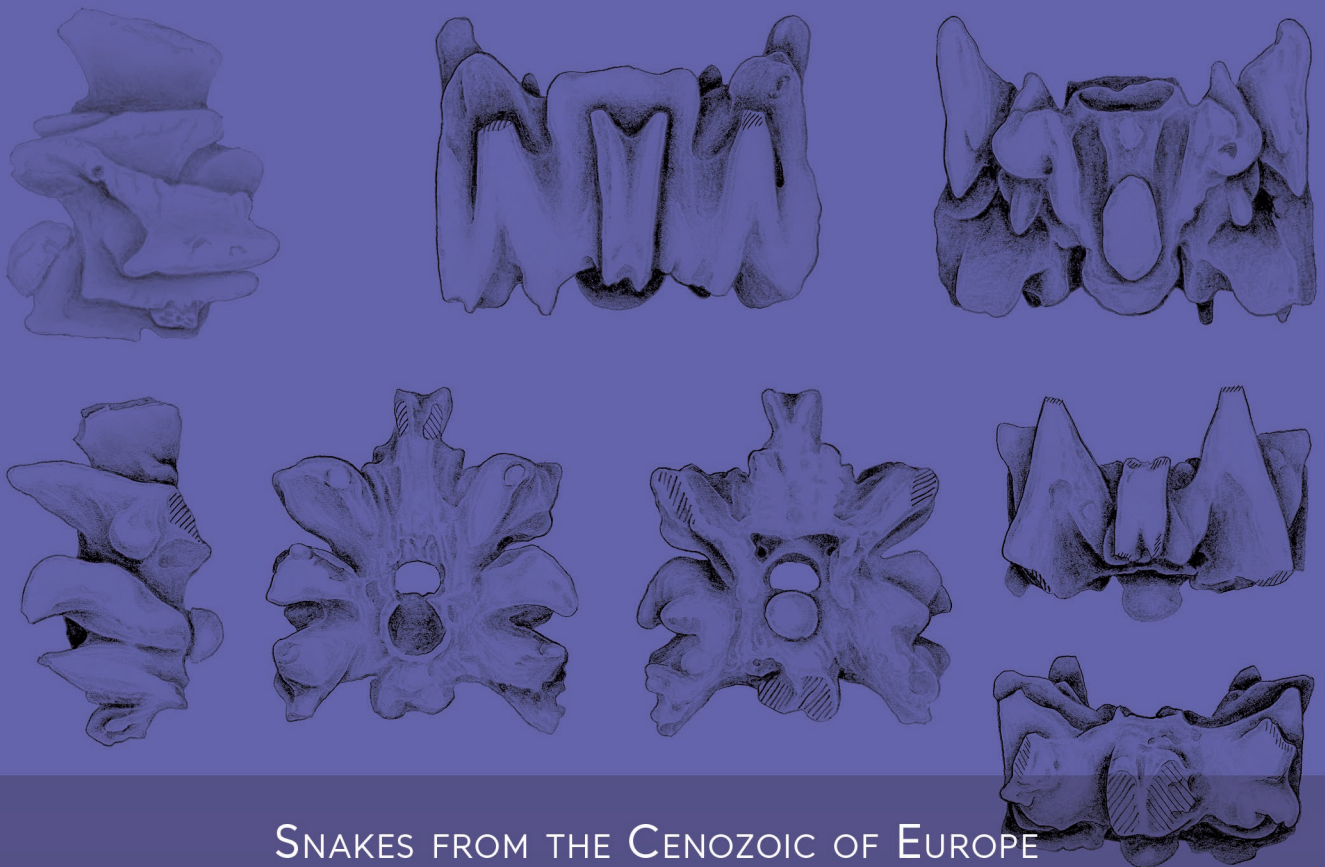


When snake vertebrae go to an extreme – revision,
vertebral morphology, and intracolumnar variation
of the enigmatic snake *Cadurceryx* Hoffstetter
& Rage, 1972, from the Eocene of Europe

Zbigniew SZYNDLAR & Georgios L. GEORGALIS



SNAKES FROM THE CENOZOIC OF EUROPE

– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

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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

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ABSTRACT

We provide a thorough documentation of the vertebral morphology and intracolumnar variation of the enigmatic snake *Cadurceryx* Hoffstetter & Rage, 1972, from the Eocene of France. Based on abundant vertebrae, pertaining to practically all portions of the column, originating from the middle Eocene (MP 16) of Lavergne in the Phosphorites du Quercy, we conduct a revision of the taxon, provide an emended diagnosis, and highlight a number of distinctive vertebral features that differentiate it from all other snakes. Most prominently, *Cadurceryx* is characterized by the presence of additional apophyses throughout the trunk, cloacal, and caudal vertebrae, which form (at least partly) true articular joints linking neighbouring vertebrae (additional intervertebral articulations). These additional apophyses are: pterapophyses (present in all vertebrae), extensions of zygapophyses and neural spine, as well as extensions of pleurapophyses (present in caudal vertebrae). We further present additional trunk and/or caudal vertebrae from several other localities in the area of the Phosphorites du Quercy: the middle Eocene (MP 16) of Malpérié, the late Eocene (MP 17) of La Bouffie and Rosières 2, the late Eocene (MP 18) of Sainte Néboule, and from imprecise localities from the “old Quercy collections”. We further conduct a critical evaluation of the original description of the taxon. Based on all these, we conclude that a single species of *Cadurceryx* was present in France during the middle and late Eocene, i.e., the type species *Cadurceryx filholi* Hoffstetter & Rage, 1972. A second species of the genus, *Cadurceryx pearchi* Holman, Harrison & Ward, 2006, known exclusively from caudal vertebrae from the late Eocene (MP 17) of Hordle Cliff, England, is herein also assessed; based on a critical approach of the original publication that established the English species, coupled with the presentation of some new caudal vertebrae from

KEY WORDS
Serpentes,
vertebrae,
skeletal description,
Paleogene.

its type locality, we consider that *Cadurceryx pearchi* represents a *nomen dubium*, with the material potentially pertaining to ?*Cadurceryx* sp. or some indeterminate erycid or charinid snake. We provide a thorough overview of the geographic and stratigraphic distribution of *Cadurceryx*. Through a detailed comparison with extinct and extant snakes, we discard affinities of *Cadurceryx* with erycids or charinaids, taking also into consideration that this grouping, according to molecular data, is not monophyletic and that the evolution of complex caudal vertebral morphologies in erycids and charinaids is likely homoplastic. Accordingly, the shared distinctive features of *Cadurceryx* with erycids and charinaids (presence of additional apophyses in caudal vertebrae that form true articular joints linking neighbouring vertebrae) are herein also regarded as homoplastic. Instead, we show that *Cadurceryx* possesses a vertebral synapomorphy of tropidophiids, namely the prominent blade-like hypapophysis on trunk vertebrae, that in posterior trunk vertebrae possesses a distinct, straight anteroventral corner, plus additional shared vertebral features. Accordingly, we herein tentatively envisage *Cadurceryx* as a tropidophiid with convergently evolved apophyseal morphologies with erycids and charinaids. Finally, we attempt a speculative interpretation of the functional morphology of the complex structures of the vertebrae of *Cadurceryx*, tentatively suggesting that these true articular joints linking neighbouring vertebrae may have offered increased rigidity across the vertebral column and may have acted as an antipredator mechanism.

RÉSUMÉ

Quand les vertèbres des serpents atteignent l'extrême – révision, morphologie vertébrale et variation intracolonnaire du mystérieux serpent Cadurceryx Hoffstetter & Rage, 1972, de l'Eocène européen.

Nous fournissons une documentation complète de la morphologie vertébrale et de la variation intracolonnaire du serpent énigmatique *Cadurceryx* Hoffstetter & Rage, 1972, de l'Eocène de France. Sur la base de vertèbres abondantes, appartenant à pratiquement toutes les parties de la colonne, originaires de l'Eocène moyen (MP 16) de Lavergne dans les Phosphorites du Quercy, nous effectuons une révision du taxon, fournissons une diagnose corrigée et mettons en évidence un certain nombre de caractéristiques vertébrales distinctives qui le différencient de tous les autres serpents. Plus particulièrement, *Cadurceryx* est caractérisé par la présence d'apophyses supplémentaires dans les vertèbres du tronc, du cloaque et de la caudale, qui forment (au moins en partie) de véritables articulations reliant les vertèbres voisines (articulations intervertébrales supplémentaires). Ces apophyses supplémentaires sont : des ptéropophyses (présentes dans toutes les vertèbres), des extensions de zygapophyses et d'épines neurales, ainsi que des extensions de pleuropophyses (présentes dans les vertèbres caudales). Nous présentons également des vertèbres tronculaires et/ou caudales supplémentaires provenant de plusieurs autres localités de la région des Phosphorites du Quercy : l'Eocène moyen (MP 16) de Malpérié, l'Eocène supérieur (MP 17) de La Bouffie et Rosières 2, l'Eocène supérieur (MP 18) de Sainte Néboule, et de localités imprécises des « anciennes collections du Quercy ». Nous effectuons également une évaluation critique de la description originale du taxon. Sur la base de tous ces éléments, nous concluons qu'une seule espèce de *Cadurceryx* était présente en France pendant l'Eocène moyen et supérieur, à savoir l'espèce type *Cadurceryx filholi* Hoffstetter & Rage, 1972. Une seconde espèce du genre, *Cadurceryx pearchi* Holman, Harrison & Ward, 2006, connue exclusivement à partir de vertèbres caudales de l'Eocène supérieur (MP 17) de Hordle Cliff, en Angleterre, est également évaluée ici ; sur la base d'une approche critique de la publication originale qui a établi l'espèce anglaise, couplée à la présentation de quelques nouvelles vertèbres caudales de sa localité type, nous considérons que *Cadurceryx pearchi* représente un *nomen dubium*, le matériel appartenant potentiellement à ?*Cadurceryx* sp. ou un serpent érycidé ou charinid indéterminé. Nous fournissons un aperçu complet de la distribution géographique et stratigraphique de *Cadurceryx*. Grâce à une comparaison détaillée avec des serpents éteints et actuels, nous écartons les affinités de *Cadurceryx* avec les érycidés ou les charinidés, prenant également en compte que ce groupement, selon les données moléculaires, n'est pas monophylétique et que l'évolution des morphologies vertébrales caudales complexes chez les érycidés et les charinidés est probablement homoplasique. Par conséquent, les caractéristiques distinctives communes de *Cadurceryx* avec les érycidés et les charinidés (présence d'apophyses supplémentaires dans les vertèbres caudales qui forment de véritables articulations reliant les vertèbres voisines) sont également considérées ici comme homoplasiques. Au lieu de cela, nous montrons que *Cadurceryx* possède une synapomorphie vertébrale des tropidophiidés, à savoir l'hypapophyse proéminente en forme de lame sur les vertèbres du tronc, qui, dans les vertèbres postérieures du tronc, possède un coin antéroventral droit distinct, ainsi que d'autres caractéristiques vertébrales communes. En conséquence, nous envisageons ici provisoirement *Cadurceryx* comme un tropidophiidé présentant des morphologies apophysaires convergentes avec les érycidés et les charinidés. Enfin, nous proposons une interprétation spéculative de la morphologie fonctionnelle des structures complexes des vertèbres de *Cadurceryx*, suggérant provisoirement que ces véritables articulations reliant les vertèbres voisines auraient pu offrir une rigidité accrue à la colonne vertébrale et agir comme un mécanisme anti-prédateur.

MOTS CLÉS
Serpentes,
vertèbres,
description du squelette,
Paléogène.

INTRODUCTION

Snake vertebrae are characterized by a combination of unique anatomical features, including a distinctive zygosphen-zygantrum articulation, that can readily differentiate them from all other squamates (Auffenberg 1963; Hoffstetter & Gasc 1969; Rage 1984b; Szyndlar 1984; Szyndlar & Georgalis 2023). Besides the basic structures observed across snakes, additional, bizarre anatomical structures or protuberances can also be observed across distantly related groups, such as the pterapophyses of palaeophiids (Rage 1983; Rage *et al.* 2003; Georgalis *et al.* 2021b; Georgalis 2023; Datta & Bajpai 2025), the distinct zygapophyseal expansions observed across an array of distantly related caenophidians (e.g. Hoffstetter 1939; Smith 1943; Bogert 1964; Fritts & Smith 1969; Hoffstetter & Gasc 1969; Slowinski 1994; Sheil 1998; Sheil & Grant 2001; Zaher *et al.* 2019), or the highly complex caudal vertebrae of erycids and charinaids (Bogert 1968a; Szyndlar 1994; Szyndlar & Georgalis 2023). Particularly for the latter, these rather complex structures on their caudal vertebrae, have been one of the principal characters that have in the past united the Old World Erycidae Bonaparte, 1831 (*sensu* Pylon *et al.* 2014) and the New World Charinaidae Gray, 1849 (*sensu* Burbrink *et al.* 2020).

Indeed, this taxonomic arrangement uniting the Old World erycids and the New World charinaids into an expanded concept of Erycidae or Erycinae Bonaparte, 1831 had practically met the almost absolute consensus across snake researchers during the second half of the 20th century (e.g. Hoffstetter 1955; Romer 1956; Kuhn 1966; Underwood 1967, 1976; Bogert 1968a; Hoffstetter & Rage 1972; Rage 1984b; McDowell 1987; Szyndlar 1987, 1991; Kluge 1993; Szyndlar & Schleich 1994; Holman 2000). Phylogenetic analyses based on morphology have found support of this grouping (e.g. Kluge 1993; Gauthier *et al.* 2012; Scanferla *et al.* 2016; Smith & Scanferla 2021), with its monophyly being primarily based on the caudal vertebral apophyses as synapomorphies (e.g. Gauthier *et al.* 2012). However, molecular data robustly and universally reject monophyly of Erycidae + Charinaidae, placing instead the latter as the sister group of ungaliophiids (Lawson *et al.* 2004; Vidal *et al.* 2007; Lynch & Wagner 2009; Wiens *et al.* 2012; Pylon *et al.* 2013; Reynolds *et al.* 2014; Hsiang *et al.* 2015; Figueroa *et al.* 2016; Harrington & Reeder 2017; Burbrink *et al.* 2020), a topology recovered also in total evidence (morphology + molecules) phylogenies (Zaher *et al.* 2023; Palci *et al.* 2024; Croghan *et al.* 2025).

A number of fossil forms, primarily from the Paleogene and Neogene of Europe and North America, has been referred to either of these two extant families (or even to the extant genera *Eryx* Daudin, 1803b, *Charina* Gray, 1849, and *Lichanura* Cope, 1861), a taxonomic assignment facilitated also by the presence of these complex structures on the caudal vertebral region (e.g. Szyndlar 1991; Szyndlar & Schleich 1994; Smith & Scanferla 2021). Nevertheless, certain extinct taxa from the Paleogene and Neogene of Europe and North America with distinctive caudal vertebral morphology (e.g. Hoffstetter & Rage 1972; Rage 1977; Zerova 1989) cannot be confidently

assigned to either erycids and charinaids and, taking into consideration that this grouping is a polyphyletic accumulation of non-related snakes, they have been tentatively collectively lumped as “erycines” (see Smith & Georgalis 2022).

One such prominent case of a bizarre “erycine” of imprecise affinities is the genus *Cadurceryx* Hoffstetter & Rage, 1972, from the Eocene of Western Europe. The genus was originally established by Hoffstetter & Rage (1972) in order to accommodate the species *Cadurceryx filholi* Hoffstetter & Rage, 1972, based on vertebral material from the Eocene of the Phosphorites du Quercy, France. The taxon was characterized by unique vertebral morphology, most prominently the presence of bizarre additional apophyses. A few additional fossil vertebrae, either identified to the species level (as *Cadurceryx filholi*), or only tentatively to the same species (as *Cadurceryx* cf. *filholi*), or only to the genus level (as *Cadurceryx* sp.), were subsequently described and illustrated from some further middle and late Eocene localities in France (Hoffstetter & Rage 1972; Rage 1984b, 1988, 2013). Furthermore, a second species of the genus, *Cadurceryx pearchi* Holman, Harrison & Ward, 2006, was later established upon material from the late Eocene (MP 17) of Hordle Cliff, England, by Holman *et al.* (2006), thus expanding significantly the geographic distribution, as well as the taxonomic diversity, of the genus.

Nevertheless, even though vertebrae of *Cadurceryx* have always appeared as bizarre to several ophidian palaeontologists in the past more than 50 years, a proper knowledge of the vertebral morphology and intracolumnar variation of this enigmatic and intriguing taxon is lacking. In the present paper, we document in detail abundant vertebrae of *Cadurceryx filholi*, pertaining to practically all portions of the vertebral column, from the middle Eocene (MP 16) locality of Lavergne in the Phosphorites du Quercy, France. We provide detailed descriptions and figures, focusing on the additional vertebral apophyses of this snake and its intracolumnar variation. We provide photographs of the holotype vertebra for the first time and present also additional vertebrae from certain other localities from Quercy. A critical evaluation of the original description of the taxon by Hoffstetter & Rage (1972) is conducted. We also revise the status of the English taxon *Cadurceryx pearchi*, based on its original description by Holman *et al.* (2006) but also on new caudal vertebrae from its type locality. Through detailed comparisons with several extinct and extant snakes, we finally discuss the potential taxonomic affinities of *Cadurceryx* within other snakes.

MATERIAL AND METHODS

The new fossil material from the middle Eocene (MP 16) of Lavergne described herein pertains to the collections of SU. In addition, we re-document previously published specimens from the “old collections” of Quercy, the middle Eocene (MP 16) of Malpéridé, and the late Eocene (MP 17) of Rosières 2, from the collections of MNHN, NHMW, and UM. Finally, we provide figures of previously undescribed vertebrae of *Cadurceryx filholi* from the Quercy late Eocene

localities of La Bouffie (MP 17) and Sainte Néboule (MP 18), from the collections of UM, plus of *Cadurceryx pearchi* from the late Eocene (MP 17A) of Christchurch Bay at Hordle Cliff, England, from the collections of NHMUK.

The UM *Cadurceryx* material from Sainte-Néboule and La Bouffie was collected by palaeontologists from UM and other French institutes (Monique Vianey-Liaud, Jean Sudre, Louis De Bonis, Jean-Yves Crochet, Bernard Sigé, and Bernard Marandat) in expeditions held during the 1970s-1980s. The single NHMW specimen from the “old collections” of Quercy belongs to a long “forgotten” collection of reptiles and amphibians that were acquired by the NHMW in the 19th century and only recently (2019) rediscovered by GLG; they all originate from imprecise localities, with the age of the specimen of the present study probably lying somewhere in the middle and late Eocene (for details on the herpetofaunal elements of this NHMW collection, see Georgalis *et al.* 2021a, c, 2023). The NHMUK specimens from Christchurch Bay at Hordle Cliff, England, were collected by Roy Gardner in 1981.

The drawings of the vertebrae from Lavergne, Malpérié, and Rosières 2, were made by ZS. Photographs were made by GLG. Terminology of snake vertebrae follows Szyndlar & Georgalis (2023). In particular for vertebrae of erycid and charinaid snakes, it follows Szyndlar (1994) and Szyndlar & Georgalis (2023).

INSTITUTIONAL ABBREVIATIONS

ICPS	Institut Català de Paleontologia Miquel Crusafont, Sabadell;
MNHN	Muséum national d'Histoire naturelle, Paris;
MSUVP	Michigan State University Museum of Vertebrate Paleontology, East Lansing, Michigan;
NHMUK	Natural History Museum, London;
NHMW	Naturhistorisches Museum Wien, Vienna;
SU (formerly UPVI)	Sorbonne Université, Paris (formerly Université de Paris VI);
UM	Institut des Sciences de l'Évolution, Université de Montpellier.

SYSTEMATIC PALAEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
?TROPIDOPHIIDAE Brongersma, 1951

Cadurceryx Hoffstetter & Rage, 1972

Cadurceryx Hoffstetter & Rage, 1972: 91.

TYPE SPECIES. — *Cadurceryx filholi* Hoffstetter & Rage, 1972.

OTHER VALID SPECIES. — None (for details, see below).

EMENDED DIAGNOSIS. — *Cadurceryx* can be differentiated from all other snakes by the presence of additional apophyses throughout the trunk, cloacal, and caudal vertebrae, which form (at least partly) true articular joints linking neighbouring vertebrae (additional intervertebral articulations). These additional apophyses are: pterapophyses (present in all vertebrae), extensions of zygapophyses and neural spine, as well as extensions of pleurapophyses (present in caudal vertebrae). Moreover, there is a progressive increase of

the complexity of succeeding vertebrae in the trunk portion of the column, from relatively simple anterior trunk vertebrae to moderately complex mid-trunk vertebrae, finally followed by highly complex vertebrae (“Posterior trunk vertebrae”). *Cadurceryx* is further diagnosed by the combination of the following features: centrum distinctly wider than long; presence of broad hypapophyses throughout the trunk and anterior cloacal vertebrae, which in posterior trunk vertebrae becomes even broader and possesses a distinct anteroventral corner forming approximately a right angle; presence of haemapophyses on more posterior caudal vertebrae; pterapophyses more prominent in mid- and posterior trunk vertebrae; pterapophyses extending forwards and backwards in trunk vertebrae, but extending almost exclusively forwards in caudal vertebrae; presence of a rather thick and occasionally anteriorly bifurcated neural spine in dorsal view; distinct interzygapophyseal connections present in trunk vertebrae but completely absent in cloacal and caudal vertebrae; in posterior trunk vertebrae, the posterior extensions of prezygapophyses and anterior extensions of postzygapophyses fuse with each other forming a thick bar; absence of paracotylar foramina.

