Additional anatomical information on the Eocene minute boas *Messelophis variatus* and *Rieppelophis ermannorum* (Messel Formation, Germany)

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Abstract

The minute fossil boas *Messelophis variatus* and *Rieppelophis ermannorum* are the most abundant snakes recovered from the early-middle Eocene paleolake of Messel (Germany). This work describes several additional specimens referable to these taxa from the same deposit. Novel anatomical information gathered here provides further support for their phylogenetic affinity with the small North–Central American boas of the family Charinidae.

Key words

Introduction

The early–middle Eocene *Konservat-Lagerstätte* of Messel (Germany) has yielded the best-preserved specimens of Paleogene snakes (SCANFERLA & SMITH, 2020), especially Booidea, providing a unique opportunity to understand the early stages in the evolution of this charismatic clade of alethinophidian snakes. Among the c. 160 snake specimens recovered so far in public institutions, *Messelophis variatus* and *Rieppelophis ermannorum* are notable for being the most abundant of identified species (SMITH *et al.*, 2018). *Rieppelophis ermannorum* was first described by BASZIO (2004) based on 14 specimens, and *M. variatus* by SCHAAL & BASZIO (2004) based on 15 specimens. Their anatomy and phylogenetic relationships were re-studied by SCANFERLA *et al.* (2016). Recently, new specimens of these fossil minute boas became available, which exhibit new relevant information about their skull anatomy. Here we describe the novel traits and discuss how they impact the inferred phylogenetic relationships of these fossil tiny boas.

Materials and methods

The study presented herein is based on the analysis of new specimens of *Messelophis variatus* and *Rieppelophis ermannorum* (see Table 1) deposited in the Messel collection of the Senckenberg Research Institute in Frankfurt am Main (SMF-ME). All specimens were completely extricated from the matrix and embedded in epoxy resin. Due to the transparent nature of the epoxy plates, we could study the embedded side of some specimens of *M. variatus* (e.g., SMF-ME 1828 a+b) in order to reveal new and noteworthy anatomical information.
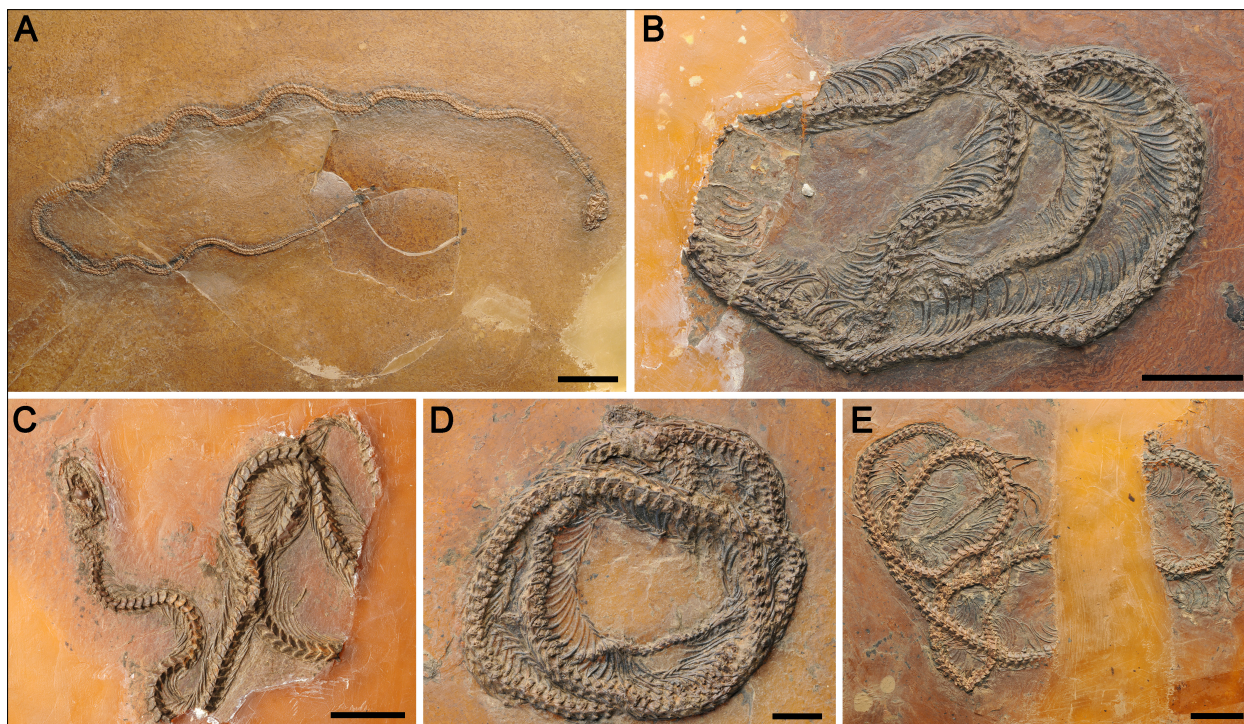
Fig. 1. Overview of the specimens examined in this work, referred to *Messelophis variatus* (SMF ME 11266, A; SMF ME 513a, B) and *Rieppelophis ermannorum* (SMF ME 10863a, C; SMF ME 1087a, D; SMF ME 1542a+b, E). Scale bars equal to 20 mm.

