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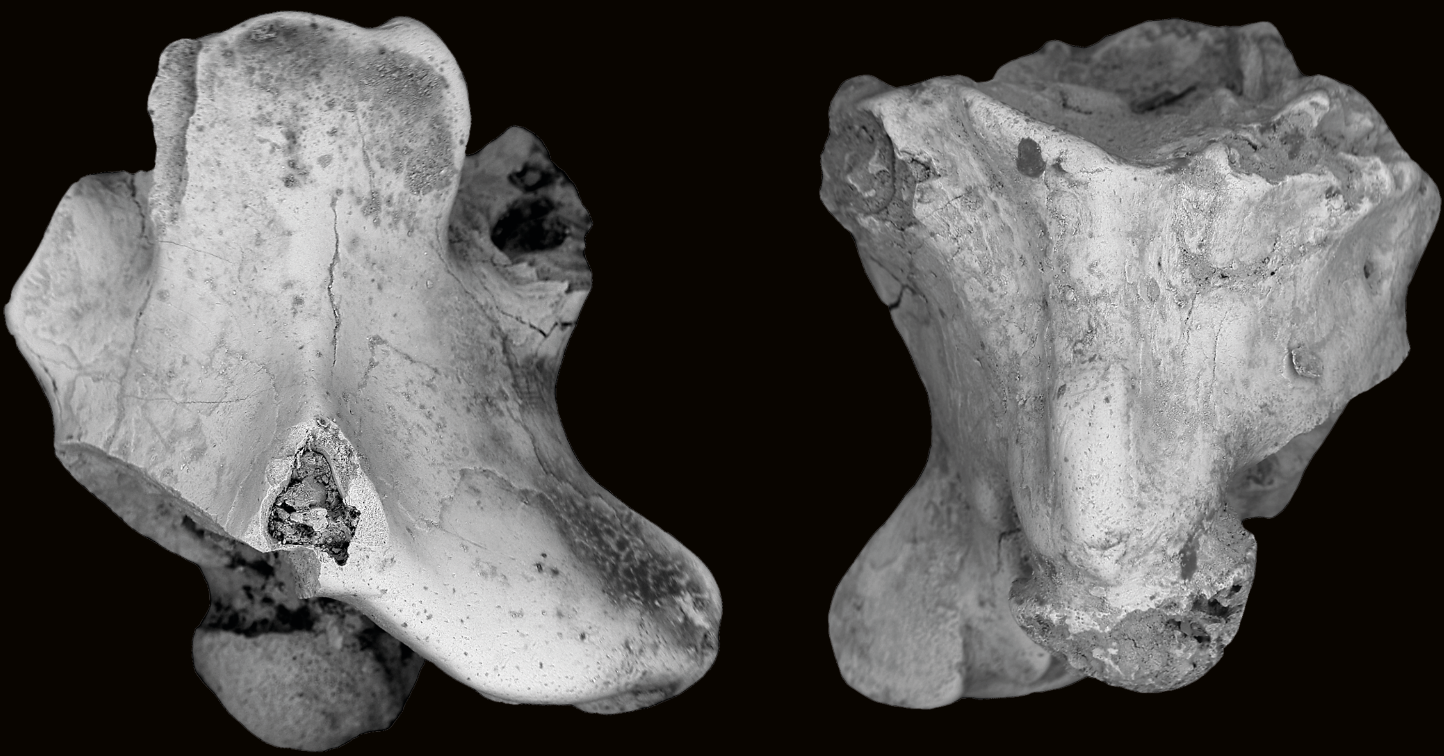

Snakes from the Cenozoic of Europe – towards a macroevolutionary and palaeobiogeographic synthesis

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Late Eocene-early Oligocene snakes from the Transylvanian Basin (Romania)

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ABSTRACT
We report herein the fossil record of snakes recovered from one late Eocene (Priabonian) and two early Oligocene (Rupelian) localities from western Romania. The only late Eocene fossil vertebrate site with snake content is Treznea, which yielded a small sized booid snake assigned to Ungaliophiidae indet. The early Oligocene locality of Cetățuia Hill, Cluj-Napoca, documents an ungaliophiid (cf. *Messelophis variatus* Baszio, 2004), while that of Suceag 1 yielded an ungaliophiid (cf. *M. variatus*), a member of Alethinophidia *incertae sedis* (*Falseryx* cf. *neervelpensis*) and an indeterminate alethinophidian snake. Part of the identified snakes represent an older fauna, known from the middle Eocene of Germany (i.e., *Messelophis* Baszio, 2004) and surviving up to the early Oligocene, while the others (e.g. *Falseryx* Szyndlar & Rage, 2003) may be seen as newcomers that appeared in Europe after the so-called "Grande Coupure". The low diversity of snake faunas in the studied localities is due to the insular conditions of that territory, with rare intermittent terrestrial connections to the more diverse snake faunas of cratonic Europe.

KEY WORDS
Fossil record,
Alethinophidia,
palaeoenvironment,
palaeogeography,
Palaeogene,
Ungaliophiidae,
Eastern Europe.

RÉSUMÉ
Serpents de l'Éocène tardif-Oligocène précoce du bassin transylvanien (Roumanie).
Nous rapportons ici le registre des serpents fossiles récupérés dans une localité de l'Éocène tardif (Priabonien) et deux localités de l'Oligocène précoce (Rupélien) de l'ouest de la Roumanie. Le seul site à vertébrés fossiles de l'Éocène tardif contenant des serpents est celui de Treznea, où l'on a trouvé un serpent booïdé de petite taille identifié comme Ungaliophiidae indet. La localité de l'Oligocène précoce de la colline de Cetățuia, Cluj-Napoca, comprend un ungaliophiidé (cf. *Messelophis variatus* Baszio, 2004), tandis que celle de Suceag 1 comprend un ungaliophiidé (cf. *M. variatus*), un membre de Alethinophidia *incertae sedis* (*Falseryx cf. neervelpensis*) et un serpent alethinophidien indéterminé. Une partie des serpents identifiés représente une faune plus ancienne, connue depuis l'Éocène moyen d'Allemagne (*Messelophis* Baszio, 2004) et ayant survécu jusqu'au début de l'Oligocène, tandis que les autres (*Falseryx* Szyndlar & Rage, 2003) peuvent être considérés comme de nouveaux venus apparus en Europe après la « Grande Coupure ». La faible diversité des faunes de serpents dans les localités étudiées est due aux conditions insulaires de ce territoire, avec de rares connexions terrestres intermittentes avec les faunes de serpents plus diversifiées de l'Europe cratonique.

MOTS CLÉS
Registre fossile,
Alethinophidia,
paléogéographie,
paléoenvironnement,
Paléogène,
Ungaliophiidae,
Europe de l'Est.