Cadurceryx filholi Hoffstetter & Rage, 1972
(Figs 1-18)

Cadurceryx filholi Hoffstetter & Rage, 1972: 91.

TAXONOMIC HISTORY. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 (new genus and species). Note that the “Taxonomic history” section here deals only with novel nomenclatural acts, new taxonomic combinations, or novel taxonomic renderings of the taxon, similarly to the style proposed in other recent reptilian papers (e.g. Joyce 2016; Georgalis & Joyce 2017; Georgalis *et al.* 2021c; Georgalis 2025).

TYPE MATERIAL. — **Holotype.** France • 1 specimen (a posterior trunk vertebra [not anterior cloacal vertebra as stated by Rage 1984b]); Phosphorites du Quercy (imprecise locality); probably between middle and late Eocene; MNHN.FQU16301 (formerly MNHN Qu 301) (Hoffstetter & Rage 1972: fig. 6a, pl. I.1; Rage 1984b: fig. 16e; this paper, Fig. 1).

TYPE LOCALITY AND AGE. — Similar to most other fossil specimens from the so called “old collections” of Quercy, there are no precise locality data for the holotype of *Cadurceryx filholi*, apart from the general information that it originates from the area of the Phosphorites du Quercy. However, this information is rather general, taking into consideration that the Phosphorites du Quercy include at least 170 fissure filling localities, distributed over a broad geographic area, encompassing large parts of the current Departments of Lot, Tarn-et-Garonne, Tarn, and Aveyron, all in the administrative region of Occitanie (Rage 2006; Sigé & Hugueney 2006; Georgalis *et al.* 2021a, c; Pelissié *et al.* 2021). They also stratigraphically span over a considerable time period, from the early Eocene (MP 8+9) until the Early Miocene (MN 3); however, most of the respective fossiliferous localities range between the late middle Eocene (MP 16) and the late Oligocene (MP 28) (Rage 2006; Sigé & Hugueney 2006; Georgalis *et al.* 2021a, c; Pelissié *et al.* 2021).

NEW AND OTHER MATERIAL STUDIED HEREIN. — *Lavergne* (MP 16): two pairs of two fused mid-trunk vertebrae (SU.PAL.2019.0.303.1 and SU.PAL.2019.0.303.12), two anterior trunk vertebrae (SU.PAL.2019.0.303.4 and SU.PAL.2019.0.303.5), two mid-trunk vertebrae (SU.PAL.2019.0.303.6 and SU.PAL.2019.0.303.7), one posterior trunk vertebra (SU.PAL.2019.0.303.8), two cloacal vertebrae (SU.PAL.2019.0.303.9 and SU.PAL.2019.0.303.10), nine caudal vertebrae

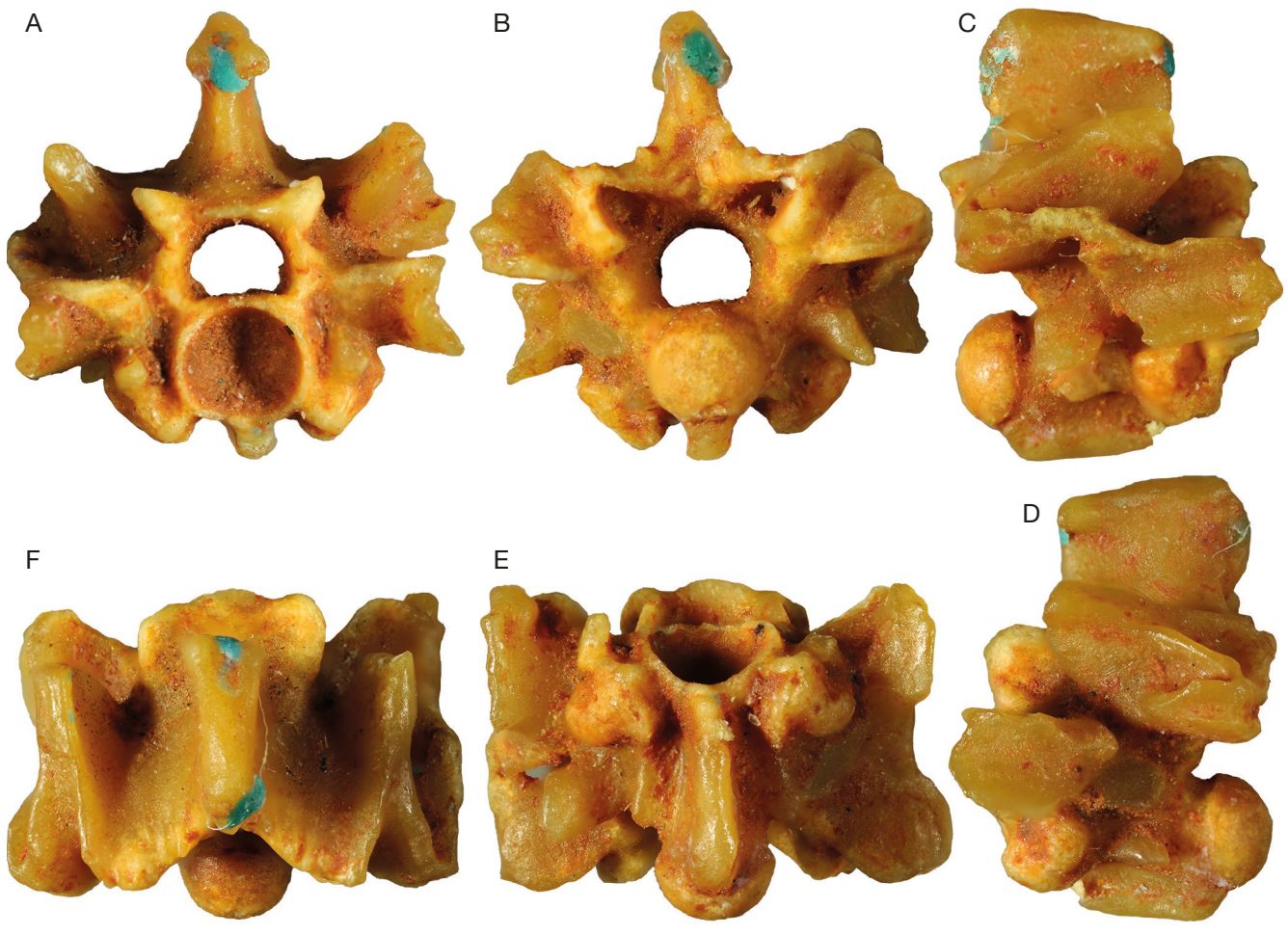


FIG. 1. — Holotype posterior trunk vertebra MNHN.F.QU16301 from the middle or late Eocene of the “Old Collections” of the Phosphorites du Quercy, in anterior (A), posterior (B), right lateral (C), left lateral (D), ventral (E), and dorsal (F) views. Scale bar: 2 mm.

(SU.PAL.2019.0.303.11 - SU.PAL.2019.0.303.19), two fused caudal vertebrae (SU.PAL.2019.0.303.3), and 70 vertebrae (of which 13 trunk, 8 cloacal, and 49 caudal vertebrae; SU.PAL.2019.0.303.20 - SU.PAL.2019.0.303.89). *Malpérié* (MP 16): two caudal vertebrae (UM MAL 501 and UM MAL 503). *La Bouffie* (MP 17): 51 trunk vertebrae (UM BFI 3011 - UM BFI 3048, UM BFI 3082, UM BFI 3104, UM BFI 3117, UM BFI 3151 - UM BFI 3158, UM BFI 3160, and UM BFI 3161), one ?cloacal (or anterior caudal) vertebra (UM BFI 3159), and seven caudal vertebrae (UM BFI 3049 - UM BFI 3051, UM BFI 3115, UM BFI 3116, UM BFI 3119, and UM BFI 3121). *Rosières 2* (MP 17): one caudal vertebra (UM ROS2 266). *Sainte Néboule* (MP 18): 10 caudal vertebrae (UM SNB 5135 - UM SNB 5142, UM SNB 5233, and UM SNB 5234). “Old collections” of Quercy (localities imprecisely known, middle or late Eocene): two trunk vertebrae (MNHN.F.QU16304 and NHMW 2019/0064/0001).

LOCALITIES AND AGE. — All localities of Lavergne, Malpérié, La Bouffie, Rosières 2, and Sainte Néboule are situated in the area of the Phosphorites du Quercy in southern France. Lavergne and Malpérié are the oldest among them, pertaining to the MP 16 zone of the middle Eocene, while Rosières 2 and Sainte Néboule are late Eocene, with Rosières 2 (MP 17) slightly older than Sainte Néboule (MP 18) (Biochrom’97 1997). As for the two vertebrae from the “old collections” of Quercy (MNHN.F.QU16304 and NHMW 2019/0064/0001), similarly to the case of the holotype, they originate from imprecisely known localities and therefore their age could lie anywhere within middle to late Eocene.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION. — Middle and late Eocene of France. For a detailed account of all known occurrences of the taxon, see Discussion below.

EMENDED DIAGNOSIS. — As for the genus (see above).

DESCRIPTION

The descriptions are based on the abundant vertebral sample from Lavergne. The vertebrae of *Cadurceryx* from Lavergne represent all major regions of the column (Figs 2; 3), except for anteriormost trunk (in particular atlas and axis) and possibly the last trunk vertebra, i.e., those (or that) preceding immediately the cloacal region. All vertebrae, as characteristic of the so called constrictor snakes (i.e., booids and pythonoids), have centra distinctly wider than long. The vertebrae are relatively small, in a few largest trunk vertebrae the centrum length is 3.0 to 3.5 mm, centrum width 4.2 to 4.6 mm, whereas centrum length/neural arch width ratio 0.7 to 0.8. Apart from the vertebral structures found in all ophidians, virtually all vertebrae throughout the column possess additional apophyses providing (at least partly) articular joints between adjacent bones. These are: pterapophyses (present in all vertebrae), extensions of zygapophyses and neural spine, as well as extensions of pleurapophyses (in caudal vertebrae).

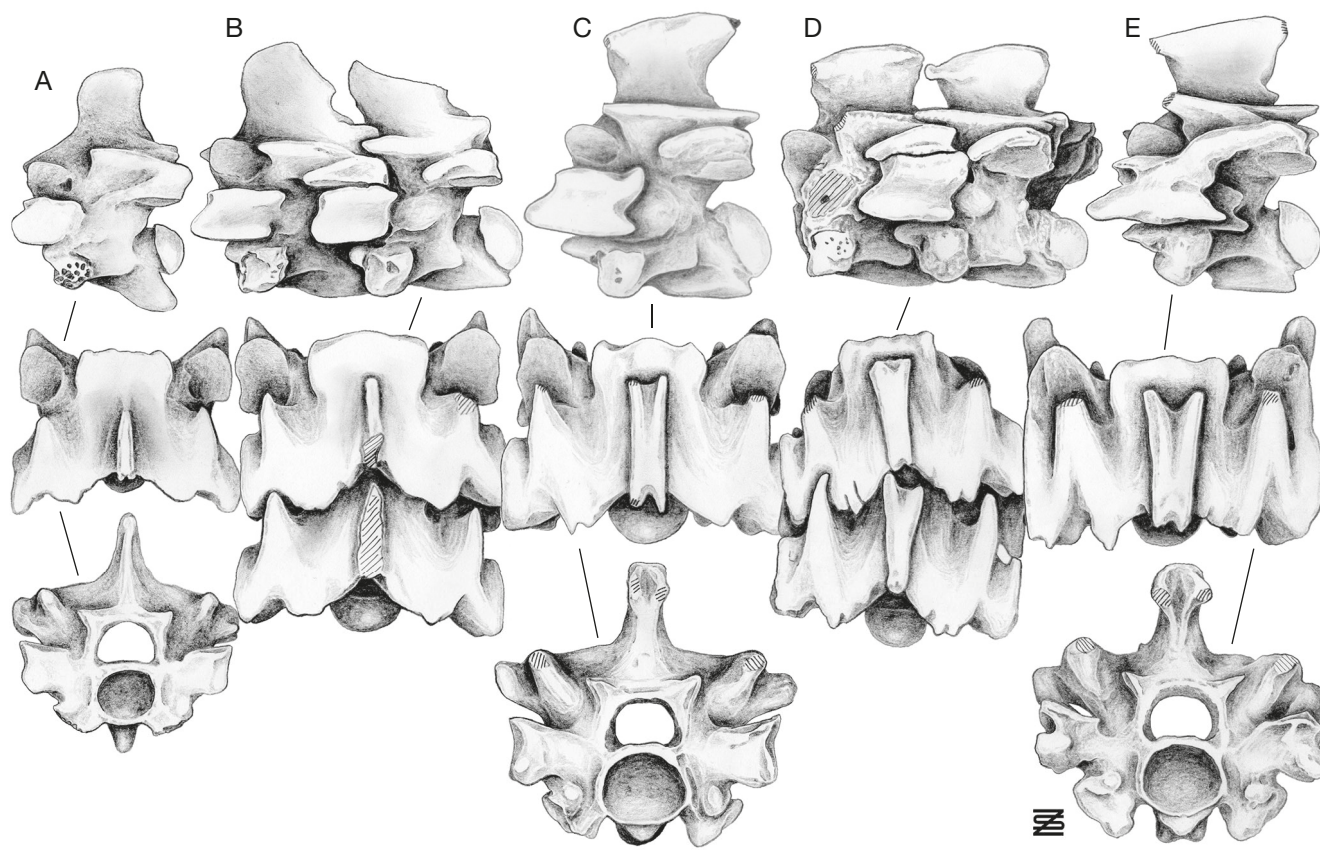


FIG. 2. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne: hypothesized sequence of vertebrae in the trunk portion of the column, in left lateral, dorsal, and anterior views. A, SU.PAL.2019.0.03.4; B, SU.PAL.2019.0.03.1; C, SU.PAL.2019.0.03.6; D, SU.PAL.2019.0.03.2; E, SU.PAL.2019.0.03.8. Scale bar: 5 mm.

The distinctive feature observed in the morphology of the trunk vertebrae of *Cadurceryx* is a progressive increase of the complexity of succeeding elements, from relatively simple anterior trunk vertebrae (see section “Anterior trunk vertebrae” below) to moderately complex mid-trunk vertebrae (“Mid-trunk vertebrae”), finally followed by highly complex vertebrae (“Posterior trunk vertebrae”). This unique morphological pattern (if we consider the morphology of additional apophyses) resembles closely the patterns characteristic of caudal (but not trunk!) portion of the column in both extant and extinct (the fossil genus *Bransateryx* Hoffstetter & Rage, 1972, at least) “erycine” snakes. The morphology of the post-trunk (i.e., cloacal and caudal) vertebrae, also provided with additional apophyses, is rather homogenous throughout the tail skeleton; in other words, there are no striking differences between the vertebrae coming from different parts of the cloacal/caudal portion of the column.

Anterior trunk vertebrae (Fig. 4)

We use this term to refer to a number (typically a few dozen in most alethinophidian snakes) of vertebrae located immediately behind the head and provided with distinct (but successively reduced in size) hypapophyses (taxa like elapids and natricids, provided with hypapophyses throughout the trunk portion of the column, are noteworthy exceptions).

This trait is observed in 10 vertebrae from Lavergne, available for this study. The hypapophysis is subsquare in shape in lateral view and rather short; its posteroventral termination reaches the level of the condyle. Apart from the presence of the latter structure, the morphology of the anterior trunk vertebrae of *Cadurceryx* is relatively simple compared with those located more posteriorly. The anterior trunk vertebrae, however, possess small but distinct pterapophyses beginning atop the postzygapophyseal area of the neural arch and directed anteriorly. At first glance, these structures look like the postzygapophyseal wings observed in *Eryx*, rather than pterapophyses (cf. Szyndlar 1994: fig. 5A), because they have the form of spurs projecting forwards but not backwards. However, in more posterior vertebrae located close to the anterior/mid-trunk transition (attributed to this region due to the presence of reduced and much different-shaped hypapophyses) the pterapophyses are produced into a short spur projecting backwards, as well (Fig. 5A).

The neural arch is moderately vaulted, but the difference between the vaulting of the arch of the anterior trunk vertebrae and of those located more posteriorly is not significant, unlike in most other snakes. The neural spine is as high as long in lateral view and not flattened dorsally. The subcentral ridges and subcentral grooves are prominent. The prezygapophyseal accessory processes are relatively short, strongly built, but are not expanded laterally or posteriorly.

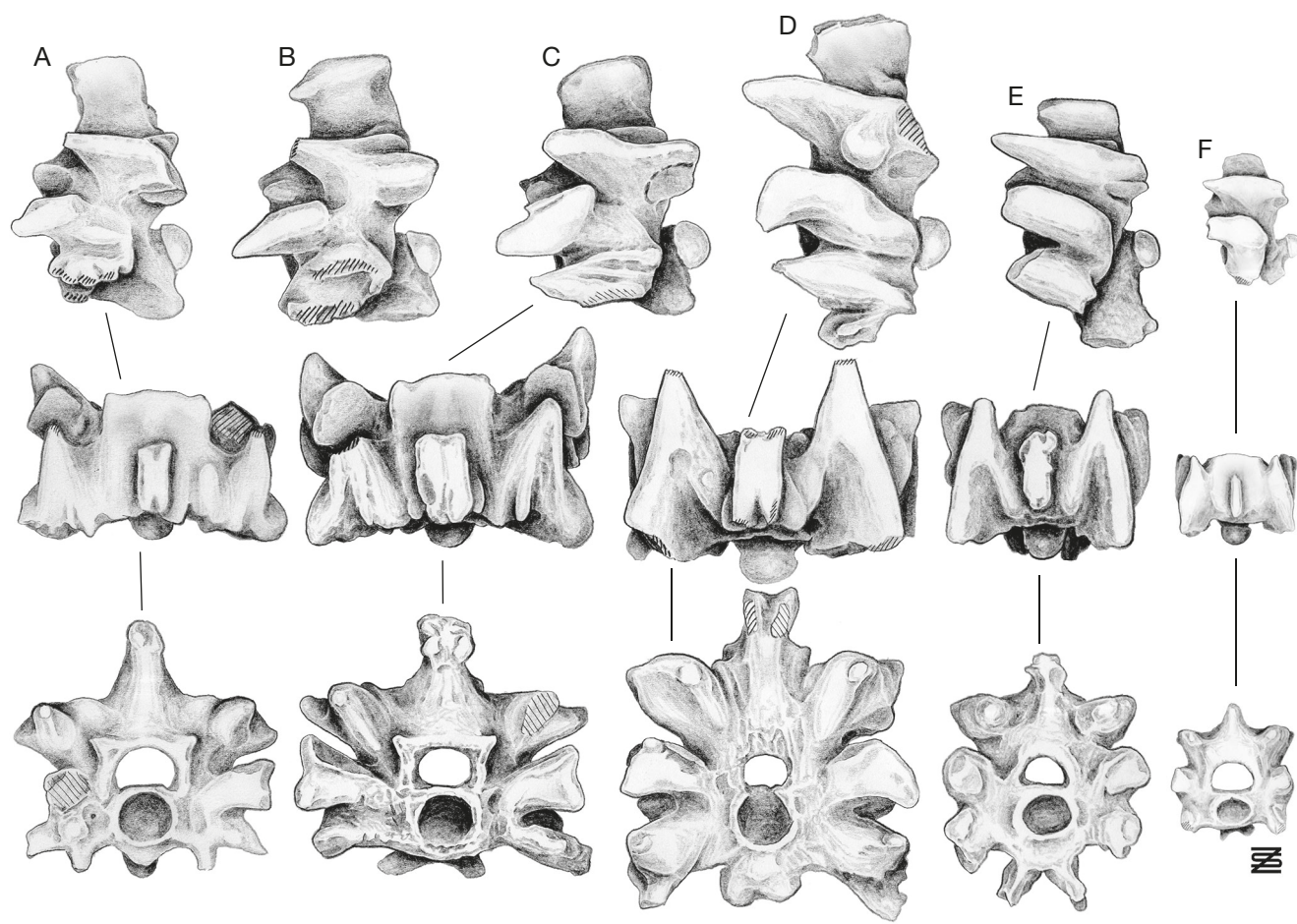


FIG. 3. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne: hypothesized sequence of vertebrae in the cloacal and caudal portion of the column, in left lateral, dorsal, and anterior views. **A**, SU.PAL.2019.0.03.9; **B**, SU.PAL.2019.0.03.10; **C**, SU.PAL.2019.0.03.12 (mirror view of right lateral side); **D**, SU.PAL.2019.0.03.13; **E**, SU.PAL.2019.0.03.16 (mirror view of right lateral side); **F**, SU.PAL.2019.0.03.17. Scale bar: 5 mm.