Table 1. List of the specimens employed in this study. SMF-ME 1087, 1542 and 2013 were collected in the 1980s and are newly referred; SMF-ME 10863 and 11266 were collected since description of the species and are newly referred.

Messelophis variatus	*Rieppelophis ermannorum*
SMF-ME 2013	SMF-ME 1087
SMF-ME 11266	SMF-ME 1542
	SMF-ME 10863

Taxonomic terms are used as follows: Booidea sensu Pyron *et al.* (2014), Caenophidia sensu Hoffstetter (1939), Constrictores sensu Georgalis & Smith (2020), Henophidia sensu Gauthier *et al.* (2012).

Results

The affinities of studied specimens here referred to *Messelophis variatus* and *Rieppelophis ermannorum* are firmly established based on numerous cranial and postcranial traits. Such features, previously depicted in a recent redescription of both species (Scanferla *et al.*, 2016) include the general morphology of cranial bones, number of tooth positions in toothed elements (mostly maxilla and dentary), vertebral shape (e.g. development of neural spine, absence/presence of laminar haemapophyses) and vertebrae count.

Novel anatomical characters for *Messelophis variatus*

Palatine. SMF-ME 11266 (Fig. 1A) provides a ventral view of a small portion of the left palatine articulated with the pterygoid (Fig. 2A). The general aspect indicates that this portion corresponds to the anterior dentigerous process present in most alethinophidian snakes, although another unidentified bone covers its anterior tip. It preserves six tooth positions, but only three teeth are present, which are larger than the pterygoid teeth.

Pterygoid. Most of the left pterygoid is present in SMF-ME 11266, only missing part of the quadrate ramus and the lateral edge corresponding to the ectopterygoid articulation (Fig. 2A). There are approximately nine tooth positions. The tooth row is located entirely in the palatine ramus and reaches the centre of the pterygoid. Some teeth are preserved anteriorly, showing the difference in size with respect of the palatine teeth. As in most booids (Fig. 2B), a medial wing for the attachment of the pterygoideus muscles is present, although it is broken distally and thus its shape cannot be ascertained. The lateral edge of the quadrate ramus is incomplete, but the preserved portion indicates a slender, delicate shape.

