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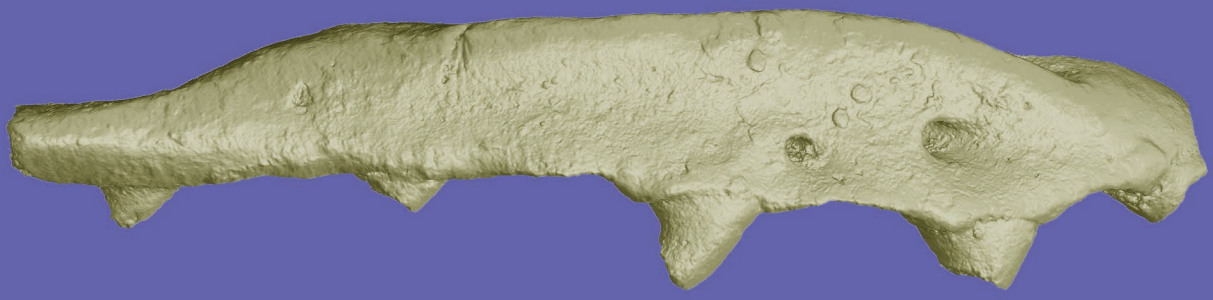

Snakes from the Cenozoic of Europe
– towards a macroevolutionary and palaeobiogeographic synthesis

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The first snake from the lower Eocene (MP 10-11) of the Cos locality, Phosphorites du Quercy, France

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ABSTRACT
Squamate faunas from the early Eocene of Europe are rare. We here describe an isolated maxilla from the early Eocene (MP 10-11) Cos locality in southwestern France. This specimen represents the only find of snake from this locality and represents the oldest described and figured cranial remain of Constrictores (i.e., the group encompassing boas and pythons) from the Cenozoic of Europe, being older than Messel, Geiseltal, Hordle, and all Quercy localities where snakes have been previously documented. The maxilla from Cos bears some resemblance with *Palaeopython* Rochebrune, 1880, which could then represent the oldest known occurence of this taxon. However, based on this single available element, we refer it as Constrictores indet.

KEY WORDS
Constrictores,
Paleogene,
Europe,
Quercy,
maxilla.

RÉSUMÉ
Le premier serpent de l'Éocène inférieur (MP 10-11) de la localité de Cos, Phosphorites du Quercy, France.
Les faunes de squamates du début de l'Éocène en Europe sont rares. Nous décrivons ici un maxillaire isolé provenant de Cos, une localité de l'Éocène inférieur (MP 10-11) du Sud-Ouest de la France. Ce spécimen représente la seule découverte de serpent issue de cette localité et représente le plus ancien reste crânien de Constrictores (boas et pythons) décrit et figuré au Cénozoïque en Europe, étant plus ancien que Messel, Geiseltal, Hordle et toutes les localités du Quercy où des serpents ont été précédemment documentés. Le maxillaire de Cos présente une certaine ressemblance avec *Palaeopython* Rochebrune, 1880, qui pourrait alors représenter la plus ancienne occurrence connue de ce taxon. Cependant, sur la base de ce seul élément disponible, nous l'attribuons à Constrictores indet.

MOTS CLÉS
Constrictores,
Paléogène,
Europe,
Quercy,
maxillaire.

