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A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India

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The early Eocene (Ypresian) Cambay Formation of Vastan Lignite Mine in Gujarat, western India, has produced a diverse assemblage of snakes including at least ten species that belong to the Madtsoiidae, Palaeophiidae (*Palaeophis* and *Pterosphenus*), Boidae, and several Caenophidia. Within the latter taxon, the Colubroidea are represented by *Russelophis crassus* sp. nov. (Russellophiidae) and by *Procerophis sahnii* gen. et sp. nov. *Thaumastophis missiaeni* gen. et sp. nov. is a caenophidian of uncertain family assignment. At least two other forms probably represent new genera and species, but they are not named; both appear to be related to the Caenophidia. The number of taxa that represent the Colubroidea or at least the Caenophidia, i.e., advanced snakes, is astonishing for the Eocene. This is consistent with the view that Asia played an important part in the early history of these taxa. The fossils come from marine and continental levels; however, no significant difference is evident between faunas from these levels. The fauna from Vastan Mine includes highly aquatic, amphibious, and terrestrial snakes. All are found in the continental levels, including the aquatic palaeophiids, whereas the marine beds yielded only two taxa. Vastan Mine is only the second locality in which the palaeophiids *Palaeophis* and *Pterosphenus* co-occur. The composition of the fauna from Vastan is on the whole similar to that of the early Eocene of Europe; however, comparisons with early Eocene faunas of other continents are not possible because they are poorly known or unknown.

Key words: Serpentes, Caenophidia, Eocene, Vastan, India.

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Introduction

Fossil snakes from Asia are poorly known. The discovery of localities yielding fossils from this continent is therefore of great interest. The early Eocene Vastan Lignite Mine (Gujarat, India) is one of these rare localities (Rana et al. 2004). Vastan Mine is located northeast of Surat in Gujarat Province, western India. It includes marine and continental beds belonging to the Cambay Formation, of middle to late Ypresian age (Rana et al. 2004; Rose et al. 2006; Sahni et al. 2006). The snake fauna from the Vastan Mine is diverse and comes mostly from the continental lenses but also from the underlying marine beds that are both situated within one meter above lignite 2 (see Sahni et al. 2006 and Rana et al. 2008). Several of the snakes represent new taxa at the genus and species level, but some of them are not named pending discovery of better preserved specimens.

Institutional abbreviations.—GU/RSR/VAS, Department of Geology, H.N.B. Garhwal University, Uttaranchal, India, R.S. Rana collection from Vastan (hereafter referred to as VAS in the text).

Systematic paleontology

Order Squamata Oppel, 1811

Suborder Serpentes Linnaeus, 1758

Family ?Madtsoiidae Hoffstetter, 1961

Remarks.—The Madtsoiidae are primarily Gondwanan and they entered southernmost Europe during the latest Cretaceous. From Gondwana, they are known from the Late Cretaceous–Eocene of South America and Africa, the latest Cretaceous of Madagascar, and the Eocene–Pleistocene of Australia.

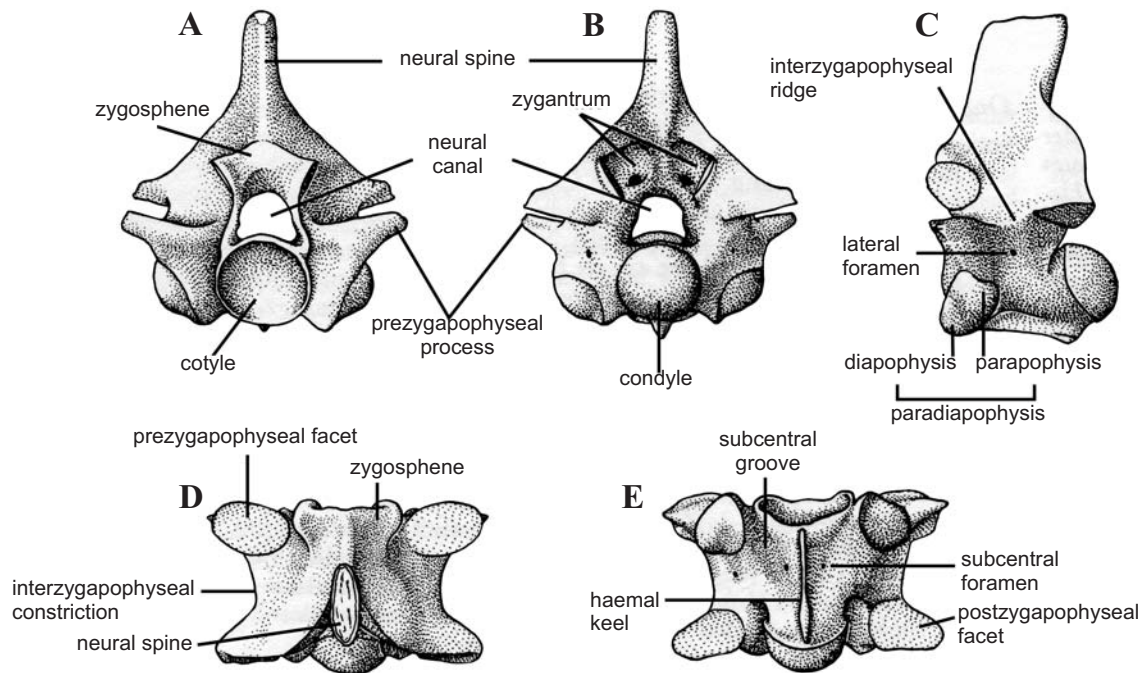


Fig. 1. Nomenclature of a snake vertebra (mid-trunk), as exemplified by the living *Python regius* (Boidae), anterior (A), posterior (B), left lateral (C), dorsal (D), and ventral (E) views (modified from Rage 1984).

lia (Rage 1998); in India, they were formerly reported from the latest Cretaceous (Rage et al. 2004) and perhaps the early Eocene (Rage et al. 2003).

?Madtsoiidae indet.

Fig. 2A.

Material.—One incomplete trunk vertebra (VAS 1049) from the continental beds of the early Eocene Cambay Formation, Vastan Lignite Mine, Gujarat, India.

Description and comparisons.—This vertebra is short and wide and its zygosphenes are comparatively narrow and thick. Such morphology occurs in booids and madtsoiids. The lack of any trace of prezygapophyseal processes and the marked lateral protrusion of the diapophyses suggest referral to the Madtsoiidae. Unfortunately, the posterior part of the neural arch, which bears an apomorphic character of the group, is broken away. Therefore, referral to madtsoiids cannot be definitely confirmed. However, if this specimen really belongs to madtsoiids, comparisons within this family are of interest. VAS 1049 is very short, which clearly distinguishes it from the small madtsoiids except for *Rionegrophis* (latest Cretaceous of South America), which is referred to this family with reservation (Albino 1987). The pronounced shortening is reminiscent of all large madtsoiids and *Rionegrophis*. The large madtsoiids are *Wonambi* (Plio-Pleistocene of Australia; Scanlon 2005), *Yurlunggur* (Oligocene and Miocene of Australia; Scanlon 2006), and the species of the *Madtsoia*–*Gigantophis* assemblage (Late Cretaceous of Africa, Madagascar and southeasternmost Europe; Paleocene and Eocene of South America, Eocene of Africa; Rage 1998). However, aside from its size, VAS 1049 differs from these

large forms in having a markedly broader section of neural canal and more laterally projecting prezygapophyses. Finally, in addition to vertebral shortness, VAS 1049 shares two characters with *Rionegrophis*, namely the triangular section of the neural canal and the marked dorsal position of the subcentral ridges with regard to the haemal keel. These three features may suggest affinities between these two snakes. Unfortunately, they are represented each by a single, poorly preserved vertebra, which prevents reliable inference. VAS 1049 differs from the madtsoiids formerly reported from India in being markedly shortened.

Family Palaeophiidae Lydekker, 1888

Genus *Palaeophis* Owen, 1841

Type species: *Palaeophis toliapicus* Owen, 1841; Ypresian, early Eocene, western Europe.

