Early Eocene snakes from Kutch, Western India, with a review of the Palaeophiidae

Jean-Claude RAGE
Département Histoire de la Terre, USM 0203, UMR Muséum-CNRS 5143,
Muséum national d'Histoire naturelle, 8 rue Buffon, F-75231 Paris cedex 05 (France)
jcrage@mnhn.fr

Sunil BAJPAI
Department of Earth Sciences, Indian Institute of Technology,
Roorkee 247 667 (India)
sunilfes@iitr.ernet.in

Johannes G. M. THEWISSEN
Department of Anatomy, Northeastern Ohio Universities College of Medicine,
Rootstown, Ohio 44272 (USA)
thewisse@neoucom.edu

Brahma N. TIWARI
Wadia Institute of Himalayan Geology, Mahadeo Singh Road, Dehradun 248 001 (India)

ABSTRACT

The early Eocene of Panandhro Mine (northwestern India) has produced a rich snake fauna largely dominated by palaeophiids. Three families are present: Palaeophiidae, ?Madtsoiidae or Boidae, and an indeterminate family of Colubroidea. The Palaeophiidae include two species: *Pterosphenus kutchensis* n. sp., that shows peculiar features, and *Pt. biswasi* n. sp. They are the earliest representatives of the genus. Madtsoiidae or Boidae are represented by only two specimens that do not permit distinction between these two families. If these fossils belong to the Boidae, then they might be the earliest representatives of that family in Asia. The colubroid from this site ranks among the earliest Cenozoic representatives of the group. The possibility that it belongs to the Colubridae cannot be excluded; if this is the case, it would be the earliest known colubrid. Nearly all specimens belong to *Pterosphenus* Lucas, 1899 that was a highly aquatic genus. It lived in shallow water, probably in marine environment close to the coasts and/or in freshwater.

KEY WORDS
Reptilia,
Serpentes,
Colubroidea,
Palaeophiidae,
Madtsoiidae,
Boidae,
Ypresian,
Eocene,
India,
palaeoenvironment,
new species.

RÉSUMÉ

Serpents de l'Éocène inférieur de Kutch, ouest de l'Inde ; revue des Palaeophiidae.
L'Éocène inférieur de Panandhro Mine (nord-ouest de l'Inde) a fourni une
faune de serpents riche et nettement dominée par les Palaeophiidae. Trois
familles sont présentes : Palaeophiidae, ? Madtsoiidae ou Boidae, et une famille
indéterminée de Colubroidea. Les Palaeophiidae comprennent deux espèces :
Pterosphenus kutchensis n. sp., qui montre des caractères particuliers, et *Pt. bis-
wasi* n. sp. Il s'agit des plus anciens représentants du genre. Madtsoiidae ou
Boidae ne sont représentés que par deux spécimens qui ne permettent pas de
distinguer les deux familles. Si ce sont des Boidae, ils pourraient être les plus
anciens représentants de la famille en Asie. Le colubroïde est l'un des plus
anciens représentants du groupe dans le Tertiaire. Son appartenance aux
Colubridae ne peut pas être exclue ; dans ce cas il s'agirait du plus ancien
Colubridae. Presque tous les spécimens appartiennent à *Pterosphenus* Lucas,
1899, genre fortement aquatique. Il vivait en eau peu profonde, dans des envi-
ronnements probablement marins près des côtes et/ou en eau douce.

INTRODUCTION

A rich lower vertebrate fauna was recovered for
the first time from the early Eocene (Ypresian)
sediments associated with lignites near
Panandhro, District Kutch (= Kachchh), Gujarat
State, on the western margin of India (Fig. 1).
This recent discovery (Bajpai & Thewissen 2002)
includes snakes, in addition to fishes, turtles,
crocodiles and whales. This fauna, possibly one
of the oldest records of Cenozoic vertebrates in
India, was recovered from an approximately 2 m
thick horizon of grey silty shales occurring in a
number of pits in the Panandhro Lignite Mine
(under Gujarat Mineral Development
Corporation Ltd.). These pits are: HD Pit (also
called North Pit), Akri Pit, and Channel Pit. The
snake bearing silty shales form part of the
Panandhro Formation of Saraswati & Banerjee
(1984) or its broadly correlatable unit designated
as Naredi Formation by Biswas (1992). Both of
these formations have been considered to be
Ypresian (early Eocene) in age, the latter on the
basis of benthic foraminifera including *Assilina
granulosa* (d'Archiac, 1847) and *A. spinosa* Davies
& Pinfold, 1937 (Biswas 1992). The Naredi
Formation in the lignite mines consists mainly of
lignite seams, lignitic and grey carbonaceous clays

and occasional ochreous muds. The top of the
Naredi Formation consists of lateritic clays that
are believed to represent a late early Eocene
unconformity of regional extent (Biswas 1992).
Overlying the Naredi sediments is the Harudi
Formation (dated as middle Eocene) which has
long been known to yield fossils of archaeocete
whales (Bajpai & Thewissen 1998).