Basicranium. Both SMF-ME 11266 and SMF-ME 513a (Fig. 1B) offer a ventral view of the basicranial elements (Fig. 2A,C). The parabasisphenoid bone resembles in many aspects that of other small booids such as *Exiliboa placata* (Fig. 2D). The parasphenoid rostrum is elongated and exhibits a narrow base, which is slightly concave.
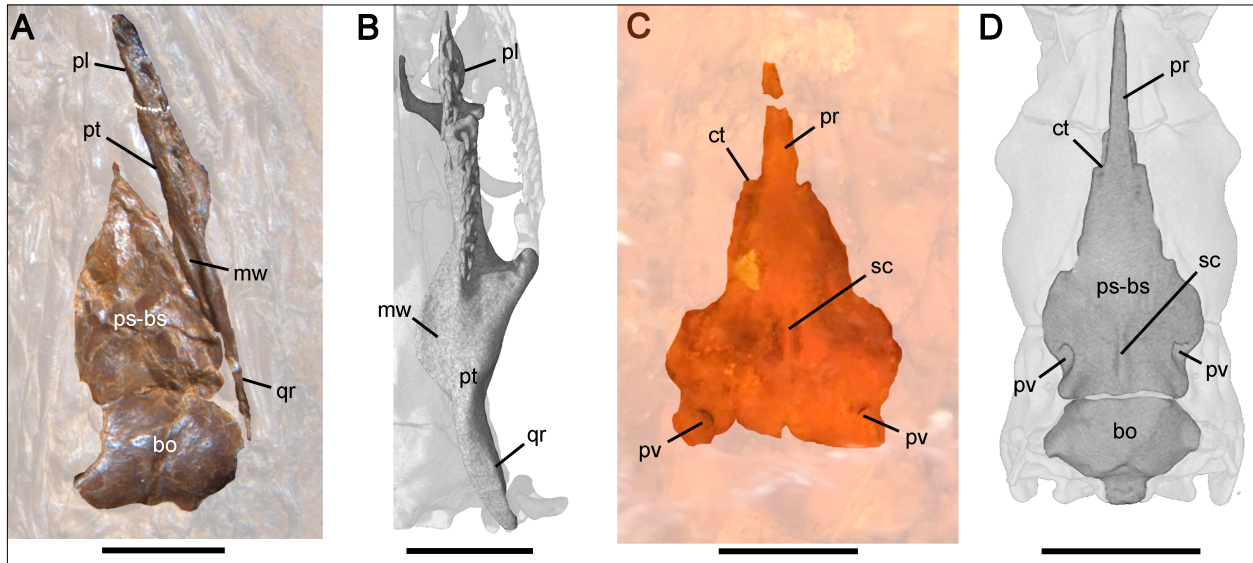
Fig. 2. Comparison of specimens referred to *Messelophis variatus* with the charinid booid *Exiliboa placata*. A, Ventral view of SMF-ME 11266; B, 3D reconstruction based on CT data of the left palatopterygoid bar of *Exiliboa placata* (FMNH 207669); C, embedded side of SMF-ME 513a; D, ventral view of the 3D reconstruction of the basicranium of *Exiliboa placata* based on CT data. bo, basioccipital; ct, crista trabecularis; mw, medial wing; pl, palatine; pr, parasphenoidal rostrum; ps-bs, parabasisphenoid; pt, pterygoid; pv, posterior foramen of the Vidian canal; qr, quadrate ramus; sc, sagittal crest of the parabasisphenoid bone. Scale bars equal to 2 mm.

The cristae trabecularis are well developed, but they do not reach the frontals. There is a small sagittal crest restricted to the posterior region near to the suture with the basioccipital, thus delimiting a shallow concave surface on either side. As in booids, the right posterior Vidian canal is larger than the left. The basioccipital can be observed in ventral view in SMF-ME 11266 (Fig. 2A). Its ventral surface is smooth, lacking the sagittal crest or protuberances present in large booids.

Novel anatomical characters for *Rieppelophis ermannorum*

Septomaxilla-Vomer. Fragmentary left and right septomaxillla and right vomer are preserved in SMF-ME 10863a (Fig. 1C, 3A). These bones can be observed in ventral and lateral views due to a small degree of crushing. As in most henophidians, the sidewall of the opening of the Jacobson's organ is formed largely by the septomaxilla rather than the vomer, a condition shared with non-caenophidian snakes (Fig. 3B). The posterior dorsal (vertical) lamina of the vomer is well developed. The only preserved portion of the left septomaxilla corresponds with the posterior process of the lateral flange, which is elongated and distally expanded as in many alethinophidians (Fig. 3B).