INTRODUCTION

The European late Eocene – early Oligocene transition corresponds to a major reconfiguration of the faunal assemblages, called "Grande Coupure" or "Terminal Eocene Events" (Pomerol & Premoli-Silva 1986), firstly described by Stehlin (1909). In the snake faunas, the above event is marked, among others, by the extinction of the large terrestrial constrictors, and the appearance of colubriform snakes in the early Oligocene (Ivanov *et al.* 2000; Rage & Augé 2010; Georgalis *et al.* 2021b; Smith & Georgalis 2022). The fossil record of Palaeogene snakes, including the Eocene-Oligocene transition, is well-documented in the western European assemblages (e.g. Hoffstetter & Rage 1972; Rage 1973, 1974, 1984, 2006; Rage & Ford 1980; Rage & Augé 1993, 2003, 2010; Szyndlar & Rage 2003; Baszio 2004; Szyndlar *et al.* 2008; Scanferla *et al.* 2016; Georgalis *et al.* 2020, 2021b, 2025; Scanferla & Smith 2020a, b; Smith & Scanferla 2021; Smith & Georgalis 2022), but in contrast, almost nothing is known from the eastern European regions, with only a few exceptions of palaeophiid remains (see Smith & Georgalis 2022). The main reason of the above circumstance is due to the missing productive fossil localities, especially because that territory was mostly covered by epicontinental seas during the Palaeogene (e.g. see Rage & Roček 2003; Popov *et al.* 2004); another reason is that less field work was done in the area, when compared to Western Europe. The fossil record from the Transylvanian Basin, the only source in Romania of Palaeogene lower vertebrates, includes crocodilians (Codrea & Fărcaș 2002; Sabău *et al.* 2021; Venczel & Codrea 2022; Venczel 2023), turtles (Koch 1894; Lörenthey 1903; Szalai 1934; Vremir 2013; Georgalis & Joyce 2017), and lissamphibians (Venczel *et al.* 2013; Venczel & Codrea 2018; Venczel *et al.* 2024) derived from several continental deposits of late Eocene (MP 20, Priabonian) and of early Oligocene (MP 23-24, Rupelian) ages. A preliminary report on the early Oligocene squamates of that area (Codrea & Venczel 2018) includes also lizards (*Ophisaurus* sp.) and snakes ("*Eoanilius*" sp. and undetermined "Tropidophiidae"). In this paper, we provide an updated taxonomic identification for the latter two forms. The fossil snake material is represented by isolated vertebrae, recovered from the late Eocene (MP 20, Priabonian) locality of Treznea, and from two early Oligocene (MP 23-24, Rupelian) localities (Cetățuia Hill and Suceag 1), all located in Cluj County, Romania (Fig. 1). Herein we describe the snake remains recovered from the above localities, evaluate their taxonomic positions and systematic relationships, as well as their biogeographic and palaeoenvironmental implications.

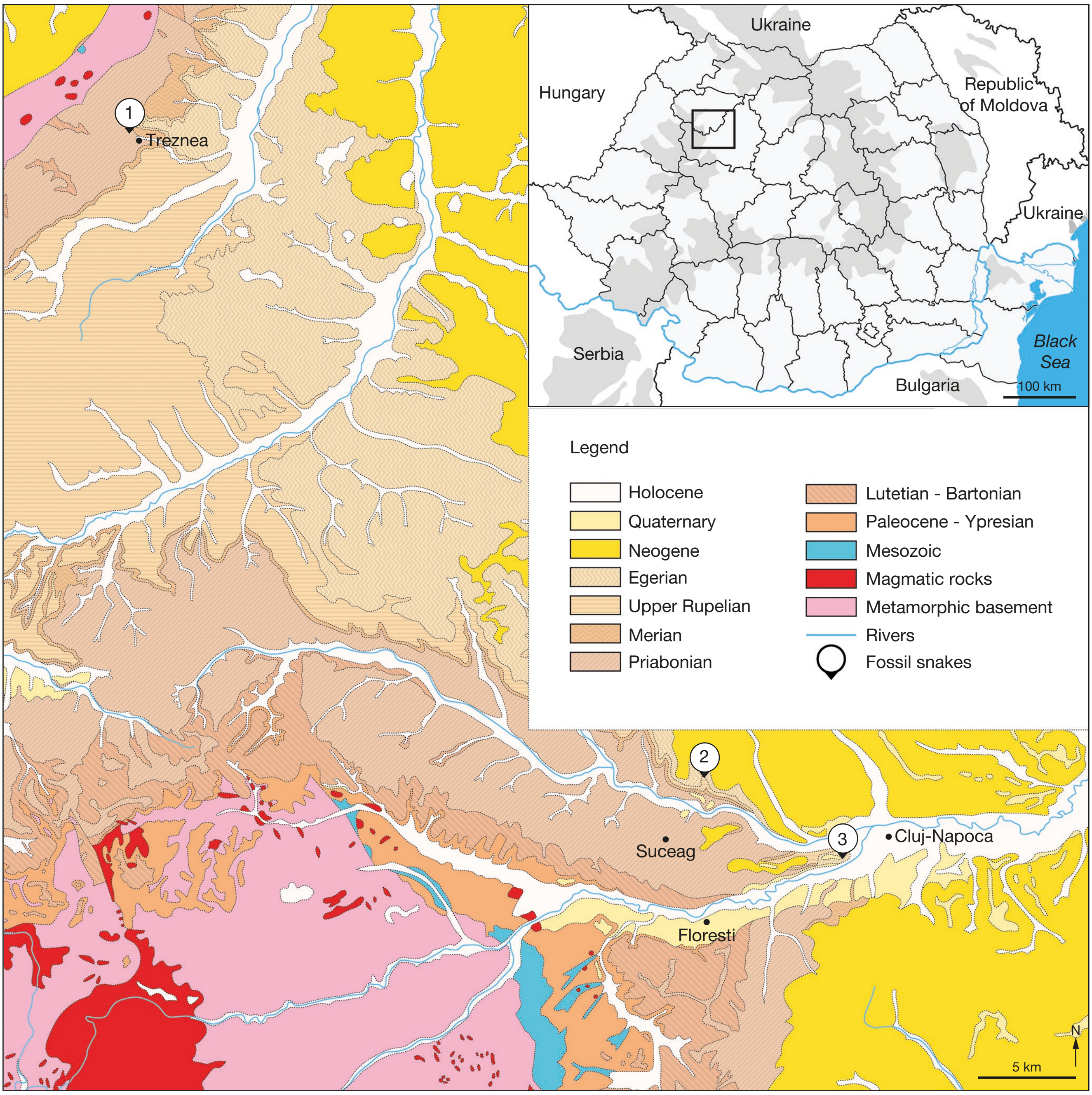

FIG. 1. — Geological map showing the Gilău and Meseș sedimentary areas and location of the Paleogene microvertebrate localities from NW Transylvania (modified after Răileanu *et al.* 1967): **1**, Treznea (late Eocene, Priabonian, Turbuța Formation); **2**, Suceag 1 (early Oligocene, Rupelian, Dâncu Formation); **3**, Cetățuia Hill, Cluj-Napoca (early Oligocene, Rupelian, Dâncu Formation).

