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Sneaking past the Grande Coupure: diversity of snakes across the Eocene-Oligocene transition (MP 19-22) from Dams (Quercy, SW France)

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Sneaking past the Grande Coupure: diversity of snakes across the Eocene-Oligocene transition (MP 19-22) from Dams (Quercy, southwestern France)

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ABSTRACT
The locality of Dams (Quercy, southwestern France) has yielded two distinct fossil assemblages, one from the late Eocene (MP 19) and a second from the early Oligocene (MP 22); it is one of the few examples of a locality with infillings across the Eocene-Oligocene transition. A minimum of 21 taxa (13 mammals, six lissamphibians) have been previously identified in Dams. Study of the snake remains from Dams yields two distinct assemblages, with a total of 11 taxa. The Eocene assemblage (five taxa) includes *Eoanilius* aff. *europae*, *Platyspondylia sudrei* Rage, 1988 and three constrictors, i.e., *Palaeopython* sp., "*Palaeopython*" *neglectus* Rochebrune, 1884 and an unnamed constrictor. The Oligocene assemblage (six taxa) includes *Eoanilius* aff. *oligocenicus* three unnamed alethinophidian species, two constrictors, i.e., *Bavarioboa crocheti* Szyndlar & Rage, 2003 and an unnamed constrictor species, and the caenophidian "*Coluber*" cf. *cadurci*. Among the 11 snake taxa from Dams, "*Palaeopython*" *neglectus* is identified for the first time from a precise locality and several unnamed Eocene and Oligocene alethinophidians are identified and described for the first time. The constrictor *Bavarioboa* Szyndlar & Schleich, 1993 is identified for the first time in the early Oligocene, pushing its appearance in the fossil record from the MP 25 back to MP 22. Comparison between the two assemblages highlights a complete turnover at the species level, with a single genus, *Eoanilius* Rage, 1974, present in both infillings.

KEY WORDS
Snakes,
Quercy phosphorites,
Eocene-Oligocene transition,
France,
anatomy,
Paleogene.

RÉSUMÉ
Ramper au travers de la Grande Coupure : diversité des serpents au cours de la transition Eocène-Oligocène (MP 19-22) de Dams (Quercy, Sud-Ouest de la France).
La localité de Dams (Quercy, Sud-Ouest de la France) a fourni deux assemblages fossiles distincts, un premier daté de l'Eocène Supérieur (MP 19) et un second de l'Oligocène inferieur (MP 22) ; c'est l'un des rares exemples d'une localité présentant des remplissages datant de la transition entre l'Eocène et l'Oligocène. Un minimum de 21 taxons (13 mammifères et six lissamphibiens) a été précédemment identifié à Dams. L'étude des restes de serpents de Dams révèle également deux assemblages, avec un total de onze taxons. L'assemblage Eocène (cinq taxons) est composé d'*Eoanilius* aff. *europae*, *Platyspondylia sudrei* Rage, 1988 et trois constrictors, *Palaeopython* sp., '*Palaeopython*' *neglectus* Rochebrune, 1884 et d'un constrictor indéterminé. L'assemblage Oligocène (sept taxons) est composé d'*Eoanilius* aff. *oligocenicus* Szyndlar, 1994, trois alethinophides indéterminés, deux constrictors, *Bavarioboa crocheti* Szyndlar & Rage, 2003 et un constrictor indéterminé, et un colubroide, '*Coluber*' cf. *caducri*. Parmi les onze taxons de Dams, '*Palaeopython*' *neglectus* est identifié pour la première fois dans une localité précise et datée dans le Quercy, et des espèces indéterminées d'alethinophides et de constrictor de l'Eocène et Oligocène sont identifiées et décrites pour la première fois. Le constrictor *Bavarioboa* Szyndlar & Schleich, 1993 est identifié pour la première fois dans l'Oligocène inferieur, repoussant ainsi sa première apparition dans le registre fossile du MP 25 au MP 22. La comparaison entre les deux assemblages identifiés indique un renouvellement complet au niveau des espèces, avec un seul genre, *Eoanilius* Rage, 1974, présent dans les deux assemblages.

MOTS CLÉS
Serpents,
phosphorites du Quercy,
transition Eocène-Oligocène,
France,
anatomie,
Paléogène.

INTRODUCTION

The Quercy Phosphorites represent an assemblage of more than 200 fossiliferous localities in Southwestern France (Pélissié *et al.* 2021). They have been known since the end of the 19th century for their rich and diverse continental fauna and flora, ranging from the middle Eocene to the Early Miocene (Pélissié *et al.* 2021). Studies of mammals from the Quercy area has revealed an important turnover around the Eocene-Oligocene transition, dubbed the 'Grande Coupure' (Stehlin 1909; Escarguel & Legendre 2006; Weppe *et al.* 2023) and enhanced by major climatic and tectonic changes. Snakes are also present within fossiliferous localities of the Quercy, although less numerous than mammals (as most member of the herpetofauna; Rage 2006). More than 25 species of snakes have been identified within the Quercy (Rage 2006, 2012), and have been the subject of numerous studies (Filhol 1877; Rochebrune 1880, 1884; de Stefano 1905; Hoffstetter & Rage 1972; Rage 1974, 1978, 1984; 1988, 2006, 2012; Szyndlar & Rage 2003; Georgalis *et al.* 2021, 2025; Smith & Georgalis 2022; Georgalis 2025; Szyndlar & Georgalis 2025; Čerňanský *et al.* 2026; and references therein). Snakes are considered to have been strongly impacted during the 'Grande Coupure', with a decrease of their specific diversity by half (from 13 to seven; Rage 2006) and an almost complete turnover at the specific level (a single species and two genera survive the 'Grande Coupure'; Rage 2006, 2012). However, the fossil record of snakes during the early Oligocene remains very limited (Rage & Szyndlar 2005; Szyndlar *et al.* 2008; Rage & Augé 2015; Smith & Georgalis 2022; Venczel *et al.* 2025), which might impact current hypotheses on diversity dynamics for this group.

The Dams phosphate pit in the commune of Caylus (Quercy, Tarn-et-Garonne) presents an interesting opportunity to enhance our knowledge of the snake diversity in the Quercy around the 'Grande Coupure'. This locality houses four distinct karstic infillings, two dated from the late Eocene (DAM1, DAM2; MP 19) and two from the early Oligocene (DAM3, DAM4; MP 22; Weppe *et al.* 2020; Lemierre & Orliac 2025). Here we identify and describe late Eocene and early Oligocene snake assemblages from Dams. We then compare both assemblages to other contemporary Quercy localities and discuss the evolution of snake diversity across the Eocene-Oligocene transition in the Quercy area.

MATERIAL AND METHODS

In this work we describe snake remains from three localities of Dams, one from the Eocene (DAM2 [MP19]) and two from the Oligocene (DAM3, DAM4 [MP22]. Specimens were photographed using a Canon EOS 5D with a 65 mm lens. All specimens are housed in the collection of the Institute of Sciences of Evolution of the University of Montpellier (Montpellier, France) under the collection UM-DAM2-XX/ UM-DAM3-XXX and UM-DAM4-XX.

Abbreviations

DAM2, DAM3, DAM4	localities of Dams;
UM	University of Montpellier.

Anatomical nomenclature

The anatomical nomenclature is derived from Georgalis *et al.* (2021) and Szyndlar & Georgalis (2023).

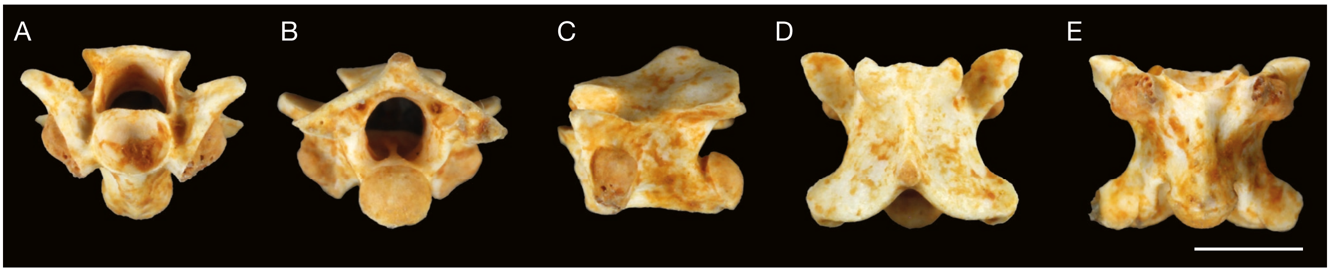

Fig. 1. — *Platyspondylia* Rage, 1974 from the late Eocene (MP 19) of Dams. UM-DAM2-21, *Platyspondylia sudrei* Rage, 1988, trunk vertebra in: **A**, anteroventral; **B**, posterior; **C**, left lateral; **D**, dorsal; **E**, ventral views. Scale bar: 1 mm.

SYSTEMATIC PALAEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
ALETHINOPHIDIA *incertae sedis*
Platyspondylia Rage, 1974

Platyspondylia sudrei Rage, 1988
(Fig. 1)

Platyspondylia sudrei Rage, 1988: 22.

Referred specimens. — Two trunk vertebrae (UM-DAM2-21 and UM-DAM2-22).

Description

The vertebrae are very small, and nearly equivalent in length and width (Fig. 1A-E). The neural arch is broad and shallow. The neural spine is low and rounded, with the anterior slope beginning approximately at the posterior margin of the zygosphene (Fig. 1C). The posterior margin of the neural arch has a shallow medial notch (Fig. 1D). The centrum features strong interzygapophyseal constriction (Fig. 1D, E). The cotyle is rounded and similar in size to the neural canal (Fig. 1A). The prezygapophyses are inclined dorsally and, in an anterior view, are located above the floor of the neural canal (Fig. 1A). Present also are short prezygapophyseal accessory processes (Fig. 1D, E). The paradiapophyses form a single articular facet on each side of the vertebrae (Fig. 1C). No paracotylar foramina are present. The zygosphene has a dorsal bulge in an anterior view (Fig. 1A). In a dorsal view, the zygosphene margin has three lobes; the medial lobe is rounded and broad and flanked by the two lateral, triangular lobes that extend anteriorly to medial lobe (Fig. 1D). The condyle is rounded and is as tall and wider than the neural canal (Fig. 1B). The postzygapophyses terminate at a mediolateral point in the posterior view, giving the postzygapophyses a triangular shape, which falls at approximately the middle of the neural canal (Fig. 1D). The haemal keel is narrow and poorly defined (Fig. 1E).

Attribution

These middle trunk vertebrae can be assigned to *Platyspondylia* based on the following combination of traits: 1) small size; 2) low neural spine; 3) zygosphene with three lobes, one medial and mediolaterally broad and two lateral and mediolaterally narrow; 4) prezygapophyses inclined above the floor of the neural canal in an anterior view; 5) weakly developed prezygapophyseal processes; and 6) paradiapophyses with no subdivisions and that reaches the ventral lip of the cotyle (see Rage 1974; Szyndlar & Rage 2003). Within *Platyspondylia*, we ascribe this to *Platyspondylia sudrei* rather than the type species *Platyspondylia lepta* Rage, 1974, based on the: 1) lower neural arch; and 2) a wider articular surface of the paradiapophyses (see Rage 1974, 1988; Čerňanský *et al.* 2026). It also differs from the late Oligocene *Platyspondylia germanica* Szyndlar & Rage, 2003 in having: 1) a convex anterior margin of the zygosphene (straight in *P. germanica*); and 2) an inclined anterior margin of the neural spine.

