

Another wanderer from the Paleocene-
Eocene Thermal Maximum?
A new species of the North American snake genus
Cheilophis Gilmore, 1938 from the early Eocene of France

Georgios L. GEORGALIS & Bastien MENNECART

SNAKES FROM THE CENOZOIC OF EUROPE

– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

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Another wanderer from the Paleocene-Eocene Thermal Maximum? A new species of the North American snake genus *Cheilophis* Gilmore, 1938 from the early Eocene of France

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ABSTRACT

We here document new snake vertebral material from the early Eocene (MP 10) of Cuis, France, that we describe as a new species of *Cheilophis* Gilmore, 1938, a genus that was so far exclusively known from the Paleocene and Eocene of North America. The new taxon bears several anatomical features with the type, and so far, only known species of *Cheilophis* from North America. However, there are also important differences that allow us to recognize it as a new congeneric species. If our identification is correct, this first observed occurrence of *Cheilophis* from France adds another shared terrestrial vertebrate genus between Europe and North America, reinforcing biogeographic hypotheses about dispersals between the two landmasses around the Paleocene-Eocene Thermal Maximum (PETM).

RÉSUMÉ

Un autre vagabond du maximum thermique du Paléocène-Éocène? Une nouvelle espèce du genre de serpent nord-américain Cheilophis Gilmore, 1938 de l'Éocène précoce de France.

Nous documentons ici des vertèbres d'une nouvelle espèce de serpent provenant de l'Éocène inférieur (MP 10) de Cuis en France, que nous attribuons à *Cheilophis* Gilmore, 1938, un genre jusqu'à présent exclusivement connu durant l'Éocène de l'Amérique du Nord. Ce nouveau taxon présente plusieurs caractéristiques anatomiques en commun avec l'espèce type d'Amérique du Nord du genre *Cheilophis*, qui est jusqu'à présent la seule espèce connue. Mais nous observons également des différences importantes qui nous permettent de reconnaître les spécimens de Cuis comme appartenant à une nouvelle espèce congénérique. Si notre détermination est confirmée, cette première occurrence du genre *Cheilophis* observée en France ajoute un autre genre de vertébré terrestre partagé entre l'Europe et l'Amérique du Nord, renforçant les hypothèses biogéographiques concernant les dispersions entre les deux masses continentales à proximité du Maximum Thermique du Paléocène-Éocène (PETM).

KEY WORDS
Serpentes,
vertebral morphology,
dispersals,
Paléogène,
new species.

MOTS CLÉS
Serpentes,
morphologie des
vertèbres,
dispersions,
Paléogène,
espèce nouvelle.

INTRODUCTION

The presence of closely related, or even congeneric, terrestrial and fresh-water taxa in Europe and North America during the early and middle Eocene has been suggested to represent the product of dispersal(s) among the two landmasses during the Paleocene–Eocene Thermal Maximum (PETM) (e.g. McKenna 1975; Escarguel 1999; Smith & Smith 2010; Smith 2011; Rage 2013; Smith 2017; De Bast & Smith 2017; Georgalis & Joyce 2017; Hooker 2018; Smith & Georgalis 2022; Solé *et al.* 2022; Čerňanský *et al.* 2023, 2024; Mayr *et al.* 2024). This pattern has been repeatedly witnessed among numerous vertebrate groups, including amphibians, reptiles, flightless birds, and mammals (McKenna 1975; West & Dawson 1978; Estes & Hutchison 1980; Escarguel 1999; Smith *et al.* 2006; Smith & Smith 2010; Smith 2011; Rage 2013; Buffetaut & Angst 2014; Roček *et al.* 2014; Georgalis & Joyce 2017; Hooker 2018; Mourer-Chauviré & Bourdon 2020; Smith & Scanferla 2021; Smith & Georgalis 2022; Solé *et al.* 2022; Čerňanský *et al.* 2023, 2024; Conedera *et al.* 2024; Mayr *et al.* 2024). In particular, among reptiles, congeneric taxa in the Paleogene of both North America and Europe are documented for turtles (Georgalis & Joyce 2017; Pérez-García & Smith 2021), crocodylians (Brochu 2013), choristoderans (Sigogneau-Russell & Russell 1978; Erickson 1987), lizards (Sullivan 1979; Augé 2005, 2012; Smith 2009, 2011; Rage 2013; Smith *et al.* 2018; Augé *et al.* 2022; Čerňanský *et al.* 2023, 2024), and of course, snakes (Smith & Georgalis 2022).

Indeed, during the Eocene, Europe and North America hosted congeneric species of the snake genus *Dunnophis* Hecht *in* McGrew *et al.*, 1959 (see Rage 1973, 1974) and *Calamagras* Cope, 1873 (see Rage 1977). In addition, *Totlandophis* Holman & Harrison, 1998, was first recognized in the British late Eocene (Holman & Harrison 1998) but a congeneric species was subsequently established from the early Oligocene of Florida, United States (Holman & Harrison 2001). Although the congeneric affinities of some of these species have not been adequately tested (or these are even disputed, particularly the case of the European *Calamagras*; see Smith 2013; Smith & Georgalis 2022), these taxa have been used to suggest similar ophidian elements in the European and North American Eocene. In any case, it is currently accepted that certain, including non-congeneric but still closely related, snake taxa occurred in the Eocene of both Europe and North America (Smith & Scanferla 2021; Smith & Georgalis 2022). Besides, of course, there were also the aquatic snakes of the genus *Palaeophis* Owen, 1841, species of which were present in both the European and North American Eocene (see Smith & Georgalis 2022), but species of this genus are also known to inhabit the marine realm (Rage 1983; Georgalis *et al.* 2021a; Smith & Georgalis 2022), thus achieving a rather broad geographic distribution.

We here describe new vertebral material from the early Eocene (MP 10) of Cuis, East of Paris, France, which we refer to the North American genus *Cheilophis* Gilmore, 1938, previously known exclusively from the Paleocene and early Eocene of the United States. The new material from

France possesses several features in common with the type (and so far, only known) species of the genus, *Cheilophis huerfanoensis* Gilmore, 1938, but still enough differences that allow us to establish it as a new congeneric species. If our identification is correct, the new taxon from France adds a further genus of snakes shared in both the European and North American Eocene.

MATERIAL AND METHODS

The fossil material described herein is permanently curated in the collections of the Natural History Museum of Basel (NMB). NMB collections are extensive for specimens from Cuis, including casts from the Lille Museum registered in 1940, and even older collections bought before. These old collections include mostly large mammals. Nevertheless, all fossil specimens of the new taxon described herein were found during more recent excavations, between 1976 and 1982. For comparative purposes, abundant material of extinct and extant snakes was studied at the collections of GMH, ISEZ, MGPT-MDHC, MNCN, MNHN, NHMUK, NHMW, PIMUZ, SMF-PH, and UM.