MATERIAL AND METHODS

The specimens described here originate from about 1 500 kg of sediment collected between 2008 and 2024 from the fossil localities of Treznea, Suceag 1 and Cetățuia Hill. The samples were dried and screen-washed using a sieve set with mesh sizes ranging between 0.3 and 3 mm. The resulting isolated skeletal remains were sorted under a binocular microscope and identified by applying standard taxonomic criteria. The scanning electron microscopy (SEM) micrographs have been produced at the Museo Nacional de Ciencias Naturales, Madrid, whereas the digital photographs were taken using a Canon RF digital camera equipped with a 60-mm f/2.8 macro lens. The specimens described herein are housed in the Palaeontology-Stratigraphy Museum of the Geological Department of the Babeș-Bolyai University, Cluj-Napoca, Romania (abbreviated, UBB V).

ANATOMICAL TERMINOLOGY AND TAXONOMIC CONVENTIONS

All measurements were taken in millimeters, and the standard anatomical orientation system is used throughout this paper; measurements of vertebrae are after Auffenberg (1963) and

Szyndlar (1984), the osteological terms are from Szyndlar & Rage (2003), whereas the classification of snakes follows Szyndlar & Georgalis (2023).

SYSTEMATIC PALAEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
ALETHINOPHIDIA *incertae sedis*

Falseryx Szyndlar & Rage, 2003

Falseryx Szyndlar & Rage, 2003: 59.

Remarks

The genus *Falseryx* Szyndlar & Rage, 2003, was originally established as a member of Boinae Gray, 1825 or Tropidophiinae Brongersma, 1951 (Szyndlar & Rage 2003), 'Tropidophiidae' (Szyndlar *et al.* 2008), Tropidophiidae Brongersma, 1951 (Ivanov 2022), and finally classified as Alethinophidia *incertae sedis* (Smith & Georgalis 2022). The uncertainties regarding the phylogenetic position of *Falseryx* stem primarily from the fact that it is known exclusively from vertebrae. There is a single published vertebral synapomorphy of tropidophiids: the presence of an anteroventral straight corner of the hypapophyses of trunk vertebrae (Smith & Georgalis 2022; Szyndlar & Georgalis 2023; Zaher *et al.* 2024); notably, this feature is absent in *Falseryx*, which has a haemal keel instead of a hypapophysis in its mid- and posterior trunk vertebrae, hinting further that this genus does not belong to tropidophiids.

Falseryx neervelpensis Szyndlar, Smith & Rage, 2008

Falseryx cf. *neervelpensis*
(Fig. 2)

Material. — Suceag 1: 11 trunk vertebrae (UBB V 1042/1-2; UBB V 1043/1-9).

Description

UBB V 1042/1, is the largest available specimen representing a middle trunk vertebra, lacking its prezygapophyseal areas and the right posterolateral side of its neural arch. In dorsal view, the vertebra appears slightly longer than wide featuring a relatively deep interzygapophyseal constriction, whereas the posterior notch of the neural arch is also deep, bordered by the nearly straight posteromedian margins of the neural arch (Fig. 2A). The neural spine, representing about one third of the length of the neural arch, is extremely low and widened, and without an anterior or posterior overhang; tiny tubercles are present on its dorsal anterior limit. The anterior margin of the zygosphene is slightly convex, with two protruding lateral lobes (the left one is damaged). In ventral view, the centrum is longer than wide (centrum length (CL) ≈ 3.85 mm; centrum width (CW) ≈ 3.26 mm; CL/CW ≈ 1.18), whereas the haemal keel is prominent, somewhat broadened anteriorly and posteriorly, but tapers near the condylar neck; on the right side a distinct subcotylar tubercle is preserved. The subcentral grooves are indistinct, whereas the subcentral foramina are present; on the right side a distinctly large subcentral foramen is preserved. Only the right paradiapophysis is preserved; it strongly projects laterally and features a well-developed tubercle on the anterior margin of the prezygapophyseal buttress (Fig. 2B). The surface of the left postzygapophysis preserves numerous lines of arrested growths (LAGs) (for their interpretation, see Venczel *et al.* 2015), of which six are more discernible, considered as indication of intermittent seasonal growths (Venczel *et al.* 2015; Venczel 2023). In lateral view, the haemal keel is prominent and its ventral margin is relatively straight, whereas the subcentral ridges are weakly defined (Fig. 2C). In anterior view, the roof of the zygosphene is straight with the lateral lobes tilting upward; the cotylar rim is damaged (Fig. 2D). In posterior view, the neural arch is depressed, slightly convex dorsally and preserves on the left dorsal side of the postzygapophysis a low bony ridge extending anteroposteriorly. No parazygantral foramen is preserved (Fig. 2E).

The remaining trunk vertebrae are smaller and fragmentary, exhibiting some morphological variation compared to the UBB V 1042/1 specimen. The neural spine is consistently low and strongly broadened and with either parallel lateral margins (Fig. 2F), or distinct posterior widening (Fig. 2G). Some specimens feature a well-developed median lobe on the zygosphene (Fig. 2F, G). In the UBB V 1042/2 specimen, the paradiapophyses are well-preserved and somewhat differentiated into diapophyseal and parapophyseal portions. The portions of prezygapophyseal buttresses between the paradiapophyses and prezygapophyseal processes, as seen in *Falseryx neervelpensis* (see Szyndlar *et al.* 2008), are developed into prominent, anteriorly facing tubercles (Fig. 2H). In anterior view, the outline of the cotyle appears circular, without paracotylar foramina (Fig. 2I). In UBB V 1043/1, representing an anterior trunk vertebra (Fig. 2J, K), the neural arch appears more vaulted and less elongated, whereas the haemal keel is more prominent and extends posteriorly beyond the condylar neck.

Remarks

The size and morphology of the above-described vertebrae from Suceag 1 are closely resemble those of *Falseryx neervelpensis* known from the early Oligocene (MP 21) locality of Boutersem TGV, Belgium. In particular, the prominent tubercles protruding anteriorly on the prezygapophyseal buttresses are highly similar to those observed in this species (Szyndlar *et al.* 2008: figs 1, 2). The vertebrae of the type species of the genus (i.e., *Falseryx petersbuchi* Szyndlar & Rage, 2003), known from the Early Miocene (MN 4) localities of Petersbuch 2, Germany and Dolnice, Czech Republic (Szyndlar & Rage 2003), also bear resemblance to the specimens from Suceag 1. However, they lack the tubercles developed on the prezygapophyseal buttresses, which are considered diagnostic of *F. neervelpensis* (see Szyndlar *et al.* 2008).