INTRODUCTION

The Paleogene was an important time in snake evolution (Smith & Georgalis 2022; Georgalis *et al.* 2025). For example, large constrictor snakes (Constrictores *sensu* Georgalis & Smith 2020), including both boas and pythons, form a diverse and ecologically prominent group of terrestrial faunal assemblages in the European Paleogene. The earliest record of Constrictores from the Cenozoic of Europe is known from the late Paleocene (MP 6) of Rivecourt, France, based on two trunk vertebrae described by Smith *et al.* (2014), followed by vertebral material that was referred to *Paleryx* Owen, 1850, by Hecht & Hoffstetter (1962; but was never figured) from the earliest Eocene (MP 7) of Dormaal, plus few vertebral remains from the early Eocene (MP 7) of Silveirinha, Portugal, described by Rage & Augé (2003), and some briefly mentioned (but so far undescribed) material from Le Quesnoy (Nel *et al.* 1999). A dentary of a large snake was reported from the Paleocene of Walbeck, Germany by Kuhn (1940), and judging from its mentioned size it could be indeed a member of Constrictores. However, this material was never figured and is now probably lost (Georgalis *et al.* 2021), so a further proper identification cannot be made. Another potential alethinophidian is known from the early to middle Paleocene of Hainin and could eventually pertain to Constrictores. However, this was only briefly described in a thesis (Van Dyck 1983) and its precise affinities are impossible to resolve. Subsequently, Constrictores achieved an impressive diversity and abundance throughout the European Eocene (Georgalis & Scheyer 2019; Zaher & Smith 2020; Georgalis *et al.* 2021; Smith & Georgalis 2022; Smith & Scanferla 2022); they represent the dominant snake group of the continent, as it is testified by an array of vertebral but also cranial remains, as well as spectacular complete skeletons from the fossil Konservat-Lagerstätten of Messel and Geiseltal in Germany (Barnes 1927; Kuhn 1939; Schaal 2004; Smith & Scanferla 2016, 2021, 2022; Scanferla *et al.* 2016; Smith *et al.* 2018; Scanferla & Smith 2020a, b; Zaher & Smith 2020; Georgalis *et al.* 2021; Smith & Scanferla 2022; Palci *et al.* 2024).

Overall, the large Constrictores from the Eocene of Europe have been referred to four genera: *Palaeopython* Rochebrune, 1880, known from France and Switzerland, *Eoconstrictor* Scanferla & Smith, 2020, known from Germany and Switzerland, *Paleryx* Owen, 1850, from the Eocene of England, and *Phosphoroboa* Georgalis, Rabi & Smith, 2021, from the Eocene of France (see, e.g. Scanferla & Smith 2020b; Georgalis *et al.* 2021; Smith & Georgalis 2022; Palci *et al.* 2024). In general, middle Eocene Constrictores from Europe are known mostly from localities with exeptional fossilization conditions (i.e., Fossil-Lagerstätte localities), such as Messel (Smith *et al.* 2018; Scanferla & Smith 2020a, b; Smith & Scanferla 2021; Chuliver *et al.* 2022), and Geiseltal (Kuhn 1939; Georgalis *et al.* 2021; Palci *et al.* 2024), but isolated vertebral and cranial remains have also been recovered from a small number of localities, particularly the Phosphorites du Quercy in France, but also Switzerland and Germany (Rage 1984, 1988, 2013; Rage & Augé 2010; Georgalis & Scheyer 2019; Georgalis *et al.* 2021). On the contrary, early Eocene remains of Constrictores from Europe are less adequately known (see Smith & Georgalis 2022).

In this paper, we describe the first snake remain from the Cos locality (44°13'11.20"N, 1°44'58.21"E) in France. Regarding squamates, only anguimorphs (Čerňanský *et al.* 2023a, b; see the first paper for the geological setting and a map) and a pan-gekkotan (Čerňanský *et al.* 2023c) have been so far described from this site. The Cos fissure is the seventh pre-middle Eocene locality of Phosphorites du Quercy known and is one of the oldest (MP 10-11 [MP 10b in Lihoreau *et al.* 2025]; the age of the Cos locality is estimated to be between *c.* 50 and *c.* 48 Ma, the late Ypresian; see Godinot *et al.* 2021; Vianey-Liaud *et al.* 2022, 2024).

MATERIAL AND METHODS

The studied fossil material is deposited at the Institut des Sciences de l'Évolution, University of Montpellier, cataloged under individual UM-COS-numbers. The standard anatomical orientation system is used throughout this paper. All specimens were scanned using the micro-computed tomography (µCT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a phoenix v|tome|x L 240 micro-CT. The CT data sets were analysed using VG Studio Max 3.1. and Avizo 8.1.

INSTITUTIONAL ABBREVIATION

UM-COS Cos collection, Institut des Sciences de l'Évolution, Université de Montpellier.

SYSTEMATIC PALEONTOLOGY

Squamata Oppel, 1811b
Serpentes Linnaeus, 1758
Alethinophidia Nopcsa, 1923
Constrictores Oppel, 1811a
(*sensu* Georgalis & Smith 2020)

Constrictores indet.
(Fig. 1)

MATERIAL. — **Southwestern France** • 1 right maxilla; UM-COS-1014.

