

SUPPLEMENTARY APPENDIX 4.S1: Catalog of Palaeogene snakes¹

Given the uncertainties in the phylogenetic affinities of most of the formally named snake taxa, we elect to give an alphabetical catalog that may be consulted regardless of higher taxonomic changes. The entries in this catalog comprise all currently valid species as well as certain composites for unnamed distinct, potentially distinct or indeterminate taxa (found in Table 4.1). Species that are currently considered nomina dubia, nomina nuda, and junior synonyms of valid taxa are omitted from this catalog. In a few cases we make remarks on genera or higher taxa, which are left-justified rather than centred; the monophyly of many of them is untested or in doubt. While ‘wastebasket taxa’ and ‘taxa of convenience’ are not without merit, we do not wish to foster the impression that these are clades.

A full table of (we believe) all known occurrences can be found in Supplementary Appendix 4.S2, where also all valid species are listed, with indications of their type localities (abbreviated there as ‘TL’), as well as all species that are currently considered invalid (e.g., nomina nuda, nomina dubia, or junior synonyms of valid taxa). With regard to species-level taxonomy, we have accepted the generic attributions of species as maintained by the last reviser. For species diversity, we have tried to follow the original authors in determining whether a fossil taxon, whether named or not, is distinct (as with ‘Caenophidian indet. A’ from Vastan; Rage et al., 2008). We also allow once per broad geographic region (viz., Africa, Asia, Australia, Europe, North America, South America) that an unnamed species from a higher taxon is distinct, even if the authors do not state this. For instance, Rage et al. (2008) described vertebrae of an unnamed ‘boid’ from Vastan Mine, India. Smith et al. (2016) also described vertebrae of an unnamed ‘boid’ from Tadkeshwar Mine, India, and noted several differences to the unnamed taxon from Vastan. We consider the species from Vastan, the first described, to be distinct, but not that from Tadkeshwar, as there was no clear statement that the taxa were distinct.

***Afrotortrix draaensis* Rage et al., 2021**

Described on the basis of 25 trunk vertebrae from the early-middle Eocene of Algeria (Rage et al., 2021). No additional material reported; intracolumnar variation well known. Genus monotypic. Diagnostic features with respect to other “anilioids” (Rage et al., 2021): paracotylar foramina present, zygapophyses less inclined, no marked V-shaped notch in posterior border of neural arch, and tubercular neural spine. Rage et al. (2021) documented characters that permit reference of this taxon to the “anilioid” grade and considered it the only secure “anilioid” known from Africa.

***Alamitophis tingamarra* Scanlon, 2005**

Described (originally as *Alamitophis* cf. *argentinus*, later as a new species) on the basis of 9 vertebrae from throughout the column, rib fragments, and a partial dentary from the lower Eocene Tingamarra locality of Queensland, Australia (Scanlon, 1993; 2005). No additional material reported. Intracolumnar variation well known. Diagnostic features with respect to other Madtsoiidae (Scanlon, 2005): small size, more elongate centrum, smooth median prominence on the anterior margin of the zygosphenon, weak subcentral ridges, and only weakly angled zygapophyses. As envisaged by Scanlon

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(2005), Vasile et al. (2013) recovered *A. tingamarra* as the sister species of *A. elongatus*, another referred species from the Upper Cretaceous of Argentina, whereas Rio and Mannion (2017) found no evidence for the monophyly of *Alamitophis*.

***Amananulam sanogoi* McCartney et al., 2018**

Described on the basis of 1 partial mid-trunk vertebra from the Palaeocene of the Trans-Saharan Seaway (Gao Trench), Mali (McCartney et al., 2018). No additional material reported. Intracolumnar variation unknown. However, we here note that the 2 articulated vertebrae from the Palaeocene of the Dahomey Embayment described by Stromer (1910) as a constrictor similar to *Calamagras* fit closely with the diagnosis of Nigerophiidae and especially of *A. sanogoi* (including oblique paradiapophyses); we regard this material as *Amananulam* sp. Genus monotypic. Diagnostic features with respect to other nigerophiids (McCartney et al., 2018): haemal keel restricted to the posterior quarter of centrum, zygosphene thick, dorsally concave neural arch, and neural spine restricted to posterior third of neural arch. McCartney et al. (2018) referred it to Nigerophiidae on the basis of the anteroposteriorly short neural spine, the weakness of the interzygapophyseal and subcentral ridges, and the ventrally directed paradiapophyses.

***Amaru scagliai* Albino, 2018**

Described on the basis of 33 whole or partial trunk vertebrae from Estancia Pampa Grande, northwestern Argentina (Albino, 2018). No additional material reported. Intracolumnar variation unknown. Genus monotypic. The following are the main features that in combination were given to distinguish the taxon (Albino, 2018): neural arch not depressed, long and long neural spine, zygosphene wider than cotyle and with tongue-like anteromedian projection, centrum shorter than neural arch width, prominent subcentral ridges, paracotylar foramina absent, and para- and diapophyses well differentiated. Albino (2018) considered the taxon to belong to 'Macrostromata' on the basis of the V-shaped notch on the posterior border of the neural arch and excluded it from Caenophidia on the basis of vertebral proportions and the lack of paracotylar foramina. She noted similarities to Constrictores in overall shape and zygosphene form, but gave the well-differentiated para- and diapophyses as a feature inconsistent with this. As a clade 'Macrostromata' is not recognized in the present classification, we consider the taxon to be Alethinophidia *incertae sedis*.

'anilioids' indet.

The vertebrae of many basal alethinophidians (*Anilius*, Uropeltidae, *Cylindrophis*) have been characterised by a suite of shared features including a depressed neural arch, highly reduced neural spine, and weak or absent haemal keel (e.g., Hoffstetter and Gasc, 1969; Rage, 1984a) (see Head, 2021: for a critical phylogenetic review). Relatively similar morphologies are also seen in 'Scolecophidia', although in that group the para- and diapophyses are scarcely distinguishable and large prezygapophyseal processes are present (Rage, 1984a), which raises the prospect that this gestalt is primitive for crown snakes, in which case the identification of 'anilioid' could not even be construed to be 'basal alethinophidian' (see also comments under *Coniophis* sp. below). If Longrich et al.'s (2012) attribution of cranial elements to the genotype *C. precedens* is correct, it would strengthen this assertion.

That being said, indeterminate 'anilioids' were reported from the Palaeocene and Eocene of Tiupampa, Bolivia, and Laguna Umayo, Peru (Rage, 1991), and the lower and middle Eocene and upper Oligocene of France (Augé et al., 1997; Szyndlar and Rage,

2003). Zerova and Chkhikvadze (1984, cited in Danilov and Averianov, 1999) reported the presence of an 'aniliid' in the lower Eocene of Kyrgyzstan. Reports of 'aniliids' from Messel (Keller and Schaal, 1992), repeated in Morlo et al. (2004), could not be confirmed (Smith, 2013), nor can the affinities of purported 'aniliids' from Geiseltal, Germany, figured by Krumbiegel et al. (1983: figs. 117-118).

***Anilioides nebraskensis* Holman, 1976**

First described on the basis of 12 trunk vertebrae from two localities in the upper Oligocene of the Great Plains, USA, and placed amongst basal alethinophidians (Holman, 1976). Another vertebra was later reported (Holman, 1977d). Intracolumnar variation unknown. Holman (2000) pointed out that to Auffenberg (1963), the author of the genus (typified by the Miocene *Anilioides minuatus*), 'Aniliidae' included not only *Cylindrophis*, *Anomochilus*, Uropeltidae and *Anilius* but also *Xenopeltis* and *Loxocemus*. The genus was originally distinguished principally by the presence of a keel on the dorsal surface of the zygosphene, which Auffenberg (1963) presumed was a continuation of the neural spine, and the upturned lateral edges of the zygosphene. Curiously, *A. nebraskensis* lacks the keeled zygosphene, and Holman (2000) considered its attribution to the genus questionable. Its relationships are unknown (Rage, 1984a; Holman, 2000).

***Anomalophis bolcensis* (Massalongo, 1859)**

Originally described as *Archaeophis bolcensis* on the basis of 3 sections of vertebral column (anterior, middle, and posterior) together with their associated ribs from the lower Eocene of Monte Bolca, Italy (Massalongo, 1859). No additional material reported. Intracolumnar variation not well documented. Genus monotypic. Diagnostic features include (Rage, 1984a): vertebrate elongate, interzygapophyseal constriction weak, ventral surface of centrum somewhat flattened, zygosphene thick, para- and diapophyses not distinct, neural spine low with long anterior keel, neural canal small, vertebra foramina not visible, ribs only weakly curved and without tubercular processes. Auffenberg (1959) considered it distinct from co-occurring *Archaeophis proavus* and transferred it to the new genus *Anomalophis* but did not comment on its relationships. Rage (1984a) considered it a 'colubroid' (probably equivalent to Colubroides here). Zaher et al. (2019) found support for such a placement in the neural spine, which is blade-like (uniformly thin) and invades the zygosphenal roof, but considered its relationships ambiguous.

***Archaeophis proavus* Massalongo, 1859**

Described on the basis of a skeleton with skull including skin impressions from the lower Eocene of Monte Bolca, Italy (Massalongo, 1859). No additional material reported. Diagnostic features (Janensch, 1906a; Rage, 1984a): moderate size (total length <1.0 m), skull pointed, teeth numerous, palatine(?) long, pterygoid(?) short, total vertebral count 565, articular processes very small, scales small and numerous, gastrosteges lacking. No known snake has so many vertebrae.

'*Archaeophis*' *turkmenicus* Tatarinov, 1963

First described on the basis of sections of vertebral columns and jaw fragments from the lower Eocene of Neotethyan Turkmenistan (Tatarinov, 1963). A skull was later reported (Tatarinov, 1988; see also Alifanov, 2012). Diagnostic features, mostly with respect to *A. proavus* (Rage, 1984a): skull not pointed, teeth less numerous, maxilla with ascending process, vertebrae well ossified, articular processes well developed, and pterapophyses present. The strong differences in skull form led Rage (1984a) to state it

pertains to a new genus. Accordingly, we only tentatively place it in the same genus with the Italian genotype, *A. proavus*.

Genus *Bavarioboa* Szyndlar and Schleich, 1993

Genus named for *Bavarioboa hermi* from a Miocene fissure fill in southern Germany (Szyndlar and Schleich, 1993). In addition to the species listed below, new Palaeogene material was reported for *Bavarioboa* sp. (Szyndlar and Rage, 2003; Rage and Szyndlar, 2005; Szyndlar and Hoşgör, 2012). The reader is referred to Szyndlar and Rage (2003) for a detailed list of diagnostic features. Some of the more distinctive features are: paracotylar foramina variably present, a thickening of the neural spine and hypapophysis in posterior trunk vertebrae, Meckelian groove delimited anteriorly by bone, dorsal pterygoid keel, and boa-like palatine-ptyerygoid articulation. Szyndlar and Rage (2003) regarded the many Oligocene and Miocene species of *Bavarioboa* as closely related and assigned the genus to 'Boinae'. In the classification of Pyron et al. (2014), their 'Boinae' corresponds to the families Sanziniidae, Candoiidae, and Boidae, which do not form a clade, including in the most recent, broad-scale study (Burbrink et al., 2020), although they remain part of Booidea. The pterygoid-ectopterygoid articulation was found by Georgalis and Smith (2020) to be a synapomorphy of Booidea sensu Pyron et al. (2014), so we follow Szyndlar and Rage (2003) and include *Bavarioboa* here as part of the booid radiation.

***Bavarioboa bachensis* Szyndlar and Rage, 2003**

Described on the basis of 8 trunk vertebrae from the middle Oligocene of Quercy, France (Szyndlar and Rage, 2003). No additional material reported. Intracolumnar variation poorly known. Diagnostic features with respect to other *Bavarioboa* (Szyndlar and Rage, 2003): posterior borders of neural arch straight in posterior view, prezygapophyses broad below their articulation, broader and flattened haemal keel, and stronger subcentral ridges.

***Bavarioboa crocheti* Szyndlar and Rage, 2003**

Described on the basis of about 860 vertebrae from the throughout the column as well as cranial elements (ptyerygoid, dentaries) from the upper Oligocene of two localities at Quercy, France (Szyndlar and Rage, 2003). No additional material reported. Intracolumnar variation well known. Diagnostic features with respect to other *Bavarioboa* (Szyndlar and Rage, 2003): haemal keel biconcave, median lobe of zygosphenon ventrally displaced, rounded anterodorsal corner of neural spine on mid-trunk vertebrae, variably thickened neural spine on mid-trunk vertebrae, and variably thicker zygosphenon.

***Bavarioboa herrlingensis* Szyndlar and Rage, 2003**

Described on the basis of 277 vertebrae from throughout the column as well as cranial elements (maxilla, dentaries) from the upper Oligocene of a fissure fill in southern Germany (Szyndlar and Rage, 2003). No additional material reported. Intracolumnar variation well known. Diagnostic features with respect to other *Bavarioboa* (Szyndlar and Rage, 2003): more vaulted neural arch, prezygapophyseal processes never visible in dorsal view, paradiapophyses triangular in lateral view, rounded anterodorsal corner of neural spine on mid-trunk vertebrae, variably thicker zygosphenon, prezygapophyses not inclined and only slightly elevated over floor of neural canal, and neural spines not thickened.

***Bavarioboa minuta* Szyndlar and Rage, 2003**

Initially called “boine D” by Szyndlar (1994). Described on the basis of 365 vertebrae from throughout the column as well as cranial elements (maxilla, tooth bone fragments) from the upper Oligocene of a fissure fill in southern Germany (Szyndlar and Rage, 2003). No additional material reported. Intracolumnar variation well known. Diagnostic features with respect to other *Bavarioboa* (Szyndlar and Rage, 2003): smaller size and neural spine not extending over zygosphene.

***Bavarioboa vaylatsae* Szyndlar and Rage, 2003**

Described on the basis of 42 trunk vertebrae from the middle Oligocene of Quercy, France (Szyndlar and Rage, 2003). No additional material has been reported. Intracolumnar variation was briefly considered. Diagnostic features with respect to other *Bavarioboa* (Szyndlar and Rage, 2003): three-lobed zygosphene, longer prezygapophyseal processes, and round haemal keel.

Genus *Boavus* Marsh, 1871

This taxon was established for several species from the Bridger Basin of Wyoming (Marsh, 1871). It has generally been considered a ‘boine’ (Rage, 1984a; Holman, 2000), which for said authors included also pythons, whereas McDowell (1975) entertained ‘trepidophiid’ affinities based on skull structure. Except perhaps for the strong neural spine, all vertebral features given by those authors as diagnostic of ‘boines’ are plesiomorphic. There is no phylogenetic support for a close relationship of all species of *Boavus* listed below, much less clear evidence for their higher taxonomic affinity. *Boavus* is best regarded as a form taxon for larger constrictors from the later Palaeogene of North America. Indeterminate material of *Boavus* sp. has also been reported (Galbreath, 1953; Holman, 1979; Sullivan and Holman, 1996; Holman, 2000).

***Boavus affinis* Brattstrom, 1955**

Described on the basis of 4 mid-trunk vertebrae from the middle Eocene of coastal California (Brattstrom, 1955). Numerous (24) additional vertebrae were later reported from the same area (Brattstrom, 1958). Intracolumnar variation unknown. The only illustration is an anterior view of the type specimen (Brattstrom, 1955: fig. 1A). Diagnostic features (Brattstrom, 1955): large size, with massive zygosphene, strong haemal keel and subcentral ridges, haemal keel continuous with condyle, neural canal triangular but depressed in cross-section, and paracotylar foramina present.

***Boavus brevis* Marsh, 1871**

Described on the basis of 3 trunk vertebrae from the middle Eocene of the Bridger Basin of Wyoming (Marsh, 1871), although only the type can be located (Gilmore, 1938). No new material reported. Intracolumnar variation unknown. Diagnostic features with respect to other *Boavus* (Gilmore, 1938; Holman, 2000): centrum short with low (=depressed?) neural arch, cotyle angularly and transversely oval, zygosphene only moderately thick with small median swelling, paracotylar foramina absent, and neural spine anteroposteriorly short.

***Boavus idelmani* Gilmore, 1938**

Described on the basis of a nearly complete skeleton from the middle Eocene of Fossil Lake, Wyoming (Gilmore, 1938). The type and only known specimen is lost, but a cast exists. No additional material reported. Diagnostic features (Holman, 2000: , after Gilmore 1938 and Rage 1984b): small size, about 227 precloacal vertebrae,

hypapophyses of anterior trunk vertebrae not long and compressed, pterygoid probably with ectopterygoid process, postorbital probably not reaching frontal, elongate frontals, triangular parietal table developed anteriorly, mid-sagittal crest present on parietal. It was referred to *Boavus* on the basis of overall similarity of the quadrate and mandible (Gilmore, 1938).