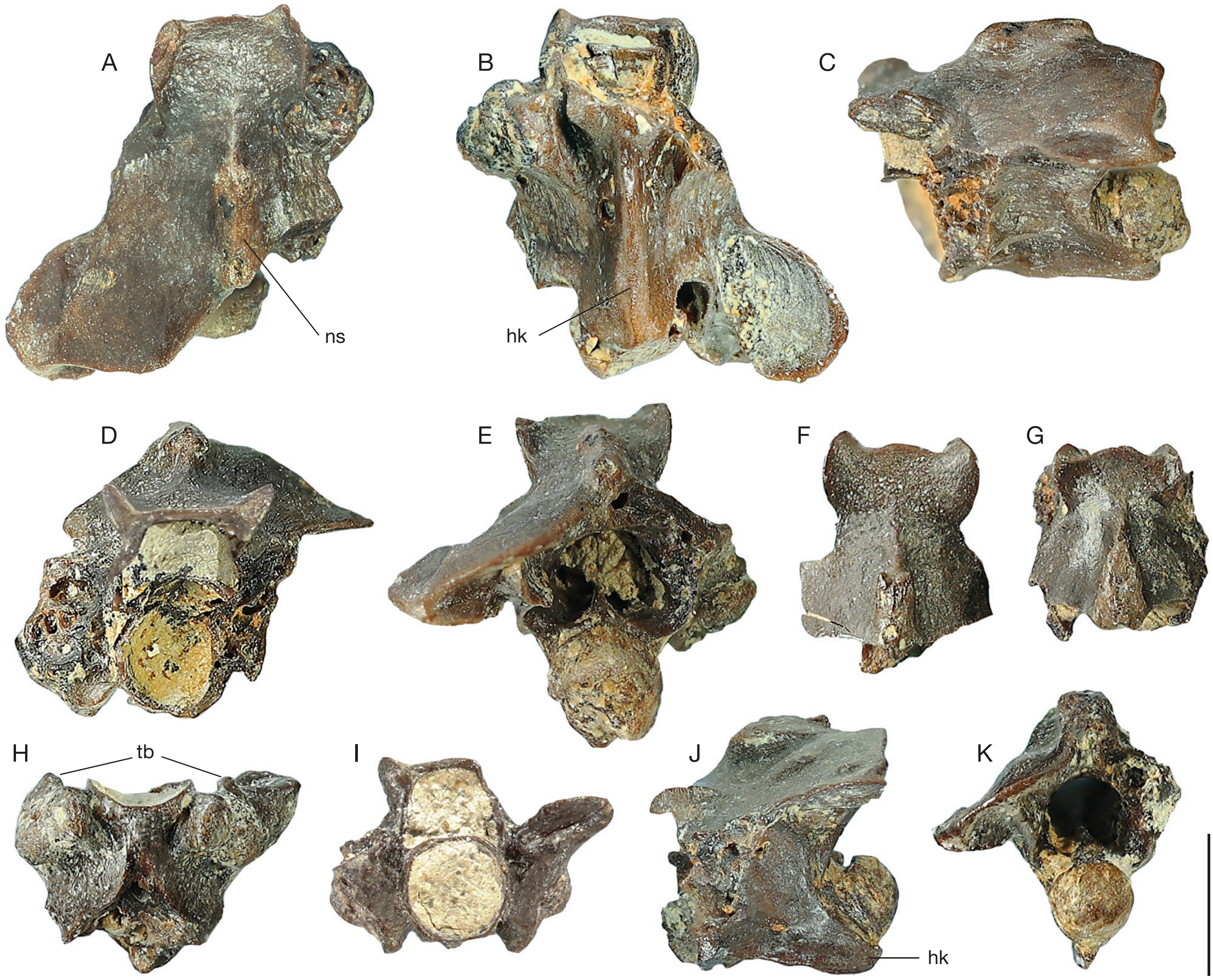

Fig. 2. — Isolated trunk vertebrae of *Falseryx* cf. *neervelpensis*: **A**-**E**, middle trunk vertebra (UBB V 1042/1) in dorsal (**A**), ventral (**B**), left lateral (**C**), anterior (**D**) and posterior (**E**) views; **F**-**I**, partial trunk vertebrae (UBB V 1043/2, 1043/3 and 1042/2) in dorsal (**F**, **G**), ventral (**H**) and anterior (**I**) views; **J**-**K**, anterior trunk vertebra (UBB V 1043/1) in left lateral (**J**) and posterior (**K**) views. Abbreviations: **hk**, haemal keel; **ns**, neural spine; **tb**, tubercul on the prezygapophyseal buttress. Scale bar: 2 mm.

CONSTRICTORES Oppel, 1811
(*sensu* Georgalis & Smith 2020)
BOOIDEA Gray, 1825 (*sensu* Pyron *et al.* 2014)

Ungaliophiidae McDowell, 1987
(*sensu* Burbrink *et al.* 2020)

Remarks

Ungaliophiidae were previously classified as a subfamily within Tropidophiidae (originally Ungaliopheinae of McDowell 1987). However, based on molecular data, ungaliophiids are considered to be much more distantly related to tropidophiids and instead represent distinct booids. This taxonomic classification is usually regarded as a subfamily within Charinaidae Gray, 1849 (Ungaliophiinae of Pyron *et al.* 2014; Georgalis & Smith 2020), or as a distinct family of Booidea, the Ungaliophiidae (Burbrink *et al.* 2020; Szyndlar & Georgalis 2023; Zaher *et al.* 2023). Parsimony analyses have recovered the latter as the sister clade of Charinaidae (Burbrink *et al.* 2020) (for further details see also Szyndlar & Georgalis 2023). *Messelophis* Baszio, 2004, is a genus of fossil dwarf boas from the middle Eocene of Messel locality, Germany, described firstly by Baszio (2004), based mainly on the morphology of its vertebrae. Another species of the genus, *Messelophis ermannorum* Schaal & Baszio, 2004, also from Messel, was later reassigned to a new genus by Scanferla *et al.* (2016): *Rieppelophis* Scanferla, Smith & Schaal, 2016. The latter genus appears in parsimony analyses as the sister taxon of *Messelophis*, while *Messelophis* + *Rieppelophis* has been recovered as the sister taxon of *Exiliboa* + *Ungaliophis* (Scanferla & Smith 2020a, b).

