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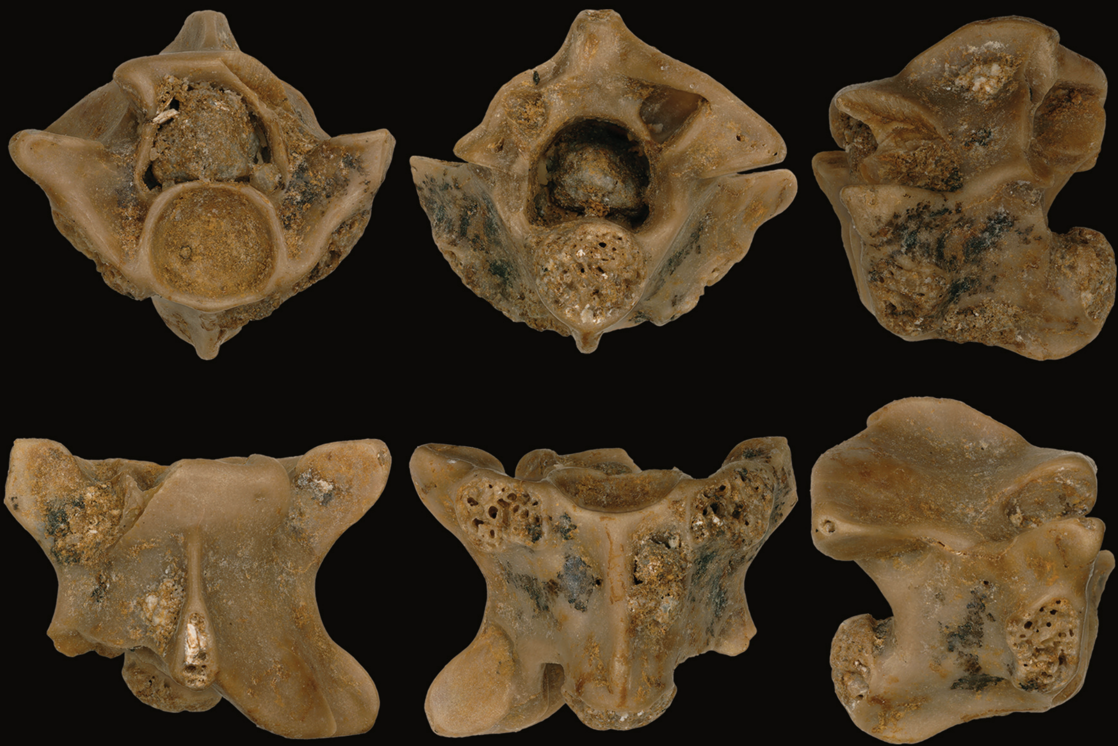
Georgios L. GEORGALIS & Bastien MENNECART



SNAKES FROM THE CENOZOIC OF EUROPE
– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

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Humble beginnings of the Cenozoic European snake glory: new Paleocene remains of snakes from Cernay, France

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ABSTRACT
Although snakes in Europe achieved an extreme and fascinating diversity during the Cenozoic, particularly during the Eocene, their Paleocene fossil record in the continent is very scarce and inadequately known, consisting of only a very few isolated and incomplete remains that have been described from only three localities. We here document snake vertebrae from the late Paleocene (MP 6) of Cernay, Paris Basin, France. Even if rather limited, the Cernay material reveals the presence of two different taxa: one with potential affinities with the genus *Dunnophis* Hecht *in* McGrew *et al.*, 1959 and a second, indeterminate, morphotype of a larger constrictor. A discussion and evaluation of the diagnostic features and the geographic and stratigraphic distribution of the genus *Dunnophis* is presented. The new Cernay material adds to our poor knowledge of Paleocene European snakes, but also of the coeval herpetofaunas in general.

KEY WORDS
Serpentes,
Constrictores,
Dunnophis,
vertebral morphology,
Paleogene.

RÉSUMÉ

Les modestes débuts de la gloire des serpents européens au Cénozoïque : nouveaux restes de serpents du Paléocène découverts à Cernay, en France.

Bien que les serpents européens aient atteint une diversité extrême et fascinante au cours du Cénozoïque, en particulier durant l'Éocène, leur registre fossile du Paléocène demeure très limité et mal connu sur ce continent. Il ne se compose en effet que de quelques restes isolés et incomplets décrits dans seulement trois localités. Nous présentons ici des vertèbres de serpents provenant du Paléocène supérieur (MP 6) de Cernay, dans le Bassin de Paris, en France. Bien que restreint, le matériel de Cernay, composé de trois vertèbres, révèle la présence de deux taxons distincts : l'un présentant des affinités potentielles avec le genre *Dunnophis* Hecht *in* McGrew *et al.*, 1959, et un second morphotype indéterminé correspondant à un plus grand constricteur. L'évaluation des caractères diagnostiques du genre *Dunnophis* ainsi que de sa distribution géographique et stratigraphique sont discutés. Ce nouveau matériel de Cernay contribue non seulement à combler nos lacunes concernant les serpents européens du Paléocène, mais également à améliorer la connaissance des herpétofaunes contemporaines de cette époque.