The X-ray microtomography of the holotype and paratype specimens of the new taxon was performed using a nanoCT[®] system nanotom[®] (phoenix X-ray, GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany) hosted at the Biomaterials Science Center of the University of Basel (Switzerland), following these parameters: 1 440 equiangular radiographs were taken over 360° using an accelerating voltage of 170 kV and a beam current of 30 mA for a resolution of 10 µm. Specimen reconstruction has been made using Aviso Lite 9.0. 3D surface model reconstructions (.PLY files) of the holotype and paratype specimens of the new taxon are openly available in the online repository Morphosource (<https://www.morphosource.org/>). For details, see the section “Availability of materials and data” below.

Taxonomy follows Smith & Georgalis (2022). Anatomical terminology and measurements of snake vertebrae follow Georgalis *et al.* (2021b) and Szyndlar & Georgalis (2023).

ABBREVIATIONS

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;
ISEZ	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.

Other abbreviations

CL	centrum length;
EECO	Early Eocene Climatic Optimum;
NAW	neural arch width;
PETM	Paleocene-Eocene Thermal Maximum.

LOCALITY

Close to the town of Epernay, 140 km eastward from Paris (Marne, France), the Formation of Unios and Teredinids Sands, also known as “sables à unios et térédines” or “sables à térédines” in French, has yielded a very rich and diverse vertebrate fauna, notably in the localities of Grauves, Monthelon, Mancy, and Cuis (e.g. Stehlin 1909; Russell *et al.* 1982; Laurain *et al.* 1985; Duprat 1997). These sands have been deposited during a global retrograding deltaic context (Duprat 1997). The presence of both marine and freshwater fish, along with the wide variety of mammals (over 50 species have been recorded), confirm that these coarse sands belong to estuarine environments (Laurain *et al.* 1985; Duprat 1997). The faunal content indicates a local age of late Cuisian, which corresponds to late Ypresian, early Eocene (Jaeger 1971; Laurain *et al.* 1985; Duprat 1997). The Cuis fauna (Fig. 1), as well as the one from Monthelon and Mancy, has been attributed to the MP 10 reference level (Biochrom'97 1997; Escarguel *et al.* 1997). In Cuis, many mammals have been discovered, including several species of the rodent *Ailuravus* (Wood 1976), diverse carnivorous mammals (Mesonychidae: Solé *et al.* 2017; Hyaenodonta: Solé *et al.* 2021), perissodactyls (Vautrin *et al.* 2021; Bronnert & Métais 2023), and artiodactyls (Erfurt & Métais 2007; Boivin *et al.* 2018). The Cuis locality was first defined as a biochronological reference by Thaler (1966) (see also Jaeger 1971). However, the locality of Grauves was ultimately chosen as the reference locality for MP 10 (Godinot 1987; Biochrom'97 1997). The numerical age of the Cuis fauna is estimated to 49.86 ± 0.455 Ma (Escarguel *et al.* 1997), during the elevated temperatures of the Early Eocene Climatic Optimum.

SYSTEMATIC PALAEOONTOLOGY

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

Genus *Cheilophis* Gilmore, 1938

TYPE SPECIES. — *Cheilophis huerfanoensis* Gilmore, 1938.

EMENDED DIAGNOSIS. — *Cheilophis* can be differentiated from all other snakes by its unique combination of features: wide haemal keel (on the posterior mid- and posterior trunk vertebrae) that

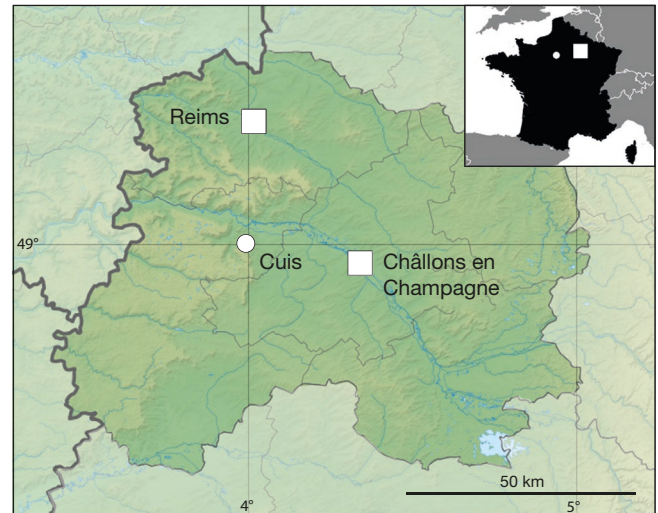


Fig. 1. — Map of the Department of Marne, showing the position of the locality of Cuis; in the inset, map of France, showing the position of Cuis (square) and the city of Paris (circle).

bears a constriction at around its mid-length and becomes wider and blunt wedged-shaped at its posterior termination; distinct “notches” of the haemal keel in ventral view; ventral expansion of the haemal keel in lateral view; thick neural spine that is mostly confined at the posterior portion of the neural arch; relatively thin zygosphenes with a distinct median lamina (“lip”) and prominent lateral lobes; moderately vaulted neural arch; deep posterior median notch of the neural arch; deep interzygapophyseal constriction; almost circular cotyle and condyle; widely extended parapophyseal process of the paradiapophyses; almost horizontal to only slightly dorsally inclined prezygapophyses; and large prezygapophyseal and postzygapophyseal articular facets. In addition to these vertebral characters, Rage (1984b) also indicated the following cranial features as diagnostic for the genus: palatal process of the maxilla directed backwards; surangular lamina of the compound bone higher than the prearticular; coronoid present.

Cheilophis periplanetes n. sp. (Figs 2–7)

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TYPE MATERIAL. — **Holotype.** France • 1 specimen (a trunk vertebra); Cuis; Formation of Unios and Teredinids Sands; 49.86 ± 0.455 Ma; MP 10, late Ypresian (early Eocene); NMB T.S.1100 (Figs 2; 3). **Paratype.** France • 1 specimen (a trunk vertebra); Cuis; Formation of Unios and Teredinids Sands; 49.86 ± 0.455 Ma; MP 10, late Ypresian (early Eocene); NMB T.S.1101 (Figs 4; 5).

