

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

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SNAKES FROM THE CENOZOIC OF EUROPE

- TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

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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 occurrence of this taxon. However, based on this single available element, we refer it as Constrictores indet.

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.

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

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 exceptional 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 ($44^{\circ}13'11.20''\text{N}$, $1^{\circ}44'58.21''\text{E}$) in France. Regarding squamates, only anguimorphs (Černanský *et al.* 2023a, b; see the first paper for the geological setting and a map) and a pan-gekkotan (Černanský *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, catalogued 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

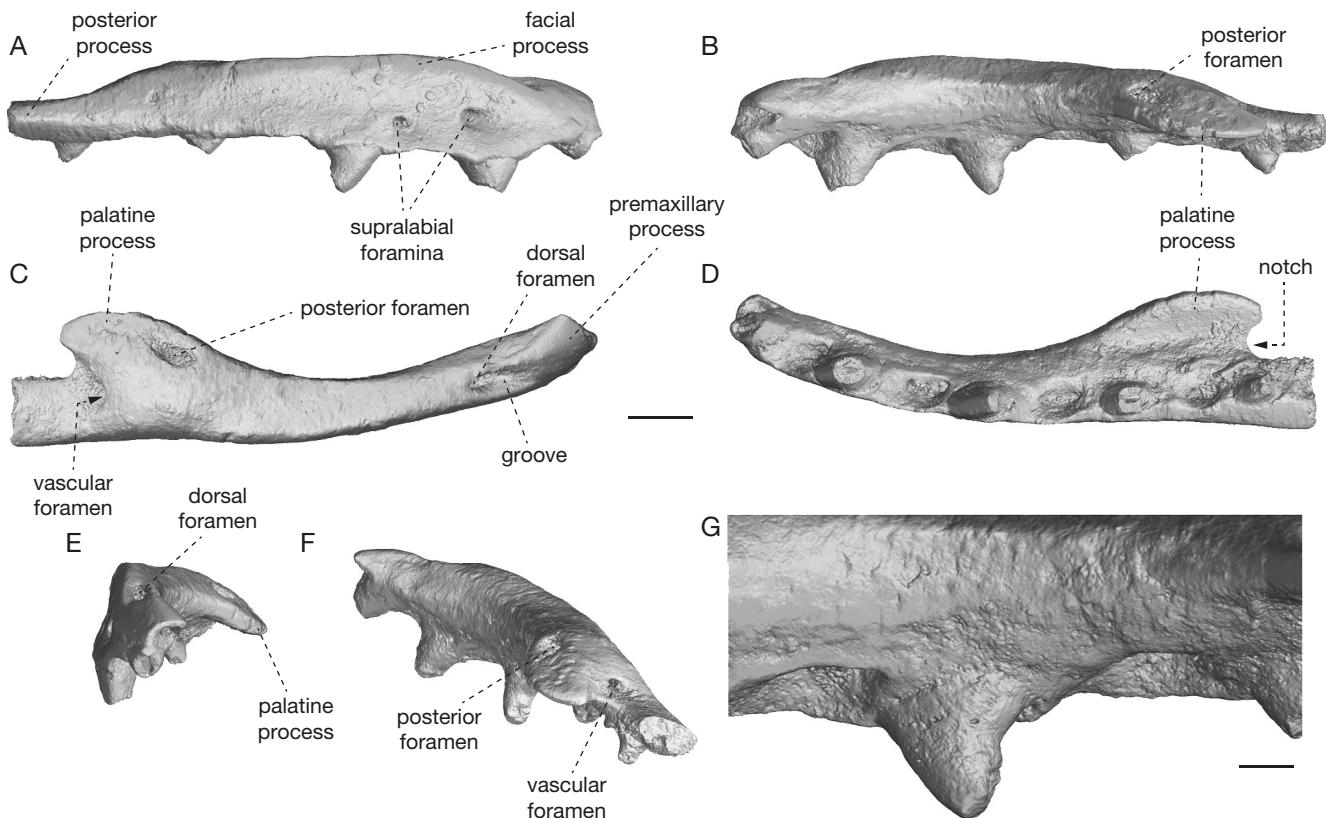


FIG. 1. — *Constrictores* indet. from the lower Eocene (MP 10-11) of the Cos locality. UM-COS-1014 right maxilla in: **A**, lateral; **B**, medial; **C**, dorsal; **D**, ventral; **E**, anterior; **F**, posterodorsomedial views. Detail of the fifth tooth in **G**, medial view. All images are micro-CT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

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