MOTS CLÉS
Serpentes,
Constrictores,
Dunnophis,
morphologie
des vertèbres,
Paléogène.

INTRODUCTION

During the Cenozoic, snakes in Europe achieved an unprecedented diversity, particularly during the Eocene (56-33.9 Ma), encompassing a fascinating array of taxa, including extreme size ranges and vertebral morphologies (Smith & Georgalis 2022; Ivanov 2022; Georgalis *et al.* 2025). Nevertheless, snake faunas from the first epoch of that Era, i.e., the Paleocene (66-56 Ma), in Europe are very poorly known, hindering significantly our understanding of the early Cenozoic evolution, origins, and palaeobiogeography of this reptile group in the continent. It is characteristic that Paleocene snakes from Europe have only been preliminarily documented, represented so far exclusively by an indeterminate constrictor from the late Paleocene (MP 6b) of Rivecourt-Petit Pâtis, Paris Basin, France (Smith *et al.* 2014), plus incomplete vertebral remains of the large aquatic genus *Palaeophis* Owen, 1841, from the Paleocene-Eocene boundary of Stolleklint Clay, Denmark (Kristensen *et al.* 2012). In addition, the Paleocene (MP 1-5) of Hainin, Belgium, seems to have yielded some snake remains; however, these have only been described in two unpublished theses (Van Dyck 1983; Folie 2006) and a conference abstract (Folie & Smith 2014). Besides these, some further mentions of Paleocene European snakes have also appeared in the literature: remains of snakes have been mentioned from the late Paleocene of Cernay, Paris Basin, France, as back as the late 19th century, in the publications of Lemoine (1878-1879, 1879, 1880, 1889) – however, these were simple mentions, without any kind of figures, or descriptions or collection numbers; a dentary of a large snake was mentioned from the late Paleocene of Walbeck, Germany, by Kuhn (1940) – however, no figure was provided and the material is currently of unknown whereabouts; and finally, remains of snakes have been also mentioned from the late Paleocene (Thanetian) of Rona, Romania, by Gheerbrant *et al.* (1999), but these were again, simply mentioned, without any kind of figures, or descriptions or collection numbers. To the contrary, the coeval North American fossil record of snakes is considerably richer and more diverse, with remains found across a number of different localities (see Holman 2000; Smith & Georgalis 2022), but obviously, the depauperate coeval European record does not afford any taxonomic comparisons and biogeographic considerations between the two landmasses.

This extreme scarceness of Paleocene European snake fossil remains drastically contrasts with the very rich Eocene fossil record of snakes from Europe, which is known for almost two centuries and across a large number of different localities (e.g., Owen 1841, 1850; Filhol 1877; Rochebrune 1880, 1884; Janensch 1906; Kuhn 1939; Rage 1973, 1974, 1978, 1980, 1983, 1984, 1988; Augé *et al.* 1997; Rage & Augé 2003, 2010; Holman *et al.* 2006; Scanferla *et al.* 2016; Georgalis & Scheyer 2019; Georgalis *et al.* 2020, 2021, 2025; Smith & Scanferla 2021; Smith & Georgalis 2022; Georgalis & Mennecart 2025; Georgalis & Jones 2025; Szyndlar & Georgalis 2025; Čerňanský *et al.* 2025, 2026), including also beautifully preserved articulated skeletons with skulls from fossil Konservat-Lagerstätte localities (Janensch 1906; Kuhn 1939; Baszio 2004; Schaal & Baszio 2004; Scanferla *et al.* 2016; Smith & Scanferla 2016, 2021; Smith *et al.* 2018; Scanferla & Smith 2020; Zaher & Smith 2020; Georgalis *et al.* 2021, 2025; Chuliver *et al.* 2022; Seghetti *et al.* 2022; Palci *et al.* 2024). As such, we cannot really witness the transition of snake faunas in Europe before and after the Paleocene-Eocene Thermal Maximum event, which played a great role in shaping the European faunal assemblages. Finally, this scarce Paleocene European snake record does not allow comparisons with the Cretaceous fossil record from Europe, which included several unique and endemic snake forms (see Head *et al.* 2022).

We here attempt to somehow fill this large gap by documenting snake vertebrae from the late Paleocene (MP 6) of Cernay in the Paris Basin, France. Although the material from Cernay is much limited and incomplete, it offers the opportunity for a cursory glimpse in the diversity and taxonomic composition of the early Cenozoic snake faunas of the region.