Eoanilius Rage, 1974
Eoanilius europae Rage, 1974

Eoanilius aff. ***europae***
(Fig. 2A-E)

Referred specimen. — One anterior trunk vertebra (UM-DAM2-23).

Description

The vertebra is very small and almost as wide as long (Fig. 2A-E). The vertebra is from the anterior portion of the vertebral column. The neural arch is depressed (Fig. 2C), with a low neural spine, extending anteriorly up to the posterior margin of the zygosphene (Fig. 2C). The posterior margin of the neural arch bears a deep medial notch (Fig. 2D). The pre- and postzygapophyses have anteroposteriorly elongated articular facets (Fig. 2D, E), and no prezygapophyseal processes are preserved. The zygosphene anterior margin is thin, straight, and seems to bear two faint lateral lobes (Fig. 2A). The articular facets of the zygosphene are oriented slightly lateroventrally (Fig. 2A). The cotyle is circular and smaller than the neural canal (Fig. 2A). The paradiapophyses are eroded but seem to form a single articular facet on each side (Fig. 2C). No paracotylar foramina are present (Fig. 2A). In ventral view, the centrum widens anteriorly (Fig. 2E). The subcentral ridges are fainted and not well delimited (Fig. 2E). A small hypapophysis extends posteriorly from the ventral surface of the centrum (Fig. 2E).

ATTRIBUTION
This anterior vertebra can be assigned to *Eoanilius* on the following combination: 1) small size; 2) neural arch depressed, 3) posterior margin of the neural arch notched; 4) small and reduced neural spine; and 5) articular facets of the zygosphene horizontal (see Rage 1974; Szyndlar & Rage 2003). Two species are known for this genus, *Eoanilius europae* and *Eoanilius oligocenicus* Szyndlar, 1994 (see Szyndlar & Rage 2003; Smith & Georgalis 2022). Our specimen does resemble *Eoanilius europae* on the following combination of characters (Rage 1974; Szyndlar 1994; Szyndlar & Rage 2003): 1) small neural spine with poorly defined anterior border; 2) paradiapophyses smaller than in *E. oligocenicus* (Szyndlar 1994); and 3) bilobed zygosphene (trilobed in *E. oligocenicus*). However, because anterior trunk vertebrae are not always diagnostic for extinct species, we assign our specimen to *Eoanilius* aff. *europae*.

Eoanilius oligocenicus Szyndlar, 1994

Eoanilius aff. ***oligocenicus***
(Fig. 2F-M)

REFERRED MATERIALS. — Two articulated trunk vertebrae (UM-DAM4-51); one trunk vertebra (UM-DAM4-52); one posterior trunk vertebra (UM-DAM4-53).

DESCRIPTION
Trunk vertebrae
The two articulated trunk vertebrae are both small, with the centrum being slightly wider than long (Fig. 2H, I). The cotyle is much wider than long and is smaller than the neural canal (Fig. 2F). The neural arch is depressed, with the neural spine forming a low, anteroposteriorly broad arch whose anterior margin reaches the level of the posterior margin of the zygosphene (Fig. 2G). The posterior margin of the neural arch has a deep, medial notch (Fig. 2G). The zygosphene is thin and bowed in anterior view with ventro-lateral articular facets (Fig. 2F). Dorsally, the zygosphene has one mediolaterally broad medial lobe and two mediolaterally narrow lateral lobes that extend anteriorly to the same level as the median lobe (Fig. 2H). No paracotylar foramen are present (Fig. 2F). In ventral view, the centrum widens anteriorly (Fig. 2H). The haemal keel appears poorly delimited (Fig. 2I).

Posterior trunk vertebra
This posterior trunk vertebra is small and wider than long (Fig. 2J-M). In the ventral view, the centrum widens posteriorly (Fig. 2M). The cotyle is also wider than tall and is smaller than the neural canal (Fig. 2J). The posteroventral portion of the vertebrae was not preserved, so the condyle is unable to be described properly. The neural arch is depressed, with the neural spine forming a low, broad arch, with a shallow, medial notch at the posterior margin (Fig. 2L). In the anterior view, the zygosphene is thin and bowed with ventro-lateral articular facets (Fig. 2J). In the dorsal view, the zygosphene has two lateral, mediolaterally narrow lobes (Fig. 2L). The prezygapophyses reach dorsally to approximately the midline of the neural canal (Fig. 2L). The paradiapophyses form a single articular facet on each side of the vertebra (Fig. 2K). A pair of small paracotylar foramina seems to be visible in anterior view (Fig. 2J). The haemal keel appears absent.

ATTRIBUTION
All vertebrae are assigned to *Eoanilius* on the following characters: 1) small size; 2) neural arch depressed; 3) posterior margin of the neural arch notched; 4) small and reduced neural spine; 5) articular facets of the zygosphene horizontal; and 6) haemal keel poorly defined (Rage 1974; Szyndlar & Rage 2003). Within this genus, our specimens resemble vertebrae of *Eoanilius oligocenicus* in: 1) having a trilobed zygosphene; 2) large paradiapophyses; and 3) distinct subcentral and lateral foramina (although their presence or absence can be ascribed to fossilization; Rage & Augé 2015). However, the lobes of the zygosphene are more projected anteriorly in *E. oligocenicus* (see Szyndlar 1994). This difference has been noticed in vertebrae from the coeval locality in Valbro (Rage & Augé 2015), and the significance of this difference is currently unknown. The presence of paracotylar foramina in UM-DAM4-53 deserves a comment. Presence of this feature has never been, to our knowledge, documented within any illustrated vertebrae assigned to *Eoanilius* (e.g., Rage 1974; Szyndlar 1994; Rage & Augé 2015), and could point either to a distinct taxon, or to a larger intrageneric diversity. Because the specimen is not well preserved, and because other foramina within *Eoanilius* are known to be depended on fossilization (Rage & Augé 2015), we consider UM-DAM4-53 does not represent a distinct taxon. Thus, we assign our three specimens to *Eoanilius* aff. *oligocenicus*, acknowledging the close resemblance to the morphology of this taxon.

'Alethinophidia indet. morphotype 1'
(Fig. 3A)

REFERRED MATERIALS. — Two trunk vertebrae (UM-DAM4-55 and UM-DAM4-62).

DESCRIPTION
This trunk vertebra is small with a centrum as wide as long, without anterior widening (anterior and posterior margins being relatively the same width; Fig. 3A, B). The cotyle is circular and larger than the neural canal (Fig. 3A1). The neural spine is short low, reduced posteriorly (Fig. 3A2, B1). The neural arch is not vaulted. The zygosphene is bowed in anterior view but is missing its median part (Fig. 3A1, B1). As such, we have no indication if the zygosphene was trilobed (lateral lobes are present; Fig. 3A2). In ventral view, the haemal keel is narrow but delimited by marked subcentral margins (Fig. 3A3, B2). The prezygapophyses are small and markedly expanded anterolaterally (Fig. 3A2, B1).

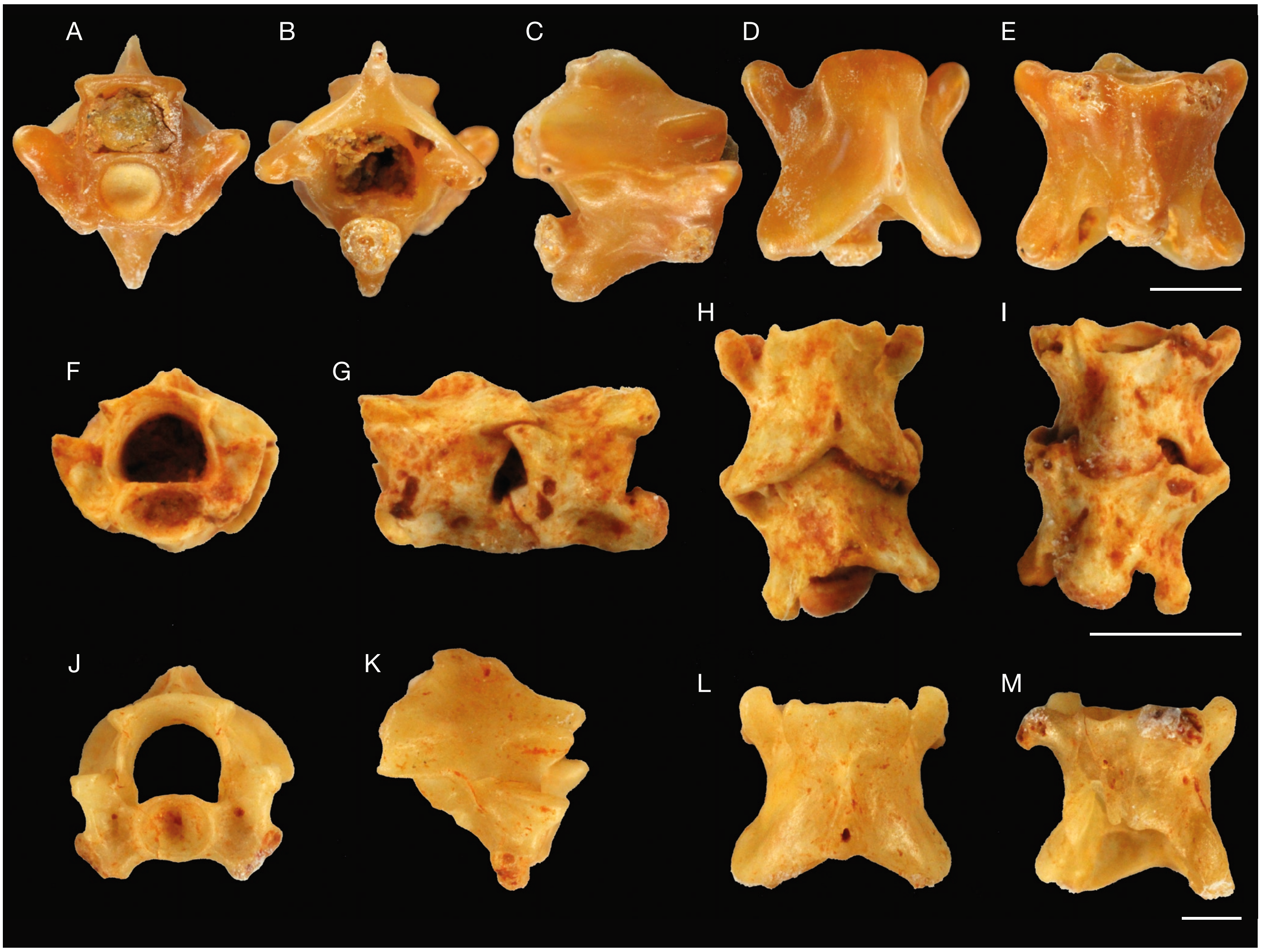

Fig. 2. — *Eoanilius* Rage, 1974 from the late Eocene (**A**-**E**) and early Oligocene (**F**-**M**) of Dams: **A**-**E**, UM-DAM2-23, *Eoanilius* aff. *europae*, anterior trunk vertebra in: **A**, anterior; **B**, posterodorsal; **C**, right lateral; **D**, dorsal; **E**, ventral views; **F**-**I**, UM-DAM4-51, *Eoanilius* aff. *oligocenicus*, two articulated trunk vertebrae in: **F**, anterior; **G**, left lateral; **H**, dorsal; **I**, ventral views; **J**-**M**, UM-DAM4-53, *Eoanilius* aff. *oligocenicus*, posterior trunk vertebra in: **J**, anterior; **K**, right lateral; **L**, dorsal; **M**, ventral views. Scale bars: 1 mm.