Mid-trunk vertebrae (Fig. 5)

In the vertebrae immediately succeeding the anterior trunk ones, the hypapophysis has a rather different shape: this structure is prominent, thick, and moderately broad in ventral view, while in lateral view, this is relatively anteroposteriorly long. Behind the cotyle rim, there is a shallow (and rather indistinct) depression in the keel (Fig. 5F). The subcentral grooves, on both sides of the hypapophysis, are deep and accompanied by prominent subcentral ridges. In most (but not all) vertebrae, the ridges terminate sharply in the form of distinct spurs before reaching the condyle, the feature well seen in lateral view (Fig. 5E).

These vertebrae are distinctly higher than long in lateral view and distinctly broader than long in ventral view. The neural arch is moderately depressed. The neural canal is significantly narrower than the suborbicular cotyle. The condyle is also rounded or slightly depressed. The paradiapophyses are relatively small, without distinct subdivision into para- and diapophyseal portions. The subcentral and lateral foramina are small but distinct (the latter, usually covered by post-prezygapophyseal structures, are hardly seen in lateral view).

The neural spine, approximately as high as long, has its anterior margin slightly overhanging and the posterior margin usually strongly overhanging. The upper margin of the neural spine can be slightly depressed and sometimes slightly bifurcated anteriorly and posteriorly, in dorsal view; the bifurcations do not overlap in neighbouring vertebrae (Fig. 5A, C).

The pterapophyses, well developed on both sides of the base of the neural spine, are elongate and protrude distinctly both anteriorly and posteriorly. As seen in the pairs of fused vertebrae, the anterior projections of pterapophyses of the more posteriorly located vertebra externally overlap the posterior projections of pterapophyses of the preceding vertebra (Fig. 5C, D).

The prezygapophyses have prominent extensions: prezygapophyseal accessory processes and posterior extensions of prezygapophyses. The prezygapophyseal accessory processes, developed beneath the elongated prezygapophyseal articular facets in the form of long laminae, project forwards and backwards. The postzygapophyses, provided with subsquare-shaped articular facets, are distinctly separated off the pterapophyses located above; anteriorly, the postzygapophyses are produced into more or less prominent anterior extensions.

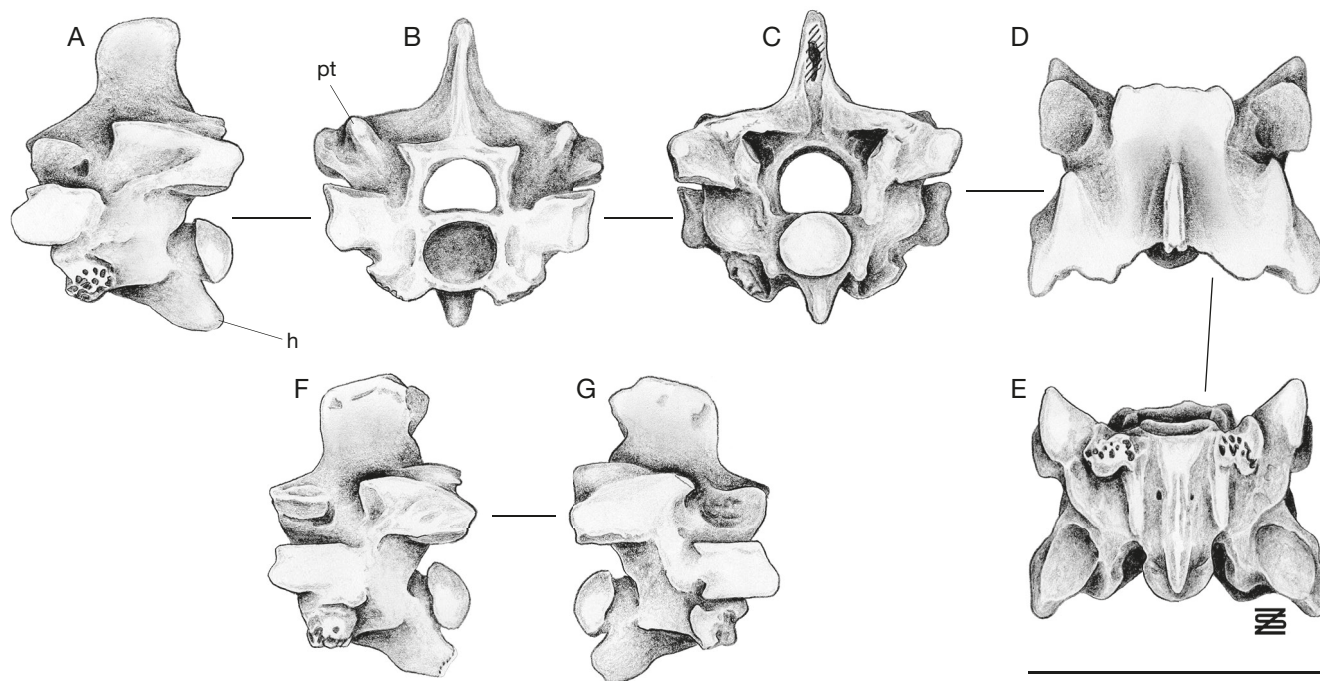


FIG. 4. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne, anterior trunk vertebrae: **A–E**, SU.PAL.2019.0.03.4 in left lateral (**A**), anterior (**B**), posterior (**C**), dorsal (**D**), and ventral (**E**) views; **F, G**, SU.PAL.2019.0.03.5 in left (**F**) and right lateral (**G**) views. Abbreviations: **h**, hypapophysis; **pt**, pterapophysis. Scale bar: 5 mm.

The posterior extensions of prezygapophyses and anterior extensions of postzygapophyses are approaching to each other but are not fused (Fig. 5E).

Posterior trunk vertebrae (Fig. 6)

Some vertebral elements of the posterior trunk vertebrae (pterapophyses, diapophyses, neural canal, cotyles and condyles, zygosphenes, and zygantra) do not differ significantly from those of the mid-trunk vertebrae. Other elements, however, are apparently overgrown and/or significantly enlarged.

The main difference between the vertebrae described below and those described in the preceding section is progressing complexity of the vertebral structures, observed in particular (but not only) in the development of additional apophyses. At first glance, the most striking feature differentiating the mid-trunk and posterior trunk vertebrae is, in the latter vertebrae, the significant enlargement of the posterior extensions of prezygapophyses and anterior extensions of postzygapophyses that fuse with each other forming a thick bar, especially well visible in lateral views (Fig. 6A). Hence, each bar, resulting from the fusion of the zygapophyseal extensions, is distinctly separated from the main body of the vertebra by a large foramen. In rare cases, the fusion may be incomplete on one side of a vertebra (Fig. 6J).

The neural spine is of similar height as in mid-trunk vertebrae but thicker (in anterior and posterior views), more flattened dorsally, and with more distinct anterior and posterior bifurcations.

In lateral view, the hypapophysis is more prominent and relatively higher (i.e., extending further downward) than in mid-trunk vertebrae and provided with more prominent (deeper) depression behind the cotyle rim (Fig. 6A, F).

A characteristic feature of the hypapophysis in this portion of the vertebral column is its distinct anteroventral corner that forms approximately a right angle.

In a few vertebrae, there exist distinct spurs originating from the centrum wall above the postero-dorsal part of the paradiapophyses and projecting posteriorly (*“une apophyse incline vers le bas et l’arrière”* of Hoffstetter & Rage 1972). These structures, although quite prominent, can be obscured by overgrown posterior parts of the prezygapophyseal accessory processes and hence hardly visible in lateral view (Fig. 6A); instead, they are well seen, immediately behind the paradiapophyses, in ventral view (Fig. 6E).

The posterior trunk vertebrae are more depressed than those from the preceding regions of the column. This difference is most apparent in the most posterior trunk vertebrae (usually termed “posteriormost trunk” or “last trunk”, i.e., the last and possibly penultimate vertebrae), described in the following paragraphs.

The available material from Lavergne contains four such vertebrae that no doubt originate from the very end of the trunk portion of the column (Fig. 6H, I, J–O). The most characteristic feature distinguishing them from more anterior trunk vertebrae is the increasing height (i.e., downward projection) of their hypapophyses (Fig. 6I–K); these can be termed “cloacal hypapophyses”. These hypapophyses are even more prominent than preceding vertebrae and their anteroventral corner is even more distinct and straighter. Another important feature of these vertebrae is an apparent reduction in size of the posterior projections of pterapophyses; interestingly, the same morphological pattern is observed in the anterior trunk vertebrae (see below) as well as those from the cloacal and caudal regions (see above).

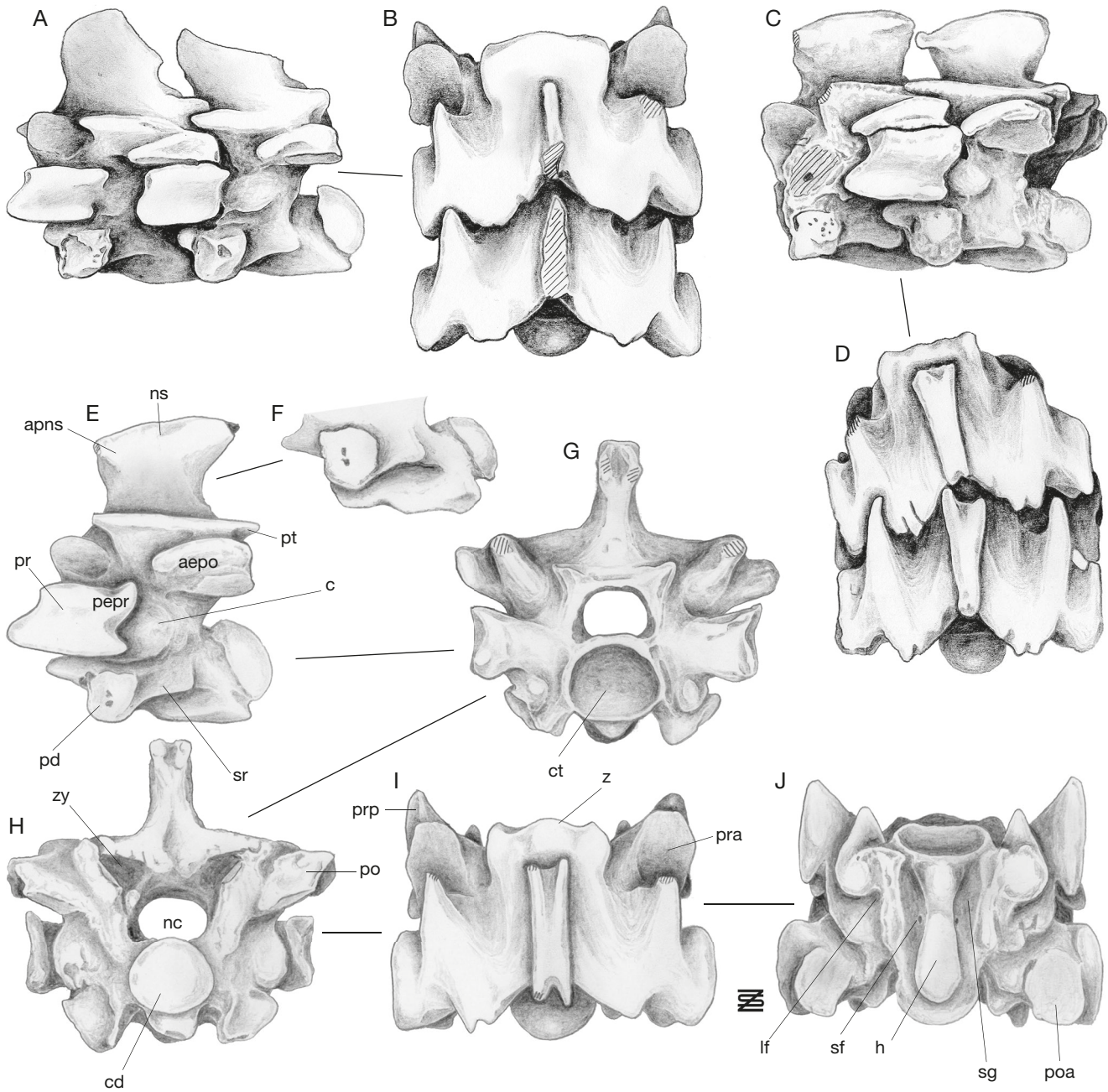


FIG. 5. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne, mid-trunk vertebrae: **A, B**, two fused vertebrae SU.PAL.2019.0.03.1 in left lateral (**A**) and dorsal (**B**) views; **C, D**, two fused vertebrae SU.PAL.2019.0.03.2 in left lateral (**C**) and dorsal (**D**) views; **E–J**, SU.PAL.2019.0.03.6 in left lateral (**E**), left lateroventral (**F**), anterior (**G**), posterior (**H**), dorsal (**I**), and ventral (**J**) views. Abbreviations: **aepo**, anterior extension of postzygapophysis; **apns**, articular process of neural spine; **c**, centrum; **cd**, condyle; **ct**, cotyle; **h**, hypapophysis; **lf**, lateral foramen; **nc**, neural canal; **ns**, neural spine; **pd**, paradiapophysis; **pepr**, posterior extension of prezygapophysis; **po**, postzygapophyseal articular facet; **pra**, prezygapophyseal articular facet; **prp**, prezygapophyseal accessory process; **pt**, pterapophysis; **sf**, subcentral foramen; **sg**, subcentral groove; **sr**, subcentral ridge; **z**, zygosphen; **zy**, zygantrum. Scale bar: 5 mm.

Concluding, most vertebral elements observed in the available posteriormost trunk and anteriormost cloacal vertebrae display very similar (unless almost identical) morphological patterns (the presence of lymphapophyses in cloacal vertebrae is an obvious exception). Unfortunately, there exists one significant deviation from this “smooth” trunk-to-cloacal transition, namely the presence of interzygapophyseal connections in the former vs. their complete disappearance in the latter (in fact, in all following vertebrae until the tail tip).

This “sharp transition” may indicate that *Cadurceryx* could actually possess (an) additional trunk vertebra(e) immediately preceding the cloacal region, which is unfortunately absent in the available fossil material.

Cloacal vertebrae (Fig. 7)

The material from Lavergne makes it possible to reconstruct roughly the cloacal and caudal portions of the vertebral column. Interestingly, the structure of virtually all

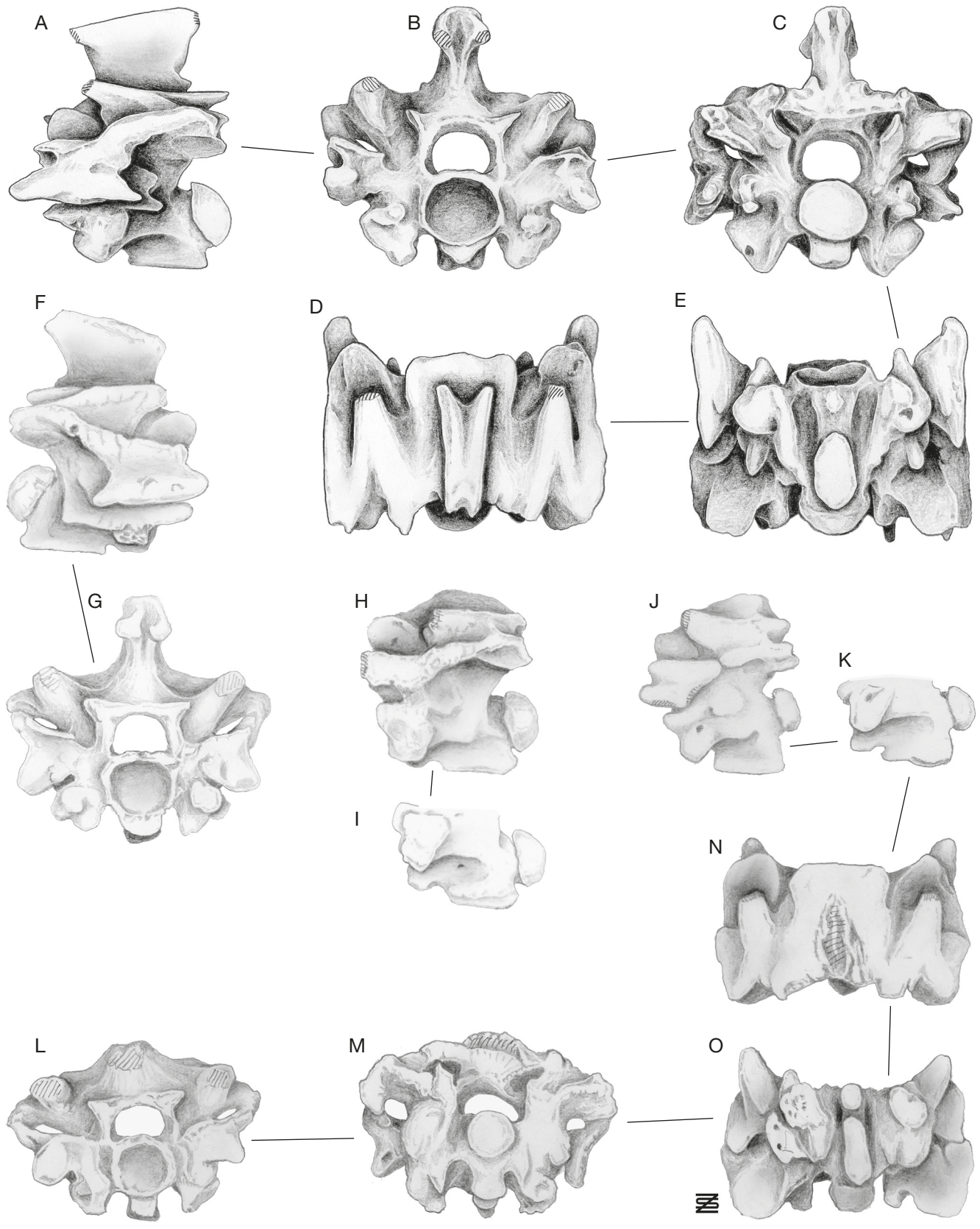


FIG. 6. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne, mid-/posterior trunk vertebrae: **A-E**, SU.PAL.2019.0.03.8 in left lateral (**A**), anterior (**B**), posterior (**C**), dorsal (**D**), and ventral (**E**) views; **F, G**, SU.PAL.2019.0.03.22 in right lateral (**F**) and anterior (**G**) views; **H, I**, SU.PAL.2019.0.03.21 in left lateral (**H**) and left lateroventral (**I**) views; **J-O**, SU.PAL.2019.0.03.20 in left lateral (**J**), left lateroventral (**K**), anterior (**L**), posterior (**M**), dorsal (**N**), and ventral (**O**) views. Scale bar: 5 mm.

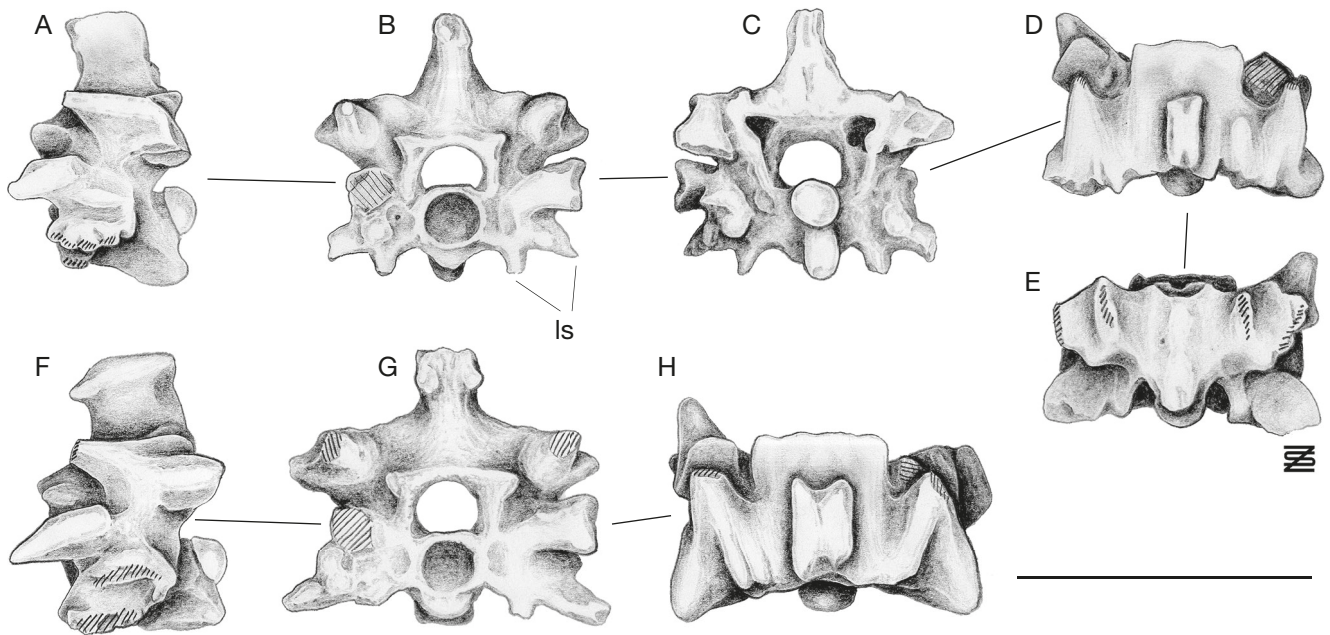


FIG. 7. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne, cloacal vertebrae: **A-E**, SU.PAL.2019.0.03.9 in left lateral (**A**), anterior (**B**), posterior (**C**), dorsal (**D**), and ventral (**E**) views; **F-H**, SU.PAL.2019.0.03.10 in left lateral (**F**), anterior (**G**), and dorsal (**H**) views. Abbreviation: **ls**, lymphapophysis. Scale bar: 5 mm.