MATERIAL AND METHODS

The fossil material described herein is permanently curated in the collections of the Natural History Museum of Basel (NMB). The material originates from the fossil locality of Cernay, in the Paris Basin, France. The age of the locality is considered to pertain to the late Paleocene (MP 6). More information on the geological settings and the faunal assemblage of Cernay can be found in Georgalis & Mennecart (2026).

For comparative purposes, abundant material of extinct and extant snakes was studied at the collections of GMH, ISEA, MGPT-MDHC, MNCN, MNHN, NHMUK, NHMW, PIMUZ, SMF-PH, and UM. Taxonomy follows Szyndlar & Georgalis (2023). Anatomical terminology and measurements of snake vertebrae follow Georgalis *et al.* (2021) and Szyndlar & Georgalis (2023).

Institutional abbreviations

GMH	Geiseltalmuseum of Martin-Luther Universität Halle-Wittenberg, now referred to as the Geiseltalsammlung, housed as part of the Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle;
ISEA	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków;
MGPT-MDHC	Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMUK	Natural History Museum, London;
NHMW	Naturhistorisches Museum Wien, Vienna;
NMB	Naturhistorisches Museum Basel;
PIMUZ	Palaeontological Institute of the University of Zurich;
SMF-PH	Paleoherpetology collection, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main;
UM	Institut des Sciences de l'Évolution, Université de Montpellier.

SYSTEMATIC PALAEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
CONSTRICTORES Oppel, 1811
(*sensu* Georgalis & Smith, 2020)

Genus *Dunnophis* Hecht *in* McGrew *et al.*, 1959

Type species. — *Dunnophis microechinus* Hecht *in* McGrew *et al.*, 1959.

cf. ***Dunnophis*** sp.
(Fig. 1)

Material examined. — **France** • Two trunk vertebrae (NMB Cy.1166 and [tentatively also] NMB Cy.1167).

Description

The description is based on the most complete specimen, NMB Cy.1166. The trunk vertebra NMB Cy.1166 is incomplete, missing part of the neural arch, while both paradiapophyses and the condyle are rather eroded (Fig. 1A-F). The vertebra is relatively small, with a centrum length 2.2 mm and a neural arch width 2.1 mm. In anterior view (Fig. 1A), the zygosphene is moderately thin and straight, with its width being larger than that of the cotyle. The neural canal is large and rounded with very short lateral sinuses. The prezygapophyses are dorsally inclined. The cotyle is large and elliptical. Deep paracotylar fossae exist on either right and left side of the cotyle; there are no paracotylar foramina. In posterior view (Fig. 1B), the posterior margin of the neural arch is almost completely damaged; nevertheless, it seems that the neural arch was depressed. The paradiapophyses (both eroded, but the left one being in a better preservation state) seem to be wide and slightly extend ventrolaterally. The condyle is partly eroded (particularly at its ventral part), but it seems to have been moderately large and slightly elliptical. In dorsal view (Fig. 1F), the neural spine is restricted solely to the posterior half of the neural arch; its thickness gradually augments towards its posteriormost edge. Nevertheless, the posteriormost margin of the neural spine, as well as that of the neural arch, is damaged. The zygosphene is distinctly trilobate, with two prominent lateral lobes, resembling small horns, plus a wide central lobe. The prezygapophyseal articular facets are small and elongated. The interzygapophyseal constriction is shallow. In ventral view (Fig. 1E), the centrum is slightly longer than wide (ratio centrum length / neural arch width: 1.04). The haemal keel is wide and crosses almost the entire midline of the centrum, commencing anteriorly from approximately the ventral level of the cotyle and terminating posteriorly only slightly prior to the ventral level of the condyle. A large and deep subcentral foramen is situated on the left side of the haemal keel (approximately at its midline length); whether there is also an additional subcentral foramen at the right side of the haemal keel cannot be evaluated because of the presence of sediment at this portion. The subcentral grooves are deep. The postzygapophyseal articular facets are massive and rather broad. There are no prezygapophyseal accessory processes. In lateral view (Fig. 1C, D), the neural spine is rather short, being solely developed at the posterior half of the neural arch; its dorsalmost margin is nevertheless damaged. A single, small, lateral foramen is situated below each of the interzygapophyseal ridges. The subcentral ridges are prominent and convex, giving also to the ventral margin of the centrum a distinctly convex shape. The haemal keel protrudes ventrally.

The second vertebra (NMB Cy.1167) is much more incomplete, missing much of the neural arch, neural spine, paradiapophyses, and right prezygapophysis, the entire zygosphene and left postzygapophysis, while its ventral surface (including the haemal keel) is rather eroded (Fig. 1G-L). Nevertheless, NMB Cy.1167 overall resembles the above-described and better-preserved NMB Cy.1166 in terms of its elongation and dimensions (centrum length: 2.4 mm; neural arch width: 2.4 mm), the seemingly depressed neural arch, and the neural spine confined to the posterior half of the neural arch.