Attribution

This unnamed form represented by UM-DAM4-55 differs from *Eoanilius* aff. *oligocenicus* in having: 1) a narrow haemal keel; 2) well delimited subcentral margins; and 3) circular cotyle and condyle. As such, they represent a second distinct alethinophidian taxon from the Oligocene assemblage of Dams. It does differ from *Platyspondylia* in having well delimited subcentral margins and circular cotyle and condyle. It also differs from the Oligocene *Falseryx neervelpensis* Szyndlar, Smith & Rage, 2008 in: 1) having a smaller neural spine; and 2) lacking prezygapophyseal accessory processes. Thus, it likely represents a distinct unnamed taxon from the Oligocene, here informally referred as 'Alethinophidia indet. morphotype 1'.

'Alethinophidia indet. morphotype 2'
(Fig. 3B)

Referred material. — One trunk vertebra (UM-DAM4-62).

Description

This trunk vertebra is small and poorly preserved (Fig. 3B). The centrum slightly widens anteriorly (Fig. 3B2). The neural spine is reduced to a small tubercle on the posterior region of the neural arch (Fig. 3B1). The prezygapophysis is elongated anterolaterally but small (Fig. 3B1). The haemal keel is well-delimited by subcentral ridges (Fig. 3B2).

Attribution

This vertebra is poorly preserved. It does differ from *Eoanilius* aff. *oligocenicus* and *Platyspondylia* in having well-delimited subcentral ridges. It does also differ from *Falseryx neervelpensis* in having a very small and reduced neural spine. It seems to differ from the 'Alethinophidia indet. morphotype 1' in having a wider haemal keel and would represent a second alethinophidian morphotype, here referred as 'Alethinophidia indet. morphotype 2'. However, because UM-DAM4-62 is poorly preserved, it is difficult to assess if it represents a distinct taxon from the 'Alethinophidia indet. morphotype 1' or whether the differences can simply be attributed to intracolumnar variation.

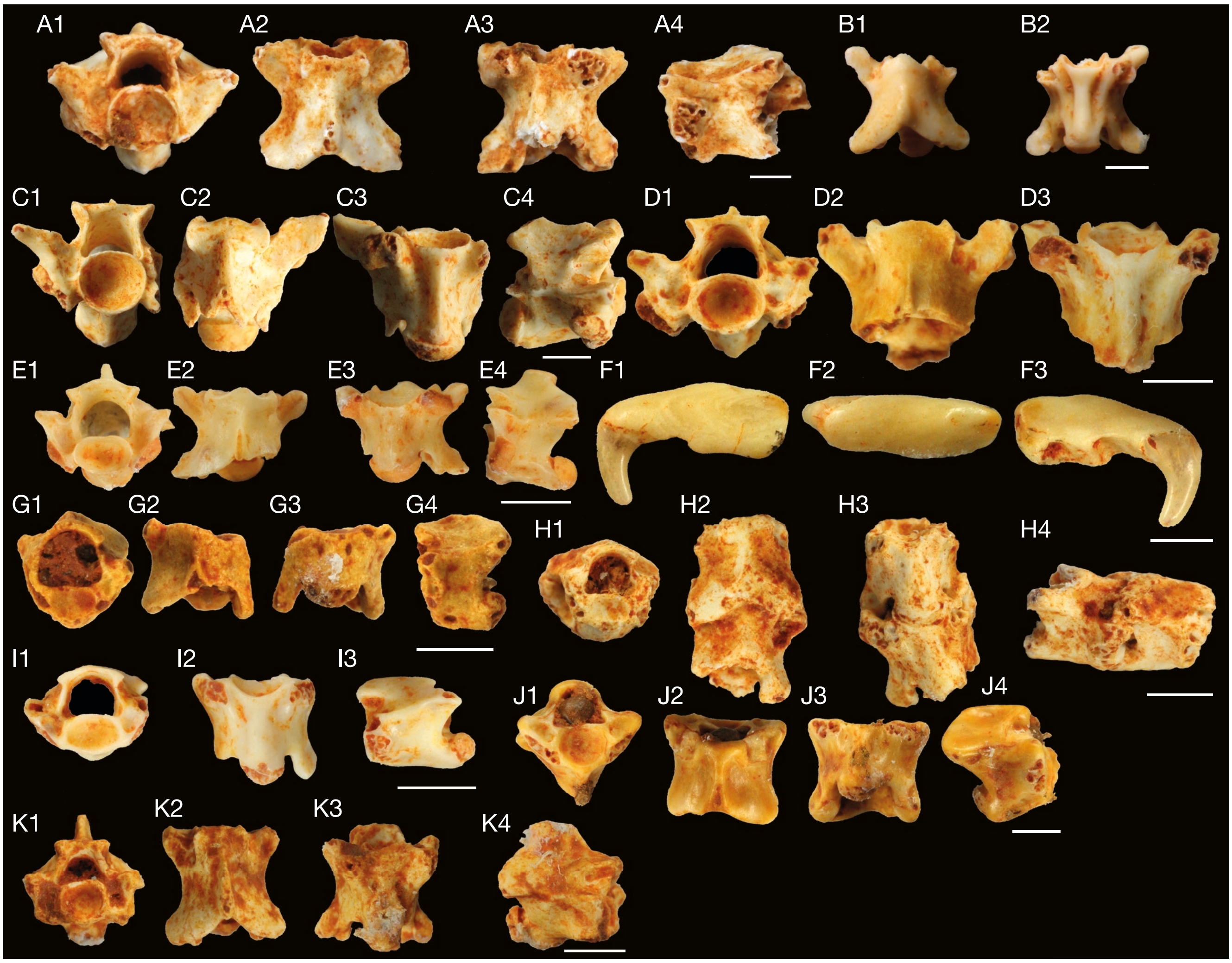

FIG. 3. — Alethinophidia indet. from the early Oligocene (MP 22) of Dams: **A**, UM-DAM4-55, ‘Alethinophidia indet. morphotype 1’, trunk vertebra in: **A1**, anterior; **A2**, dorsal; **A3**, posterior; **A4**, left lateral views; **B**, UM-DAM4-62, ‘Alethinophidia indet., morphotype 2’, trunk verterba in: **B1**, dorsal; **B2**, ventral views; **C**-**E**, ‘Alethinophidia indet., morphotype 3’, trunk vertebrae: **C**, UM-DAM4-56 in: **C1**, anteroventral; **C2**, dorsal; **C3**, ventral; **C4**, right lateral views; **D**, UM-DAM4-58 in: **D1**, anterior; **D2**, dorsal; **D3**, ventral views; **E**, UM-DAM4-59 in: **E1**, anterior; **E2**, dorsal; **E3**, ventral; **E4**, left lateral views; **F**, Alethinophidia indet., UM-DAM4-54 maxilla in: **F1**, labiolingual; **F2**, dorsal; **F3**, labiolingual views; **G**-**J**, Alethinophidia indet., trunk vertebrae; **G**, UM-DAM4-63 in: **G1**, anterior; **G2**, dorsal; **G3**, ventral; **G4**, left lateral views; **H**, UM-DAM4-60 in: **H1**, anterior; **H2**, dorsal; **H3**, ventral; **H4**, left lateral views; **I**, UM-DAM4-61 in: **I1**, anterior; **I2**, dorsal; **I3**, left lateral views; **J**, UM-DAM4-57 in: **J1**, anterior; **J2**, dorsal; **J3**, ventral; **J4**, right lateral views; **K**, UM-DAM4-64, cloacal vertebra in: **K1**, anterior; **K2**, dorsal; **K3**, ventral; **K4**, right lateral views. Scale bars: 1 mm.

‘Alethinophidia indet. morphotype 3’
(Fig. 3C-E)

REFERRED MATERIALS. — Three trunk vertebrae (UM-DAM4-56, 58, 59).

DESCRIPTION

These three trunk vertebrae (UM-DAM4-56, 58, 59; Fig. 3C-E). They differ from those assigned to ‘Alethinophidia indet. morphotypes 1 and 2’ in: 1) being larger; 2) having the lateral lobes of the zygosphene anteroposteriorly expanded to form lateral ridges (Fig. 3C2, D2, E2); 3) having the articular facets of the prezygapophyses expanded anterolaterally (rhomboidal shaped structure); 4) having a neural spine extending more anteriorly; and 5) having a more developed neural spine (Fig. 3C4, E4).

ATTRIBUTION

As mentioned above, these vertebrae differ from the one assigned to the ‘Alethinophidia indet. morphotype 1’ and the ‘Alethinophidia indet. morphotype 2’, They also differ from *Eoanilius* in: 1) having a more developed median lobe on the zygosphene; and 2) having a neural spine more extended anteroposteriorly and more developed dorsally. Hence, it represents a third Oligocene alethinophidian morphotype from the Oligocene of Dams. This species does resemble *Falseryx neervelpensis*, in: 1) having distinct prezygapophyseal accessory processes; and 2) well developed lateral lobes and trilobed condition on the zygosphene (Szyndlar *et al.* 2008). However, it differs in: 1) having a more developed neural spine and a more distinct central lobe on the zygosphene; and 2) lacking the prezygapophyseal buttresses developed into prominent tubercles. This Oligocene taxon also differs from

Platyspondylia in having a more anteroposteriorly developed and taller neural spine. Thus, it likely represents a distinct unnamed taxon from the Oligocene, here informally referred as 'Alethinophidia indet. morphotype 3'.

Alethinophidia indet.
(Fig. 3F-K)

REFERRED MATERIAL. — One incomplete left maxilla (UM-DAM4-54); three trunk vertebrae (UM-DAM4-57, UM-DAM4-60, and UM-DAM4-61); two articulated trunk vertebrae (UM-DAM4-63); one cloacal vertebra (UM-DAM4-64).

DESCRIPTION
Maxilla
UM-DAM4-54 is small, and only the anterior portion of the bone is preserved (Fig. 3F). It preserves one recurved tooth at the most anterior tooth position, along with two tooth positions without teeth preserved; the empty sockets are angled anteroventrally (Fig. 3F3). The anterior most tooth extends anteriorly exactly with the anterior boundary of the maxilla (Fig. 3F) and has been rounded due to weathering.

Trunk vertebrae
Four specimens (UM-DAM4-57, 60, 61, 63; Fig. 3G-I) of trunk vertebrae that cannot be assigned to any of the three identified alethinophidians. Three of them (UM-DAM4-60, 61, 63) differ from the two unnamed alethinophidians in: 1) having a haemal keel poorly defined; and 2) having a dorsoventrally compressed cotyle. It can be further differentiated from the 'unnamed alethinophidian 1' in being narrower. It can also be differentiated from the 'unnamed alethinophidian 2' in: 1) having a very reduced neural spine; and 2) small zygapophyses (Fig. 3G2, H2).