LOCALITY AND HORIZON. — Cos, fissure fill in the Quercy region (southwestern France); lower Eocene (MP 10-11 interval).

DESCRIPTION

Maxilla

The maxilla UM-COS-1014 is fairly preserved, although incomplete – the specimen corresponds to the anterior half of a right bone, while its posterior termination is broken off (Fig. 1). The maximum anteroposterior length of this bone is 9.3 mm. The preserved portion of the maxilla bears nine and half tooth positions (five partly preserved teeth are still attached to the bone). It is elongated (Fig. 1A, B) and slightly anteromedially curved in dorsal and ventral views (Fig. 1C, D); the anterior portion of the bone is convex laterally, forming

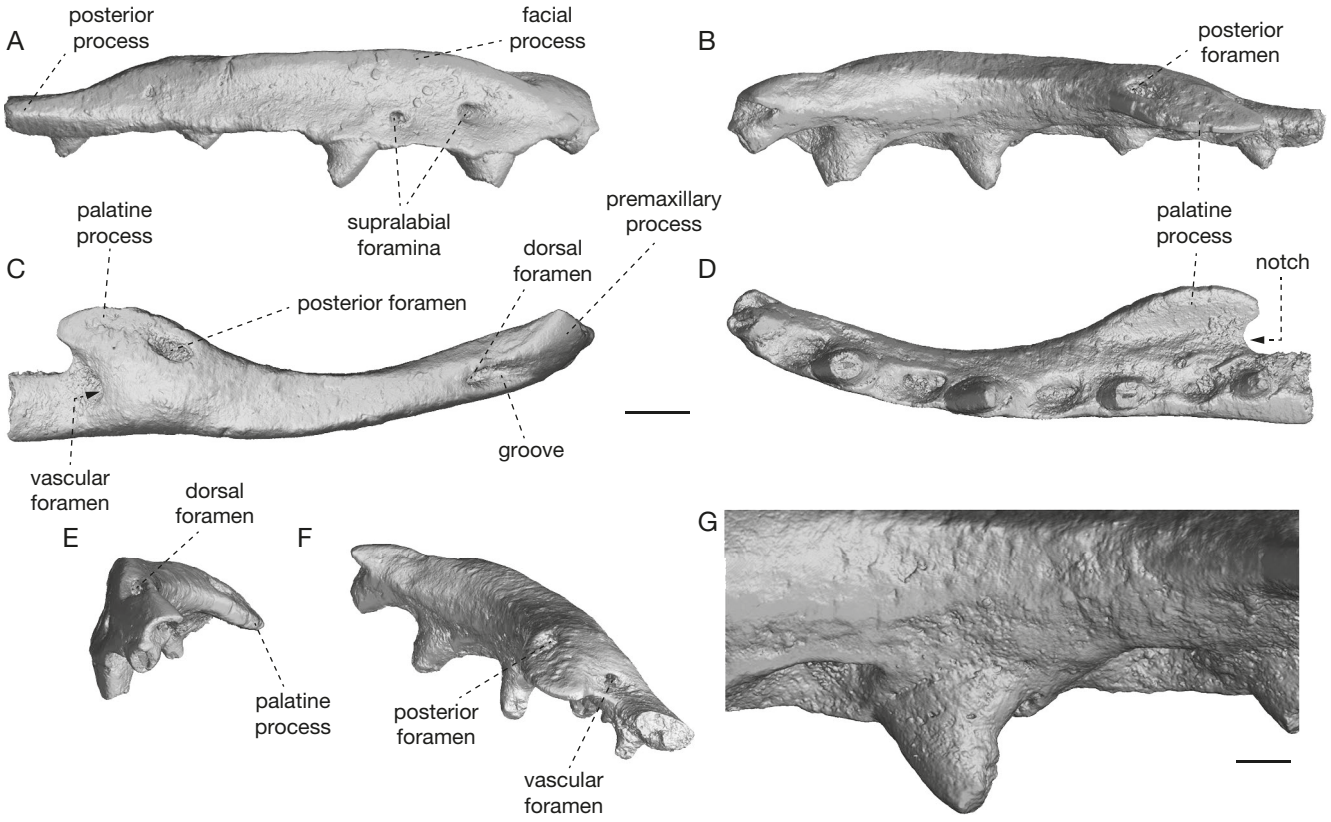

FIG. 1. — Constrictores indet. from the lower Eocene (MP 10-11) of the Cos locality. UM-COS-1014 right maxilla in: **A**, lateral; **B**, medial; **C**, dorsal; **D**, ventral; **E**, anterior; **F**, posterodorsomedial views. Detail of the fifth tooth in **G**, medial view. All images are micro-CT visualizations. Scale bars: A-F, 1 mm; G, 0.35 mm.