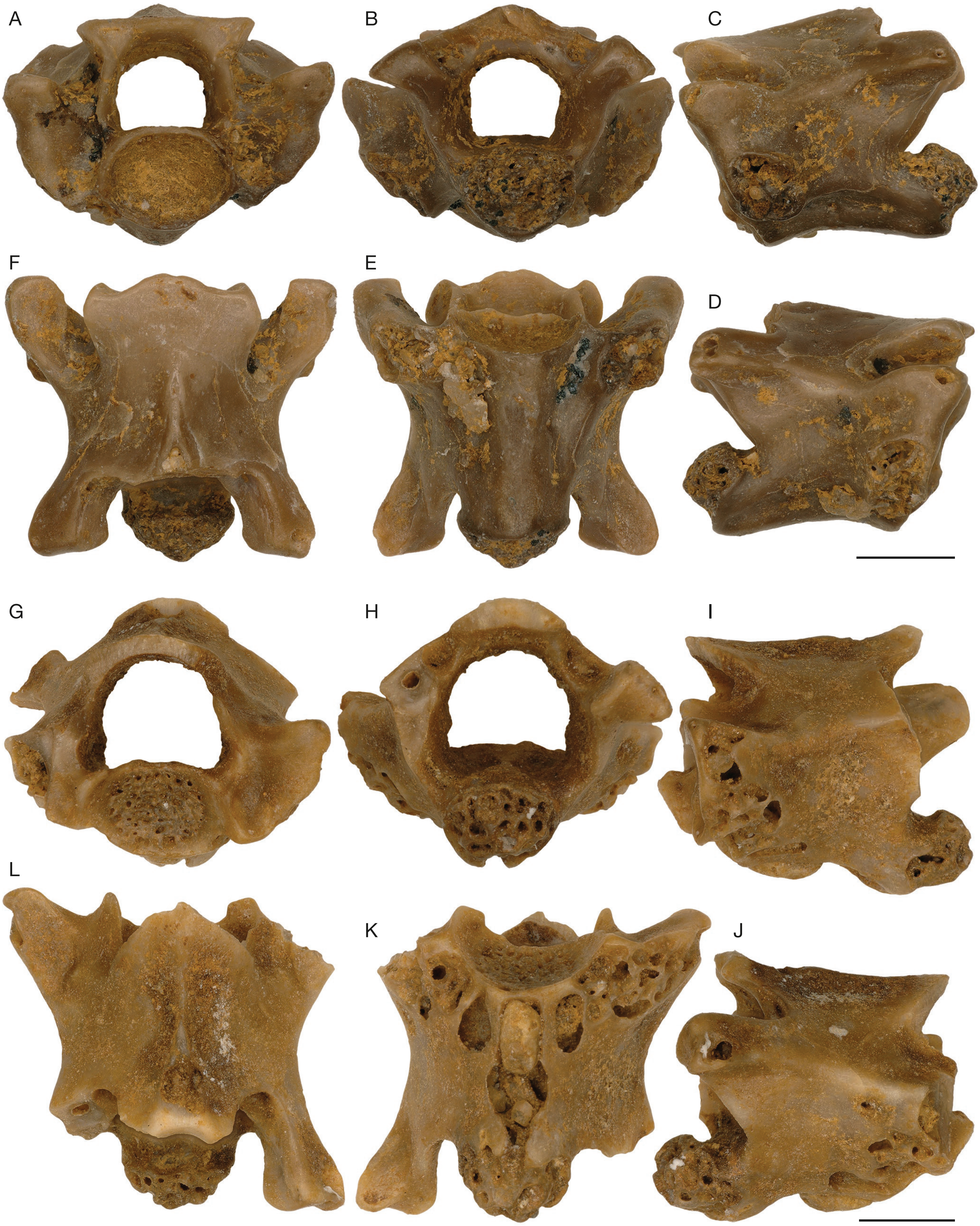

FIG. 1. — cf. *Dunnophis* sp. from Cernay: **A**-**F**, trunk vertebra (NMB Cy.1166) in anterior (**A**), posterior (**B**), left lateral (**C**), right lateral (**D**), ventral (**E**), and dorsal (**F**) views; **G**-**L**, trunk vertebra (NMB Cy.1167) in anterior (**G**), posterior (**H**), left lateral (**I**), right lateral (**J**), ventral (**K**), and dorsal (**L**) views. Scale bars: 1 mm.