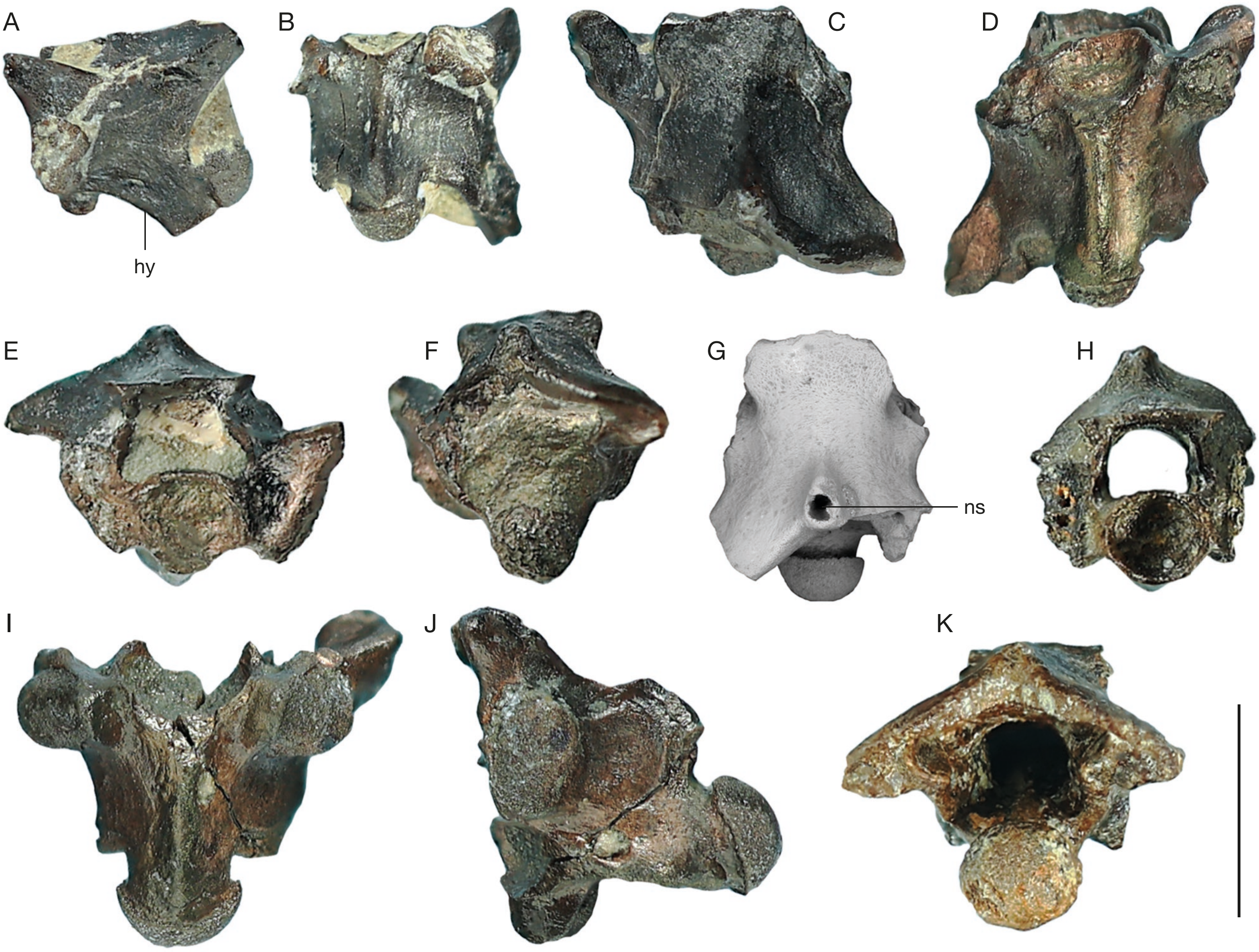

Fig. 3. — Isolated trunk vertebrae of cf. *Messelophis variatus*: **A**, **B**, anterior trunk vertebra (UBB V 1045) in left lateral (**A**) and ventral (**B**) views; **C**-**F**, middle trunk vertebra (UBB V 1046/1) in dorsal (**C**), ventral (**D**), anterior (**E**) and posterior views (**F**); **G**, **H**, partial trunk vertebra (UBB V 1046/2) in dorsal (**G**) and anterior (**H**) views; **I**-**J**, partial trunk vertebra (UBB V 1046/3) in ventral (**I**) and left ventrolateral (**J**) views; **K**, partial trunk vertebra (UBB V 1047/2) in posterior view. Abbreviations: **hy**, hypapophysis; **ns**, neural spine. Scale bar: 2 mm.

Genus *Messelophis* Baszio, 2004
Species *Messelophis variatus* Baszio, 2004

cf. *Messelophis variatus*
(Figs 3A-K; 4A-I)

Material. — Cetățuia Hill: one anterior trunk vertebra (UBB V 1045), four trunk vertebrae (UBB V 1046/1-4); Suceag 1: eight trunk vertebrae (UBB V 1047/1-8), one caudal vertebra (UBB V 1044).

Description

The specimen UBB V 1045 represents a partial anterior trunk vertebra with the roof of its neural arch broken off (Fig. 3A, B). The centrum is slightly longer than wide and features a salient and posteroventrally projecting hypapophysis. Two small subcentral foramina are present and the paradiapophyses appear robust and undifferentiated, however their surfaces are strongly eroded.

One of the best preserved mid-trunk vertebrae from the Cetățuia Hill locality is represented by UBB V 1046/1(Fig. 3C-F); however, in the specimen the right prezygapophysis and the left postzygapophysis are completely broken off, whereas the lateral margin of the left prezygapophysis, the ventral margin of the cotylar lip and the posterior tip of the condyle are also missing. The estimated centrum length of the UBB V 1046/1 specimen approaches 2.42 mm, whereas its centrum width approaches 2.39 mm; in the UBB V 1047/1 specimen from Suceag 1 locality (Fig. 4A-C) the centrum length reaches 2.64 mm, whereas its centrum width equals 2.46 mm. In dorsal view, the most striking feature is that the neural spine is extremely short and point-like, positioned on the upraised dorsoposterior border of the neural arch, whereas the area in front of the neural spine is flat (Figs 3C, G, H; 4A, D, E); however, in all the specimens the distal tip of the neural spine is broken off (Figs 3G, H; 4H). The interzygapophyseal constriction is moderate and a well-defined posterior notch is present on the neural arch. The anterior margin of the zygosphene is provided with two lateral lobes and with a less developed median lobe (Figs 3C; 4A). In ventral view, the haemal keel is well-defined, more salient in the specimens from Cetățuia Hill (Figs 3D, I; 4F),