slightly bent rod-shaped projection. Its dorsal surface is pierced by a dorsal foramen (*sensu* Scanlon 2001), located at the level of the third tooth position (counted from anterior). Anteriorly, a distinct but short groove runs from that foramen. It continues anteriorly to the lateral side of the bone. The premaxillary process is smooth and rounded (Fig. 1C). As typical for snakes, the maxilla lacks an articulation facet for the premaxilla. The medial margin of the anterior portion of the maxilla shows a stronger concavity, because from the sixth tooth position, the bone gradually widens posteriorly protruding into the palatine process (prefrontal process *sensu* Szyndlar 1984). The palatine process is broad (it occupies an area from the sixth to ninth tooth positions). It is slightly hooked posteriorly (it projects posteromedially into a short process separated posteriorly from the rest of the bone by a rounded notch; Fig. 1D). Thus, it has the shape of a "shark dorsal fin" in dorsal and ventral views (Fig. 1C, D). The dorsal surface of the palatine process is pierced by a large posterior foramen (Fig. 1C) of the superior dental canal (*sensu* Anthony & Serra 1950). This foramen is located in the anterior region of the process and is also visible in medial view. Another foramen which is called the vascular foramen (*sensu* Anthony & Serra 1950) is located more posteriorly on the dorsal surface of the dental portion of the maxilla (slightly anterolaterally from the posterior notch of the palatine process). The CT scan reveals that all three foramina present on the dorsal surface of the bone converge in the same internal alveolar canal in which the two supralabial foramina (see below) also open. In posterior view, the palatine process is slightly inclined medioventrally (Fig. 1F). Thus, a shallow longitudinal depression is present between the dental portion and the process (Fig. 1D).

In lateral view, the bone is low and presents a poorly defined suborbital margin. Note, however, that a well-visible vestige of the facial process (*sensu* Gauthier *et al.* 2012) rises at the level of the anterior dorsal foramen and disappears at roughly the level of the palatine process. The external surface of the bone is pierced by two supralabial foramina in the anterior region. The larger of these two is the anterior one and it is located at the level of the posterior area of the third tooth position (counted from anterior). The smaller posterior supralabial foramen is located at the level of the posterior area of the fourth tooth position (counted from anterior). The rest of the external surface is smooth. The posterior portion of the maxilla, i.g., the posterior process, is broken off. Thus, it is unknown if it was flared or not. The presence or absence of an ectopterygoid process cannot be assessed.

Dentition

The dentition is ankylosed-subthecodont. The teeth are mesiodistally wide, especially at their bases, however, they are also mediolaterally compressed. Although the tooth apiced are mostly broken off (the best preserved tooth is the fifth one, Fig. 1G), they are clearly recurved. The anterior teeth appear to be the largest; the tooth size gradually decreases posteriorly.

Comments

The number and size of supralabial foramina is an important feature for Constrictores. The size of these foramina depends on the number of nerve fibres and size of blood vessels that serve the sensory tissue of heat-sensing circumoral epithelium in snakes. In maxilla, this tissue is innervated by the maxillary and/or ophthalmic branch of the trigeminal, and perfused by branches of the superior maxillary artery, which pass through the supralabial foramina (Young 1988).

DISCUSSION

The maxilla UM-COS-1014 is one of the oldest snake cranial remains from Europe, being older than Messel, Geiseltal, Hordle, and all Quercy snake-yielding localities. In fact, Cenozoic localities that yielded snake cranial remains in Europe, only the early Eocene (Ypresian) locality of Monte Bolca, Italy, that yielded the complete skeleton (with skull) of the enigmatic snake *Archaeophis proavus* Massalongo, 1859 (Janensch 1906; Seghetti *et al.* 2022), could be older than Cos; in any case, *Archaeophis* Massalongo, 1859 is clearly not a constrictor and thus, the Cos maxilla represents the oldest cranial remain of a constrictor that has been described and figured from the Cenozoic of Europe. It should be noted, however, that the slightly older snake fauna of Prémontré (MP 10, Ypresian – estimated at about 50.4 to 50.3 Mya) from France has yielded cranial material of "Boidae non Erycinae" that was mentioned and very briefly described (but not figured) by Augé *et al.* (1997).

