence of Lacertidae in Europe already in ~MP 5. This is consistent with recent molecular analyses in which the crown ages were recovered for Lacertidae in the Paleocene or around the Cretaceous-Tertiary (K/T) transition (Vidal and Hedges 2009; Hipsley et al. 2009; Garcia-Porta et al. 2019).

All vertebrae described here are allocated to Lacertidae, because their morphology resembles the one present in lacertids (see, e.g., Čerňanský et al. 2015a: fig. 4I-M for a fossil one, Tschopp 2016 for extant ones), but more precise allocation is impossible. It should be noted, however, that the vertebral morphology of *Camptognathosaurus* is currently unknown. In fact, it cannot be fully excluded that some specimens, like MLU.GeoS. 4066, might belong to *Camptognathosaurus*. Two reasons might support it: (1) this taxon is the most numerous in regard to preserved elements in Walbeck, and (2) the presence of a low neural spine is reported for *Cryptolacerta* too (Müller et al. 2011), which is similar to *Camptognathosaurus* in many aspects (see comparison above).

One question arises regarding the original attribution of *Camptognathosaurus* to amphisbaenians by Folie et al. (2013). Vertebrae of modern amphisbaenians can be easily recognized in the fossil record (although an allocation at the family level is very difficult) by the following combinations of features (see Estes 1983): (1) depressed centrum with a flat ventral surface; (2) roughly parallel lateral margins in ventral aspect; (3) massive synapophyses; (4) absence of zygosphene; and (5) and a sinusoidal neural arch lacking a neural spine. No vertebra from Walbeck possesses a combination of these features. One

can argue that according to Folie et al. (2013), the members of polyodontobaenids (if *Camptognathosaurus* belonged to this clade) exhibit many plesiomorphic features in jaws. Thus, this could also be expected from elements from other body parts. Some specimens, such as MLU.GeoS. 4066 are interesting. It possesses roughly parallel lateral margins in ventral view and quite large subcentral foramina (Fig. 6G). Other morphological character states (i.e., the presence of the neural spine), however, do not support an allocation of any vertebrae currently known from Walbeck to Amphisbania but rather show affinity to lacertids. For this reason, in this study, we prefer to assign tentatively all herein-described vertebrae as Lacertidae. Moreover, if *Camptognathosaurus* belongs not to crown Lacertidae, but, at least, to the total clade, such an allocation would not be entirely inconsistent even if some of these vertebrae would prove to belong to this taxon.

Scincoidea

The allocation of the right (MLU.GeoS.4057) and left (MLU.GeoS.4058) maxillae to Scincoidea (the clade includes Scincidae, Cordyliformes and Xantusiidae, see Zheng and Wiens 2016) is supported (see remarks above). Previously, Folie et al. (2005) described material from the middle Paleocene of Belgium as *Scincoideus haininensis*. Although the crown tips of this taxon do not possess striae similar to the Walbeck material, and the tooth apices also have a rather blunt appearance, some differences still can be observed. For example, the last posterior supralabial foramen is located at the level of the eighth tooth position (counted from posterior), whereas in the maxilla from Walbeck it is located at the level of the third tooth position (in MLU.GeoS.4058). However, the Belgian material requires a detailed revision because there are doubts about its allocation to Scincoidea. This taxon is rather considered to be a member of Lacertoidea (see Smith and Gauthier 2013; Čerňanský et al. 2020a). More complete Walbeck specimens are needed for a proper comparison.

Palaeogeographic note for the Paleocene

Besides Walbeck in Germany and Rivecourt-Petit Pâtis (MP 6b) and Cernay-lès-Reims (MP 6a) both France, the material of “*cf. Camptognathosaurus parisiensis*” is also described from the locality Montchenot (Paris Basin, MP 6; Augé et al. 2021). This locality is geographically close to Cernay. Based on the occurrence of the same taxon, it might seem likely that the whole area, including the French localities and the German Walbeck locality, might have formed one palaeogeographical unit (e.g., an island or part of the continent above the sea level) in the Paleocene. Note, however, that a dispersion over sea cannot be fully excluded as this is not uncommon for lizards (e.g., Losos 2009; Čerňanský et al. 2020c),

in which even fossorial forms such as amphisbaenians are found on islands. Although palaeodistribution of *Campygnathosaurus* is important, it is difficult to make the strong argument that today's northern France and Germany were really united by a land connection on this basis. Future research of new localities and various types of organisms might shed light on the paleogeography of Europe during the Paleocene.

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Supplementary material 1

Updated phylogenetic matrices

Authors: Andrej Čerňanský, Davit Vasilyan

Data type: nexus

Explanation note: Updated phylogenetic matrices in TNT. file format used for the phylogenetic analyses in this study.

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Link: <https://doi.org/10.3897/fr.27.109123.suppl1>

Supplementary material 2

Consensus tree with Bremer values

Authors: Andrej Čerňanský, Davit Vasilyan

Data type: tif

Explanation note: A New Technology (NT) search in TNT produced two equally parsimonious trees. Here is the consensus tree of these two trees.

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Link: <https://doi.org/10.3897/fr.27.109123.suppl2>

Supplementary material 3

Parsimonious tree with Bremer values

Authors: Andrej Čerňanský, Davit Vasilyan

Data type: tif

Explanation note: A New Technology (NT) search in TNT produced two equally parsimonious trees. Here is the tree with Bremer values.

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