***Boavus occidentalis* Marsh, 1871**

The genotype species, described on the basis of 8 mid-trunk vertebrae from the middle Eocene of the Bridger Basin, Wyoming (Marsh, 1871). Additional material, including long strings of vertebrae and cranial elements (mandible, quadrate), reported from the type area (Gilmore, 1938), and compared to it from the lower Oligocene of the Great Plains (Sullivan and Holman, 1996). Intracolumnar variation known for the preloacal series (Gilmore, 1938). Diagnostic features (Rage, 1984a): trunk vertebrae with thick zygosphenes and sharp haemal keel, and quadrate moderately elongate with large dorsal portion.

Genus *Borealilysia* Head, 2021

Established by Head (2021), the type species being *Coniophis carinatus* Hecht, 1959. Head (2021) determined that it shares four apomorphies with *Anilius*: prezygapophyses elevated to just shorter than zygosphenes, neural spine with short anterior lamina running much of neural arch length, neural arch depressed, and weakly developed, medially emarginated haemal keel on mid- and posterior preloacal vertebrae. He consequently referred it to Aniliidae.

***Borealilysia carinata* (Hecht, 1959)**

First described (as *Coniophis carinatus*) on the basis of 1 trunk vertebra from the middle Eocene of the Bridger Basin, Wyoming, by Hecht (in McGrew et al., 1959), who simultaneously noted that 'several' more specimens were present in closely related localities. Intracolumnar variation not addressed, only potential ontogenetic variation. However, it is worth noting that Hecht described the species *Coniophis platycarinatus* from virtually the same localities, and this species has been regarded as representing the posterior trunk of *B. carinata* (Smith, 2013; Head, 2021). No new material reported.

***Borealilysia gunnelli* Head, 2021**

Described on the basis of 2 articulated trunk vertebrae from the middle Eocene of the Bridger Basin, Wyoming (Head, 2021). Diagnostic features with respect to *B. carinata* (Head, 2021): thicker, shorter prezygapophyses, higher angle of prezygapophyses, and smaller accessory ridges on roof of neural arch.

***Bransateryx vireti* Hoffstetter and Rage, 1972**

First described on the basis of several thousand vertebrae from throughout the column as well as cranial bones (maxillae, palatines, pterygoids, quadrate, dentaries) from the upper Oligocene of central France (Hoffstetter and Rage, 1972). Much additional Oligocene material has been reported (Szyndlar, 1994; Augé and Rage, 1995; Szyndlar and Rage, 2003; Rage and Szyndlar, 2005). Genus monotypic (cf. Szyndlar, 1987; see Szyndlar and Rage, 2003), so we note here that additional material was reported for or compared to *Bransateryx* sp. (Hoffstetter and Rage, 1972; Astruc et al., 2003). Diagnostic features with respect to 'erycines' (Rage, 1984a): posterior caudal vertebrae very short and tall with several complex, supernumerary processes and palatine with choanal process.

***Cadurceryx filholi* Hoffstetter and Rage, 1972**

First described on the basis of 9 vertebrae from the old Quercy collections, probably from the upper Eocene (Hoffstetter and Rage, 1972). Much additional material reported for or compared to the species from the middle to upper Eocene of Quercy and a few other areas of western Europe (Hoffstetter and Rage, 1972; Crochet et al., 1981; Rage, 1988a; 2013). We also note here that additional material has been reported for *Cadurceryx* sp. (Hoffstetter and Rage, 1972; Rage, 1978; Crochet et al., 1981). Diagnostic features of the genus (Rage, 1984a) at a time when it was monotypic (cf. Holman et al., 2006): caudal vertebrae very short with supernumerary processes, and supernumerary processes present also on some precloacal vertebrae. The latter feature is unusual and seen otherwise in North American *Pterygoboa* (Holman, 2000).

***Cadurceryx pearchi* Holman et al., 2006**

Described on the basis of 5 caudal vertebrae from the upper Eocene of Hordle Cliff, England (Holman et al., 2006). No new material reported. Intracolumnar variation unknown. Diagnostic features of caudal vertebrae with respect to *C. filholi* (Holman et al., 2006): cotyle larger than neural canal and knoblike tubercle present on prezygapophysis. The well-developed supernumerary processes on caudal vertebrae mark this species as an 'erycine', but it is unknown whether they extended into the precloacal area, as in *C. filholi*. It is remarkable, though not unheard of (Maul et al., 2015), for so many caudal vertebrae to be preserved without precloacal vertebrae.

***Cadurcobia insolita* Rage, 1978**

Described on the basis of about 180 vertebrae from the upper Eocene of Quercy, France (Rage, 1978). This species might correspond to Rage's 'Boid D' (J.-C. Rage, pers. comm. to KTS, 2010), as detailed under ∇ Constrictores *incertae sedis*. Additional material reported from other Quercy localities (Crochet et al., 1981) and compared to it from the middle Eocene (Rage and Augé, 2010). Intracolumnar variation described. Genus monotypic. Rage (1978) gave the unusual combination of a tall neural spine and (what he considered to be) a depressed ('surbaissé') neural arch as diagnostic of the species. In contrast, Holman et al. (2006) considered the neural arch to be 'moderately vaulted'. Rage (1978) noted similarities to *Geringophis vetus* (see below) and to some species of *Tropidophis* (see Bogert, 1968) but regarded the relationships of *C. insolita* as unresolved.

∇ Caenophidia *incertae sedis*, unnamed taxa

Indeterminate or unnamed caenophidians have been reported from the lower Eocene of France (Augé et al., 1997) and the middle Eocene of Pondaung, Myanmar (Head et al., 2005).

Genus *Calamagras* Cope, 1873

Calamagras is one of the most widely recognised fossil snake genera. In addition to the species listed below, *Calamagras* sp. has been reported from the Eocene of the North Sea Basin (Hecht and Hoffstetter, 1962) and the Isle of Wight and Hordle Cliff (Milner et al., 1982; Holman et al., 2006), and from the Oligocene of the Brule Formation (Holman, 1987; 2000), of peninsular Florida (Hayes, 2000), and of Mongolia (Böhme, 2007). As noted below, there is evidence that *C. weigeli* is related to Ungaliophiinae, a member of Charinidae (Pyron et al., 2014). One of those pieces of evidence is an elongation of the trunk vertebrae, so that the ratio between centrum length and neural

arch width (CL/NAW) is ≥ 1.1 , unlike in all other constrictors (except *Xenopeltis*). This elongation of the vertebrae is additionally present in the type specimens of *C. murivorus*, *C. angulatus*, and *C. truxalis*, suggesting these also may pertain to the total clade of Ungaliophiinae (Smith, 2013). To the extent that other species depart morphologically from Ungaliophiinae, it is expected that many are not properly referred to *Calamagras* (Smith, 2013). Two skeletons of *Calamagras* sp. co-preserved with a skull identified as *Ogmophis* sp. were also reported from a lower Oligocene locality (Breithaupt and Duvall, 1986; Breithaupt, 1997), and a skull of the former was illustrated (Breithaupt, 1997: fig. 2). These will surely play a key role in the determination of systematic affinity of some *Calamagras* spp.

***Calamagras angulatus* Cope, 1873**

First described on the basis of a single trunk vertebra from the lower Oligocene of the Cedar Creek area of Colorado (Cope, 1873). Additional material has been reported from throughout the Oligocene of the Great Plains (Holman, 1976; Sullivan and Holman, 1996; Maddox and Wall, 1998), and more still compared to it (Holman, 1977d). Intracolumnar variation unknown. The main diagnostic feature with respect to other *Calamagras* is apparently the depressed neural arch (cf. specific and generic diagnoses in Holman, 2000). The CL/NAW ratio is 1.1, potentially a synapomorphy of the species with Ungaliophiinae (Smith, 2013). Clearly this hypothesis must be tested by study of additional material from the type area.

'*Calamagras*' gallicus Rage, 1977

Described on the basis of 1 caudal (the holotype) and about 30 trunk vertebrae from various localities in lower Eocene of the Paris Basin (Rage, 1977). One of the referred trunk vertebrae was illustrated photographically by Schaal and Baszio (2004: fig. 2). Additional material reported from the lower Eocene of the Paris Basin (Augé et al., 1997). Diagnostic features (Rage, 1977): caudal vertebrae very short with small pterapophyses and a low thick neural spine. The caudal vertebrae indeed show apomorphies shared by 'erycines', in particular the accessory process (very weak though it may be), the proportions, and the loss of zygosphene-zygantral accessory articulations. The recognition of 'erycine' polyphyly means that these shared apomorphies are not synapomorphies of a clade, and it is consequently unknown whether the species is related to the New or Old World 'erycines'. Given the occurrence of *Rageryx schmidi* at Messel, it is entirely possible that this species is on the stem of Charinainae, but new material will be required to assess its relationships (Smith and Scanferla, 2021a).

***Calamagras murivorus* Cope, 1873**

This, the genotype species, was first described on the basis of 6 articulated trunk vertebrae from the lower Oligocene of the Cedar Creek area of Colorado (Cope, 1873). Additional material reported by Gilmore (1938). Intracolumnar variation unknown. Holman (2000) regarded this species as distinct but failed to provide a diagnosis apart from characters of the genus, of which *Calamagras murivorus* is the type species. The CL/NAW ratio is 1.1, potentially a synapomorphy of the species with Ungaliophiinae (Smith, 2013). Clearly this hypothesis must be tested by study of additional material from the type area. Note that Holman (2000) regarded both *C. truxalis* and *C. talpivorus* to be synonyms of *C. murivorus*, but Smith (2013) reported that the CL/NAW ratio of *C. talpivorus* is low (<1.0), like a more typical constrictor and unlike *C. murivorus*.

'*Calamagras*' *platyspondylus* Holman, 1976

First described (as *C. platyspondyla*) on the basis of 10 vertebrae from several upper Oligocene localities in the Great Plains (Holman, 1976). An additional vertebra reported from the upper Oligocene of Florida (Holman and Harrison, 2001). Intracolumnar variation unknown. The main diagnostic feature given by Holman (1976) was the broad haemal keel. A 'relatively wide, robust, well-differentiated haemal keel' was also given in the diagnosis of *C. weigeli* (Holman, 2000; see below). It may be noted that the CL/NAW ratio of the holotype of *C. platyspondylus* is about 0.96 (based on Holman, 1976: fig. 1B); it therefore appears to lack the apomorphic vertebral elongation of the total clade of Ungaliophiinae (see Smith, 2013). Note also that the species epithet is emended to conform to the masculine gender of the genus name.

'*Calamagras*' *primus* Hecht, 1959

First described on the basis of 1 trunk vertebra from the middle Eocene of the Bridger Basin of Wyoming (Rocky Mountains). Hecht (in McGrew et al., 1959) reported additional vertebrae from the type locality, apparently uncatalogued, but they remain undescribed. Vertebrae have been compared to this species from the San Juan Basin, New Mexico (Sullivan and Lucas, 1988). Diagnostic features (Hecht in McGrew et al., 1959): neural spine thin with reduced 'knob' (tip?), convex zygosphene and depressed cotyle. None of these features is clearly apomorphic. The CL/NAW ratio of the holotype shows that it is not elongate, unlike the genotype species (Smith, 2013).

'*Calamagras*' *turkestanicus* Danilov and Averianov, 1999

Described on the basis of about 50 trunk vertebrae from the lower Eocene Alay Formation (Averianov, 1997) of Neotethyan Kyrgyzstan (Danilov and Averianov, 1999). Intracolumnar variation briefly described. The vertebrae are short and wide; most noteworthy of the diagnostic features is the depression of the neural arch, even on anterior vertebrae (Danilov and Averianov, 1999). Beyond Constrictores, its relationships are unknown.

***Calamagras weigeli* Holman, 1972**

First described on the basis of 2 trunk vertebrae from the upper Eocene Cypress Hills of Saskatchewan (Holman, 1972). Many additional material and tentatively 2 cranial bones reported from the upper Eocene Medicine Pole Hills of North Dakota by Smith (2013), who described intracolumnar variation and estimated the proportion of caudal to trunk vertebrae as 0.14. Diagnostic features (Holman, 2000): haemal keel wide and robust, subcentral ridges moderate, neural spine short and thick, and neural arch vaulted. Smith (2013) noted in *C. weigeli* two synapomorphies of Ungaliophiinae among constrictors: elongate trunk vertebrae, with the CL/NAW ratio ≥ 1.1 (Rage, 2008; Smith, 2013), and haemapophyses lacking on all caudal vertebrae (Szyndlar and Rage, 2003; Smith, 2013). Smith and Scanferla (2021a) found unambiguous phylogenetic support for a close relationship between *C. weigeli* and Ungaliophiinae, although whether the species is recovered in the crown or on the stem depended on phylogenetic methods. Where caudal vertebrae are known in other Palaeogene species related to Ungaliophiinae – viz. *Messelophis variatus* and *Rieppelophis ermannorum* below – these retain haemapophyses, indicating that *C. weigeli* is closer to the crown (if not in it).

***Cheilophis huerfanoensis* Gilmore, 1938**

Described on the basis of a series of >130 trunk vertebrae, presumed to represent a single individual from the Huerfano Formation of the Rocky Mountains (Gilmore, 1938; Rage, 1984b). Rage (1984b) conducted additional preparation and was able to isolate some of the vertebrae and also revealed skull bones (maxilla, compound bone). Genus monotypic. Some reports of material from elsewhere were erroneous (Holman, 2000); other material was reported from the Palaeocene of the San Juan Basin (Sullivan and Lucas, 1988) and East Coast (Cook and Ramsdell, 1991). The diagnosis includes some rather widespread features but Rage (1984b) emphasised the posterior extension of the parapophysis. Rage (1984b) regarded this species as a 'boine', but his concept of Boinae also included pythons; hence, we include it as Constrictores *incertae sedis*. The association of vertebral and cranial material makes this species potentially important.

***Chubutophis grandis* Albino, 1993**

Described on the basis of 1 trunk vertebra from the San Jorge Basin, Argentina (Albino, 1993). No new material reported. Intracolumnar variation unknown. Genus monotypic. Diagnostic features (Albino, 1993): very large size, centrum very short, neural spine tall and anteroposteriorly short, zygosphenes thick, zygapophyseal articulations inclined, neural canal triangular and small, haemal keel flattened and posteriorly prominent, cotyle and condyle depressed, paracotylar foramina present, paradiapophyses robust and elevated. Albino (1993) assigned it to 'Boinae' based on the small prezygapophyseal processes, tall neural arch and strong neural spine. This assignment corresponds to Constrictores *incertae sedis* in the present classification. This is a large constrictor, with a centrum length exceeding 17 mm.

'*Coluber*' *cadurci* Rage, 1974

Described on the basis of many ('plusieurs') vertebrae from throughout the column from lower Oligocene localities of Quercy, France (Rage, 1974). Additional material reported from the lower and upper Oligocene of Quercy (Augé and Rage, 1995; Sigé et al., 1998; Rage and Augé, 2015). Diagnostic features (Rage, 1974): hypapophysis lacking on mid- and posterior trunk vertebrae (potentially apomorphic: Smith, 2013), tall narrow haemal keel on mid-dorsal vertebrae, neural arch depressed ('surbaissé'), long prezygapophyseal processes, and long and low neural spine. The diagnosis is inadequate, as it describes a morphology common to many colubrids (sensu Zaher et al., 2019). There is a widespread assumption that the species does not represent *Coluber*, at least in the modern conception of that genus, but no positive evidence has presented to support that; the generic partitioning of *Coluber* with all its current species distributed solely in the New World, favour such an assumption. Head et al. (2016) regarded this as the earliest record of the total clade of Colubroidea + Elapoidea.

▽Colubriiformes *incertae sedis*, unnamed taxa

Indeterminate or unnamed members of the total clade of Colubriiformes (sensu Zaher et al., 2009), which together with Xenodermidae form the inclusive clade Colubroidea – mostly described as 'colubrids' or 'colubroids' by the authors in question – have been reported from the upper Eocene of the Medicine Pole Hills, USA (Smith, 2013), the upper Eocene of the Krabi Basin, Thailand (Rage et al., 1992), the lower or middle Eocene of Algeria (Rage et al., 2021), the lower Oligocene of Oman (Thomas et al. 1991), the lower Oligocene of a fissure fill in peninsular Florida (Holman and Harrison, 2001; up to 3 taxa, none of them illustrated), an upper Oligocene fissure fill in southern Germany (Böhme, 2008; 2 taxa), the upper Oligocene of the Sperrgebiet, Namibia (originally regarded as middle Eocene; Rage et al., 2013), and the upper Oligocene of

Rukwa Rift Basin of Tanzania (McCartney et al., 2014; McCartney et al., 2021; 6 taxa). Three of these records (∇ Colubroidea from the Medicine Pole Hills and ∇ Elapidae and Lamprophiidae from the Rukwa Rift Basin) are treated as separate entries.