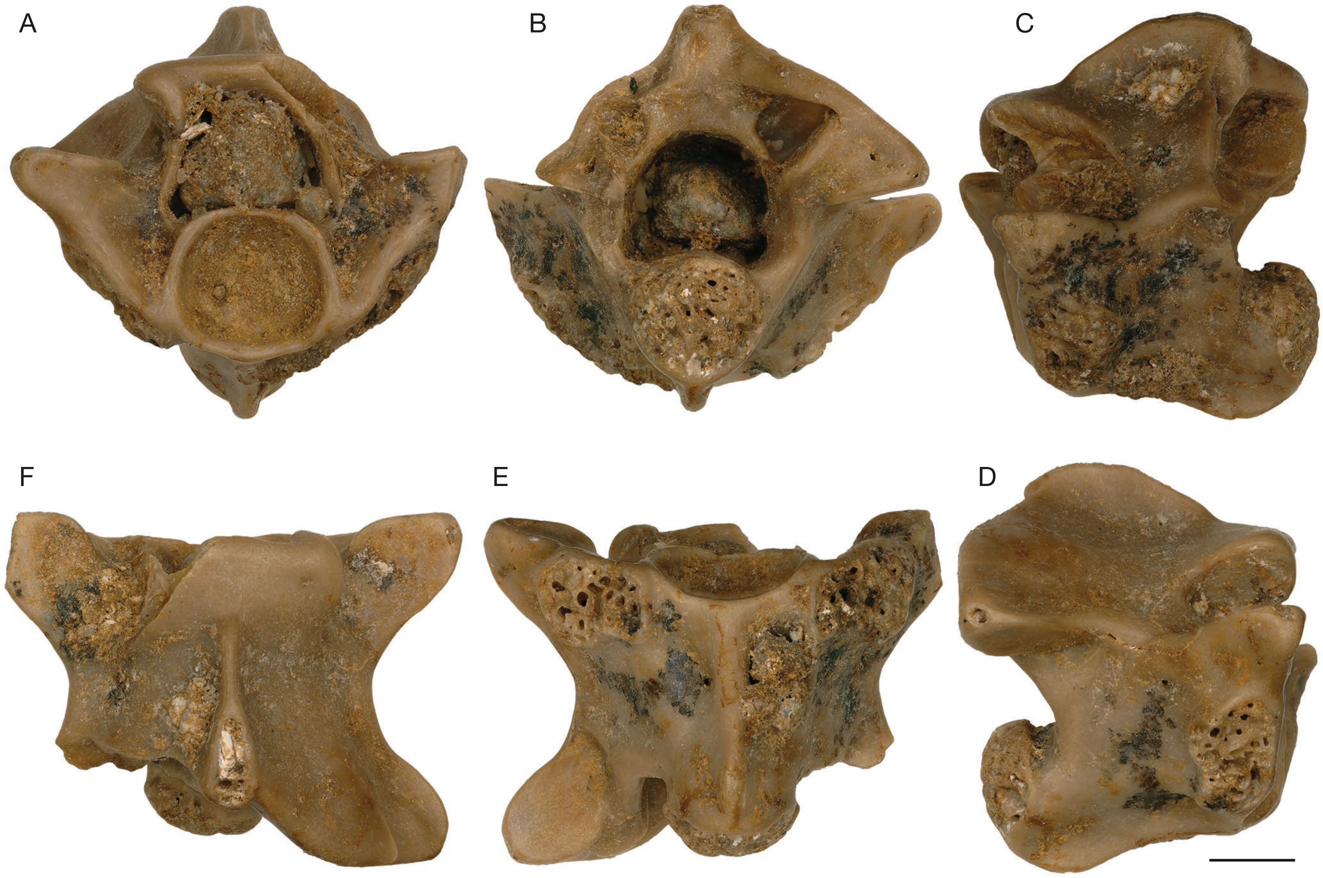

FIG. 2. — Constrictores indet. (morphotype 2) from Cernay. Trunk vertebra (NMB Cy.1165) in anterior (**A**), posterior (**B**), left lateral (**C**), right lateral (**D**), ventral (**E**), and dorsal (**F**) views. Scale bar: 1 mm.

REMARKS

NMB Cy.1166 (and possibly also NMB Cy.1167) belong to a moderately small snake form with a somehow elongated centrum (ratio of centrum length to neural arch width ≥ 1), a relatively depressed neural arch, elongated prezygapophyseal articular facets, a very short neural spine that is confined in the posterior third of the neural arch, and no prezygapophyseal accessory processes. These features approach the morphology of the genus *Dunnophis* (Hecht 1959; Rage 1973, 1974, 1984; Venczel *et al.* 2025; Čerňanský *et al.* 2026). However, as it is also analyzed below (see Discussion), these features of *Dunnophis* are also shared also with other extinct and extant taxa; this fact, along with the incomplete preservation of the two vertebrae from Cernay, leads us to tentatively refer them as cf. *Dunnophis* sp.

Constrictores indet. (morphotype 2)
(Fig. 2)

MATERIAL EXAMINED. — **France** • A trunk vertebra (NMB Cy.1165).