Basicranium. The parabasisphenoid can be observed in SMF-ME 1087a (Fig. 1D, 3C). The ventral view exhibits a morphology similar to *Messelophis variatus* and *Exiliboa placata*, with a short but conspicuous sagittal crest located in the posterior third of the bone defining two shallow concavities for muscle origin. Both posterior apertures of the Vidian canal are present near to the lateral edges of the basisphenoid region, the right being larger than the left foramen as in booids. The basioccipital can be observed in ventral view in SMF-ME 1087a (Fig. 3C). The suture between this bone and the parabasisphenoid is straight. As in most small booids, the basioccipital has a bulbous shape with a smooth ventral surface, lacking the sagittal crest or protuberances present in large booids.

Prootic. This neurocranial element is well preserved in SMF-ME 1542a+b (Fig. 1E) and SMF-ME 10863a (Fig. 3D). The prootic is similar to that of small extant booid snakes such as *Lichanura* and *Exiliboa*. The anterior (V_2) trigeminal foramen is delimited anteriorly by the parietal due to the weak development of the dorsal and ventral anterior processes of the prootic. The ophidiosphenoid is present as a broad strip of bone that separates the anterior (V_2) from the posterior (V_3) foramen. Ventral to the anterior end of this structure there is a small foramen that topologically corresponds to the laterosphenoid foramen described by RIEPPEL (1979), which is the passage for the cid-nerve. Ventral to the posterior trigeminal foramen (V_3) there is a small foramen that corresponds with the hyomandibular branch of the facial nerve (VII_h). Additionally, a