∇ Colubroidea *incertae sedis*

Described (as ‘Colubrid Indet.’) on the basis of 4 trunk and 4 postcloacal vertebrae from the Medicine Pole Hills, Great Plains, USA (Smith, 2013). No additional material reported. Intracolumnar variation described from throughout the column. Main features: elongate shape (ratio of centrum length to neural arch width 1.2–1.3), elongate prezygapophyseal processes, sharp and uniformly narrow haemal keel in mid- and posterior trunk (Smith, 2013; Zaher et al., 2019). The absence of hypapophyses in the mid- and posterior trunk of Colubroidea is potentially apomorphic within Colubrimorpha (Smith, 2013) but occurs also in another colubrid lineage, i.e., Pareidae (Zaher et al., 2019). Smith (2013) noted overall similarity to the ‘racer’ clade of North American colubroids. The main features are not clearly apomorphic, but as they occur in combination only in Colubroidea, Zaher et al. (2019) regarded this unnamed taxon as the oldest known record of the total clade of Colubroidea.

***Conantophis alachuaensis* Holman and Harrison, 2000**

Described on the basis of 4 vertebrae from an Oligocene fissure fill in peninsular Florida (Holman and Harrison, 2000). No additional material reported. Genus monotypic. Intracolumnar briefly described. Main diagnostic features (Holman and Harrison, 2000): small, neural arch highly depressed, relatively large zygapophyseal articulations, concave zygosphenal roof, and thick, salient, ventrally bowed haemal keel. Based on certain similarities to *Tropidophis*, and Holman and Harrison (2000) tentatively suggested that the closest living relatives of *Conantophis* might lie with that taxon. As clear apomorphic features were not adduced in support of this suggestion, we consider it to be Constrictores *incertae sedis*.

***Coniophis* sp.**

Coniophis Marsh, 1892 was the earliest named fossil ‘anilioid’. Given that many of its features are plesiomorphic, there is widespread recognition that it is probably a wastebasket taxon circumscribing any number of relatively primitive, fossorial snakes (Sanders et al., 2010). Notably, the association of dentigerous cranial elements with the type species, the Cretaceous *Coniophis precedens*, led Longrich et al. (2012) to consider it a stem snake (see also Hecht, 1982).

Fossils have been reported for or compared to *Coniophis* from numerous Palaeogene localities on different continents. In North America these range from the middle Palaeocene to upper Eocene (Estes, 1976; Holman, 1979; Smith, 2013), including an unconfirmed report of a vertebra from the Huerfano Formation (Hecht in McGrew et al., 1959: , p. 139). [Note that *Coniophis carinata* Hecht, 1959 has been transferred to the new genus *Borealilysia* (Head, 2021); see above.] In Europe these range from the middle to upper Eocene (Crochet et al., 1981; Rage, 1988a; Rage and Augé, 2010). In Africa these are two localities from the upper Paleocene and lower Eocene of Morocco (Augé and Rage, 2006). In South America these are two localities from the Palaeocene of Peru (Rage, 1981; 1991) and Itaboraí (Rage, 1998).

∇ Constrictores *incertae sedis*

In addition to the named taxa treated elsewhere, large numbers of vertebrae have been referred to taxa that must be considered as indeterminate members of the total

clade of Constrictores: from the Palaeocene through Eocene of South America (Rage, 1991; Albino, 1993; Rage, 2001; Bloch et al., 2008; Albino, 2012), from the entire Palaeogene of Europe (see Supplementary Appendix 4.S2), from the Palaeocene, Eocene and upper Oligocene of Afro-Arabia (Thomas et al., 1991; Augé and Rage, 2006; McCartney et al., 2014; McCartney and Seiffert, 2016; Rage et al., 2021), and the Eocene of Asia (Rage, 1987; Rage et al., 1992; Rage et al., 2003; Rage et al., 2008; Smith et al., 2016). Most notable of the South American occurrences is a vertebra tentatively referred to the genus *Boa* from the upper Eocene of Argentina (Albino, 1993).

Most notable of the European occurrences are the 'lettered boids' (Boid C, D, etc.) from the Phosphorites du Quercy indicated by Bonis et al. (1973) and Crochet et al. (1981) and subsequently appearing elsewhere (e.g., Rage, 1984c). There is no certain relationship between the 'lettered' taxa and some taxa later described, so these must be considered as Constrictores indet.. Nevertheless, the following correspondences between 'lettered' and actual taxa were given by J.-C. Rage (pers. comm. to KTS, 2010):

'Boidae M = *Platyspondylia sudrei* from Le Bretou

Boidae K = Boidae K from Lissieu

Boidae J = cf. *Palaeopython cadurcensis* from Le Bretou

Boidae D = devrait (?) être *Cadurcoboia insolita* d'après me etiquette de Escamps A

Boidae E = *Phosphoroboa filholii*, d'après me etiquette de Escamps A'

In addition, 'Boidae I' was subsequently formally named as *Bavarioboa crocheti* Szyndlar and Rage (2003). Further work in Quercy collections and perhaps archival study of Rage's notes will be important to certify his intentions.

Beyond the many vertebrae, there is also cranial material of an unnamed constrictor from the late Eocene of the Fayum, Egypt (McCartney and Seiffert, 2016). Indeterminate cranial material of constrictors is also known from Europe, originating from the Phosphorites du Quercy (i.e., one of the syntypes of *Elaphis boulei*, a paralectotype of *Palaelaphis antiquus*, the holotype of *Palaelaphis robustus*, the paralectotypes of *Paleryx cayluxi*, and a paralectotype of *Tachyophis nitidus*) and Geiseltal (Szyndlar and Rage, 2003; Georgalis et al., 2021c). Even mummified specimens of indeterminate constrictors, comprising scales and vertebrae, are known from the Phosphorites du Quercy, e.g., the lectotype and certain paralectotypes of *Rageophis lafonti* (Filhol, 1877; Szyndlar and Rage, 2003).

***Coprophis dakotaensis* Parris and Holman, 1978**

Described on the basis of 4 poorly preserved vertebrae, apparently from one individual, in a mammalian coprolite from the lower Oligocene of South Dakota (Great Plains). No additional material reported. Genus monotypic. The higher taxonomic affinity of this species was considered uncertain (Rage, 1984a; Holman, 2000), but we follow Sullivan and Holman (1996) in considering it a constrictor. Parris and Holman (1978) listed a combination of eight features as diagnostic of the species. We note that these features – and also the vertebral elongation (*Coprophis dakotaensis* has a CL/NAW ratio of 1.15; KTS pers. obs.) – are common in species of *Calamagras* also from the Brule Formation, and revision might reveal *Coprophis* to be a junior synonym of *Calamagras*.

***Corallus priscus* Rage, 2001**

Described on the basis of 38 trunk vertebrae from the lower Eocene fissure fills of São José de Itaboraí, Brazil (Rage, 2001). An additional 15 trunk vertebrae from the same area were compared to *Corallus* (Rage, 2001). Intracolumnar variation well known. Diagnostic features with respect to extant *Corallus* spp. (Rage, 2001): regularly curved interzygapophyseal constriction, neural arch taller, posteromedian notch in

neural arch shallower, and variable presence of paracotylar foramina. Rage (2001) allied it with *Corallus* on the basis of three characters: zygapophyseal articulations horizontal, neural arch vaulted and neural spine high. Head (2015) concurred.

***Crythosaurus mongoliensis* Gilmore, 1943**

Described on the basis of a partial skull from the lower Oligocene of Hsanda Gol, Mongolia (Gilmore, 1943). No new material reported. Genus monotypic. Although Gilmore (1943) gave a diagnosis, he assumed it was an amphisbaenian, so we do not repeat the diagnosis here. McDowell (1979) and Estes (1983) both concluded that it is an 'erycine' booid, while Wallach et al. (2014) went further, recombining it into the extant genus *Eryx* (as *Eryx mongoliensis*). We agree with its similarities to "erycines" but keep it in its own genus.

***Dawsonophis wyomingensis* Holman, 1979**

Described on the basis of 2 fragmentary vertebrae from the middle Eocene of the Wind River Basin (between Bridger and Bighorn basins). Genus monotypic. Diagnostic features (Holman, 1979; 2000): 'thin' flat zygosphene, 'long' neural arch, the shape of the haemal keel and the 'moderately vaulted' (Holman, 1979: 104) or 'vaulted' (Holman, 2000: 38) neural arch. None of these features is clearly apomorphic. Its relationships to other constrictors are unknown (Holman, 1979; Rage, 1984a). However, Holman (2000) even speculated that it could represent a new 'subfamily' (probably equivalent to family today).

Genus *Dunnophis* Hecht, 1959

Established for *Dunnophis microechinus* Hecht, 1959. Additional material was referred or compared to *Dunnophis* sp. from the Palaeocene of Montana (Estes, 1976: , questionably), the middle Eocene of the Wind River Basin, Wyoming (Holman, 1979), the lower, middle and upper Eocene of western Europe (Hecht and Hoffstetter, 1962; Rage and Ford, 1980; Milner et al., 1982; Russell et al., 1982; Augé et al., 1997; Duffaud and Rage, 1997), and the Palaeocene of Morocco (Augé and Rage, 2006). Except for the complete absence of prezygapophyseal processes, the generic diagnosis (Rage, 1984a) comprises plesiomorphies or apomorphies shared with other taxa, so there is little phylogenetic evidence that the three named species are closely related. Hecht drew the attention of Bogert (1968) to this genus, and the latter author noted the similarities of proportion to the extant ungaliophiine *Exiliboa placata*. Indeed, the elongate character of the vertebrae is consistent with attribution of *Dunnophis* to the total clade of Ungaliophiinae, and if they are related then species of *Dunnophis*, possessing haemapophyses (where caudal vertebrae are known), would be outside the crown and basal to *Calamagras weigeli* (Smith, 2013). We feel that the present evidence is too thin and regard these species as *Constrictores incertae sedis*.

***Dunnophis cadurcensis* Rage, 1974**

Described on the basis of many ('plusieurs') vertebrae, including caudals, from the upper Eocene of Quercy, France (Rage, 1974). Intracolumnar variation briefly described. Additional material reported for or compared to the species from the middle and upper Eocene of France (Rage, 1978; Crochet et al., 1981; Rage, 1988a; Rage and Augé, 2010). Diagnostic features with respect to other species (Rage, 1984a): median lobe of zygosphene narrow, subcentral grooves not reaching condyle (questioned by Augé et al., 1997), and neural spine anteroposteriorly long (reaching zygosphene).

***Dunnophis matronensis* Rage, 1973**

Described on the basis of numerous ('nombreuses') vertebrae from the lower Eocene of the Paris Basin (Rage, 1973). Intracolumnar variation unknown. Additional material reported from the lower to middle Eocene of western Europe (Augé et al., 1997; Nel et al., 1999; Rage and Augé, 2003; 2010). Diagnostic features with respect to other species (Rage, 1984a): median lobe of zygosphene wide and rounded, subcentral grooves only on anterior half of centrum (questioned by Augé et al., 1997), and neural spine low and anteroposteriorly short with anterior keel.

***Dunnophis microechinus* Hecht, 1959**

The genotype, described on the basis of 5 vertebrae from the middle Eocene of the Bridger Basin, Wyoming, by Hecht (in McGrew et al., 1959), who also stated that further material is present in Marsh's collections at the Yale Peabody Museum. No additional material reported. Intracolumnar variation unknown. Diagnostic features with respect to other species (Rage, 1984a): median lobe of zygosphene narrow, subcentral grooves running from cotyle to condyle (questioned by Augé et al., 1997), neural spine low and anteroposteriorly short and without anterior keel. We further note that Hecht (in McGrew, 1959) used two different spellings for the species epithet: "*microechinis*" and "*microechinus*". We here choose the latter spelling as the valid one, judging that it is more grammatically correct, although we acknowledge that the former has had a relatively more common appearance in the literature.

▽*Elapidae incertae sedis*

Two taxa (Morphotypes A and B) were described (but not named) from the upper Oligocene Rukwa Rift Basin of Tanzania, each on the basis of 1 posterior trunk vertebra (McCartney et al., 2014). Intracolumnar variation unknown. No additional material reported. In addition to more general colubriiform characters, Morphotype A has the following main features: low and thick hypapophysis with flattened, laterally expanded ventral edge, and postzygapophyseal foramen lacking (McCartney et al., 2014). McCartney et al. (2014) noted similarity of the hypapophysis to some *Naja*. Zaher et al. (2019) regarded Morphotype A as the oldest known representative of the total clade of Elapidae.

Genus *Eoanilius* Rage, 1974

Established by Rage (1974) for *E. europae*. Szyndlar (1994) described a second species, *E. oligocenicus*, that is extremely similar to the genotype. Apomorphic evidence has not been presented for the monophyly of the genus, but we have no reason to doubt the two are closely related. McDowell (1987) and Szyndlar (1994) saw its relationships specifically with *Anilius* rather than Uropeltidae or Cyliodrophiidae, in particular because of the neural spine, which is rudimentary but present (presumably a plesiomorphic feature). Except for the absence of haemapophyses in the caudal vertebrae, these elements lack apomorphic features of 'anilioids' (Head, 2021). Until a revision has been accomplished, we regard *Eoanilius* spp. as Alethinophidia *incertae sedis*.

***Eoanilius europae* Rage, 1974**

First described on the basis of about 40 vertebrae and a quadrate from the upper Eocene of Quercy (Rage, 1974). Intracolumnar variation briefly considered. Additional

material reported from the upper Eocene of Quercy (Crochet et al., 1981) and questionably from the upper Eocene of Hordle Cliff, England (Milner et al., 1982); the latter record is considered uncertain as it was simply mentioned without any kind of figure or description (Rage and Augé, 1993). Diagnostic features with respect to extant *Anilius* and *Cylindrophis* (Rage, 1974): zygosphene wider than condyle throughout column and cotyle circular throughout column; additionally, a haemal keel is present in the posterior trunk, and haemapophyses were absent on the single caudal vertebra (see also *E. oligocenicus* below). Smith (2013) raised the prospect that the holotype and referred vertebrae could pertain to a constrictor and the referred quadrate to an 'anilioid'; Head (2021) thought it possible that it is a fossorial constrictor.

***Eoanilius oligocenicus* Szyndlar, 1994**

First described on the basis of 130 vertebrae from throughout the column from four Oligocene fissure fill localities in southern Germany (Szyndlar, 1994). Intracolumnar variation briefly considered. Additional material reported from the upper Oligocene of southern Germany (Böhme, 2008) and compared to the species ('aff.', 'cf.') from the lower Oligocene of Quercy (Sigé et al., 1998; Rage and Augé, 2015) as well as the Miocene (e.g., Venczel and Sanchíz, 2006; Syromyatnikova et al., 2019), demonstrating an extensive range. Diagnostic features with respect to *E. europae* (Szyndlar, 1994; Rage and Augé, 2015): stronger neural spine with well-defined anterior border, conspicuous haemal keel, three-lobed zygosphene, and larger paradiapophyses.

Genus *Eoconstrictor* Scanferla and Smith, 2020a

The genus was established by Scanferla and Smith (2020a) to accommodate *Palaeopython fischeri* from Messel. The phylogenetic analysis conducted by the same authors recovered *Eoconstrictor* to lie on the stem of Boidae (sensu Pyron et al. 2014). Subsequently, the Geiseltal taxon *Paleryx spinifer* was referred to the same genus by Georgalis et al. (2021c).

***Eoconstrictor fischeri* (Schaal, 2004)**

First described (as *Palaeopython fischeri*) on the basis of 7 articulated vertebrae (the holotype, in two sections) and 10 partial or complete skeletons from the lower-middle Eocene locality of Messel, Germany (Schaal, 2004). New skeletons reported from the type locality (Smith and Scanferla, 2016), and vertebrae compared to it from the middle to upper Eocene Dielsdorf, Switzerland (Georgalis and Scheyer, 2019) and from Geiseltal (Georgalis et al., 2021c). Georgalis et al. (2021c) described intracolumnar variation in vertebrae from the type locality and provide an updated diagnosis including vertebral characters and the mostly skull characters established by Scanferla and Smith (2020a). Scanferla and Smith (2020a) determined that the species is not closely related to *Palaeopython* and placed it in the new genus *Eoconstrictor*. Their phylogenetic analyses found it to be related to Neotropical boas, Boidae sensu Pyron et al. (2014).

***Eoconstrictor spinifer* (Barnes, 1927)**

Described from the Eocene of Geiseltal (Barnes, 1927). The type material was known to include some cranial elements and vertebrae. Georgalis et al. (2021c) restudied that material, discovered that it contained additional cranial elements (basioccipital, prootic, parietal, pterygoid, maxilla) and anterior trunk vertebrae and that it probably represents a single individual. Its relationships were recently clarified by Georgalis et al. (2021c), who reassessed its generic placement and recombined it into *Eoconstrictor*.