Overall, among large Paleogene snakes, the maxilla from Cos bears much resemblance with *Palaeopython* (for this taxon, see Geogalis *et al.* 2021; Smith & Scanferla 2022). In the Cos maxilla, the number of supralabial foramina is two (contra four in *Eoconstrictor fischeri* [Schaal, 2004] [see Sanferla & Smith 2020b] and only one in *Eoconstrictor spinifer* [Barnes, 1927] [see Georgalis *et al.* 2021 and *Eoconstrictor barnesi* Palci, Onary, Lee, Smith, Wings, Rabi & Georgalis, 2023 [see Palci *et al.* 2024]); note that for the English taxon *Paleryx rhombifer* Owen, 1850, no maxilla is so far known (Georgalis *et al.* 2021). Among *Palaeopython* spp., the number of labial foramina is only two in *Palaeopython schaali* Smith & Scanferla, 2022 (see Smith & Scanferla 2022).

The curvature of the lateral margin of the maxilla also points affinities with Messelopythonidae Smith & Scanferla, 2022, the pythonoid group that also *Palaeopython* belongs. In general, features that support a referal of the Cos maxilla to *Palaeopython* are: the sigmoidal curvature of the lateral margin of the maxilla; the anteroposteriorly short palatine process of the maxilla; the low number (two) of labial foramina. Unfortunately, another important diagnostic feature of *Palaeopython*, the flaring posterior process of the maxilla is not visible in our specimen, as this respective part is mostly broken.

Accordingly, although a referal of the Cos maxilla to *Palaeopython* seems plausible, based on the incompleteness and limiteness of the existing material, we here identify this specimen solely as Constrictores indet. Nevertheless, if the Cos maxilla indeed belongs to *Palaeopython*, then it would represent the oldest occurrence of this genus, as with an age of MP 10-11, it would be older than *Palaeopython schaali* from Messel (MP 11; Smith & Scanferla 2022), *Palaeopython ceciliensis* Barnes, 1927, from Geiseltal (late early or middle Eocene; Georgalis *et al.* 2021), and *Palaeopython* sp. from Laprade (Quercy) and Lissieu (both MP 14; Rage & Augé 2010).

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Availability of materials and data

The maxilla is cataloged and accessible in the fossil reptile collection of the Institut des Sciences de l'Évolution, University of Montpellier in France. A digital surface model of the figured fossil is available on Morphosource and Virtual Collections: UM-COS-1014: https://www.morphosource.org/concern/media/000645744?locale=en

REFERENCES

Anthony J. & Serra R. G. 1950. — Anatomie de l'appareil de la morsure chez "*Eunectes murinus*" L. (Boidae). *Revista Brasileira de Biologia* 10: 23-44.

Augé M. L., Duffaud S., de Broin F., Rage J-C. & Vasse D. 1997. — Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin parisien) : une herpétofaune de référence pour l'Eocène inférieur. *Géologie de la France* 1: 23-33.

Barnes B. 1927. — Eine eozäne Wirbeltier-Fauna aus der Braunkohle des Geiseltals. *Jahrbuch des Halleschen Verbandes für die Erforschung der mitteldeutschen Bodenschätze, Neue Folge* 6: 5-24.