REFERRED SPECIMENS. — Five trunk vertebrae (NMB T.S.1063, NMB T.S.1067, NMB T.S.1071, NMB T.S.1084, and NMB T.S.1092). Tentatively also, an anterior trunk vertebra (NMB T.S.1065) and two caudal vertebrae (NMB T.S.1048 and NMB T.S.1066).

TYPE LOCALITY AND AGE. — All specimens originate from the locality of Cuis; MP 10 (around $49.86 \text{ Ma} \pm 0.455$), early Eocene.

ETYMOLOGY. — The new species epithet is from the Greek word “periplanetes” (“περιπλανήτης”), which means “wanderer”, reflecting the potential wandering that occurred during the dispersals among North America and Europe.



FIG. 2. — Holotype trunk vertebra (NMB T.S.1100) of *Cheilophis periplanetes* n. sp. in anterior (A), posterior (B), dorsal (C), ventral (D), right lateral (E), and left lateral (F) views. Scale bar: 1 mm.

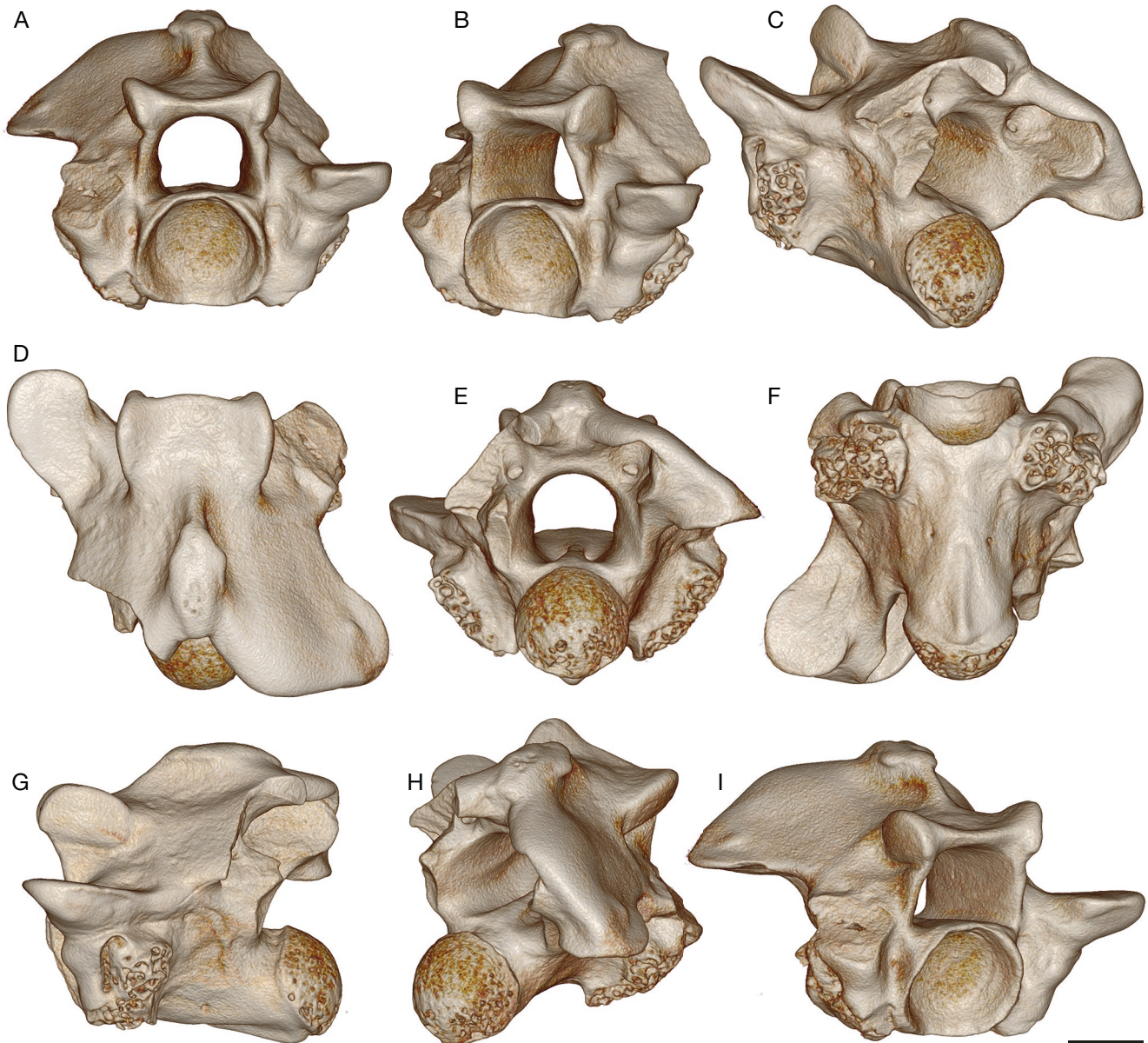


FIG. 3. — 3D μ CT images of holotype trunk vertebra (NMB T.S.1100) of *Cheilophis periplanetes* n. sp. in anterior (A), left anterodorsolateral (B), left posterolateral (C), dorsal (D), posterior (E), ventral (F), left lateral (G), posterodorsal (H), and right anterolateral (I) views. Scale bar: 1 mm.

DIAGNOSIS. — *Cheilophis periplanetes* n. sp. can be referred to the genus *Cheilophis* on the basis of the full list of diagnostic vertebral features of the genus (see above). *Cheilophis periplanetes* n. sp. can be differentiated from the type and only other known species of *Cheilophis*, i.e., *Cheilophis huerfanoensis*, by its much smaller size (centrum length [CL] almost half in size), shorter centrum, the absence of prezygapophyseal accessory processes, the more massive prezygapophyseal and postzygapophyseal articular facets, the shorter neural spine, the rare presence of paracotylar foramina, and the more dorsally expanded lateral lobes of the zygosphenes.

DESCRIPTION

Holotype

The holotype vertebra (NMB T.S.1100) is incomplete, missing most of the left postzygapophysis and part of the right prezygapophysis, while the paradiapophyses are eroded (Figs 2; 3).