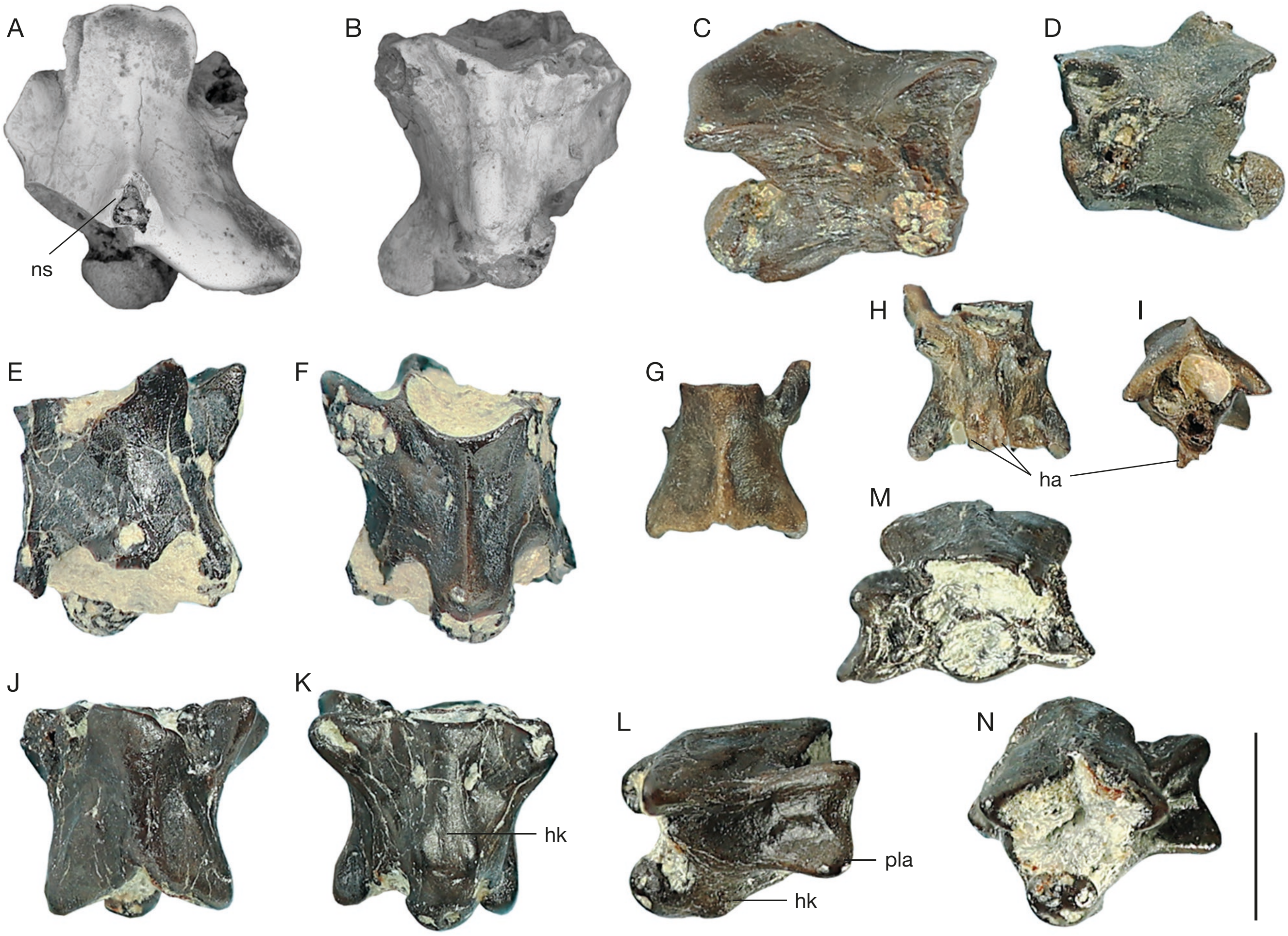

Fig. 4. — Isolated trunk vertebrae of cf. *Messelophis variatus*: (**A**-**I**) and Ungaliophiidae indet. (**J**-**N**): **A**-**C**, middle trunk vertebra (UBB V 1047/1) in dorsal (**A**), ventral (**B**) and right lateral (**C**) views; **D**, middle trunk vertebra (UBB V 1047/3) in left lateral view; **E**, **F**, middle trunk vertebra (UBB V 1046/4) in dorsal (**E**) and ventral (**F**) views; **G**-**I**, caudal vertebra (UBB V 1044) in dorsal (**G**), ventral (**H**) and posterior (**I**) views; **J**-**N**, caudal vertebra (UBB V 1048) in dorsal (**J**), ventral (**K**), right lateral (**L**), anterior (**M**) and posterior (**N**) views. Abbreviation: **ha**, haemapophysis; **hk**, haemal keel; **ns**, neural spine; **pla**, pleurapophysis. Scale bar: 2 mm.

whereas in those from Suceag 1, it is somewhat widened and flattened (Fig. 4B). The subcentral foramina are present and of variable size, the subcentral grooves are weakly defined, whereas the paradiapophyses project strongly laterally; the prezygapophyseal process is vestigial (Fig. 3I, J). In lateral view, the vertebrae appear moderately flattened with the neural arch elevated near the neural spine (Fig. 4C, D). The paradiapophyses are undifferentiated and robustly built, as seen in specimen UBB V 1046/3 (Fig. 3J). In anterior view, the neural arch is slightly flattened, the neural spine is relatively low, whereas the cotyle is circular and the paracotylar foramina are lacking; the zygosphenal roof is almost horizontal (Fig. 3E, H). In posterior view, the neural arch appears slightly convex, the condyle is rounded, whereas the parazygantral foramina are lacking (Fig. 3F, K).

A single caudal vertebra (UBB V 1044), representing a small sized individual (however, about five lines of the arrested growths are observed on its prezygapophysis indicating that it was an adult snake), possesses a low neural spine extending from the base of the zygosphene to the posterior notch of the neural arch (Fig. 4G). The centrum is longer than wide, whereas the neural arch is depressed possessing a weak interzygapophyseal constriction (Fig. 4H); below the right prezygapophysis, a tiny prezygapophyseal accessory process is preserved, and the prezygapophysis itself is elongated. In ventral view, the pleurapophyses are broken off; however, the remnants of the paired haemapophyses are partially preserved (Fig. 4H, I).

Remarks

Some of the phenotypical features of the vertebrae described above closely resemble those of *Messelophis variatus* (e.g. presence of an extremely short "point-like" neural spine, developed near the posterior border of the neural arch and the paracotylar foramina absent). Similar to the specimens of our study, the vertebrae of *M. variatus* are elongated, with extremely short neural spines developed at the posterior border of the neural arch, the paracotylar foramina are absent and the prezygapophyseal accessory processes are weakly developed (Baszio 2004; Schaal & Baszio 2004; Scanferla *et al.* 2016: fig. 1B). Moreover, in the holotype of *M. variatus* (SMF-ME 1828 A-B), exposing a short portion of the ventral side of its vertebral column (MV pers. obs.), and in the recently

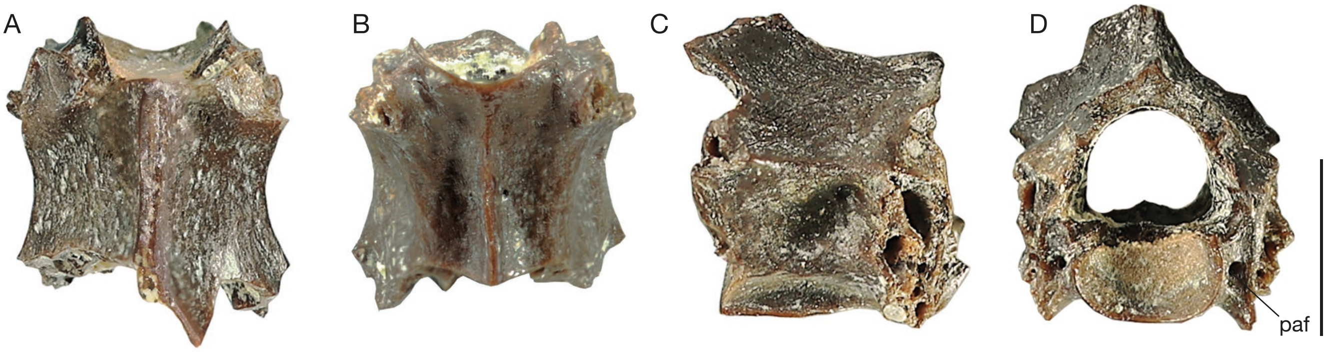

Fig. 5. — Isolated trunk vertebra of Alethinophidia indet.: **A**-**D**, incomplete middle trunk vertebra (UBB V 1049) in dorsal (**A**), ventral (**B**), right lateral (**C**) and anterior (**D**) views. Abbreviation: **paf**, paracotylar foramen. Scale bar: 2 mm.

referred specimen SMF-ME 513a from the early middle Eocene of Messel, Germany, exposing the ventral side of its vertebral column (Scanferla & Smith 2020b: fig. 1B), the trunk vertebrae possess prominent haemal keels of variable shape (i.e., of gladiate or spatulate-shape, *sensu* Auffenberg 1963). The caudal vertebra UBB V 1044, similarly to *M. variatus*, possesses a low neural spine and provided with paired haemapophyses (Scanferla *et al.* 2016: fig. 18A); however, in *M. variatus* the haemapophyses appear laminar, whereas in UBB V 1044 the remnants of the latter structure comparatively are less elongated anteroposteriorly.

A number of comparable attributes of the studied specimens should be noted also in the fossil genus *Dunnophis* Hecht *in* McGrew *et al.*, 1959, which was originally designated based on isolated vertebrae as an *incertae sedis* snake from the late early Eocene of North America (Hecht 1959), and recorded later from the Eocene of Western Europe (e.g. Rage 1973, 1974, 1984, 2006; Rage & Ford 1980; Rage & Augé 2003, 2010; see Smith & Georgalis 2022), and even from the late Palaeocene of Morocco (Augé & Rage 2006). Among the peculiar features of *Dunnophis*, as noted by the above authors, are the following: the centrum is depressed, narrow and longer than wide; the extremely short neural spine is developed near the margin of the deep posterior notch of the neural arch; the prezygapophyseal processes are absent or vestigial; and the caudal vertebrae, rarely present in the fossil material, likely possessed haemapophyses, as seen in the North American type species of the genus, *Dunnophis microechinis* Hecht *in* McGrew *et al.*, 1959 (see Hecht 1959: plate 56: 7-10). Resemblance between *Dunnophis* and *Ungaliophis* Müller, 1880 was already noted by Bogert (1968), while similarity between *Dunnophis* and *Messelophis* was mentioned by Baszio (2004). Rage & Augé (2010) suggested that *Messelophis* might be considered a junior synonym of *Dunnophis*. On the other hand, the specimens from the early Oligocene of Romania described herein, share with the two recent genera of ungaliophiids (i.e., *Exiliboa* Bogert, 1968, and *Ungaliophis*) a number of phenotypic features, as follows: lightly built vertebrae with their centrum longer than wide, the presence of a prominent haemal keel in the trunk vertebrae (according to Szyndlar & Georgalis, 2023, the haemal keel is less developed in *Ungaliophis*), the absence of paracotylar foramina, and weakly developed or vestigial prezygapophyseal accessory processes. Some of these characters (e.g. elongation of the trunk vertebrae and presence of haemal keel in the caudal vertebrae) have been considered synapomorphies of Ungaliophiidae within the clade of Constrictores (Smith 2013).

Ungaliophiidae indet.
(Fig. 4J-N)

Material. — Treznea: one posterior caudal vertebra (UBB V 1048).

Description

The only available caudal vertebra (UBB V 1048) is known from the Treznea locality (Fig. 4J-N). It appears well-preserved; however, its surface displays some signs of erosion. The neural arch is strongly depressed and the neural spine is reduced to a low keel. In ventral and lateral views, the centrum possesses a prominent haemal keel, connected to a rounded condyle. The haemal keel is somewhat enlarged posteriorly and displays on the posteroventral side two small knobs (Fig. 4K).

Remarks

The main feature of the single available specimen (UBB V 1048) is the presence of a well-developed haemal keel on the subcentral surface, reminiscent of *Rieppelophis ermannorum* (Schaal & Baszio, 2004), in which the haemapophyses in the caudal vertebrae are replaced by paired knobs (Scanferla *et al.* 2016: fig. 18B). Additionally, it shares similarities with recent ungaliophiids (*Exiliboa* and *Ungaliophis*), which possess a distinct haemal keel in the caudal vertebrae, instead of paired haemapophyses (Szyndlar & Georgalis 2023).

Alethinophidia indet.
(Fig. 5)

Material. — Suceag 1: one trunk vertebra (UBB V 1049).

Description

The fragmentary trunk vertebra is small, missing the anterior portion of its neural arch, the anterior part of the zygosphene, the dorsal section of the neural spine, the zygapophyses, the dorsal parts of the cotyle and the condyle. Although the dorsal part of the neural spine is lacking, its broken surface suggests that it was rather long, extending from the base of the zygosphene onto the posterior notch of the neural arch (Fig. 5A). In ventral view, the haemal keel is salient and narrow, with subcentral foramina present; the subcentral ridges are well-defined (Fig. 5B). In anterior and lateral views, the neural arch appears lightly built and moderately vaulted; the dorsal part of the cotyle is broken but its remnants suggest potential dorsoventral flattening; both sides of the cotyle is flanked by large paracotylar foramina (Fig. 5C, D).

REMARKS

The overall morphology of the trunk vertebra resembles that of colubriform snakes, exhibiting the following characteristics: a lightly built neural arch, a reconstructed centrum distinctly longer than wide, a presumably long neural spine, a prominent and narrow haemal keel, and distinct paracotylar foramina (see Zaher *et al.* 2019). However, due to its fragmentary state, the specimen cannot be assigned more precisely within alethinophidian snakes.