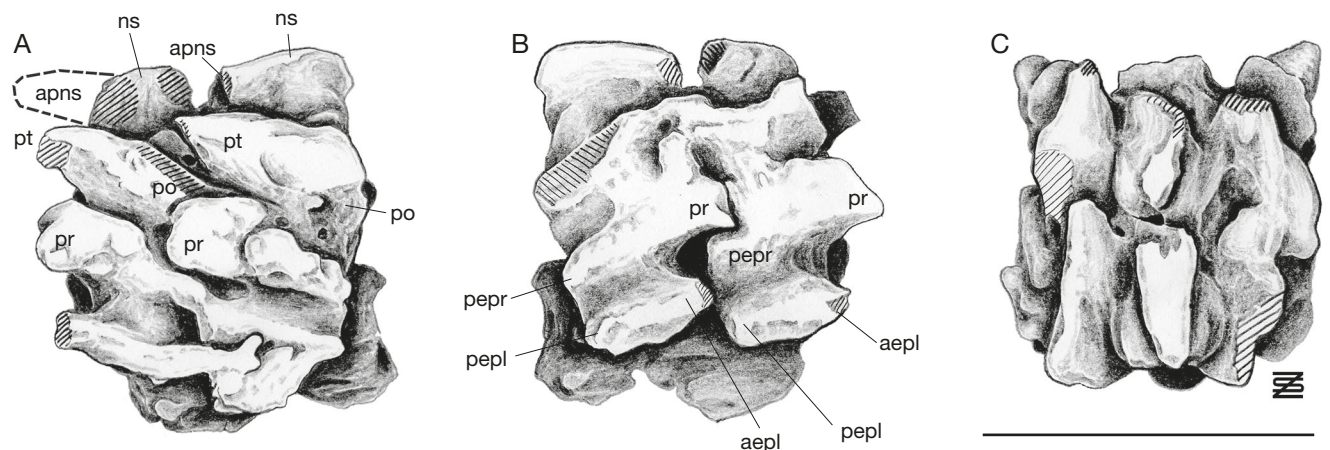


FIG. 8. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne, intervertebral articulation between two caudal vertebrae. SU.PAL.2019.0.03.3 in left lateral (**A**), right lateral (**B**), and dorsal (**C**) views. Abbreviations: **aepl**, anterior extension of pleurapophysis; **apns**, articular process of neural spine; **ns**, neural spine; **pepl**, posterior extension of pleurapophysis; **pepr**, posterior extension of prezygapophysis; **po**, postzygapophysis; **pr**, prezygapophysis; **pt**, pterapophysis. Scale bar: 5 mm.

vertebrae coming from this region of the column is rather homogenous, from the cloaca to the tail tip. This situation is in contrast to that observed in the extant genus *Eryx* and the extinct *Bransateryx*, where the simply built cloacal and anterior caudal vertebrae are followed by more and more complex ones, with the highest rate of complexity appearing in posteriormost caudal vertebrae.

As in other snakes, the cloacal vertebrae of *Cadurceryx* clearly differ from the caudal vertebrae by having (remnants of) lymphapophyses instead of pleurapophyses. Besides, they display quite complex morphology in the upper portion of vertebral bodies and in this aspect they do not differ substantially from the following caudal vertebrae.

The available material from Lavergne consists of 10 cloacal vertebrae. Two of them, provided with short hypapophyses (resembling those of the last trunk vertebrae), are considered anterior cloacal vertebrae. The remaining eight cloacal vertebrae are provided with (remnants of) haemapophyses, hence, they are considered to be located more posteriorly in the cloacal portion of the column.

In most examined snakes, in particular in snakes with complex vertebrae, the cloacal vertebrae morphologically closely resemble the posteriormost trunk vertebrae (obviously, except for the subcentral structures). Unfortunately, in the case of *Cadurceryx* from Lavergne, vertebrae that could be interpreted with full certainty as posteriormost trunk ones have not been

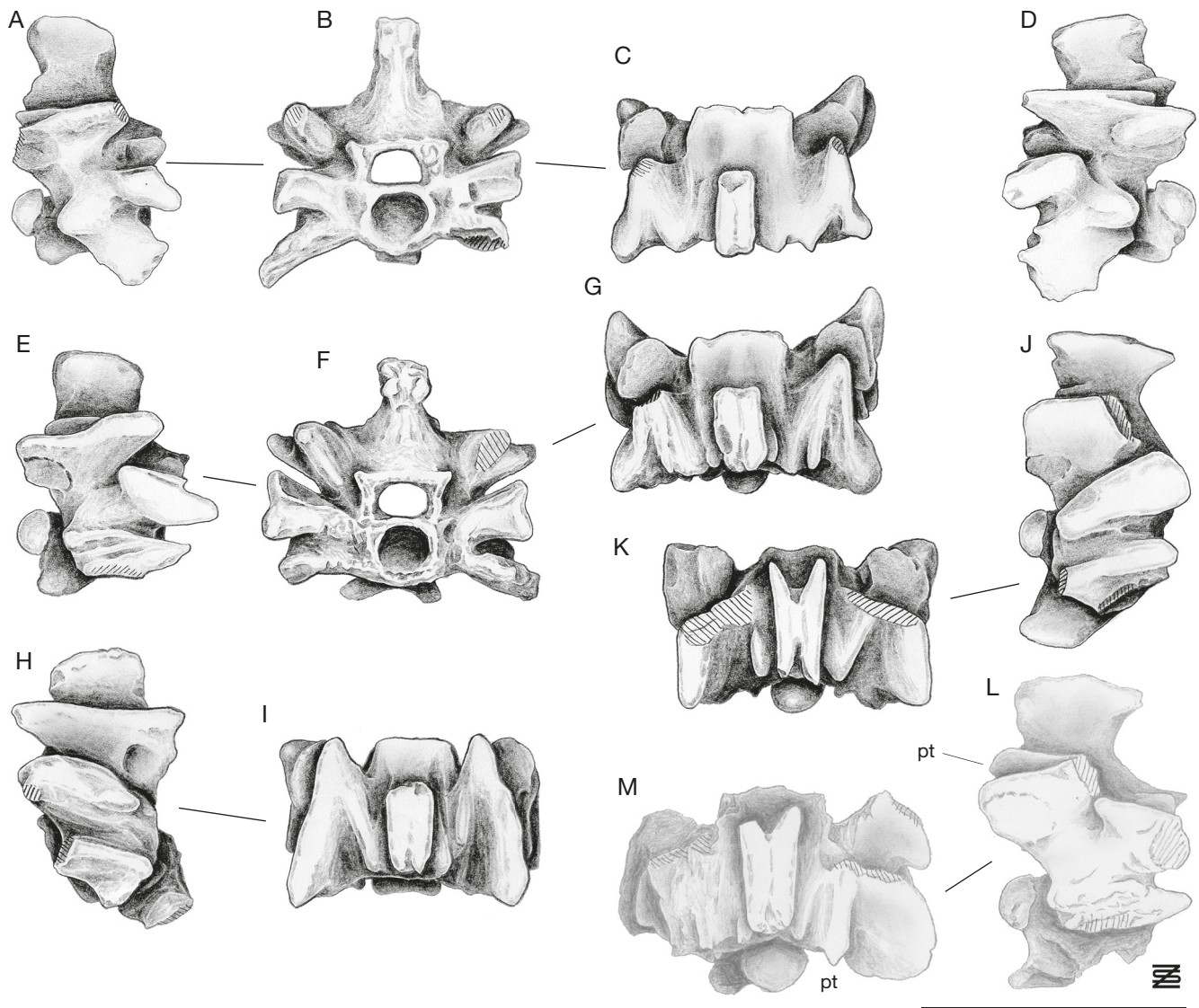


FIG. 9. – *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne, caudal (more anterior) vertebrae: **A–C**, SU.PAL.2019.0.03.11 in right lateral (**A**), anterior (**B**), and dorsal (**C**) views; **D**, SU.PAL.2019.0.03.18 in left lateral view; **E–G**, SU.PAL.2019.0.03.12 in right lateral (**E**), anterior (**F**), and dorsal (**G**) views; **H, I**, SU.PAL.2019.0.03.14 in left lateral (**H**) and dorsal (**I**) views; **J, K**, SU.PAL.2019.0.03.15 in left lateral (**J**) and dorsal (**K**) views; **L, M**, SU.PAL.2019.0.03.19 in right lateral (**L**) and dorsal (**M**) views. Abbreviation: **pt**, pterapophysis. Scale bar: 5 mm.

found (see below). Their possible presence could shed light on the enigmatic transition between the “trunk-like” and “cloacal/caudal” patterns of complexity.

Caudal vertebrae (Figs 8–10)

Sixty caudal vertebrae have been picked off the available Lavergne material. Anteriormost caudal vertebrae possess a hypapophysis, while, as characteristic of most snakes, succeeding caudal vertebrae are provided with paired haemapophyses; unfortunately, these latter structures are broken in virtually all available caudal vertebrae. As mentioned in the preceding paragraphs, the vertebrae coming from the tail region display rather homogenous morphology. However, protruding vertebral elements (in particular pterapophyses, as well as extending parts of prezygapophyses and pleurapophyses) are less strongly developed in the vertebrae

interpreted as located more anteriorly (Fig. 9) than those located more posteriorly (Fig. 10).

Compared with trunk vertebrae, most caudal vertebrae are relatively much higher than long in lateral view, as well as distinctly broader than long in ventral view. The neural arch is depressed. The neural canal is relatively very small (except for vertebrae pertaining to juvenile individuals, e.g. Fig. 10L). The neural spine is moderately small and short in lateral view, but relatively thick in anterior/posterior views and sometimes depressed dorsally.

The postzygapophyses are simply built. With one exception only (Fig. 10A), the postzygapophyses are devoid of any anterior extensions. Although the prezygapophyses are developed into prominent posterior extensions, the latter structures are never fused with postzygapophyses, unlike in the posterior trunk vertebrae.

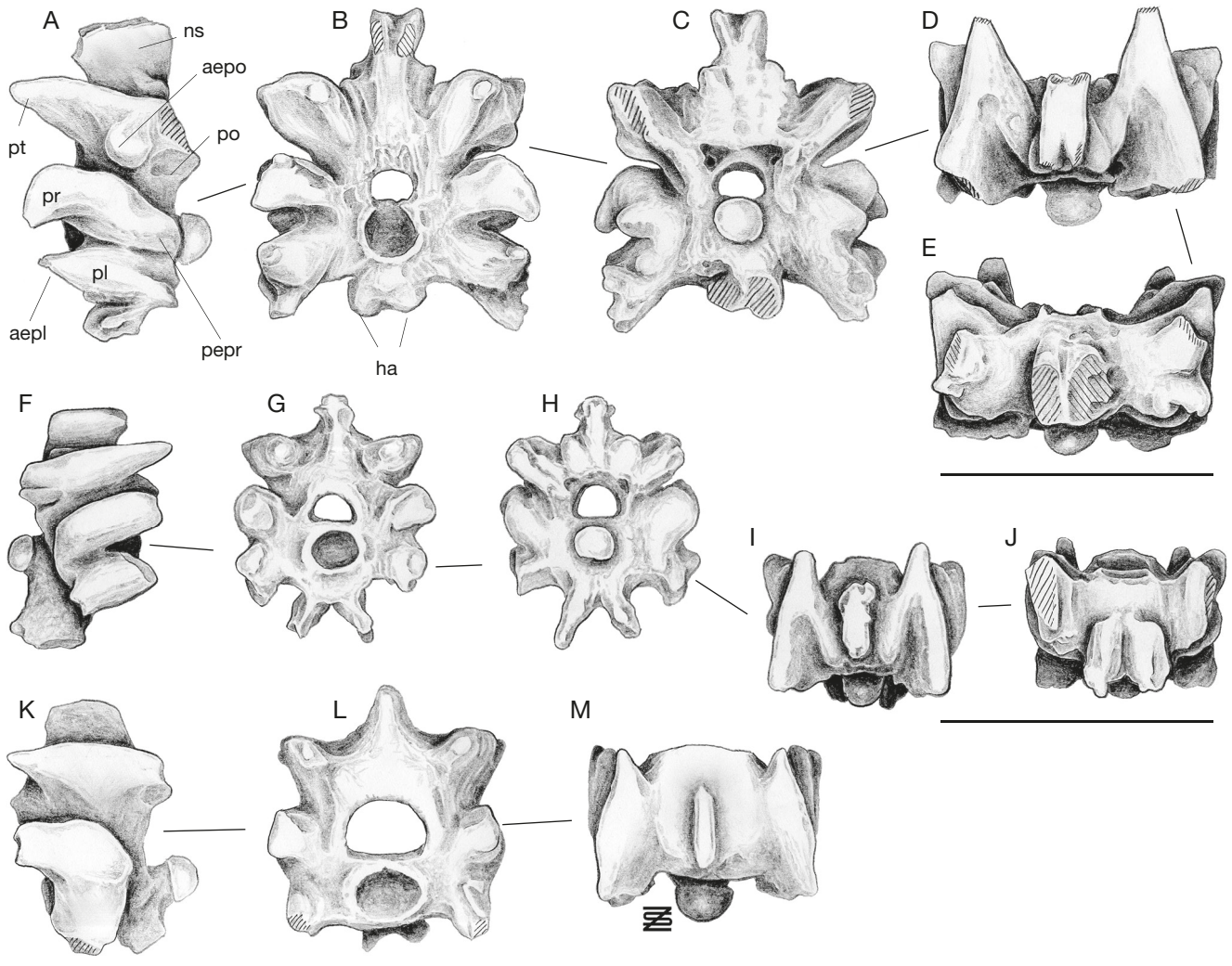


Fig. 10. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Lavergne, caudal (more posterior) vertebrae: **A-E**, SU.PAL.2019.0.03.13 in left lateral (**A**), anterior (**B**), posterior (**C**), dorsal (**D**), and ventral (**E**) views; **F-J**, SU.PAL.2019.0.03.16 in right lateral (**F**), anterior (**G**), posterior (**H**), dorsal (**I**), and ventral (**J**) views; **K-M**, SU.PAL.2019.0.03.17 in left lateral (**K**), anterior (**L**), and dorsal (**M**) views. Abbreviations: **aepl**, anterior extension of pleurapophysis; **aepo**, anterior extension of postzygapophysis; **ha**, haemapophysis; **ns**, neural spine; **pepr**, posterior extension of prezygapophysis; **pl**, pleurapophysis; **po**, postzygapophysis; **pr**, prezygapophysis; **pt**, pterapophysis. Scale bars: 5 mm.

The prominent pterapophyses are maintained in the entire post-trunk portion of the column, but, however, in overwhelming majority of the post-trunk vertebrae they are extending exclusively forwards and not backwards, therefore unlike as in the trunk vertebrae of *Cadurceryx* itself as well as caudal vertebrae of *Eryx* and *Bransateryx*, having pterapophyses provided with distinct both anterior and posterior projections. Despite the lack of the backward projections, the pterapophyses belonging to more posterior caudal vertebrae of *Cadurceryx* may have overlapped those of their anterior neighbours. Surprisingly, as seen in two fused caudal vertebrae (Fig. 8C), the (left) pterapophysis belonging to the posterior vertebra overlaps the (left) pterapophysis of the anterior vertebra from inside and not outside, as characteristic of the trunk vertebrae (see below). Notably, in a few caudal vertebrae of *Cadurceryx*, there exist minute protuberances above the postzygapophyseal region that may mimic vestigial rear projections of pterapophyses (Fig. 9H), whereas

one caudal vertebra from Lavergne (Fig. 9L-M) has pterapophyses distinctly separated off the postzygapophyses and provided with distinct posterior projections.

The pleurapophyses (although badly preserved in most caudal vertebrae) were no doubt strongly built structures, stretching latero-ventrally. The pleurapophyses are provided with prominent anterior and posterior extensions, from above distinctly separated by a deep furrow from the prezygapophyses and their posterior extensions. As seen in two fused caudal vertebrae (Fig. 8B), the anterior extension of pleurapophysis is wedged between the posterior extension of prezygapophysis (from above) and the posterior extension of pleurapophysis of the preceding vertebra (from below). This condition does not differ from that observed in the recent genus *Eryx*, while in the Oligo-Miocene genus *Bransateryx* the anterior extension of pleurapophysis is articulated from above by the posterior extension of pleurapophysis of the preceding vertebra (Szyndlar 1994).

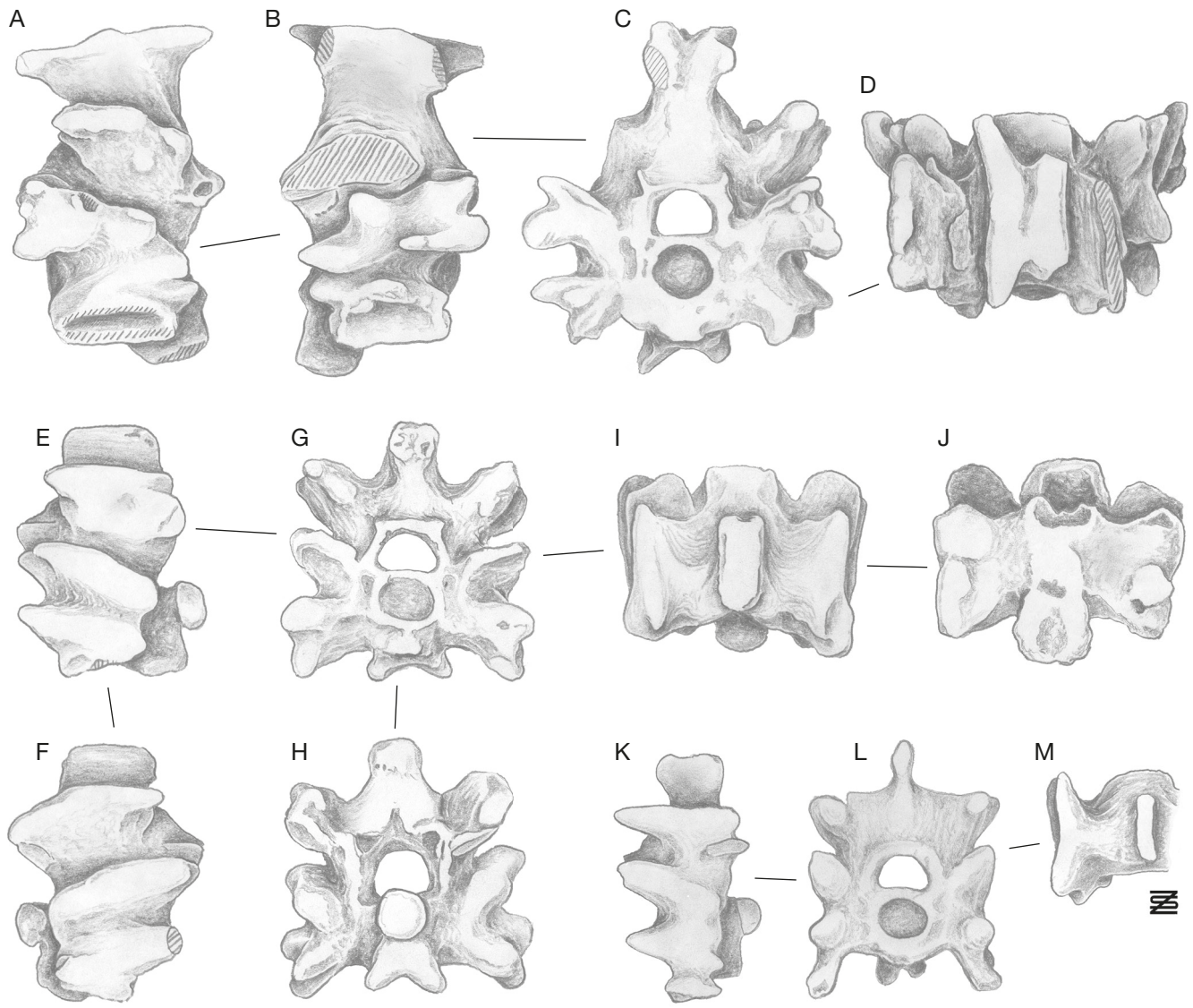


FIG. 11. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Malpérié (A–J) and Rosières 2 (K–M), caudal vertebrae: A–D, UM MAL 501 in right lateral (A), left lateral (B), anterior (C), and dorsal (D) views; E–J, UM MAL 503 in left lateral (E), right lateral (F), anterior (G), posterior (H), dorsal (I), and ventral (J) views; K–M, UM ROS 266 in left lateral (K), anterior (L), and dorsal (M) views. Scale bar: 5 mm.