Čerňanský A., Tabuce R. & Vidalenc D. 2023a. — Anguimorph lizards from the early Eocene (MP 10–11) of the Cos locality, Phosphorites du Quercy, France and the early evolution of Glyptosaurinae in Europe. *Journal of Vertebrate Paleontology* 42 (5): e2211646. https://doi.org/10.1080/02724634.2023.2211646

Čerňanský A., Tabuce R. & Vidalenc D. 2023b. — A replacement name for *Sullivania* Čerňanský *et al.*, 2023, non *Sullivania* Palmer, 1947. *Journal of Vertebrate Paleontology* 42 (6): e2231254. https://doi.org/10.1080/02724634.2023.2231254

Čerňanský A., Daza J. D., Tabuce R., Saxton E. & Vidalenc D. 2023c. — An early Eocene pan-gekkotan from France could represent an extra squamate group that survived the K/Pg extinction. *Acta Palaeontologica Polonica* 68 (4): 695-708. https://doi.org/10.4202/app.01083.2023

Chuliver M., Scanferla A. & Smith K. T. 2022. — Live birth in a 47-million-year-old snake. *Science of Nature* 109: 56. https://doi.org/10.1007/s00114-022-01828-3

GAUTHIER J. A., KEARNEY M., MAISANO J. A., RIEPPEL O. & BEHLKE A. D. 2012. — Assembling the squamate tree of life: perspectives from the pheno-type and the fossil record. *Bulletin of the Peabody Museum of Natural History* 53: 3-308.

GEORGALIS G. L. & SCHEYER T. M. 2019. — A new species of *Palaeopython* (Serpentes) and other extinct squamates from the Eocene of Dielsdorf (Zurich, Switzerland). *Swiss Journal of Geosciences* 112: 383-417. https://doi.org/10.1007/s00015-019-00341-6

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. https://doi.org/10.26049/VZ70-3-2020-03

GEORGALIS G. L., RABI M. & SMITH K. T. 2021. — Taxonomic revision of the snakes of the genera *Palaeopython* and *Paleryx* (Serpentes, Constrictores) from the Paleogene of Europe. *Swiss Journal of Palaeontology* 140: 18. https://doi.org/10.1186/s13358-021-00224-0

GEORGALIS G. L., ZAHER H. & LAURIN M. 2025. — Introduction to: Snakes from the Cenozoic of Europe – towards a macroevolutionary and palaeobiogeographic synthesis, in GEORGALIS G. L., ZAHER H. & LAURIN M. (eds), Snakes from the Cenozoic of Europe – towards a macroevolutionary and palaeobiogeographic synthesis. *Comptes Rendus Palevol* 24 (3): 45-49. https://doi.org/10.5852/cr-palevol2025v24a3

GODINOT M., BLONDEL C., ESCARGUEL G., LÉZIN C., PÉLISSIÉ T., TABUCE R. & VIDALENC D. 2021. — Primates and Plesiadapiformes from Cos (Eocene; Quercy, France). *Geobios* 66-67: 153-176. https://doi.org/10.1016/j.geobios.2021.03.004

HECHT M. K. & HOFFSTETTER R. 1962. — Note préliminaire sur les amphibiens et les squamates du Landénien supérieur et du Tongrien de Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 38: 1-30.

JANENSCH W. 1906. — Über *Archaeophis proavus* Mass., eine Schlange aus dem Eocän des Monte Bolca. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 19: 1-33.

KUHN O. 1939. — Die Schlangen (Boidae) aus dem Mitteleozän des Geiseltales. *Nova Acta Leopoldina, Neue Folge* 7 (47): 119-133.

KUHN O. 1940. — Crocodilier- und Squamatenreste aus dem oberen Paleocän von Walbeck. *Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B* 1940 (1): 21-25.

LIHOREAU F., YANS J., BENAMMI M., GIRARD F., BALLAS G., BOURGET H., BOYRIE C., CAILLAUD J., CHARRUAULT A.-L., GERNELLE K., SOLÉ F., VALENTIN X., VAUTRIN Q., VIANEY-LIAUD M. & TABUCE R. 2025. — Impact of the EECO on mammalian faunas: new Ypresian localities from Montpellier (France), a multidisciplinary approach. *Proceedings of the Geologists' Association* 101092. https://doi.org/10.1016/j.pgeola.2025.01.001

LINNAEUS C. 1758. — *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentii Salvii, Stockholm, 824 p. https://doi.org/10.5962/bhl.title.542

MASSALONGO A. 1859. — *Specimen photographicum animalium quorumdam plantarumque fossilium agri Veronensis*. Vicentinius et Franchinius Excudebant, Verona, 101 p.

NEL A., DE PLÖEG G., DEJAX J., DUTHEIL D., DE FRANCESCHI D., GHEERBRANT E., GODINOT M., HERVET S., MENIER J. J., AUGÉ M., BIGNOT A., CAVAGNETTO C., DUFFAUD S., GAUDANT J., HUA S., JOSSANG A., DE LAPPARENT DE BROIN F., POZZI J. P., PAICHELER J. C., BEUCHET F. & RAGE J.-C. 1999. — Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France). *Comptes Rendus de l'Académie des Sciences, Series IIA – Earth and Planetary Science* 329 (1): 65-72. https://doi.org/10.1016/S1251-8050(99)80229-8

NOPCSA F. 1923. — *Eidolosaurus* und *Pachyophis*. Zwei neue Neocom-Reptilien. *Palaeontographica* 65: 99-154.

OPPEL M. 1811a. — Suite du 1er. mémoire sur la classification des reptiles. Ord. II. Squammata mihi. Sect. II. Ophidii. Ord. III. Ophidii, Brongniart. *Annales du Museum d'histoire Naturelle, Paris* 16: 376-393.

OPPEL, M. 1811b. — *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben.* Joseph Lindauer, Munich, 87 p. https://doi.org/10.5962/bhl.title.4911

OWEN R. 1850. — Part III. Ophidia (*Palæophis*, &c.), *in* OWEN R. (ed.), *Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds*. Palæontographical Society of London, London: 51-63.

PALCI A., ONARY S., LEE M. S. Y., SMITH K. T., WINGS O., RABI M. & GEORGALIS G. L. 2024. — A new booid snake from the Eocene (Lutetian) Konservat-Lagerstätte of Geiseltal, Germany, and a new phylogenetic analysis of Booidea. *Zoological Journal of the Linnean Society* 202 (2): zlad179. https://doi.org/10.1093/zoolinnean/zlad179

RAGE J.-C. 1984. — Serpentes, *in* WELLNHOFER P. (ed.), *Encyclopedia of Paleoherpetology*. Part 11. Gustav Fischer, Stuttgart, New York, 80 p.

RAGE J.-C. 1988. — Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. I Amphibiens et Reptiles. *Palaeontographica Abteilung A* 205: 3-27.

RAGE J.-C. 2013. — Mesozoic and Cenozoic squamates of Europe. *Palaeobiodiversity and Palaeoenvironments* 93: 517-534. https://doi.org/10.1007/s12549-013-0124-x

RAGE J.-C. & AUGÉ M. 2003. — Amphibians and squamate reptiles from the lower Eocene of Silveirinha (Portugal). *Ciências da Terra, Universidade Nova de Lisboa* 15: 103-116.

RAGE J.-C. & AUGÉ M. 2010. — Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. *Geobios* 43 (2): 253-268. https://doi.org/10.1016/j.geobios.2009.08.002

ROCHEBRUNE A. T. DE 1880. — Revision des ophidiens fossiles du Museum d'Histoire Naturelle. *Nouvelles Archives du Muséum d'Histoire Naturelle, 2ème Série* 3: 271-296.

SCANLON J. D. 2001. — *Montypythonoides*: the Miocene snake *Morelia riversleighensis* (Smith and Plane, 1985) and the geographical origin of pythons. *Memoirs of the Association of Australasian Palaeontologists* 25: 1-35.

SCANFERLA A. & SMITH K. T. 2020a. — Additional anatomical information on the Eocene minute boas *Messelophis variatus* and *Rieppelophis ermannorum* (Messel Formation, Germany). *Vertebrate Zoology* 70: 615-620.

SCANFERLA A. & SMITH K. T. 2020b. — Exquisitely preserved fossil snakes of Messel: insight into the evolution, biogeography, habitat preferences and sensory ecology of early boas. *Diversity* 12: 100. https://doi.org/10.3390/d12030100

SCANFERLA, A., SMITH K. T. & SCHAAL S. F. K. 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 (1): 182-206. https://doi.org/10.1111/zoj.12300

SCHAAL S. 2004. — *Palaeopython fischeri* n. sp. (Serpentes: Boidae), eine Riesenschlange aus dem Eozän (MP 11) von Messel. *Courier Forschungsinstitut Senckenberg* 252: 35-45.

SEGHETTI S. M., GEORGALIS G. L., TSCHOPP E. & DELFINO M. 2022. — A historical overview of the reptile fauna from the Eocene Bolca Fossil-Lagerstätte (Italy). *Bollettino della Società Paleontologica Italiana* 61: 119-143. https://doi.org/10.4435/BSPI.2022.14

SMITH K. T. & GEORGALIS G. L. 2022. — The diversity and distribution of Palaeogene snakes; a review, with comments on vertebral sufficiency, *in* GOWER D. & ZAHER H. (eds), *The Origin and Early Evolution of Snakes*. Cambridge University Press, Cambridge: 55-84. https://doi.org/10.1017/9781108938891.006

SMITH K. T. & SCANFERLA A. 2016. — Fossil snake preserving three trophic levels and evidence for an ontogenetic dietary shift. *Palaeobiodiversity and Palaeoenvironments* 96: 589-599. https://doi.org/10.1007/s12549-016-0244-1

SMITH K. T. & SCANFERLA A. 2021. — A nearly complete skeleton of the oldest definitive erycine boid (Messel, Germany). *Geodiversitas* 43 (1): 1-24. https://doi.org/10.5252/geodiversitas2021v43a1

SMITH K. T. & SCANFERLA A. 2022. — More than one large constrictor lurked around paleolake Messel. *Palaeontographica, Abteilung A: Palaeozoology – Stratigraphy* 323: 75-103. https://doi.org/10.1127/pala/2021/0119

SMITH T., QUESNEL F., PLÖEG G. DE, FRANCESCHI D. DE, MÉTAIS G., DE BAST E. , SOLÉ F., FOLIE A., BOURA A., CLAUDE J., DUPUIS C., GAGNAISON C., IAKOVLEVA A., MARTIN J., MAUBERT F., PRIEUR J., ROCHE E., STORME J.-Y., THOMAS R., TONG H., YANS J. & BUFFETAUT E. 2014. — First Clarkforkian equivalent Land Mammal Age in the Latest Paleocene basal Sparnacian Facies of Europe: fauna, flora, paleoenvironment and (bio)stratigraphy. *PLoS ONE* 9 (1): e86229. https://doi.org/10.1371/journal.pone.0086229

SMITH K. T., ČERŇANSKÝ A., SCANFERLA A. & SCHAAL S. 2018. — Lizards and snakes: warmth-loving sunbathers, *in* SMITH K. T., SCHAAL S. F. K. & HABERSETZER J. (eds), *Messel, An Ancient Greenhouse Ecosystem*. Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main: 122-147.

SZYNDLAR Z. 1984. — Fossil snakes from Poland. *Acta Zoologica Cracoviensia* 28 (1): 1-156.

VAN DYCK M. C. 1983. — *Étude de la faune herpétologique du "Montien" continental de Hainin (Hainaut, Belgique) et d'autres gisements paléogènes du Nord-Ouest de l'Europe.* Thèse de la faculté des Sciences, Université Catholique de Louvain, 199 p.

VIANEY-LIAUD M., VIDALENC D., ORLIAC M. J., MAUGOUST J., LÉZIN C. & PÉLISSIÉ T. 2022. — Rongeurs de la localité éocène de Cos (Tarnet-Garonne, Quercy, France). Comparaison avec les rongeurs de localités de la transition Éocène inférieur/Éocène moyen. *Geodiversitas* 44 (26): 753-800. https://doi.org/10.5252/geodiversitas2022v44a26

VIANEY-LIAUD M., LIHOREAU F., SOLÉ F., GERNELLE K., VAUTRIN Q., BRONNERT C., BOURGET H., VIDALENC D. & TABUCE R. 2024. — A revision of the late early Eocene mammal faunas from Mas de Gimel and Naples (Montpellier, Southern France) and the description of a new theridomorph rodent. *Geodiversitas* 46 (10): 387-422. https://doi.org/10.5252/geodiversitas2024v46a10

YOUNG B. A. 1988. — The cephalic vascular anatomy of three species of sea snakes. *Journal of Morphology* 196 (2): 195-204. https://doi.org/10.1002/jmor.1051960208

ZAHER H. & SMITH K. T. 2020. —Pythons in the Eocene of Europe reveal a much older divergence of the group in sympatry with boas. *Biology Letters* 16 (12): 20200735. https://doi.org/10.1098/rsbl.2020.0735

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