The vertebra has a centrum length (CL) of 3 mm and a neural arch width (NAW) of 3.2 mm. In anterior view (Figs 2A; 3A), the zygosphenes are moderately thin and bears a distinct median lamina, resembling a lip. There are two distinct lateral lobes on the zygosphenes that protrude much dorsally, like horns. The neural canal is semicircular (i.e., like an arch, rounded above and flat below). The prezygapophyses are almost horizontal, being only very slightly dorsally extended. The cotyle is large and almost circular. There are no paracotylar foramina. In posterior view (Figs 2B; 3E), the neural arch is moderately vaulted, with a vaulting ratio (sensu Georgalis *et al.* 2021b) equal to 0.47. The zygantral roof is relatively thick. The condyle is large and circular. In dorsal view (Figs 2C; 3D), the neural spine is very thick and is mostly confined to the posterior half of the neural arch. The zygosphenes are trilobed,

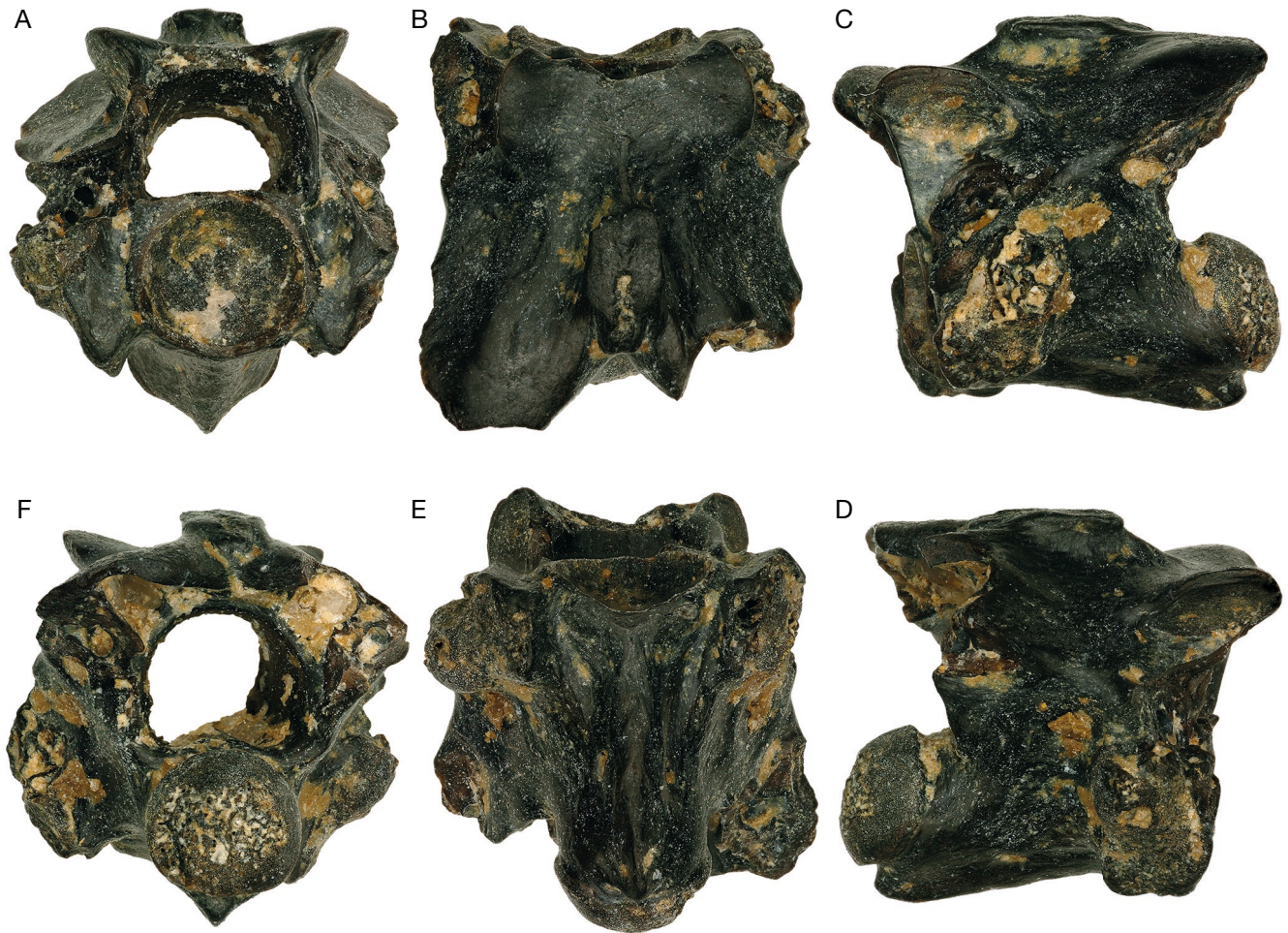


FIG. 4. — Paratype trunk vertebra (NMB T.S.1101) of *Cheilophis periplanetes* n. sp. in anterior (A), dorsal (B), left lateral (C), right lateral (D), ventral (E), and posterior (F) views. Scale bar: 1 mm.

with the two lateral lobes being more prominent than the central one. The prezygapophyses project anterolaterally. The prezygapophyseal articular facets are large and oval. The interzygapophyseal constriction is deep (unlike other Eocene European constrictors, such as *Eoconstrictor* Scanferla & Smith, 2020, and *Palaeopython* Rochebrune, 1880). The posterior median notch of the neural arch is deep. In ventral view (Figs 2D; 3I), the centrum is wider than long (ratio CL/NAW equal to 0.94). The haemal keel runs along most of the midline of the centrum; it commences anteriorly almost at the ventral level of the cotyle and terminates posteriorly at the level of the condyle. The width of the haemal keel is not consistent throughout its length; instead, there is a prominent constriction at the anterior half of the centrum and it becomes gradually wider and more prominent towards its posterior termination. Notably, there are distinct “notches” around its posterior portion. The subcentral grooves are deep. Subcentral foramina are present. The paradiapophyses are much eroded and their exact shape and size cannot be precisely deciphered, but it seems that they were not divided (or were only slightly divided) into distinct diapophyses and parapophyses. There are no prezygapophyseal accessory processes. The postzygapophyseal articular facets are massive and

broad. In lateral view (Figs 2E, F; 3G), the neural spine is very short; it commences far behind the level of the zygosphenes and gradually increases in height, being developed mostly at the posterior half of the neural arch. The zygosphenal facets are broad. The subcentral ridges are almost straight. The haemal keel protrudes ventrally at the level of the posterior half of the centrum, with its height gradually developed and culminating around its posteriormost edge. Judging from the width of the haemal keel, the vaulting of the neural arch, and the height of the neural spine, we assume that the vertebra originates somewhere from the mid- or posterior mid-trunk portion of the vertebral column.