Remarks.—*Palaeophis* includes several species whose vertebrae are slightly to strongly compressed laterally. Two assemblages of species, or grades, may be distinguished (Rage 1984; Rage et al. 2003). The primitive grade comprises species whose vertebrae are weakly compressed and that have low pterapophyses, whereas species of the advanced grade have vertebrae clearly compressed laterally and well-developed pterapophyses. However, this genus may be a paraphyletic assemblage including all palaeophiine species that do not belong to *Pterospheenus*.

Stratigraphic and geographic range.—Latest Cretaceous of Africa; Paleocene of Africa and North America; early Eocene of Africa, North America, Europe, Central Asia and India; middle Eocene of Africa, North America, Europe and

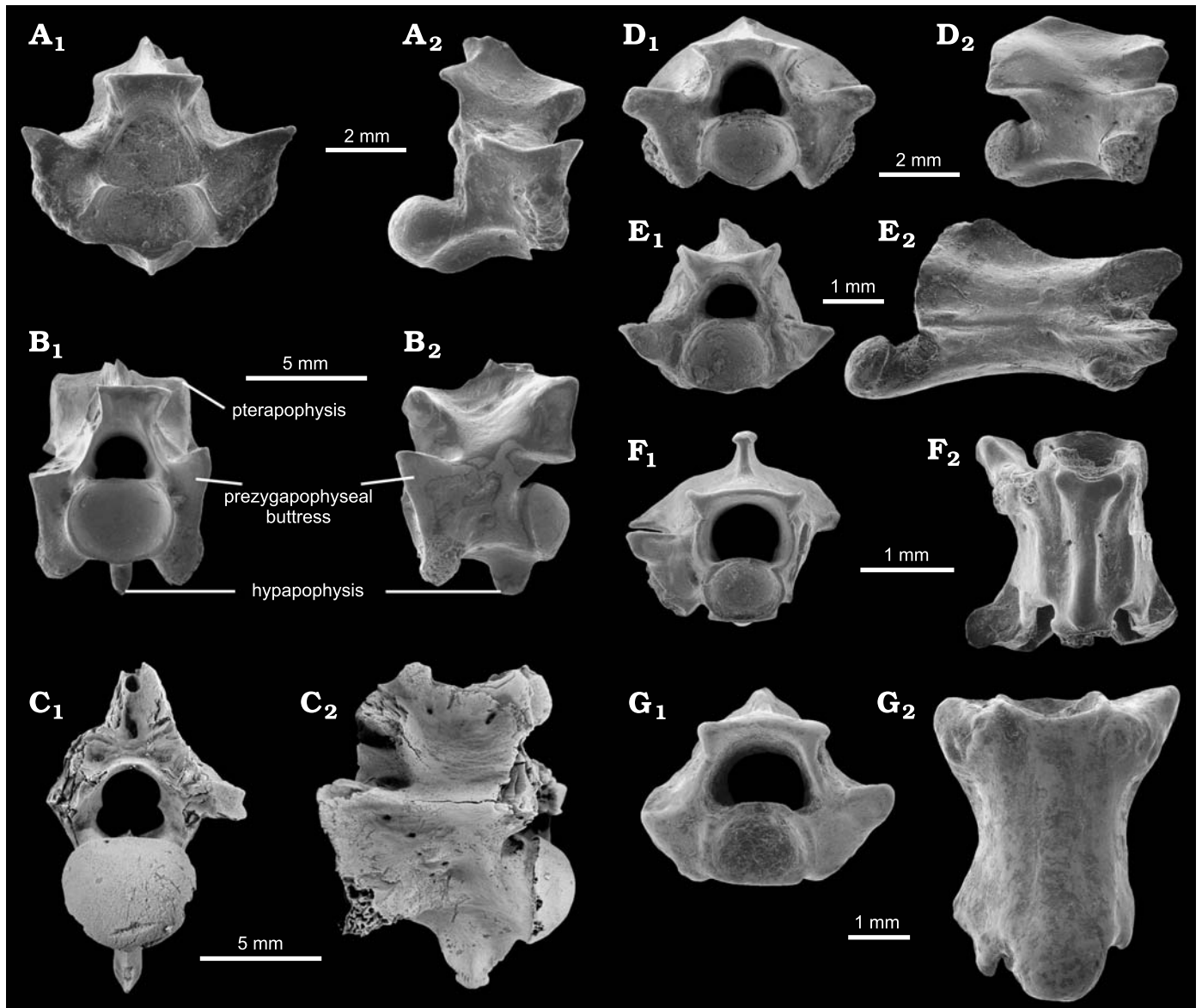


Fig. 2. Snakes from the early Eocene of Vastan (Cambay Formation, Gujarat, western India). **A.** ?Madtsoiidae indet., VAS 1049, trunk vertebra, anterior (A₁) and right lateral (A₂) views. **B.** Palaeophiidae, *Palaeophis* sp., VAS 1037, trunk vertebra, anterior (B₁) and left lateral (B₂) views. **C.** Palaeophiidae, *Pterosphenus* sp., VAS 1009, trunk vertebra, posterior (C₁) and left lateral (C₂) views. **D.** Boidae indet., VAS 1010, trunk vertebra, anterior (D₁) and right lateral (D₂) views. **E.** ?Russellophiidae indet., VAS 1050, trunk vertebra, anterior (E₁) and right lateral (E₂) views. **F.** Caenophidian snake, gen. et sp. indet. A, VAS 1021, trunk vertebra, anterior (F₁) and ventral (F₂) views. **G.** Caenophidian snake, gen. et sp. indet. B, VAS 1051, trunk vertebra, anterior (G₁) and ventral (G₂) views.

Central Asia; late Eocene of North America and perhaps Central Asia (Rage et al. 2003; Parmley and De Vore 2005).

Palaeophis sp.

Fig. 2B.

Material.—Twenty-two vertebrae: Three trunk (VAS 1001, 1002, 1005) and two caudal (VAS 1003, 1004) vertebrae from the marine beds; fifteen trunk (VAS 1007, 1008, 1024–1031, 1034–1037, 1055) and two caudal (VAS 1032, 1033) vertebrae from the continental beds. All from the early Eocene Cambay Formation, Vastan Lignite Mine, Gujarat, India.

Description and comparisons.—The characters of palaeo-

phiids are clearly apparent: vertebrae more or less compressed laterally; presence of pterapophyses and of a hypapophysis; paradiapophyses located low on the centrum; articular surface of the paradiapophyses simple; prezygapophyseal buttresses compressed, forming a vertical ridge that extends from the dorsal part of the diapophysis to the tip of the articular facet; prezygapophyseal facets small. In addition, the base of the neural spine is clearly separated from the anterior border of the zygosphenon, which points to the genus *Palaeophis*. Strong variation affects the lateral compression; it is difficult to determine whether it represents intracolumnar variation or indicates the presence of more than one species. We suspect that

two species are present, belonging to the “primitive” and “advanced” grades of *Palaeophis* respectively, but this cannot be confirmed based on the specimens at hand.

Genus *Pterosphenus* Lucas, 1899

Type species: Pterosphenus schucherti Lucas, 1899; Jacksonian, latest Eocene, southeastern USA.

Stratigraphic and geographic range.—Early Eocene of India; middle Eocene of eastern Asia and North America; late Eocene of Africa, North and South America, and perhaps Central Asia (Rage et al. 2003; Head et al. 2005).

Pterosphenus sp.

Fig. 2C.

Material.—One trunk vertebra (VAS 1009) from the continental beds of the early Eocene Cambay Formation, Vastan Lignite Mine, Gujarat, India.

Description and comparisons.—A single, poorly preserved vertebra represents *Pterosphenus*. It is strongly compressed laterally. The zygosphenal roof is arched dorsally and the top of the anterior border of the zygosphenon forms the base of the anterior border of the neural spine. This feature characterizes *Pterosphenus* (except most vertebrae of *Pt. kutchensis* Rage, Bajpai, Thewissen, and Tiwari, 2003) and is unknown in *Palaeophis* (Rage 1983). The paradiapophyses of this vertebra are markedly separated from each other, which demonstrates that it cannot be referred to *Pt. kutchensis* (early Eocene of India) in which paradiapophyses originate from a common base (Rage et al. 2003). This specimen does not provide other information at species level; it is referred to as *Pterosphenus* sp. The fossil from Vastan Mine may be the earliest representative of the genus.