RESULTS AND DISCUSSION

The present contribution represents the first detailed report on Palaeogene snake remains from the territory of the Transylvanian Basin. The studied material is scanty and only three fossil localities yielded isolated vertebrae assignable to three different groups of snakes, as follows: 1) Treznea (late Eocene, Priabonian, Turbuța Formation): Ungaliophiidae indet.; 2) Suceag 1 (early Oligocene, Rupelian, Dâncu Formation): *Falseryx* cf. *neervelpensis* (Alethinophidia incertae sedis), cf. *Messelophis variatus* (Ungaliophiidae), and Alethinophidia indet.; and 3) Cetățuia Hill, Cluj-Napoca (early Oligocene, Rupelian, Dâncu Formation): cf. *Messelophis variatus* (Ungaliophiidae).

The fossil record of ungaliophiid snakes with *Messelophis-Rieppelophis-Dunnophis* phenotypical appearance, based on the review of Szyndlar *et al.* (2008), covers in North America the time span from the middle Palaeocene (Estes 1976) to the end of the Eocene (Holman 2000), whereas in Europe, these taxa are known from the earliest Eocene (MP 7) of Portugal (Rage & Augé 2003) into to the early Oligocene (MP 22) of Germany (Szyndlar & Rage 2003), and material from Africa has been tentatively referred to *Dunnophis* (late Paleocene of Adrar Mgorn 1, Morocco; Augé & Rage 2006). Accordingly, the clade survived the so-called “Grande Coupure” bio-event and the occurrence of *Messelophis* in the early Oligocene (MP 23-24) localities of Cetățuia Hill and Suceag 1, Romania may correspond to their last occurrence on the European territory. The presence of these small booids during the Eocene-early Oligocene of Eastern Europe may result from a distributional scenario outlined by Scanferla & Smith (2020a) (i.e., a transoceanic dispersal from the presumed South American origin into Europe, through Africa; or conversely, following a mostly terrestrial route from South America into Europe, through North America). Regardless of which version of the above scenario is more compelling, and taking into consideration that during this time interval large areas of the European continent were covered by epicontinental seas (Rage & Roček 2003; Popov *et al.* 2004), the dispersal of dwarf boas from the western part of the European continent into more eastern areas was possible through ephemeral terrestrial connections, or through other unknown circumstances. However, the key factor in their dispersal and survival in new areas was the existence of preferred habitats throughout their range of distribution. The microhabitat preference of *Messelophis*, according to multivariate analyses of Scanferla & Smith (2020a), was similar to that of arboreal snakes; consequently, the small booid from the studied localities probably inhabited forested palaeoenvironments.

The oldest fossil record of the genus *Falseryx* is known from the early Oligocene (MP 21) of Belgium (Szyndlar *et al.* 2008); it is also recorded from the latest Oligocene (MP 30) of Kargi, Turkey (Georgalis *et al.* 2021a); the Miocene fossil record is known from the earliest Miocene (MN 1) of Kilçak, Turkey (Syromyatnikova *et al.* 2019), the Early Miocene of Czech Republic (Szyndlar & Rage 2003), the Early and Middle Miocene (MN 2-MN 7 + 8) of Germany (Szyndlar & Rage 2003; Čerňanský *et al.* 2015, 2016) and the Early Miocene (MN 4) of Spain (Szyndlar & Rage 2003). The fossil record from the early Oligocene (MP 23-24) of Romania, described herein, fills the gap between the early and late Oligocene localities and implies a potential pathway for the distribution of vertebrates between the western and southeastern part of the continent and potential connections with Anatolia. In fact, the Oligocene localities of Suceag 1 (Romania) and Kargi (Turkey), from where remains of *Falseryx* are known, were part of a larger insular biogeographic province extending from southeastern Europe to Anatolia, the so-called Balkanatolia (Licht *et al.* 2022). Szyndlar *et al.* (2008) considered that the most reasonable explanation for the appearance of *Falseryx* in the early Oligocene of Europe is its immigration from Asia, followed by its disappearance from the western part of the continent; this was further supported by the eventual documentation of the genus in the late Oligocene of Anatolia by Georgalis *et al.* (2021a). Nevertheless, the genus was present in the geologically younger Balkanatolian localities that document the second wave of its range extension into Europe during the Early Miocene (Ivanov 2022).

Little is known about the closer systematic relationships and habitat preference of *Falseryx*. Szyndlar & Rage (2003) considered it as a member of Boidae, and indeed these authors observed similar features in an anterior caudal vertebra of *F. petersbuchi* Szyndlar & Rage, 2003 (see Szyndlar & Rage 2003: fig. 27P-T), provided with a prominent hypapophysis, that structure occurring in some members of boids and pythonids (Boinae and Pythoninae in their terminology). The trunk vertebrae of *Falseryx* resemble also *Bransateryx*, and therefore these were seen initially as a member of the latter genus (Szyndlar 1987; Szyndlar & Schleich 1993). Furthermore, Szyndlar *et al.* (2008) observed a close resemblance in the subcentral morphology of the posterior caudal vertebrae of *F. neervelpensis* and *Rottophis atavus* (Meyer, 1855), known from the latest Oligocene (MP 30) of Germany, both possessing distinct haemal keels, instead of haemapophyses. Nevertheless, in light of recent review of Smith & Georgalis (2022), *Falseryx* and *Rottophis* Szyndlar & Böhme, 1996, are considered (in the absence of synapomorphies with Boidae) Alethinophidia incertae sedis.

The presence of LAGs exposed in one of the vertebrae of *Falseryx* cf. *neervelpensis*, as in the case of the late Eocene alligatoroid crocodilian *Diplocynodon* from Leghia, Romania (Venczel 2023), may indicate a seasonal palaeoclimate in connection with terrestrial cooling in Northern Europe (Hren *et al.* 2013), and start of reconfigurations of the forest-dominated ecosystems well before the Eocene-Oligocene terminal event, as outlined by Wu *et al.* (2024).

CONCLUSIONS

The fossil record from the late Eocene-early Oligocene timespan of the Transylvanian basin, as documented in the present work, includes one ungaliophiid snake (cf. *Messelophis variatus*), an Alethinophidia *incertae sedis* snake (*Falseryx* cf. *neervelpensis*) and an indeterminate alethinophidian snake with potential colubriform attributes. Despite the scantiness of the available remains, the composition of this snake assemblage is in agreement with the fossil record around the so called "Grande Coupure", known from the western and south-eastern part of the European continent. The ungaliophiid snake (cf. *Messelophis variatus*) may be considered an early Oligocene survivor of a rather diverse booid snake fauna existing in earlier stages of the European Eocene, whereas *Falseryx* may be considered a newcomer, which shifted its range into the western part of the continent using the southern pathway for vertebrates, the so-called Balkanatolia.

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