***Falseryx neervelpensis* Szyndlar et al., 2008**

Described on the basis of 87 vertebrae from throughout the column from the lower Oligocene of Belgium (Szyndlar et al., 2008). Intracolumnar variation well known. No new material reported, although we note that material is referred to *Falseryx* sp. from the upper Oligocene of Anatolia (Georgalis et al., 2021a). Diagnostic features with respect to the Neogene (genotype) species, *Falseryx petersbuchi* (Szyndlar et al., 2008): trunk vertebrae with longer centra, shallower interzygapophyseal constriction, deeper median notch in neural arch, lower and thicker neural spine, median lobe of zygosphene small or absent, larger tubercles on prezygapophyseal buttresses, smaller and higher paradiapophyses, larger vertebral foramina, and cloacal and postcloacal vertebrae with smaller hypapophyses. Szyndlar et al. (2008) referred the species to 'Tropidophiidae' (a concept embracing Ungaliophiinae and Tropidophiidae s.s.), noting that it displays similarity to both extant clades (trunk vertebrae more similar to Ungaliophiinae, caudal vertebrae more similar to Tropidophiidae s.s.). Smith (2013) and Syromyatnikova et al. (2019) also reported that vertebral proportions are apparently derived as in Ungaliophiinae. Given these contradictory data, we consider the species as *Alethinophidia incertae sedis*.

***Floridaophis auffenbergi* Holman, 1999**

Described on the basis of 1 trunk vertebra from a lower Oligocene fissure fill in peninsular Florida (Holman, 1999). No additional material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Holman, 1999): vertebra wider than long, neural arch vaulted, zygosphene sharply convex in dorsal view, neural spine taller anteriorly than posteriorly, haemal keel only moderately wide and tapering posteriorly, and epizygapophyseal spines absent. Holman (1999) regarded it as a 'colubrid' (roughly equivalent to Colubriiformes here) because of the lightly built structure, long and thin neural spine, well-developed prezygapophyseal processes, and strong division of para- and diapophyses.

Genus *Geringophis* Holman, 1976

Established for *G. depressus* from the upper Oligocene. Diagnostic features with respect to 'erycines', with which it was considered to be allied (Holman, 2000): very small size, vertebrae wider than long with flaring postzygapophyses, depressed neural arch, long and tall neural spine, and distinct haemal keel. Material of *Geringophis* sp. was reported from the Oligocene of peninsular Florida (Hayes, 2000; Holman and Harrison, 2001). Holman (2000) regarded it as an 'erycine', probably on account of size and the depressed neural arch (the only feature in the subfamily diagnosis that could be scored for the known material), but clear apomorphic evidence is lacking. The genus is supposed to have survived into the Neogene, represented by another species, *Geringophis yatkolai* (Holman, 1977c, 2000).

***Geringophis depressus* Holman, 1976**

This is the type species (Holman, 1976) and the youngest of the Palaeogene species attributed to the *Geringophis*. Described on the basis of 3 trunk vertebrae from the upper Oligocene of the Great Plains. Another vertebra reported from the same region (Holman, 1977d). Holman (2000) gave diagnostic features that are mostly widespread amongst constrictors, but the combination of a very depressed neural arch and a long tall neural spine (with posterior tubercle) is fairly unique.

***Geringophis robustus* Holman and Harrison, 2001**

Described on the basis of 3 trunk vertebrae from the I-75 locality, an Oligocene fissure-fill locality from peninsular Florida (Holman and Harrison, 2001). No new material of it has been reported. Diagnostic features with respect to congeners (Holman and Harrison, 2001): overall 'robustness' and thick neural spine.

***Geringophis vetus* Holman, 1982a**

Described on the basis of 1 trunk vertebra from the lower Oligocene of the Great Plains (Nebraska). Additional material has since been reported from the same region (Sullivan and Holman, 1996; Maddox and Wall, 1998). Diagnostic features with respect to congeners (Holman, 1982b; 2000): (slightly) longer neural spine without posterior tubercle and minor features of the centrum.

***Gigantophis garstini* Andrews, 1901**

This large madtsoiid was described on the basis of a large but unknown number of vertebrae, including an articulated section of about 20, and a posterior compound bone fragment (which was later considered only tentatively referable; Andrews, 1906) from the upper Eocene of the Fayum, Egypt (Andrews, 1901). Rio and Mannion (2017) estimated a total length of up to 6.9 m. Intracolumnar variation was addressed by Rio and Mannion (2017). Since then further material from the Fayum, including skull bones (Andrews, 1906; McCartney and Seiffert, 2016) has been described as well as material from the middle Eocene of Dor al Talha, Libya (Hoffstetter, 1961). Rage et al. (2014) also identified *Gigantophis* sp. from the Palaeocene of the 'southern cluster' in Pakistan, but the generic identity was questioned by Rio and Mannion (2017), who considered the genus to be restricted to Africa and monotypic. Diagnostic features with respect to other Madtsoiidae (Rio and Mannion, 2017): exceptionally large size, broad haemal keel with rhombic terminus in mid-trunk vertebrae, weak subcentral ridges, low neural spine, and (in posterior trunk vertebrae) an angled centrum and depressed neural canal. According to Vasile et al. (2013) the species is the sister to *Yurlunggur camfieldensis* from the Miocene of Australia (Scanlon, 1992), whereas Rio and Mannion (2017) could not resolve its close relations.

***Goinophis minusculus* Holman, 1976**

Described on the basis of 1 partial trunk vertebra from the upper Oligocene of the Great Plains (Holman, 1976). An additional vertebra from the same region was later compared to it (Holman, 1977d). Genus monotypic. The species is reportedly characterised by a unique combination of lizard-like (triangular centrum, undivided paradiapophyses = synapophyses) and snakelike features, especially of the zygosphenes (Holman, 1976; 2000). Rage (1984a) regarded the combination as so peculiar that he considered it possible that *Goinophis minusculus* is what would today be called a stem snake.

***Headonophis harrisoni* Holman, 1993**

Described on the basis of 1 trunk vertebra from the upper Eocene of the Isle of Wight (Holman, 1993). No additional material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Holman, 1993): zygapophyses narrow and anteroposteriorly oriented, prezygapophyseal processes absent, synapophyses undivided, paracotylar foramina present in fossae, neural arch moderately flattened, and haemal keel massive. Holman (1993) regarded the neural spine as 'long', but we concur with Rage et al. (2008) that it appears anteroposteriorly short, unlike in Colubriiformes.

Holman (1993) noted similarities to *Anomalophis* and Russellophiidae. In view of these comparisons, we feel that assignment only to ∇ Caenophidia *incertae sedis* is justified.

***Hechtophis austrinus* Rage, 2001**

Described on the basis of 72 trunk vertebrae from the lower Eocene fissure fills of São José de Itaboraí, Brazil (Rage, 2001). Intracolumnar variation well known. No new material has since been reported, although 35 additional vertebrae from Itaboraí were compared to the species. Genus monotypic. Diagnostic features (Rage, 2001): ‘deep’ interzygapophyseal constriction, laterally directed zygapophyses, neural arch neither vaulted nor depressed, and paracotylar foramina. None of these features is clearly apomorphic; even paracotylar foramina are widespread in Caenophidia and fossil Simoliophiidae and Madtsoiidae as well as some clades of Booidea and therefore are of uncertain polarity (Rage, 2001). Rage (2001) considered the species to be related to ‘erycines’ because he thought it was close to *Lichanura*; he did not provide apomorphic evidence to support that assertion. Especially relevant would be evidence from caudal vertebrae (Szyndlar and Rage, 2003; Smith, 2013), which were not identified.

Genus *Helagras* Cope, 1883a

Established for *H. prisciformis* by Cope (1883b). Holman (1983) described a second species, *H. orellanensis*, which he referred to the same genus on account of having a ‘thick tuberous neural spine entirely confined to the posterior part of the neural arch’ (Holman, 2000: 74), a diagnostic feature taken from Gilmore (1938). A tuberous neural spine is potentially synapomorphic.

***Helagras orellanensis* Holman, 1983**

Described on the basis of 1 isolated and 2 articulated trunk vertebrae from the lower Oligocene of the Great Plains (Holman, 1983). No additional material reported; intracolumnar variation unknown. Diagnostic features with respect to the genotype species (Holman, 1983): taller neural spine and slightly depressed cotyle and condyle. Note that the paratype shows a strong haemal keel, unlike the holotype, contradicting one of the diagnostic features. Holman (1983) regarded the species as ‘Henophidia’ *incertae sedis* and then later as an ‘erycine’ (Holman, 2000). No apomorphic features have been adduced in support of ‘erycine’ affinities.

***Helagras prisciformis* Cope, 1883a**

This is the type species and the older of the two referred to *Helagras*. First described on the basis of 2 articulated trunk vertebrae from the Palaeocene of the San Juan Basin, New Mexico (Cope, 1883b). Well over 200 additional vertebrae were later reported from the same region (Gilmore, 1938), so although intracolumnar variation is unknown it should be attainable. The most distinctive features were those Cope (1883b) gave for the genus, namely an opening of the zygantral roof to expose the lateral edges of the zygosphene. Gilmore (1938), however, showed that this is an artefact (possibly the result of corrosion, as in large constrictor vertebrae from Geiseltal; Georgalis et al., 2021c). This leaves the species poorly diagnosed (Rage, 1984a), despite the abundant referred material. Holman (1983) regarded the species as ‘Henophidia’ *incertae sedis* and then later, like Rage (1984a), as an erycine (Holman, 2000). No apomorphic features have been adduced in support of ‘erycine’ affinities.

***Hoffstetterella brasiliensis* Rage, 1998**

Described on the basis of 8 vertebrae from the lower Eocene fissure fills of São José de Itaboraí, Brazil, by Rage (1998), who also compared additional material to it. Intracolumnar variation well known. No additional material reported. Genus is monotypic. Diagnostic features with respect to other ‘anilioids’ (Rage, 1998): neural spine more prominent, posterior notch in neural arch deeper, a posteromedial extension of the diapophysis, commonly slitlike subcentral foramina, and small subcotylar tubercles. Rage (1998) allowed that the neural spine and posterior notch of the neural arch were more reminiscent of macrostomatan snakes (see also Head, 2021), and for this reason we included as *Alethinophidia incertae sedis*.

***Hordleophis balconae* Holman, 1996**

Described on the basis of 4 trunk vertebrae from the upper Eocene of southern England (Holman, 1996). No additional material reported; intracolumnar variation unknown. Genus monotypic. The diagnosis is inadequate. Holman (1996) gave the following features as particularly important for systematic assignment to ‘Boinae’: neural arch not depressed and without accessory processes, prezygapophyseal processes small, and neural spine well developed. These features are not clearly apomorphic and do not appear to be fully adequate for systematic assignment. Pending revision, we regard it as *Constrictores incertae sedis*.

***Huberophis georgiensis* Holman, 1977c**

Described on the basis of 1 posterior trunk vertebra from the middle Eocene of the East Coast, USA (Holman, 1977a). No additional material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Holman, 1977a): general proportions, low and short neural spine, prominent subcentral ridges and grooves, and prezygapophyseal processes absent. The neural spine and centrum features are positionally variable and indicate the holotype pertains to the posterior trunk, as Rage (1984a) recognised. It is conceivable that the apparent absence of prezygapophyseal processes is artifactual, as these are commonly eroded, especially when small. In general proportions the species is similar to referred posterior trunk vertebrae of *Ogmophis compactus* (Smith, 2013: fig. 10K-O). Holman (2000) speculated that the species might be related to ‘*Calamagras*’.

***Itaboraiophis depressus* Rage, 2008**

Described on the basis of 10 trunk vertebrae from the lower Eocene fissure fills of São José de Itaboraí, Brazil (Rage, 2008). No additional material reported; intracolumnar variation well known. Main diagnostic features (Rage, 2008): parazygosphenal foramina present, tall neural spine, neural arch ‘strongly depressed’ and hypapophyses or deep haemal keels absent on posterior trunk vertebrae. Rage (2008) regarded the phylogenetic relationships of this snake to be unknown beyond *Constrictores*.

***Kataria anisodonta* Scanferla et al., 2013**

Described on the basis of a partial skull from the Palaeocene of Tiupampa, Bolivia (Scanferla et al., 2013). No additional material reported. Genus monotypic. As a skull-based taxon, comparison with most other fossil snakes is impossible. Derived diagnostic features (Scanferla et al., 2013): elongate vomer with reduced contribution to vomeronasal fenestra, a single foramen piercing the cavity of Jacobson’s organ, 21 maxillary teeth with a diastema separating the ultimate tooth from the others, ectopterygoid with ventral articulation on the palatine, a broad choanal process, and frontal and parietal contributions to the optic fenestra. Using a morphological data set,

Scanferla et al. (2013) inferred this species to be a 'derived macrostomatan', a clade that included Bolyeriidae, Tropicophiidae and Caenophidia; the position did not change when a molecular topology was enforced. Hsiang et al. (2015) inferred a similar phylogenetic position in a pure morphological analysis, but in a combined Bayesian analysis *K. anisodonta* shifted to the stem of Tropicophiidae (which now is the extant sister taxon to *Anilius*). Thus, discrepancies in the broad-scale tree topology of extant snakes makes the position of this species uncertain.

Lamprophiidae *incertae sedis*

Described on the basis of 1 posterior trunk vertebra from the upper Oligocene of the Rukwa Rift Basin, Tanzania (McCartney et al., 2021). Intracolumnar variation unknown. No additional material reported. This unnamed taxon shares the following apomorphic features with lamprophiine lamprophiids (McCartney et al., 2021): broad, flange-like prezygapophyseal process, broad laminar process of the postzygapophyses, and longitudinal ridge on the posterodorsal part of the neural arch (all presumably paired). These highly unusual processes (reminiscent of 'erycines') support an affinity with Lamprophiinae and make this unnamed taxon the oldest record of crown Lamprophiidae (McCartney et al., 2021).

Genus *Madtsoia* Simpson, 1933

Simpson (1933) first described an unusual 'boid' snake from the lower Eocene of Argentina, which he named *Madtsioia bai*. Other species have since been referred to it, also from much older sediments and other Gondwanan landmasses (Hoffstetter, 1961; LaDuke et al., 2010), although broader phylogenetic analyses have failed to recover them as a clade (Vasile et al., 2013; Rio and Mannion, 2017).

***Madtsioia bai* Simpson, 1933**

First described on the basis of 45 mostly articulated trunk vertebrae in two sections (5 mid-trunk vertebrae, the remainder much closer to the vent) and associated ribs of one individual plus 3 additional vertebrae from the lower Eocene of the San Jorge Basin, Argentina (Simpson, 1933). Hoffstetter (1959) estimated the size of the holotype animal at 7-8 m. Intracolumnar variation reasonably well known. Simpson (1935) reported from the Eocene of Gaiman (=Cerro Pan de Azúcar), Argentina, vertebral fragments similar to, but not quite as large as, those of *M. bai*. Hoffstetter (1959) reported a fragment of a large dentary from the same area with a primitively high number (3) of mental foramina; he ascribed it to *M. cf. bai*. Simpson (1933) also suggested that a smaller vertebral centrum from the Upper Cretaceous might pertain to the same species.

***Madtsioia camposi* Rage, 1998**

Described on the basis of 178 vertebrae from all parts of the column as well as a maxilla, palatine and dentary from the lower Eocene fissure fills of São José de Itaboraí, Brazil (Rage, 1998). Intracolumnar variation well known; no additional material reported. The height of the neural spine was given as diagnostic of the species with respect to other species of *Madtsioia*, and the species is additionally characterised by a strong facial process of the maxilla, a palatine with a dorsal process and posteriorly situated maxillary process, and a short and deep dentary (Rage, 1998). Though noting similarity in the morphology of cranial elements to *M. bai*, Rage (1998) regarded the generic attribution as tentative.

Madtsoiidae indet.

Additional material has been referred or compared to *Madtsoia* sp., ?*Madtsoia* sp. or cf. *Madtsoia* sp. from the lower Eocene of Australia (Scanlon, 1993; 2005) and the middle Palaeocene through Oligocene of Argentina (Albino, 1993; Albino and Brizuela, 2014). Indeterminate madtsoiid material was also reported from the Eocene of Argentina (Albino, 1993), the upper Palaeocene and lower Eocene of Morocco (Augé and Rage, 2006), and the lower Eocene of the lignite mines of India (Rage et al., 2003; Rage et al., 2008; Smith et al., 2016). Two vertebral specimens from Palaeocene of the 'southern cluster' of Pakistan, described by Rage et al. (2014) as pertaining to *Gigantophis* sp., were considered as Madtsoiidae indet. by Rio and Mannion (2017).

***Messelophis variatus* Baszio, 2004**

Described on the basis of a nearly complete skeleton (the holotype) and 14 other vertebral sections or partial skeletons from the lower-middle Eocene of Messel, Germany (Baszio, 2004). Intracolumnar variation known. Additional material was reported by Scanferla et al. (2016) and Scanferla and Smith (2020b). The genus is now monotypic. See Scanferla et al. (2016) for a detailed diagnosis; major features include: a toothed premaxilla with an ascending process, finger-like medial foot process of the prefrontal, forked maxillary process of ectopterygoid, short supratemporal, c. 300 elongate preclacal vertebrae with small neural spines, and postclacal vertebrae with haemapophyses. Scanferla et al. (2016) inferred that *M. variatus* formed a clade with *Rieppelophis ermannerorum*, which Scanferla and Smith (2020a) determined is on the stem of Ungaliophiinae.