Paratype

The paratype vertebra (NMB T.S.1101) is incomplete, missing both prezygapophyses and the right postzygapophysis (Figs 4; 5). The vertebra is small, with a centrum length (CL) equal to 2.8 mm and a neural arch width (NAW) equal to 3 mm. The paratype vertebra NMB T.S.1101 bears an overall resemblance to the holotype, exhibiting typical features of the species, such as the thin zygosphenes with the distinct “lip”, the prominent lateral lobes of the zygosphenes, the dorsoventrally short neural spine that is mostly confined to the

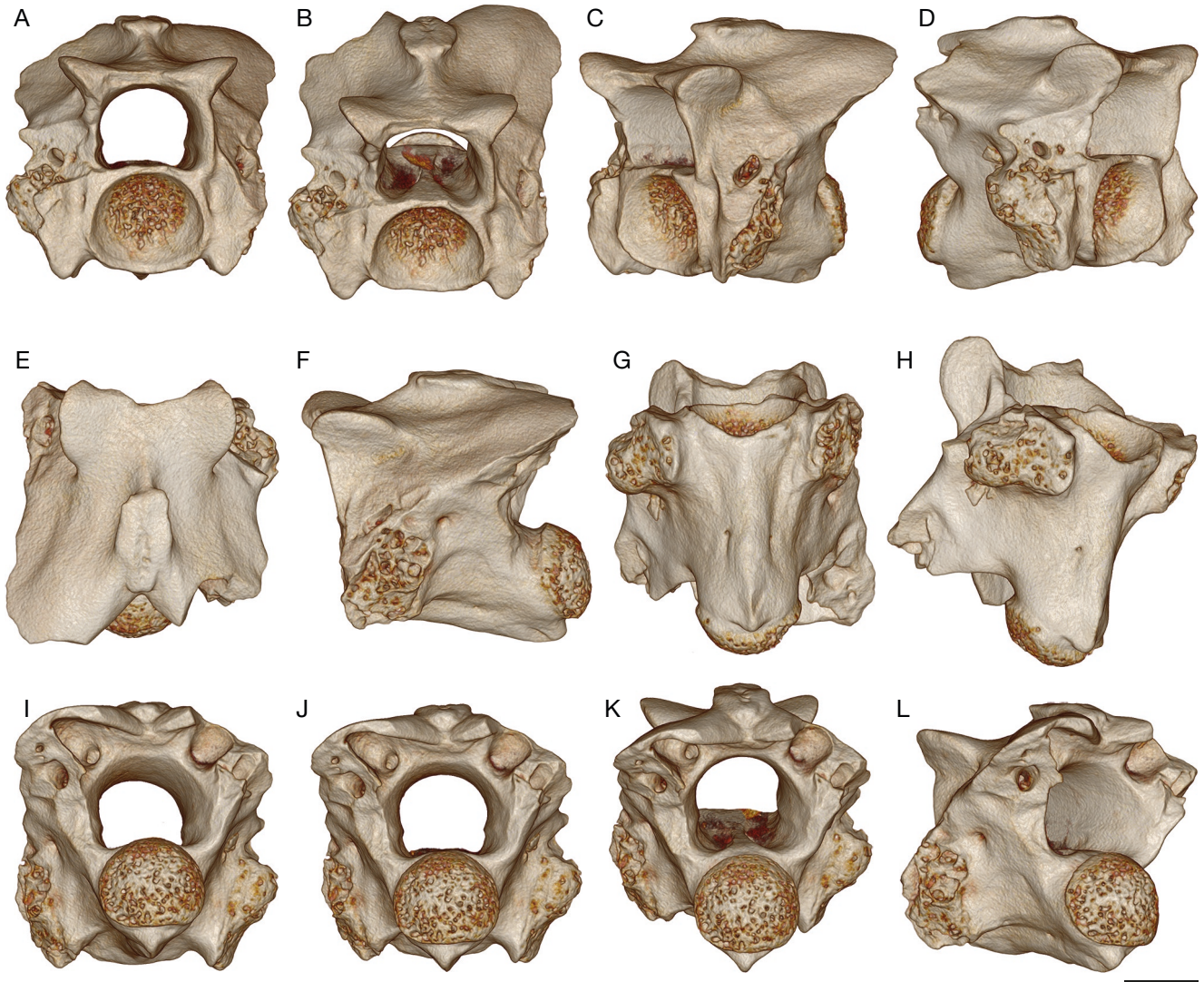


FIG. 5. — 3D μ CT images of paratype trunk vertebra (NMB T.S.1101) of *Cheilophis periplanetes* n. sp. in anterior (A), anterodorsal (B), left anterolateral (C), right anterolateral (D), dorsal (E), left lateral (F), ventral (G), ventrolateral (H), posteroventral (I), posterior (J), posterodorsal (K), and left posterolateral (L) views. Scale bar: 1 mm.

posterior portion of the neural arch, and the wide haemal keel with distinct “notches”. Nevertheless, there are some striking features observed in the paratype. Most prominently, the paratype vertebra exhibits the thickest neural spine known for the species (Figs 4B; 5E). Interestingly, the paratype vertebra NMB T.S.1101 demonstrates the widely extended parapophyseal process of the paradiapophyses (Fig. 5A, B), a feature that was highlighted as diagnostic for *Cheilophis* by Rage (1984a). This structure is otherwise not preserved in any other specimen of the new taxon (including the holotype [though a hint about such extended parapophyseal process might be observed on the right side of this specimen]) and thus, its observation in NMB T.S.1101 is of particular importance, as it further reinforces a referral of the new taxon from Cuis to the North American *Cheilophis*. The neural arch of NMB T.S.1101 is exceedingly depressed (Figs 4F; 5J), with a vaulting ratio (sensu Georgalis *et al.* 2021b) reaching only 0.16. The haemal keel is wide, and, similarly to the holotype, there

are distinct “notches” around its posterior portion (Figs 4E; 5G, H). What is further notable for NMB T.S.1101 is the presence of a small paracotylar foramen on the right of the cotyle (Figs 4A; 5A, B, D) – our observation of the μ CT files of this specimen confirms that this foramen goes relatively deeply into the vertebra. We attribute all these differences to intracolumnar variation. Judging from these features, we consider that the paratype vertebra NMB T.S.1101 originates from the posterior mid-trunk portion of the column (more posterior than the holotype).