The fourth vertebra, UM-DAM4-57, has a centrum wider than long (Fig. 3J3). The cotyle is slightly elongated, wider than tall, and approximately the same size as the neural canal (Fig. 3J1). In the anterior view, the zygosphene is bowed (Fig. 3J1) with no lobes in the dorsal view (Fig. 3J2). The prezygapophyses are oriented dorsolaterally, although the apices are weathered. The paradiapophyses form a large, deep single articular facet on the side of the vertebra (Fig. 3J4). There are also no paracotylar foramina. The interzygapophyseal ridge is well-defined (Fig. 3J4). The neural spine is anteroposteriorly extended, with a deep notch on the posterior margin (Fig. 3J2). The condyle is weathered but maintains a rounded shape and not well-differentiated from the centrum (Fig. 3J3, J4). The haemal keel is low, broad, and rounded (Fig. 3J3).

Cloacal vertebra
The vertebra (UM-DAM4-64) is small, with a centrum that is longer than wide (Fig. 3K). The cotyle is rounded, slightly wider than tall, and larger than the neural canal (Fig. 3K1). In the anterior view, the zygosphene is thick and the dorsal margin forms a flat, horizontal surface (Fig. 3K1). In dorsal view, the zygosphene has two, very small and pointed lateral lobes (Fig. 3K2). The prezygapophyses are oriented laterally, forming a horizontal dorsal margin (Fig. 3K2). The paradiapophyses form a large, deep single articular facet on the side of the vertebrae (Fig. 3K4). The neural spine is tall, forming a broad ridge that starts anteriorly at the approximate posterior margin of the prezygapophysis (Fig. 3K2, K4). The anterior margin of the neural spine is flat and posterio-distally oriented, and the posterior margin is dorsally convex (Fig. 3K4). The neural spine also has a small notch on the posterior aspect (Fig. 3K2). The haemal keel is deep and mediolaterally broad, located on the posterior portion of the centrum closer to the condyle (Fig. 3K3, K4). The condyle is round and well-differentiated from the centrum (Fig. 3K3).

ATTRIBUTION
The maxilla can be assigned to Alethinophidia based on its dentition, made of subthecodont teeth, the latter curved posteriorly in a "hook" shape (Georgalis *et al.* 2021). It cannot be assigned more precisely among snakes. Three trunk vertebrae (UM-DAM4-60, 61, 63) are similar to vertebrae assigned to *Eoanilius* in: 1) having a poorly defined haemal keel; 2) very reduced neural spine; 3) small zygapophyses; and 4) dorsoventrally compressed cotyle (Fig. 3G-I). However, they are too poorly preserved, especially in the zygosphene region, to be assigned to *Eoanilius* with certainty. UM-DAM4-57, 64 are too poorly preserved to allow comparisons.

CONSTRICTORES Oppel, 1811
(*sensu* Georgalis & Smith, 2020)
PYTHONOIDEA Fitzinger, 1826
(*sensu* Wallach, Williams & Boundy, 2014)
MESSELOPYTHONIDAE Smith & Scanferla, 2022
Palaeopython Rochebrune, 1880

Palaeopython sp.
(Fig. 4)

REFERRED SPECIMENS. — Two articulated trunk vertebrae (UM-DAM2-15); one trunk vertebra (UM-DAM2-16).

DESCRIPTION
The two articulated vertebrae (Fig. 4) are massive (62 mm centrum length; 83 mm neural arch width). In anterior view, the zygosphene is wider than the cotyle on the anterior vertebra. The neural canal is wide and trapezoidal shaped (Fig. 4A). The zygosphene is thick, with large articular facets ventrolaterally oriented (Fig. 4A). The zygosphene bears two prominent lateral lobes. The prezygapophyses bear large articular facets dorsomedially oriented. They bear small zygapophyseal processes (Fig. 4D, E). The interzygapophyseal ridge is well-marked. The synapophyses are weakly divided between dia- and parapophysis. No paracotylar foramen is present. In anterior view, the neural arch is vaulted, with its posterior region higher than its anterior one. In dorsal view, the neural spine extends anteriorly at the base of the zygosphene. The neural spine is thick and moderately high. It extends posteriorly past the medial notch on the posterior margin of the

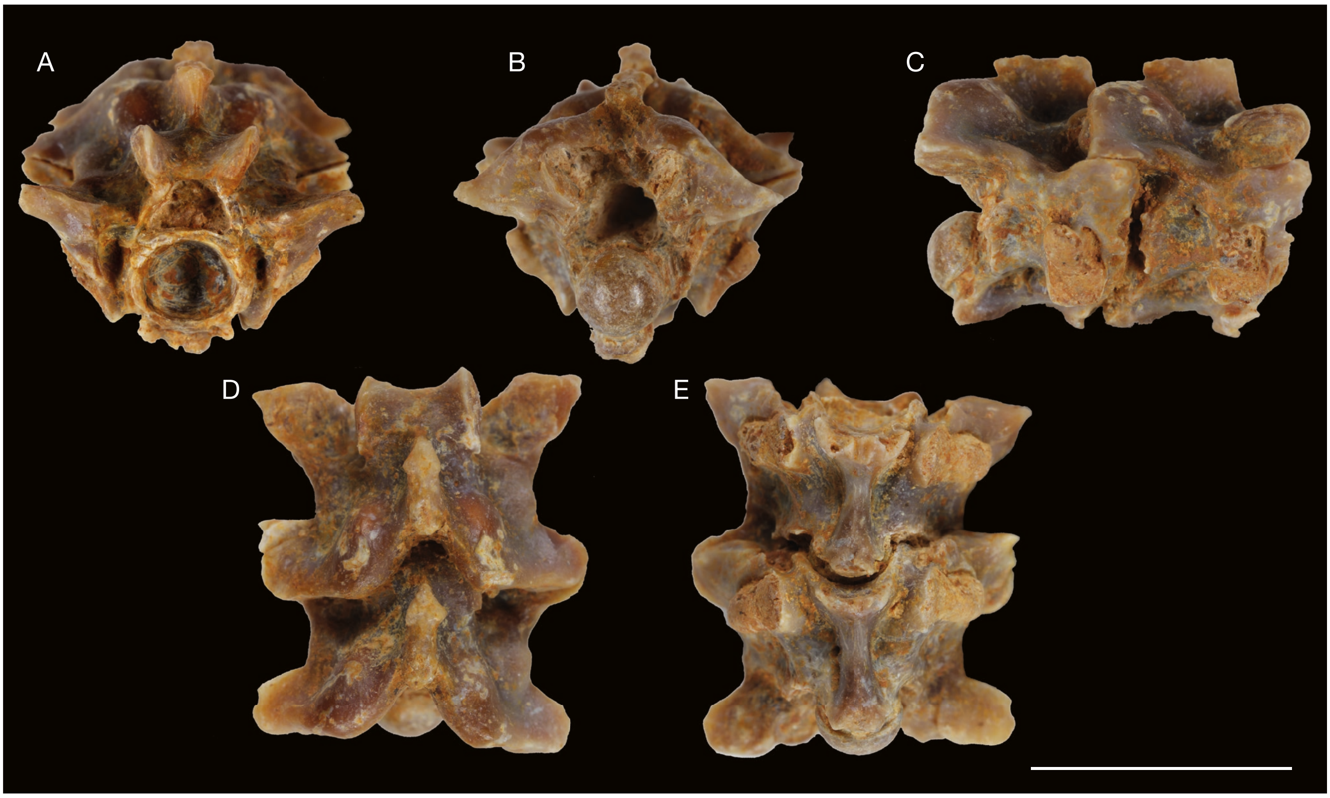

Fig. 4. — *Palaeopython* Rochebrune, 1880 from the late Eocene (MP 19) of Dams. UM-DAM2-15, *Palaeopython* sp., two articulated vertebrae in: **A**, anterior; **B**, ventral; **C**, right lateral; **D**, dorsal; **E**, ventral views. Scale bar: 10 mm.

neural arch. In posterior view, the zygantrum of the posterior vertebra is deep and marked by elongated zygantral mounds. In ventral view, a small subcentral foramen is present on the second vertebra. The centrum is roughly triangular, with its anterior margin wider than its posterior margin. The subcentral ridges are well marked. The haemal keel is well-marked and rather thin. The condyle is smaller than the zygosphene and well distinct from the main body of the centrum.

Attribution

Both specimens are referred to the large messelopythonid *Palaeopython* based on the: 1) very thick zygosphene; 2) asymmetrical interzygapophyseal constriction; 3) deep paracotylar fossae; and 4) zygosphene broadly concave with anterolateral horns (i.e., lateral lobes; Georgalis *et al.* 2021). Four species of *Palaeopython* are currently recognized as valid: *Palaeopython cadurcensis* (Filhol, 1877) from Quercy (see Georgalis *et al.* 2021); *Palaeopython ceciliensis* Barnes, 1927, from Geiseltal, Germany (see Georgalis *et al.* 2021); *Palaeopython helveticus* Georgalis & Scheyer, 2019, from Dielsdorf, Switzerland (see Georgalis & Scheyer 2019); and *Palaeopython schaali* Smith & Scanferla, 2022 from Messel, Germany (see Smith & Scanferla 2022). The vertebrae from DAM2 differ from *Palaeopython helveticus* (see Georgalis & Scheyer 2019) in having: 1) a thicker zygosphene; and 2) a less vaulted neural arch. They also differ from *Palaeopython ceciliensis* (see Barnes 1927; Georgalis *et al.* 2021) in having: 1) zygapophyseal facet oriented more dorsomedially; 2) prezygapophyses more laterally expanded and "squared off"; and 3) lacking a weak zygosphenal tubercle. Dams specimens also differ from the recently described *Palaepython schaali* (see Smith & Scanferla 2022) in: 1) having a thicker zygosphene with anterolateral horns; and 2) having a lower neural spine. Vertebrae from Dams do resemble *Palaeopython cadurcensis* in their differences from the other three *Palaeopython* species but are considerably smaller than most known *P. cadurcensis* vertebrae, especially as the articulated vertebrae seem to belong to a relatively mature individual. Thus, we refer these specimens to *Palaeopython* sp.

BOOIDEA Gray, 1825
(*sensu* Pyron, Reynolds & Burbrink, 2014)
Bavarioboa Szyndlar & Schleich, 1993

Bavarioboa crocheti Szyndlar & Rage, 2003
(Fig. 5)

Bavarioboa crocheti Szyndlar & Rage, 2003: 28.

Referred specimens. — Four trunk vertebrae (UM-DAM4-65 – UM-DAM4-68).