small piece of the right prootic corresponding with the ventral region of this bone can be observed in SMF-ME 1087a (Fig. 2C), which permits the observation of the laterosphenoid foramen and just posteriorly the foramen of the palatine ramus of the facial nerve (VII_p) in a configuration that mirrors charinid boas (Fig. 3). In contrast to large booids, the crista prootica is weakly developed and barely covers the stapedial footplate dorsolaterally as in charinid booids.
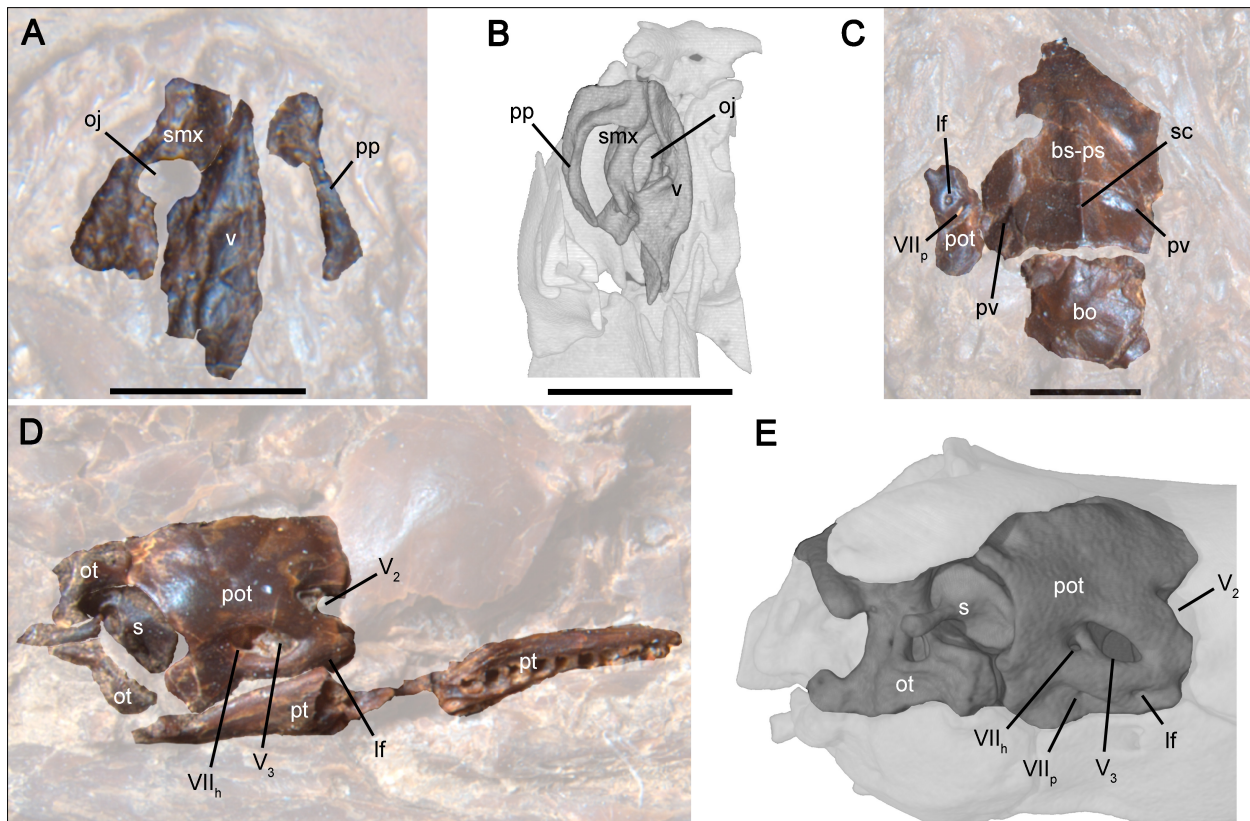
Fig. 3. Comparison of specimens referred to *Rieppelophis ermannorum* with the charinid booid *Exiliboa placata*. A, ventral view of the skull of SMF-ME 1087a showing the vomer-septomaxilla bones; B, 3D reconstruction based on CT data of the snout bones of *Exiliboa placata* (FMNH 207669) in ventrolateral view; C, ventral view of the skull of SMF-ME 1087a showing the basicranial bones; D, Lateral view of the skull of SMF-ME 10863a; E, 3D reconstruction based on CT data of the neurocranium of *Exiliboa placata* in right lateral view. bo, basioccipital; lf, laterosphenoid foramen; oj, opening of the Jacobson´s organ; ot, otooccipital; pot, prootic; pp, posterior process of the lateral flange of septomaxilla; ps-bs, parabasisphenoid; pt, pterygoid; pv, posterior foramen of the Vidian canal; s, stapes; sc, sagittal crest of the parabasisphenoid; smx, septomaxilla; v, vomer; V_2, foramen for the maxillary branch of the trigeminal nerve; V_3, foramen for the mandibular branch of the trigeminal nerve; VII$_h$, hyomandibular ramus of the facial nerve; VII$_p$, palatine ramus of the facial nerve. Scale bars equal to 2 mm.