ADDITIONAL MATERIAL OF *CADURCERYX FILHOLI* FROM THE PHOSPHORITES DU QUERCY

Besides the abundant vertebral material from Lavergne described above, which pertains to practically almost all portions of the column, we present here additional vertebrae of *Cadurceryx filholi* from other localities in the area of the Phosphorites du Quercy. These include caudal vertebrae from Malpérié (MP 16; Fig. 11A–J) and Rosières 2 (MP 17; Fig. 11K–M) that were previously described and figured by Hoffstetter & Rage (1972), plus several undescribed trunk and caudal vertebrae from La Bouffie (MP 17; Figs 12–16), and a few caudal vertebrae from Sainte Néboule (MP 18; Fig. 17). Moreover, we present also two further trunk vertebrae from the “old collections” of Quercy: one vertebra (MNHN.F.QU16304; Fig. 18A–F), originally described and figured by Hoffstetter & Rage (1972: fig. 6B), and one previously undescribed vertebra from the collections of NHMW (NHMW 2019/0064/0001; Fig. 18G–L).

All these vertebrae match well with the morphology and intra-columnar variation observed in the above documented Lavergne sample. We therefore assign all of them to *Cadurceryx filholi*. This resemblance further prompts us to consider that a single species of *Cadurceryx*, i.e., the type species *Cadurceryx filholi*, was present in all these studied localities and perhaps, in general in France during the middle and late Eocene. It is further worth noting that the snake sample from Sainte Néboule, although it comprised vertebrae of several other snake taxa (GLG, personal observation), yielded only caudal vertebrae of *Cadurceryx* but not a single trunk one (see also Discussion below).

A CRITICAL APPROACH OF HOFFSTETTER & RAGE’S (1972) ORIGINAL DESCRIPTION AND OTHER EARLY DOCUMENTATIONS OF *CADURCERYX*

The genus *Cadurceryx*, with the type (and then only known) species *Cadurceryx filholi*, was originally described by Hoffstetter

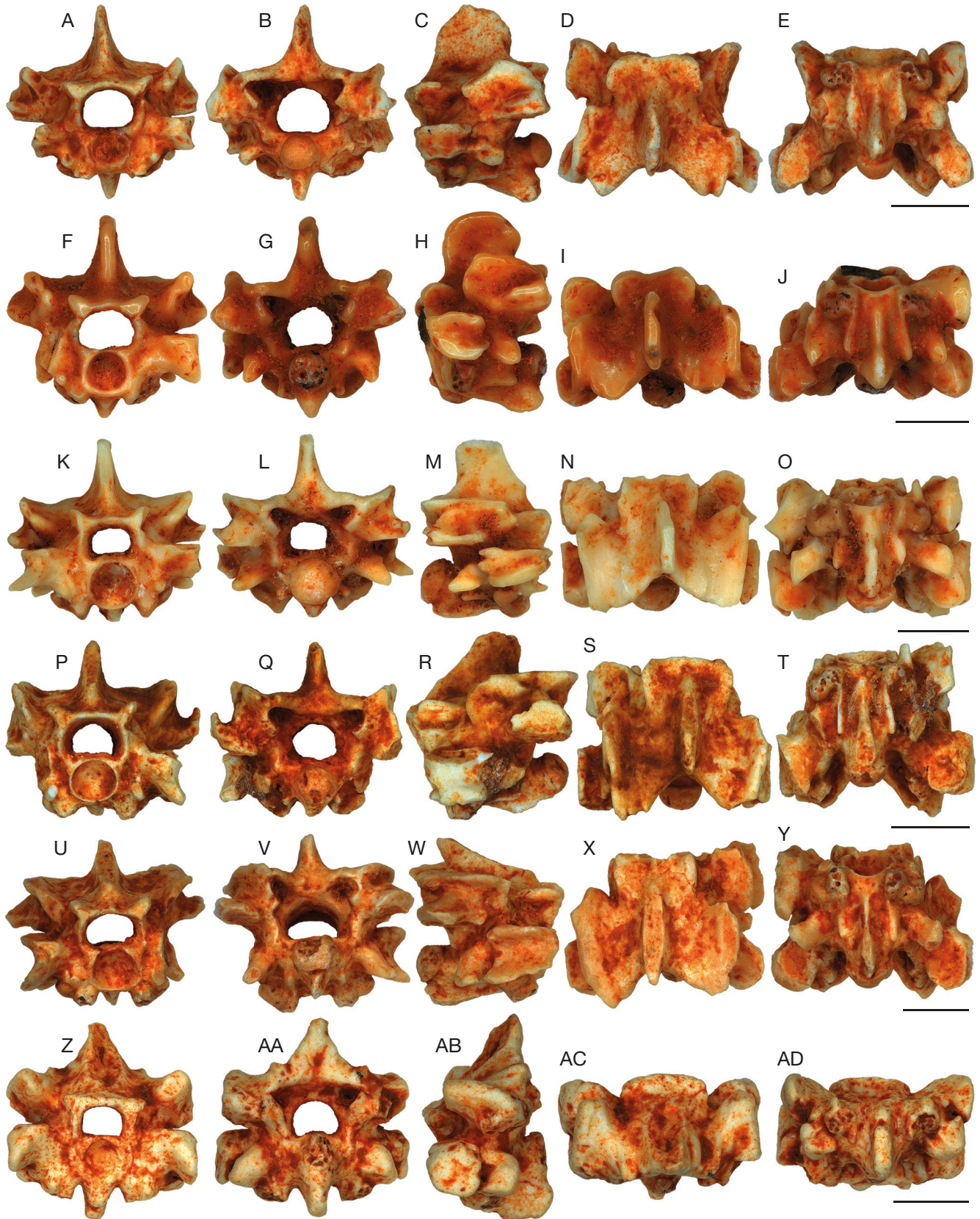


FIG. 12. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from La Bouffie, trunk vertebrae: **A-E**, UM BFI 3019 in anterior (**A**), posterior (**B**), left lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F-J**, UM BFI 3041 in anterior (**F**), posterior (**G**), left lateral (**H**), dorsal (**I**), and ventral (**J**) views; **K-O**, UM BFI 3014 in anterior (**K**), posterior (**L**), right lateral (**M**), dorsal (**N**), and ventral (**O**) views; **P-T**, UM BFI 3044 in anterior (**P**), posterior (**Q**), left lateral (**R**), dorsal (**S**), and ventral (**T**) views; **U-Y**, UM BFI 3028 in anterior (**U**), posterior (**V**), right lateral (**W**), dorsal (**X**), and ventral (**Y**) views; **Z-AD**, UM BFI 3043 in anterior (**Z**), posterior (**AA**), left lateral (**AB**), dorsal (**AC**), and ventral (**AD**) views. Scale bars: 2 mm.

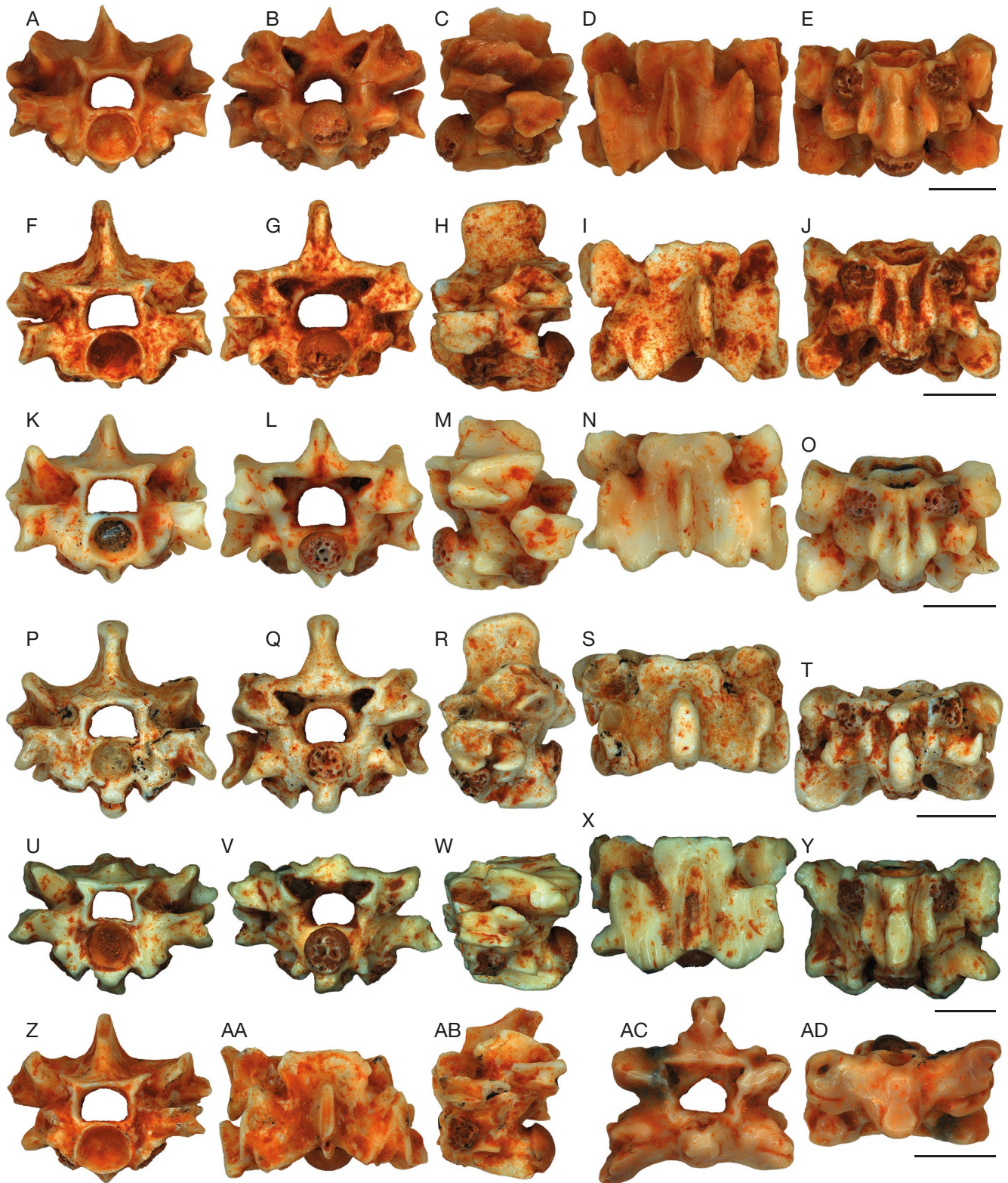


FIG. 13. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from La Bouffie, trunk vertebrae: **A–E**, UM BFI 3013 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F–J**, UM BFI 3030 in anterior (**F**), posterior (**G**), left lateral (**H**), dorsal (**I**), and ventral (**J**) views; **K–O**, UM BFI 3016 in anterior (**K**), posterior (**L**), right lateral (**M**), dorsal (**N**), and ventral (**O**) views; **P–T**, UM BFI 3045 in anterior (**P**), posterior (**Q**), left lateral (**R**), dorsal (**S**), and ventral (**T**) views; **U–Y**, UM BFI 3082 in anterior (**U**), posterior (**V**), left lateral (**W**), dorsal (**X**), and ventral (**Y**) views; **Z–AB**, UM BFI 3034 in anterior (**Z**), dorsal (**AA**), and left lateral (**AB**) views; **AC, AD**, UM BFI 3033 in posterior (**AC**) and ventral (**AD**) views. Scale bars: 2mm.

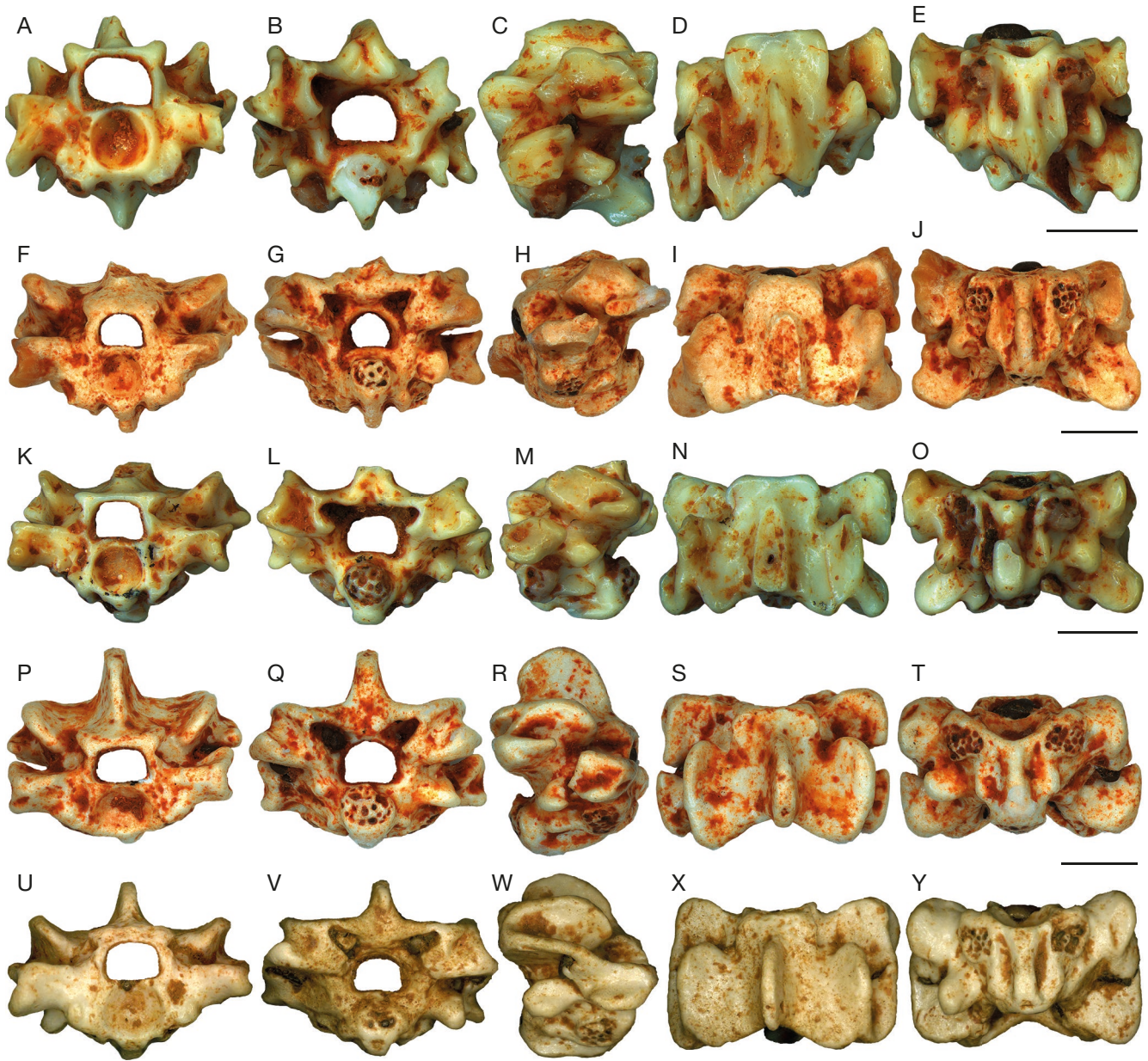


FIG. 14. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from La Bouffie, trunk vertebrae: **A–E**, UM BFI 3117 in anterior (**A**), posterior (**B**), left lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F–J**, UM BFI 3012 in anterior (**F**), posterior (**G**), left lateral (**H**), dorsal (**I**), and ventral (**J**) views; **K–O**, UM BFI 3104 in anterior (**K**), posterior (**L**), left lateral (**M**), dorsal (**N**), and ventral (**O**) views; **P–T**, UM BFI 3017 in anterior (**P**), posterior (**Q**), right lateral (**R**), dorsal (**S**), and ventral (**T**) views; **U–Y**, UM BFI 3151 in anterior (**U**), posterior (**V**), right lateral (**W**), dorsal (**X**), and ventral (**Y**) views. Scale bars: 2 mm.

& Rage (1972), based on remains (exclusively isolated vertebrae) coming from several Eocene sites of France. The holotype vertebra (MNHN.F.QU16301), originating from an unidentified locality in the Phosphorites du Quercy (“anciennes collections”), was defined by Hoffstetter & Rage (1972) as “une vertèbre complexe à tubercules costaux”, owing to its complex morphology, as originating from the posterior portion of the column; subsequently Rage (1984b) treated the holotype as a probably anterior cloacal vertebra. The astonishing statement of Rage (1984b) that the holotype vertebra of *Cadurceryx filholi* may have come from the cloacal region of the column seems apparently to be an unintentional mistake (although certainly difficult to be explained how the mistake was made)!

Jean-Claude Rage, who on many occasions in the 1990s and early 2000s was discussing with ZS about *Cadurceryx*, never actually supported the above opinion; what is more, the only figure of a trunk vertebra of *Cadurceryx* (UM [formerly USTL] LAV 1275), morphologically not differing from the holotype, published by Rage (2013: fig. 3h, i) was described in the caption as just “trunk vertebra”. In any case, as we demonstrated in the descriptions above, the morphology of the holotype specimen matches that of a posterior trunk vertebra. Eight other trunk vertebrae, also belonging to the old collections of the Phosphorites du Quercy, were referred to *C. filholi*, as well (Hoffstetter & Rage 1972). Of them, four vertebrae display the complex morphology (MNHN.F.QU16304; Hoffstetter

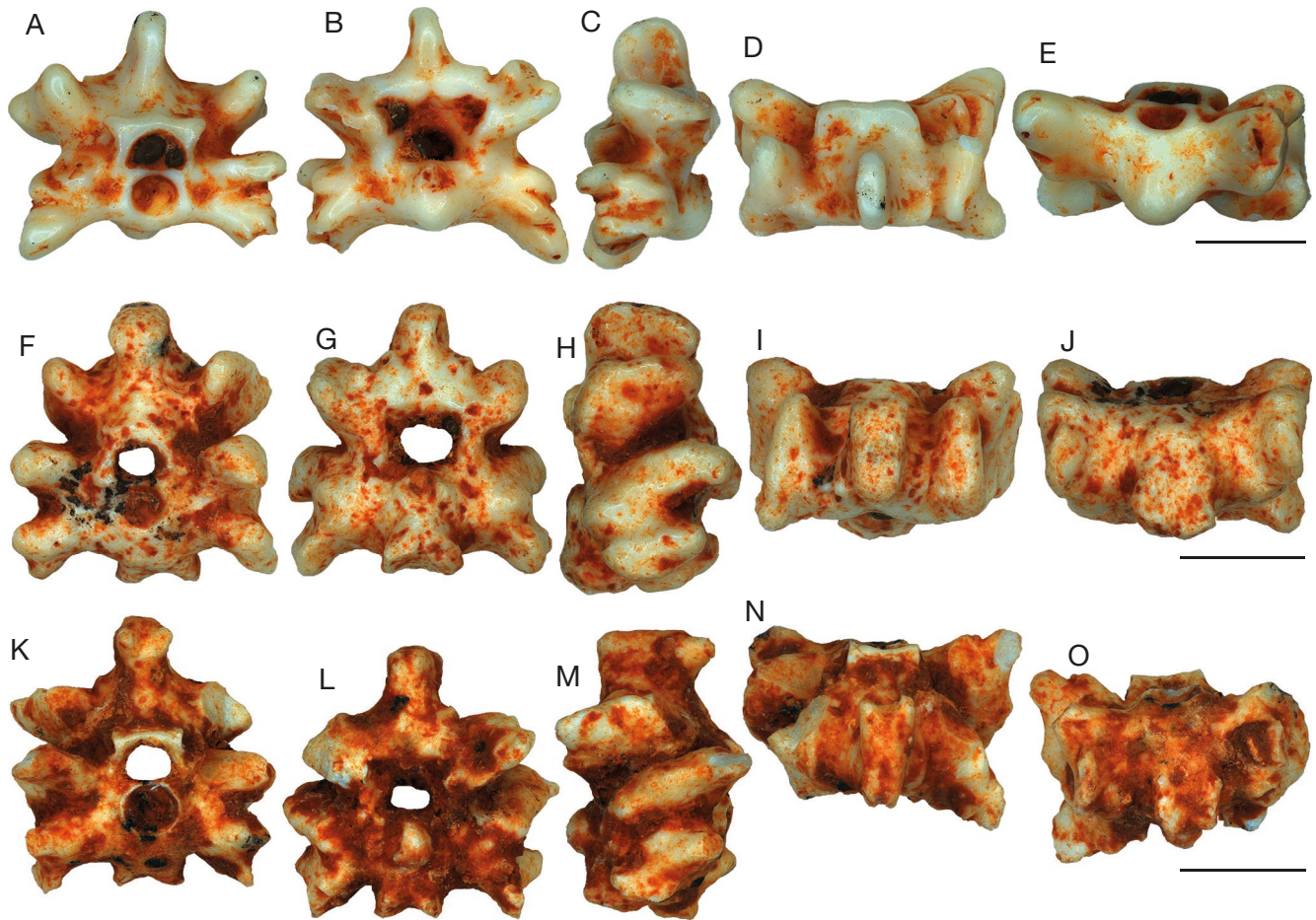


FIG. 15. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from La Bouffie, caudal vertebrae: **A-E**, UM BFI 3048 in anterior (**A**), posterior (**B**), left lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F-J**, UM BFI 3049 in anterior (**F**), posterior (**G**), right lateral (**H**), dorsal (**I**), and ventral (**J**) views; **K-O**, UM BFI 3050 in anterior (**K**), posterior (**L**), right lateral (**M**), dorsal (**N**), and ventral (**O**) views. Scale bars: 2 mm.

& Rage 1972: fig. 6B; this paper, Fig. 17A-F), similarly to the holotype, whereas four others (MNHN.F.QU16306; Hoffstetter & Rage 1972: fig. 6C) are simply built, devoid of any additional apophyses (“*vertèbres dorsales typiques*”). Hoffstetter & Rage (1972) attributed the latter vertebrae to the anterior trunk portion of the column of *C. filholi*, justifying that decision with their similarity to trunk vertebrae of the extant “erycine” snakes (“*présentent le style des Erycinae*”), in which they envisaged *Cadurceryx* to pertain. Hoffstetter & Rage (1972) noticed that, at first glance, the complexity pattern of the trunk vertebrae of *Cadurceryx* closely resembles (but not in all aspects) that characteristic of caudal vertebrae of the living ericids and charinaids.

Apart from the remains belonging to the “old collections” from the Phosphorites du Quercy, Hoffstetter & Rage (1972) described also a number of vertebrae from precisely dated Eocene localities in France. These were identified as either *Cadurceryx* cf. *filholi* or *Cadurceryx* sp., and originated from the middle Eocene (MP 16) of Robiac and the late Eocene (MP 17) Quercy localities of Malpérié and Les Pradigues. Among them, Hoffstetter & Rage (1972) found a few complex caudal (or cloacal) vertebrae (“*vertèbres caudales typiques*”) (UM MAL 501 and UM MAL 503; Hoffstetter & Rage 1972:

95, fig. 6D, pl. I fig. 4; this paper, Fig. 11A-J). They noticed that these vertebrae are less complex than the preceding trunk vertebrae (“*vertèbres complexes à tubercules costaux*”) and identified them as belonging to *Cadurceryx* sp. (and not *C. filholi*).

At least one vertebra from Malpérié (UM MAL 502), described briefly and illustrated by Hoffstetter & Rage (1972: pl. I, fig. 3), with reduced protruding elements accompanying the zygapophyses and provided with a distinct (and small anteroposteriorly) hypapophysis, apparently pertained (in the light of our present study; see above) to the anterior trunk portion of the column. Hoffstetter & Rage (1972), however, referred it as a “*vertèbre complexe à tubercules costaux*”, therefore as coming from the posterior trunk portion of the column, whereas its hypapophysis (short but distinct) was unexpectedly considered a haemal keel (“*carène hémale*”). This (rather strange) judgement may have resulted from the absolute (?) conviction of these authors that all anterior trunk vertebrae of *Cadurceryx* were simply built, therefore the vertebra in question should have originated from another region of the column.

In the section devoted to the fossils from Malpérié, Hoffstetter & Rage (1972: 95) mentioned the presence of vertebrae provided with cloacal hypapophyses (“*hypapophyse « cloacale » ou « précloacale »*”), the feature characteristic of posteriormost

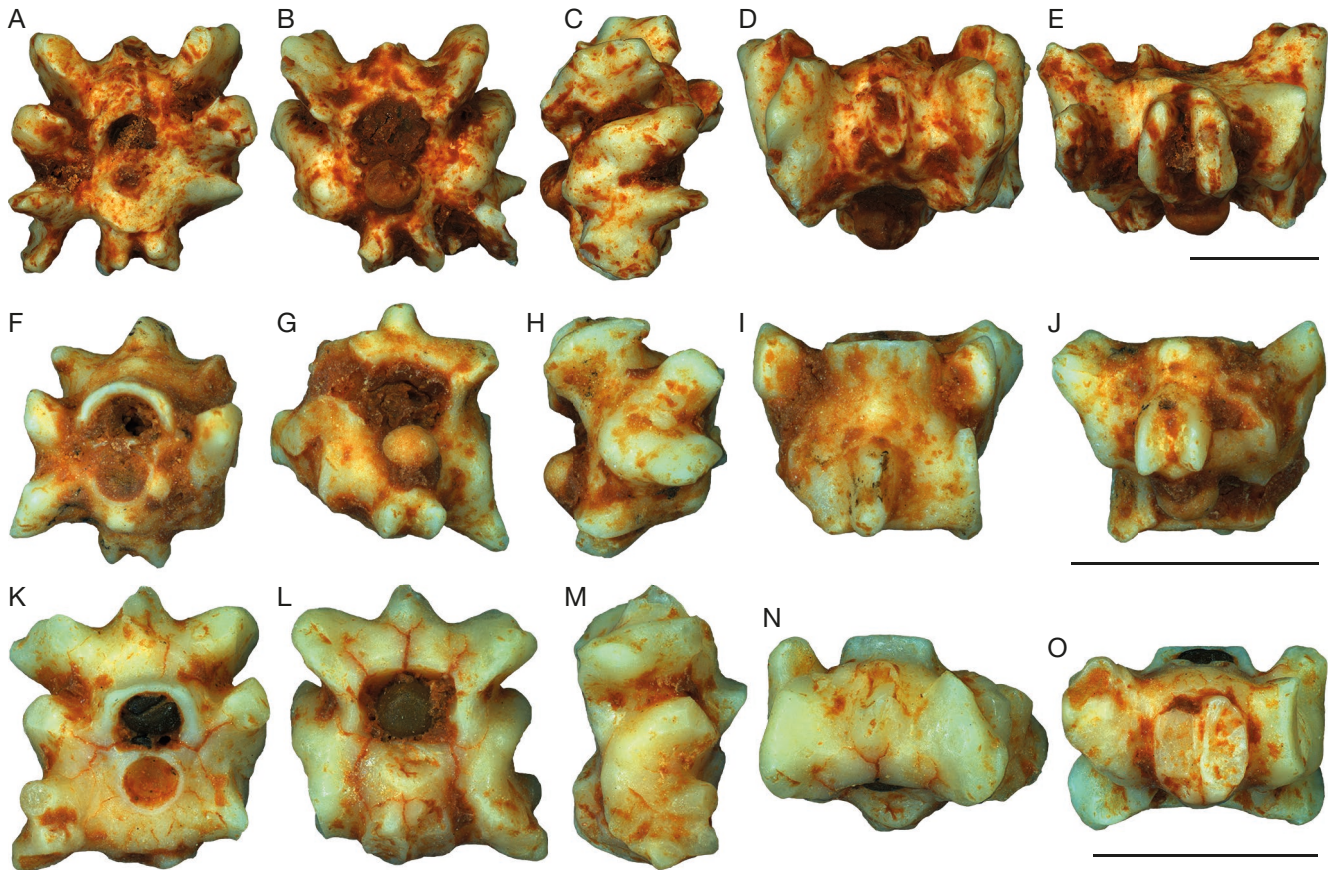


FIG. 16. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from La Bouffie, caudal vertebrae: **A–E**, UM BFI 3115 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F–J**, UM BFI 3119 in anterior (**F**), posterior (**G**), right lateral (**H**), dorsal (**I**), and ventral (**J**) views; **K–O**, UM BFI 3121 in anterior (**K**), posterior (**L**), right lateral (**M**), dorsal (**N**), and ventral (**O**) views. Scale bars: 2 mm.

trunk vertebrae, i.e., those located immediately before cloacal vertebrae. It is not certain, based on Hoffstetter & Rage's (1972) text, whether these vertebrae belonged to the fossils coming from Malpérié or another locality; we have been unable to trace these vertebrae.

The caudal vertebrae from Malpérié (originally referred to *Cadurceryx* sp.) attracted a special attention of Hoffstetter & Rage (1972: 95), who observed (considering this fact as curious) that they are a little less complex (“*un peu moins complexes*”) than the preceding (i.e., trunk) ones. These authors also noticed that the arrangement of additional apophyses surmounting the caudal vertebrae differs from that observed in the trunk vertebrae, in particular “*les ptéropophyses sont confondues avec la lame qui surmonte les postzygapophyses* [= anterior extensions of postzygapophyses]” (Hoffstetter & Rage 1972: 95). It is difficult, however, to guess from the above statement which of the either two structures is lacking. In our opinion, the anterior extensions of postzygapophyses are the elements missing in the caudal (and also cloacal) vertebrae, whereas the prominent pterapophyses are maintained in the entire post-trunk portion of the column. This explains the absence of interzygapophyseal fusions in post-trunk vertebrae (see below).

Subsequently to this 1972 original description, *Cadurceryx* was mentioned (but not described in detail) from several Eocene localities in the Phosphorites du Quercy (see also

Discussion below). In the literature, there exist illustrations of three previously undescribed vertebrae. Of them, two caudal vertebrae were illustrated: *Cadurceryx* cf. *filholi* from Le Bretou (MP 16) (UM BRT 1317; Rage 1988: fig. 17) and *Cadurceryx filholi* from Rosières 2 (MP 17) (UM ROS2 266; Rage 1984b: fig. 16D; this paper, Fig. 11K–M). As revealed by our current study, these two vertebrae rather “deviate” from the morphology “typical” of *Cadurceryx filholi*; it is unclear if this deviation could reflect some species level distinction, but we tentatively treat it here as some kind of intraspecific variation. The third illustrated specimen (shown in anterior and dorsal views) is a trunk vertebra from Lavergne (UM [formerly USTL] LAV 1275; Rage 2013: fig. 3h, i).

Finally, Szyndlar & Rage (2003), based on unpublished observations, briefly reported that additional apophyses in *Cadurceryx* were not restricted to the posterior trunk portion of the column but that they were also present on more anteriorly located trunk vertebrae.

As a further note, based on the herein documentation that *Cadurceryx* possessed complex structures and additional apophyses throughout its vertebral column, from its beginning to the end of the tail, it is evident that the trunk vertebrae devoid of additional apophyses that were presented in the original Hoffstetter & Rage (1972) publication (“*vertèbres*

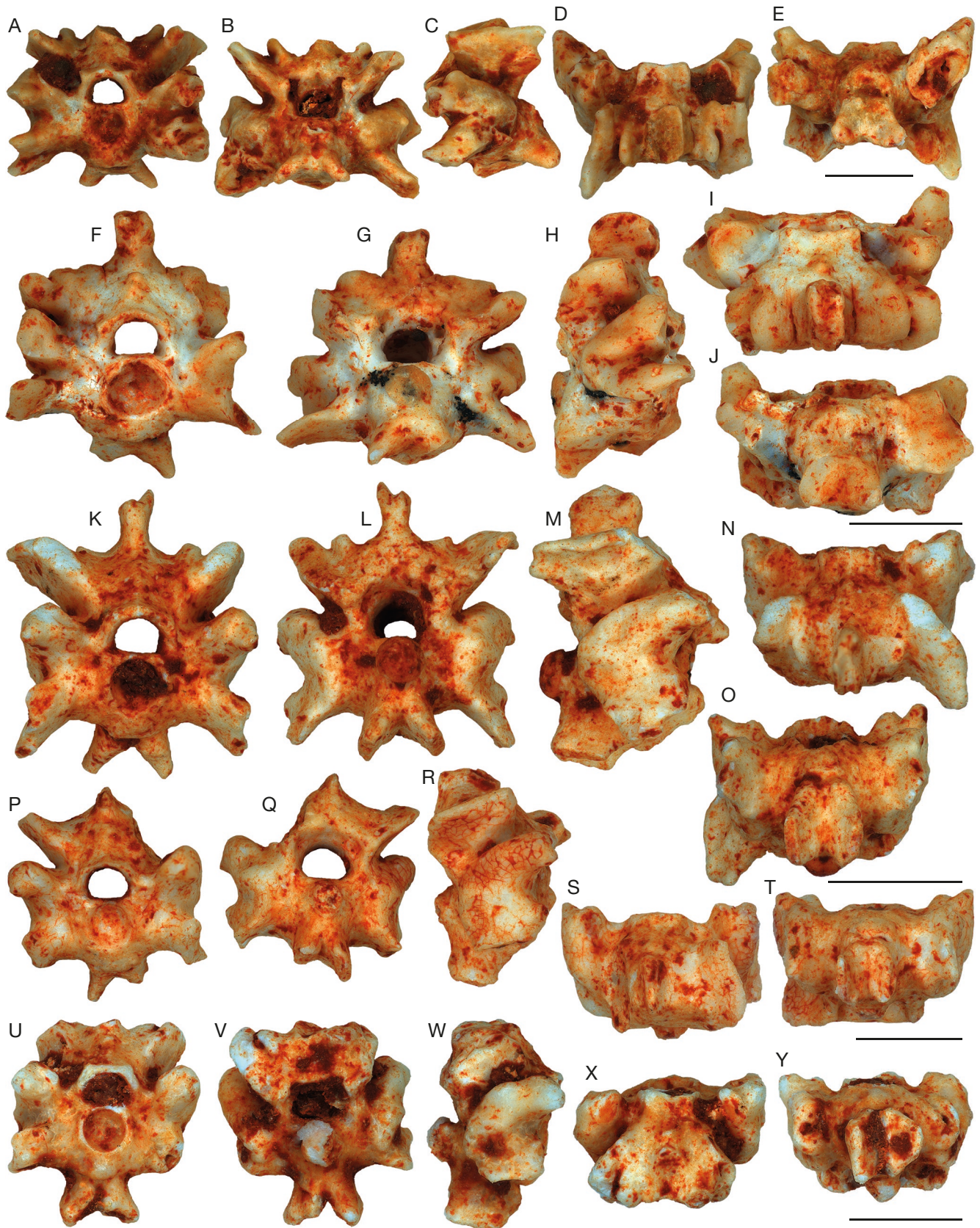


FIG. 17. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from Sainte Néboule, caudal vertebrae: **A-E**, UM SNB 5136 in anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views; **F-J**, UM SNB 5137 in anterior (F), posterior (G), right lateral (H), dorsal (I), and ventral (J) views; **K-O**, UM SNB 5138 in anterior (K), posterior (L), right lateral (M), dorsal (N), and ventral (O) views; **P-T**, UM SNB 5139 in anterior (P), posterior (Q), right lateral (R), dorsal (S), and ventral (T) views; **U-Y**, UM SNB 5140 in anterior (U), posterior (V), right lateral (W), dorsal (X), and ventral (Y) views. Scale bars: 2 mm.

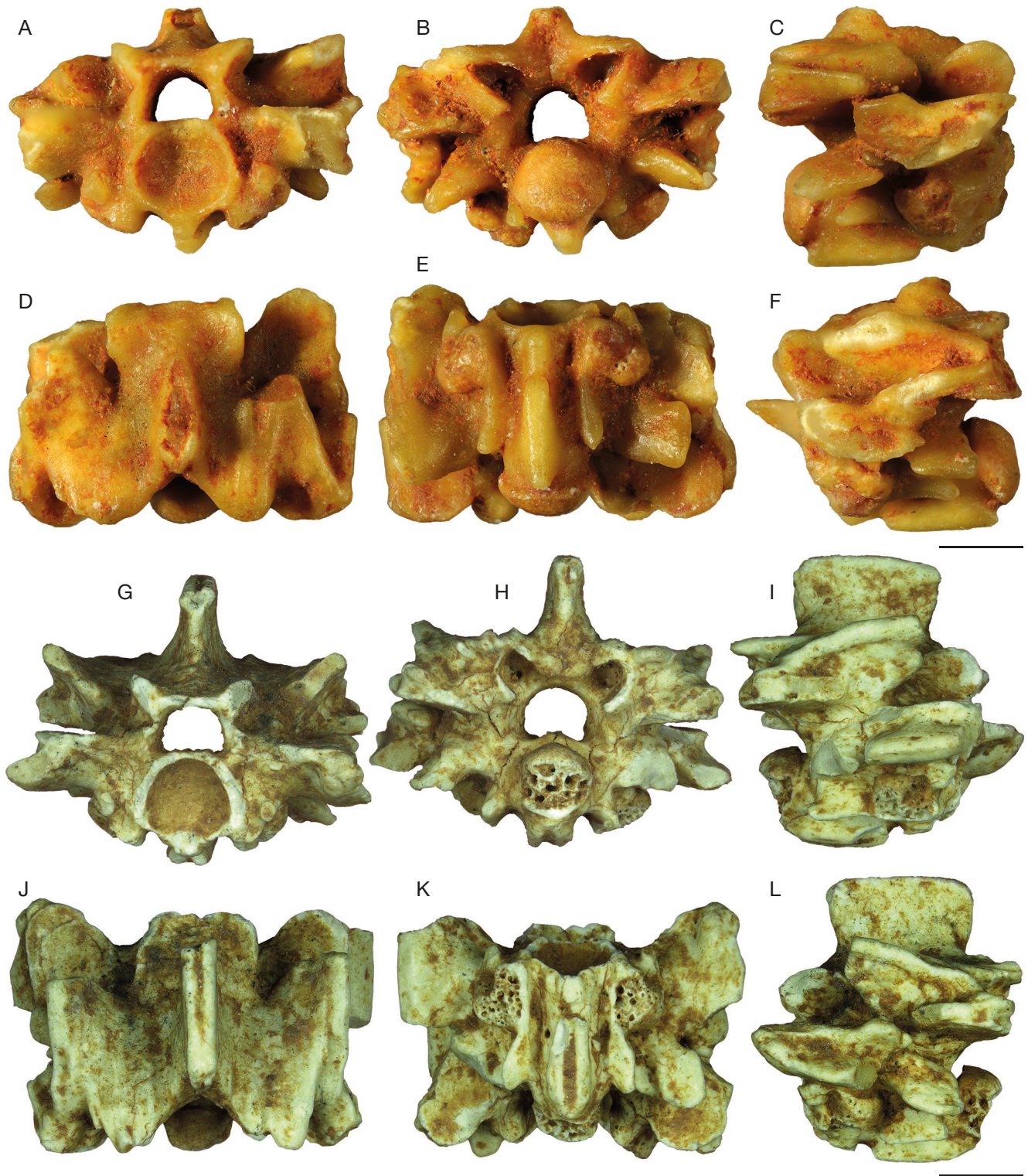


FIG. 18. — *Cadurceryx filholi* Hoffstetter & Rage, 1972 from the “old collections” of Quercy (locality[ies] imprecisely known, middle or late Eocene), trunk vertebrae: **A–F**, MNHN.F.QU16304 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), ventral (**E**), and left lateral (**F**) views; **G–L**, NHMW 2019/0064/0001 in anterior (**G**), posterior (**H**), right lateral (**I**), dorsal (**J**), ventral (**K**), and left lateral (**L**) views. Scale bars: 2 mm.

dorsales typiques” of Hoffstetter & Rage 1972; e.g. specimens MNHN.F.QU16306; see Hoffstetter & Rage 1972: fig. 6C) cannot belong to this taxon and instead they are here reidentified as belonging to some other snake (provisionally referred here as *Constrictores* indet.).

STATUS OF THE ENGLISH MATERIAL REFERRED TO *CADURCERYX*

The first snake remains identified as *Cadurceryx* outside of France were reported from the Eocene of England. The oldest fossil, a single “*Cadurceryx*-like caudal vertebra”,

was reported from the middle Eocene locality of Creechbarrow (MP 16) by Hooker (1986), with this record being reproduced as *Cadurceryx* sp. by Milner (1986) and cf. *Cadurceryx* sp. indet. by Benton & Spencer (1995). Unfortunately, these were all simple mentions and no description or figure or that material was published. The presence of other material of *Cadurceryx* sp. was mentioned also from the late Eocene of Hordle Cliff (MP 17) by Milner (1986); also in this case, no information about the above fossil(s) was provided.

Nevertheless, other excavations in Hordle Cliff, starting at the 1990s, yielded new fossil ophidian remains, which were eventually housed in the collections of MSUVP. Of them, five caudal vertebrae from the collections of MSUVP were described as the new species *Cadurceryx pearchi* by Holman *et al.* (2006). Interestingly, the above paper did not include any mention about possible presence or absence of trunk vertebrae in the examined MSUVP material, while four other snake papers that were also based on the Hordle Cliff material from the MSUVP collections (Holman 1993, 1996; Holman & Harrison 1998a, b), provided no evidence for the existence of trunk vertebrae of *Cadurceryx*. Accordingly, there is no evidence whether trunk vertebrae were actually absent in this MSUVP collection or they (if present) were ignored by the above authors. Anyway, possible absence of trunk vertebrae in the situation when caudals are present, seems astonishing (but this is anyway not the only such case for this taxon; see also Discussion below).

Apparently, in order to compare the newly erected species *Cadurceryx pearchi* with the type species *Cadurceryx filholi*, Holman *et al.* (2006) used only one illustration of a caudal vertebra referred to the latter species, published in the snake volume of *Handbuch der Paläoherpetologie* by Rage (1984b: fig. 16D; this paper, Fig. 11K–M). The choice of this vertebra (UM ROS2 266; originating from Rosières 2) seems unfortunate, because its morphology, especially in the anterior aspect, notably deviates from that characteristic of most caudal vertebrae of *Cadurceryx*. However, the reason for which Holman *et al.* (2006) chose just this vertebra seems quite clear: it was (and so far still is!) the only illustrated caudal vertebra identified to the species level as *Cadurceryx filholi*. At those times, illustrations of three other caudal vertebrae referred to *Cadurceryx* were available in the literature (two from Malpéridé: UM MAL 501 and UM MAL 503; Hoffstetter & Rage 1972: fig. 6D; pl. I, fig. 4; this paper, Figs 11A–D, E–H; and one from Le Bretou: UM BRT 1317; Rage 1988: fig. 17), but they were ignored by Holman *et al.* (2006), probably because they were identified either only to the genus level for the material of Malpéridé (*Cadurceryx* sp. of Hoffstetter & Rage 1972) or were not confidently identified anyway to the species level (*Cadurceryx* cf. *filholi* of Rage 1988). Ironically, the two vertebrae from Malpéridé (as we can state today) display clearly the morphology characteristic of the species *C. filholi*, unlike the caudal one from Rosières 2.

Hence, the diagnosis of *Cadurceryx pearchi* seems inaccurate, because it reflects exclusively the differences between the single vertebra from Rosières 2 and the English holotype

(MSUVP 2061; Holman *et al.* 2006: figs 2, 3), stating that: 1) *C. pearchi* has the cotyle larger than the neural canal, while in *C. filholi* vice versa; and 2) the prezygapophyses of *C. pearchi* are produced into knoblike tubercles, absent in *C. filholi*. However, the relatively broad neural canal in the Rosières fossil (feature 1) apparently results from the juvenile age of the snake (e.g. Georgalis & Scheyer 2019; Szyndlar & Georgalis 2023). Regarding the second diagnostic trait of *C. filholi* (feature 2), namely the “anterior ends of prezygapophyses [...] produced into knoblike tubercles”, it is very difficult to guess what the latter term means based on Holman’s *et al.* (2006: 58) text and figures. The only reasonable explanation is that the authors used the term “knoblike tubercle” as a synonym of “prezygapophyseal accessory process”. The prezygapophyseal accessory processes (prominent in most cases), however, occur in caudal vertebrae of *C. filholi*; no doubt, their absence in the vertebra from Rosières results again from the juvenile age of the snake.

To close the comments on the paper by Holman *et al.* (2006), we should add that one of the paratypes of *Cadurceryx pearchi* (MSUVP 2059) was listed as “Caudal [sic] vertebrae of *Pterygoboa* sp. indet. (MSUVP 2059)” on their caption of the drawing of the specimen (Holman *et al.* 2006: 57, fig. 3i–l), although the same (single) vertebra was described as “Caudal [sic] vertebrae of *Cadurceryx pearchi* sp. nov. paratype (MSUVP 2059)” on their caption of the photograph of the specimen (Holman *et al.* 2006: 56, fig. 2g–i). This is most probably a misspelling, as we see no reason why Holman *et al.* (2006) regarded this particular specimen as belonging to *Pterygoboa*. In any case, there is so far no evidence that the genus *Pterygoboa* Holman, 1976, a bizarre “erycine” from the Oligo-Miocene of North America was ever present in England or Europe in general; besides, the vertebral morphology of *Pterygoboa* (that is also characterized by the presence of additional apophyses) is drastically different from *Cadurceryx* (Holman 1976, 1998; Mead & Schubert 2013).

Here we present a few caudal vertebrae from the late Eocene (MP 17A) of Christchurch Bay at Hordle Cliff (Mammal Bed, Totland Bay Member), England, from the collections of NHMUK (Figs 19–21). These specimens are apparently the same ones mentioned in the faunal list of Milner (1986). Interestingly, in this NHMUK sample, among numerous vertebrae of several other snake taxa from Hordle Cliff, there were only a few *Cadurceryx*-like caudal vertebrae available and not a single trunk vertebra. Nevertheless, the vertebrae still seem to pertain to different regions of the caudal vertebral column, as it can be attested by the differences regarding the anteroposterior length and dorsoventral height across the specimens (Figs 19–21). In any case, the new English caudal vertebrae bear practically no important differences from the known caudal vertebrae of *Cadurceryx filholi* from the Phosphorites du Quercy.

These being said, to summarize, the English form from Hordle Cliff seems to could potentially belong to *Cadurceryx*, although the absence of any trunk vertebra renders such

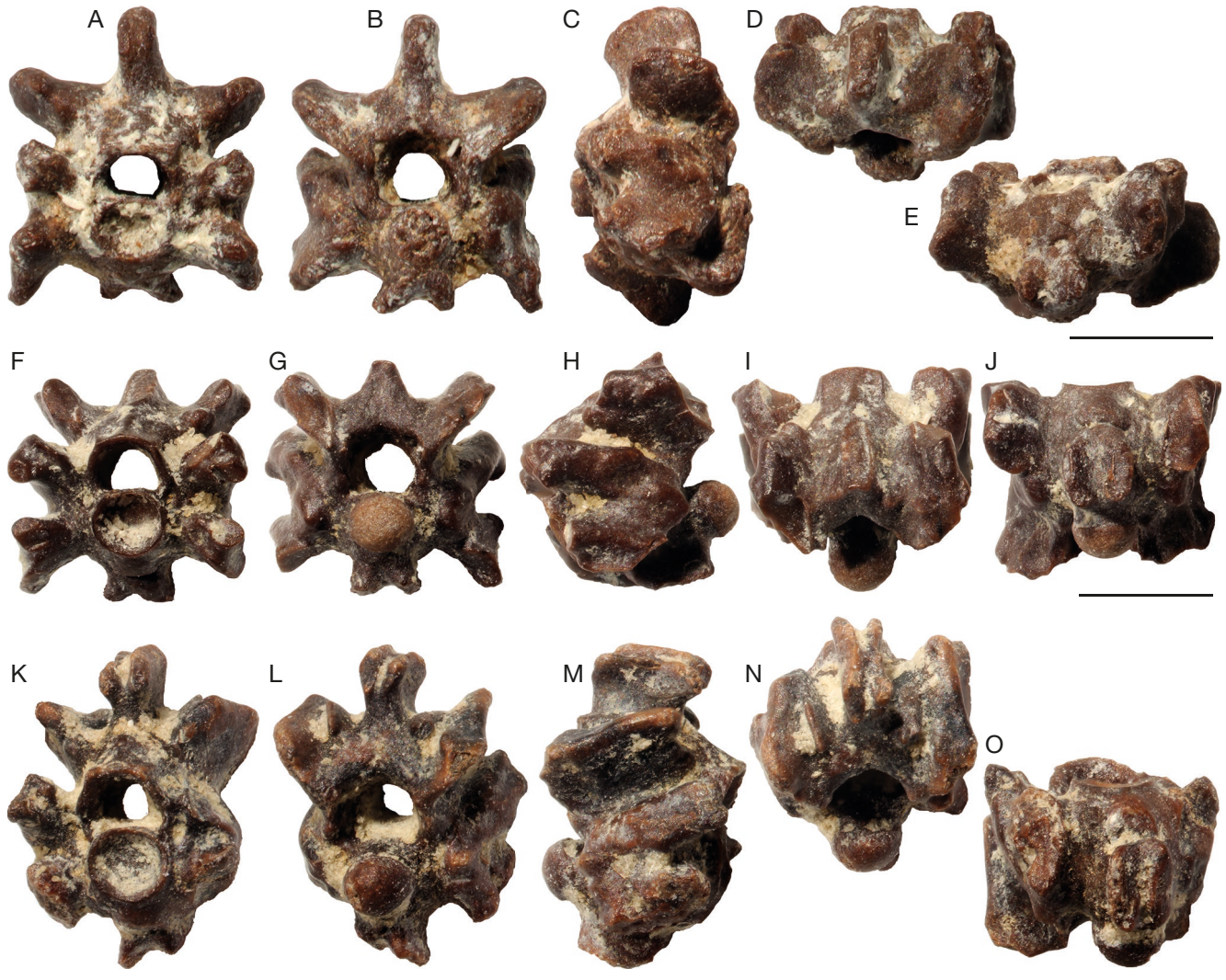


FIG. 19. — ?*Cadurceryx* sp. from Hordle Cliff, caudal vertebrae: **A–E**, NHMUK PV R 10803 in anterior (**A**), posterior (**B**), right (ventro)lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F–J**, NHMUK PV R 10805 in anterior (**F**), posterior (**G**), left lateral (**H**), dorsal (**I**), and ventral (**J**) views; **K–O**, NHMUK PV R 10804 in anterior (**K**), posterior (**L**), right lateral (**M**), (postero)dorsal (**N**), and ventral (**O**) views. Scale bars: 2 mm.

taxonomic identification as tentative (at max). Nevertheless, based on the diagnosis of Holman *et al.* (2006), coupled with the observation of the NHMUK caudal vertebrae, a species level distinction of the English *Cadurceryx* from the French species *Cadurceryx filholi* (although possible) cannot be demonstrated with certainty. The holotype of *Cadurceryx pearchi* and all known specimens from England are all incomplete caudal vertebrae and the diagnosis proposed by Holman *et al.* (2006) refers to variable features. Accordingly, *Cadurceryx pearchi* is considered to be a *nomen dubium*, with the material potentially pertaining to an indeterminate species of *Cadurceryx* (i.e., ?*Cadurceryx* sp.). Only new and more complete material from the Eocene of England, ideally comprising also trunk vertebrae, will eventually show whether indeed a distinct species of this genus was inhabiting England or whether they are conspecific with the French species *Cadurceryx filholi* or even whether these “puzzling” caudal vertebrae from Hordle pertain instead to a (different) taxon (potentially an erycid or a charinaid).

DISCUSSION

TAXONOMIC AFFINITIES OF *CADURCERYX* WITHIN SNAKES

Ever since its original establishment by Hoffstetter & Rage (1972), *Cadurceryx* has met a relatively frequent appearance in the literature (e.g. Rage 1973, 1974, 1975, 1977, 1978, 1984a, b, 1987, 1988, 2006, 2012, 2013; Underwood 1976; Holman 1977, 1998; Estes & Hutchison 1980; Rage & Ford 1980; Crochet *et al.* 1981; Hooker 1986; Milner 1986; McDowell 1987; Carroll 1988; Zerova 1989; Kluge 1993; Rage & Augé 1993; Szyndlar 1994; Szyndlar & Schleich 1994; Benton & Spencer 1995; Duffaud & Rage 1997; Szyndlar & Rage 2003; Szyndlar & Alférez 2005; Holman *et al.* 2006; Wallach *et al.* 2014; Boundy 2021; Georgalis *et al.* 2021a, c; Smith & Scanferla 2021; Smith & Georgalis 2022; Villa *et al.* 2022; Shi *et al.* 2023; Szyndlar & Georgalis 2023; Lemierre & Georgalis 2025). Nevertheless, almost all of these frequent appearances consisted of simple mentions of the name or reviews of what



FIG. 20. — ?*Cadurceryx* sp. from Hordle Cliff, caudal vertebrae: **A-E**, NHMUK PV R 10806 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F-J**, NHMUK PV R 10807 in anterior (**F**), posterior (**G**), right anterolateral (**H**), dorsal (**I**), and ventral (**J**) views; **K-O**, NHMUK PV R 10808 in anterior (**K**), posterior (**L**), left lateral (**M**), dorsal (**N**), and ventral (**O**) views. Scale bars: 2 mm.

was already known, while practically, the description of new material (Rage 1984b, 1988, 2013; Holman *et al.* 2006) or at least any pragmatic documentation or commentary of its anatomy (e.g. Szyndlar & Rage 2003; Smith & Scanferla 2021) have been literally minimal.

The most characteristic feature of *Cadurceryx*, i.e., the bizarre additional apophyses and structures of its vertebrae, managed to intrigue ophidian researchers since the time of Hoffstetter & Rage (1972). McDowell (1987) already commented that the “horizontally expanded” prezygapophyseal accessory

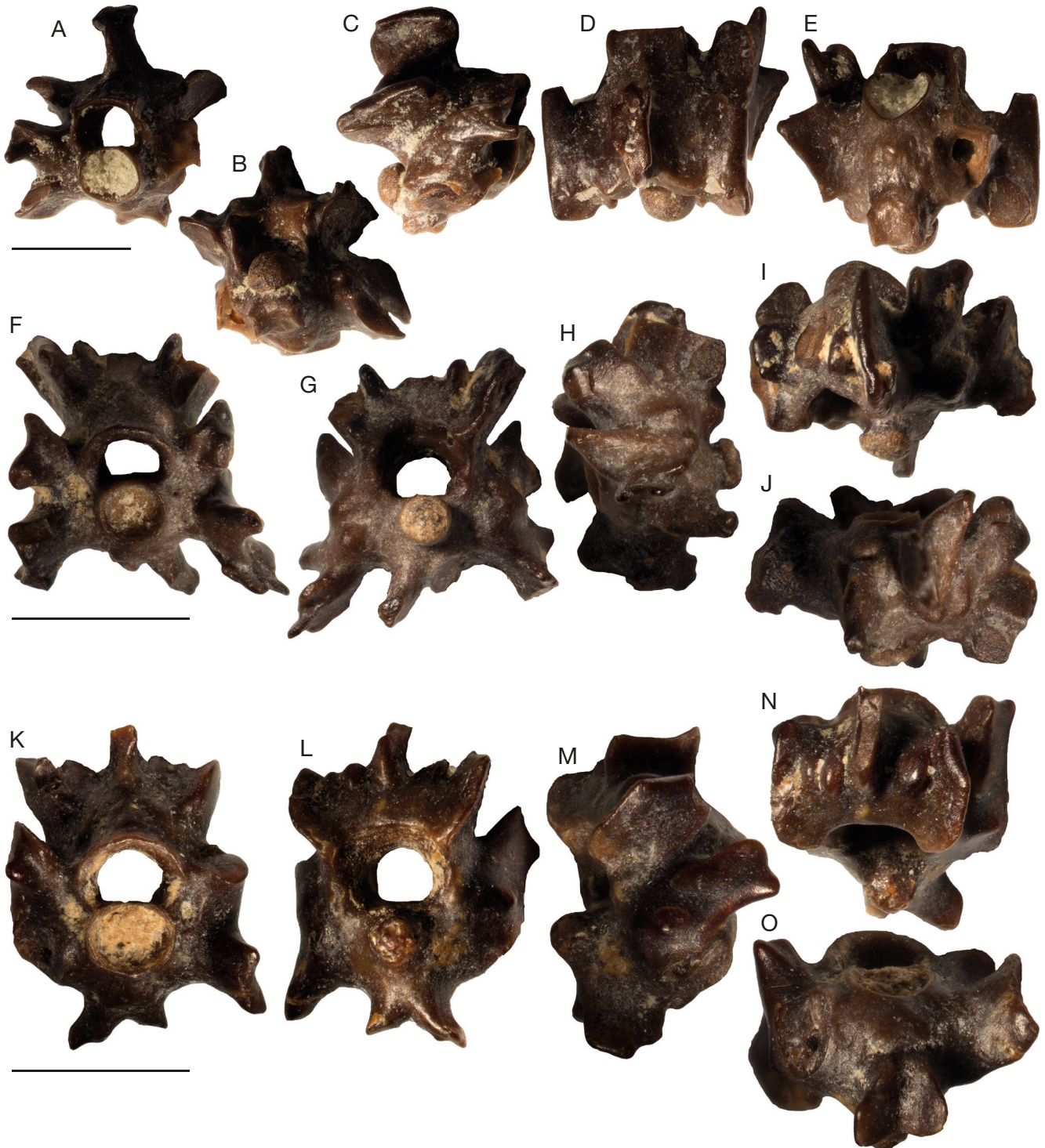


FIG. 21. — ?*Cadurceryx* sp. from Hordle Cliff, caudal vertebrae: **A-E**, NHMUK PV R 38880 in anterior (**A**), posteroventral (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F-J**, NHMUK PV R 38881 in anterior (**F**), posterior (**G**), left ventrolateral (**H**), right dorsolateral (**I**), and ventral (**J**) views; **K-O**, NHMUK PV R 38883 in anterior (**K**), posterior (**L**), right lateral (**M**), dorsal (**N**), and ventral (**O**) views. Scale bars: 2 mm.

processes could differentiate *Cadurceryx* from other constrictor snakes. It was so far believed that the complex structures and apophyses were, like in erycids and charinaids, practically confined (or at least primarily present) in the caudal series (e.g. Hoffstetter & Rage 1972; Rage 1984b, 1988; Holman *et al.* 2006) and practically, for this reason previously published

trunk vertebrae, such as the holotype MNHN.F.QU16301, were treated as cloacal or even caudal vertebrae (e.g. Hoffstetter & Rage 1972; Rage 1984b). Accordingly, *Cadurceryx* was practically always and uniformly envisaged as a member of the traditional concept of Erycidae or Erycinae (Hoffstetter & Rage 1972; Rage 1984b, 1988; Carroll 1988; Holman *et al.*

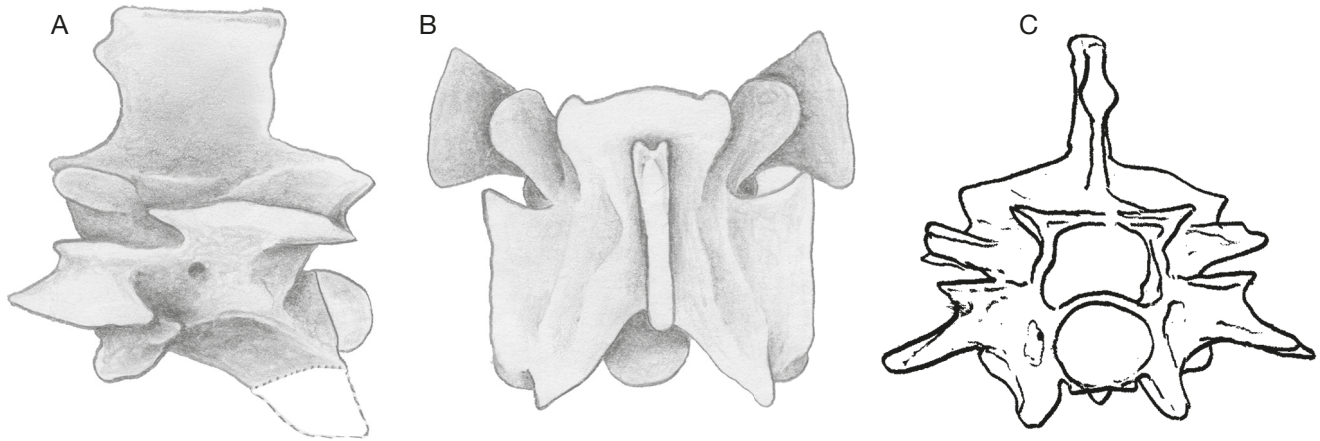


FIG. 22. — Vertebra of the extant lamprophiid *Mehelya* sp. in left lateral (A), dorsal (B), and anterior (C) views. This vertebra, along with several others originated from the stomach content of an African Mongoose and they were received from Ulrich Joger to ZS for study.

2006; Wallach *et al.* 2014; Boundy 2021; Smith & Georgalis 2022). As it was highlighted above (see Introduction), this traditional grouping uniting *Eryx*, *Charina*, and *Lichanura* was considered as monophyletic and met wide acceptance across the 20th century; however, according to molecular phylogenetic analyses, this traditional grouping appears instead to be polyphyletic, because charinaids (i.e., *Charina* and *Lichanura*) are not closely related to *Eryx*, but are more related to ungaliophiids. In any case, the only work that seemed to cast doubt on the erycine affinities of *Cadurceryx* was in fact a brief statement of Szyndlar & Rage (2003: 11) that *Cadurceryx* and the North American *Pterygoboa* were not considered as members of the traditional concept of erycines, because the “additional vertebral apophyses in both snakes are not restricted to the caudal portion of the column; instead, uniformly shaped additional apophyses occur throughout the vertebral column (unpublished observation), which cast doubts on their assignment to the Erycinae”. Our herein detailed documentation of the vertebral morphology and intracolumnar variation of *Cadurceryx filholi* fully confirms this preliminary statement of Szyndlar & Rage (2003) and the French taxon is demonstrated to possess additional apophyses throughout the vertebral column. Moreover, *Pterygoboa* also possesses complex structures in its trunk vertebrae (though it is not certain to what extent across the column), but in any case, these structures are much more simplified (Mead & Schubert 2013).

At this point, it is worth mentioning, that a number of extant caenophidian snakes, distantly related to each other, possess distinct zygapophyseal expansions and peculiar elaborations in their trunk vertebrae. Prominent such examples include the Asian xenodermid *Xenodermus* Reinhardt, 1836, the Asian colubrid *Cercaspis* Wagler, 1830 (sometimes considered a junior synonym of *Lycodon* Boie in Fitzinger, 1826; e.g. Pyron *et al.* 2013; Wallach *et al.* 2014), the American dipsadids *Emmochliophis* Fritts & Smith, 1969, *Leptodeira* Fitzinger, 1843 (but not all its species), *Nothopsis* Cope, 1871, and *Synopsis* Peracca, 1896, the African lamprophiids *Gonionotophis* Boulenger, 1893, *Limaformosa* Broadley, Tolley,

Conradie, Wishart, Trape, Burger, Kusamba, Zassi-Boulou & Greenbaum, 2018, and *Mehelya* Csiki, 1903, and the Asian elapid *Bungarus* Daudin, 1803a (see descriptions and figures in Hoffstetter 1939; Smith 1943; Bogert & Duellman 1963; Bogert 1964; Fritts & Smith 1969; Hoffstetter & Gasc 1969; Slowinski 1994; Sheil 1998; Sheil & Grant 2001; Zaher *et al.* 2019; McCartney *et al.* 2021; see also this paper, Fig. 22). These bizarre morphologies include wing-like expansions on the prezygapophyses (*Cercaspis*, *Nothopsis*, *Limaformosa*, *Mehelya*, and *Bungarus*), or wing-like expansions on the postzygapophyses (*Emmochliophis* and *Xenodermus*), or lateral wing-like expansions of the entire vertebra (*Synopsis*) (see Smith 1943; Bogert 1964; Fritts & Smith 1969; Hoffstetter & Gasc 1969; Holman 1976; Slowinski 1994; Sheil 1998; Sheil & Grant 2001; Zaher *et al.* 2019). Nevertheless, it has to be highlighted that any resemblance between the additional apophyses of *Cadurceryx* and all these snakes is only superficial: in *Cadurceryx* (as well as in caudal vertebrae of erycids and charinaids), the additional apophyses form true articular joints linking neighbouring vertebrae, unlike in other snakes.

Another interesting and prominent anatomical feature of (many but not all specimens of) *Cadurceryx* is the thick and (on many occasions) anteriorly bifurcated neural spine in dorsal view. Such bifurcation is relatively rare in snakes but it has still been observed across trunk (and occasionally also caudal) vertebrae of distantly related taxa, such as the North American Oligo-Miocene “erycine” *Pterygoboa*, the European Oligo-Miocene “erycine” *Albaneryx* Hoffstetter & Rage, 1972, and a few extant taxa of tropidophiids, charinaids, pythonids, xenodermids, dipsadids, and psammophiids, as well as in caudal vertebrae of *Bransateryx* and *Eryx* (see descriptions and/or figures in Bogert 1964, 1968a; Holman 1967; Hoffstetter & Gasc 1969; Hoffstetter & Rage 1972; Hoge & Federsoni 1974; Rage 1984b; Sheil & Grant 2001; Mead & Schubert 2013; Zaher *et al.* 2019; Szyndlar & Georgalis 2023).

A further distinctive feature of the trunk and cloacal vertebrae of *Cadurceryx*, is the presence of hypapophysis, unlike a “simple” haemal keel observed in erycids and charinaids.

Notably, the hypapophysis of mid- and posterior trunk of *Cadurceryx* is, in lateral view, rather anteroposteriorly long, prominent, and usually possesses a distinct anteroventral corner that forms approximately a right angle, while in ventral view, this structure is rather thick. Interestingly, this morphology matches perfectly with tropidophiids (Smith & Georgalis 2022; Szyndlar & Georgalis 2023; Zaher *et al.* 2024). Particularly for the “distinct anteroventral corner that forms approximately a right angle”, this is considered to represent a vertebral synapomorphy of Tropidophiidae (Smith & Georgalis 2022; Szyndlar & Georgalis 2023; Zaher *et al.* 2024) and can be indeed rather prominent across different species of the two known extant genera of the group, i.e., *Tropidophis* Bibron in Ramón de la Sagra, 1838-1843, and *Trachyboa* Peters, 1860 (e.g. see figures in Syromyatnikova *et al.* 2021; Szyndlar & Georgalis 2023; Zaher *et al.* 2024); furthermore, as pointed out by Szyndlar & Georgalis (2023: 750), in tropidophiids the hypapophyses of trunk vertebrae can “occasionally show a different degree of inclination that protrudes much anteriorly” (e.g. figures in Bogert 1968a, b; Dowling & Duellman 1978; Lee & Scanlon 2002), which is also the case of certain trunk vertebrae of *Cadurceryx*. Besides, the presence of hypapophyses in cloacal and anteriormost caudal vertebrae and of haemapophyses in more posterior caudal vertebrae of *Cadurceryx* also matches the pericloacal subcentral structures pattern observed in Tropidophiidae (Szyndlar & Georgalis 2023). Finally, minute pterapophyses are also present in all vertebrae of *Trachyboa* (but not in *Tropidophis*) (see Szyndlar & Georgalis 2023).

All these being said, it seems challenging to assess the exact phylogenetic and taxonomic affinities of *Cadurceryx*. Certain features, such as the low value of the centrum length/neural arch width ratio (< 1.1) are indicative of Constrictores Oppel, 1811 (*sensu* Georgalis & Smith 2020), i.e., the group encompassing boas (including, among others, also Erycidae and Charinaidae) and pythons (Georgalis & Smith 2020; Szyndlar & Georgalis 2023); however, this feature is not exclusive to this group and can be in fact observed across an array of other non-caenophidian snakes that do not pertain to Constrictores (see Szyndlar & Georgalis 2023). As explained above, erycids and charinaids seem to possess a considerable resemblance with *Cadurceryx* in terms of the additional apophyses, which form true articular joints linking neighbouring vertebrae, unlike other snakes that possess additional apophyses; however, as clearly demonstrated here, these additional apophyses in *Cadurceryx* are present also throughout the whole vertebral column and not “simply” in the caudal series, as is the case of erycids and charinaids. Moreover, as it was also highlighted above, molecular evidence strongly suggests that Erycidae and Charinaidae do not form together a monophyletic group but are only distantly related within booids; therefore, if these phylogenetic topologies are accurate, evolution of complex caudal vertebral morphologies in charinaids and erycids is homoplastic, which would further cast doubt on the systematic affinities of fossil taxa based on overall similar morphologies.

On the other hand, the striking (and unique among snakes) resemblance of the broad hypapophyses with a distinct straight anteroventral corner in *Cadurceryx*, coupled with other features, such as the presence of pterapophyses (shared with the extant *Trachyboa*), the similar ratio of centrum length to neural arch width and the similar pattern of pericloacal subcentral structures, match the diagnosis of Tropidophiidae. Nevertheless, certain structures of *Cadurceryx*, including the additional apophyses of all vertebrae, instead rather deviate from this group.

To sum up, taking into consideration that the shared hypapophyseal morphology of *Cadurceryx* and Tropidophiidae represents a vertebral synapomorphy of the latter group (Smith & Georgalis 2022; Szyndlar & Georgalis 2023; Zaher *et al.* 2024), coupled with the fact that under molecular topologies, vertebral characters present in erycids and charinaids are homoplastic, we herein tentatively envisage *Cadurceryx* as a tropidophiid with convergently evolved apophyseal morphologies with erycids and charinaids. Of course, only complete articulated skeletons, ideally comprising also skull remains, may confirm or refute such taxonomic referral. Note that tropidophiids are currently present only in tropical Americas, however, fossil record implies for a much broader distribution, as it can be attested by an unnamed form from the late Eocene of Fayum, Egypt (McCartney & Seiffert 2016), while other potential occurrences from the Paleogene of Europe, such as *Szyndlaria* Rage & Augé, 2010, from the middle Eocene of France (Rage & Augé 2010), could also belong to this group (see Smith & Georgalis 2022; Zaher *et al.* 2024).

Species level taxonomy and geographic and stratigraphic distribution of Cadurceryx

Regarding the species level taxonomy of *Cadurceryx*, two species have been in the past referred to this genus: the type species, *Cadurceryx filholi*, from various middle and late Eocene localities of France (mainly, but not exclusively, in the area of the Phosphorites du Quercy; see below for a complete list of all occurrences), and *Cadurceryx pearchi* from the late Eocene (MP 17) of the locality of Hordle Cliff in England. Besides, Rage (1978) had already left open the possibility that an additional species of *Cadurceryx* was present in Quercy, an assumption he based on abundant (though then undescribed) material from Lavergne – more particularly, Rage (1978: 209) considered that the form from the localities of Lavergne and Sainte Néboule could represent a distinct taxon than *Cadurceryx filholi*. In our revision, the genus is conceived as monotypic, i.e., only the type species, *Cadurceryx filholi*, is treated as valid, with the other previously referred species of the genus, *Cadurceryx pearchi* from England, treated as a *nomen dubium*. As such, the herein studied material from localities in Quercy, spanning from the middle (MP 16) to late (MP 18) Eocene, is treated all as pertaining to *Cadurceryx filholi*, while the English material should be better regarded (at best) solely up to the genus level, as ?*Cadurceryx* sp. and we cannot even exclude that it represents some erycid or charinaid taxon.

It should be noted though that besides France and potentially also England, *Cadurceryx* has also been mentioned from Spain, as an undescribed and unfigured occurrence from the late Eocene (MP 17) locality of Sossis by Szyndlar & Schleich (1994), a claim reproduced also later by Szyndlar & Alf  rez (2005). Subsequent studies by one of us (ZS) of ophidian remains coming from this locality have revealed the presence of seven fragmentary trunk and caudal vertebrae (ICPS 116770 - ICPS 116772 and ICPS 116777 - ICPS 116780), which is temporarily identified as cf. *Cadurceryx* sp. (ZS, unpublished observation). Although superficially resembling the French remains of *Cadurceryx filholi*, the Spanish fossils may have represented a distinct species. Unfortunately, due to the scarcity and fragmentary nature of the latter material, ultimate conclusions cannot be drawn at the present time.

Stratigraphically (but also geographically) *Cadurceryx* seems to be rather confined. Besides the indeterminate remains from England (*Cadurceryx pearchi* of Holman *et al.* 2006 and the vertebrae from Hordle Cliff presented above) and the undescribed vertebrae from Spain, which could pertain (or not) to *Cadurceryx*, the genus is known exclusively from France. In summary, *Cadurceryx filholi* is known from: the middle Eocene of Lavergne (MP 16; Rage 2013; this paper), Le Bretou (MP 16; *Cadurceryx* cf. *filholi* of Rage 1988), and Robiac (MP 16; *Cadurceryx* sp. of Hoffstetter & Rage 1972), and the late Eocene of La Bouffie (MP 17; this paper), Les Pradigues (MP 17; *Cadurceryx* cf. *filholi* of Hoffstetter & Rage 1972), Malp  ri   (MP 17; *Cadurceryx* sp. of Hoffstetter & Rage 1972; this paper), Sainte N  boule (MP 18, this paper), Rosi  res 2 (Rage 1984b), and of course the “old collections” of Quercy, which could be dated anywhen between the middle and late Eocene (Hoffstetter & Rage 1972; this paper); it is worth noting that all these localities, with the exception of Robiac, are situated within the area of the Phosphorites du Quercy.

Besides these confirmed occurrences, simple mentions of the taxon, mostly in faunal lists, have been made for the late Eocene of Aubrelong 2 (MP 17; Crochet *et al.* 1981), Lebrati  re (MP 17; Crochet *et al.* 1981), Les Clapi  s (MP 17; Crochet *et al.* 1981), Perri  re (MP 17; Crochet *et al.* 1981), Rosi  res 5 (MP 17; Crochet *et al.* 1981), Gousnat (MP 18; Crochet *et al.* 1981), Monteils (MP 18; Maitre *et al.* 2006), Co  nac (MP 19; Crochet *et al.* 1981), and Palembert (MP 19; *Cadurceryx* sp. of Crochet *et al.* 1981); all these localities are situated within the area of the Phosphorites du Quercy.

Interestingly, furthermore, there were two mentions in the literature that implied the probable presence of *Cadurceryx* as early as the MP 13 zone of middle Eocene: these were simply mentions in Duffaud & Rage (1997) and Rage (2012), without even explicitly stating the locality name, that cannot be evaluated. Nevertheless, unpublished observations of the late Jean-Claude Rage and his personal communications to one of us (ZS) could shed some light on this issue: Jean-Claude Rage had mentioned the presence of two caudal and two trunk vertebrae from the middle Eocene (MP 13) of Bouxviller and one ?anterior caudal and six trunk vertebrae from the coeval (MP 13) locality of Saint-Maximin, which could belong to *Cadurceryx*. If correct, these would

represent the oldest occurrence of the genus; however, only a thorough documentation of these specimens will eventually show whether they belong indeed to *Cadurceryx* or not.

It is noticeable that *Cadurceryx* is absent from the well-sampled early and early middle Eocene Fossilagerst  tte localities of Messel and Geiseltal in Germany, which have anyway yielded a diverse array of snakes, including unique articulated skeletons of multiple sizes (e.g. Kuhn 1939; Smith & Scanferla 2016, 2021, 2022; Scanferla & Smith 2020; Zaher & Smith 2020; Georgalis *et al.* 2021c, 2025; Palci *et al.* 2024). The oldest “erycine” snake from Europe, the enigmatic “*Calamagras*” *gallicus* Rage, 1977, is even older, known from the MP 10 of the Paris Basin (Rage 1977), while the MP 11 of Messel has anyway yielded the charinaid *Rageryx schmidi* Smith & Scanferla, 2021, known from a single articulated skeleton (Smith & Scanferla 2021). Accordingly, only the documentation of the afore-mentioned material from the MP 13 of Bouxviller and Saint-Maximin will reveal whether *Cadurceryx* is genuinely (or not) absent during the early and early middle Eocene. On the other hand, the genus apparently did not survive the “*Grande Coupure*” extinction event at the latest Eocene-earliest Oligocene boundary, as it is totally absent from all early Oligocene localities. Therefore, the enigmatic and so intriguing *Cadurceryx* seems to have been one of the several herpetofaunal “victims” of the climatic deteriorations and major faunal turnover that affected Europe during the Eocene-Oligocene transition.

Life history and autecology of Cadurceryx

With such a unique vertebral morphology, it is truly tempting, though inevitably and absolutely speculative, to hypothesize on the potential functional morphology of the bizarre vertebral structures of *Cadurceryx* and what would these imply on the life history and autecology of this taxon.

It is indeed hard to envisage functional implications for these extreme vertebral morphologies of *Cadurceryx*, especially when considering that the several extant snake taxa with additional apophyses on their vertebrae (*Eryx*, *Charina*, *Lichanura*, *Xenodermus*, *Cercaspis*, *Emmochliophis*, *Synophis*, *Nothopsis*, *Gonionotophis*, *Mehelya*, *Limaformosa*, *Bungarus*) display rather disparate functional morphologies: for example, the expanded caudal vertebral morphologies in charinaids and erycids have been suggested to aid as a component of anti-predator defence or defence against aggressive prey (Fr  dlov   *et al.* 2023; 2025), the massive and expanded zygapophyses of *Synophis* enable this snake to achieve increased rigidity to the point of forming a “zig-zag pattern” along the axis of the vertebral column (Sheil & Grant 2001), while the expanded zygapophyses in African files snakes (*Gonionotophis*, *Mehelya*, and *Limaformosa*) and *Bungarus* structurally support a triangular transverse body form (Jason Head, personal communication, July 2025). Besides, it is worth noting that a few tetrapods are known to possess distinct tubercles, ornamentation, or spikes in their vertebrae but nevertheless, these are observed across a wide taxonomic range, including the Cretaceous-Paleogene salamander *Piceoerpeton* Meszoely, 1967 (see Gardner 2012), the Paleogene and Neogene salamander

Chelotriton Pomel, 1853 (see e.g. Ivanov 2008; Roček 2019), the Cretaceous pipoid frog *Pachycentrata* Báez & Rage, 2004 (see Báez & Rage 1998), the chamaeleonid lizard *Brookesia* Gray, 1864 (see Molnar & Watanabe 2023), the dipsadid snake *Xenopholis* Peters, 1869 (see Boulenger 1896; Hoge & Federsoni 1974; Jansen *et al.* 2009; Kok & Means 2024), and the bizarre Eocene perplexicervicid birds (see Mayr *et al.* 2024). Notably, in perplexicervicid birds (which also inhabited the Eocene of the Phosphorites du Quercy), such tubercles are prominent in the neck region of the animal and they were recently interpreted, with the aid of histology and μ CT scanning, to represent anti-predator mechanisms, serving as “internal body armor” and protecting the neck from bites of carnivorous mammals (Mayr *et al.* 2024). Also, prominent spiked osteoderms are associated and attached on the underlying cervical vertebrae of the enigmatic Triassic diapsid reptile *Eusauropsphargis* Nosotti & Rieppel, 2003 (see Scheyer *et al.* 2017, 2019; Klein & Scheyer 2024). Moreover, distinct spikes are present on the vertebrae of the Triassic tanystropheid reptile *Akidostropheus* Schubul, Marsh & Kligman, 2025, protruding dorsally from the neural spine, and these have also been suggested to represent defensive, anti-predator structures, that protected the elongated, but vulnerable, neck of this animal (Schubul *et al.* 2025). Taking all these observations into consideration, we tentatively consider that the complex structures of the vertebrae of *Cadurceryx*, with their prominent and strong articulations (i.e., true articular joints linking neighbouring vertebrae enabling additional intervertebral articulations), restricted mobility (as these additional articular surfaces buttress each other) and may have been used to provide strong rigidity across the vertebral column, while additionally such pointy vertebral apophyses may have potentially deterred biting from predators. Of course, on the absence of more complete fossil specimens, we cannot rule out the possibility that the complex structures of *Cadurceryx* were instead serving some other functional purpose.

It is further worth highlighting that certain fossil localities have (so far) yielded only caudal vertebrae attributed to *Cadurceryx*. These are the cases of the samples we studied from Sainte Néboule and Hordle Cliff. Such total absence of trunk vertebrae of *Cadurceryx* from these two localities seems peculiar. Interestingly also, our rich sample of Lavergne, on which we primarily based our herein anatomical descriptions, also contains a proportionally higher count of caudal (60) vertebrae compared to trunk (20) ones. On the other hand though, this pattern is drastically opposite in La Bouffie, where our sample yielded a proportionally higher number of trunk vertebrae (51) versus caudal ones (only 7 or 8). Smith (2013) had suggested that the low amount of caudal vertebrae (at least, the relative proportion of trunk and caudal vertebrae) of the same taxon from a fossil locality could be indicative of a taxon with a short tail; to the contrary here, in these two localities with only caudal (and no trunk) vertebrae of *Cadurceryx*, it would be interesting (and intriguing) to apply the approach of Smith (2013) and envisage *Cadurceryx* as a long-tailed snake. If so, these would contradict other snakes with complex vertebral structures, which have low numbers

of caudal vertebrae, such as erycids and charinaids, but also tropidophiids, to which *Cadurceryx* likely belongs (see Szyndlar & Georgalis 2023). In any case, it is still hard to imagine a rather stiff and non-flexible (because of its additional apophyses and extra intervertebral articulations that buttress each other) snake like *Cadurceryx* possessing a very long tail. Of course, though, only articulated skeletons can shed affirmative light on this question.

Nevertheless, with its extreme vertebral morphology, which appears as a fascinating mosaic of different taxonomic groups, *Cadurceryx* aptly witnesses the high diversity, disparity, and beauty of snake vertebrae and vertebral structures.

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