***Messelopython freyi* Zaher and Smith, 2020**

Described on the basis of four skeletons from the lower or middle Eocene of Messel, Germany (Zaher and Smith, 2020). The holotype and one of the referred specimens were previously considered possibly pythonid (Habersetzer and Schaal, 1990; Szyndlar and Böhme, 1993). Intracolumnar variation unknown. No additional material reported. Genus monotypic. Diagnostic features (Zaher and Smith, 2020): premaxilla with 6 teeth and without midline diastema, palatine foramen in palatine, mid-sagittal crests on parietal and basisphenoid, sigmoidal lateral margin of maxilla, large and crescentic supraorbital, and ectopterygoid overlap of pterygoid reduced. Using a combined morphological-phylogenomic matrix Zaher and Smith (2020) inferred that *M. freyi* lies on the stem of crown Pythonidae. Subsequently, Smith and Scanferla (2021b) established the pythonoid family Messelopythonidae to accommodate this taxon along with *Palaeopython*.

***Morelia riversleighensis* (Smith and Plane, 1985)**

Described (originally as *Montypythonoides riversleighensis*), on the basis of a maxilla with 7 seven associated vertebrae plus 3 vertebrae and 3 isolated teeth from two other localities in Riversleigh, Australia (Smith and Plane, 1985). One of the latter localities, D Site of Faunal Zone A (Archer et al., 1989), pertains to the upper Oligocene (Woodhead et al., 2016). Scanlon (2001) gave a very thorough diagnosis of the species, which we will not deign to abridge, and noted that there are no autapomorphies.

***Natrix mlynarskii* Rage, 1988b**

Described on the basis of 3 trunk vertebrae from Quercy, France (Rage, 1988b). One of these is from a well-dated locality (Mas de Got, MP 22), and is definitely early Oligocene in age. Intracolumnar variation described. Additional material was reported for 'Natricinae indet.' from the upper Oligocene of Quercy (Augé and Rage, 1995) and (as '*Protropidonotus* sp.') an upper Oligocene fissure fill of southern Germany (Dehm, 1935), which could have affinities with *N. mlynarskii*. Diagnostic features with respect to extant *Natrix* (Rage, 1988b): mid-trunk vertebrae elongate, neural spine not low, interzygapophyseal constriction not deep, ventral surface of centrum flat or slightly concave, and straight subcentral ridges that are very strong and sharp. Strangely, *N. mlynarskii* appears to lack parapophyseal processes. Clearly overall similarity to extant natricids and their European diversity played a role in the identification. No phylogenetic evidence has been produced for or against a specific relationship to *Natrix*.

***Nebraskophis oligocenicus* Holman, 1999**

Described on the basis of 1 trunk vertebra from a lower Oligocene fissure fill in peninsular Florida (Holman, 1999). No additional material has been reported, but it should be noted that a vertebra showing all the diagnostic features given below (where known) was reported from the upper Eocene of a disused mine in Georgia (Parmley and Holman, 2003). Intracolumnar variation unknown. Diagnostic features with respect to the Neogene genotype, *Nebraskophis skinneri* Holman, 1973 from the Miocene of the Great Plains (Holman, 1999): even more reduced neural spine, condyle depressed, and haemal keel flaring somewhat posteriorly. No justification was given for its assignment to 'Colubridae' (roughly equivalent to Colubriformes here), but one can deduce that the reasoning is similar to that given for the assignment of *Floridaophis* discussed above.

'*Nessovophis*' zhyлга Averianov, 1997

Described on the basis of 13 trunk vertebrae from the lower Eocene of Neotethyan Kazakhstan (Averianov, 1997). No additional material reported; intracolumnar variation mentioned. Rage et al. (2003) concurred that the species likely is a nigerophiid but removed the type species, *Nessovophis tamdy*, to *Palaeophis*. Accordingly, a new genus name is required for this species. As the original diagnosis concerned characters differentiating species of '*Nessovophis*', we do not repeat them here.

***Nigerophis mirus* Rage, 1975b**

Described on the basis of 110 vertebrae from the Palaeocene of the Trans-Saharan Seaway (Iullemeden Basin) of Niger (Rage, 1975b). No additional material reported; intracolumnar variation described. Rage (1975b) gave the following main features as characteristic (except those characteristic of the family, fide Rage and Werner, 1999): short and anteriorly directed prezygapophyseal processes, zygosphenes thick, synapophyses, massive, small keels above postzygapophyses of anterior trunk vertebrae, and lateral foramina absent.

Genus *Ogmophis* Cope, 1883b

Established by Cope (1883a) for specimens from the John Day Basin of Oregon. Its diagnosis has long been problematic (Gilmore, 1938; Rage, 1984a; Holman, 2000). Several new species have been named, but no apomorphic evidence has been adduced for their close relation to the genotype species, *O. oregonensis* (see Smith, 2013: for a review). Complicating this state of affairs is the loss of the holotype of *O. oregonensis*, for which a neotype has not been designated. Additional material has been reported for or

compared to this genus (Gilmore, 1938; Holman, 1987; Hayes, 2000; Holman, 2000; Fremd and Whistler, 2009). Particularly interesting are the specimens from the John Day Basin (Fremd and Whistler, 2009), the type region of *O. oregonensis*. Furthermore, a skull identified as *Ogmophis* sp., which is co-preserved with two skeletons of '*Calamagras* sp.', was also reported from a lower Oligocene locality (Breithaupt and Duvall, 1986; Breithaupt, 1997).

***Ogmophis compactus* Lambe, 1908**

First described on the basis of 4 trunk vertebrae from the upper Eocene Cypress Hills of Saskatchewan (Lambe, 1908). Additional vertebral material has been reported from the Cypress Hills (Holman, 1972) and the lower Oligocene Brule Formation (Gilmore, 1938), and vertebral and cranial material from the upper Eocene Medicine Pole Hills of North Dakota (Smith, 2013). Intracolumnar variation well known (Smith, 2013). Diagnostic features (Holman, 2000): prezygapophyseal accessory processes prominent, neural spine swollen posteriorly, haemal keel wide and very distinct, and sub-central grooves deep. Smith (2013) gave the following as derived features uniting *O. compactus* from the Medicine Pole Hills with extant *Loxocemus bicolor*: extremely broad quadrate head oriented orthogonally to ventral condyle, very thin neck between quadrate head and ventral condyle, an elongate fossa on the medial surface of the anterior margin of the quadrate, obliteration of the weak mid-sagittal ridge on the parabasisphenoid at mid-length, extremely well-developed subcentral ridges and grooves on vertebrae, and broad haemal keel with undercut margins. In phylogenetic analyses by Smith and Scanferla (2021b) the species was generally recovered as a sister species to *Loxocemus* or in a polytomy with *Loxocemus* and *Xenopeltis*, depending on phylogenetic method. A partial loxocemid skull from the upper Eocene of Trans-Pecos, Texas, has also been reported but not yet described (Bhullar et al., 2009).

***Ogmophis oregonensis* Cope, 1883b**

The genotype of *Ogmophis*. Described on the basis of 4–5 trunk vertebrae from an unknown upper Oligocene horizon of the John Day Basin of central Oregon (Cope, 1883a). The type material has been lost since the time of Gilmore (1938). New material similar to *Ogmophis* has since been reported from the John Day beds (Fremd and Whistler, 2009) and could potentially form the basis of a neotype, which would be important for the systematics of North American fossil snakes. Gilmore's (1938) list of diagnostic features (ignoring that indicative of position in column) is still current: condyle and cotyle round, condyle moderately oblique, and interzygapophyseal ridge prominent. Obviously it cannot be improved without type material. It has frequently been assigned to 'erycines' (e.g., Holman, 2000), but there is no apomorphic evidence for that assertion (Smith, 2013).

***Ogmophis voorhiesi* Holman, 1977c**

Described on the basis of 3 trunk vertebrae from the middle Eocene of the East Coast, USA (Holman, 1977a). Two trunk vertebrae and a tail tip were subsequently reported from the middle Eocene of the Wind River Basin (Holman, 1979), although intracolumnar variation remains undescribed. Smith (2013) argued on the basis of proportions that the tail tip cannot belong to the same species that produced the trunk vertebrae from the same locality. Main diagnostic features (Holman, 2000): very wide and robust haemal keel and thick neural spine with 'obtuse' ends. Holman (1979) believed the tail tip to be compelling evidence of the 'erycine' affinities of this species,

but Smith (2013) questioned the purported 'erycine' features of the specimen. Accordingly, there are no apomorphic features supporting of 'erycine' affinities.

Palaeophiidae Lydekker, 1888a

Lydekker (1888a) agreed with Rochebrune (1880) that these are not closely related to pythons and named a new family. This taxon was long divided into Archaeophiinae and Palaeophiinae (Rage, 1984a), although Georgalis et al. (2020) draw attention to the weakness of the evidence for their close relation. Supposed synapomorphies, being observable only on the axial skeleton in the latter group (as no skull material is known), are: laterally compressed vertebrae, more ventrally directed synapophyses, straighter ribs, vertebral condyle directed posteriorly. No evidence has been presented against the monophyly of the taxon, so we provisionally accept it here.

Genus *Palaeophis* Owen, 1841

Established for *Palaeophis toliapicus* from the lower Eocene of the London Clay (Owen, 1841). Besides the several named species of the genus (see below), indeterminate material of *Palaeophis* sp. has been reported from a large number of Palaeocene through upper Eocene sites in North America (Parmley and Case, 1988; Erickson, 1998), Europe (Owen, 1850; Lydekker, 1888b; Doncieux and Leriche, 1908; Moroz and Savron, 1975; Rage, 1983a; Rosselet, 1991; Snetkov and Bannikov, 2010; Kristensen et al., 2012), Central Asia (Averianov, 1997), IndoPakistan (Rage et al., 2008), and southeast Asia (Head et al., 2005).

It is widely considered that *Palaeophis* is paraphyletic with respect to the more derived *Pterosphenus* (Janensch, 1906b; Hoffstetter, 1958; Holman et al., 1990 [1991]; Rage et al., 2003; Snetkov, 2011). Rage et al. (2003) proposed some provisional groupings of *Palaeophis* spp. and noted that some species may be synonyms of others (see also Gilmore, 1938). Although progress is being made (e.g., McCartney et al., 2018; Folie et al., 2021; Georgalis et al., 2021b), the alpha taxonomy is presently too convoluted to propose any new groups formally, and we abstain from presenting diagnostic characters for individual species.

***Palaeophis africanus* Andrews, 1924**

Described on the basis of 3 isolated trunk vertebrae from the Dahomey Embayment of Nigeria, with only the most complete vertebra (holotype) being originally figured (Andrews, 1924). Additional material has been reported from the middle Eocene of the Congo Basin (Folie et al., 2021) and Togo (Georgalis et al., 2021b). Furthermore, fragmentary vertebral material from the upper Eocene of the East Coast, USA has been referred to the same taxon (Parmley and DeVore, 2005), however, its conspecificity with the African species was doubted by Georgalis et al. (2021b), who confined the distribution of *P. africanus* solely to Africa.

***Palaeophis casei* Holman, 1982b**

Described on the basis of 14 isolated trunk vertebrae from the lower Eocene of the Gulf Coast, USA (Holman, 1982a). Additional material was reported from the lower Eocene of the Gulf Coast (Parmley and Case, 1988) and East Coast, USA (Weems, 1999). Comments on variation have been made (Holman, 1982a; Parmley and Case, 1988). This is the smallest known Palaeophiid, reaching a total length of only c. 50 cm (Holman, 1982a).

***Palaeophis collosaesus* Rage, 1983b**

Described on the basis of about 270 vertebrae from different parts of the column from the lower Eocene of the Trans-Saharan Seaway (Gao Trench) of Mali (Rage, 1983b). Intracolumnar variation was noted. Additional material has been reported from the same area (McCartney et al., 2018). Histological and micro anatomical studies have been conducted on the vertebrae of this taxon (Buffrénil and Rage, 1993; Houssaye et al., 2019). This is the largest species of *Palaeophis* and the largest marine snake in general, as well as one of the largest snakes of all time (Rage, 1983b; McCartney et al., 2018).

***Palaeophis ferganicus* Averianov, 1997**

Described on the basis of 7 vertebrae from different parts of the column from two localities in the lower Eocene of Neotethyan Kyrgyzstan (Averianov, 1997). Intracolumnar variation was noted. No additional material has been reported.

***Palaeophis grandis* (Marsh, 1869)**

Described on the basis of 1 trunk vertebra from the middle Eocene of the East Coast, USA (Marsh, 1869). Another specimen was reported from further south along the East Coast (Blake, 1941). The species was initially placed in its own genus, *Dinophis* Marsh, 1869 (preoccupied), for which the substitute name *Titanophis* was used by the same author (Marsh, 1877). However, it was soon after almost universally treated as a member of *Palaeophis* (Rochebrune, 1880), a view that persists in the ophidian literature today (e.g., Rage, 1984a; Wallach et al., 2014).

***Palaeophis littoralis* Cope, 1868a**

Described on the basis of 3 vertebrae from the middle Eocene of the East Coast, USA (Cope, 1868a; 1868b). Additional material has been reported from other localities in the East and Gulf Coast (Gilmore, 1938; Parmley and Case, 1988; Holman et al., 1990 [1991]; Dessem 1976 in Holman, 2000).

***Palaeophis maghrebianus* Arambourg, 1952**

Described on the basis of about 12 vertebrae, probably from a single individual, from the lower Eocene phosphates of Morocco (Arambourg, 1952). Additional material has been reported from other localities in the lower Eocene of said phosphates, including articulated sections of vertebral column (Arambourg, 1952; Houssaye et al., 2013). Histological and micro anatomical information indicated the presence of osteosclerosis, especially in vertebrae of the anterior and mid-trunk regions (Houssaye et al., 2013).

***Palaeophis nessovi* Averianov, 1997**

Described on the basis of 1 trunk vertebra from the upper Eocene of Neotethyan Kazakhstan (Averianov, 1997). Additional material has been reported from the middle Eocene of Crimea (Snetkov and Bannikov, 2010; Snetkov, 2011; Zvonok and Snetkov, 2012). Furthermore, *Palaeophis udovichenkoi* Averianov, 1997, a supposedly distinct species established from the middle Eocene of Crimea, has since been synonymized with *P. nessovi* (Snetkov and Bannikov, 2010).

***Palaeophis oweni* Zigno, 1881**

Described on the basis of 24 trunk vertebrae from different portions of the column from the middle Eocene of Monte Duello, Italy (Zigno, 1881). The taxon had been in the past few decades considered a probable junior synonym of *Palaeophis typhaeus* (e.g., Rage, 1984a), but it was recently revalidated by Georgalis et al. (2020), who

redescribed it in detail, designated as the lectotype the most complete specimen, provided photographs of the material for the first time, and gave an emended diagnosis.

***Palaeophis tamdy* (Averianov, 1997)**

Described (as *Nessovophis tamdy*) on the basis of 9 trunk vertebrae from the middle Eocene of Neotethyan Uzbekistan (Averianov, 1997). Intracolumnar variation was noted (but see Rage et al., 2003). Zvonok and Snetkov (2012) reported additional material from the middle Eocene of Crimea. Originally considered to represent a nigerophiid, Rage et al. (2003) determined it belongs to *Palaeophis*.

***Palaeophis toliapicus* Owen, 1841**

This, the genotype species, was described on the basis of three blocks with about 60–65 vertebrae and ribs from the lower Eocene of the London Clay (Owen, 1841). Additional specimens were reported for or compared to the species from the lower Eocene of the type area (Owen, 1850), the Paris Basin (Rage, 1983a; Augé et al., 1997), the North Sea Basin (Rage, 1983a), East Coast, USA (Weems and Grimsley, 1999) and Limfjord (Hoch, 1975) and the middle Eocene of Crimea (Zvonok and Snetkov, 2012).

***Palaeophis typhaeus* Owen, 1850**

Described on the basis of 4 vertebrae from the lower Eocene of southern England (Owen, 1850; Lydekker, 1888b). Additional material has been reported for (or synonymized with) the species from the lower Eocene of the London Clay and elsewhere in southern England (Owen, 1850; Lydekker, 1888b), North Sea Basin (Lydekker, 1888b; Rage, 1983a), and Paris Basin (Augé et al., 1997) and the middle Eocene of the Congo Basin (Antunes, 1964). The last collection has been reinterpreted as *P. africanus* by Folie et al. (2021), so *P. typhaeus* is known only from Europe.

***Palaeophis vastaniensis* Bajpai and Head, 2007**

Described on the basis of 3 vertebrae from a lower Eocene lignite mine of India (Bajpai and Head, 2007). Additional material was reported for (or considered probably conspecific with) the species from the same or adjacent localities (Rage et al., 2008; Smith et al., 2016).