Stapes. The right stapes is preserved and visible in natural position in SMF-ME 10863a (Fig. 3D). The stapedial shaft is partially broken at the base, but the observable portion of this structure indicates that its length is barely shorter than the diameter of the footplate, as in charinid booids. In comparison with *Messelophis variatus*, which curiously bears a small footplate like in large booids, *Rieppelophis ermannorum* has a relatively large footplate in a similar fashion to that of charinid boids and other small-sized henophidians (Fig. 3E).

Otooccipital. Only the anteriormost (otic) region of this bone can be observed in SMF-ME 10863a. The crista interfenestralis is projected anterolaterally, reaching the lateral bony rim (Fig. 3D). The crista tuberalis is not preserved, hence the conformation of the juxstastapedial recess cannot be ascertained posteriorly.

Pterygoid. An incomplete right pterygoid is present in SMF-ME 10863a, missing part of the quadrate ramus, part of the mid-region and the anterior tip of the palatine ramus (Fig. 3D). The tooth row is located in the palatine ramus and it reaches the centre of the pterygoid. There are approximately ten tooth positions, although the exact tooth count cannot be given. No teeth are preserved, although the size of the tooth sockets indicate they were notably smaller than the maxillary teeth.

Discussion

The new anatomical information described here was scored previously in a recently published work about the booid assemblage from Messel (SCANFERLA & SMITH, 2020). Both maximum parsimony and Bayesian analyses performed in that work (Fig. 4A) revealed a close affinity of the small Messel booids *Messelophis variatus, Rieppelophis ermannorum* and the new Messel charinine to North American-Central American charinine and ungaliophiine boas (see also SMITH & SCANFERLA, in press). The new traits described here, especially those of the neurocranium, permit an osteological characterization of this clade of Euro-American small booids.
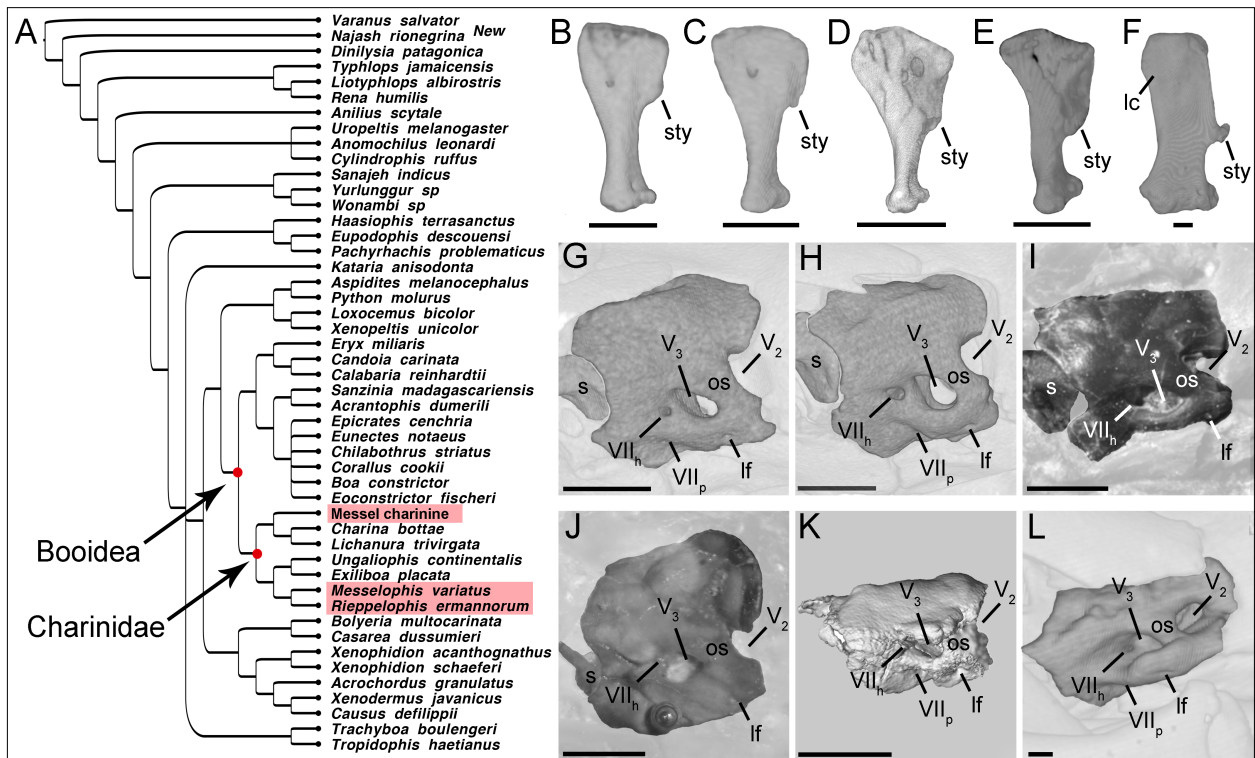
Fig. 4. Phylogenetic relationships of Messel minute boas. A, Maximum parsimony tree of a combined analysis (DNA+morphology) depicting the position of *Messelophis* and *Rieppelophis* into Charinidae boas (taken from SCANFERLA & SMITH, 2020); B−F, posterolateral view of 3D reconstructions based on HXRCT data of the left quadrate of *Charina bottae* (UMMZ 240637), *Exiliboa placata* (FMNH 207669), new Messel charinine (HLMD Me 9723, inverted), *Rieppelophis ermannorum* (HLMD Me 7915, inverted) and *Boa imperator* (FMNH 31182); G−L, lateral view of the right prootic bone of *Exiliboa placata* (FMNH 207669, based on HXRCT data), *Lichanura trivirgata* (CAS 200649, based on HXRCT data), *Rieppelophis ermannorum* (HLMD Me 7915), *Messelophis variatus* (SMF ME 1828 a+b), new Messel charinine (HLMD-Me 9723, based on HXRCT data) and *Boa imperator* (FMNH 31182, based on HXRCT data). lc, lateral crest; lf, laterosphenoid foramen; os, ophidiosphenoid; sty, stylohyal; V_2, foramen for the maxillary branch of the trigeminal nerve; V_3, foramen for the mandibular branch of the trigeminal nerve; VII_h, hyomandibular ramus of the facial nerve; VII_p, palatine ramus of the facial nerve. Scale bars equal to 1 mm.