Referred specimens – intracolumnar variation

All referred specimens are much incomplete but they nevertheless preserve certain anatomical structures that allow a taxonomic attribution to *Cheilophis periplanetes* n. sp. Especially NMB T.S.1071, NMB T.S.1084, NMB NMB T.S.1092, and NMB T.S.1063 are all rather fragmentary and/or eroded. Most available trunk vertebrae share with the

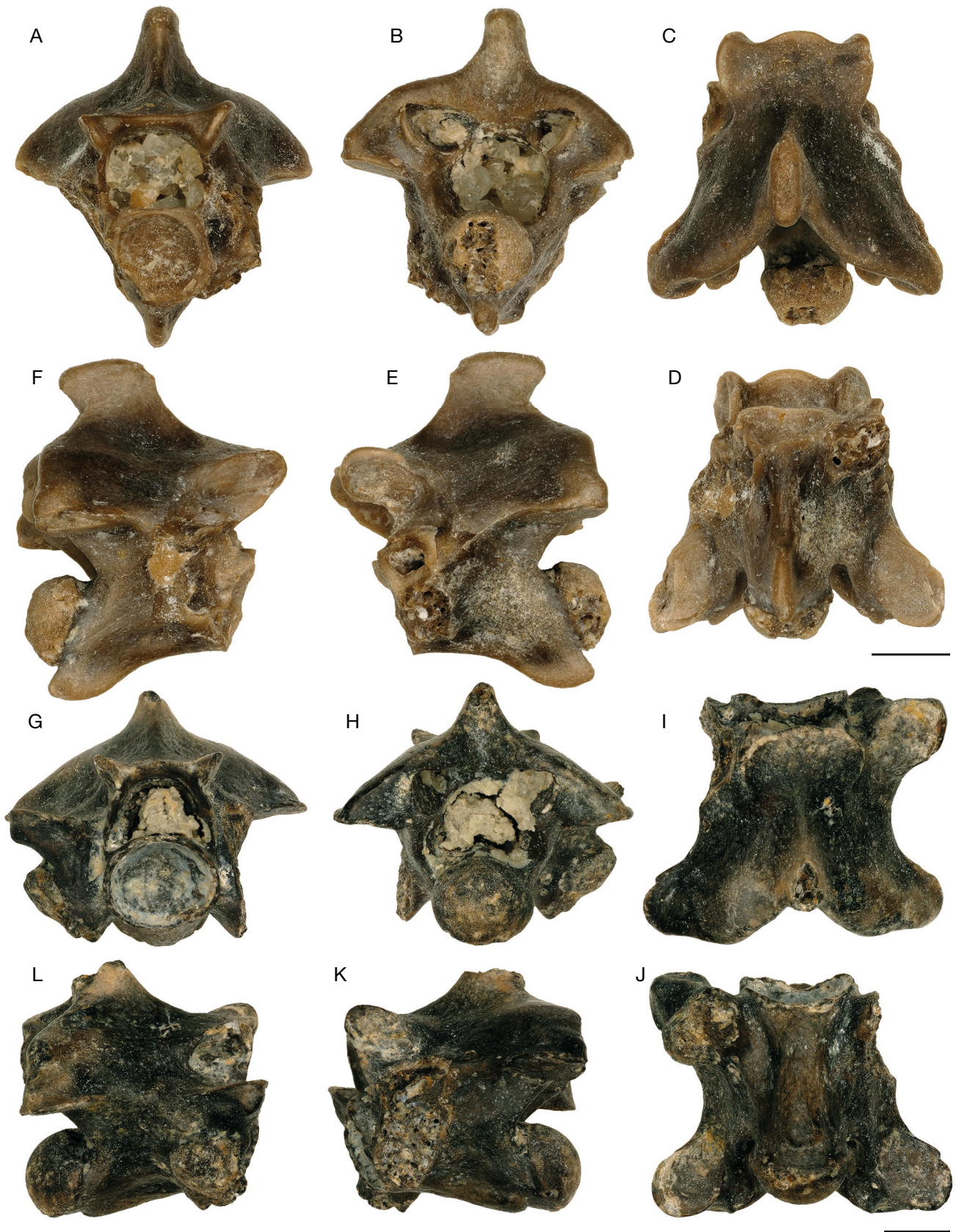


FIG. 6. — Other referred vertebrae of *Cheilophis periplanetes* n. sp.: **A-F**, anterior trunk vertebra NMB T.S.1065 in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**), left lateral (**E**), and right lateral (**F**) views; **G-L**, trunk (or cloacal) vertebra NMB T.S.1067 in anterior (**G**), posterior (**H**), dorsal (**I**), ventral (**J**), left lateral (**K**), and right lateral (**L**) views. Scale bars: 1 mm.



FIG. 7. — Caudal vertebrae tentatively referred to *Cheilophis periplanetes* n. sp.: A–E, anterior caudal vertebra NMB T.S.1048 in anterior (A), posterior (B), dorsal (C), ventral (D), and right lateral (E) views; F–J, posterior caudal vertebra NMB T.S.1066 in anterior (F), posterior (G), dorsal (H), ventral (I), and left lateral (J) views. Scale bars: 1 mm.

holotype an overall similar morphology, including a wider than long centrum, a thin zygosphenes with a median lamina (“lip”) and prominent lateral lobes that protrude dorsally, a relatively short neural spine that is mostly confined at the posterior portion of the neural arch, a moderately vaulted neural arch, absence of prezygapophyseal accessory processes, and large prezygapophyseal articular facets (Fig. 6). Nevertheless, some differences are apparent among the few available specimens, dealing with the shape and width of the haemal keel, the size of the prezygapophyseal and postzygapophyseal articular facets, and the height, anteroposterior length, and thickness of the neural spine. All these differences can most probably be attributed to intracolumnar variation (see e.g. Smith 2013; Szyndlar & Georgalis 2023) though some other kind of variation, such as ontogenetic (e.g. Georgalis & Scheyer 2019) cannot be excluded.

As is common in snakes, anterior trunk vertebrae are characterized by the presence of a hypapophysis instead of haemal keel, a more vaulted neural arch, and a higher and posteriorly inclined neural spine. The only anterior trunk vertebra from our sample is NMB T.S.1065 (Fig. 6A–F), though still a referral of this specimen to *Cheilophis periplanetes* n. sp. should be considered as tentative. NMB T.S.1065 possesses hypapophysis (instead of haemal keel), which is short and posteroventrally directed, as well as a posteriorly inclined neural spine, which is considerably higher than in other vertebrae. Other differences include the narrower centrum and the (slightly) more vaulted neural arch. Nevertheless, other typical features of the new species are still present in the specimen NMB T.S.1065, such as the thin zygosphenes with a median lamina (“lip”) and two prominent lateral lobes, and the massive postzygapophyseal articular facets.