DESCRIPTION

The trunk vertebra NMB Cy.1165 is incomplete, missing a small part of the zygosphene and most of the left postzygapophysis (Fig. 2). The vertebra is moderately large, with a centrum length of 3.1 mm and a neural arch width of 3.6 mm. In anterior view (Fig. 2A), the zygosphene is moderately thin and straight. The neural canal is large and trapezoidal. The prezygapophyses are only slightly tilted dorsally. The cotyle is large and almost circular. Deep paracotylar fossae exist on either right and left side of the cotyle; there are no paracotylar foramina. In posterior view (Fig. 2B), the zygantral roof is relatively thickened. The neural arch is vaulted, with a vaulting ratio (sensu Georgalis *et al.* 2021) equal to 0.47. The condyle is large and its ventral portion is slightly laterally compressed. In dorsal view (Fig. 2F), the neural spine commences well beyond the level of the zygosphene; it is moderately thick, with its thickness gradually augmenting towards its posteriormost portion. The zygosphene is incomplete, however, the preserved half of it denotes that it possessed one distinct median and two lateral lobes. The prezygapophyses extend laterally (to slightly anterolaterally). The prezygapophyseal articular facets are massive and broad. The interzygapophyseal constriction is deep. The posterior median notch of the neural arch is incomplete, however, the preserved part denotes that it should have been deep. In ventral view (Fig. 2E), the centrum is much wider than long (ratio centrum length / neural arch width: 0.86). The haemal keel is moderately thin and crosses almost the entire midline of the centrum, commencing anteriorly from the ventral level of the cotyle and terminating posteriorly only slightly prior to the ventral level of the condyle. Subcentral foramina are present. Both paradiapophyses are much eroded. There are no prezygapophyseal accessory processes. The postzygapophyseal articular facets are massive and rather broad. In lateral view (Fig. 2D), the neural spine is moderately short, gradually augmenting in height. The subcentral ridges are slightly convex, giving also to the ventral margin of the centrum a distinctly convex shape. The haemal keel protrudes ventrally, with this protrusion being more marked towards its posterior portion.

Remarks

NMB Cy.1165 is a moderately large form, with a centrum wider than long, a prominent haemal keel (in lateral view), a vaulted neural arch, a short neural spine that commences well beyond the level of the zygosphene, deep interzygapophyseal constriction, no paracotylar foramina, and no prezygapophyseal accessory processes. These characters match those of (many members of) Constrictores, the lineage encompassing boas and pythons (Georgalis & Smith 2020; Smith & Georgalis 2022; Szyndlar & Georgalis 2023); however, based on this single available vertebra, it is impossible to more precisely assign NMB Cy.1165 and we only refer to it as Constrictores indet. Nevertheless, it is more robust and its centrum is much wider than the above-described cf. *Dunnophis* sp., clearly belonging to a second snake taxon from the locality.

DISCUSSION

The material from Cernay is very limited, comprising solely three incomplete vertebrae. Nevertheless, this scarce material denotes the presence of two taxa in the locality, rendering Cernay as the most diverse snake fauna in the Paleocene of Europe. Indeed, as was mentioned also above, Paleocene snakes from Europe had so far been described solely from the localities of Rivecourt-Petit Pâtis, Paris Basin, France (Smith *et al.* 2014) and from the Paleocene-Eocene boundary of Stolleklint Clay, Denmark (Kristensen *et al.* 2012), plus the material from Hainin, Belgium that was described in two unpublished theses (Van Dyck 1983; Folie 2006). Among these, the fragmentary material from the marine locality of Stolleklint Clay was referred to the palaeophiid *Palaeophis* (Kristensen *et al.* 2012), while the Hainin and Rivecourt-Petit Pâtis specimens pertain to other groups. It is difficult to decipher what snakes occurred in Hainin, as they have been so far exclusively described in unpublished theses and abstracts: the first snake material from Hainin was described as cf. *Dunnophis* sp. in the unpublished thesis of Van Dyck (1983) and was subsequently considered as Alethinophidia indet. by Rage (1998); subsequently, Folie (2006) in her unpublished thesis, described snake material from that locality, which following subsequent mentions in literature seem to pertain to a scolecophidian and a constrictor (Mead 2013; Rage 2013; Folie & Smith 2014). The material from Rivecourt-Petit Pâtis consisted of two incomplete vertebrae, among which only one was figured (and only in its anterior view; Smith *et al.* 2014: fig. 7B), and was very briefly described and tentatively referred by Smith *et al.* (2014) as pertaining to an indeterminate boid; the material was subsequently reclassified as Constrictores indet. by Georgalis *et al.* (2021). Interestingly, it is tempting to observe that the Cernay material encompasses both a *Dunnophis*-like alethinophidian (like in Hainin) and a larger "boid-like" constrictor (like in Rivecourt-Petit Pâtis), but apparently, based on such limited and incomplete material, it is rather speculative to envisage any taxonomic comparisons, while of course, the Hainin *Dunnophis*-like material remains yet to be formally described.