Description

All four vertebrae are relatively large, with relatively equal length and width. The cotyle is slightly wider than tall and is larger than the neural canal (Fig. 5D, H). No paracotylar

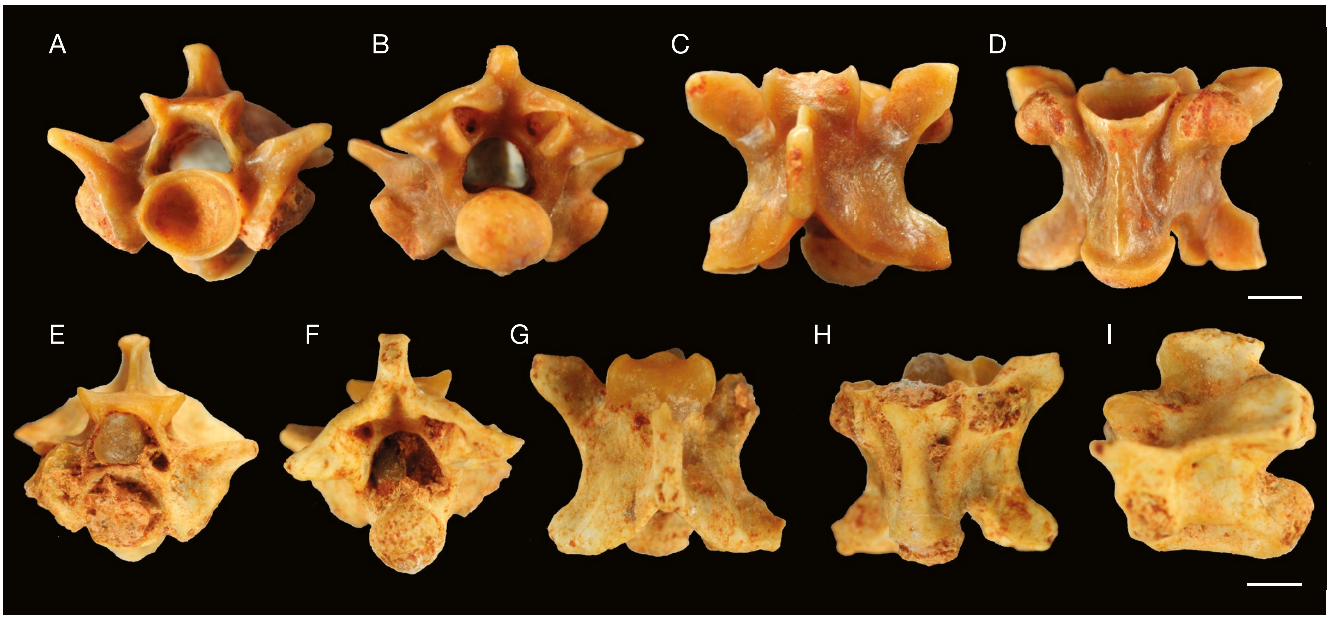

FIG. 5. — *Bavarioboa crocheti* Szyndlar & Rage, 2003 from the early Oligocene (MP 22) of Dams: **A**-**D**, UM-DAM4-65, trunk vertebra in: **A**, anterior; **B**, posterior; **C**, dorsal; **D**, ventral views; **E**-**I**, UM-DAM4-67, trunk vertebra in: **E**, anterior; **F**, posterior; **G**, dorsal; **H**, ventral: **I**, left lateral views. Scale bars: 1 mm.

foramen are present. In the anterior view, the zygosphene is horizontal and thick, with articular facets oriented ventrolaterally (Fig. 5A, E). Dorsally, the zygosphene is trilobed, with two mediolaterally narrow lateral lobes and one mediolaterally broad medial lobe (Fig. 5C, G). The prezygapophyses are elongate and dorsolaterally oriented (Fig. 5C, G). The paradiapophyses form a single articular facet, with projections extending further ventrally than the ventral margin of cotyle (Fig. 5A, I). The neural spine is thick, anteroposteriorly broad, and dorsally flat. The most dorsal portion of the neural spine forms a shelf (Fig. 5C, G, I). The posterior edge of the neural spine overhangs the posterior margin of the centrum. The condyle is slightly mediolaterally elongated and well-differentiated from the rest of the centrum (Fig. 5D, H). The postzygapophyses are horizontally oriented and taper to a point laterally (Fig. 5C). The haemal keel is shallow and not well-defined and is shaped like a biconcave lens (Fig. 5D, H).

ATTRIBUTION

We attribute these vertebrae to Oligocene *Bavarioboa* based on: 1) a straight zygosphene in anterior view; 2), prezygapophyses located above the ventral margin of the neural canal; and 3) paradiapophyses that project ventrally beyond the ventral margin of the cotyle (see Szyndlar & Rage 2003). Among known *Bavarioboa* species, all our vertebrae resemble *Bavarioboa crocheti* in: 1) having a trilobed zygosphene (sharing with coeval *Bavarioboa vaylatsae* Szyndlar & Rage, 2003); 2), a haemal keel shaped like a biconcave lens (shared with *Bavarioboa hermi* Szyndlar & Schleich, 1993 and *Bavarioboa herrlingensis* Szyndlar & Rage, 2003); and 3) thickened neural spines (see Szyndlar & Rage 2003). Hence, all vertebrae from DAM4 are assigned to *Bavarioboa crocheti*.

CONSTRICTORES *incertae sedis*

"*Palaeopython*" *neglectus* Rochebrune, 1884
(Fig. 6A-D)

REFERRED SPECIMENS. — Two trunk vertebrae (UM-DAM2-19 and UM-DAM2-20).

DESCRIPTION

The description is based on UM-DAM2-19, the most complete vertebra. The vertebra is wider than long. The vertebra is slightly deformed, with the condyle not aligned with the anteroposterior axis of the centrum (Fig. 6A). The cotyle is ovoid, wider than long (Fig. 6A). The vertebral canal is rhombohedral-shaped and narrows dorsally (Fig. 6A). The zygosphene is as wide as the cotyle. Its articular facets are lateroventrally oriented. The zygosphene is moderately thick and slightly arched in anterior view (Fig. 6A, C). It is trilobed, with a prominent median lobe. The neural arch is vaulted. The neural spine is broken near its base, assessing its height is not possible (Fig. 6B). However, it is oriented posteriorly and likely extended past the postzygapophyses. The prezygapophyses bear ovoid articular facet oriented dorsally. They bear small prezygapophyseal processes. The interzygapophyseal ridge is well-marked laterally (Fig. 6B). It extends as a small lateral blade. The synapophyses are weakly divided between dia- and parapophysis. No paracotylar foramen is present. However, the diapophysis is larger and wider than the parapophysis. In ventral view, the centrum is clearly triangular shaped, with a wider anterior region. The haemal keel is thin, but not well-marked (Fig. 6D). The subcentral ridges are present but faint (Fig. 6D).

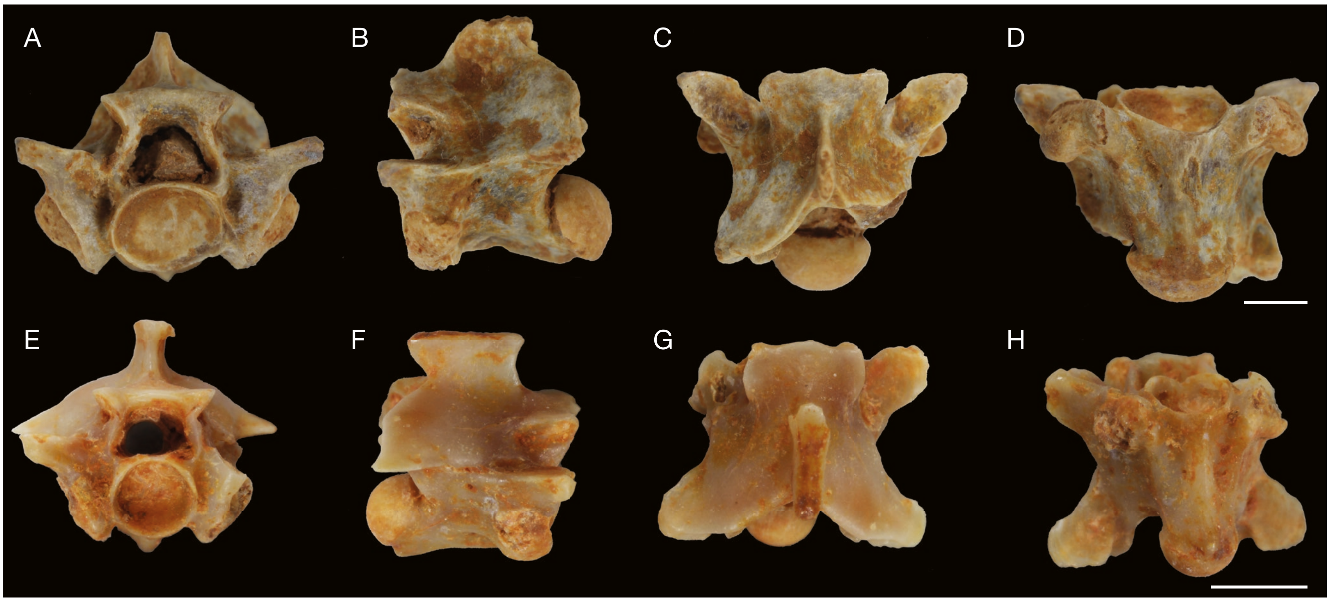

Fig. 6. — Constrictores from the late Eocene (MP 19) of Dams: **A**-**D**, UM-DAM2-19, "*Palaeopython*" *neglectus* Rochebrune, 1884, trunk vertebra in: **A**, anterior; **B**, left lateral; **C**, dorsal; **D**, ventral views; **E**-**H**, UM-DAM2-17, 'Constrictores indet. morphotype 1', trunk vertebra in: **E**, anterior; **F**, right lateral; **G**, dorsal; **H**, ventral views. Scale bars: 2 mm.

Attribution

Both vertebrae are referred to Constrictores on: 1) the presence of a centrum wider than longer, triangular shaped (i.e., widening anteriorly; Fig. 6D); 2) small prezygapophyseal accessory processes; 3) parapophyses faintly divided into two articular facets; and 4) no paracotylar foramen (Fig. 6A-D). Furthermore, our vertebrae are referred to "*Palaeopython*" *neglectus* as: 1) symmetrical interzygapophyseal constriction (asymmetrical in *Palaeopython*); 2) thinner zygosphene than *Palaeopython* and *Phosphoroboa* Georgalis, Rabi & Smith, 2021; and 3) neural spine extending anteriorly onto the zygosphene roof (Fig. 6C; see Georgalis *et al.* 2021). It should be noted that the assignment of this species to the genus *Palaeopython* is doubtful, and will likely be revised when more available material, in particular cranial remains, will be described (Georgalis *et al.* 2021).

'Constrictores indet. morphotype 1'
(Fig. 6E-H)

Referred specimens. — UM-DAM2-17, 18, two trunk vertebrae.

Description

The vertebra is wider than long. In anterior view, the cotyle is circular (Fig. 6E). The zygosphene is wider than the cotyle, and its articular facet are lateroventrally oriented (Fig. 6E). The neural canal is wider than the cotyle and is roughly rhombohedral. A single prezygapophysis is preserved (Fig. 6G). It bears a flat dorsally oriented articular facet, located above the floor of the neural canal. The interzygapophyseal ridge is poorly defined (Fig. 6F). In lateral view, a small lateral foramen is present slightly ventral to the prezygapophysis. The zygantrum seems deep. The zygosphene is thin and its neural region is flat. The zygosphene is trilobed. The synapophyses bear a single articular facet. The neural arch is not high nor vaulted. The neural spine extends anteriorly at the base of the zygosphene. The neural spine is moderately high and conserves its height on its whole length (Fig. 6F, G). It extends posteriorly past the median notch of the posterior margin of the neural arch. In ventral view, the subcentral ridges are well-marked (Fig. 6H). The haemal keel is sharp and well-defined. A pair of subcentral foramina is present.

Attribution

Those vertebrae represent a rather small constrictor, with an average centrum length of 0.30 mm. They resemble the older *Szyndlaria* Rage & Augé, 2010 in having: 1) a depressed neural arch; and 2) a thin zygosphene slighter wider than cotyle and straight in anterior view, However, it does differ in lacking: 1) a high neural spine; 2) paradiapophyses strongly projecting and in having; 3) a narrower centrum; and 4) a haemal keel not restricted to the posterior part of the centrum (hypapophysis-like haemal keel). Both vertebrae from DAM2 do matches the description (without illustrated specimens) of the 'Booidea K' (Rage & Augé 2010; part of the lettered constrictors from the Quercy; see Smith & Georgalis 2022) in having: 1) an anteroposteriorly long neural spine that is moderately high; 2) a centrum narrower than most Eocene constrictors from the Quercy; 3) a thin trilobed zygosphene with a flat roof (i.e., straight in anterior view); 4) zygapophyses clearly above the floor of the neural canal; and 5) short prezygapophyseal articular facet that are not markedly projected laterally. However, these have never been figured. Thus, we assign both vertebrae to a distinct third Eocene constrictor from Dams, here informally called 'unnamed constrictor 1', and could also represent 'Booidea K'.

‘Constrictores indet. morphotype 2’
(Fig. 7A-E)

Referred specimens. — UM-DAM3-715, 716, two anterior to mid trunk vertebrae; UM-DAM4-69–73, five mid- to posterior trunk vertebrae.

Description

Three specimens (UM-DAM4-69, 70, 72; Fig. 7A-C) represent anterior to middle trunk vertebrae. They are all procoelous, with a centrum widening anteriorly (Fig. 7A3, B3). The neural canal is trapezoidal shaped, with a broad base (Fig. 7A1, B1). The zygosphene is moderately thick, with a straight anterior margin (Fig. 7A1, A2, B1, B2). No lobes are distinct on the anterior margin of the zygosphene (Fig. 7A2, B2). The prezygapophyses bear an articular facet oriented slightly dorsomedially above the level of the floor of the neural canal (Fig. 7A1, B1). Both facets are ovoid and slightly expanded anteroposteriorly. The neural arch is not vaulted, and bears a moderately developed neural spine, extending anteriorly from the zygosphene to past the posterior notch of the neural arch posterior margin (i.e., it overhangs on the succeeding vertebra; Fig. 7A2, A4, B2, B4). The posteriormost region of the neural spine seems slightly thicker than the rest (Fig. 7A2, B2, C2). In ventral view, the centrum bears a narrow haemal keel, well delimited by the paired subcentral margins (Fig. 7A3, B3). One vertebra (UM-DAM4-72) has a haemal keel slightly broader (Fig. 7C3), and more hourglassed shaped, suggesting more posterior position than the others.

Two additional specimens (UM-DAM3-716; UM-DAM4-71) represent mid- to posterior trunk vertebrae (Fig. 7D, E). They differ from the three previous vertebrae in having a less vaulted neural arch and a broader haemal keel hourglassed-shaped (Fig. 7D1, E1).

Attribution

These vertebrae differ from the one assigned to *Bavarioboa* in having a flatter zygosphene lacking any projecting lobes. Thus, they represent a second Oligocene constrictor in Dams. Within the early Oligocene of the Quercy, two additional constrictors, ‘Booidea C’ and ‘Booidea indeterminate B’, are known (‘Boidae indeterminate in Rage & Augé 2015). Our vertebrae differ from the one assigned to ‘Booidea C’ (Rage & Augé 2015) in lacking a median lobe on the zygosphene and in having a smaller neural spine that does not project past the postzygapophyses. They also differ from the ‘Booidea indeterminate B’ in having a smaller neural spine (taller than in ‘Booidea C’ according to Rage & Augé 2015). Thus, we assign our specimens to an indeterminate species of constrictor, informally named ‘Constrictores indet. morphotype 2’.

Constrictores indet.
(Fig. 7F, G)

Referred materials. — UM-DAM3-715, UM-DAM4-73, two trunk vertebrae.

Description

The two specimens are smaller than the other constrictor vertebrae (Fig. 7F, G). They are procelous (Fig. 7F, G) with their centrum widening anteriorly. The zygosphene is moderately thickened and trilobed (Fig. 7F1, G1), with the median lobe not very prominent and slightly shifted ventrally. The prezygapophyses are not expanded laterally bear small but distinct prezygapophyseal processes (Fig. 7F2, F3). The haemal keel is not well delimited but seems hourglass shaped (Fig. 7F3). The neural arch is vaulted (Fig. 7F4, G3) and bears a neural spine extending anteriorly to the base of the zygosphene (Fig. 7F2; F4, G2, G3). The neural spine is moderately developed (Fig. 7G1, G2) and thickened distally.

Attribution

These specimens differ from ‘Constrictores indet. morphotype 2’ in having a trilobed zygosphene. They also differ from ‘Booidea C’ in having: 1) prezygapophyseal processes projecting anterolaterally; 2) a broad median lobe of the zygosphene; and 3) a smaller neural spine. They differ from the two indeterminate constrictors (‘Boidae indeterminate A’ and ‘B’; Rage & Augé 2015) from Valbro in having a smaller neural spine. Our specimens do however resemble *Bavarioboa crocheti* in having: 1) a moderately developed neural spine extending anteriorly up to the base of the zygosphene; 2) a trilobed zygosphene with the median lobe shifted ventrally; and 3) the distal portion of the neural spine thickened. However, they do differ in having the ventral shifting of the median zygosphenal lobe less pronounced; a thinner zygosphene and by their smaller size. Still, they might represent intraspecific variation or juvenile of *Bavarioboa crocheti*, or another taxon. Because we cannot confirm either hypothesis, we regard them as Constrictores indet.

CAENOPHIDIA Hoffstetter, 1939
COLUBROIDES Zaher *et al.*, 2009
“*Coluber*” *cadurci* Rage, 1974

“***Coluber***” cf. ***cadurci***
(Fig. 8)

Referred specimens. — Five trunk vertebrae (UM-DAM4-74 – UM-DAM4-78); two cloacal vertebrae (UM-DAM4-79 and 80).

Description

Most vertebrae are complete. The centrum is elongated anteroposteriorly. It bears a small and circular cotyle (Fig. 8A, B). The vertebral canal is rhombohedral and wider than the cotyle (Fig. 8A). A small paracotylar foramen is present (Fig. 8A). The zygosphene is thin and flat. Its articular facets are slightly ventrolaterally oriented. In dorsal view, the zygosphene does not bear any lobes, safe for a small anterior projection of its articular facets (Fig. 8A, D). The prezygapophyses bear dorsally oriented articular facets. These facets are ovoid and bear a prezygapophyseal process anteriorly (Fig. 8A, E). The neural arch is not vaulted. The neural spine extends from the

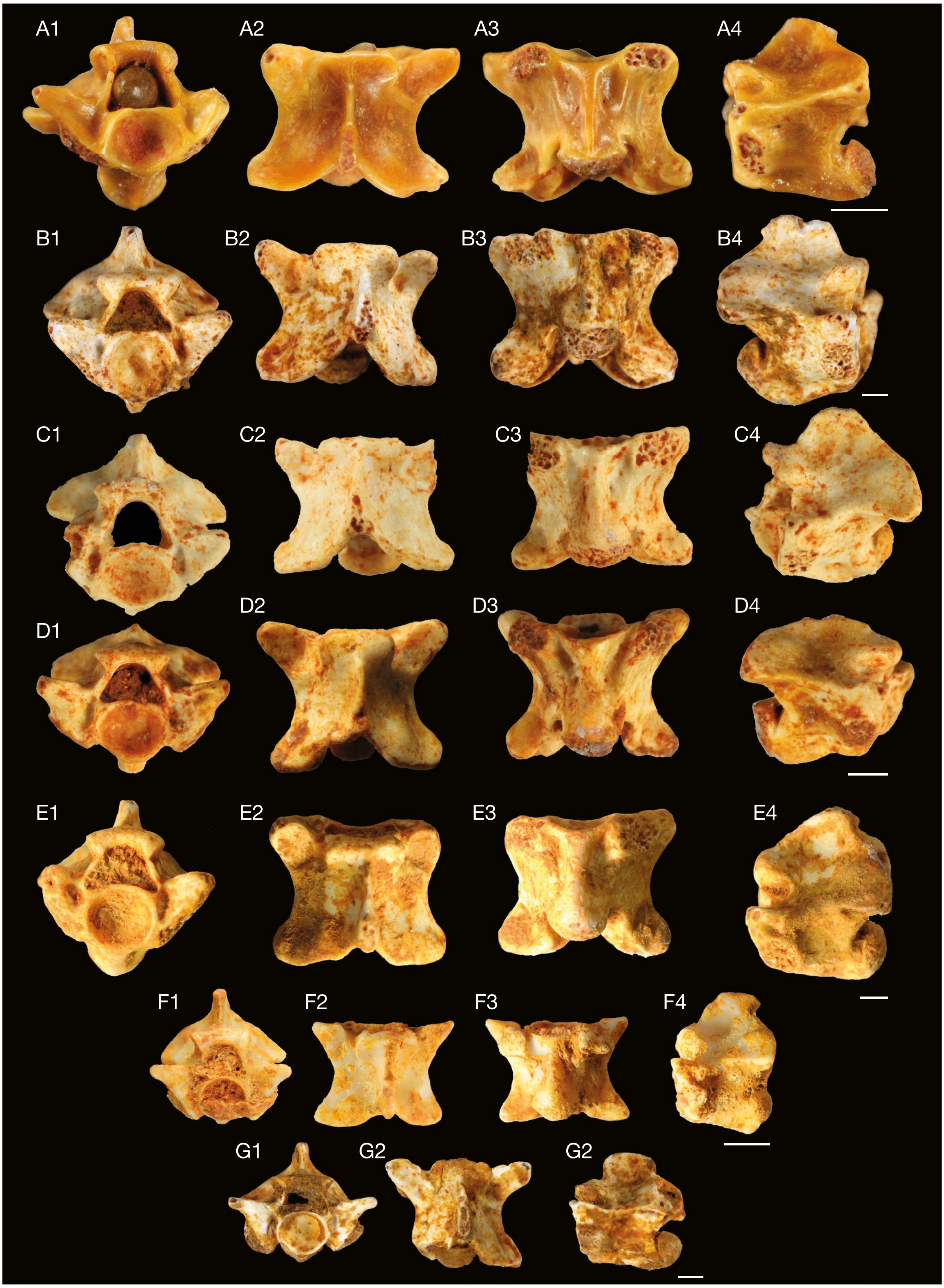

FIG. 7. — Constrictores from the early Oligocene (MP 22) of Dams: **A**-**C**, 'Constrictores indet. morphotype 2', anterior to mid trunk vertebrae: **A**, UM-DAM4-69 in: **A1**, anteroventral; **A2**, dorsal; **A3**, ventral; **A4**, left lateral views; **B**, UM-DAM4-70 in: **B1**, anterior; **B2**, dorsal; **B3**, ventral; **B4**, right lateral views; **C**, UM-DAM4-72 in: **C1**, anterior; **C2**, dorsal; **C3**; ventral; **C4**, left lateral views; **D**-**E**, 'Constrictores indet. morphotype 2', mid to posterior trunk vertebrae; **D**, UM-DAM3-716 in: **D1**, anterior; **D2**, dorsal; **D3**, ventral; **D4**, right lateral views; **E**, UM-DAM4-71 in; **E1**, anterior; **E2**, dorsal; **E3**, ventral views; **F**, **G**, Constrictores indet, trunk vertebrae: **F**, UM-DAM3-716 in: **F1**, anterior; **F2**, dorsal; **F3**, ventral; **F4**, left lateral views; **G**, UM-DAM4-73 in: **G1**, anterior; **G2**, dorsal; **G3**, left lateral views. Scale bars: 1 mm.

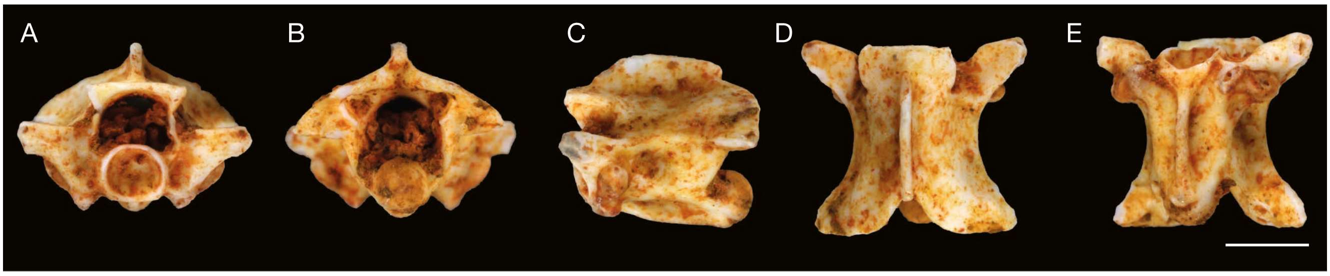

FIG. 8. — "*Coluber*" cf. *cadurci* from the early Oligocene (MP 22) of Dams. UM-DAM4-74, trunk vertebra in: **A**, anterior; **B**, posterior; **C**, left lateral; **D**, dorsal; **E**, ventral views. Scale bar: 1 mm.

zygosphene to the posterior margin of the neural arch. The spine is developed as a blade-like structure, with the same height throughout its whole length (Fig. 8B-D). The dia- and parapophyses are small. Although closely spaced together, they form two distinct articular facets (Fig. 8C). In posterior view, the zygantrum is shallow. In ventral view, the centrum is slightly triangular-shaped (Fig. 8E). The subcentral ridges are thin. The haemal keel is thin but strongly projected ventrally, forming a blade-like structure.

ATTRIBUTION

The presence of: 1) a centrum anteroposteriorly elongated; 2) a neural spine well-developed and blade-like; and 3) a haemal keel well-developed and blade-like is diagnostic for caenophidian snakes that have not continuous hypapophysis across their trunk vertebrae (Zaher *et al.* 2019). Among them, only "*Coluber*" *cadurci* Rage, 1974 is known within the Oligocene of the Quercy (Rage 2006; Smith & Georgalis 2022). Our vertebrae resemble those of "*Coluber*" *cadurci* (Rage, 1974) in: 1) having a neural spine extending on the entire length of the neural arch; and 2) having a blade-like haemal keel. However, because prezygapophyseal accessory processes are not complete (long prezygapophyseal processes are part of "*Coluber*" *cadurci* diagnosis; Rage, 1974), they are tentatively assigned to "*Coluber*" cf. *cadurci*. Note that the genus level placement of this taxon is still far from resolved we follow previous authors (e.g., Smith & Georgalis 2022) in only tentatively including it in the wastebasket genus *Coluber*.

DISCUSSION

SNAKE DIVERSITY IN DAMS

In total 41 specimens in Dams belong to snakes, representing at least 12 taxa (Table 1). Two distinct assemblages are identified, an Eocene one (9 specimens for five taxa) and an Oligocene one (32 specimens for seven taxa).

Snakes have been described from upper Eocene and lower Oligocene localities of the Quercy since more than a century (e.g., Filhol 1877; Rochebrune 1880, 1884; de Stefano 1905; Hoffstetter & Rage 1972; Rage 1974, 2006, 2012; Szyndlar & Rage 2003; Georgalis *et al.* 2021, 2025; Szyndlar & Georgalis 2025; Čerňanský *et al.* 2026). Although snakes (alongside other squamates) have been the focus of detailed studies for various localities (Rage 1978, 1988; Rage & Vergnaud-Grazzini 1978; Augé & Rage 1995; Rage & Augé 2010, 2015; Čerňanský *et al.* 2026), they remain often only mentioned in taxonomic lists (Crochet *et al.* 1981). However, several recent studies focused on selected taxa (Szyndlar & Rage 2003; Rage & Szyndlar 2005; Georgalis *et al.* 2021; Georgalis 2025; Szyndlar & Georgalis 2025) allowed for a better comprehension of snake diversity in the region and its evolution throughout the late Eocene-Oligocene time span.

Based on the literature (following the reviews of Rage 1974; 2006; Smith & Georgalis 2022) and this study, snakes of the MP 19 (late Eocene) of the Quercy are represented by the following taxa (at the species level): 1) the alethinophidian *Cadurceryx filholi* Hoffstetter & Rage, 1972; 2) "*Coniophis*" sp. (Alethinophidia indet.); 3) *Cadurcoboa insolita* Rage, 1978 (Constrictores *incertae sedis*); 4) *Dunnophis cadurcensis* Rage, 1974 (Alethinophidia *incertae sedis*); 5) *Eoanilius europae* (Alethinophidia *incertae sedis*); 6) *Palaeopython cadurcensis* (Constrictores); 7) "*Palaeopython*" *neglectus* (Constrictores *incertae sedis*); 8) *Phosphoroboa filholii* (Rochebrune, 1880) (Booidea *incertae sedis*); and 9) *Platyspondylia sudrei* (Alethinophidia *incertae sedis*). It should be noted that over the past decades, several 'lettered boids' (Constrictores *incertae sedis*) have been mentioned in taxonomic lists and reviews of Quercy localities (Crochet *et al.* 1981; Rage 2006, 2012; Rage & Augé 2010, 2015; Čerňanský *et al.* 2026). Because few have been described, and none (so far) illustrated, it is still difficult to assess wherever they represented distinct taxa from the one mentioned above. We do follow Smith & Georgalis (2022) review and consider at least three of them to represent distinct taxa from the above mentioned: 1) 'Booidea C'; 2) 'Booidea K'; and 3) 'Booidea L' (see also Čerňanský *et al.* 2026). In total, at least 12 snakes can be recognized within MP 19 localities in the Quercy.

In the Quercy area, we were unable to find detailed work on snakes from a locality coeval with the Eocene assemblage of Dams (MP 19), although taxonomic lists are available for seven localities (Coânac-1; Escamps; Palembert; Rosieres 1, 2, 3, 4; Crochet *et al.* 1981; Smith & Georgalis 2022) and detailed work on precise taxa are known (e.g., *Cadurceryx filholi* in Rage 1984 and Szyndlar & Georgalis 2025; *Phosphoroboa filholii* in Georgalis *et al.* 2021). Among them, Escamps is the most diverse snake locality, with the following taxa identified (following Crochet *et al.* 1981; update for 'lettered boids follow Smith & Georgalis 2022): 1) *Cadurcoboa insolita*; 2) *'Coniophis'* sp.; 3) *Dunnophis cadurcensis*; 4) *Eoanilius europae*; 5) *Palaeopython cadurcensis*; 6) *Phosphoroboa filholii*; 7) *Platyspondylia sudrei*; 8) 'Booidea C'; 9) an unnamed constrictor ('Booidea K'); and 10) 'Booidea L'. Out of those eight taxa identified in Escamps, half of them are also identified in Dams (see Table 1). It should be noted that there is, to our knowledge, no illustration of the 'lettered boids' present in Escamps available, and descriptions of their vertebral morphology are not all available (see Rage & Augé 2010; 2015, for a description of the morphology of 'Booidea K' and 'Booidea C' respectively). The diversity of snakes in Dams seems to be poorer than in Escamps (five *vs* eight) but resembles the diversity present in other coeval Quercy localities (between one and six in the above-mentioned localities). Interestingly, we identify "*Palaeopython*" *neglectus* in the late Eocene assemblage of Dams. This taxon has been erected on specimens from the Old Quercy collections and identified in unknown Eocene localities in the Quercy (Georgalis *et al.* 2021), and its presence in the Eocene assemblage of Dams allows to confirm its late Eocene age.

Early Oligocene snakes seem to have received, like the rest of the herpetofauna, less attention than their late Eocene counterparts, with detailed work available for far fewer localities (Augé & Rage 1995; Szyndlar & Rage 2003; Rage & Szyndlar 2005; Szyndlar *et al.* 2008; Rage & Augé 2015; Smith & Georgalis 2022; Venczel *et al.* 2025).

Based on the literature (Augé & Rage 1995; Rage 2006; Rage & Augé 2015; Smith & Georgalis 2022) and this study, we consider snakes of the MP 22 in the Quercy area to be represented by the following taxa (at the specific level): 1) *Eoanilius* aff. *oligocenicus* (Alethinophidia *incertae sedis*); 2) *Bavarioboa crocheti* (Booidea *incertae sedis*); 3) "*Coluber*" *cadurci* (Colubroides); 4) "*Natrix*" *mlynarskii* (?Natricidae); 5) 'Booidea C'; 6-8) at least three indeterminate constrictors ('Constrictores indet. morphotype 2' from this study; 'Booidea indeterminate A', 'B' from Rage & Augé 2015); and 9-11) three unnamed alethinophidians of uncertain affinities ('unnamed alethinophidian 1' and '2' from this study). Thus, at least 11 snake taxa are identified within MP 22 localities in the Quercy.

Snakes have been described and illustrated from a single Quercy locality for the early Oligocene, Valbro (MP 22; Rage & Augé 2015). Within Valbro, at least five snake taxa can be recognized: 1) *Eoanilius* aff. *oligocenicus*; 2) 'Booidea C'; 3) "*Coluber*" *cadurci*; 4) an indeterminate constrictor, 'Booidea indeterminate A'; and 5) an indeterminate constrictor, 'Booidea indeterminate B' ('Boidae indeterminate A and B in Rage & Augé 2015). Only two of these taxa are also identified in the Oligocene assemblage of Dams: 1) *Eoanilius* aff. *oligocenicus*; and 2) "*Coluber*" *cadurci* (represented by "*Coluber*" cf. *cadurci* in Dams). However, small non-constrictor snakes are more diverse in Dams (three-four *vs* one in Valbro) and constrictors from Dams seem to be larger (5-7 mm of centrum length *vs* 3.7-4.5 mm centrum length in Valbro), despite a smaller number of specimens (32 in Dams *vs* 106 in Valbro).

Thus, among the twelve snakes present in Dams, we identify four new taxa for the Quercy Phosphorites, three unnamed Oligocene non-constrictors alethinophidians and an unnamed Oligocene constrictor. The diversity of the Eocene assemblage is similar to other coeval localities (except the rich and diverse locality of Escamps) even though the number of available is small (nine). The diversity of the Oligocene assemblage is slightly higher than its coeval locality Valbro.