These snakes share a particular configuration of the general shape and arrangement of the foramina of the prootic bone. Specifically, the foramen for the maxillary branch of the trigeminal nerve is closed anteriorly by the parietal in adult individuals, and the laterosphenoid foramen is located just below the anteroventral part of the ophidiosphenoid (Fig. 4G−L). The palatine branch of the facial nerve is located just below of the foramen for the hyomandibular branch of the facial nerve (this condition cannot be observed in *Messelophis variatus*). The quadrate bone is another distinctive element of these snakes, which is characterized by an expanded and planar cephalic condyle with the stylohyal attached directly to its posterior region, and a persistent foramen in the lateral surface of the cephalic condyle (Fig. 4B−E). The planar cephalic condyle was observed also in late embryos and juvenile specimens of some extant boids, but during post-natal growth a laterally oriented crest develops along the anterior edge of the cephalic condyle (SCANFERLA, 2016). Remarkably, the quadrate of the adult specimens of the Messel boa *Eoconstrictor fischeri* (SCANFERLA & SMITH, 2020: supplementary material) mirrors that of charinids due to the presence of a conspicuous foramen and a pla-nar shape (i.e. without the laterally oriented crest), but the stylohyal is attached to a medial crest as in Neotropi-cal boas and other booid subclades.

The anatomical information provided by the new specimens of *Messelophis* and *Rieppelophis* provides fur-ther support for the affinities of Messel small boas with North American-Central American charinid snakes. This Euro-American lineage probably dispersed in the late Paleocene or early Eocene, around the Paleocene-Eocene Thermal Maximum. These favourable climatic condi-tions permitted small tropical to subtropical reptiles as well as other ectothermic vertebrates to cross high lati-tude land bridges such as Greenland (e.g., AUGÉ, 2005; SMITH, 2009; GEORGALIS & JOYCE, 2017). Possibly, cli-matic deterioration at the end of the Paleogene let to the extinction of this clade in Europe. However this explana-tion is a little simplistic, because there are persistent cur-rent representatives of this clade in temperate, relatively high latitudes in North America (*Charina* spp.) but also some species (*Ungaliophis* spp.) in tropical environments of Central America.

The chief difficulty in understanding the origin and fate of charinids from Messel is that their relations to oth-

er fossil Paleogene snakes are virtually unknown. Most other taxa are known only from vertebrae (e.g., Rage, 1974; Szyndlar & Rage, 2003), and vertebrae are demonstrably less informative than cranial elements with regard to phylogenetic relationships (Smith & Georgalis, in press). Potential relatives of Charinidae from the time before Messel include *'Calamagras' gallicus* (see Smith & Scanferla, in press) and *Dunnophis matronensis*. *Dunnophis cadurcensis* is known from the late Eocene and species referred to the genus *Platyspondylia* cross the Eocene-Oligocene boundary; both of these taxa are potential ungaliophiine relatives (Bogert, 1968; Szyndlar & Rage, 2003), although the best case for a stem ungaliophiine outside of Messel remains late Eocene *Calamagras weigeli* from North America (Smith, 2013). At present, however, the precise relations of these taxa are unknown (see Smith & Georgalis, in press).