***Palaeophis virginianus* Lynn, 1934**

Described on the basis of 2 trunk vertebrae, presumed by the author to come from the same individual, from the upper Palaeocene of the East Coast, USA (Lynn, 1934). Much additional material has been reported from the Palaeocene through middle Eocene of the East and Gulf Coast (Holman, 1977a; Holman and Case, 1988; Parmley and Case, 1988; Holman et al., 1990 [1991]; Weems, 1999; Dessem 1976 in Holman, 2000).

***Palaeophis zhylan* (Nessov, 1984)**

Described on the basis of 4 trunk vertebrae from the upper Palaeocene or lower Eocene of Neotethyan Kazakhstan (Nessov and Udovichenko, 1984). No additional material has been reported. Originally placed in its own genus, *Vialovophis* Nessov, 1984, and considered to represent a new family, Vialovophiidae Nessov, 1984, it was subsequently shown to be referable to *Palaeophis* by Rage et al. (2003).

Genus *Palaeopython* Rochebrune, 1880

Established by Rochebrune (1880) to accommodate *Python cadurcensis* Filhol, 1877 and his new species *P. filholii*, both based on various remains from the old collections (probably middle or upper Eocene) of Quercy. The genus is thoroughly reviewed by Georgalis et al. (2021c), and we therefore dispense with details. There is no clear apomorphic evidence that unites all named species. Wallach et al. (2014) placed *Palaeopython* spp. on the pythonoid line but provided no justification. More recently, *Palaeopython* was grouped together with *Messelopython* into the pythonoid family Messelopythonidae by Smith and Scanferla (2021b).

***Palaeopython cadurcensis* (Filhol, 1877)**

This species, from Quercy, is the type of the genus. Georgalis et al. (2021c) designated a vertebral lectotype and determined that paralectotype cranial elements (maxilla, dentary) are properly referred. The same authors further described additional vertebral material from the old collections of the Phosphorites du Quercy and provided an emended diagnosis. In addition, they synonymized *Paleryx cayluxi* with *Palaeopython cadurcensis* (Georgalis et al., 2021c). For details, we refer the reader to that work.

***Palaeopython ceciliensis* Barnes, 1927**

Described on the basis of one fragmentary vertebra from the Lutetian of Geiseltal, Germany (Barnes, 1927). Georgalis et al. (2021c) assigned much new material to this species from other excavation pits at Geiseltal and discussed intracolumnar variation. Cranial elements have not been described. For details, we refer the reader to that work.

***Palaeopython helveticus* Georgalis and Scheyer, 2019**

Described on the basis of 7 vertebrae from the Eocene of the Zurich area in Switzerland (Georgalis and Scheyer, 2019); the authors thoroughly studied ontogenetic variation with the application of micro-CT. Georgalis et al. (2021c) treated it together with other species in the genus.

***Palaeopython schaali* Smith and Scanferla, 2021b**

Described on the basis of two well preserved skeletons with skulls from Messel, representing the most complete material referred to *Palaeopython* (Smith and Scanferla, 2021b). The articulated skeletons of *Palaeopython schaali* enabled a direct documentation of otherwise unknown features of this genus, which indicated its close affinities with the also co-occurring *Messelopython* (Smith and Scanferla, 2021b). For more details, we refer the reader to that work.

***“Palaeopython” neglectus* Rochebrune, 1884**

Described on the basis of vertebral material and a mummy from Quercy (Rochebrune, 1884). A single trunk vertebra was subsequently designated as the lectotype (Rage, 1984a). Georgalis et al. (2021c) treated it together with other species in the genus, described more vertebral material, and casted doubt on its generic attribution. For details, we refer the reader to that work.

***Paleryx rhombifer* Owen, 1850**

First described on the basis of a mid-trunk vertebra from Hordle in southern England (Owen, 1850). Additional material was referred by Lydekker (1888b). As has been previously suggested (Rage and Ford, 1980; Rage, 1984a), we regard the second species of that genus described from Hordle, i.e., *Paleryx depressus*, as a junior synonym

of *P. rhombifer*. The taxon is reviewed in detail by Georgalis et al. (2021c), who described additional vertebral as well as cranial material. Its phylogenetic relationships remain unknown, though based on its cranial material, booid affinities were excluded by Georgalis et al. (2021c).

***Paraepicrates brevispondylus* Hecht, 1959**

Described on the basis of 1 trunk vertebra from the middle Eocene of the Bridger Basin in the Rocky Mountains (Hecht in McGrew et al., 1959). No new material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Hecht in McGrew et al., 1959): short-based and gradually rising neural spine, shallow posterior notch in neural arch, small prezygapophyseal accessory processes, moderately thick zygosphenes, and overhanging neural spine. It has generally been treated as related to the larger constrictors (Rage, 1984a; e.g., Holman, 2000), but Kluge (1988) saw the short-based neural spine and shallow notch as diagnostic features of *Lichanura*.

***Paraplatyspondylia batesi* Holman and Harrison, 1998b**

Described on the basis of 25 trunk vertebrae from two horizons in the upper Eocene of southern England (Holman and Harrison, 1998b). No new material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Holman and Harrison, 1998b): low and long neural spine, prezygapophyses squared anteriorly, deep paracotylar fossae. More detailed comparison of this genus with its namesake *Platyspondylia*, and especially in consideration of individual and intracolumnar variation, would be instructive. Holman et al. (2006) considered the systematic affinities of this snake to be unknown. Smith (2013) considered that it is not very distinguishable from *Platyspondylia* spp.

***Paraungaliophis pricei* Rage, 2008**

Described on the basis of 2 trunk vertebrae from the lower Eocene fissure fills of São José de Itaboraí (Rage, 2008). No additional material reported; intracolumnar variation unknown. Due to the elongation of the vertebrae, with CL/NAW of 1.16 (based on Rage, 2008: fig. 1v), Rage (2008) considered it related to Ungaliophiinae. As with *Dunnophis* (see above), we consider this evidence too tenuous and consider it as *Constrictores incertae sedis*.

***Patagoniophis australiensis* Scanlon, 2005**

First described on the basis of 38 vertebrae from throughout the column, rib fragments and a partial dentary from the lower Eocene of the Tingamarra locality in Australia (Scanlon, 1993; 2005). No new material reported; intracolumnar variation well known. Diagnostic features with respect to the genotype, *Patagoniophis parvus* Albino, 1986 from the Upper Cretaceous of Argentina (Scanlon, 2005): smaller size, the shape of the subcentral ridges, and the large and less arched zygosphenes. Rio and Mannion (2017) recovered *P. australiensis* in a mostly South American-Australian clade (with two Cretaceous European members).

***Paulacoutophis perplexus* Rage, 2008**

Described on the basis of 12 vertebrae from the lower Eocene fissure fills of São José de Itaboraí, Brazil (Rage, 2008). No additional material reported; intracolumnar and individual variation well known. Genus monotypic. Diagnostic features (Rage, 2008): parazygosphenal foramina present, slanting anterior margin of neural spine, neural arch and centrum not depressed, and posterior expansion of diapophysis. Trunk

vertebrae also commonly show a remarkable feature: a transverse ridge that delimits the posterior margin of the zygosphen. Rage (2008) regarded the species as most similar to large booids but ultimately of uncertain systematic affinity.

***Phosphoroboa filholii* (Rochebrune, 1880)**

Described on the basis of a posterior trunk vertebra from an unknown locality in the Phosphorites du Quercy (Rochebrune, 1880). This species might correspond to Rage's 'Boid E' (J.-C. Rage, pers. comm. to KTS, 2010), as detailed under ∇ Constrictores *incertae sedis*. Much new material was reported from the upper Eocene of Quercy by Rage (1974), who considered intracolumnar variation in the vertebrae and also described a pterygoid. The pterygoid, he believed, shows a boa-like anterior articulation. The species is reviewed in detail by Georgalis et al. (2021c), who described much new vertebral and cranial material (as well as the pterygoid of Rage 1974) and removed it from the genus *Palaeopython*, placing it into its own booid genus *Phosphoroboa*. For more details, we refer the reader to Georgalis et al. (2021c).

Genus *Platyspondylia* Rage, 1974

Established by Rage (1974) for *Platyspondylia leptota*, the genus was revised by Szyndlar and Rage (2003). They assigned *Platyspondylia* to 'Tropidophiidae' 'mainly based on its cranial osteology' (p. 75) – and most especially the quadrate bone – but did not specify to which of the two groups of 'tropidophiids' they saw the greatest resemblance. Szyndlar et al. (2008) found resemblance of the trunk vertebrae with *Ungaliophis* but refrained from any further conclusion due to the fact that all known caudals of *Platyspondylia leptota* possessed haemapophyses. Indeed, However, Vianey-Liaud et al. (2014), on the basis of slightly older finds from the Oligocene of France, showed that a population referred to *Platyspondylia* sp. had anterior caudal vertebrae with a ventral, median groove and haemapophyses appearing only in the middle caudals.

Szyndlar and Rage (2003) appear to have agreed with McDowell (1987) that the palatine and compound bone are sufficiently similar to *Ungaliophis* to refer the species to Ungaliophiinae (although McDowell did not specify exactly how), adding that the quadrate also supports this referral (also without specifying exactly why). Note that similar morphologies of the quadrate are also known in *Boavus occidentalis* (Gilmore 1938) and now in several Messel booids as well, which are related to Ungaliophiinae and to Boidae (Scanferla and Smith 2020b).

There is no positive (apomorphic) evidence for tropidophiid (s.s.) affinities of *Platyspondylia leptota* or *P. germanica*, and the proportions of trunk vertebrae partly contradict them, insofar as some vertebrae are elongate as in Ungaliophiinae. In contrast, the ventrally grooved anterior caudal vertebrae of *Platyspondylia* sp. from Saint-Privat-des-Vieux are said to be consistent with tropidophiid (s.s.) affinities (Vianey-Liaud et al., 2014). While grooved anterior caudals have not been taken to be the tropidophiid (s.s.) pattern, this evidence of reduction of haemapophyses on anterior caudals is more consistent with Tropidophiidae (s.s.) as described by Szyndlar and Rage (2003) than the named species of *Platyspondylia*.

In view of this contradictory evidence, we regard *Platyspondylia* spp. as *Alethinophidia incertae sedis*.

Much material has been referred to *Platyspondylia* sp. over the years from the Oligocene of France and Germany (Szyndlar, 1994; Augé and Rage, 1995; Sigé et al., 1998; Szyndlar and Rage, 2003; Vianey-Liaud et al., 2014) and probably also Anatolia (Georgalis et al., 2021a).

***Platyspondylia germanica* Szyndlar and Rage, 2003**

Described on the basis of 7 trunk vertebrae, 1 caudal vertebra and a maxilla from an upper Oligocene fissure fill in the Swabian Jura (Szyndlar and Rage, 2003). No additional material reported; intracolumnar and individual variation somewhat known. The maxilla is broken posteriorly. Features of the palatine process of the maxilla and especially of the vertebrae were given to differentiate the species from congeners (Szyndlar and Rage, 2003).

***Platyspondylia lepta* Rage, 1974**

The genotype, described on the basis of over 200 trunk and tail vertebrae as well as skull elements (palatine, quadrate, compound bone) from the upper Oligocene of Quercy, France (Rage, 1974). Nearly 300 vertebrae and more skull elements (including maxilla) were reported from two other localities in Quercy (Szyndlar and Rage, 2003). However, the maxilla is broken posteriorly. Intracolumnar variation well known. Features of the palatine process of the maxilla and especially of the vertebrae were given to differentiate the species from congeners (Szyndlar and Rage, 2003). All known caudal vertebrae have haemapophyses (Szyndlar and Rage, 2003).

***Platyspondylia sudrei* Rage, 1988a**

Described on the basis of 27 isolated vertebrae from the upper Eocene of one locality in the Phosphorites du Quercy (Rage, 1988a). This species might correspond to Rage's 'Boid K' (J.-C. Rage, pers. comm. to KTS, 2010), as detailed under ∇ Constrictores *incertae sedis*. No new material reported; intracolumnar variation well known. Minor features of the palatine process of the maxilla and especially of the vertebrae were given to differentiate the species from congeners (Rage, 1988a; Szyndlar and Rage, 2003).

***Platyspondylophis tadkeshwarensis* Smith et al., 2016**

Described on the basis of 7 isolated vertebrae from a lower Eocene lignite mine of India (Smith et al., 2016). No additional material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features with respect to other Madtsoiidae (Smith et al., 2016): large size, strongly depressed centrum, horizontal and transversely directed prezygapophyses, strong paradiapophyses, small neural spine, and no parazygantral foramina (only fossae). The last feature is curious, because the presence of such foramina is typically considered diagnostic of Madtsoiidae (e.g., Rage, 1984a; Scanlon, 1992; Mohabey et al., 2011). Smith et al. (2016) considered this species to pertain to the clade of large madtsoiids.

***Plesiotortrix edwardsi* Rochebrune, 1884**

Described on the basis of 3 articulated trunk vertebrae from an unknown level at Quercy, France (Rochebrune, 1884). No additional material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Rage, 1984a): neural arch fairly vaulted and neural canal fairly tall. Clearly, it is in need of restudy. Rage (1984a) recognised that it is a constrictor, not an 'anilioid', and tentatively, but without justification, assigned it to 'Boinae' (which at the time also included pythons). We consider it Constrictores *incertae sedis*.

***Procerophis sahnii* Rage et al., 2008**

Described on the basis of 8 vertebrae from throughout the column from a lignite mine in India (Rage et al., 2008). Additional material reported from a nearby

contemporaneous mine (Smith et al., 2016). Intracolumnar variation reasonably well known. Diagnostic features (Smith et al., 2016): lightly built vertebrae, laminar prezygapophyseal buttresses with weak anteriorly directed processes, wide and thin zygosphenes, long and blade-like neural spine, well marked subcentral ridges, and variably paracotylar foramina. Rage et al. (2008) considered the species to be close to Nigerophiidae on the basis of the prezygapophyses but also showing similarity of proportion to arboreal colubroids. El-Hares et al. (2022) described a trunk vertebra from the late Eocene of the Fayum, Egypt, which they tentatively referred to the same genus, as cf. *Procerophis* sp.

Genus *Pterosphenus* Lucas, 1899

Rage et al. (2003) presented a new diagnosis of *Pterosphenus*. The genus had an enormous geographic distribution, encompassing North and South America, Africa, and Asia. Besides the named species listed below, indeterminate material of *Pterosphenus* sp. has been reported from the lower Eocene lignite mines of India (Bajpai and Thewissen, 2002; Rage et al., 2003; Rage et al., 2008), middle Eocene of the 'central cluster' of IndoPakistan (Gingerich et al., 1979), upper Eocene of the East Coast, USA (Parmley and DeVore, 2005), and upper Eocene of the Fayum (McCartney and Seiffert, 2016).

***Pterosphenus biswasi* Rage et al., 2003**

Described on the basis of 4 trunk vertebrae from a lower Eocene lignite mine of India (Rage et al., 2003). No additional material reported; intracolumnar variation unknown.

***Pterosphenus kutchensis* Rage et al., 2003**

Described on the basis of 106 vertebrae from a lower Eocene lignite mine of India (Rage et al., 2003). No additional material reported; ontogenetic and intracolumnar variation well known.

***Pterosphenus schucherti* Lucas, 1899**

Described on the basis of about 40 vertebrae, considered by Gilmore (1938) to pertain to one individual, from the middle Eocene of the Gulf Coast, USA (Lucas, 1899). Considerable additional material has been reported for or compared to the species from the middle to upper Eocene of the Gulf Coast (Gilmore, 1938; Westgate and Ward, 1981; Westgate, 1984; McPherson and Manning, 1986; Parmley and Case, 1988; Westgate, 1989; see also Breard and Stringer, 1995; Dessem 1976 and Breard 1978 in Holman, 2000), peninsular Florida (Hutchison, 1985), and the East Coast (Miller, 1955; Holman, 1977a; Parmley and Case, 1988; Parmley and DeVore, 2005).

***Pterosphenus schweinfurthi* (Andrews, 1901)**

Described (as *Moeriophis schweinfurthi*) on the basis of an unknown number of vertebrae from the upper Eocene of the Fayum (Andrews, 1901). Additional material has been reported for or compared to the species from the type area (Andrews, 1906; Janensch, 1906b; McCartney and Seiffert, 2016), the middle Eocene of Dor el Talha, Libya (Hoffstetter, 1961) and the Congo Basin (Antunes, 1964), and the middle and upper Eocene of Morocco (Zouhri et al., 2018, 2021)

***Pterosphenus sheppardi* Hoffstetter, 1958**

Described on the basis of 5 articulated trunk vertebrae with ribs from the upper Eocene of Ancon, Ecuador (Hoffstetter, 1958). No additional material reported; intracolumnar variation unknown.

***Pterygoboa* sp.**

The distinctive genus is typically identified in the Miocene of North America (Holman, 2000), but Mead and Schubert (2013) reported 17 'highly fragmented' vertebrae of this taxon from an upper Oligocene marginal marine environment of Florida. They were not illustrated (although similar Miocene material was) but were described as showing the accessory processes on trunk vertebrae that characterise the genus.