SNAKE DIVERSITY IN THE QUERCY ACROSS THE LATE EOCENE-EARLY OLIGOCENE

Based on published and unpublished literature, snakes have been considered to undergo a major extinction event at the "Grande Coupure" in the Quercy and Western Europe (Szyndlar & Rage 2003; Rage 2006, 2012, 2013; Vasilyan 2018; Georgalis *et al.* 2021, 2025; Smith & Georgalis 2022), with the extinction of almost all Eocene taxa (Rage 2006, 2012). Because most Eocene taxa do not have a precise phylogenetic position (see Smith & Georgalis 2022), it is difficult to assess how affected some families were. However, it is admitted that lineages represented by large Eocene constrictors, namely (in the Quercy) *Palaeopython* and *Phosphoroboa*, and other mid-sized Eocene constrictors disappear from the Quercy and Western Europe during the 'Grande Coupure' (Georgalis *et al.* 2021). A single constrictor, 'Booidea C', has been considered to survive the Eocene-Oligocene transition (Rage 2006, 2012; Rage & Augé 2015; Smith & Georgalis 2022). However, because no formal description nor illustration exist for this informal taxon, we cannot confirm that Eocene and Oligocene specimens represent the same taxon, or even a constrictor. Two alethinophidian genera of uncertain phylogenetic affinities, *Eoanilius* and *Platyspondylia*, also survive into the Oligocene, but are likely represented by different species, suggesting a turnover (Szyndlar & Rage 2003; Rage 2012). The early Oligocene snake diversity is considered to be dominated by relatively small-sized snakes, with the appearance of the medium sized *Bavarioboa* at the start of the late Oligocene (Szyndlar & Rage 2003). Furthermore, the diversity of snakes is considered to critically decrease by more than half and remains low during the early Oligocene (Szyndlar & Rage 2003; Szyndlar *et al.* 2008; Szyndlar & Hoşgör 2012; Venczel *et al.* 2025).

In Dams, we did identify several mid- to large sized constrictors in the Eocene assemblage (although the largest, *Palaeopython cadurcensis*, is probably absent). We also identify two medium sized constrictors in the early Oligocene assemblage of Dams, including *Bavarioboa crocheti*. However, both differ from the Eocene constrictors, in coherence with the almost complete turnover recovered in this group. *Platyspondylia* and *Eoanilius* are present in the Eocene assemblage, but only *Eoanilius* is identified in the Oligocene one, seemingly represented by a distinct species from the Eocene one. Lastly, we recover the caenophidian "*Coluber*" cf. *cadurci* in the Oligocene assemblage, in coherence with its appearance in the fossil record in the early Oligocene (Rage 2006, 2012; Smith & Georgalis 2022). With the new taxa identified in Dams, especially

TABLE 1. — List of snake species identified in Dams and coeval localities of Escamps (late Eocene, MP 19) and Valbro (early Oligocene, MP 22).

	Eocene DAM2 (MP 19)	**Oligocene DAM3 + DAM4 (MP 22)**	**Escamps MP 19**	**Valbro MP 22**
Alethinophidia *incertae sedis*	*Platyspondylia sudrei* Rage, 1988	*Eoanilius* aff. *oligocenicus*	“*Coniophis*” sp.	*Eoanilius* aff. *oligocenicus*
	Eoanilius aff. *europae*	Alethinophidia indet. morphotype 1’	*Dunnophis cadurcensis* Rage, 1974	–
	–	Alethinophidia indet. morphotype 2’	*Eoanilius europae* Rage, 1974	–
	–	Alethinophidia indet. morphotype 3’	*Platyspondylia sudrei*	–
Constrictores	*Palaeopython* sp.	*Bavarioboa crocheti* Szyndlar & Rage, 2003	*Palaeopython cadurcensis*	“Booidea C”
	“*Palaeopython*” *neglectus* Rochebrune, 1884	‘Constrictores indet. morphotype 2’	*Phosphoroboa filholii* (Rochebrune, 1880)	“Booidea indeterminate A”
	‘Constrictores indet. morphotype 1’	–	*Cadurcoboa insolita* Rage, 1978	“Booidea indeterminate B”
	–	–	“Booidea C”	–
	–	–	“Booidea K”	–
	–	–	“Booidea L”	–
Caenophidia	–	“*Coluber*” cf. *cadurci*	–	“*Coluber*” *cadurci* Rage, 1974

in the Oligocene assemblage, the diversity of snakes in the Quercy only decreases by less than a fifth at the Eocene-Oligocene transition, However, we cannot draw conclusion in the absence of additional detailed work on additional Upper Eocene and lower Oligocene localities.

Comparisons between the Quercy area and the rest of Western Europe is difficult due to: 1) the limited number of late upper Eocene localities outside of the Quercy (Smith & Georgalis 2022: appendix 4.2); and 2) the absence of geographically close Upper Eocene and Lower Oligocene localities outside the Quercy.

For the MP 19, two localities have been identified in Western Europe: 1) Fishbourne, Isle of Wight, United Kingdom (Headon Hills Fm, MP18-19 according to Smith & Georgalis 2022); and 2) Mormont Saint-Loup, Switzerland. In both localities, the number of identified snakes is low (four and two taxa respectively) compared to most coeval Quercy localities (four to eight taxa in most localities), and very poor if compared to the entire Quercy assemblage (12 taxa). No taxa from the Quercy area are recovered in Fishbourne, while both taxa from Mormont Saint-Loup are recovered in Quercy localities (*Dunnophis cadurcensis* and ?*Palaeopython*); however, the snakes from the latter Swiss locality are in need of revision, as they have been only briefly described and figured in a 19th century work (Pictet *et al.* 1855-1857).

For the early Oligocene, localities that are more western are available, ranging from the MP 21 to the MP 23 (Smith & Georgalis 2022: appendix 4.2). Among them, localities of Ehrenstein 12 and Herrlingen 7, in Germany, are coeval to the Oligocene assemblage of Dams (MP 22; Szyndlar 1994; Smith & Georgalis 2022). The snakes of Ehrenstein 12 are almost as diverse (at least five taxa; Szyndlar 1994; Smith & Georgalis 2022) as the Oligocene assemblage of Dams but remains very poor compared to the Quercy one (five taxa *vs* ten in the Quercy). A single taxon might be recovered in both the Quercy and German assemblage, *Eoanilius oligocenicus* (if specimens referred to *Eoanilius* aff. *oligocenicus* can be referred to this taxon, as this taxon appears to be widespread across several Oligocene and Early Miocene localities in Europe and Western Asia (see Syromyatnikova *et al.* 2019; Ivanov 2022; Smith & Georgalis 2022). Interestingly, a single constrictor is present in the German assemblage, while they make up half of the diversity in the Quercy one. In addition, some taxa from Ehrenstein 12 are recovered in the late Oligocene assemblage of the Quercy (Szyndlar 1994; Rage 2006; Smith & Georgalis 2022). This might suggest: 1) different palaeoenvironment between the Quercy and southern Germany, with the former more suited for constrictor snakes; 2) better survival rates among constrictors from the Quercy during the Eocene-Oligocene transition; 3) high endemism for snakes within the Quercy area; and/or 4) an earlier establishement in Germany (compared to the Quercy area) of snake taxa from eastern Europe and Asia, arriving in the region during the earliest Oligocene (Ivanov 2000; Szyndlar & Rage 2003). However, additional material is needed before going further into studying and discussing palaeogeographic and diversity dynamics of the group.

Size and ecology as a mean of survival?

As mentioned above, the diversity of snakes during the early Oligocene was considered poor, with only small-sized taxa identified from the MP 21 to the MP23 (Szyndlar & Rage 2003; Rage & Szyndlar 2005; Szyndlar *et al.* 2008). Furthermore, the absence of medium to large-sized snake until the MP 25 has been considered a marker of a slow recovery of snake diversity (Rage & Szyndlar 2005; Szyndlar *et al.* 2008). Most of these taxa have historically been interpreted as fossorial snakes (Szyndlar & Rage 2003), an ecology that would have allowed either better chance of survival to the climatic changes at the Eocene-Oligocene boundary or facilitate an implantation in a more arid and opened environment (Rage 2006). In Dams, we do see a complete turnover in the medium to large-sized snakes, with a slight decrease in diversity (three to two; Table 1), while one genus of small sized snake is present in both assemblages, and their diversity increases (two to four; Table 1). Interestingly, two medium-sized snakes, *Bavarioboa crocheti* and the 'unnamed constrictor 1' are present in the Oligocene assemblage (Table 1). Their vertebrae are of a similar size to the ones of medium-sized snakes from the Eocene assemblage and are larger than most of those recovered in the coeval locality of Valbro (5-7 mm *vs* 4.3-4.5 mm maximum centrum length). This would be in contradiction with a slower recovery of medium to large sized snakes in Europe, being absent from the fossil record for less than 2 Ma (instead of almost 4 Ma in previous hypotheses; Szyndlar *et al.* 2008),

In the Oligocene assemblage of Dams, we do recover several small alethinophidian taxa with a vertebral morphology traditionally used to infer fossoriality: short low neural spine, poorly delimited haemal keel, centrum not wide (Rage 1974; Szyndlar & Rage 2003; Szyndlar & Georgalis 2023). These "fossorial" taxa would represent half of the snakes in the Oligocene assemblage, seemingly supporting the hypothesis of a better resilience to climatic and environmental changes. However, it should be noted that recent studies of complete extinct snakes (Scanferla & Smith 2020; Zaher & Smith 2020; Smith & Scanferla 2021, 2022; Smith & Georgalis 2022; Palci *et al.* 2024), including ones with vertebral features associated with fossoriality, have shown radically different palaeoecological interpretations when including body proportions or cranial anatomy. Furthermore, a recent study has proposed that fossoriality increased extinction rates within snakes (Cyriac & Kodamdaramaiah 2018; Li & Wiens 2021), which would contradict the hypothesis of a better resilience to climatic and environmental changes. Thus, it is possible this ecology had a lesser impact in survival and diversification of snakes during this period,

CONCLUSION

The study of the snake specimens recovered from three karstic infillings from Dams allow to identify at least 12 species in two distinct assemblages. The late Eocene assemblage (MP 19, one infilling), despite the small number of specimens, is composed of five distinct species, *Eoanilius* aff. *europae*, *Palaeopython* sp. (Constrictores), the constrictor "*Palaeopython*" *neglectus*, the alethinophidian *Platyspondylia sudrei* and an unnamed species of constrictor ('Constrictores indet. morphotype 1'). Within this assemblage, "*Palaeopython*" *neglectus* is identified for the first time in a precise locality, as it was previously known solely from the "Old collections" of Quercy. The early Oligocene assemblage (MP 22, two infillings) is composed of seven distinct species, *Eoanilius* aff. *oligocenicus*, three indeterminate alethinophidians ('Alethinophidia indet. morphotypes 1-3'), *Bavarioboa crocheti*, an indeterminate constrictor ('Constrictores indet. morphotype 2') and *Coluber* cf. *cadurci*. Within this assemblage, the three indeterminate alethinophidians and the indeterminate constrictor are identified for the first time in the Quercy area, almost doubling the number of snake taxa for the MP 22 in the Quercy. This assemblage is also the oldest occurrence of *Bavarioboa* in the fossil record and extends the temporal range of this genus back to the early Oligocene. Comparison between the two assemblages highlights a complete turnover at the species level, and a single genus, *Eoanilius*, is present in both. This complete turnover, at the species level, is similar at the Quercy regional level, in which a single taxon, 'Booidea C', might have survived. Additional material and local scale revisions are needed for further investigation into the diversity dynamics of the group.

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