Infraorder Henophidia Nopcsa, 1923

Superfamily Booidea Gray, 1825

Family Boidae Gray, 1825

Boidae indet.

Fig. 2D.

Material.—Three trunk vertebrae (VAS 1010, 1038, 1052) from the continental beds of the early Eocene Cambay Formation, Vastan Lignite Mine, Gujarat, India.

Remarks.—These vertebrae do not show any character that would differentiate them from the standard boid morphology. The marked variation of the size of the specimens suggests that more than one taxon is present. VAS 1052 is indeed distinctively smaller than the two other vertebrae and it does not show juvenile features.

Infraorder Caenophidia Hoffstetter, 1939

Remarks.—The Caenophidia are regarded as the most advanced snakes. They include the Acrochordoidea and Colubroidea, which are sister groups. The Acrochordoidea comprise the living Acrochordidae and the extinct Nigerophiidae. The Colubroidea include the living Atractaspididae, Elapidae,

Viperidae, and paraphyletic colubrids, and the extinct Anomalophiidae and Russellophiidae, which are regarded as primitive colubroids. McDowell (1987) assigned the Anomalophiidae and Russellophiidae, as well as the Palaeophiidae, to the Acrochordoidea; but Rage and Prasad (1992: 90) noted that the character that links these families to the Acrochordidae (i.e., the morphology of the prezygapophyses) may be an adaptation to aquatic life without systematic value.

Superfamily Colubroidea Oppel, 1811

Family Russellophiidae Rage, 1978

Comments.—The Russellophiidae include only two named genera: *Russellophis* from the Eocene of Western Europe and *Krebsophis* from the Cenomanian of Sudan (Rage and Werner 1999). In addition, an indeterminate genus is likely present in the Paleocene of Brazil (Rage 1998). Russellophiids are known only from vertebrae. They are easily characterized by a suite of characters: vertebrae elongate; neural arch very vaulted; prezygapophyseal facets horizontal or weakly inclined, generally below the horizontal contrary to almost all other snakes; prezygapophyseal buttresses compressed, forming an anterolateral vertical ridge; frequent presence of a tubercle on the anterior face of the latter ridge; absence of prezygapophyseal processes; ventral face of centrum narrow, well-limited laterally by marked subcentral ridges; absence of hypapophyses in the mid- and posterior trunk regions.

The material from Vastan Mine includes a new species of russellophiid that appears to be morphologically intermediate between *Russellophis* and *Krebsophis*. It is tentatively referred to *Russellophis*.

Genus *Russellophis* Rage, 1975

Type species: Russellophis tenuis Rage, 1975; Ypresian, early Eocene, western Europe.

Remarks.—Aside from the species from Vastan (assuming the latter actually belongs to *Russellophis*), the genus was previously known only by the type species and by indeterminate forms. The type species is restricted to the standard levels MP 8+9 and MP 10 (Ypresian, early Eocene) of western Europe. *Russellophis* sp. was reported from the earliest Eocene (MP 7) to the late Eocene (MP 19) (Rage and Augé 1993).

Stratigraphic and geographic range.—Eocene of western Europe and likely India.

Russellophis crassus sp. nov.

Fig. 3.

Etymology: Latin *crassus*, thick, in reference to the vertebral morphology.

Type material: Holotype: One mid-trunk vertebra (VAS 1039). Paratypes: Eight vertebrae: six trunk (VAS 1011, 1012, 1040–1042, 1056) and two caudal (VAS 1013, 1043) vertebrae. All from the continental beds of the early Eocene Cambay Formation.

Other material: Two larger trunk vertebrae (VAS 1044, 1045) from the continental beds may represent overgrown specimens, but their assignment to the species cannot be confirmed.

Type locality: Vastan Lignite Mine, northeast of Surat, Gujarat, India.

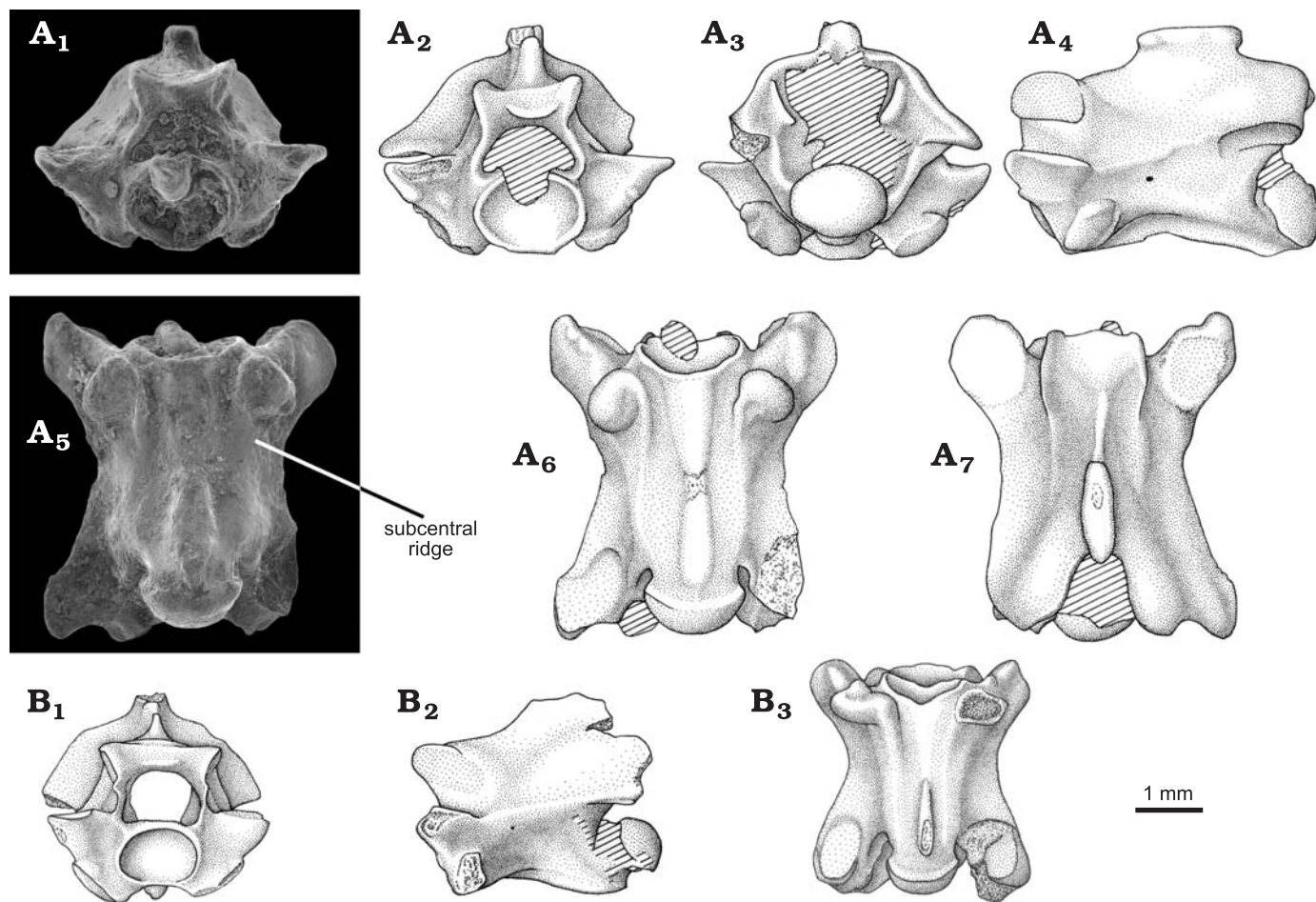


Fig. 3. Russellophiid snake, *Russellophis crassus* sp. nov., from the early Eocene of Vastan (Cambay Formation, Gujarat, western India). **A.** VAS 1039, mid-trunk vertebra, holotype, in anterior (A_1 , A_2), posterior (A_3), left lateral (A_4), ventral (A_5 , A_6), and dorsal (A_7) views. **B.** VAS 1011, trunk vertebra from the anterior/mid-trunk transition in anterior (B_1), left lateral (B_2), and ventral (B_3) views.