Acknowledgements

References

Augé, M. (2005). Evolution des lézards du Paléogene en Europe. *Mémoires du Muséum National d'Histoire Naturelle*, **192**, 1–369.

Baszio, S. (2004). *Messelophis variatus* n. gen. nov. sp. from the Eocene of Messel: a tropidopheine snake with affinities to Erycinae (Boidae). *Courier Forschungsinstitut Senckenberg*, **252**, 47–66.

Bogert, C. M. (1968). A new genus and species of dwarf boa from southern Mexico. *American Museum Novitates*, **2354**, 1–38.

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

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

Georgalis, G. L. & Smith, K. T. (2020). Constrictores Oppel, 1811 – the available name for the taxonomic group uniting boas and pythons. Vertebrate Zoology, **70**, 291–304.

Pyron, R. A., Reynolds, R. E. & Burbrink, F. T. (2014). A taxonomic revision of boas (Serpentes: Boidae). Zootaxa, **3846**, 249–260.

Rage, J-C. (1974). Les serpents des Phosphorites du Quercy. *Palaeovertebrata*, **6**, 274–303.

Rieppel, O. (1979). The evolution of the basicranium in the Henophidia (Reptilia: Serpentes). *Zoological Journal of Linnean Society*, **66**, 411–431.

Scanferla, A. (2016). Postnatal ontogeny and the evolution of macrostomy in snakes. *Royal Society Open Science*, **3**, 160612.

Scanferla, A. & Smith, K. T. (2020). Exquisitely preserved fossil snakes of Messel: insight into the evolution, biogeography, habitat preferences and sensory ecology of early boas. *Diversity*, **12**, 100.

Scanferla, A., Smith, K. T. & Schaal, S. (2016). Revision of the cranial anatomy and phylogenetic relationships of the Eocene minute boas *Messelophis variatus* and *Messelophis ermannorum* (Serpentes, Booidea). *Zoological Journal of the Linnean Society* 176: 182–206.

Schaal, S. & Baszio, S. (2004). *Messelophis ermannorum* n. sp., eine neue Zwergboa (Serpentes: Boidae: Tropidopheinae) aus dem Mittel-Eozän von Messel. *Courier Forschungsinstitut Senckenberg*, **252**: 67–77.

Smith, K. T. (2009). Eocene lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Reptilia: Squamata). *Bulletin of the Peabody Museum of Natural History*, **50**, 219–306.

Smith, K. T. (2013). New constraints on the evolution of the snake clades Ungaliophiinae, Loxocemidae and Colubridae (Serpentes), with comments on the fossil history of erycine boids in North America. *Zoologischer Anzeiger*, **252**, 157–182.

Smith, K. T. & Scanferla, A. (in press). A nearly complete skeleton of the oldest definitive erycine boid (Messel, Germany). *Geodiversitas*

Smith, K. T. & Georgalis, G. L. (in press). The diversity and distribution of Palaeogene snakes: a review, with comments on vertebral sufficiency *in*: Gower, D. A. & Zaher, H. (eds) *A Contribution to the Origin and Early Evolution of Snakes*. London, Linnean Society.

Smith, K. T., Čerňanský, A., Scanferla, A. & Schaal, S. (2018). Lizards and snakes – Warmth-loving sunbathers, pp. 123-148 *in*: Smith, K.T., Schaal, S. & Habersetzer, J. (eds) *Messel – An Ancient Greenhouse Ecosystem*. Frankfurt am Main, Senckenberg.

Szyndlar, Z. & Rage, J-C. (2003). *Non-erycine Booidea from the Oligocene and Miocene of Europe*. Kraków, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences.