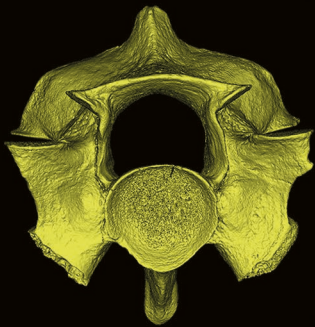


A new peculiar early diverging caenophidian snake (Serpentes) from the late Eocene of Hordle Cliff, England

Georgios L. GEORGALIS & Marc E. H. JONES



SNAKES FROM THE CENOZOIC OF EUROPE

– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

Edited by Georgios L. GEORGALIS, Hussam ZAHER & Michel LAURIN

DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :

Gilles Bloch, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF (*, took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article) :

Michel Laurin* (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR : Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT : Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS : Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS :

Micropaléontologie/*Micropalaeontology*

Lorenzo Consorti (Institute of Marine Sciences, Italian National Research Council, Trieste)

Paléobotanique/*Palaeobotany*

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Anais Boura (Sorbonne Université, Paris)

Métazoaires/*Metazoa*

Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléoichthyologie/*Palaeoichthyology*

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/*Mesozoic amniotes*

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/*Turtles*

Walter Joyce (Universität Freiburg, Switzerland)

Lépidosauromorphes/*Lepidosauromorphs*

Hussam Zaher (Universidade de São Paulo)

Oiseaux/*Birds*

Jingmai O'Connor (Field Museum, Chicago)

Paléomammalogie (mammifères de moyenne et grande taille)/*Palaeomammalogy (large and mid-sized mammals)*

Grégoire Métais (CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, Paris)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/*Palaeomammalogy (small mammals except for Euarchontoglires)*

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/*Palaeomammalogy (Euarchontoglires)*

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/*Palaeoanthropology*

Aurélien Mounier (CNRS/Muséum national d'Histoire naturelle, Paris)

Archéologie préhistorique (Paléolithique et Mésolithique)/*Prehistoric archaeology (Palaeolithic and Mesolithic)*

Nicolas Teyssandier (CNRS/Université de Toulouse, Toulouse)

Archéologie préhistorique (Néolithique et âge du bronze)/*Prehistoric archaeology (Neolithic and Bronze Age)*

Marc Vander Linden (Bournemouth University, Bournemouth)

RÉFÉRÉS / REVIEWERS : <https://sciencepress.mnhn.fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER :

Made from the Figures of the article.

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol* is indexed by:

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /
Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on:

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*

Adansonía, Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie*.

L'Académie des sciences publie aussi / *The Académie des sciences also publishes:*

Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)

ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

A new peculiar early diverging caenophidian snake (Serpentes) from the late Eocene of Hordle Cliff, England

Georgios L. GEORGALIS

Institute of Systematics and Evolution of Animals,
Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków (Poland)
georgalis@isez.pan.krakow.pl (corresponding author)

Marc E. H. JONES

Science Group: Fossil Reptiles, Amphibians and Birds Section,
Natural History Museum, Cromwell Road, SW7 5BD London (United Kingdom)

Submitted on 4 December 2024 | Accepted on 9 August 2025 | Published on 7 November 2025

[urn:lsid:zoobank.org:pub:182D1817-2CD6-4289-B9DA-7144AEC882DD](https://zoobank.org/pub:182D1817-2CD6-4289-B9DA-7144AEC882DD)

Georgalis G. L. & Jones M. E. H. 2025. — A new peculiar early diverging caenophidian snake (Serpentes) from the late Eocene of Hordle Cliff, England, 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 (25): 505–530. <https://doi.org/10.5852/cr-palevol2025v24a25>

ABSTRACT

We here describe a new genus and species of snake, based on several trunk and caudal vertebrae, originating from the late Eocene (MP 17a) of Hordle Cliff, England. We investigated the fossil material via both visual microscopy and micro-computed tomography (μCT) scanning, focused on its intracolumnar variation, and extensively compared it with other Paleogene snake taxa from England and continental Europe. The new small taxon is characterized by an array of bizarre and distinctive vertebral features that can differentiate it from all other snakes. Its morphology is similar to that of russellophiids; however, some anatomical features differ drastically from those observed in the latter group and therefore, defy such family-level placement. In addition, the new English taxon bears some striking resemblance with extant acrochordids, particularly with the species *Acrochordus granulatus* (Schneider, 1799). Accordingly, we consider that the new taxon most likely represents an early diverging caenophidian, potentially being even a member of Acrochordidae Bonaparte, 1831, far outside the so far known stratigraphic and geographic distribution of the latter group. It further adds to the astonishing diversity of vertebral morphologies of European Paleogene snakes.

KEY WORDS
Squamata,
Caenophidia,
Russellophiidae,
Acrochordidae,
vertebral morphology,
new genus,
new species.

RÉSUMÉ

Un nouveau serpent caenophidien (Serpentes) particulier à divergence précoce de la fin de l'Éocène de Hordle Cliff, Angleterre.

Nous décrivons ici un nouveau genre et une nouvelle espèce de serpents, basés sur plusieurs vertèbres troncales et caudales, originaires de la fin de l'Éocène (MP 17a) de Hordle Cliff, en Angleterre. Nous avons étudié le matériel fossile à la fois par microscopie visuelle et par tomographie à microscopie (μCT), en nous concentrant sur sa variation intracolonnaire et en le comparant de manière approfondie à d'autres taxons de serpents du Paléogène d'Angleterre et d'Europe continentale. Le nouveau petit taxon est caractérisé par un ensemble de caractéristiques vertébrales bizarres et distinctives qui peuvent le différencier de tous les autres serpents. Sa morphologie se rapproche quelque peu de celle des russellophiidés, cependant, certaines de ses caractéristiques anatomiques sont radicalement différentes de celles observées dans ce dernier groupe et défient donc un tel placement au niveau de la

MOTS CLÉS
Squamata,
Caenophidia,
Russellophiidae,
Acrochordidae,
morphologie vertébrale,
genre nouveau,
espèce nouvelle.

famille. De plus, le nouveau taxon anglais présente une ressemblance frappante avec les acrochordidés existants, particulièrement avec l'espèce *Acrochordus granulatus* (Schneider, 1799). En conséquence, nous considérons que le nouveau taxon représente très probablement un caenophidien divergent précoce, pouvant même être un membre des Acrochordidae Bonaparte, 1831, bien en dehors de la distribution stratigraphique et géographique connue jusqu'à présent de ce dernier groupe. Il ajoute en outre à l'étonnante diversité des morphologies vertébrales des serpents européens du Paléogène.

INTRODUCTION

Snakes from the Eocene of England have been known for almost two centuries. They comprise some of the earliest important finds in the history of palaeophidology, described by one of the most prominent palaeontologists and anatomists of the time, Sir Richard Owen. Indeed, the early Eocene of England yielded the first remains of the iconic giant snake *Palaeophis* Owen, 1841 (see Owen 1841, 1850), whereas the late Eocene of Hordle Cliff, yielded the first fossil constrictor snake to be described, *Paleryx* Owen, 1850 (see Owen 1850). Since then, Eocene English fossil snakes have been the focus of several studies, including the description of new material, the establishment of new taxa, and/or the redocumentation of important species that were named in the 19th century (Lydekker 1888a, b; Rage & Ford 1980; Holman 1993, 1996; Holman & Harrison 1998a, b; Holman *et al.* 2006; Georgalis *et al.* 2021b).

Here we describe a new genus and species of a very peculiar, small snake from the late Eocene of Hordle Cliff. This material was briefly mentioned and discussed for a couple of sentences (but not figured) in Milner *et al.* (1982) as “Caenophidian 2”. It was noted to have some general resemblance with the genus *Russellophis* Rage, 1975, which back then was known only from early Eocene of France. We conduct a detailed anatomical documentation of the material and provide extensive comparisons with other coeval snakes from Europe.

MATERIAL AND METHODS

All fossil specimens of the new taxon, described here, are permanently curated at the collections of the Natural History Museum, London (NHMUK). All specimens of the new taxon were collected by Roy Gardner in 1981. He collected matrix and processed it using screen washing techniques and most microvertebrate remains were separated using sieves with a 1 mm mesh.

Digital models were made for five of the specimens: NHMUK PV R 10795 (holotype); NHMUK PV R 10796; NHMUK PV R 10797; NHMUK PV R 10798 (paratype); NHMUK PV R 38946. These models were made at the Natural History Museum UK using X-ray micro-Computed Tomography with the Zeiss Xradia 520 Versa. Specimens were packed individually in small plastic tubes and scanned separately. Settings comprised 140 kV and 72 µA, exposure 3 ms, to produce TIFF

slices with a voxel size of 0.00447 × 0.00447 × 0.00447 mm. The TIFFs stacks were then opened as volumes in Avizo 3D 2021.2 (Thermo Fisher Scientific, Waltham, Massachusetts, United States). The volumes were cropped before segmentation. Segmentation initially involved selecting a threshold which closely represented the external surface of the bone. Manual segmentation tools (e.g. lasso, draw) were then used to remove remaining matrix. Typically, every other slide was segmented and the selection was interpolated. For each bone two surface files were made: to document the segmentation a surface file was made with Smoothing set to none; for the figures a surface file was made with Smoothing set to Unconstrained smoothing. These bone surface files were exported as a Stanford PLY. All these models are available at the online repository of Morphosource: <https://www.morphosource.org/projects/000658862>.

Taxonomy follows Smith & Georgalis (2022). Anatomical terminology follows Georgalis *et al.* (2021b), Head (2021), and Szyndlar & Georgalis (2023).

INSTITUTIONAL ABBREVIATIONS

ISEA	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków;
MNHN	Muséum national d'Histoire naturelle, Paris;
MSUVP	Michigan State University Museum of Vertebrate Paleontology, East Lansing, Michigan;
NHMUK	Natural History Museum, London.

LOCALITY

Hordle (also known in the older literature as Hordwell) Cliff is a locality of the Headon Hill Formation, in southern England (Edwards & Daley 1997). Besides snakes, among reptiles, the locality has yielded a diverse assemblage of turtles, crocodylians, and lizards (Owen & Bell 1849; Huxley 1859; Seeley 1876; Lydekker 1887, 1888a, b, 1889; Hooley 1905; Milner *et al.* 1982; Benton & Spencer 1995; Klembara & Green 2010; Georgalis & Joyce 2017). The locality is particularly known for its rich and considerably diverse mammal fauna (e.g. Hooker *et al.* 2005; Hooker & Harrison 2008). More precisely, the material described herein, as well as all fossil specimens collected by Roy Gardner (from Fareham, Hampshire) in the 1980's originates from the Mammal Bed, which is the same site that yielded also some of the material collected by the Marchioness of Hastings during the 19th century (see Milner *et al.* 1982; Benton & Spencer



FIG. 1. — Holotype trunk vertebra NHMUK PV R 10795 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views. Scale bar: 1 mm.

1995). The exact spot where the new snake taxon was found is in Christchurch Bay, on the Hampshire coast, in the stretch of the Hordle Cliff, between Becton Bunny in the west and Long Mead End in the east (see Milner *et al.* 1982). The age of the Mammal Bed locality of Hordle Cliff correspond to the MP 17a zone, i.e., with an age of approximately 36.91 ± 0.326 Ma (Biochrom'97 1997; Escarguel *et al.* 1997). For more information on the geology of the locality, see Milner *et al.* (1982) and Edwards & Daley (1997).

SYSTEMATIC PALAEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
CAENOPHIDIA Hoffstetter, 1939

Paradoxophidion n. gen.

[urn:lsid:zoobank.org:act:447C8D95-2A3D-4A4A-A41C-D068C458797A](https://doi.org/10.1017/S0022272022000000)

TYPE SPECIES. — *Paradoxophidion richardoweni* n. gen., n. sp.

DIAGNOSIS. — As for the type and only known species.

ETYMOLOGY. — The new genus name derives from the Greek words “παράδοξος” (“paradoxos”) meaning “paradox”/“weird”, and “ὄφιδιον” (“ophidion”) meaning “snake”, in referral of the weird combination of vertebral features present in the new taxon. Gender of the new genus name is neuter.

Paradoxophidion richardoweni n. gen., n. sp.
(Figs 1-14; Appendices 1; 2)

[urn:lsid:zoobank.org:act:DF7D9EEA-52E4-4E8E-8DFC-AC001D0D2E64](https://doi.org/10.1017/S0022272022000000)

TYPE MATERIAL. — **Holotype. England** • 1 specimen (a trunk vertebra); Christchurch Bay, Hordle Cliff; Headon Hill Formation; 36.91 ± 0.326 Ma; MP 17, Priabonian (late Eocene); NHMUK PV R 10795 (Figs 1; 2).

Paratype. England • 1 specimen (a trunk vertebra); Christchurch Bay, Hordle Cliff; Headon Hill Formation; 36.91 ± 0.326 Ma; MP 17, Priabonian (late Eocene); NHMUK PV R 10798 (Figs 3; 4).

REFERRED SPECIMENS. — 18 trunk vertebrae (NHMUK PV R 10792, NHMUK PV R 10794, NHMUK PV R 10797, NHMUK PV R 38879, NHMUK PV R 38942, NHMUK PV R 38943,

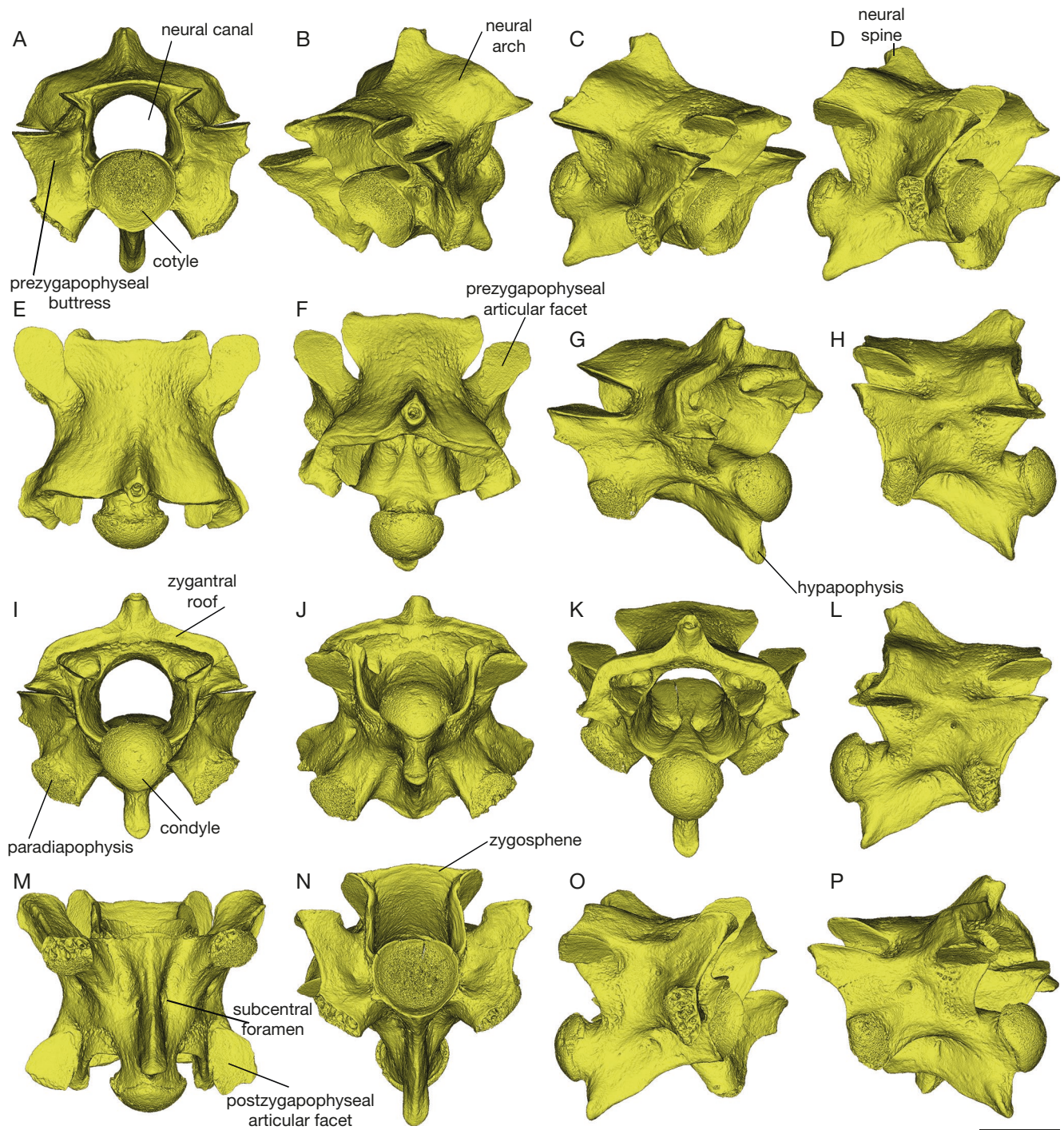


FIG. 2. — 3D μ CT images of holotype trunk vertebra NHMUK PV R 10795 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), left anterodorsolateral (B), right anterodorsolateral (C), right ventrolateral (D), dorsal (E), posterodorsal (F), left posterolateral (G), left lateral (H), posterior (I), posteroventral (J), posterodorsal (K), right lateral (L), ventral (M), anteroventral (N), right ventrolateral (O), and left posterolateral (P) views. Scale bar: 1 mm.

NHMUK PV R 38944, NHMUK PV R 38945, NHMUK PV R 38946, NHMUK PV R 38950, NHMUK PV R 38952–NHMUK PV R 38954, and NHMUK PV R 38956–NHMUK PV R 38960), two ?cloacal vertebrae (NHMUK PV R 38947 and NHMUK PV R 38948), and nine caudal vertebrae (NHMUK PV R 10791, NHMUK PV R 10793, NHMUK PV R 10796, NHMUK PV R 10799, NHMUK PV R 10800, NHMUK PV R 38941, NHMUK PV R 38949, NHMUK PV R 38951, and NHMUK PV R 38955).

TYPE LOCALITY AND AGE. — All specimens originate from the locality of Christchurch Bay at Hordle Cliff, Hampshire, England; Mammal Bed, Totland Bay Member, MP 17 (approximately 36.91 ± 0.326 Ma), late Eocene.

GEOGRAPHIC AND STRATIGRAPHIC RANGE. — Taxon known exclusively from the type locality.

DIAGNOSIS. — *Paradoxophidion richardoweni* n. gen., n. sp. is unique among all snakes in possessing the following characters:

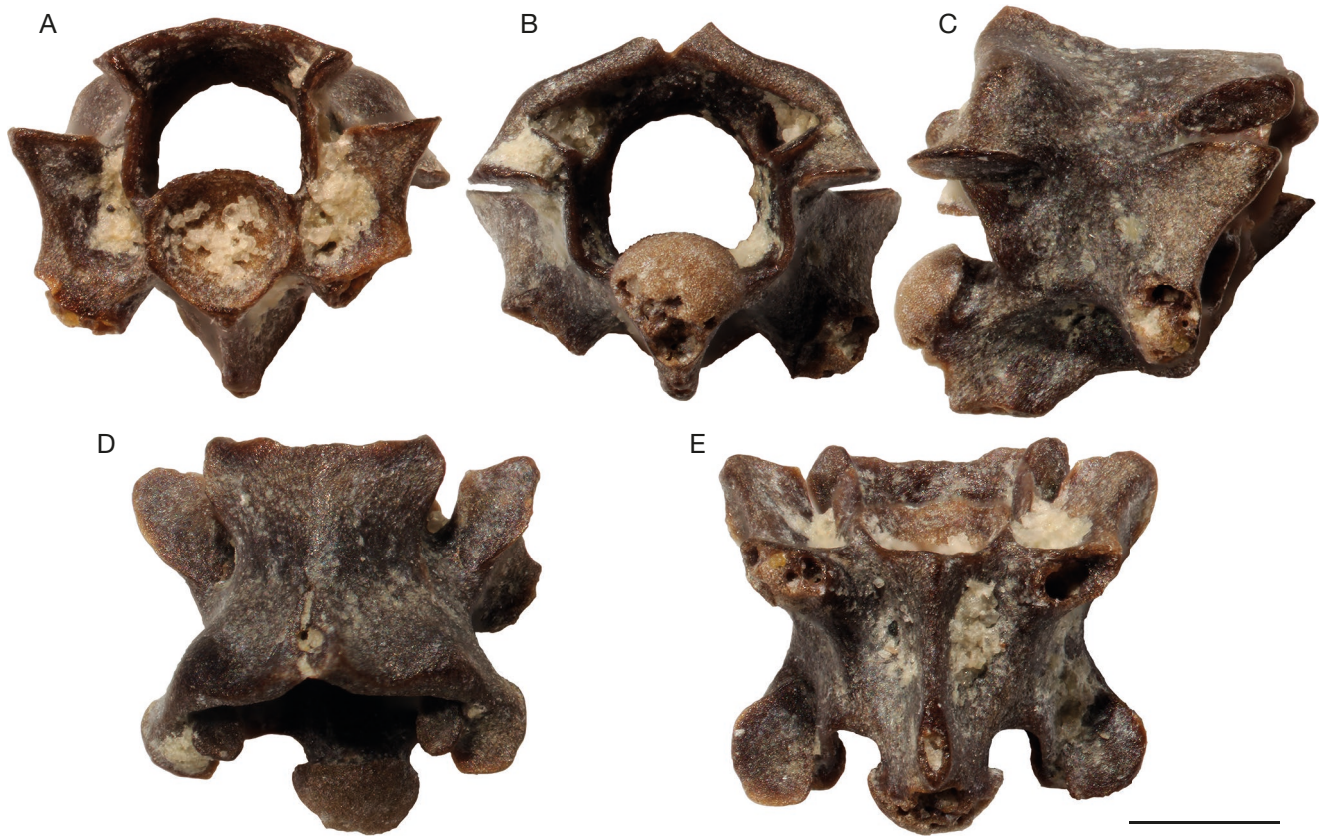


FIG. 3. — Paratype trunk vertebra NHMUK PV R 10798 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), posterior (B), right lateral (C), dorsal (D), and ventral (E) views. Scale bar: 1 mm.

hypapophysis with a triangular shape in lateral view; vaulted neural arch with a peculiar dome-shaped arching; thick and transversely expanded zygantral roof (i.e., “thickened posterior margin of the neural arch” *sensu* Head 2021); and the contact of the paradiapophyses with the lateral margins of cotyle well dorsal to the level of its ventral margin. *Paradoxophidion richardoweni* n. gen., n. sp. can be further differentiated from all other snakes by the following combination of features: small vertebral size, with centrum length (CL) ranging around 2 mm; moderately (dorsoventrally) short neural spine that is almost strictly confined to the posteriormost portion of the neural arch; presence of hypapophysis across all trunk vertebrae, that is prominent and much ventrally expanded in lateral view and narrow in ventral view; presence of prominent prezygapophyseal buttresses that are compressed and form a more or less vertical ridge; presence of a small, pterapophysis-like, tubercle on each side of the neural arch; paradiapophyses not clearly divided into diapophyses and parapophyses; paradiapophyses facing ventrally in anterior view and reaching below the ventral level of the cotyle; absence of paracotylar foramina; very small and circular cotyle and condyle; absence of paracotylar ventrolateral processes; occasional presence of a short median ventral process/tubercle in the ventral margin of the cotyle; zygosphenes very thin and always larger than the cotyle; very large neural canal; absence of parazygosphenal foramina; caudal vertebrae with elongated and slender pleurapophyses; anterior caudal vertebrae with a haemal keel; and mid-caudal and posterior caudal vertebrae with paired haemapophyses. For detailed comparisons with other snakes, see Discussion below.

ETYMOLOGY. — The new species name honours Sir Richard Owen (1804–1892), one of the greatest palaeontologists and comparative anatomists of all time. Richard Owen was the first to describe

fossil remains of snakes from Hordle Cliff, as well as one of the first researchers that provided a thorough documentation of the snake vertebral column, focusing on its anatomical structures and the intracolumnar variation. Richard Owen was also the founder of the Natural History Museum in London (1881), where all known specimens of the new taxon are permanently curated. The name also alludes to the Richard Owen Fund of the Palaeontographical Society that was awarded to the first author (GLG) in 2023 and enabled him to study the fossil specimens of this new taxon at NHMUK.

DESCRIPTION

Holotype (NHMUK PV R 10795)

The holotype trunk vertebra NHMUK PV R 10795 of *Paradoxophidion richardoweni* n. gen., n. sp. is practically complete, with only some erosion observed in its right paradiapophysis and (perhaps also) the dorsalmost part of the neural spine (Figs 1; 2; Appendix 1). In anterior view (Figs 1A; 2A), the zygosphenes are very thin and are much wider than the cotyle. The dorsal roof of the zygosphenes is slightly convex. The neural canal is very large. The prezygapophyses are only slightly dorsally inclined. Prominent prezygapophyseal buttresses are present, forming a somewhat vertical ridge; these commence dorsally from the level of the prezygapophyses and terminating ventrally towards the level of the paradiapophyses. The cotyle is very small and circular. There are no paracotylar foramina. There are no paracotylar ventrolateral processes. The paradiapophyses

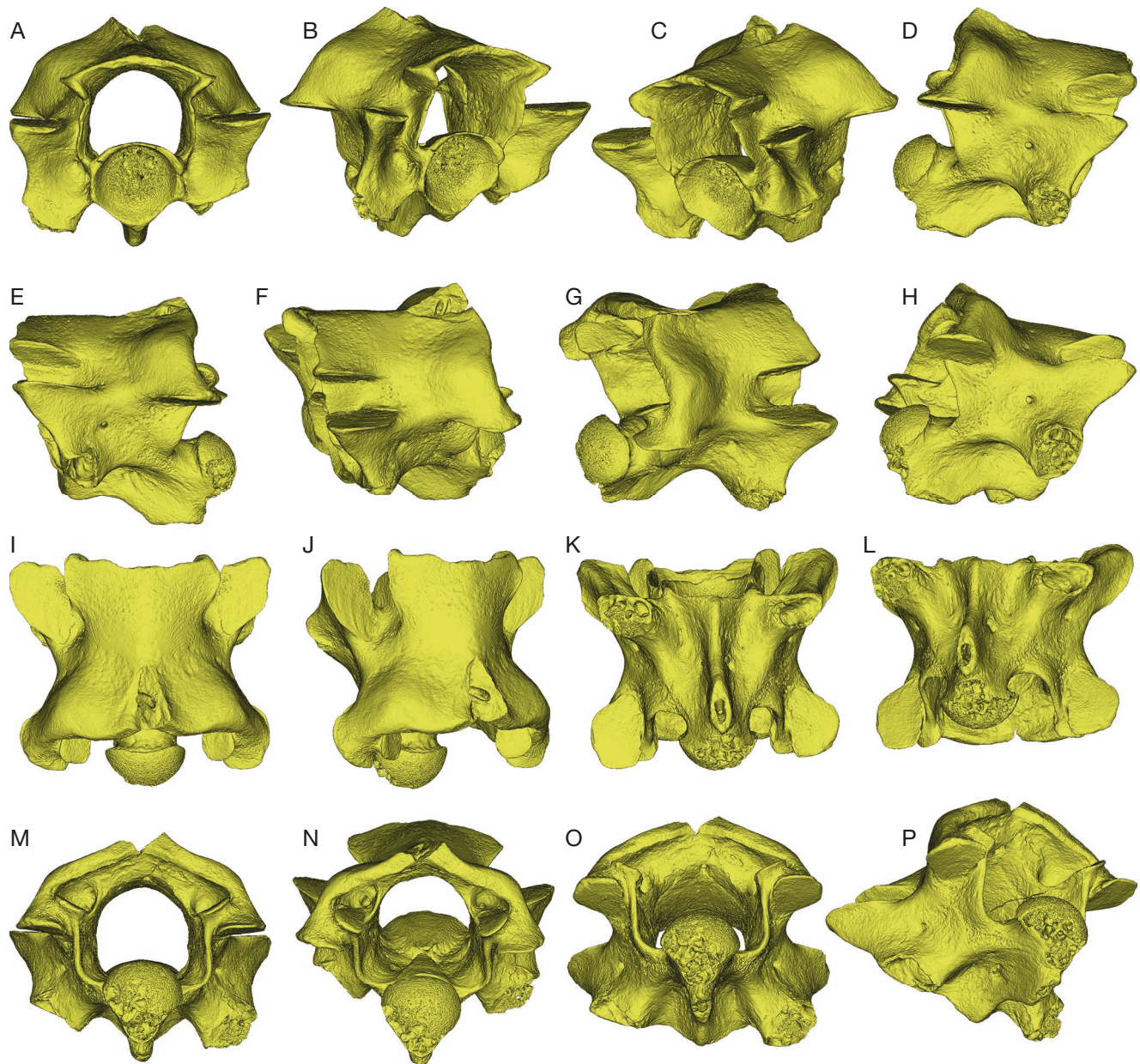


FIG. 4. — 3D μ CT images of paratype trunk vertebra NHMUK PV R 10798 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), right anterolateral (B), left anterolateral (C), right lateral (D), left lateral (E), left anterolateral (F), right posterodorsolateral (G), right posteroventrolateral (H), dorsal (I), left dorsolateral (J), ventral (K), left ventrolateral (L), posterior (M), posterodorsal (N), posteroventral (O), and left posteroventrolateral (P) views. Scale bar: 1 mm.

are distinct from the centrum and extend ventrally, below the level of the ventral lip of the cotyle; the paradiapophyses contact the lateral margins of the cotyle well above the level of its ventral margin. The hypapophysis is relatively thick and is very elongated, extending much ventrally. In posterior view (Figs 1B; 2I), the zygantral roof is very thick (i.e., “thickened posterior margin of the neural arch” *sensu* Head 2021). The neural arch is moderately vaulted, with a vaulting ratio (*sensu* Georgalis *et al.* 2021b) equal to 0.42, and possesses a peculiar dome-shaped arching. The condyle is small and circular. The paradiapophyses (only the left one is almost complete, with a slight breakage in its parapophyseal surface; the right one is eroded), are massive and they

seem not to be divided into diapophyseal and parapophyseal portions. In dorsal view (Figs 1D; 2E), the base of the neural spine is strictly confined to the posterior half of the neural arch. The zygosphenes possess two distinct lateral lobes. The prezygapophyses are small, slightly extending anterolaterally. The prezygapophyseal articular facets are relatively small and oval. The interzygapophyseal constriction is moderately deep. A posterior median notch of the neural arch is almost absent. In ventral view (Figs 1E; 2M), the centrum is slightly wider than long ($CL/NAW = 0.95$). The hypapophysis extends across most of the midline of the centrum, commencing anteriorly from the base of the cotyle and terminating posteriorly well before the condyle.



FIG. 5. — Trunk vertebra NHMUK PV R 38946 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views. Scale bar: 1 mm.

The condyle is situated in a distinct condylar neck. The sub-central grooves are deep. The postzygapophyses are moderately large and somewhat triangular. There are no prezygapophyseal accessory processes, however, small, russellophiid-like spines are present below the prezygapophyseal articular facets. In lateral view (Figs 1C; 2H, L), the neural spine is relatively dorsoventrally short, while it is slender and anteroposteriorly relatively short; it abruptly commences augmenting in height in the posterior half of the centrum and is much posteriorly inclined. A small, pterapophysis-like, tubercle is present posteriorly on each side of the neural arch. A large lateral foramen is situated below the interzygapophyseal ridges. The subcentral ridges are strongly convex. The hypapophysis is large and almost triangular; it commences anteriorly from the tip of the cotyle but it is mostly developed towards the posterior half of the centrum, where it becomes prominent and extends rather ventrally.

Paratype and referred specimens – intracolumnar variation

All available trunk vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp. are rather small, with CL ranging around 2 mm or even less (Figs 3–9). The paratype (NHMUK PV R 10798; Figs 3; 4) and all referred specimens share with the holotype a rather similar vertebral morphology, though some differences can be observed, which can be attributed

to intracolumnar variation. The centrum is anteroposteriorly short and relatively wide in all trunk vertebrae. Among them, notably, NHMUK PV R 38943 (Fig. 8K–O) is rather anteroposteriorly short and laterally wide, i.e., wider than every other available vertebra of the species ($CL/NAW = 0.77$). This shape is probably due to intracolumnar variation, as this vertebra (NHMUK PV R 38943) is also characterized by a much vaulted neural arch (vaulting ratio *sensu* Georgalis *et al.* 2021b equal to 0.48). Still though, even this vertebra has a prominent hypapophysis, while all other distinctive features (e.g. shape and thickness of the zygantrum, paradiapophyses being distinct from the centrum and ventrally expanded, posterior confinement and size of the neural spine) perfectly match the morphology of the remaining vertebrae. The zygosphenes in trunk vertebrae most usually possess two (more or less) distinct lateral lobes and no median lobe in dorsal view, while in anterior view, it is slender and slightly arched (e.g. NHMUK PV R 38944 [Fig. 9A, D] and the holotype [NHMUK PV R 10795; Figs 1A, D; 2A, E]) to very arched (e.g. NHMUK PV R 38942 [Fig. 8F], NHMUK PV R 38943 [Fig. 8K]). Nevertheless, there are cases, where a median lobe is present and the lateral lobes are incipient (NHMUK PV R 10797; Figs 7E; 8D). Although prezygapophyseal accessory processes are absent in other specimens, tall, blade-like

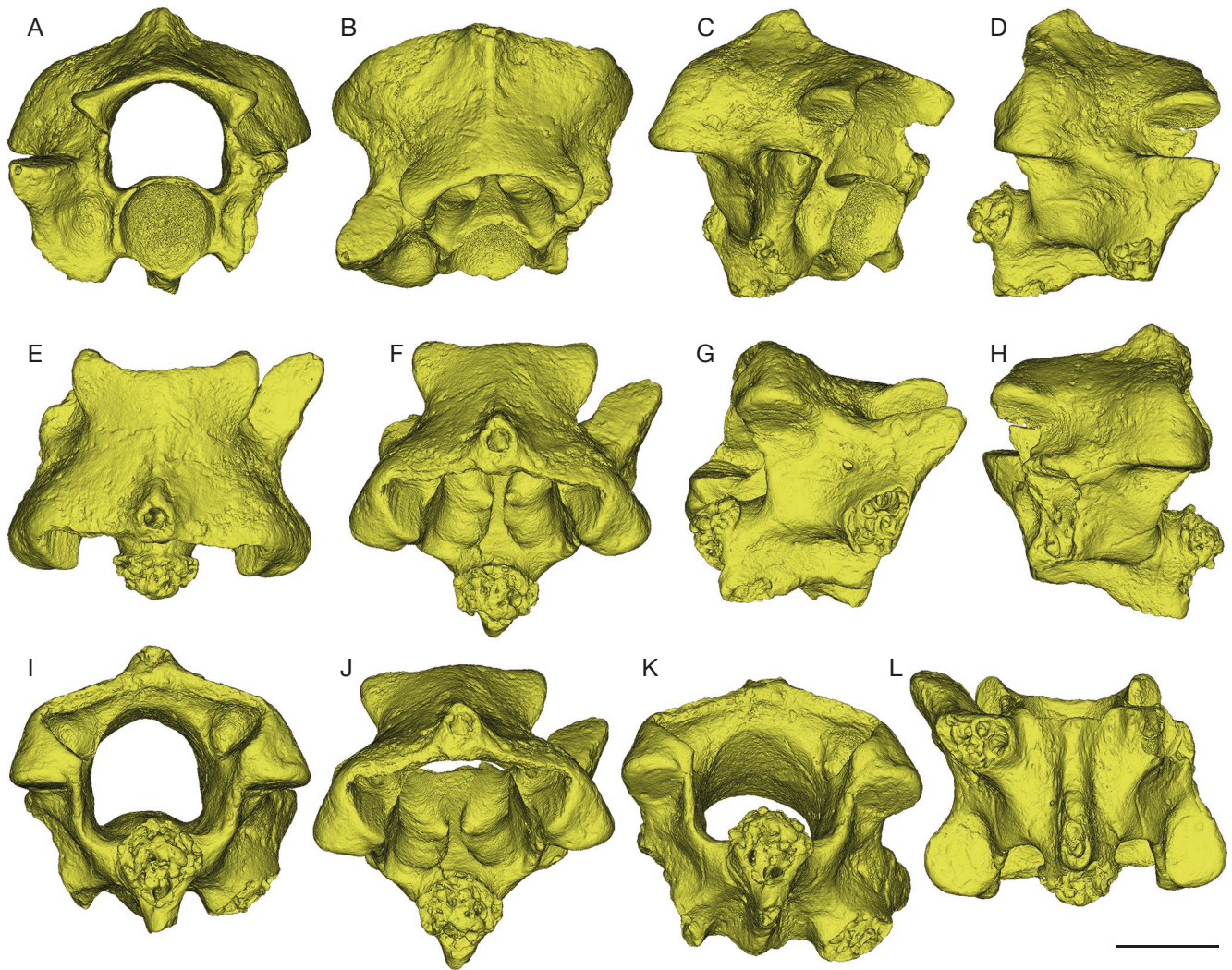


FIG. 6. — 3D μ CT images of trunk vertebra NHMUK PV R 38946 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), anterodorsal (B), right anterolateral (C), right lateral (D), dorsal (E), posterodorsal (F), right ventrolateral (G), left lateral (H), posterior (I), posterodorsal (J), posteroventral (K), and ventral (L) views. Scale bar: 1 mm.

processes extending anterolaterally beyond the margins of the prezygapophyseal articular facets are clearly visible in NHMUK PV R 10797 (Figs 7; 8D-E). Like in the holotype, all vertebrae possess, on each side of the neural arch, a small, pterapophysis-like, tubercle. The posterior median notch of the neural arch is either absent or (at maximum) rather shallow. Lateral foramina are present. Subcentral foramina are variably present across trunk vertebrae: usually a single one on the left side of the hypapophysis; however, there are cases that these are doubled, i.e., one across each side of the hypapophysis (NHMUK PV R 38950; Fig. 9J). The zygantal roof is thickened in all vertebrae, giving a dome-shaped appearance. Interestingly, paracotylar ventrolateral processes (a plesiomorphy for alethinophidian snakes) are absent in all specimens of the new taxon. The paradiapophyses are prominent, much ventrally expanded, and seem not to be divided into diapophyses and parapophyses (like in *Russellophis* but unlike caenophidians). The prezygapophyseal buttresses are prominent in all vertebrae.

Some variation is also observed in the neural spine across trunk vertebrae. This structure is strictly confined in the posteriormost portion of the neural arch in all specimens. The dorsoventral height of the neural spine slightly varies: it is mostly short and usually somehow posteriorly inclined.

The most important variation though regards the shape, size, and direction of the hypapophysis, which differs across trunk vertebrae. The hypapophysis can be rather broad and prominent in some trunk vertebrae. Such broad hypapophysis (in lateral view) is observed in the holotype (NHMUK PV R 10795; Figs 1C; 2H, L), the paratype (NHMUK PV R 10798; Figs 3C; 4D, E), and the referred vertebra NHMUK PV R 38946 (Figs 5C; 6D, H). In contrast, vertebrae NHMUK PV R 10792, NHMUK PV R 38944 (Fig. 9C), NHMUK PV R 38950 (Fig. 9H), and NHMUK PV R 10792 (Fig. 9M) have a more slender and somehow acute hypapophysis (in lateral view). In some trunk vertebrae, the hypapophysis is shorter in lateral view, with its posterior edge slightly dorsoventrally high (e.g. NHMUK PV R 10797 [Figs 7D; 8C]).

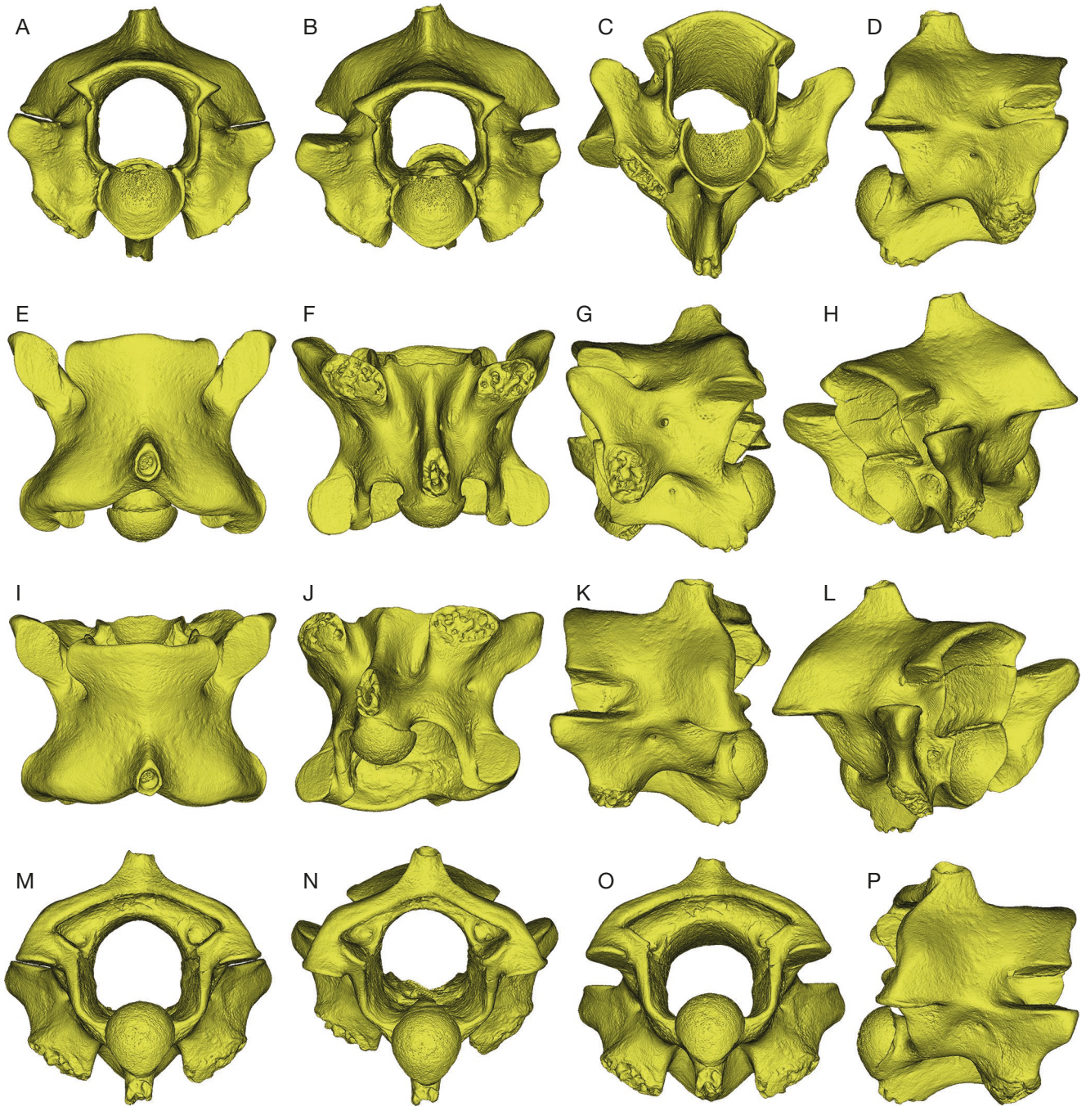


FIG. 7. — 3D μ CT images of trunk vertebra NHMUK PV R 10797 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), anterodorsal (B), anteroventral (C), right lateral (D), dorsal (E), ventral (F), left ventrolateral (G), left anterolateral (H), anterodorsal (I), posteroventrolateral (J), left dorsolateral (K), right anterolateral (L), posterior (M), posterodorsal (N), posteroventral (O), and right dorsolateral (P) views. Scale bar: 1 mm.

It is difficult to assess the intracolumnar position of the available trunk vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp. This is particularly the case for the specimens with very broad hypapophyses (NHMUK PV R 10795 [holotype; Figs 1; 2], NHMUK PV R 10798 [paratype; Figs 3; 4], and NHMUK PV R 38946 [Fig. 5]). NHMUK PV R 38942 is probably an anterior trunk vertebra, due to the fact that its neural arch is more vaulted (vaulting ratio *sensu* Georgalis *et al.* 2021b equal to 0.54) and the hypapophysis is thinner in

lateral view, seeming more posteroventrally directed (Fig. 8F-J). Finally, NHMUK PV R 38945 seems to represent the anteriormost available vertebra, as it can be attested by its very slender, long, and posteroventrally directed hypapophysis, the vaulted neural arch, and the tiny prezygapophyseal articular facets – this specimen also has the thinnest zygantral roof.

NHMUK PV R 38947 (Fig. 10A-E) and NHMUK PV R 38948 (Fig. 10F-J) likely represent cloacal vertebrae. These are wider and anteroposteriorly shorter than trunk



FIG. 8. — Trunk vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp.: A–E, NHMUK PV R 10797 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views; F–J, NHMUK PV R 38942 in anterior (F), posterior (G), right lateral (H), dorsal (I), and ventral (J) views; K–O, NHMUK PV R 38943 in anterior (K), posterior (L), right lateral (M), dorsal (N), and ventral (O) views. Scale bars: 1 mm.

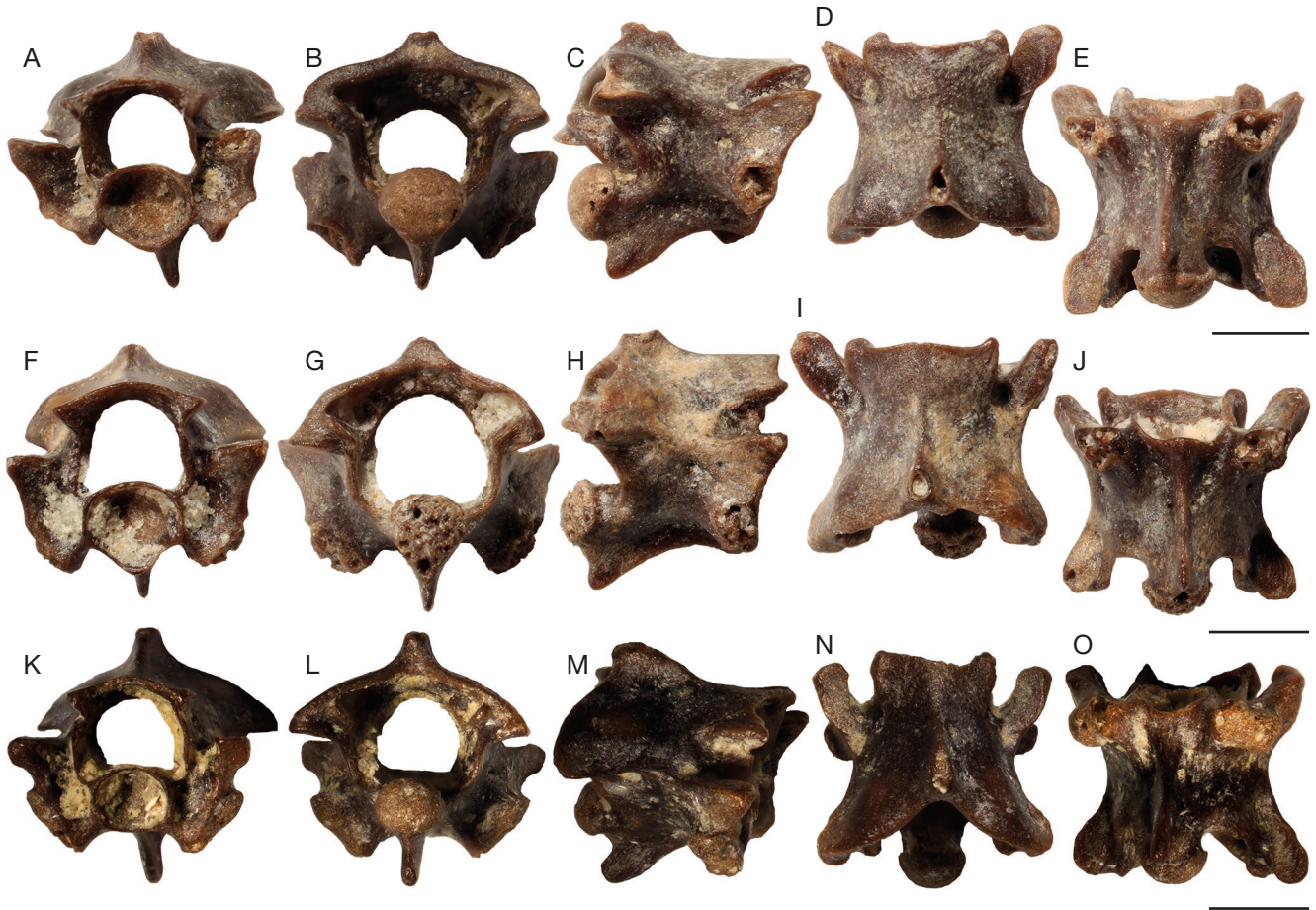


FIG. 9. — Trunk vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp.: A–E, NHMUK PV R 38944 in anterior (A), posterior (B), right lateral (C), dorsal (D), and ventral (E) views; F–J, NHMUK PV R 38950 in anterior (F), posterior (G), right lateral (H), dorsal (I), and ventral (J) views; K–O, NHMUK PV R 10792 in anterior (K), posterior (L), right lateral (M), dorsal (N), and ventral (O) views. Scale bars: 1 mm.

vertebrae, a pattern particularly observed in NHMUK PV R 38947 (Fig. 10E). These vertebrae are characterized by the presence of lymphapophyses instead of paradiapophyses. They both preserve the bases of the dorsal and ventral lymphapophyseal processes, which are separated by a wide and somehow concave arc. These structures are better preserved in NHMUK PV R 38947, in which, apart from the bases, there also remain portions of the left lymphapophyseal processes (Fig. 10A, B). There are no lymphapophyseal foramina among the lymphapophyses. The neural spine in NHMUK PV R 38948 (Fig. 10H) is dorsoventrally shorter and anteroposteriorly longer than the preceding trunk vertebrae, with its base crossing around half of the midline of the neural arch. Both cloacal vertebrae have hypapophyses. The hypapophysis extends across the whole midline of the centrum in ventral view.

Nine caudal vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp. are available in our sample. NHMUK PV R 10796 (Figs 11; 12; Appendix 2), NHMUK PV R 10799 (Fig. 13A–E), and NHMUK PV R 10793 (Fig. 13M–Q) are anterior caudal vertebrae. This is most probably the case also for NHMUK PV R 10791 (Fig. 13K–L), NHMUK PV R 10800 (Fig. 13F–J) and NHMUK PV R 38951 (Fig. 13R–

U), though we cannot exclude that they could alternatively represent instead posteriormost trunk or cloacal vertebrae. Almost all of these vertebrae are wider compared to the trunk vertebrae described above. These are characterized by the presence of a short hypapophysis/haemal keel, instead of paired haemapophyses; such hypapophysis/haemal keel is relatively sharp and thin in ventral view, while it is dorsoventrally rather short in lateral view. The pleurapophyses are incomplete in all specimens, with the exception of NHMUK PV R 10796, where the right pleurapophysis is complete, being very elongated and slender (Figs 10; 11) and, to a lesser degree, NHMUK PV R 10793, which preserves part of the left pleurapophysis (Fig. 13M, N). Unlike trunk vertebrae, where subcentral foramina are usually small to medium-sized, in certain anterior caudal vertebrae, these are considerably large (e.g. NHMUK PV R 10791 [Fig. 13K]; NHMUK PV R 10796 [Figs 11E; 12D, N]). Notably, in three specimens of the new taxon, the anterior caudal vertebra NHMUK PV R 10791 (Fig. 13K) and, to a lesser degree also the anterior caudal vertebra NHMUK PV R 10793 (Fig. 13Q) and the paratype trunk vertebra NHMUK PV R 10798 (Figs 3E; 4K, L), there is short median ventral process/tubercle in the ventral margin of the cotyle. NHMUK PV R 38941 (Fig. 14A–E),

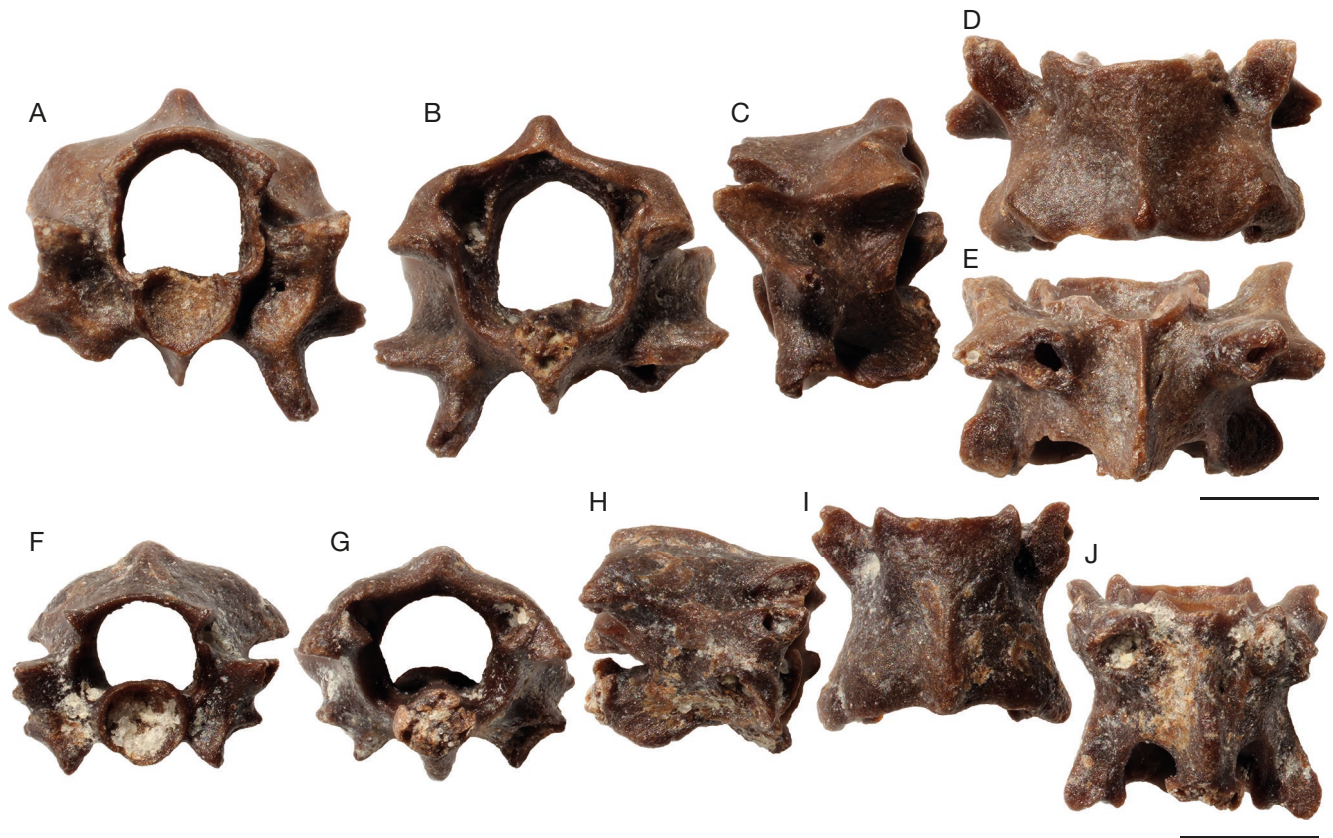


FIG. 10. — Cloacal vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp. A-E, NHMUK PV R 38947 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views; F-J, NHMUK PV R 38948 in anterior (F), posterior (G), right lateral (H), dorsal (I), and ventral (J) views. Scale bars: 1 mm.

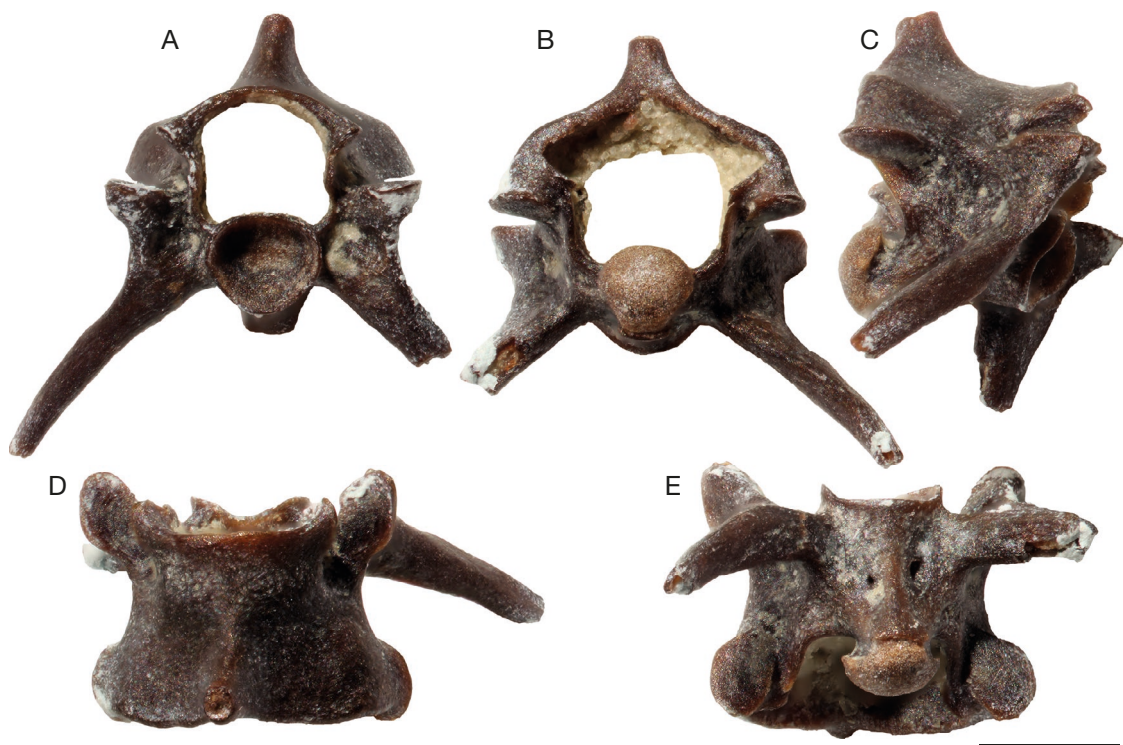


FIG. 11. — Anterior caudal vertebra NHMUK PV R 10796 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), posterior (B), right lateral (C), dorsal (D), and ventral (E) views. Scale bar: 1 mm.

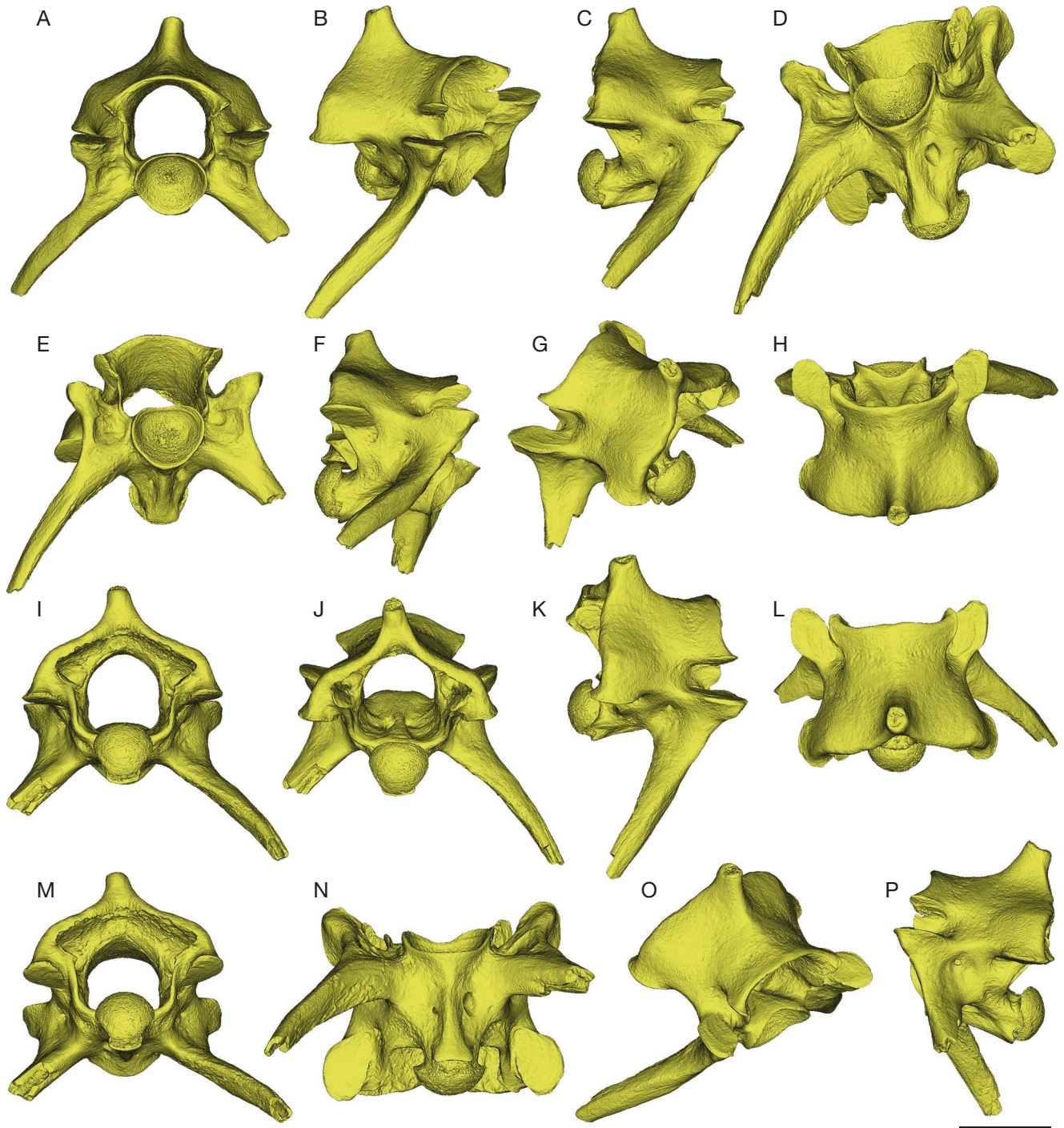


FIG. 12. — 3D μ CT images of anterior caudal vertebra NHMUK PV R 10796 of *Paradoxophidion richardoweni* n. gen., n. sp. in anterior (A), right anterolateral (B), right lateral (C), anteroventral (D, E), right ventrolateral (F), left dorsolateral (G), anterodorsal (H), posterior (I), posterodorsal (J), right posterolateral (K), dorsal (L), posteroventral (M), ventral (N), anterodorsal (O), and left lateral (P) views. Scale bar: 1 mm.

NHMUK PV R 38949 (Fig. 14F–J), and NHMUK PV R 38955 represent more posterior caudal vertebrae and they have a pair of haemapophyses (instead of hypapophysis) and a relatively longer centrum. These haemapophyses are rather short, not protruding much ventrally below the centrum. Like in the preceding trunk vertebrae, the neural spine is confined to the posteriormost portion of the neural arch; however, in NHMUK PV R 38949 (Fig. 14I) and NHMUK PV R 38955

this structure is anteroposteriorly longer than remaining caudal vertebrae. The ventral surface of the centrum can bear also a pair of subcentral foramina, but these vary in size and degree of symmetry. Other features of the caudal series, which are also observed in the trunk vertebrae, include the thickening of the zygantrum, the thin zygosphenes, the large neural canal, the small, pterapophysis-like, tubercle on each side of the neural arch, and the small and circular cotyle and condyle.



FIG. 13. — Anterior caudal vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp.: A-E, NHMUK PV R 10799 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views; F-J, NHMUK PV R 10800 in anterior (F), posterior (G), right lateral (H), ventral (I), and dorsal (J) views; K-L, NHMUK PV R 10791 in ventral (K) and posterior (L) views; M-Q, NHMUK PV R 10793 in anterior (M), posterior (N), left ventrolateral (O), dorsal (P), and ventral (Q) views; R-V, NHMUK PV R 38951 in anterior (R), posterior (S), right lateral (T), dorsal (U), and ventral (V) views. Scale bars: 1 mm.



FIG. 14. — Posterior caudal vertebrae of *Paradoxophidion richardoweni* n. gen., n. sp.: **A–E**, NHMUK PV R 38941 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F–J** NHMUK PV R 38949 in anterior (**F**), posterior (**G**), left lateral (**H**), dorsal (**I**), and ventral (**J**) views. Scale bars: 1 mm.

DISCUSSION

COMPARISONS WITH RUSSELLOPHIIDS

Paradoxophidion n. gen. resembles Russellophiidae Rage, 1978a, an enigmatic group of aquatic or semiaquatic snakes, probably lying somewhere within caenophidians (Rage 1978a, 1984; Rieppel 1988; Rage *et al.* 2008; Head *et al.* 2016, 2022; McCartney & Seiffert 2016; Zaher *et al.* 2019; Smith & Georgalis 2022). The type genus of this family, *Russellophis*, is known from the early Eocene of France, Belgium, and India (Rage 1975, 1978a; Rage *et al.* 2008; Smith & Georgalis 2022), but other potential russellophiids are also known from the Late Cretaceous (Campanian) of Sudan, the early Eocene of France and Brazil, the middle Eocene of France, and the late Eocene of Egypt (Rage & Werner 1999; Rage 2008; McCartney & Seiffert 2016; Head *et al.* 2022; Smith & Georgalis 2022).

Paradoxophidion n. gen. shares with russellophiids certain characteristic features, such as the moderately (dorsoventrally) short neural spine that is strictly confined to the posteriormost portion of the neural arch, the vaulted neural arch with a peculiar dome-shaped arching, the shape and thickness of the zygantral roof (i.e., thickened posterior margin of the neural arch), the presence of small spines below the prezygapophyseal articular facets, the prominent prezygapophyseal buttresses that are compressed and form a more or less vertical ridge, the paradiapophyses that are not clearly divided into diapophyses and parapophyses and that face ventrally in anterior view and reach below the ventral level of the cotyle, the absence of paracotylar foramina, and a very large neural canal (characters from Rage 1984; Rage *et al.* 2008). For comparative purposes, photographs of the holotype (MNHN.F.CB1603) and a referred vertebra

(MNHN.F.CB1623) of *Russellophis tenuis* Rage, 1975, from the early Eocene (MP 8/9) type locality of Condé-en-Brie in the Paris Basin, France, are presented here in Figure 15.

However, there are some important differences between the new taxon from Hordle and russellophiids. Most importantly, the English taxon possesses a prominent hypapophysis (particularly large, broad, and ventrally inclined in some vertebrae) instead of haemal keel across all trunk vertebrae, whereas in Russellophiidae hypapophyses are confined solely to the anterior trunk vertebrae and then substituted by haemal keels in succeeding trunk vertebrae (Rage 1984; Rage *et al.* 2008). Moreover, *Paradoxophidion* n. gen. lacks a supposedly diagnostic feature of *Russellophis*, i.e., the ventrolateral inclination of the prezygapophyseal articular facets in anterior view (which is otherwise visible in several [but not all] known specimens of *Russellophis*; see Rage 1975, 1984; Rage *et al.* 2008). Instead, in the new English taxon, the prezygapophyses are almost horizontal to very slightly dorsally inclined. Other major differences of *Paradoxophidion* n. gen. from russellophiids, include the elongation of the centrum and the distinctiveness of the subcentral ridges: *Russellophis* and other known russellophiid records are all characterized by a very elongated centrum, that is much longer than wide, and distinct subcentral ridges (Rage 1975, 1984; Rage *et al.* 2008; Georgalis *et al.* 2025; this paper, Fig. 15E, K). Instead, the centrum of *Paradoxophidion* n. gen. is relatively anteroposteriorly short and laterally wide, compared to any published russellophiids. Among published russellophiids, only perhaps the unnamed form from the late Eocene of Fayum, Egypt, has such an anteroposteriorly short and laterally narrow centrum (see McCartney & Seiffert 2016: fig. 7A). Finally, *Paradoxophidion richardoweni* n. gen., n. sp. is smaller than all known russellophiids: it has a CL around 2 mm, while this value is 3.6 mm in *Russellophis tenuis* from

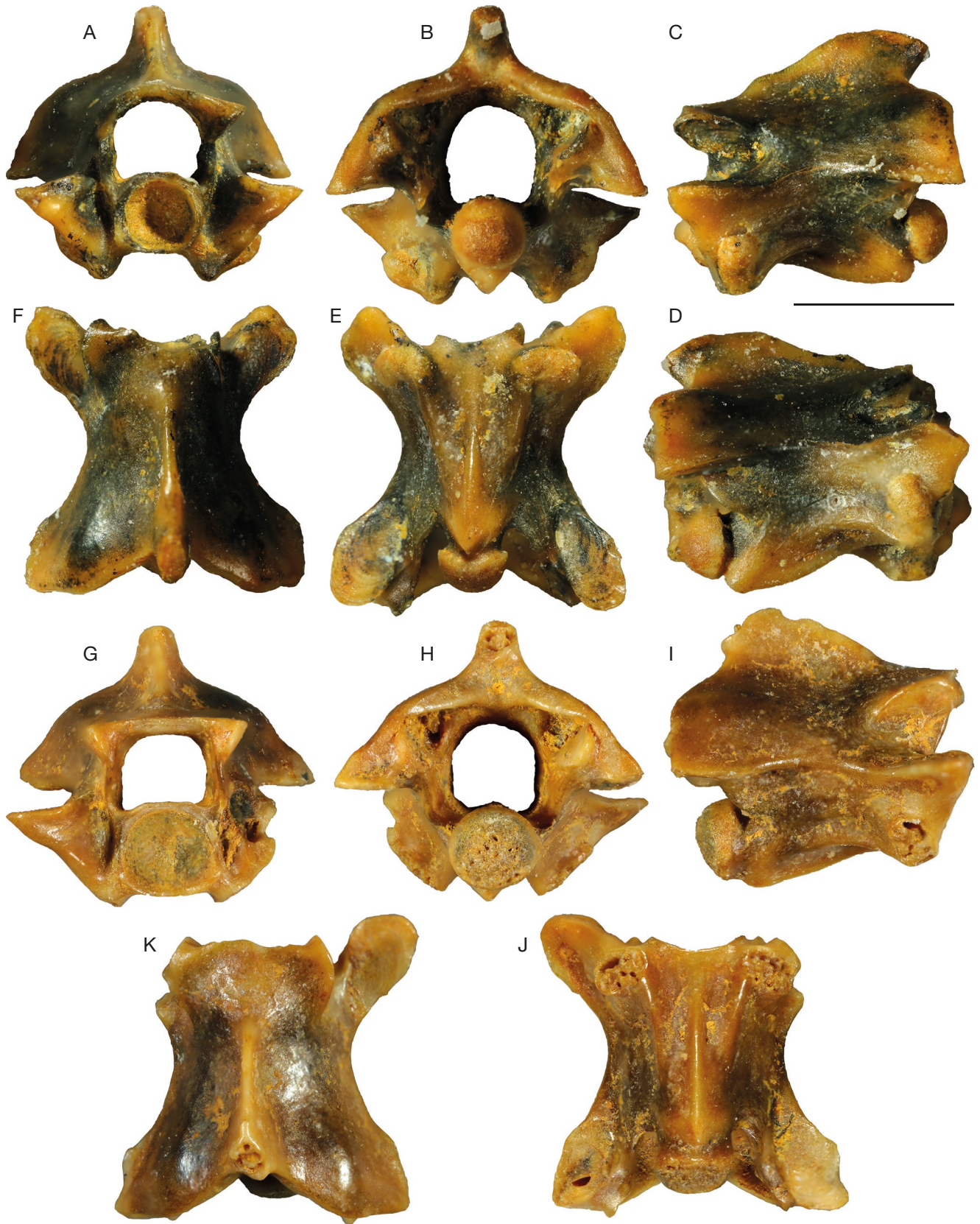


FIG. 15. — *Russellophis tenuis* Rage, 1975 from the early Eocene (MP 8/9) type locality of Condé-en-Brie in the Paris Basin, France: **A-F**, holotype trunk vertebra (MNHN.F.CB1603) in anterior (**A**), posterior (**B**), left lateral (**C**), right (ventro)lateral (**D**), ventral (**E**), and dorsal (**F**) views; **G-K**, trunk vertebra (MNHN.F.CB1623) in anterior (**G**), posterior (**H**), right lateral (**I**), ventral (**J**), and dorsal (**K**) views (this specimen has been previously figured in Rage 1983: fig. 10). Scale bar: 2 mm.

the early Eocene of France and Belgium (Rage 1975, 1984), more than 4 mm in *Russellophis crassus* Rage, Folie, Rana, Singh, Rose & Smith, 2008, from the early Eocene of India (Rage *et al.* 2008), and 3.3 mm in *Krebsophis thobanus* Rage & Werner, 1999, from the Late Cretaceous (Campanian) of Sudan (Rage & Werner 1999; age after Head *et al.* 2022).

Comparisons regarding caudal vertebral morphology among *Paradoxophidion richardoweni* n. gen., n. sp. and russellophiids are hard to make because of the scarcity of such descriptions for the latter group. As a matter of fact, the sole known caudal vertebrae for russellophiids are: one caudal vertebra of *Russellophis tenuis* described (but not figured) by Rage (1975) and two caudal vertebrae of *Russellophis crassus* described (but again not figured) by Rage *et al.* (2008) as possessing pleurapophyses and haemapophyses. In any case, the relatively high proportion of caudal vertebrae (compared to the available trunk vertebrae; i.e., 9 out of 31) of the new taxon in our NHMUK sample is interesting; it evokes the suggestion of Smith (2013) that high percentages of caudal vertebrae of one species in a single fossil locality denote snakes with longer tails, however, certainly more material is required in order to assess such proportions.

COMPARISONS WITH OTHER PALEOGENE ENGLISH AND CONTINENTAL EUROPEAN TAXA

Paradoxophidion richardoweni n. gen., n. sp. differs significantly from all other named snake taxa from Hordle Cliff and other late Eocene localities in England, i.e., *Cadurceryx pearchi* Holman, Harrison & Ward, 2006, *Paraplatyspondylia batesi* Holman & Harrison, 1998b, *Hordleophis balconae* Holman, 1996, *Totlandophis thomasaе* Holman & Harrison, 1998a, *Vectophis wardi* Rage & Ford, 1980, *Paleryx rhombifer* Owen, 1850, and *Headonophis harrisoni* Holman, 1993.

More particularly, *Paradoxophidion richardoweni* n. gen., n. sp. can be readily differentiated from *Cadurceryx pearchi* by the absence of complex structures on the caudal vertebrae (see Holman *et al.* 2006).

Paradoxophidion richardoweni n. gen., n. sp. can be differentiated from *Paraplatyspondylia batesi* (type and only known species of the genus *Paraplatyspondylia* Holman & Harrison, 1998b) by its neural spine being confined solely to the posteriormost portion of the neural arch (unlike the dorsoventrally short but anteroposteriorly long neural spine of *Paraplatyspondylia*), the presence of hypapophysis instead of haemal keel on trunk vertebrae, and the prominent prezygapophyseal buttresses (see Holman & Harrison 1998a).

Paradoxophidion richardoweni n. gen., n. sp. can be differentiated from *Hordleophis balconae* (type and only known species of the genus *Hordleophis* Holman, 1996a) by its neural spine being extremely small and confined solely to the posteriormost portion of the neural arch (unlike the dorsoventrally very high and anteroposteriorly long neural spine of *Hordleophis*), the presence of hypapophysis instead of haemal keel on trunk vertebrae, and the prominent prezygapophyseal buttresses (see Holman 1996). Moreover, the validity of *Hordleophis* needs to be further assessed as this taxon bears some resemblance with the genus *Cadurcobia* Rage, 1978b, from the middle

and late Eocene of France (Rage 1978b; Rage & Augé 2010), a resemblance that was already suggested by Rage & Augé (2010), mainly in reference to the high neural spine and the depressed neural arch. However, the sole available illustrations of the holotype trunk vertebra (MSUVP 1361) of *Hordleophis balconae* and of one (among the three) paratype trunk vertebrae (MSUVP 1362) presented in Holman (1996: figs 1, 2) hinder any definite conclusions. Even more, long before the establishment of *Hordleophis*, Milner *et al.* (1982) had listed material that they assigned to ?*Cadurcobia* sp. from Hordle Cliff, however, this was never figured or described.

Paradoxophidion richardoweni n. gen., n. sp. can be differentiated from *Totlandophis thomasaе* (type species of *Totlandophis* Holman & Harrison, 1998a) by being much smaller and its neural spine being extremely small and confined solely to the posteriormost portion of the neural arch (unlike the dorsoventrally higher and anteroposteriorly much longer neural spine of *Totlandophis thomasaе*), the presence of hypapophysis instead of haemal keel in trunk vertebrae, the much slenderer prezygapophyseal articular facets, and the less shallow posterior median notch of the neural arch (see Holman & Harrison 1998a).

Paradoxophidion richardoweni n. gen., n. sp. can be differentiated from *Vectophis wardi* (type and only known species of the genus *Vectophis* Rage & Ford, 1980) by its neural spine being extremely small and confined solely to the posteriormost portion of the neural arch (unlike the dorsoventrally higher and anteroposteriorly much longer neural spine of *Vectophis*), the more depressed neural arch, the less shallow posterior median notch of the neural arch, the not so prominent subcentral grooves, the presence of hypapophysis instead of haemal keel across trunk vertebrae, the prominent prezygapophyseal buttresses, and the different shape of the zygantrum and, the less vaulted neural arch (see Rage & Ford 1980).

Paradoxophidion richardoweni n. gen., n. sp. nov. can be differentiated from *Paleryx rhombifer* (sole currently recognized valid species of the genus *Paleryx*) according to its much smaller overall size, the shape and size of the neural spine that is confined solely to the posteriormost portion of the neural arch (instead of the much more prominent neural spine of *Paleryx* that is dorsoventrally higher and anteroposteriorly longer), the presence of hypapophysis instead of haemal keel, the prominent prezygapophyseal buttresses, the thinner zygosphenes, and the thinner prezygapophyseal articular facets (see Georgalis *et al.* 2021b).

Paradoxophidion richardoweni n. gen., n. sp. can be differentiated from *Headonophis harrisoni* (type species of the genus *Headonophis* Holman, 1993) by its shorter centrum, the paradiapophyses being distinct from the centrum and much ventrally directed, the neural spine being extremely small and confined solely to the posteriormost portion of the neural arch (unlike the dorsoventrally higher and anteroposteriorly longer neural spine of *Headonophis*), the shallow posterior median notch of the neural arch, the absence of paracotylar foramina, the less thick (and usually) dorsoventrally higher hypapophysis, the less dorsally inclined prezygapophyses, and the prominent prezygapophyseal buttresses (see Holman 1993).

Nevertheless, it has to be highlighted that the sole published figure of the holotype trunk vertebra of *Headonophis harrisoni* (MSUVP 1342) is poorly illustrated (Holman 1993: fig. 1), the holotype trunk vertebra is rather incomplete, and the only supposedly referred material are four cloacal or caudal vertebrae that were briefly described in Holman *et al.* (2006) but never figured.

Outside the English Eocene, *Paradoxophidion richardoweni* n. gen., n. sp. greatly differs from other Paleogene small snakes from continental Europe (with the exception of the above-discussed russellophiids). More particularly, *Paradoxophidion* can be differentiated from *Eoanilius europae* Rage, 1974 (type species of the genus *Eoanilius* Rage, 1974), from the late Eocene of France, and *Eoanilius oligocenicus* Szyndlar, 1994, from the early Oligocene to Early Miocene of Germany, by being larger and dorsoventrally taller, and possessing a more slender zygosphen, hypapophyses throughout the trunk region, the prominent prezygapophyseal buttresses, the paradiapophyses being distinct from the centrum and much ventrally directed, the smaller prezygapophyseal articular facets, and a thinner neural spine in dorsal view that covers an even smaller area onto the neural arch (see Rage 1974, 1984). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from the two European species of the genus *Dunnophis* Hecht in McGrew *et al.*, 1959, i.e., *Dunnophis cadurcensis* Rage, 1974, from the middle and late Eocene of France, and *Dunnophis matronensis* Rage, 1973, from the early and middle Eocene of France and Portugal, by its shorter centrum, its thinner neural spine in dorsal view that covers an even smaller area onto the neural arch, the presence of hypapophysis instead of haemal keel across trunk vertebrae, the paradiapophyses being distinct from the centrum and much ventrally directed, and the prominent prezygapophyseal buttresses (see Rage 1973, 1974, 1984; Augé *et al.* 1997; Rage & Augé 2003, 2010). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from *Szyndlaria aureomontensis* Rage & Augé, 2010, from the middle Eocene of France, and *Cadurcoba insolita* Rage, 1978b, from the late Eocene of France, by its much smaller size, the shape and size of the neural spine that is confined solely to the posteriormost portion of the neural arch (instead of the much prominent and tall neural spine of *Szyndlaria* Rage & Augé, 2010, and *Cadurcoba* Rage, 1978b), the more vaulted neural arch, the prominent hypapophyses, and the prominent prezygapophyseal buttresses (see Rage 1978b; Rage & Augé 2010). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from *Falseryx neervelpensis* Szyndlar, Smith & Rage, 2008, from the early Oligocene of Belgium, by the shape and size of the neural spine that is confined solely to the posteriormost portion of the neural arch (instead of the short but still anteroposteriorly long neural spine of *Falseryx*) and the paradiapophyses being distinct from the centrum and much ventrally directed (see Szyndlar *et al.* 2008). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from “*Calamagras*” *gallicus* Rage, 1977, from the early Eocene of France, by the shape and size of the neural spine that has its base commencing more posteriorly on the neural arch and being confined solely to the posteriormost

portion of the neural arch, the presence of hypapophysis instead of haemal keel on trunk vertebrae, the less thick neural spine in caudal vertebrae, and the absence of complex structures on the caudal vertebrae (see Rage 1977). *Paradoxophidion richardoweni* n. gen., n. sp. can be readily differentiated from *Cadurceryx filholi* Hoffstetter & Rage, 1972, from the middle and late Eocene of France, and *Rageryx schmidi* Smith & Scanferla, 2021, from the latest early to earliest middle Eocene of Germany, by the absence of complex structures on its caudal vertebrae and a completely different morphology of the trunk vertebrae (see Hoffstetter & Rage 1972; Rage 2013; Smith & Scanferla 2021; Szyndlar & Georgalis in press). *Paradoxophidion richardoweni* n. gen., n. sp. can be readily differentiated from *Rottophis atavus* (Meyer, 1855), from the late Oligocene of Germany, by its smaller size, the shape and size of the neural spine that is confined solely to the posteriormost portion of the neural arch (instead of the short but still anteroposteriorly long neural spine of *Rottophis* Szyndlar & Böhme, 1996), the slenderer prezygapophyseal articular facets, the less dorsally inclined prezygapophyses, and the much thinner zygosphen (see Szyndlar & Böhme 1996). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from the three known species of *Platyspondylia* Rage, 1974, by the shape and size of the neural spine that is confined solely to the posteriormost portion of the neural arch (instead of the short but still anteroposteriorly long neural spine of *Platyspondylia*), the presence of hypapophyses across trunk vertebrae, and the paradiapophyses being distinct from the centrum and much ventrally directed (see Rage 1974, 1988a). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from *Messelophis variatus* Baszio, 2004, and *Rieppelophis ermannorum* (Schaal & Baszio, 2004), from the latest early to earliest middle Eocene of Germany, by the presence of hypapophyses across all trunk vertebrae and the more vaulted neural arch, its thinner zygosphen, and its neural spine that is confined to the posteriormost portion of the neural arch (see Baszio 2004; Schaal & Baszio 2004; Scanferla *et al.* 2016). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from *Anomalophis bolcensis* (Massalongo, 1859), from the early Eocene of Italy by its less elongated centrum, the neural spine that is shorter and confined solely to the posterior portion of the neural arch, the more massive and prominent paradiapophyses that are distinct from the centrum and much ventrally directed, and the presence of hypapophyses (instead of haemal keels) across all trunk vertebrae (see Auffenberg 1959). *Paradoxophidion richardoweni* n. gen., n. sp. can be differentiated from *Woutersophis novus* Rage, 1980, from the early Eocene of Belgium, by its not so elongated centrum, the presence of hypapophyses across trunk vertebrae, the much thinner zygosphen, and the much shorter neural spine that is confined to the posterior portion of the neural arch (see Rage 1980).

Finally, other Paleogene taxa from Europe are much greater in size compared to *Paradoxophidion* n. gen. (e.g. members of the genera *Palaeopython* Rochebrune, 1880, *Phosphoroboa* Georgalis, Rabi & Smith, 2021b, *Eoconstrictor* Scanferla & Smith 2020, *Messelopython* Zaher & Smith,

2020, *Bransateryx* Hoffstetter & Rage, 1972, and *Bavarioboa* Szyndlar & Schleich, 1993; see Hoffstetter & Rage 1972; Rage 1984; Szyndlar & Rage 2003; Georgalis & Scheyer 2019; Scanferla & Smith 2020; Zaher & Smith 2020; Georgalis *et al.* 2021b; Smith & Scanferla 2022; Palci *et al.* 2024) and/or differ significantly in their vertebral morphology (e.g. palaeophiids, archaeophiids; see Rage 1984; Georgalis *et al.* 2020, 2021a; Georgalis 2023).

TAXONOMIC AFFINITIES OF *PARADOXOPHIDION*

RICHARDOWENI N. GEN., N. SP.

The new taxon *Paradoxophidion richardoweni* n. gen., n. sp. exhibits a mosaic of features that are present across distantly related groups of alethinophidian snakes. Even though certain features of *Paradoxophidion* n. gen. approach the morphology of russellophiids, there are also other features that preclude such taxonomic referral. It appears actually challenging to assign *Paradoxophidion* n. gen. to a particular group of snakes with confidence, as its unique vertebral morphology differs from known groups of either non-caenophidians (Szyndlar & Georgalis 2023) and caenophidians (see Hoffstetter & Gasc 1969; Zaher *et al.* 2019). The proportion of CL/NAW <1 could at first glance be indicative of constrictors (see Georgalis & Smith 2020; Szyndlar & Georgalis 2023) but this character is further observed across other groups of non-constrictor snakes (see Szyndlar & Georgalis 2023), including the caenophidian group of acrochordids (Hoffstetter & Gayrard 1964; Head 2005). Similarly, the presence of prominent hypapophyses across the trunk vertebral column is observed across an array of distantly related snake groups, including both non-caenophidian (e.g. tropidophiids, bolyeriids, candoiids, palaeophiids) and caenophidian (e.g. acrochordids, xenodermids, natricids, elapids, homalopsids, viperids) snakes (see Zaher *et al.* 2019; Szyndlar & Georgalis 2023). The paradiapophyses not clearly divided into diapophyseal and parapophyseal portions is more typical of non-caenophidian snakes (see Szyndlar & Georgalis 2023), as in caenophidians, paradiapophyses are most usually clearly divided into distinct diapophyses and parapophyses (Zaher *et al.* 2019); in fact, this very feature, coupled with the absence of prezygapophyseal accessory processes, had led Rage (1984) to conclude that russellophiids lie more basally within the lineage of Colubroidea Zaher, Grazziotin, Cadle, Murphy, Cesar de Moura-Leite & Bonatto, 2009 (Colubroidea in his terminology). Nevertheless, as will be highlighted in detail below, the paradiapophyses of *Paradoxophidion* n. gen. are much strongly reminiscent of acrochordids, in terms of their shape and ventral extension. Szyndlar & Georgalis (2023) recently emphasized the taxonomic importance and utility of the subcentral structures of the vertebrae around the trunk to caudal transition (“pericloacal vertebrae” *sensu* Smith 2013). *Paradoxophidion* n. gen. exhibits a haemal keel (or “short hypapophysis”) in its posteriormost trunk, cloacal, and anterior caudal vertebrae, which ultimately becomes transitioned into paired short haemapophyses into succeeding posterior caudal vertebrae. A similar pattern can be observed in some extant snake groups, such as tropidophiids and some constrictors (Szyndlar & Georgalis 2023).

Aside from the above discussed similarities to russellophiids, it should be highlighted that the greatest degree of resemblance between *Paradoxophidion* n. gen. and some particular snake group is shared with Acrochordidae Bonaparte, 1831. Acrochordids are a group of fully aquatic snakes, currently distributed across marine and freshwater areas stretching from India to the western edge of the Pacific Ocean (McDowell 1979; Sanders *et al.* 2010). The family comprises solely a single valid genus, *Acrochordus* Hornstedt, 1787, with only three extant species (*Acrochordus arafurae* McDowell, 1979, *Acrochordus granulatus* [Schneider, 1799], and the type species, *Acrochordus javanicus* Hornstedt, 1787; see McDowell 1979; Sanders *et al.* 2010) and a fossil record confined to the Neogene of southern Asia, including a single, massive, extinct species, *Acrochordus dehmi* Hoffstetter, 1964 (Hoffstetter 1964; West *et al.* 1991; Rage *et al.* 2001; Head 2005; Head *et al.* 2007; Sanders *et al.* 2010; Kapur *et al.* 2021). The lineage likely represents one of the basalmost groups (if not the basalmost one) of extant caenophidians, being recovered as the sister group of Colubroidea in recent phylogenies (Slowinski & Lawson 2002; Lawson *et al.* 2005; Lee *et al.* 2007; Vidal *et al.* 2007; Zaher *et al.* 2009, 2019, 2023; Sanders *et al.* 2010; Pyron *et al.* 2011, 2013; Hsiang *et al.* 2015; Figueroa *et al.* 2016; Streicher & Wiens 2016; Zheng & Wiens 2016; Burbrink *et al.* 2020). Accordingly, despite the relatively young so far existing fossil record, the lineage of Acrochordidae is considered rather old, with divergence date estimates varying between the early Eocene (56 Ma; Sanders *et al.* 2010; Zaher *et al.* 2019) and late Oligocene (Head *et al.* 2016). Acrochordids are characterized by extreme and unique anatomical features and life history traits, including distinctive features in their skull and vertebrae (Hoffstetter & Gayrard 1964; McDowell 1979; Rieppel & Zaher 2001; Head 2005; Head *et al.* 2007; Sanders *et al.* 2010).

Paradoxophidion n. gen. shares with *Acrochordus* a number of important vertebral features: presence of hypapophyses throughout the trunk column; the paradiapophyses are distinct from the centrum, narrow, more ventrally than laterally oriented and extend well below the ventral margin of the cotyle; a large neural canal; presence of a small, pterapophysis-like, tubercle on each side of the neural arch; the (occasional) presence of a short median ventral process/tubercle in the ventral margin of the cotyle; and prezygapophyseal accessory processes consisting of vertically oriented blades, as observed in at least one specimen (NHMUK PV R 10797) of the new English taxon (Hoffstetter & Gayrard 1964; McDowell 1979; Rage 1984; Head 2005; Head *et al.* 2007; Sanders *et al.* 2010); for further comparative purposes, we present here the intracolumnar variation of the trunk vertebrae of a skeleton (ISEA R/497) of *Acrochordus arafurae* (Fig. 16). Moreover, the size, cross-sectional shape, and orientation of the reduced neural spine of *Paradoxophidion* n. gen. possesses a striking similarity to that of *Acrochordus granulatus* (see Hoffstetter & Gayrard 1964: fig. 6), a species that was for long time placed in its own genus, *Chersydrus* Cuvier, 1817, and which possesses significant vertebral differences from other *Acrochordus* spp. (most notably, the absence

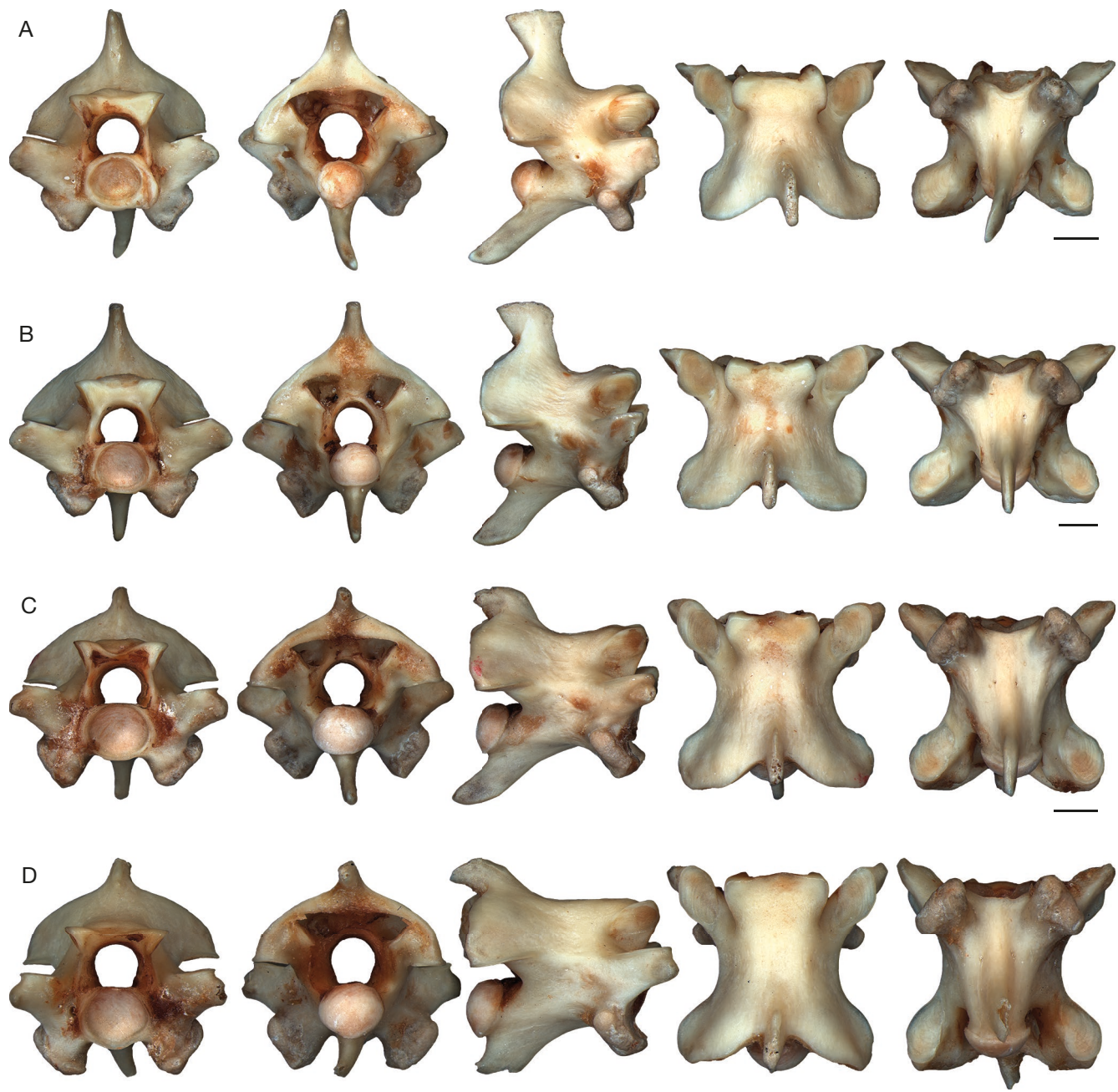


FIG. 16. — Intracolumnar variation of trunk vertebrae in the extant acrochordid *Acrochordus arafurae* McDowell, 1979 (specimen ISEA R/497): **A**, 41st vertebra; **B**, 71st vertebra; **C**, 116th vertebra; **D**, posterior trunk (158th) vertebra. Views in each row correspond to anterior, posterior, right lateral, dorsal, and ventral respectively. Scale bars: 2 mm.

of parazygosphenal foramina in *A. granulatus*; Hoffstetter & Gayraud 1964; Rage 1984; Head 2005; Sanders *et al.* 2010). It is further worth highlighting that two striking shared features of *Paradoxophidion* n. gen. and *Acrochordus*, i.e., the presence of small, pterapophysis-like, tubercles on the neural arch and the occasional presence of a short median ventral process/tubercle in the ventral margin of the cotyle (potentially serving as an attachment site for perilymphatic ligaments), were interpreted by McDowell (1979) as being homologous features with the pterapophyses and anterior hypapophyses of palaeophiids.

These being said, it seems rather likely that *Paradoxophidion* represents a basal caenophidian (Fig. 17). It is even possible that the English taxon belongs to Acrochordidae, as an early member of the group, much away from its so far known stratigraphic and geographic (extant and fossil) distribution. Nevertheless, we cannot exclude the alternative possibility that it belongs to some other group of early diverging caenophidians. Among extant taxa, the subsequently early diverging caenophidians after acrochordids according to most phylogenetic analyses (e.g. Zaher *et al.* 2019), are xenodermids and pareids, both of which exhibit much different



FIG. 17. — Hypothetical life reconstruction of *Paradoxophidion richardoweni* n. gen., n. sp. Credits: Artwork by Jaime Chirinos.

vertebral morphology than *Paradoxophidion* n. gen. (particularly pareids, which even lack hypapophyses throughout the trunk column; Zaher *et al.* 2019). In any case, the discovery of *Paradoxophidion* n. gen. as an early diverging caenophidian in the Eocene of England, is of particular significance, as only a few Eocene taxa from Europe have been regarded as true members of Caenophidia (Head *et al.* 2016; Zaher *et al.* 2019; Smith & Georgalis 2022). These records are the above discussed *Russellophis* from the early Eocene of France and Belgium (Rage 1975, 1983) and *Headonophis* from the late Eocene of England (Holman 1993; Holman *et al.* 2006), plus the genera *Anomalophis* Auffenberg, 1959, from the early Eocene of Italy (Auffenberg 1959; Seghetti *et al.* 2022), and potentially also, *Vectophis* from the late Eocene of England (Rage & Ford 1980; Zaher *et al.* 2019) and the nigerophiid *Woutersophis* Rage, 1980 from the early Eocene of Belgium (Rage 1980, 1983). In addition, there are indeterminate finds of russellophiids from the middle Eocene (MP 16) of Le Bretou, Quercy, France (Rage 1988a), and an indeterminate caenophidian from the early Eocene (MP 10) of Prémontré,

France (Augé *et al.* 1997). In the “nearby” area of northern Africa, Eocene caenophidians are also known, represented by cf. *Procerophis* sp. from Fayum, Egypt (El-Hares *et al.* 2022), a genus otherwise known from the early Eocene of India (Rage *et al.* 2008), and the thaumastophiid *Renenutet* McCartney & Seiffert, 2016, also from Fayum (McCartney & Seiffert 2016; Zaher *et al.* 2021; El-Hares *et al.* 2022); in addition, an as yet unnamed colubriiform has been described from the early-middle Eocene of Glib Zegdou HGL50 (Hammada Gour Lazib50), Algeria (Rage *et al.* 2021). Besides these records, a few other Eocene caenophidian remains are known from other continents (Zaher *et al.* 2021; Smith & Georgalis 2022). Despite this low number of fossil occurrences, it is evident that Eocene caenophidians had already achieved some relative diversity, as it is attested by the disparity of vertebral morphologies, sometimes combining a mosaic of features that is otherwise observed across different extant caenophidian groups (Head *et al.* 2016; Zaher *et al.* 2019, 2021). It is further worth noticing that the area of England seems to be an “epicenter” of this Eocene caenophidian diversity (but this

could also well reflect sampling biases), as three different taxa are now known from the region (*Vectophis*, *Headonophis*, and *Paradoxophidion* n. gen.); however, as highlighted above, we cast doubt on the status and even the validity of *Headonophis*, while we should leave open the possibility that *Vectophis* could alternatively represent some non-caenophidian snake, as it has been suggested also elsewhere (e.g. Rage & Ford 1980; Rage 1984; Rage *et al.* 2008; Smith & Georgalis 2022).

The imprecise affinities of the new taxon from Hordle Cliff within Caenophidia hinder direct biogeographic inferences. Nevertheless, if *Paradoxophidion* n. gen. belongs indeed to Russellophiidae, then the new English taxon, with an age of MP 17a (i.e., 37.8–37.5 Ma), would represent the last occurrence of the European continent, as Russellophiidae is supposed to have become extinct in Europe around the middle Eocene (MP 16 [40–37.8 Ma], locality of Le Bretou, France; Rage 1988b). It could also represent the most recent global record, with only potential exception being the unnamed form from Fayum, Egypt, which has an age approximately 37 Ma (McCartney & Seiffert 2016). If *Paradoxophidion* n. gen. belongs to Acrochordidae, it would then support divergence date estimates that place the split of that group already by the Eocene and moreover indicate a rather extraordinary geographic expansion for acrochordids, which are otherwise known exclusively from the Neogene and Quaternary of southern Asia and the western Pacific Ocean.

Furthermore, the identification of *Paradoxophidion* n. gen. casts some doubt on the supposed occurrence of *Russellophis* from England. Indeed, the presence of a caenophidian resembling *Russellophis* from the late Eocene of Christchurch Bay at Hordle Cliff, England was first reported in Milner *et al.* (1982), but that was apparently based on the same NHMUK material here designated as the new taxon *Paradoxophidion richardoweni* n. gen., n. sp. Subsequently, Milner (1986) mentioned such supposed presence of *Russellophis* sp. from Christchurch Bay at Hordle Cliff, but also from two additional English localities: the middle Eocene of Huntingbridge Division and the latest Eocene/earliest Oligocene (MP 20/21) of the Bembridge Limestone (Isle of Wight), however, again all these occurrences were not accompanied by any kind of figure, description, or collection number that could verify these records and identifications. Eventually, Holman *et al.* (2006), mentioned (but not figured) one further anterior trunk vertebra (MSUVP 2065) from the Hordle Cliff, which he considered as identical to *Russellophis tenuis*. Furthermore, Holman *et al.* (2006) erroneously mentioned that the English localities from which Milner (1986) had reported *Russellophis* were the middle Eocene (MP 16) of Creechbarrow in Dorset and the Lower Headon Beds (i.e., Hordle Cliff). Moreover, Milner (1986) mentioned the presence of a form dubbed as “Acrochordid 1” from the Lower Headon Beds, however, this was not accompanied by any kind of description, figure or collection number. We here cannot comment about the taxonomic status of the other supposed British occurrences of russellophiids and/or acrochordids mentioned in Milner (1986) and Holman

et al. (2006), but at least for the case of the material from Hordle Cliff from the NHMUK collection, it does not belong to *Russellophis* but instead represents the new taxon *Paradoxophidion richardoweni* n. gen., n. sp.

Finally, *Paradoxophidion* represents an important addition to our knowledge of Eocene faunas from England, which have been predominantly studied for their mammals (e.g. Hooker *et al.* 2005; Vasileiadou *et al.* 2022), and offers a small step forwards in tracing reptile communities and diversity across the Paleogene and especially around the “Grande Coupure” at the Eocene-Oligocene transition (Hooker 2010), and how they may have changed due to ecological and environmental factors and perturbations.

Acknowledgements

GLG acknowledges funding from the research project no. 2023/49/B/ST10/02631 financed by the National Science Center of Poland (Narodowe Centrum Nauki). GLG also acknowledges travel support from the 2023 Richard Owen Fund of the Palaeontographical Society, which enabled him to travel to London and study the NHMUK collection. We thank Agnese Lanzetti and Brett Clark for μ CT scanning five of the specimens of the new taxon; Andrew Milner and Jerry Hooker for encouragement and discussion; Olaf Lizak for help with photographing the *Acrochordus* specimen from the ISEA collection; and Brett Clark for advice on videos of μ CT models. For access to comparative material of *Russellophis*, *Vectophis*, and other snakes at the collections of MNHN, GLG is grateful to Nour-Eddine Jalil and acknowledges travel support from SYNTHESYS FR-TAF_Call4_035 (MNHN) that enabled him to study these specimens. We also thank Jaime Chirinos for the life reconstruction of the new taxon, presented in Figure 17. We finally thank the reviewers, Krister Smith, Jason Head, and two anonymous ones, for their useful comments and suggestions, which enhanced the quality of the paper.

REFERENCES

- AUFFENBERG W. 1959. — *Anomalophis bolcensis* (Massalonga), a new genus of fossil snake from the Italian Eocene. *Breviora* 114: 1–16. <https://www.biodiversitylibrary.org/page/3190823>
- AUGÉ M., DUFFAUD S., LAPPARENT DE BROIN F. DE, 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 (2): 23–33.
- BASZIO S. 2004. — *Messelophis variatus* n. gen. n. sp. from the Eocene of Messel: a tropidopheine snake with affinities to Erycinae (Boidae). *Courier Forschungsinstitut Senckenberg* 252: 47–66.
- BENTON M. J. & SPENCER P. S. 1995. — Fossil Reptiles of Great Britain. *Geological Conservation Review Series* 10. Chapman and Hall, London, 386 p. <https://doi.org/10.1007/978-94-011-0519-4>
- BIOCHROM'97 1997. — Synthèses et Tableaux de corrélations, in AGUILAR J.-P., LEGENDRE S. & MICHAUX J. (eds), *Actes du Congrès Biochrom'97, Montpellier, 14–17 avril: biochronologie mammalienne du cénozoïque en Europe et domaines reliés*. École pratique des hautes études, Institut de Montpellier (Mémoires et travaux de l'Institut de Montpellier; 21), Montpellier: 768–805.

- BONAPARTE C. L. 1831. — Saggio di una distribuzione metodica degli animali vertebrati. *Giornale Arcadico di Scienze, Lettere, ed Arti*, Roma 49: 3-77. <https://doi.org/10.5962/bhl.title.48624>
- BURBRINK F. T., GRAZZIOTIN F. G., PYRON R. A., CUNDALL D., DONNELLAN S., IRISH F., KEOGH J. S., KRAUS F., MURPHY R. W., NOONAN B., RAXWORTHY C. J., RUANE S., LEMMON A. R., LEMMON E. M. & ZAHER H. 2020. — Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology* 69 (3): 502-520. <https://doi.org/10.1093/sysbio/syz062>
- EDWARDS N. & DALEY B. 1997. — Stratigraphy of the Totland Bay Member (Headon Hill Formation, Late Eocene) at Hordle Cliff, Hampshire, southern England. *Tertiary Research* 18: 35-50.
- EL-HARES M. A., ZAHER H., EL-MEKAWY D., EL-SAYED S., SEIFFERT E. R. & SALLAM H. M. 2022. — New records of legless squamates from the lowest upper Eocene deposits of the Fayum Depression, Egypt. *Journal of Vertebrate Paleontology* 41 (4): e1992770. <https://doi.org/10.1080/02724634.2021.1992770>
- ESCARGUEL G., MARANDAT B. & LEGENDRE S. 1997. — Sur l'âge numérique des faunes de mammifères du Paléogène d'Europe Occidentale, en particulier celles de l'Éocène inférieur et moyen. in AGUILAR J.-P., LEGENDRE S. & MICHAUX J. (eds), *Actes du Congrès BiochroM'97, Montpellier, 14-17 avril: biochronologie mammalienne du cénozoïque en Europe et domaines reliés*. École pratique des hautes études, Institut de Montpellier (Mémoires et travaux de l'Institut de Montpellier; 21), Montpellier: 442-460.
- FIGUEROA A., MCKELVY A. D., GRISMER L. L., BELL C. D. & LAILVAUX S. P. 2016. — A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS ONE* 11 (9): e0161070. <https://doi.org/10.1371/journal.pone.0161070>
- GEORGALIS G. L. 2023. — First potential occurrence of the large aquatic snake *Pterospheus* (Serpentes, Palaeophiidae) from Nigeria, with further documentation of *Pterospheus schweinfurthi* from Egypt. *Alcheringa* 47 (3): 327-335. <https://doi.org/10.1080/03115518.2023.2217874>
- GEORGALIS G. L. & JOYCE W. G. 2017. — A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. *Bulletin of the Peabody Museum of Natural History* 58 (1): 115-208. <https://doi.org/10.3374/014.058.0106>
- 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 (3): 291-304. <https://doi.org/10.26049/VZ70-3-2020-03>
- GEORGALIS G. L., DEL FAVERO L. & DELFINO M. 2020. — Italy's largest snake: Redescription of *Palaeophis oweni* from the Eocene of Monte Duello, near Verona. *Acta Palaeontologica Polonica* 65 (3): 523-533. <https://doi.org/10.4202/app.00711.2019>
- GEORGALIS G. L., GUINOT G., KASSEKNE K. E., AMOUDJI Y. Z., JOHNSON A. K. C., CAPPETTA H. & HAUTIER L. 2021a. — An assemblage of giant aquatic snakes (Serpentes, Palaeophiidae) from the Eocene of Togo. *Swiss Journal of Palaeontology* 140 (20), 18 p. <https://doi.org/10.1186/s13358-021-00236-w>
- GEORGALIS G. L., RABI M. & SMITH K. T. 2021b. — Taxonomic revision of the snakes of the genera *Palaeopython* and *Paleryx* (Serpentes, Constrictores) from the Paleogene of Europe. *Swiss Journal of Palaeontology* 140 (18), 140 p. <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>
- HEAD J. J. 2005. — Snakes of the Siwalik Group (Miocene of Pakistan): systematics and relationship to environmental change. *Palaeontologia Electronica* 8.1.18A: 1-33.
- HEAD J. J. 2021. — A South American snake lineage from the Eocene Greenhouse of North America and a reappraisal of the fossil record of “anilioid” snakes. *Geobios* 66-67: 55-65. <https://doi.org/10.1016/j.geobios.2020.09.005>
- HEAD J. J., MOHABEY D. M. & WILSON J. A. 2007. — *Acrochordus* Hornstedt (Serpentes, Caenophidia) from the Miocene of Gujarat, Western India: Temporal constraints on dispersal of a derived snake. *Journal of Vertebrate Paleontology* 27 (3): 720-723. [https://doi.org/10.1671/0272-4634\(2007\)27\[720:AHSCFT\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[720:AHSCFT]2.0.CO;2)
- HEAD J. J., MAHLOW K. & MÜLLER J. 2016. — Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidea, Colubridae. *Palaeontologia Electronica* 19.2.2FC: 1-21. <https://doi.org/10.26879/625>
- HEAD J. J., HOWARD A. F. C. & MÜLLER J. 2022. — The first 80 million years of snake evolution: the Mesozoic fossil record of snakes and its implications for origin hypotheses, biogeography, and mass extinction, in GOWER D. & ZAHER H. (eds), *The Origin and Early Evolution of Snakes*. Cambridge University Press, Cambridge: 26-54. <https://doi.org/10.1017/9781108938891.005>
- HECHT M. K. 1959. — Amphibians and Reptiles, in MCGREW P. O., BERMAN J. E., HECHT M. K., HUMMEL J. M., SIMPSON G. G. & WOOD A. E. (eds), *The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming*. *Bulletin of American Museum of Natural History* 117: 130-146.
- HOFFSTETTER R. 1939. — Contribution à l'étude des Elapidæ actuels et fossiles et de l'ostéologie des Ophidiens. *Archives du Muséum d'Histoire Naturelle de Lyon* 15: 1-78.
- HOFFSTETTER R. 1964. — Les Serpents du Néogène du Pakistan (couches des Siwaliks). *Bulletin de la Société Géologique de France, 7e série* 6 (4): 467-474. <https://doi.org/10.2113/gssgf-bull.S7-VI.4.467>
- HOFFSTETTER R. & GASC J. 1969. — Vertebrae and ribs of modern reptiles, in GANS C., BELLAIRS A. D'A. & PARSONS T. S. (eds), *Biology of the Reptilia. Volume 1. Morphology A*. Academic Press, London and New York: 201-310.
- HOFFSTETTER R. & GAYRARD Y. 1964. — Observations sur l'ostéologie et la classification des Acrochordidae (Serpentes). *Bulletin du Muséum national d'Histoire Naturelle* 36: 677-696.
- HOFFSTETTER R. & RAGE J.-C. 1972. — Les *Erycina* fossiles de France (Serpentes, Boidae). Compréhension et histoire de la sous-famille. *Annales de Paléontologie* 58: 81-124.
- HOLMAN J. A. 1993. — A new genus of primitive colubroid snake from the Upper Eocene, Isle of Wight, England. *Tertiary Research* 14: 151-154.
- HOLMAN J. A. 1996. — A new genus of diminutive boid snake from the upper Eocene of Hordle Cliff, Hampshire, England. *Tertiary Research* 17: 11-13.
- HOLMAN J. A. & HARRISON D. L. 1998a. — A new genus of small boid snake from the upper Eocene of Hordle Cliff, Hampshire, England. *Acta Zoologica Cracoviensia* 41: 29-33.
- HOLMAN J. A. & HARRISON D. L. 1998b. — A new genus of snake (Serpentes: Boidae) from the Upper Eocene of Hordle Cliff, Hampshire, England. *Acta Zoologica Cracoviensia* 41: 23-27.
- HOLMAN J. A., HARRISON D. L. & WARD D. J. 2006. — Late Eocene snakes from the Headon Hill Formation, southern England. *Cainozoic Research* 5: 51-62.
- HOOKE J. J. 2010. — The 'Grande Coupure' in the Hampshire Basin, UK: taxonomy and stratigraphy of the mammals on either side of this major Palaeogene faunal turnover, in WHITTAKER J. E. & HART M. B. (eds), *Micropalaeontology, sedimentary environments and stratigraphy: a tribute to Dennis Curry (1912–2001)*. The Geological Society of London, London: 147-215. <https://doi.org/10.1144/TMS004.8>

- HOOKE J. J. & HARRISON D. L. 2008. — A new clade of omomyid primates from the European Paleogene. *Journal of Vertebrate Paleontology* 28 (3): 826-840. [https://doi.org/10.1671/0272-4634\(2008\)28\[826:ANCOOP\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2008)28[826:ANCOOP]2.0.CO;2)
- HOOKE J. J., COOK E. & BENTON M. J. 2005. — British Tertiary fossil mammal GCR sites, in BENTON M. J., COOK E. & HOOKE J. J. (eds), *Mesozoic and Tertiary Fossil Mammals and Birds of Great Britain. Geological Conservation Review Series* 32: 68-124.
- HOOLEY R. W. 1905. — On a new Tortoise from the Lower Headon Beds of Hordwell, *Nicoria headonensis* sp. nov. *Geological Magazine* 2 (2): 66-68. <https://doi.org/10.1017/S0016756800129255>
- HSIANG A. Y., FIELD D. J., WEBSTER T. H., BEHLKE A. D. B., DAVIS M. B., RACICOT R. A. & GAUTHIER J. A. 2015. — The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. *BMC Evolutionary Biology* 15 (87). <https://doi.org/10.1186/s12862-015-0358-5>
- HUXLEY T. H. 1859. — On the dermal armour of *Crocodylus hastingsiae*. *Quarterly Journal of the Geological Society of London* 15: 678-680. <https://doi.org/10.1144/GSL.JGS.1859.015.01-02.74>
- KAPUR V. V., PICKFORD M., CHAUHAN G. & THAKKAR M. G. 2021. — A middle Miocene (~14 Ma) vertebrate assemblage from Palasava, Rapar Taluka, Kutch (Kachchh) District, Gujarat State, western India. *Historical Biology* 33 (5): 595-615. <https://doi.org/10.1080/08912963.2019.1648451>
- KLEMBARA J. & GREEN B. 2010. — Anguimorph lizards (Squamata, Anguimorpha) from the Middle and Upper Eocene of the Hampshire Basin of Southern England. *Journal of Systematic Palaeontology* 8 (1): 97-129. <https://doi.org/10.1080/14772011003603531>
- LAWSON R., SLOWINSKI J. B., CROTHER B. I. & BURBRINK F. T. 2005. — Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 37 (2): 581-601. <https://doi.org/10.1016/j.ympev.2005.07.016>
- LEE M. S. Y., HUGALL A. F., LAWSON R. & SCANLON J. D. 2007. — Phylogeny of snakes (Serpentes): combining morphological and molecular data in likelihood, Bayesian and parsimony analyses. *Systematics and Biodiversity* 5 (4): 371-389. <https://doi.org/10.1017/S1477200007002290>
- 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>
- LYDEKKER R. 1887. — Note on the Hordwell and other crocodylians. *Geological Magazine* 4 (7): 307-312. <https://doi.org/10.1017/S001675680019377X>
- LYDEKKER R. 1888a. — *Catalogue of Fossil Reptiles and Amphibians in the British Museum (Natural History). Part I. Containing the Orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria*. British Museum (Natural History), London, 309 p.
- LYDEKKER R. 1888b. — Notes on Tertiary Lacertilia and Ophidia. *Geological Magazine* 5 (3): 110-113. <https://doi.org/10.1017/S0016756800173480>
- LYDEKKER R. 1889. — *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History): Part III. The Order Chelonina*. British Museum (Natural History), London, 239 p.
- MASSALONGO A. 1859. — *Specimen photographicum animalium quorundam plantarumque fossilium agri Veronensis*. Vicentini et Franchini Excudebant, Verona, 101 p.
- MCCARTNEY J. A. & SEIFFERT E. R. 2016. — A late Eocene snake fauna from the Fayum Depression, Egypt. *Journal of Vertebrate Paleontology* 36 (1): e1029580. <https://doi.org/10.1080/02724634.2015.1029580>
- MCDOWELL S. B. 1979. — A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part III. Boinae and Acrochordoidea (Reptilia, Serpentes). *Journal of Herpetology* 13 (1): 1-92. <https://doi.org/10.2307/1563761>
- MEYER H. VON 1855. — [untitled; in Mittheilungen an Professor Bronn gerichtet]. *Neues Jahrbuch für Mineralogie Geologie und Paläontologie* 1855: 326-337.
- MILNER A. C. 1986. — Amphibians and squamates from the Palaeogene of England, in ROČEK Z. (ed.), *Studies in Herpetology*. Charles University, Prague and Societas Europaea Herpetologica, Prague: 685-688.
- MILNER A. C., MILNER A. R. & ESTES R. 1982. — Amphibians and Squamates from the Upper Eocene of Hordle Cliff, Hampshire — a preliminary report. *Tertiary Research* 4: 149-154.
- NOPCSA F. 1923. — *Eidolosaurus* und *Pachyophis*. Zwei neue Neocom-Reptilien. *Palaeontographica* 65: 99-154.
- OWEN R. 1841. — Description of some ophiolites (*Palaeophis toliapicus*) from the London Clay of Sheppey, indicating an extinct species of serpent. *Transactions of the Geological Society Second Series* 2 (6): 209-210. <https://doi.org/10.1144/transgslb.6.1.209>
- OWEN R. 1850. — Part III. Ophidia (*Palaeophis*, &c.), in OWEN R. (ed.), *Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds*. Palaeontographical Society of London, London: 51-63.
- OWEN R. & BELL T. 1849. — Part I: Chelonina, in OWEN R. & BELL T. (eds), *Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds*. Palaeontographical Society of London, London: 1-76. <https://doi.org/10.5962/bhl.title.61856>
- 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>
- PYRON R. A., BURBRINK F. T., COLLI G. R., DE OCA A. N. M., VITT L. J., KUCZYNSKI C. A. & WIENS J. J. 2011. — The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution* 58 (2): 329-342. <https://doi.org/10.1016/j.ympev.2010.11.006>
- PYRON R. A., BURBRINK F. T. & WIENS J. J. 2013. — A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 93. <https://doi.org/10.1186/1471-2148-13-93>
- RAGE J.-C. 1973. — Présence de *Dunnophis* (Reptilia, Serpentes) dans l'Eocène et l'Oligocène européens. *Compte rendu sommaire des séances de la Société Géologique de France* 1973 (3): 76-78.
- RAGE J.-C. 1974. — Les Serpents des Phosphorites du Quercy. *Palaeovertebrata* 6: 274-303.
- RAGE J.-C. 1975. — Un Caenophidien primitif (Reptilia, Serpentes) dans l'Eocène inférieur. *Compte rendu sommaire des séances de la Société Géologique de France* 1975 (2): 46-47.
- RAGE J.-C. 1977. — An erycine snake (Boidae) of the genus *Calamagras* from the French lower Eocene, with comments on the phylogeny of the Erycinae. *Herpetologica* 33 (4): 459-463. <https://www.jstor.org/stable/3891716>
- RAGE J.-C. 1978a. — L'origine des Colubroïdes et des Acrochordoïdes (Reptilia, Serpentes). *Comptes rendus de l'Académie des sciences Série 4* 286 (8): 595-597.
- RAGE J.-C. 1978b. — 5. Squamates, in GEZE B., RAGE J.-C., VERGNAUD-GRAZZINI F., DE BROIN F., BUFFETAUT E., MOURIER-CHAUVIRE C., CROCHET J.-Y., SIGÉ B., SUDRE J., REMY A., LANGE-BADRE L., DE BONIS L., HARTENBERGER J. L. & VIANEY-LIAUD M. (eds), *La poche à Phosphate de Ste-Néoule (Lot) et sa faune de vertébrés du Ludien supérieur*. *Palaeovertebrata* 8: 201-215.
- RAGE J.-C. 1980. — Un Serpent marin nouveau de l'Eocène de Belgique. Le problème des Serpents marins du Paléogène. *Comptes rendus de l'Académie des sciences, Série 4* 291: 469-471.
- RAGE J.-C. 1983. — Les serpents aquatiques de l'Eocène européen. Définition des espèces et aspects stratigraphiques. *Bulletin du Muséum national d'Histoire naturelle, Série 4, Section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie* 5: 213-241.

- RAGE J.-C. 1984. — Serpentes, in WELLNHOFER P. (ed.), *Encyclopedia of Paleoherpétology*, part 11. Gustav Fischer, Stuttgart, New York, 80 p.
- RAGE J.-C. 1988a. — 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. 1988b. — The oldest known colubrid snakes. The state of the art. *Acta Zoologica Cracoviensia* 31 (13): 457-474.
- RAGE J.-C. 2008. — Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part III. Ungaliophiinae, Booids incertae sedis, and Caenophidia. Summary, update, and discussion of the snake fauna from the locality. *Palaeovertebrata* 36 (1-4): 37-73. <https://doi.org/10.18563/pv.36.1-4.37-73>
- 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>
- RAGE J.-C. & FORD R. L. E. 1980. — Amphibians and squamates from the Upper Eocene of the Isle of Wight. *Tertiary Research* 3: 47-60.
- RAGE J.-C. & WERNER C. 1999. — Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: the earliest snake assemblage. *Palaeontologia Africana* 35: 85-110.
- RAGE J.-C., GUPTA S. S. & PRASAD G. V. R. 2001. — Amphibians and squamates from the Neogene Siwalik beds of Jammu and Kashmir, India. *Paläontologische Zeitschrift* 75 (2): 197-205. <https://doi.org/10.1007/BF02988013>
- RAGE J.-C., FOLIE A., RANA R. S., SINGH H., ROSE K. D. & SMITH T. 2008. — A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India. *Acta Palaeontologica Polonica* 53 (3): 391-403. <https://doi.org/10.4202/app.2008.0303>
- RAGE J.-C., ADACI M., BENSALAH M., MAHBOUBI M., MARIVAUX L., MEBROUK F. & TABUCE R. 2021. — Latest Early-early Middle Eocene deposits of Algeria (Glib Zegdou, HGL50), yield the richest and most diverse fauna of amphibians and squamate reptiles from the Palaeogene of Africa. *Palaeovertebrata* 44: e1 32 pp.
- RIEPEL O. 1988. — A review of the origin of snakes. *Evolutionary Biology* 22: 37-130. https://doi.org/10.1007/978-1-4613-0931-4_2
- RIEPEL O. & ZAHER H. 2001. — The development of the skull in *Acrochordus granulatus* (Schneider) (Reptilia: Serpentes), with special consideration of the otico-occipital complex. *Journal of Morphology* 249 (3): 252-266. <https://doi.org/10.1002/jmor.1053>
- ROCHEBRUNE A. T. DE 1880. — Révision des ophidiens fossiles du Muséum d'Histoire naturelle. *Nouvelles Archives du Muséum d'Histoire naturelle*, série 2, 3: 271-296.
- SANDERS K. L., MUMPUNI, HAMIDY A., HEAD J. J. & GOWER D. J. 2010. — Phylogeny and divergence times of filesnakes (*Acrochordus*): inferences from morphology, fossils and three molecular loci. *Molecular Phylogenetics and Evolution* 56 (3): 857-867. <https://doi.org/10.1016/j.ympev.2010.04.031>
- SCANFERLA A. & SMITH K. T. 2020. — Exquisitely preserved fossil snakes of Messel: Insight into the evolution, biogeography, habitat preferences and sensory ecology of early boas. *Diversity* 12 (3): 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. & BASZIO S. 2004. — *Messelophis ermannorum* n.sp., eine neue Zwergboa (Serpentes: Boidae: Tropidopheinae) aus dem Mittel-Eozän von Messel. *Courier Forschungsinstitut Senckenberg* 252: 67-77.
- SCHNEIDER J. G. 1799. — *Historiae amphibiorum naturalis et literariae. Fasciculus primus, continens Ranas, Calamitas, Bufones, Salamandras et Hydros in genera et species descriptos notisque suis distinctos*. Friederici Frommanni, Jena, 264 p. <https://doi.org/10.5962/bhl.title.78757>
- SEGNETTI 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 (2): 119-143. <https://doi.org/10.4435/BSP.2022.14>
- SEELEY H. G. 1876. — On remains of *Emys hordwellensis* (Seeley) from the Lower Hordwell Beds in the Hordwell Cliff, contained in the Woowardian Museum of the University of Cambridge. *Quarterly Journal of the Geological Society* 32: 445-450. <https://doi.org/10.1144/GSL.JGS.1876.032.01-04.51>
- SLOWINSKI J. B. & LAWSON R. 2002. — Snake phylogeny: evidence from nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* 24 (2): 194-202. [https://doi.org/10.1016/S1055-7903\(02\)00239-7](https://doi.org/10.1016/S1055-7903(02)00239-7)
- SMITH K. T. 2013. — New constraints on the evolution of the snake clades Ungaliophiinae, Loxocemidae and Colubridae (Serpentes), with comments on the fossil history of erycine boids in North America. *Zoologischer Anzeiger* 252 (2): 157-182. <https://doi.org/10.1016/j.jcz.2012.05.006>
- 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 Evolutionary History of Snakes*. Cambridge University Press, Cambridge: 55-84. <https://doi.org/10.1017/9781108938891.006>
- 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 (1-3): 75-103. <https://doi.org/10.1127/pala/2021/0119>
- STREICHER J. W. & WIENS J. J. 2016. — Phylogenomic analyses reveal novel relationships among snake families. *Molecular Phylogenetics and Evolution* 100: 160-169. <https://doi.org/10.1016/j.ympev.2016.04.015>
- SZYNDLAR Z. 1994. — Oligocene snakes of southern Germany. *Journal of Vertebrate Paleontology* 14 (1): 24-37. <https://doi.org/10.1080/02724634.1994.10011536>
- SZYNDLAR Z. & BÖHME W. 1996. — Redescription of *Tropidonotus atavus* von Meyer, 1855 from the upper Oligocene of Rott (Germany) and its allocation to *Rottophis* gen. nov. (Serpentes, Boidae). *Palaeontographica A* 240 (4-6): 145-161. <https://doi.org/10.1127/pala/240/1996/145>
- SZYNDLAR Z. & GEORGALIS G. L. 2023. — An illustrated atlas of the vertebral morphology of extant non-caenophidian snakes, with special emphasis on the cloacal and caudal portions of the column. *Vertebrate Zoology* 73: 717-886. <https://doi.org/10.3897/vz.73.e101372>
- SZYNDLAR Z. & GEORGALIS G. L. in press. — When snake vertebrae go to an extreme – revision, vertebral morphology, and intracolumnar variation of the enigmatic snake *Cadurceryx* Hoffstetter & Rage, 1972, from the Eocene of Europe, in GEORGALIS G. L., ZAHER H. & LAURIN M. (eds), *Snakes from the Cenozoic of Europe – towards a macroevolutionary and palaeobiogeographic synthesis*. *Comptes Rendus Palevol*.
- SZYNDLAR Z. & RAGE J.-C. 2003. — *Non-erycine Booidea from the Oligocene and Miocene of Europe*. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, 111 p.
- SZYNDLAR Z. & SCHLEICH H.-H. 1993. — Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern Germany. *Stuttgarter Beiträge zur Naturkunde B* 192: 1-47.

- SZYNDLAR Z., SMITH R. & RAGE J.-C. 2008. — A new dwarf boa (Serpentes, Booidea, 'Tropidophiidae') from the Early Oligocene of Belgium: a case of the isolation of Western European snake faunas. *Zoological Journal of the Linnean Society* 152 (2): 393–406. <https://doi.org/10.1111/j.1096-3642.2007.00357.x>
- VASILEIADOU K., HOOKER J. J. & COLLINSON M. E. 2022. — Taphonomy of an Eocene micromammal assemblage in a lake-margin depositional setting elucidates an ancient food web. *Palaeontologia Electronica* 25: a16. <https://doi.org/10.26879/1214>
- VIDAL N., DELMAS A.-S., DAVID P., CRUAUD C., COULOUX A. & HEDGES S. B. 2007. — The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. *Comptes Rendus Biologies* 330 (2): 182–187. <https://doi.org/10.1016/j.crvi.2006.10.001>
- WEST R. M., HUTCHISON J. H. & MUNTHE J. 1991. — Miocene vertebrates from the Siwalik Group, western Nepal. *Journal of Vertebrate Paleontology* 11 (1): 108–129. <https://doi.org/10.1080/02724634.1991.10011378>
- 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>
- ZAHER H., GRAZZIOTIN F. G., CADLE J. E., MURPHY R. W., CESAR DE MOURA-LEITE J. & BONATTO S. L. 2009. — Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia* 49 (11): 115–153. <https://doi.org/10.1590/S0031-10492009001100001>
- ZAHER H., MURPHY R. W., ARREDONDO J. C., GRABOSKI R., MACHADO-FILHO P. R., MAHLOW K., MONTINGELLI G. G., QUADROS A. B., ORLOV N. L., WILKINSON M., ZHANG Y.-P. & GRAZZIOTIN F. G. 2019. — Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS ONE* 14 (5): e0216148. <https://doi.org/10.1371/journal.pone.0216148>
- ZAHER H., FOLIE A., BOTALLO QUADROS A., RANA R. S., KUMAR K., ROSE K. D., FAHMY M. & SMITH T. 2021. — Additional vertebral material of *Thaumastophis* (Serpentes: Caenophidia) from the early Eocene of India provides new insights on the early diversification of colubroidean snakes. *Geobios* 66–67: 35–43. <https://doi.org/10.1016/j.geobios.2020.06.009>
- ZAHER H., MOHABEY D. M., GRAZZIOTIN F. G. & MANTILLA J. A. W. 2023. — The skull of *Sanajeh indicus*, a Cretaceous snake with an upper temporal bar, and the origin of ophidian wide-gaped feeding. *Zoological Journal of the Linnean Society* 197 (3): 656–697. <https://doi.org/10.1093/zoolinnean/zlac001>
- ZHENG Y. & WIENS J. J. 2016. — Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution* 94 (Part B): 537–547. <https://doi.org/10.1016/j.ympev.2015.10.009>

Submitted on 4 December 2024;

accepted on 9 August 2025;

published on 7 November 2025.

APPENDICES

APPENDIX 1. — Flythrough video of the μ CT of the holotype trunk vertebra NHMUK PV R 10795 of *Paradoxophidion richardoweni* n. gen., n. sp. in horizontal cross-section without background. Available at: https://doi.org/10.5852/cr-palevol2025v24a25_s1

APPENDIX 2. — Flythrough video of the μ CT of the caudal vertebra NHMUK PV R 10796 of *Paradoxophidion richardoweni* n. gen., n. sp. in oblique view with horizontal cross-sections. Available at: https://doi.org/10.5852/cr-palevol2025v24a25_s2