Type horizon: Early Eocene (middle to late Ypresian) continental beds of Cambay Formation.

Diagnosis.—Differs from *Russellophis tenuis* and *Krebsophis thobanus* Rage and Werner, 1999 in having a narrower and thicker zygosphene. Further differs from *R. tenuis* by its more massive build, larger cotyle and condyle, and more dorsally placed paradiapophyses. Further distinguished from *K. thobanus* by its lamellar and high neural spine, paradiapophyses more extended dorsoventrally, thinner roof of zygantrium, and by the continuity between ventral edge of parapophyses and subcentral ridges.

Description of the holotype.—The holotype is a nearly complete mid-trunk vertebra whose measurements are as follows (in mm): width through prezygapophyses: 4.3; width of zygosphene: 1.6; length of centrum from edge of cotyle to tip of condyle: 3.9; width of interzygapophyseal constriction at narrowest circumference: 2.5.

In anterior view the vertebra is not depressed. The zygosphene is thick and relatively narrow, its roof is concave dorsally, a thin horizontal median lobe standing out against the bulk of the zygosphene. The section of the neural canal is low

and nearly as wide as the zygosphene. The cotyle is almost circular, its width being similar to those of the zygosphene and neural canal. The prezygapophyses strongly project laterally, they lack any trace of prezygapophyseal processes. The prezygapophyseal articular facets are slightly inclined below the horizontal. The paradiapophyses are located rather low but they do not protrude clearly below the cotyle and they face somewhat ventrally. The paracotylar foramina are absent.

In dorsal view, the vertebra is markedly elongate. The interzygapophyseal constriction is shallow and asymmetrical, its most constricted part being shifted anteriorly. The prezygapophyseal facets are nearly circular, without a discernible major axis. The anterior border of the zygosphene forms three weakly projecting lobes (a wide median lobe and narrow lateral ones). The shape of the posterior median notch is obscured by matrix, but it is probably not shallow. The neural spine is lamellar and composed of two portions: a posterior thick part occupying less than one-third of the vertebral length and a thinner anterior part reaching the posterior limit of the zygosphenal roof.

In lateral aspect, the posterior, thick part of the neural spine is rather high. The zygosphenal facets are broad and

situated markedly above the zygapophyseal plane. The pre-zygapophyseal buttress is compressed; it forms a ridge that reaches the lateral tip of the articular facet. A small anterior tubercle is present on this ridge at the level of the top of the paradiapophysis; the tubercle is prolonged posteriorly as a blunt ridge on the lateral face of the buttress. The interzygapophyseal ridge is very salient. The paradiapophysis is rather small and strongly inclined, the top of the diapophysis being located approximately below the posterior limit of the pre-zygapophyseal facet; the articular surface is not subdivided into dia- and parapophyseal areas. The subcentral ridge is well-marked and arched dorsally. The lateral foramina are present.

In ventral view, the surface of the centrum is narrow, flat, limited laterally by well-defined subcentral ridges that hardly diverge anteriorly. The ventral rim of each parapophysis extends posteriorly and grades into the subcentral ridge. The haemal keel is of moderate width; its ventral edge is blunt.

In posterior view, the neural arch is very vaulted and it swells out above the zygantrum. The roof of the zygantrum is thin. Parazygantral foramina are absent.

Intracolumnar variation.—One vertebra (VAS 1011), from the transition between the anterior and mid-trunk regions, differs from the holotype, i.e., from mid-trunk vertebrae, in having a wider zygosphenes, a narrower and deeper haemal keel, less marked subcentral ridges, and paradiapophyses projecting below the cotyle. Posterior trunk vertebrae have the neural arch less vaulted than in more anterior vertebrae (but it remains markedly vaulted). Their haemal keel is wider and more poorly defined in the posterior half of centrum; it is anteriorly limited by short and narrow subcentral grooves. The caudal vertebrae retain a very vaulted neural arch; they differ from posterior trunk ones only in having pleurapophyses (or lymphapophyses) and haemapophyses. It should be noted that there is no conspicuous variation in length or height of the neural spine within the vertebral column.

Intraspecific variation.—The prezygapophyseal facets may be horizontal or slightly inclined either below the horizontal or (in one vertebra) above the horizontal. The tubercle on the anterior face of the prezygapophyseal buttress is not always present. In lateral aspect, the long axis of the paradiapophysis is strongly inclined (e.g., the holotype) or less inclined. These variations are apparently not correlated with the position of the vertebrae in the vertebral column. One feature that cannot be seen on the holotype is observable on other vertebrae: the posterior median notch in the neural arch is deep.

Discussion.—*Russellophis crassus* displays all features of the Russellophiidae (see above). It clearly differs from *Russellophis tenuis* and *Krebsophis thobanus*, the only other known species of the family. The narrow and deep zygosphenes sharply distinguishes *R. crassus* from the two other species in which it is wide to very wide and thin. In addition, although this cannot be regarded as a specific feature, *R. crassus* is larger than *K. thobanus* and *R. tenuis*. In the largest

vertebra of *R. crassus* (VAS 1012), the length of the centrum reaches 3.8 mm although the extremity of the condyle is broken off (it was probably over 4 mm); this measurement is 3.3 mm and 3.6 mm in the largest vertebrae of *K. thobanus* and *R. tenuis*, respectively.

R. crassus is further distinguished from *R. tenuis* by its markedly more massive build, its larger cotyle and condyle, and its less ventrally placed paradiapophyses. In addition, in some vertebrae of *R. crassus* the axis of the paradiapophyses is more inclined posterodorsally than in *R. tenuis*. The tubercle that occurs on the anterior face of the prezygapophysis may be absent in *R. crassus*, whereas it is always present in *R. tenuis* (although sometimes unilaterally).

R. crassus differs from *K. thobanus* in having a lamellar and rather high neural spine, paradiapophyses more extended dorsoventrally, and a markedly thinner roof of the zygantrum despite the massive build of the vertebrae. Moreover, in *R. crassus*, as in *R. tenuis*, the ventral edge of each parapophysis is continuous with the subcentral ridge; in *K. thobanus*, the parapophysis appears to be distinct from the ridge.

Rage and Werner (1999) distinguished *Krebsophis* from *R. tenuis* on the basis of the following characters: (1) vertebrae of *Krebsophis* more heavily-built, although the size is similar; (2) cotyle and condyle larger in *Krebsophis*; (3) neural spine, a low keel for most of its length in *Krebsophis*, a rather high lamina in *R. tenuis*; (4) paradiapophyses more dorsally placed in *Krebsophis*; (5) interzygapophyseal and subcentral ridges more prominent in *Krebsophis*.

R. crassus displays features that occur either in *Krebsophis* or *R. tenuis*. Among the features listed above, it shares characters 1, 2, 4, and 5 with *Krebsophis*. Only character 3 is common to *R. crassus* and *R. tenuis*. However, character 5 directly results from the massiveness (character 1) of the vertebrae; these two characters should not be regarded as distinct. On the other hand, two characteristics shared by *R. crassus* and *R. tenuis* should be added: the thin zygantral roof and the connection between the ventral rim of parapophysis and subcentral ridge. Another character may discriminate between *Krebsophis* on one hand, and *R. crassus* and *R. tenuis* on the other hand: in *Krebsophis*, the dorsoventral extent of the paradiapophysis seems reduced, whereas in the two other species it is “normal”. Finally, on the basis of the morphology of the neural spine, the relation between paradiapophyses and subcentral ridges, the morphology of paradiapophyses, and the thin zygantral roof, the species from Vastan is tentatively referred to *Russellophis*.

?*Russellophiidae* gen. et sp. indet.

Fig. 2E.

Material.—One trunk vertebra (VAS 1050) from the continental beds of the early Eocene Cambay Formation, Vastan Lignite Mine, Gujarat, India.

Description and comparisons.—This vertebra is characterized by its very strong, unusual elongation. The ventral face of the centrum is very narrow, flat, and limited by poorly

marked subcentral ridges; contrary to what is usual in snakes, the ridges are more apparent in the posterior part of the vertebra than anteriorly. The haemal keel is very thin. The prezygapophyseal buttress is identical to that of russellophiids and a small anterior tubercle is present. The prezygapophyseal facets are inclined below the horizontal. The zygosphene is approximately as wide as the cotyle and its roof is concave dorsally. The paradiapophyses are situated low and they face rather ventrally. The neural spine is restricted to the posterior part of the neural arch; it is prolonged anteriorly by a faint ridge. The neural arch is very vaulted.

This vertebra is astonishing. Its elongation is reminiscent of that of extant highly arboreal colubrids. On the other hand, aside from strong elongation, it displays a combination of characters that is typical of the Russellophiidae (see above). Only the poor development of the subcentral ridges is not characteristic of russellophiids. The anterior face of the specimen, with a zygosphene as wide as the cotyle and concave dorsally, is consistent with that of *Russellophis crassus*. Therefore, VAS 1050 might be interpreted as a posterior trunk vertebra of this species, because vertebrae of the posterior trunk region (but not the posteriormost ones) are more elongated than those of the mid-trunk. However, this vertebra is markedly more elongate than the caudal vertebrae of *R. crassus*, so assignment to this taxon does not appear to be possible. In Europe, no such vertebra has been found despite the fact that *Russellophis* is relatively frequent in the Eocene.

Colubroidea indet.

Genus *Procerophis* nov.

Etymology: Latin *procerus*, elongate, in reference to the vertebral morphology.

Type species: *Procerophis sahnii* sp. nov. from Vastan Lignite Mine, northeast of Surat, Gujarat, India; monotypic.

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

Procerophis sahnii sp. nov.

Fig. 4.

Etymology: After Ashok Sahnii (Panjab University, India), for his contributions to the vertebrate paleontology of India.

Type material: Holotype: One posterior trunk vertebra (VAS 1014). Paratypes: Seven vertebrae: one anterior trunk (VAS 1015), two mid-trunk (VAS 1016, 1046), one posterior trunk (VAS 1057), one posteriormost trunk (VAS 1047), and two caudal (VAS 1048, 1058) vertebrae. All from the continental beds of the early Eocene Cambay Formation.

Type locality: Vastan Lignite Mine, northeast of Surat, Gujarat, India.

Type horizon: Early Eocene (middle to late Ypresian) continental beds of Cambay Formation.

Diagnosis.—Differs from all other snakes, except *Nigerophis*, in having prezygapophyseal buttresses compressed, forming a vertical ridge, prolonged by anteriorly oriented prezygapophyseal processes. Differs from *Nigerophis* in having very lightly built vertebrae, a wide and thin zygosphene, a blade-like and long neural spine, well-marked subcentral ridges, and paracotylar foramina (irregularly occurring).

Description of the holotype.—The holotype is a well-preserved vertebra; only its neural spine is damaged. It comes from the posterior trunk region, but it is not a posteriormost trunk vertebra. Usually, the vertebra selected as the holotype is from the mid-trunk. But, in the present case, only two mid-trunk vertebrae are available; one (VAS 1016) is poorly preserved, whereas the other (VAS 1046) is clearly larger (perhaps overgrown) than the other specimens and seemed inappropriate to be selected as the holotype.

The holotype is small, elongate, and very lightly built. Its measurements are as follows (in mm): total length from prezygapophysis to postzygapophysis (prezygapophyseal process excluded): 3.8; width through prezygapophyses: 3.2; width of zygosphene: 1.8; length of centrum from edge of cotyle to tip of condyle: 3.5; width of interzygapophyseal constriction at smallest circumference: 1.9.

In anterior view, the vertebra is wide and slightly depressed. The section of the neural canal is large and its lateral walls are thin. The zygosphene is wide and thin, its roof being slightly convex dorsally. The prezygapophyseal articular facets are nearly horizontal; the prezygapophyseal plane lies clearly above the floor of the neural canal. No part of each prezygapophyseal buttress projects laterally beyond the articular facet, but a strong prezygapophyseal process projects anteriorly. The cotyle is somewhat depressed and it is narrower than the neural canal. A large paracotylar foramen is present on the right side only.

In dorsal view, the vertebra is markedly elongate. The interzygapophyseal constriction is shallow and the apex of its curvature is shifted anteriorly. The zygosphene is wide, it forms three lobes; the lateral lobes are acute whereas the median lobe is wide. The articular facets of the prezygapophyses are elongate and narrow, their major axis being oblique; on either side, a blunt prezygapophyseal process projects anteriorly beyond the facet. The neural spine is thin and long; anteriorly it reaches the roof of the zygosphene. The posterior median notch is shallow.

In lateral aspect, the neural spine is rather high. The zygosphenal articular facets are elongate anteroposteriorly. The prezygapophyseal buttress is compressed, forming a blunt keel that originates just dorsal to the diapophysis. The prezygapophyseal process appears as an anterior projection of the latter keel; it is compressed laterally and its lateral face is slightly concave. The interzygapophyseal ridge is strongly marked and it juts out as a crest in its posterior part. A small, incipient epizygapophyseal spine hardly protrudes posteriorly. The paradiapophyses are small; their articular surfaces are eroded. The condyle is small; it is borne by an elongate neck. The lateral foramina are present.

In posterior view, the neural arch is depressed. The zygosphenal roof is thin. Some foramina open lateral to the zygantrum, but they are not located in fossae.

In ventral view, the centrum is elongate and well-limited laterally by sharp subcentral ridges. The latter ridges are almost parallel. The haemal keel is wide, spatulate and well-

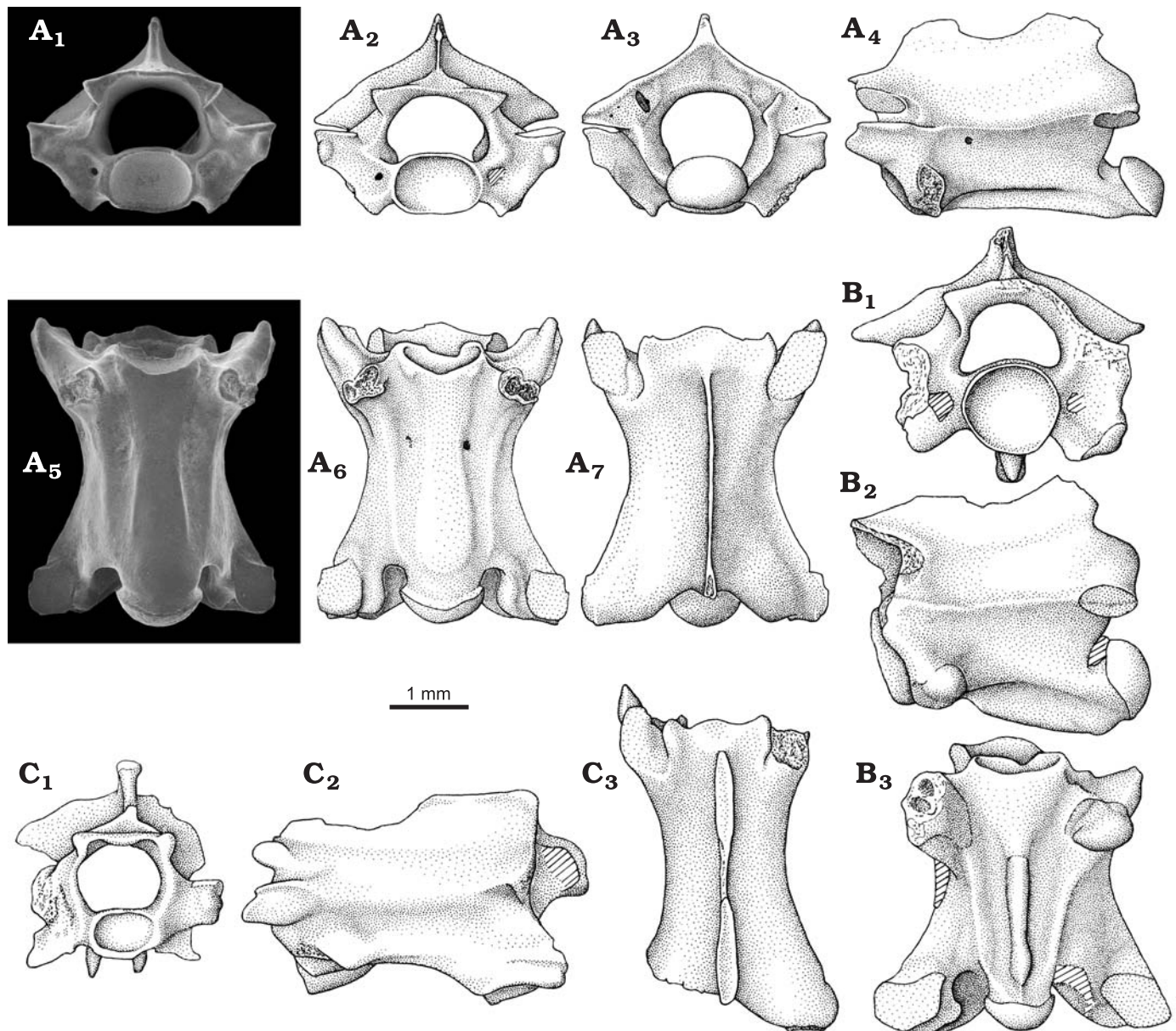


Fig. 4. Colubroid snake, *Procerophis sahnii* gen. and sp. nov., from the early Eocene of Vastan (Cambay Formation, Gujarat, western India). A. VAS 1014, posterior trunk vertebra, holotype, anterior (A₁, A₂), posterior (A₃), left lateral (A₄), ventral (A₅, A₆), and dorsal (A₇) views. B. VAS 1047, posteriormost trunk vertebra, anterior (B₁), left lateral (B₂), and ventral (B₃) views. C. VAS 1048, caudal vertebra, anterior (C₁), left lateral (C₂), and dorsal (C₃) views.

marked off from the centrum. The surface of the centrum is slightly concave. The subcentral foramina are present.

Intracolumnar variation.—The only available anterior trunk vertebra displays the differences that are usually observed between vertebrae from the anterior and mid- or posterior trunk regions. Compared with the holotype, the anterior trunk vertebra is shorter, its neural arch is more vaulted (but it remains weakly vaulted), the paradiapophyses are more distant from the centrum, the ventral face of the centrum is poorly limited laterally and it widens anteriorly, and a hypapophysis is present.

Vertebrae from the mid-trunk region are more elongate than the anterior trunk vertebra but less elongate than the posterior trunk vertebrae. Their neural arch is almost as

vaulted as in the anterior trunk vertebra. Their centrum is elongate but it slightly widens anteriorly. The haemal keel is markedly thinner than that of the holotype and it is not spatulate, its lateral borders being subparallel.

Posterior, but not posteriormost, trunk vertebrae are illustrated by the holotype. One posteriormost trunk vertebra is available. It differs from the holotype in having paradiapophyses more distant from the centrum and cotyle, articular surfaces of paradiapophyses facing more ventrally, deep subcentral grooves, and a deeper and narrower haemal keel. The caudal vertebrae are very elongate and narrow. They are provided with haemapophyses and pleura- or lymphapophyses.

Intraspecific variation.—The presence of paracotylar foramina is confirmed in only two vertebrae; lateral and subcentral

foramina also occur irregularly. Epizygapophyseal spines are present only in the holotype and in the anterior trunk vertebra (not verifiable on VAS 1016). The articular surface of the paradiapophyses is preserved in a single vertebra (VAS 1047): the dia- and parapophyseal areas appear to be poorly differentiated from each other and their sizes are similar.

Discussion.—The light build and marked elongation of the vertebrae as well as the presence of prezygapophyseal processes and paracotylar foramina (although the latter occur irregularly) clearly point to the Colubroidea. However, in extant colubroids, the prezygapophyseal process arises from the non-compressed prezygapophyseal buttress, just below the articular facet, and it projects laterally or slightly anterolaterally. In the extinct families assigned to the Colubroidea, the Anomalophiidae and Russellophiidae, the prezygapophyseal buttress is compressed and it forms a vertical ridge, which is reminiscent of *Procerophis*. In these two families, however, the ridge extends from the diapophysis to the tip of the articular facet and there is no prezygapophyseal process; the ridge does not project beyond the articular facet. In *Procerophis*, the ridge does not reach the tip of the facet as a result of the presence of the prezygapophyseal process, the latter appearing as an outgrowth of the ridge. A similar condition is known in *Nigerophis*, the only nigerophiid in which the morphology of the prezygapophysis is well-known. Nigerophiids do not appear to be colubroid snakes; they are referred to the Acrochordoidea (Rage 1984; McDowell 1987). It is of interest to note that the prezygapophyseal buttress of the extant Acrochordidae displays a morphology that is intermediate between that of Anomalophiidae and Russellophiidae on one hand, and that of *Procerophis* and *Nigerophis* on the other hand. In the Acrochordidae, the buttress is compressed and forms a vertical ridge, as in anomalophiids and russellophiids, but the dorsal part of the ridge protrudes beyond the facet; however, it does not form a process.

Based on the morphology of the prezygapophyses, *Procerophis* appears to be close to the nigerophiids, i.e. the Acrochordoidea. Nevertheless, the very light build, marked elongation that recalls extant arboreal colubrids, and blade-like, long neural spine are colubroid features. Apart from the prezygapophyses, vertebrae of *Procerophis* are similar to those of various modern colubrids. Unfortunately, available vertebral characters are not sufficiently numerous to allow reliable phylogenetic analysis. Moreover, some of them are not discrete (lightening, elongation) and others are affected by polymorphism (paracotylar foramina, epizygapophyseal spines). Thus, despite the morphology of the prezygapophyses, *Procerophis* is referred to the Colubroidea; the association of its very light build and strong vertebral elongation is inconsistent with acrochordoids. Because of the morphology of the prezygapophyses and the reduced paradiapophyses in which the two articular areas are hardly distinct from each other, *Procerophis* cannot be referred to an extant colubroid family. Moreover, in having paracotylar foramina and prezygapophyseal processes, *Procerophis* is more advanced than both the Anomalophiidae and Russellophiidae.

Therefore, like various other fossils, *Procerophis* is a colubroid that cannot be referred to a known family. Among these fossils, *Procerophis* is reminiscent of *Headonophis harri-soni* Holman, 1993 from the latest middle Eocene (formerly regarded as late Eocene) of England. However, *Headonophis* lacks prezygapophyseal processes and its neural spine is short anteroposteriorly (Holman 1993). Other Colubroidea incertae sedis include some unnamed forms and *Vectophis wardi* Rage and Ford, 1980. The oldest colubroid is an unnamed snake from the Cenomanian of Sudan (Rage and Werner 1999); unfortunately, its prezygapophyses are unknown. This fossil differs from *Procerophis sahnii* mainly in having less depressed vertebrae and clearly shorter posterior trunk and caudal vertebrae. Augé et al. (1997) reported a Colubroidea incertae sedis from the early Eocene of France. This snake differs from *Procerophis* in having less elongate vertebrae, clearly shorter prezygapophyseal processes, and a neural spine shorter anteroposteriorly. The species of Colubroidea previously reported from the early Eocene of India (Rage et al. 2003) has vertebrae more massively built and shorter than those of *Procerophis*, and parazygosphenal foramina are present. Based on the presence of parazygosphenal and multiple paracotylar foramina, Head et al. (2005) suggested that this snake may belong to acrochordoids. The vertebra from the late middle Eocene of Myanmar assigned to the Colubroidea by Head et al. (2005) differs markedly from *Procerophis* in being more blocky and shorter than those from Vastan Mine. *Vectophis*, from the same beds as *Headonophis*, was tentatively regarded as a colubroid by Rage et al. (2003). Its vertebrae mainly differ from those of *Procerophis* in being clearly shorter and higher. Whatever its precise relationships, *Procerophis* is a very distinctive snake.

Caenophidia incertae sedis

Genus *Thaumastophis* nov.

Etymology: Greek *Thaumastos*, astonishing, in reference to the prezygapophyseal morphology.

Type species: *Thaumastophis missiaeni* sp. nov. from Vastan Lignite Mine, northeast of Surat, Gujarat, India; monotypic.

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

Thaumastophis missiaeni sp. nov.

Fig. 5.

Etymology: After Pieter Missiaen (University of Ghent, Belgium), for his contribution to the Indian Eocene vertebrate project.

Type material: Holotype: One mid-trunk vertebra (VAS 1017). Paratypes: Three vertebrae: two mid- (VAS 1018, 1019) and one posterior trunk (VAS 1020) vertebrae. All from the continental beds of the early Eocene Cambay Formation.

Type locality: Vastan Lignite Mine, northeast of Surat, Gujarat, India.

Type horizon: Early Eocene (middle to late Ypresian) continental beds of Cambay Formation.

Diagnosis.—Differs from all other snakes in having prezygapophyses strongly compressed anteroposteriorly below the articular facets, forming laminar deep prezygapophyseal processes that slightly protrude laterally. Vertebrae lightly

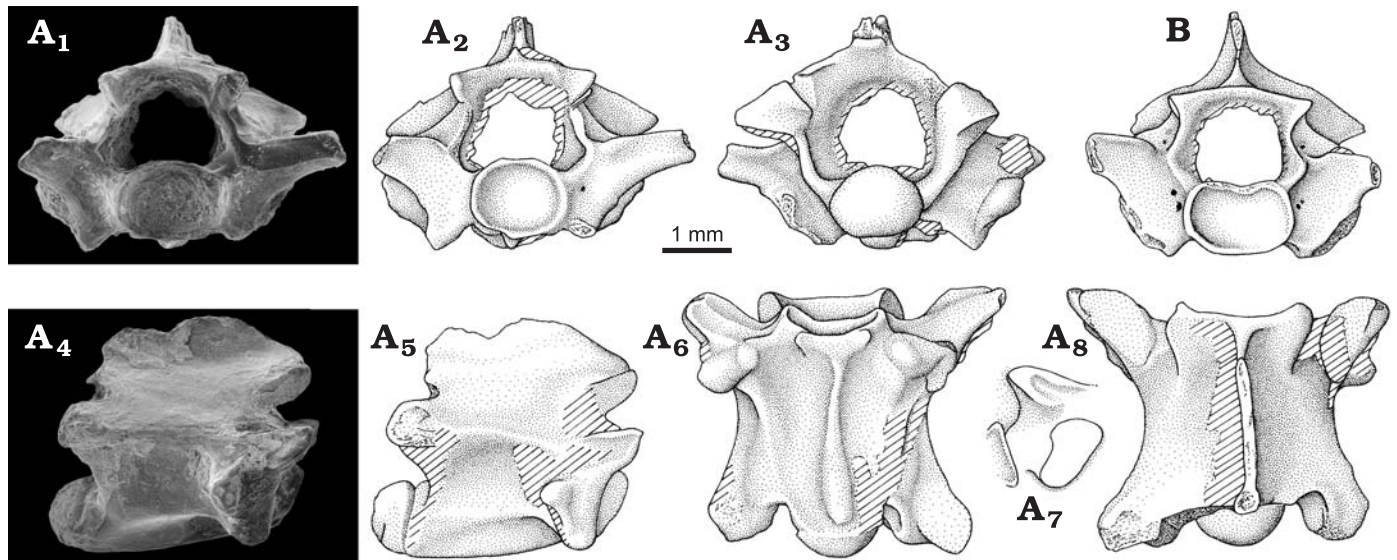


Fig. 5. Caenophidian snake, *Thaumastophis missiaeni* gen. and sp. nov., from the early Eocene of Vastan (Cambay Formation, Gujarat, western India). A. VAS 1017, mid-trunk vertebra, holotype, anterior (A₁, A₂), posterior (A₃), right lateral (A₄, A₅), ventral (A₆), and dorsal (A₈) views; anterolateral view (A₇) of left prezygapophysis of holotype. B. VAS 1018, mid-trunk vertebra, anterior view, showing variation in the number of foramina.

built and slightly elongate. Dia- and parapophyseal areas distinct. Neural spine blade-like and long. Centrum narrow, flat ventrally.

Description of the holotype.—The holotype is a slightly damaged mid-trunk vertebra that is lightly built and slightly elongate. Measurements (in mm): width of zygosphenes: 2; length of centrum from edge of cotyle to tip of condyle: 3.1; width of interzygapophyseal constriction at narrowest circumference: 2.5.

In anterior view, the vertebra is wide. The zygosphenes are thin, wide and slightly arched dorsally. The section of the neural canal is broad, almost as wide as the zygosphenes. The cotyle is round and markedly narrower than the neural canal. Small ventrolateral tubercles are present below the cotyle. The prezygapophyses strongly project laterally. The prezygapophyseal processes are deep and they slightly project laterally beyond the prezygapophyseal facets. The prezygapophyseal facets are hardly slanting above the horizontal. The paradiapophyses slightly project below the cotyle. A paracotylar foramen is present on the left side only.

In dorsal view, the vertebra is slightly elongate. The interzygapophyseal constriction is moderately deep. The prezygapophyseal facets are elongate, their major axis being oblique. The anterior border of the zygosphenes is concave. The posterior border of the neural arch is damaged. The neural spine is laminar, rather thin and long; it reaches the anterior border of the zygosphenes.

In lateral view, the neural spine is rather high; its anterior border arises obliquely from the anterior border of the zygosphenes. The prezygapophyseal buttress is strongly compressed anteroposteriorly as a deep lamina below the articular facet; it is recurved posteroventrally and it forms a short prezygapophyseal process. The interzygapophyseal ridge is

salient. The paradiapophysis is elongate dorsoventrally; the diapophysis bulges and it is distinct from the clearly flatter and broader parapophysis. The ventral border of the haemal keel is slightly convex ventrally.

In ventral view, the surface of the centrum is flat and narrow. The subcentral ridges are moderately salient but well-marked; they weakly diverge anteriorly. The haemal keel is narrow and slightly widening posteriorly.

In posterior view, the neural arch is rather depressed. Parazygantral foramina are absent.

Intracolumnar variation.—Aside from vertebrae from the mid-trunk region, only one poorly preserved, eroded posterior trunk vertebra is available. It only shows that, as is usual, the paradiapophyses are more distant from the centrum than in mid-trunk vertebrae.

Intraspecific variation.—In one mid-trunk vertebra (VAS 1018), the anterior border of the zygosphenes is nearly straight in dorsal view, the anterior border of the neural spine originates posteriorly to the zygosphenal edge, the lamina beneath the prezygapophyseal facet is vertical (not recurved), and the ventral border of the haemal keel is almost straight in lateral aspect. The posterior median notch of the neural arch, not preserved in the holotype, is moderately deep. In VAS 1018, two paracotylar and one parazygosphenal foramina are present on each side. An additional parazygosphenal foramen perhaps opens on the right side, but this cannot be confirmed.

Discussion.—*Thaumastophis missiaeni* differs from all other snakes by a peculiar character: the prezygapophysis is strongly compressed beneath its articular facet, forming a more or less vertical, deep lamina that projects laterally as a short prezygapophyseal process. This morphology of the prezygapophyses appears to be a derived state unique to *Thau-*

mastophis missiaeni. This condition likely represents the highest degree of the compression that occurs in the Palaeophiidae, the Acrochordoidea, and the Anomalophiidae and Russellophiidae. Contrary to other snakes in which compression occurs, in *Thaumastophis* the prezygapophyses markedly project laterally. The differentiation between dia- and parapophyseal areas points to the Caenophidia. *Thaumastophis* is the earliest snake in which this character occurs. Aside from these features, the overall morphology of *Thaumastophis missiaeni* is reminiscent of the colubroids (more specifically, the light build, slight elongation, long and blade-like neural spine and narrow centrum). However, paired paracotylar foramina, coupled with the presence of parazygantral foramina (as observed in VAS 1018), suggest acrochordoids (Hoffstetter and Garrard 1964), which renders referral to the colubroids uncertain. Therefore, *Thaumastophis missiaeni* is assigned to Caenophidia incertae sedis.

Gen. et sp. indet. A

Fig. 2F.

Material.—Four trunk vertebrae: one (VAS 1006) from the marine beds; three (VAS 1021–1023) from the continental beds. All from the early Eocene Cambay Formation, Vastan Lignite Mine, Gujarat, India.

Description and comparison.—The vertebrae are elongate and relatively gracile, with a large neural canal and a thin, wide and crenate zygosphenone. The prezygapophyseal buttresses are not of the compressed type and incipient, boid-like prezygapophyseal processes are present. The neural arch is slightly vaulted; it bears a comparatively high neural spine that occupies its posterior half. The anterior and posterior borders of the neural spine are almost vertical. Paracotylar foramina are perhaps irregularly present in the bottom of deep depressions. VAS 1006 differs somewhat from the three other vertebrae in having more salient subcentral ridges, but this may be an intracolumnar variation.

This terrestrial snake represents a new taxon at the generic and species level, but none of the specimens is sufficiently complete to serve as the holotype. The family assignment is problematic. Because of its light build, this snake may belong to the poorly known primitive complex of the colubroids or to the basal caenophidian assemblage.

Gen. et sp. indet. B

Fig. 2G.

Material.—One trunk vertebra (VAS 1051) from the continental beds of the early Eocene Cambay Formation, Vastan Lignite Mine, Gujarat, India.

Description and comparison.—This single vertebra is elongate and not massive; the neural canal is large and the zygosphenone is thin. The prezygapophyseal buttresses are compressed and there is no prezygapophyseal process. The vertebra lacks paracotylar foramina. The long neural spine reaches the zygosphenal roof anteriorly; its height remains unknown. The centrum is elongate, narrow, without well-marked sub-

central ridges. The haemal keel is wide and poorly marked off from the centrum.

On the whole, this vertebra is reminiscent of *Procerophis*, but it differs from it in lacking prezygapophyseal processes and subcentral ridges, and in being less gracile. Like *Procerophis*, this specimen may belong to the Colubroidea; however, based on this single specimen, such a referral cannot be certain. This vertebra, more specifically its centrum, is reminiscent of various extant arboreal colubrids. But as shown by the absence of prezygapophyseal processes, it does not belong to the colubrids.

Discussion

The snake fauna from Vastan is diverse (Table 1). It includes at least ten species, perhaps twelve. The most primitive snakes are represented by two genera of palaeophiids and perhaps one madtsoiid. The Henophidia are represented by one boid, and the Caenophidia (i.e., advanced snakes) are the most abundant with six species. Among the latter, two, perhaps three colubroids are identified including one russellophiid that is formally recognized.

The marine beds yielded few specimens. Two taxa from this layer (the marine *Palaeophis* sp. and Caenophidia gen. et sp. indet. A, a terrestrial form) have been recovered also from the continental beds. No significant differences therefore appear between marine and continental beds.

Several taxa are aquatic. The Palaeophiidae were highly adapted to aquatic life; however, they are present even in the continental beds, which is not surprising. These snakes lived in marine water but also in brackish and freshwater environ-

Table 1. Checklist of snakes from the Eocene of Vastan Mine.

?Madtsoiidae Hoffstetter, 1961
Gen. et sp. indet.
Palaeophiidae Lydekker, 1888
<i>Palaeophis</i> sp.
<i>Pterosphenus</i> sp.
Henophidia Nopcsa, 1923
Boidae Gray, 1825
Boidae indet.
Caenophidia Hoffstetter, 1939
Colubroidea Opperl, 1811
Russellophiidae Rage, 1978
<i>Russellophis crassus</i> sp. nov.
?Russellophiidae
Gen. et sp. indet.
Colubroidea indet.
<i>Procerophis sahnii</i> gen. et sp. nov.
Caenophidia incertae sedis
<i>Thaumastophis missiaeni</i> gen. et sp. nov.
Gen. et sp. indet. A
Gen. et sp. indet. B

ments close to the coast; at least for *Pterosphenus*, mangrove perhaps represented a favorable niche (Westgate 2001; Rage et al. 2003). Until now, aside from two erroneous reports, the co-occurrence of *Palaeophis* and *Pterosphenus* in the same locality has been reported only from the latest Eocene of Hardie Mine, Georgia, USA (Parmley and De Vore 2005). Vastan is the second locality that yields both genera. *Russellophis crassus* has compressed prezygapophyseal buttresses, a morphology that is found in extant highly aquatic snakes (Acrochordidae) and in fossils that are almost always found in sediments of aquatic origin. However, *Russellophis* was not highly modified for aquatic life (absence of lateral compression of the vertebrae); it was perhaps amphibious, more or less riparian as are various extant snakes. In *Procerophis* and in gen. et sp. indet. B, the prezygapophyseal buttresses are compressed but the strong elongation of the vertebrae is similar to that of terrestrial, even arboreal extant colubrids; their mode of life cannot be inferred. The Boidae, gen. et sp. indet. A, and likely the presumed madtsoiid were terrestrial.

The composition of the fauna from Vastan is reminiscent of the early Eocene of Europe (Palaeophiidae, Boidae, primitive caenophidians including Russellophiidae). Such geographic affinities were already noticed about bats (Smith et al. 2007) and rodents (Rana et al. 2008). But it should be noted that comparisons with early Eocene faunas of other continents is not possible because they are poorly known, or even unknown. Aside from Vastan, the only early Eocene faunas (i.e. assemblages including at least two taxa) from Asia are those from Kutch, western India (Rage et al. 2003) and Andarak 2, Kirghizia (Averianov 1997; Danilov and Averianov 1999). Snakes have also been reported from the Akli Formation (Rana et al. 2005), of possible early Eocene age, but they have not yet been studied. In addition, Chorlakki (Kuldana Formation) in northern Pakistan is early middle Eocene in age (Gingerich 2003). The fauna from Chorlakki includes only terrestrial forms (Boinae sensu lato, Erycinae; Rage 1987a) whereas, like Vastan, Andarak 2 and Kutch have produced both terrestrial and aquatic snakes. However, it is not possible to reliably compare Vastan to these two localities, from which little diversity is known. Andarak 2 has yielded only the rare "*Archaeophis*" *turkmenicus* Tatarinov, 1963 (Archaeophiinae, ?Palaeophiidae), the palaeophiid *Palaeophis ferganicus* Averianov, 1997, and the boid *Calamagras turkestanicus* Danilov and Averianov, 1999. Kutch has yielded a fauna that is rich in number of specimens but is less diverse and unbalanced. Palaeophiidae (*Pterosphenus kutchensis* and *Pt. biswasi* Rage, Bajpai, Thewissen, and Tiwari, 2003) markedly outnumber other snakes (a madtsoiid or boid and an indeterminate caenophidian). There is no species common to Vastan and either of the other early Eocene localities from Asia.

At Vastan, the number of taxa that belong to the Colubroidea, or at least to the Caenophidia, is striking for the Eocene. These include *Russellophis*, *Procerophis*, *Thaumatostophis*, and perhaps gen. et sp. indet. A and B. This supports the view that Asia played an important role in the early history of advanced snakes (Rage 1987b; Head et al. 2005).

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Note added in proof

While our article was in press, it has come to our attention that *Palaeophis* sp. from Vastan was described as *Palaeophis vastaniensis* by Bajpai and Head in a paper dated Dec. 2007. They do not consider the possible presence of two species and the diagnostic characters do not appear to be clearly distinct from those of other species.

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