But what stands for *Dunnophis* or a *Dunnophis*-like snake anyway? *Dunnophis* was originally typified from North America, with its type species, *Dunnophis microechinus* Hecht *in* McGrew *et al.*, 1959, originally described from the middle Eocene of the Bridger Basin in Wyoming, United States (Hecht 1959). Subsequently, other remains from the middle Eocene and (even the) Paleocene of North America have been tentatively referred to this taxon (e.g., Estes 1976; Holman 1979; see Smith & Georgalis 2022). Furthermore, two species from Europe have been established as members of the same genus, i.e., *Dunnophis matronensis* Rage, 1973 and *Dunnophis cadurcensis* Rage, 1974. *Dunnophis matronensis* was originally established by Rage (1973) upon vertebral material from the early Eocene (MP 10) of Grauves in the Paris Basin, with the taxon being subsequently described also from the early Eocene (MP 7) of Silveirinha, Portugal (Rage & Augé 2003), the early Eocene (MP 10) of Prémontré, France (Augé *et al.* 1997), and the middle Eocene (MP 14) of Lissieu, France (Rage & Augé 2010), while it has also been mentioned (but not described or figured) from the early Eocene (MP 7) of Le Quesnoy, France (Nel *et al.* 1999). *Dunnophis cadurcensis* was originally established by Rage (1974) upon vertebral material from the late Eocene (MP 17) of Malpérié, Quercy, France, with the taxon being subsequently described also from the middle Eocene (MP 16) localities of Le Bretou (Rage 1988) and Lavergne (Čerňanský *et al.* 2026), both from Quercy, France, while it has also been mentioned (but not described or figured) from an array of localities, all from Quercy, France: the late Eocene (MP 17) of Aubrelong B (Crochet *et al.* 1981), the late Eocene (MP 17) of La Bouffie (Crochet *et al.* 1981), the late Eocene (MP 17) of Les Pradigues (Crochet *et al.* 1981), the late Eocene (MP 17) of Perrière (Crochet *et al.* 1981), the late Eocene (MP 18) of Sainte Néboule (Rage 1978), the late Eocene (MP 18-19) of Célarié (Crochet *et al.* 1981), the late Eocene (MP 18-19) of Sindou (Crochet *et al.* 1981), the late Eocene (MP 19) of Escamps (Rage 1974), and the late Eocene (MP 19) of Rosières A and B (Crochet *et al.* 1981). In addition, other unnamed forms from the Paleogene of Europe (Hecht & Hoffstetter 1962; Rage & Ford 1980; Van Dyck 1983; Augé *et al.* 1997; Rage & Augé 2010) and even northern Africa (Augé & Rage 2006) have been referred to the genus *Dunnophis*. The youngest occurrence of *Dunnophis* in Europe is supposed to be from the early Oligocene (MP 22) of Ehrenstein 12, Germany (Szyndlar & Rage 2003), however, no figures or descriptions of this material have been made and its documentation is restricted to the listing of its collection numbers (see Szyndlar & Rage 2003: 75). Nevertheless, the typical diagnostic features of *Dunnophis* (elongated centrum, neural spine confined to the posterior third [or even margin] of the neural arch, a depressed neural arch, and absence of prezygapophyseal accessory processes) are somehow more widespread features among snakes and not truly unique to *Dunnophis*, raising thus questions and doubts about the congeneric affinities of the three named species and the unnamed purported occurrences from North America, Europe, and northern Africa (Smith & Georgalis 2022). Notably, in the Eocene of Europe two other taxa seems to have similar vertebrae, i.e., *Messelophis variatus* Baszio, 2004, and *Rieppelophis ermannorum* (Schaal & Baszio, 2004), both known from several specimens, including also almost complete skeletons, from the Fossillagerstätte locality of Messel in Germany (Baszio 2004; Schaal & Baszio 2004; Scanferla *et al.* 2016; Smith *et al.* 2018; Scanferla & Smith 2020; Chuliver *et al.* 2022), with the former taxon being also recently described from the late Eocene of Romania (Venczel *et al.* 2025). Within Constrictores, *Messelophis* Baszio, 2004, and *Rieppelophis* Scanferla, Smith & Schaal, 2016, have been interpreted as probable members of Ungaliophiidae McDowell, 1987 (*sensu* Burbrink *et al.* 2020), the lineage encompassing the Dwarf Boas of the extant genera *Exiliboa* Bogert, 1968 and *Ungaliophis* Müller, 1880, currently inhabiting Central and northern South America (e.g., Scanferla & Smith 2020; Smith & Georgalis 2022; Venczel *et al.* 2025). Such taxonomic attribution was substantially aided by the known cranial morphology of *Messelophis* and *Rieppelophis* (Scanferla *et al.* 2016), but in any case, the elongation of the centrum is considered a diagnostic feature of ungaliophiids (Smith 2013; Georgalis & Smith 2020; Szyndlar & Georgalis 2023). It is therefore likely that also *Dunnophis* could pertain to ungaliophiids, however, in the absence of any cranial material, this taxonomic assumption cannot be confidently confirmed. In any case, the Cernay material denotes that this morphotype with an elongated vertebral centrum was already present since the Paleocene (supporting the similar, unpublished, observation of Van Dyck [1983] for the Hainin material).