Pythonoidea indet.

The possible occurrence of pythonids in the Palaeogene of Europe has been discussed since the time of Filhol (1877). Kuhn (1939) stated that premaxillary teeth are present in a Geiseltal specimen he referred to *Paleryx spinifer*, a potentially plesiomorphic feature retained amongst extant constrictors only in Pythonoidea. Georgalis et al. (2021c) could not confirm this and regarded the specimen as Constrictores indet. Szyndlar (1994) and Szyndlar and Böhme (1993) considered the high number of vertebrae (approaching 400) of three specimens from Messel (figs. 194-196 in Keller and Schaal, 1992) to be compelling evidence for the presence of Pythonidae. However, the first two specimens are now referred, respectively, to *Eoconstrictor fischeri* and *Messelophis variatus*, which were shown to be booids (Scanferla et al., 2016; Scanferla and Smith, 2020a). The third ("erycine") specimen illustrated by Keller and Schaal (1992) has not yet been studied in detail, but all known snake taxa from Messel except *E. fischeri* and *M. variatus* have <300 vertebrae. Augé et al. (1997) and Duffaud and Rage (1997) reported palatines from the lower and middle Eocene, respectively, of France in which a palatine foramen is present; Szyndlar and Böhme (1993) reported and illustrated a specimen from Messel that also possesses a palatine foramen. Such a foramen characterises all extant Pythonoidea but might be primitive (Szyndlar and Böhme, 1993), so the authors concluded that the taxa in question are either pythonids (at the time, a close relationship with *Xenopeltis* and *Loxocemus* was not recognised) or a new, unknown lineage of constrictors. Habersetzer and Schaal (1990) identified premaxillary teeth (questioned by Baszio, 2004) and a supraorbital bone in another specimen from Messel, features also typical of Pythonoidea.

The specimen studied by Szyndlar and Böhme (1993) later became the holotype of *Messelopython freyi* Zaher and Smith, 2020, and that studied by Habersetzer and Schaal (1990) a paratype (see above). On this background, we consider it reasonable to refer the isolated palatines from France to Pythonoidea, although we recognise that further work on those collections will be necessary in order to confirm this.

***Rageryx schmidi* Smith and Scanferla, 2021a**

Described on the basis of a nearly complete skeleton from the lower-middle Eocene locality of Messel (Smith and Scanferla, 2021a). No additional material reported; intracolumnar variation briefly described. Genus monotypic. Main diagnostic features (Smith and Scanferla, 2021a): skull with short snout and moderately extensive braincase, orbits in front of longitudinal midpoint of skull, premaxilla not protruded, parietal with mid-sagittal ridge on posterior third, shelf bounding groove for posterior opening of Vidian canal obscures foramen for palatine branch of cranial nerve VII,

supratemporal short, quadrate ramus of pterygoid with longitudinal, dorsally open groove, coronoid reduced, c. 220 precloacal vertebrae, caudal neural spines not bifurcated, distal caudal vertebrae short and tall with supernumerary processes. The supernumerary processes universally characterise (Smith, 2013) both New and Old World ‘erycines’. The phylogenetic analyses of Smith and Scanferla (2021a) and Scanferla and Smith (2020a) recovered *Rageryx schmidi* as a sister-taxon of the New World ‘erycines’, Charininae.

***Renenutet enmerwer* McCartney and Seiffert, 2016**

Described on the basis of 12 trunk vertebrae from the upper Eocene of the Fayum, Egypt (McCartney and Seiffert, 2016). Additional material reported by Zaher et al. (2021) and El-Hares et al. (2022). Some intracolumnar variation described, including both trunk (McCartney and Seiffert, 2016) and caudal vertebrae (El-Hares et al., 2022). Genus monotypic. Among the diagnostic features (McCartney and Seiffert, 2016): parazygosphenal foramina present, zygosphene gracile, hypapophyses on mid- and posterior trunk vertebrae absent, and prezygapophyseal processes conical. McCartney and Seiffert (2016) referred *R. enmerwer* to Colubriformes but did not distinguish between crown and stem. Zaher et al. (2021) placed it in their new family Thaumastophiidae together with *Thaumastophis*, on the stem of Colubriformes.

***Rieppelophis ermannonum* (Schaal and Baszio, 2004)**

First described (as *Messelophis ermannonum*) on the basis of 15 specimens (holotype: 5 articulated vertebrae), including several in which the skull is preserved, from the lower-middle Eocene of Messel (Schaal and Baszio, 2004). Additional material was reported by Scanferla et al. (2016) and Scanferla and Smith (2020b). Genus monotypic. Scanferla et al. (2016) placed it in the new genus *Rieppelophis* based on the significant differences in body form. Main diagnostic features (Scanferla et al., 2016): an untoothed premaxilla with an ascending process, nasal articulates with medial frontal pillar, finger-like medial foot process of the prefrontal, forked maxillary process of ectopterygoid, short supratemporal, c. 183 relatively long precloacal vertebrae with robust neural spines, and postcloacal vertebrae with paired protuberances rather than laminar haemapophyses. Scanferla and Smith (2020b) described additional anatomical information. Scanferla et al. (2016) inferred that *R. ermannonum* formed a clade with *Messelophis variatus*, which Scanferla and Smith (2020a) determined is on the stem of Ungaliophiinae.

***Rottophis atavus* (von Meyer, 1855)**

First described (as *Tropidonotus atavus*) on the basis of a partial skeleton from an upper Oligocene shallow lake deposit near Bonn, Germany (Meyer, 1855). At least four additional skeletons from the type locality are known (Lydekker, 1888b; Szyndlar and Böhme, 1996; Szyndlar and Rage, 2003), and there have furthermore been tentative reports of the species elsewhere (Meyer, 1860; Szyndlar, 1994; but see Szyndlar and Rage, 2003: 88). Intracolumnar variation well known. Szyndlar and Böhme (1996) redescribed it in detail and placed it in its own monotypic genus, *Rottophis*. Szyndlar and Böhme (1996) and Szyndlar and Rage (2003) observed general similarities between *Rottophis atavus* and Ungaliophiinae in the trunk vertebrae and between *R. atavus* and Tropidophiidae s.s. in the caudal vertebrae.

The most striking feature of this taxon is that caudal vertebrae at the beginning of the distal third of the tail have a haemal keel, sometimes grooved, rather than lamellar haemapophyses, which appear only on the posterior-most caudals (Szyndlar et al.,

2008). A support for tropidophiid affinities of *Rottophis* was implied by the low total number of vertebrae (around 215) in comparison with typical constrictors (Szyndlar et al., 2008).

Since cranial synapomorphies of Tropidophiidae s.s. are not preserved, it is clear that only vertebral anatomy is relevant here. The pattern of ventral structures on the caudal vertebrae of *Rottophis atavus* does not correspond closely to the pattern in Tropidophiidae s.s. as explicated by Szyndlar and Rage (2003). In *R. atavus*, the grooved haemal keels are found in the anterior part of the distal segment, and normal haemapophyses are found in subsequent vertebrae; given present morphological data, this pattern would be unique. Additionally, the mid-trunk vertebrae of *R. atavus* appear elongate, based on figures in Szyndlar and Böhme (1996), with a CL/NAW ratio of c. 1.1 (Smith, 2013). This derived feature is typical of Ungaliophiinae, not Tropidophiidae s.s. The issue of total vertebral number is an important one and should be further pursued. We note that a low number of vertebrae also appears to be present in *Xenopeltis unicolor*.

In sum, we do not believe that the evidence for tropidophiid affinities for this taxon is strong at present. The pattern of ventral structures on the centrum does not seem to correspond as closely to Tropidophiidae s.s. as has been claimed, and the proportions of the trunk vertebrae are apomorphically elongate, more similar to Ungaliophiinae. The total vertebral count is an important problem and should be further pursued. Given the character conflict, we regard this taxon for now as Alethinophidia *incertae sedis*.

***Rukwanyoka holmani* McCartney et al., 2014**

Described on the basis of 2 trunk vertebrae from the upper Oligocene of the Rukwa Rift Basin of Tanzania (McCartney et al., 2014). Variation was described, although it is unclear if it is intracolumnar or individual. No additional material reported. Diagnostic features (McCartney et al., 2014): neural spine longer than tall with anterior keel, neural arch laminae straight, zygosphenes thin and flat and anteriorly concave, paracotylar foramina present in deep fossa, and haemal keel deep and narrow. McCartney et al. (2014) assigned it to 'Boinae', which at the time included Candoiidae, Sanziniidae and Boidae sensu Pyron et al. (2014), principally by the lack of apomorphic features of other groups (Madtsoiidae, Palaeophiidae, Tropidophiidae) and the presence of paracotylar foramina, which they acknowledged are of uncertain polarity. The hypothesis has not been further tested, so for the present we regard it as Constrictores *incertae sedis*.

Genus *Russellophis* Rage, 1975a

Established for a peculiar vertebra from the lower Eocene of France of elongate, lightly built, caenophidian aspect in which the zygapophyseal articulations show a downward inclination, the opposite of essentially all other snakes (Rage, 1975a). Additional material has been referred to *Russellophis* sp. or ?Russellophiidae indet. from the lower Eocene of Itaboraí (Rage, 2008), the lower to upper Eocene of Europe (Milner, 1986; Rage, 1988a; Rage and Augé, 1993; Augé et al., 1997; Duffaud and Rage, 1997; Nel et al., 1999; Rage and Augé, 2010), the upper Eocene of the Fayum (McCartney and Seiffert, 2016), and the lower Eocene of India (Rage et al., 2008).

***Russellophis crassus* Rage et al., 2008**

Described on the basis of 9 vertebrae from throughout the column from a lower Eocene lignite mine in India (Rage et al., 2008). No additional material reported;

intracolumnar variation well known. Diagnostic features with respect to *R. tenuis* (Rage et al., 2008): narrower and thicker zygosphene, more massive build, larger cotyle and condyle, more elevated paradiapophyses.

***Russellophis tenuis* Rage, 1975a**

This, the genotype species, was described on the basis of 1 trunk vertebra from the lower Eocene of France (Rage, 1975a). Additional material has been reported from the lower to upper Eocene of Europe (Rage, 1983a; Augé et al., 1997; Holman et al., 2006). On the diagnosis, see *R. crassus*.

***Sanjuanophis froehlichii* Sullivan and Lucas, 1988**

Described on the basis of 7 associated and 1 isolated trunk vertebrae from the lower Eocene of the San Juan Basin (Sullivan and Lucas, 1988). No additional material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Sullivan and Lucas, 1988): large size, swollen haemal keel, stout zygosphene without tubercle, and tall neural spine. Sullivan and Lucas (1988) regarded this species as the largest North American constrictor.

'Scoleophidia' incertae sedis

Indeterminate scoleophidian vertebrae have been reported from 14 localities in the Palaeogene, 9 of them from western Europe: 2 vertebrae from the Palaeocene of Hainin in the North Sea Basin (Folie, 2006); 2 from the lowermost Eocene of Dormaal in the North Sea Basin (Hecht and Hoffstetter, 1962); 1 fragmentary vertebra from the middle Eocene of Saint-Maximin, Quercy (Duffaud and Rage, 1997); uncounted from four localities in the upper Eocene and one locality in the upper Oligocene of Quercy (Rage, 1974; Crochet et al., 1981; Rage and Bailon, 2005); 2 vertebrae from the upper Eocene of Sainte-Néboule, Quercy (Rage, 1978); 1 vertebra from the upper Palaeocene of Morocco (Augé and Rage, 2006); 5 vertebrae from the early to middle Eocene of Algeria (Rage et al., 2021); and 18 vertebrae from three upper Oligocene (fissure fill) localities in peninsular Florida (Mead, 2013).

Like most living scoleophidians, these remains are very small. Diagnostic features of the vertebrae (Rage, 1984a): low, depressed neural arch lacking a neural spine; long and parallel-sided centrum; oval cotyle and condyle; para- and diapophyses united as synapophysis; and prezygapophyseal accessory processes present. While distinctive, their vertebral morphology is considered homogeneous (Rage, 1984a; see Georgalis et al., 2017), and no species have been named from the Palaeogene.

***Syndlaria aureomontensis* Rage and Augé, 2010**

Described on the basis of about 4 trunk vertebrae from the middle Eocene of a fissure fill in eastern France (Rage and Augé, 2010). Some unusual aspects of intracolumnar variation were described. No additional material has since been reported. Genus monotypic. Main diagnostic features (Rage and Augé, 2010): combination of tall neural spine and depressed neural arch, together with strongly projecting paradiapophyses, ventrally arched haemal keel, and (weak) subcotylar processes. Rage and Augé (2010) found these features most consistent with 'Tropidophiidae' and so assigned the species to that taxon, but they also highlighted that certain characters are shared also with *Cadurcobia* and *Geringophis*, amongst others (see above). Head (2015) considered the haemal keel 'squared off' rather than arched and on the basis of that apomorphy the oldest record of the total clade of Tropidophiidae s.s. We consider the haemal keel to be rounded in profile, and it does not show the anterior corner

characteristic of the hypapophysis of Tropicophiidae s.s. (see below). Rage and Augé (2010) noted that caudal vertebrae are unknown, so we provisionally follow their conclusion that the assignment is not definitive. We consider it Alethinophidia *incertae sedis*.

***Tallahattaophis dunnii* Holman and Case, 1988**

Described on the basis of 1 fragmentary vertebra from the Eocene of the Gulf Coast, USA (Holman and Case, 1988). No additional material reported; intracolumnar variation unknown. Genus monotypic. Diagnostic features (Holman and Case, 1988): neural spine long and low, neural arch vaulted, prezygapophyseal accessory processes absent, and haemal keel wide and flat. To what extent the evidently eroded processes contribute to these features, is unclear. The features used by Holman and Case (1988) to assign the species to 'Boinae' (including large boas and pythons) are all plesiomorphic.

Genus *Texasophis* Holman, 1984

Established for *Texasophis fossilis* from the Neogene of North America (Holman, 1977b). The generic diagnosis (Holman, 2000) is inadequate. No phylogenetic evidence has been adduced for or against the monophyly of the genus, and most of the finds are united by an overall resemblance of their vertebrae, which are small, elongate, with a low neural spine, very low prezygapophyseal accessory processes, and a distinct haemal keel.

***Texasophis bohemicus* Szyndlar, 1987**

Described from the Neogene of the Czech Republic (Szyndlar, 1987). Additional material reported from an Oligocene fissure fill of southern Germany (Szyndlar, 1994). Intracolumnar variation described. Diagnostic features with respect to congeners (Szyndlar, 1987): size, concave posterior border of neural arch, and straight anterior border of zygosphenon.

***Texasophis galbreathi* Holman, 1984**

Described on the basis of 1 trunk vertebra from the lower Oligocene of Colorado (Holman, 1984). No new material reported; intracolumnar unknown. Diagnostic features with respect to congeners (Holman, 2000): more gracile and elongate, uniformly thinner haemal keel, and postzygapophyseal articular facets more elongate.

***Texasophis hecki* Böhme, 2008**

Described on the basis of 9 vertebrae from an upper Oligocene fissure fill of southern Germany (Böhme, 2008). No additional material reported; intracolumnar variation unknown. Diagnostic features with respect to congeners (Böhme, 2008): size, trilobate zygosphenon, subcircular pre- and postzygapophyseal articular facets, anteriorly narrower haemal keel, and horizontal prezygapophyseal processes.

***Thaumastophis missiaeni* Rage et al., 2008**

Described on the basis of 4 vertebrae from a lower Eocene lignite mine in India (Rage et al., 2008). Additional material was reported from contemporaneous nearby localities (Smith et al., 2016); in addition, Zaher et al. (2021) suggested that indeterminate 'colubroid' material from the 'southern cluster' of IndoPakistan (Rage et al., 2003) also pertains to the species. Diagnostic features (Zaher et al., 2021): laminar and slightly protruding prezygapophyses processes, parazygosphenal foramina variably

present, anteriorly thin and posteriorly slightly expanded neural spine in middle and posterior trunk, neural spine invading zygosphenal roof, para- and prezygapophyses distinct, and cotyle depressed. Zaher et al. (2021) considered that it shares two uniquely derived characters of Colubroidea (the presence of a uniformly thin, blade-like neural spine on trunk vertebrae and expanded laminar haemapophyses in the caudal vertebrae) and furthermore a derived character of Colubriiformes (the extension of the neural spine onto the zygosphenal roof); however, the posterior end of the neural spine is (still) slightly expanded, suggesting it is outside crown Colubriiformes.

***Titanoboa cerrejonensis* Head et al., 2009**

First described on the basis of 186 trunk vertebrae and ribs from the Palaeocene of the Cerrejón mine of Colombia (Head et al., 2009). Additional material, including cranial bones, has been reported but not yet described (Head et al., 2013). This is the largest known snake of all time. Diagnostic apomorphies (Head et al., 2009): extremely large size, T-shaped neural spine, and very small subcentral and lateral foramina. Preliminary phylogenetic analyses including cranial material reportedly supported an affinity with Neotropical Boidae (Head et al., 2013).