NMB T.S.1067 could be a posterior trunk vertebra (Fig. 6G–L), judging from the wide haemal keel, or even an anterior cloacal vertebra, judging from the high neural arch. However, features such as the not-so-short neural spine should make an exact intracolumnar assignment uncertain. Rage (1984b) had already highlighted that unlike most snakes, posterior trunk vertebrae of *Cheilophis huerfanoensis* did not possess short neural spines compared to preceding vertebrae, and therefore this observation may apply also to the new European species. Nevertheless, certain diagnostic features of the new species are apparent in this specimen, such as the zygosphenes with the “lip” and the distinct lateral lobes, as well as the massive prezygapophyseal and postzygapophyseal articular facets.

NMB T.S.1048 and NMB T.S.1066 are the only caudal vertebrae (Fig. 7) that are, at least tentatively, referred to *Cheilophis periplanetes* n. sp. They are characterized by the presence of haemapophyses and pleurapophyses. These specimens too possess a thick neural spine that is confined to the posterior portion of the neural arch. Judging from the elongation of their centrum and the shape of the haemapophyses, NMB T.S.1048 originates from the anterior caudal region (Fig. 7A–E), while NMB T.S.1066 represents a posterior caudal vertebra (Fig. 7F–J). Interestingly, in the anterior caudal vertebra NMB T.S.1048, the haemapophyses are short and their base is situated onto a distinct keel in the centrum (Fig. 7A, B, D, E).

DISCUSSION

The genus *Cheilophis* was so far known exclusively by its type species, *Cheilophis huerfanoensis*, originally established by Gilmore (1938) based on abundant vertebrae and ribs,

presumably pertaining to a single individual, from the early Eocene (early Bridgerian) of the Gardner locality, Huerfano Formation, Colorado, United States. Gilmore (1938) figured only a single vertebra among this bulk of material, though he provided also some information on intracolumnar variation. Rage (1984b) further prepared the fossil skeleton described by Gilmore (1938), isolated several vertebrae that were embedded on matrix, highlighted errors in the original figuring of the vertebra provided by Gilmore (1938), designated and figured a lectotype, discussed intracolumnar variation, described and figured cranial elements (a maxilla, a dentary, and a compound bone) that were also embedded in the same matrix, and provided an emended diagnosis for the taxon. During the same year, in his monumental treatise on fossil snakes, the same author further figured an additional vertebra (a posterior trunk one) from the type locality (Rage 1984a). Some limited additional material has been subsequently referred to the same species from two other localities in the United States: a single, fragmentary, trunk vertebra from the early Eocene of the San Juan Basin, New Mexico (Sullivan & Lucas 1988), plus some limited vertebral material from the late Paleocene of New Jersey (Cook & Ramsdell 1991). Another vertebra, from the Oligocene of Nebraska, that was tentatively referred to *Cheilophis* by Gilmore (1938) was subsequently referred to another snake group later by Rage (1984b) and Holman (2000). *Cheilophis huerfanoensis* was further revised by Holman (2000), while Rage (2001) further highlighted diagnostic features of *Cheilophis* and comparisons with many other extinct and extant constrictors. The taxon was ultimately reviewed by Smith & Georgalis (2022), who continued to treat it as valid, though of still unclear relationships within Constrictores.

The new material from the early Eocene (MP 10) of Cuis bears several features that allow its referral to the North American genus, *Cheilophis*, including the so-called by Gilmore (1938: 80) “outstanding” “lip-like projection on the zygosphenes”, that inspired its very name (from the Greek word “χείλος” [“cheilos”], meaning “lip”). Several other shared features can be observed between the type species and *Cheilophis periplanetes* n. sp. (see Diagnosis above). Notably, the new European taxon is considerably smaller than the American *Cheilophis huerfanoensis*, which achieved a CL of around 6 mm (vs around only 3 mm in *Cheilophis periplanetes* n. sp.).

The precise taxonomic affinities of *Cheilophis* are unresolved. Certain authors have suggested affinities of this genus with either colubriiforms (Gilmore 1938), erycid booids (Erycinae of Hoffstetter 1955; Hoffstetter & Rage 1972), boids (Boinae of Holman 2000; Wallach *et al.* 2014), or generally with constrictors (Boinae of Rage 1984a, 1984b; Boidae of Underwood 1976; Smith & Georgalis 2022). The taxonomic allocation of multiple North American taxa to erycids has been subsequently criticized and/or rejected (Szyndlar & Rage 2003; Smith 2013; Smith & Georgalis 2022) and as a matter of fact, vertebrae of erycids can only be precisely identified only if they originate from the caudal portion of the column (Szyndlar & Georgalis 2023). Affinities of *Cheilophis* with boids could be indeed the case, but it should be noted that vertebrae of

many boids and pythonids share an overall similar vertebral morphology (see Szyndlar & Georgalis 2023) and both stem boids and stem pythonids have been identified in the European Eocene (Scanferla & Smith 2020; Zaher & Smith 2020; Georgalis *et al.* 2021b, 2025; Smith & Georgalis 2022; Smith & Scanferla 2022; Palci *et al.* 2024). The herein documented presence (even if rare, i.e., in only one specimen [the paratype NMB T.S.1101]) of paracotylar foramina in the new European taxon could possibly reject pythonoid affinities (as vertebrae of this group never possess paracotylar foramina) and support instead a possible inclusion within booids, vertebrae of which occasionally possess such foramina (see Szyndlar & Georgalis 2023). Nevertheless, although affinities with Booidea seem more likely, in the absence of more complete specimens, we still prefer to follow the opinion of Smith & Georgalis (2022) and keep *Cheilophis* as an *incertae sedis* within Constrictores.

It is now well known that several dispersals of terrestrial taxa occurred between North America and Europe, around the PETM, facilitated by global warming and the drastic palaeogeographic changes that occurred at this time period (McKenna 1975; Smith *et al.* 2006; Brikiatis 2014). Various dispersal routes have been proposed to explain this biogeographic pattern of shared vertebrate taxa among Eocene Europe and North America. Burbrink & Lawson (2007) attempted to analyze such dispersal routes among the two landmasses, mainly under the prism of snakes. According to these authors, potential pathways for these dispersal routes involved (Burbrink & Lawson 2007):

- the Thulean Bridge (i.e., Europe-British Islands-southern Greenland-Queen Elizabeth Islands), which consists of paratropical/polar broad-leaved forest, with a relatively warm climate, suitable for snakes and other reptiles;
- De Geer Bridge (i.e., Scandinavia-northern Greenland-Canadian Arctic Archipelago), which consists of para-tropical to temperate woodlands, with a cool climate, not very suitable for snakes and other reptiles;
- and Greenland-Faeroes Bridge (i.e., Greenland-Faeroes bridge [island chain connection]), which consists of paratropical/sub-tropical to temperate woodlands, with a relatively cool climate, not very suitable for snakes and other reptiles.

It is worth noting that particularly the De Geer and the Thulean routes have been proposed for the dispersals of other early Paleogene reptiles, such as crocodylians (e.g. Conedera *et al.* 2024) and lizards (Čerňanský *et al.* 2024). Furthermore, even if there was not some fully terrestrial corridor but only nearby landmasses, overwater dispersal has been well documented among snakes and has been variously used to explain molecular data (e.g. Kyriazi *et al.* 2013) and extralimital occurrences of the fossil record (e.g. Georgalis & Szyndlar 2022).

Whatever the exact dispersal route of these taxa may have been, what remains unambiguous is that multiple closely related taxa existed in both North America and Europe during the Eocene. The herein recognition of *Cheilophis periplanetes* n. sp. from the early Eocene (MP 10) of France further adds one more genus that had shared presence in both landmasses during the early Paleogene. The two type localities of the two species of *Cheilophis* appear to be more



FIG. 8. — Life reconstruction of *Cheilophis periplanetes* n. sp. Credits: Artwork by Jaime Chirinos.

or less of the same age: Cuis pertains to MP 10, i.e., bears an age of 49.86 ± 0.455 Ma (Escarguel *et al.* 1997), while the Gardner Locality is situated at the upper bed of the Huerfano Formation (Sullivan 1979), with an age of 50.3–49 Ma (Rasmussen *et al.* 2020). This almost contemporary age of both type localities affords no definite assumptions about the origin of *Cheilophis*, i.e., if the genus appeared earlier in North America and subsequently dispersed to Europe or vice versa. It should be noted though that the limited vertebral material from the late Paleocene of New Jersey that was referred to *Cheilophis huerfanoensis* by Cook & Ramsdell (1991) may hint towards an American ancestry, but of course, it still remains to be confirmed whether such taxonomic identification of the New Jersey referred material is indeed correct. Accordingly, we may tentatively assume that the ancestry of *Cheilophis* as well lies in North America.

The period (MP 10) that *Cheilophis periplanetes* n. sp. has been found seems to correspond to a time interval of relative stability without major faunal events (Solé *et al.* 2019); this period is even considered as a period of endemism in Europe (Solé *et al.* 2022). Then, the dispersal of this species may have occurred earlier, probably during the Mammal Dispersal Event (MDE) at the PETM. The geographical origin of the Eocene vertebrate taxa has been strongly discussed over the past decades and Asia may represent a good candidate for several mammal groups (e.g. Godinot & Lapparent de Broin

2003; Smith *et al.* 2006; Smith & Smith 2010; Rose *et al.* 2014; De Bast & Smith 2017), while Europe and America may be for others (e.g. De Bast & Smith 2017; Boivin *et al.* 2018). Dispersals between Europe and Africa were also not uncommon during the early Eocene (e.g. Gheerbrant *et al.* 2006; Rage & Gheerbrant 2020; see discussion in Georgalis 2021). Nevertheless, Europe would have been a stepping stone most of the time to colonize North America around the PETM dispersal events (Smith *et al.* 2006; Rose *et al.* 2014; Solé *et al.* 2015). Moreover, Europe may be considered as the center of dispersion for the large flightless birds Gastornithidae (Buffetaut & Angst 2014; Mayr *et al.* 2024), while a diversity of insects may have originated from Greenland before dispersing into Northern America and Europe (Archibald & Makarkin 2006; Archibald *et al.* 2011). Regarding reptiles, many of the terrestrial / semiaquatic taxa that are shared among the European and North American Paleogene have usually their oldest occurrences (and suggested ancestry) in North America (e.g. the large trionychid *Axestemys* Hay, 1899; Vitek & Joyce 2015 vs Georgalis & Joyce 2017), but admittedly the coeval Asian and African fossil record is rather poor to afford further biogeographic implications.

The very small size (almost half centrum length, compared to the North American congeneric species) could potentially suggest different climatic and environmental adaptations between the European and North American species. In

any case, *Cheilophis*, being represented in Europe solely by the herein described material from Cuis, seems not to have survived for long in Europe. Indeed, its absence from all younger Eocene localities from Europe and elsewhere may indicate that the genus made it only for a brief period in Europe and eventually became extinct. As a matter of fact, Cuis coincides with the Early Eocene Climatic Optimum (EECO), which represents along with the PETM the highest temperatures for the last 65 Ma. Accordingly, this might explain why some “tropical” taxa and “newcomers” could not make it very long after that time in Europe.

The new material from Cuis further adds to the, so far limited, fossil record of snakes from the early Eocene of Europe. During this time interval, snake faunas in Europe are mainly represented by palaeophiids and to a lesser degree by constrictors, russellophiids, nigerophiids, archaeophiids, anomalophiids, scolecophidians, plus some alethinophidians of uncertain affinities (Smith & Georgalis 2022). As a matter of fact, early Eocene snake fossil remains from Europe have only been formally described from the Belgian localities of Dormaal, Quenast, Egem, Nederokkerzeel, and Woluwé Saint-Étienne in Van Pachtenbeke, the Danish locality of Isle of Fur, the French localities of Condé-en-Brie, La Borie, Grauves, Prémontéré, Cuise-la-Motte, and Cos, the German locality of Katharinenhof, the Italian locality of Monte Bolca, the Portuguese locality of Silveirinha, the English localities of Kingston, Isle of Sheppey, Bracklesham, and the Ukrainian locality of Sbornaya (for details and references see Smith & Georgalis 2022; see also Čerňanský *et al.* 2025). The majority of these localities yielded only palaeophiid remains, but a few continental localities (e.g. Dormaal, Condé-en-Brie, Grauves, Prémontéré, Cos, Silveirinha) yielded also some non-aquatic taxa. To these localities and taxa, we now add Cuis and the new constrictor *Cheilophis periplanetes* n. sp. (Fig. 8), which provide interesting insights into the fascinating, but still obscure, biogeography and evolution of early Eocene snakes from Europe.

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Availability of materials and data

All fossil specimens described herein are permanently curated at the collections of the Naturhistorisches Museum Basel, Switzerland. 3D surface model reconstructions (.PLY files) of the holotype and paratype specimens of *Cheilophis periplanetes* n. sp. are openly available in the online repository Morphosource (<https://www.morphosource.org/>): holotype trunk vertebra NMB T.S.1100 (Morphosource.org: Media 000741028 [ark:/87602/m4/741028]); paratype trunk vertebra NMB T.S.1101 (Morphosource.org: Media 000741048 [ark:/87602/m4/741048]).

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