As for the second snake morphotype (Constrictores indet. [morphotype 2]) documented in Cernay, this represents a larger and more robust form. It possesses the typical constrictor vertebral morphology, characterized by a massive vertebra with a wider than long centrum. This morphology, however, is widespread across extinct and extant constrictors, observed in both constrictor subgroups, i.e., booids and pythonoids (e.g., Szyndlar & Georgalis 2023). As such, it is not taxonomically informative for this single vertebra from Cernay. Nevertheless, it clearly attests that the typical constrictor morphology that would dominate snake faunas during the Eocene (Rage 1984; Georgalis *et al.* 2021; Smith & Georgalis 2022) was already present in the Paleocene of Europe.

As was mentioned above, snakes from Cernay were briefly mentioned (but never described or figured), already since the second half of the 19th century by Lemoine (1878-1879, 1879, 1880, 1889). The material from the NMB collection described herein is not the same as the one briefly mentioned in these works of Lemoine (1878-1879, 1879, 1880, 1889), which was discovered one century earlier. Lemoine's Cernay collection is deposited at the Muséum national d'Histoire naturelle Paris (Gaudry 1898; Boyer *et al.* 2012), but it actually appears that his snake specimens are currently of unknown whereabouts. Apparently, the (never published) material that Lemoine had available was more abundant and perhaps somehow diverse: Lemoine (1878-1879: 403) initially stated "*il y a de même plusieurs formes des serpents* [there are also several types of snakes]", while he subsequently became more precise in claiming that the snake vertebrae from Cernay indicated the presence of three different sized forms ("*L'existence des Serpents à cette époque est indiquée par des vertèbres de trois dimensions différentes*"; Lemoine 1879: 3). In the following year, Lemoine (1880) mentioned again the presence of snakes from Cernay, but his only comment was that they could probably achieve a length of 3 to 4 meters and that they were probably non-venomous ("*Les serpents de cette même époque semblent avoir atteint 3 a 4 mètres; ils ne paraissent pas avoir été venimeux*"; Lemoine 1880: 593). Later, the same author seemed to have reassessed their initial diversity estimation of three forms and instead stated that the snakes from Cernay consisted of two species, however, this was again a simple mention ("*Serpents (2 esp.)*"; Lemoine 1889: 233), still again without any kind of description or further data. From his mentions in his works, we can assume that Lemoine (1878-1879, 1879, 1880, 1889) had a larger amount of vertebrae available compared to the modest number of three that we only described in this paper. It is further worth noting that Gervais (1877), when describing important elements from the Lemoine's collection from Cernay, did not mention at all any snake specimen, while he discussed other reptiles from the locality (choristoderes, turtles, and crocodiles). Nevertheless, the two snake taxa described here from this NMB material match the "diversity number" of two that was mentioned by Lemoine (1889).

Even if rather limited and incomplete, the new snake fossil remains from Cernay add to our understanding of the Paleocene snake assemblages from Europe, which still remain extremely poorly known. Besides snakes, such scarce and inadequate knowledge is also the case for the rest of the herpetofauna, as the Paleocene of Europe is rather poorly documented in general for amphibians and reptiles (e.g., Gervais 1877; Herre 1939; Estes *et al.* 1967; Vergnaud-Grazzini & Hoffstetter 1972; Sigogneau-Russell & Russell 1978; Groessens-Van Dyck 1981a, b; Rage 2003; Rage & Roček 2003; Delfino *et al.* 2005; Pérez-García 2012, 2020; Matsumoto *et al.* 2013; Martin *et al.* 2014; Smith *et al.* 2014; Georgalis & Joyce 2017; Macaluso *et al.* 2025; Vasilyan & Macaluso 2025), particularly so for squamates (Kuhn 1940; Folie *et al.* 2005, 2013; Augé 2005; Augé *et al.* 2021; Čerňanský & Vasilyan 2024; Georgalis & Mennecart 2026). As such, even though significant discoveries of Paleocene European turtles, crocodiles, and choristoderes have demonstrated interesting cases of endemism and biogeography (e.g., Sigogneau-Russell & Russell 1978; Delfino *et al.* 2005; Pérez-García 2012, 2020; Matsumoto *et al.* 2013; Martin *et al.* 2014), herpetofaunas from that epoch are still inadequately known, especially when compared to the much better documented coeval mammalian faunas (Biochrom'97 1997; Solé *et al.* 2022; Tabuce *et al.* 2025) and therefore every single piece in the puzzle is really important.

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