Genus *Totlandophis* Holman and Harrison, 1998a

Established for *T. thomasaе* from the upper Eocene of Europe (Holman and Harrison, 1998a). A second species, *T. americanus*, was reported from the lower Oligocene of North America (Holman and Harrison, 2001). The latter authors seem to have regarded the upturned zygosphenon as an apomorphic character uniting the two species.

***Totlandophis americanus* Holman and Harrison, 2001**

Described on the basis of 6 trunk vertebrae from a lower Oligocene fissure fill in Florida (Holman and Harrison, 2001). No additional material reported; variation noted. Holman and Harrison (2001) gave minor features, principally of the neural arch, as distinguishing this species from the genotype, *T. thomasaе*.

***Totlandophis thomasaе* Holman and Harrison, 1998a**

This, the genotype, species was described on the basis of 18 trunk vertebrae from the upper Eocene of Hordle Cliff, England (Holman and Harrison, 1998a). No additional material reported; intracolumnar variation unknown. Holman and Harrison (1998a) regarded the slightly upturned zygosphenon as a unique feature, but the taxon was otherwise not differentiated from other fossil or living constrictors except 'Boinae'. The apparent step at the posterior margin of the zygosphenon is reminiscent of *Paulacoutophis perplexus* from Itaboraí (see above).

Tropidophiidae indet.

Early discussions of the presence of 'Tropidophiidae' in Europe took place at a time when that taxon was taken to include the dwarf boa groups Tropidophiinae (=Tropidophiidae s.s. here) and Ungaliophiinae. The monophyly of the taxon 'Tropidophiidae' so constituted has been in dubious for some time (Zaher, 1994). Because a number of fossil taxa have been assigned to the family, most notably from Europe and Africa, which would mark a significant range expansion, it is worth reviewing the morphological evidence that support Tropidophiidae s.s.

Recent morphological evidence (published synapomorphies) for the monophyly of Tropidophiidae s.s. are predominantly in the skull:

- Frontal subolfactory process descending lamina/parasphenoid rostrum relationship absent [Gauthier et al. (2012) char. 41(0)]
- Frontal supraorbital shelf present and demarcated medially by narrow shallow longitudinal furrow often bearing line of foramina on the dorsal surface of the frontal [Gauthier et al. (2012) char. 51(2)]
- Parietal, middle third wide in dorsal view [Gauthier et al. (2012) char. 92(1)]
- Maxilla suborbital ramus extends posteriorly to posterior quarter of orbit [Gauthier et al. (2012) char. 120(1)]
- Nervus ethmoidalis medialis enclosed posteriorly in septomaxilla [Gauthier et al. (2012) char. 208(3)]
- Vomeronasal organ, cupola fenestrated medially, even if only narrowly [Gauthier et al. (2012) char. 210(0)]
- Margin of vomer at opening of vomeronasal organ flat [Gauthier et al. (2012) char. 219(0)]
- Vomer septum transversely fenestrated [Gauthier et al. (2012) char. 223(1)]
- Palatine, vomerine process buttresses vomer splays laterally at tips to buttress vomer posteriorly [Gauthier et al. (2012) char. 235(1)]
- Internal articulation of palatine with pterygoid short (0) [Scanferla and Smith (2020a) char. 92(0)]
- Lateral edge of maxillary ramus of ectopterygoid slopes medially [Gauthier et al. (2012) char. 279(0); cf. Scanferla and Smith (2020a) char. 97(0): the lateral edge of the ectopterygoid is straight]
- Dorsal head of postorbital ('jugal' of Scanferla and Smith, 2020a) with prominent posterodorsal knob articulating with parietal [Scanferla and Smith (2020a) char. 54(1)]
- Trigeminal foramen or foramina enclosed by prootic [Gauthier et al. (2012) char. 321(3); also Scanferla and Smith (2020a)]
- Vidian canal caudal opening: anterior margin at basisphenoid-prootic suture [Gauthier et al. (2012) char. 337(1)]
- Supraoccipital with broad (i.e., as long as or more than parietal) contact to prootic [Scanferla and Smith (2020a) char. 118(1)]
- Maxillary tooth row extends to posterior third of orbit [Gauthier et al. (2012) char. 415(1); cf. Scanferla and Smith (2020a), char. 69(0)]
- Coronoid bone absent [Scanferla and Smith (2020a) char. 152(1)]. Note that the interpretation of this feature as a synapomorphy depended also on the species of *Tropidophis* studied, as the presence of the bone is interspecifically variable in that genus (McDowell, 1975).
- Coronoid process on lower jaw formed by compound bone only [Scanferla and Smith (2020a) char. 157(2)]

Additional osteological characters that have been mentioned in a pre-phylogenetic context (and not yet evaluated in phylogenetic analyses) include: supratemporal extending only slightly beyond cranial wall, prearticular ala with apex well behind dentary, and triangular quadrate with dorsally displaced stapedial articulation (McDowell, 1975). It should be noted in this context that while examined *Tropidophis* and *Trachyboa* have such a prearticular ala, *Ungaliophis* has a surangular ala instead, and *Exiliboa* has both. Scanferla and Smith (2020a) also document a dorsally situated stapedial articulation in *Charina bottae*. Scanferla (2016) documents strong ontogenetic variation in the posterior extent of the supratemporal and suggests that a

supratemporal that does not extend far beyond the braincase may be a paedomorphic trait of small constrictors.

Note also that Gauthier et al. (2012, char. 121) found a posterior expansion of the maxilla at the ectopterygoid articulation to be a synapomorphy uniting Tropicophiidae s.s. and Caenophidia, whereas McDowell (1975) argued that the former is distinguished from the latter by the *lack* of a posteromedial ‘process’ of the maxilla. The apparent contradiction appears to arise from the way in which the character is defined. Examined tropidophiids in fact have a distinct, narrow-based, medially directed process at the posterior end of the maxilla, broadening it, but this feature is not exactly the same as McDowell’s (1975) character, which appears to describe a general broadening for the ectopterygoid articulation without a distinct, narrow-based process (whereby his choice of the word ‘process’ for the caenophidian state is confusing). Careful examination of the CT scans of *Ungaliophis continentalis* and *Exiliboa placata* show the hint of a tropidophiid-like process there, but it is not nearly as strong or distinct as in Tropicophiidae s.s.

Furthermore, it has been recognised since Bogert (1968) that Tropicophiidae s.s. is distinguished from constrictors by the presence of hypapophyses throughout the trunk, although they may become diminished posteriorly, as in *Tropicophis feicki* (pers. obs.), noted previously by Bogert (1968). We note that in all species of Tropicophiidae s.s. examined by us, the hypapophysis of mid-trunk vertebrae is not only present and broad but additionally has a strong anteroventral corner. The corner is present even in *Tropicophis feicki*, which Bogert (1968: fig. 8C) appears to illustrate as being rounded.

Finally, Szyndlar and Böhme (1996) called attention to some remarkable features of the caudal vertebrae in constrictors, and their observations were expanded by Szyndlar and Rage (2003) and Szyndlar et al. (2008) to include Tropicophiidae s.s. According to the latter authors, a longitudinal sequence of subcentral structures is typical of Tropicophiidae s.s.: the anterior caudals bear hypapophyses, the middle caudals have typical haemapophyses, and the posterior caudals bear structures similar to haemal keels, sometimes with a median pit or groove.

Szyndlar and Böhme (1996) also examined the caudal vertebrae of constrictors. Sanziniidae (*Sanzinia* and *Acrantophis*) lack haemapophyses in the tail and have rather a haemal keel (Szyndlar and Böhme, 1996); in *Sanzinia*, at least, the haemal keel is sometimes grooved but there is no pattern of grooved and ungrooved haemal keels, the two occurring ‘at random’ (Szyndlar and Rage, 2003). On the other hand, Smith (2013) found haemapophyses to be present in *Sanzinia*. In *Calabaria*, the anterior (but not anterior-most) post-cloacal vertebrae have a haemal keel that diminishes posteriorly, and ‘indistinct outlines’ of haemapophyses are present in the remainder of the tail (Szyndlar and Böhme, 1996). In other constrictors, haemapophyses first appear at varying distance from the cloacals (on the first or second post-cloacal in Boidae and Pythonidae, on the third in *Loxocemus*, more posteriorly in *Eryx*). In no other taxon, however, did Szyndlar et al. (2008) find the tropidophiid (s.s.) pattern.

A number of taxa have been intensively discussed as or referred to Tropicophiidae s.s. over the last two decades: *Rottophis*, *Falseryx*, *Platyspondylia*, *Szyndlaria*, and an unnamed taxon from the Fayum. Given our understanding of tropidophiid osteology, it is clear that almost all of these taxa (*Rottophis*, *Falseryx*, *Platyspondylia*, *Szyndlaria*) would have to be considered stem representatives of Tropicophiidae s.s., as they lack some of the vertebral (and, where known, cranial) synapomorphies of that crown clade given above (see individual taxon entries). The only possible exception is the Fayum taxon, from which no cranial material is known. None of

the aforementioned taxa has been included in a phylogenetic analysis. There is no evidence that they form a clade.

It is worth considering the evidence of caudal vertebrae more generally. First of all, the lack of haemapophyses on anterior caudal vertebrae is not so unusual, as a varying number of the anterior-most post-cloacal vertebrae in extant constrictors lack them (Szyndlar and Böhme, 1996; see above). Thus, it is really the reduction of haemapophyses in the distal tail to a (grooved) haemal keel that is so unusual in Tropidophiidae s.s. Second, while the sequence of subcentral structures in Tropidophiidae s.s. might be unique amongst extant taxa, it is well recognised that haemapophyses have become reduced in different ways several times amongst Constrictores, the other plausible higher taxon to which some of these taxa may belong. Szyndlar and Böhme (1996) documented their loss throughout the tail in Sanziniidae (questioned for *Sanzinia* by Smith, 2013); Szyndlar et al. (2008) and Smith (2013) noted their complete loss throughout the tail in Ungaliophiinae; and Szyndlar and Böhme (1996) stated that haemapophyses are reduced to 'indistinct outlines' in *Calabaria*. In other words, haemapophyses become reduced in several different ways among known constrictors. Perhaps this has happened in some extinct lineages as well. Additionally, it is conceivable that a tropidophiid (s.s.)-like pattern is an intermediate stage on the way to a more reduced pattern, like in *Calabaria* or Ungaliophiinae.

Szyndlar et al. (2008) regarded caudal vertebral morphology to be more conservative than trunk vertebral morphology and therefore more compelling evidence of relationships. It is indubitable that caudal vertebral features are important (Szyndlar and Böhme, 1996; Szyndlar and Rage, 2003; Szyndlar et al., 2008; Smith, 2013) and were long overlooked, but they do not occupy a privileged position in a hierarchy of character evidence. Where other apomorphic character evidence in the same taxon suggest alternative relations, then they become ambiguous.

While we consider it entirely plausible that some of the taxa examined above are in fact representatives of the total clade of Tropidophiidae s.s. (and *Falseryx neervelpensis* fully complies with the tropidophiid (s.s.) caudal pattern), we feel that the evidence is not definite at present. Either apomorphic evidence is lacking (*Platyspondylia*, except perhaps *Platyspondylia* sp. from Saint-Privat-des-Vieux), or the morphological features are not derived in the same way as in Tropidophiidae s.s. (*Szyndlaria*, *Rottophis*), or derived vertebral proportions (elongation of trunk vertebrae) suggest affinities with Ungaliophiinae (*Falseryx*, *Platyspondylia*, *Rottophis*).

Only in the unnamed Fayum taxon (McCartney and Seiffert, 2016) is apomorphic morphological evidence both consistent in detail with Tropidophiidae s.s. and not contradicted by any other apomorphic evidence. The mid-trunk vertebrae of this taxon are the only described fossils that display the unique morphology of Tropidophiidae s.s.: the projecting, blade-like hypapophysis ('haemal keel' of McCartney and Seiffert, 2016) with a sharp anterior corner (see above). The taxon also has paracotylar foramina. The presence of normal haemapophyses on the single known post-cloacal vertebra does not contradict this assignment, as they occur in at least part of the tail series in extant Tropidophiidae s.s., i.e., in the mid-caudal region (Szyndlar and Rage, 2003; Szyndlar et al., 2008). There is no evidence at present bearing on the position of this taxon in the total clade of Tropidophiidae s.s. Thus, we view the Fayum taxon as the most plausible of proposed tropidophiids.

To be sure, if the total clade of Tropidophiidae s.s. was present also in Africa, it is entirely possible that it entered Europe. There is some morphological evidence that *Szyndlaria*, *Falseryx* and/or *Rottophis* are related to Tropidophiidae s.s., but given the inconsistencies, it cannot be certain whether all of them are, and at present we have no

way to decide. Therefore, we treat these taxa as *Alethinophidia incertae sedis*. We welcome further attempts to specify the phylogenetic relationships of these taxa.

***Tuscahomaophis leggetti* Holman and Case, 1992**

Described on the basis of 13 trunk vertebrae from the Palaeocene of the Gulf Coast, USA (Holman and Case, 1992). No additional material reported; intracolumnar variation unknown. Diagnostic features (Holman and Case, 1992): vertebrae short, smooth centrum with small hypapophysis at posterior end, depressed neural arch, lateral walls of posterior neural arch almost vertical, prezygapophyseal articular facets small and obliquely oriented, prezygapophyseal buttresses with sharp anterolateral border, paradiapophyses elevated, common zygantral chamber, parazygantral foramina present in fossae, and pterapophyses lacking. Holman and Case (1992) considered the species the sister of Palaeophiidae, a conclusion consistent also with Averianov's (1997: 140) views. They excluded it from Palaeophiidae because it lacks pterapophyses. We treat it as *Alethinophidia incertae sedis*.

***Vectophis wardi* Rage and Ford, 1980**

Described on the basis of over 60 vertebrae from two localities in the upper Eocene of the Isle of Wight, England. No additional material reported; intracolumnar variation well known. Genus monotypic. Main apomorphic diagnostic features (Rage and Ford, 1980): square vertebral outline; long, robust and tall neural spine; and narrow centrum. We follow Rage and Ford (1980) in considering this species *Alethinophidia incertae sedis*.

Genus *Waincophis* Albino, 1987

Established for *Waincophis australis* Albino, 1987. Material from Itaboraí was referred to *Waincophis* sp. and cf. *Waincophis* by Rage (2001). Rage (2001) gave a detailed diagnosis, amongst which the presence of paracotylar foramina is most notable. Phylogenetic evidence for the monophyly of the genus has not been presented. The genus was initially regarded as of uncertain subfamily ('el fósil no puede ser determinado con seguridad a nivel subfamiliar'; Albino, 1987: 64). Rage (2001) considered it a 'boine'. Both views would correspond to *Constrictores incertae sedis* in the present classification

***Waincophis australis* Albino, 1987**

Described on the basis of 1 vertebra from the lower Eocene of San Jorge Basin (Albino, 1987). No additional material reported; intracolumnar variation unknown. Diagnostic features (Albino, 1987), excepting those given for the genus by Rage (2001): small size, zygosphenes thin, haemal keel flattened, and cotyle and condyle slightly depressed.

***Waincophis cameratus* Rage, 2001**

Described on the basis of 49 trunk vertebrae from the lower Eocene fissure fills of Itaboraí, Brazil (Rage, 2001). An additional 5 trunk vertebrae from the same area were compared to the species (Rage, 2001). Intracolumnar variation well known. Diagnostic features with respect to congeners (Rage, 2001): large size, less depressed vertebrae, and anteroposteriorly shorter neural spine.

***Waincophis pressulus* Rage, 2001**

Described on the basis of 35 trunk vertebrae from the lower Eocene fissure fills of Itaboraí, Brazil (Rage, 2001). An additional 14 trunk vertebrae from the same area were compared to the species (Rage, 2001). Intracolumnar variation well known. Diagnostic features with respect to congeners (Rage, 2001): large size, shorter and more depressed vertebrae, narrower zygosphene, broader centrum, clearly depressed cotyle and condyle, smaller neural canal, neural spine with thick posterior portion and anterior keel, and strong median lobe on zygosphene.

***Woutersophis novus* Rage, 1980**

Described on the basis of an unknown number of trunk vertebrae from several localities in the Lutetian of the North Sea Basin around Brussels (Rage, 1980). Here we have not taken into account mere 'possible' occurrences mentioned by Rage (1980). No additional material has since been referred; intracolumnar variation was noted. Genus monotypic. The following features, amongst others, were given as diagnostic of the species, or suggested to be so (Rage, 1980; 1984a): vertebrae elongate and laterally compressed, short hypapophysis present also on mid-trunk vertebrae, synapophyses situated very deep, neural arch very vaulted. Despite differences in the shape of the centrum to *Nigerophis mirus*, Rage (1984a) maintained this species in Nigerophiidae.

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