This paper describes the snake fauna from two
closely situated localities (HD Pit and Channel
Pit) within the Panandhro Lignite Mine. The
fossils have been recovered largely by surface
collecting; large scale screenwashing is yet to be
carried out. Snake remains described in this paper
consist of vertebrae that taxonomically represent
three different families. The associated fauna will
be described separately.

The present record is of considerable significance
because fossil snakes are extremely poorly known
from the Indian Cenozoic. To the best of our
knowledge, there is just one published record of
fossil snakes from the entire Cenozoic of India at
present; it includes Acrochordidae Bonaparte,
1838 (*Acrochordus dehmi* Hoffstetter, 1964),
indeterminate Colubridae Oppel, 1811 and per-
haps Elapidae Boie, 1827 from the upper
Siwaliks of the Jammu region (Rage *et al.* 2001).
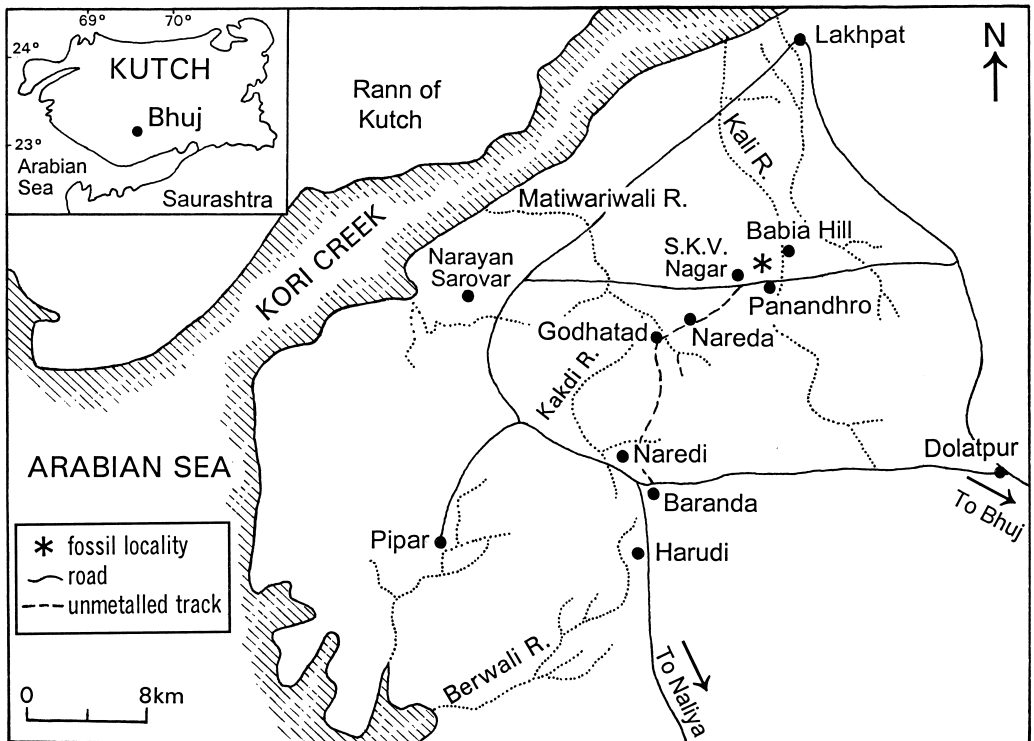The few other occurrences known from

FIG. 1. — Location of the fossiliferous locality.

elsewhere in the Indian subcontinent include those of Boidae Gray, 1825 from the early-middle Eocene Kuldana Formation of Kohat, Pakistan (Rage 1987a) and Neogene from Nepal (Conroy *et al.* 1985; West *et al.* 1991), and of Acrochordidae and Boidae from the Neogene Siwalik beds of Pakistan (Hoffstetter 1964).

The material described here is catalogued as RUSB numbers at Department of Earth Sciences, Indian Institute of Technology, Roorkee 247 667, India.

SYSTEMATICS

Family PALAEOPHIIDAE Lydekker, 1888

Palaeophiidae Lydekker, 1888.

Vialovophiidae Nessov, 1984.

The Kutch localities have yielded palaeophiid snakes that pose a peculiar problem within this family. Before considering the fossil palaeophiids from Kutch, it appears necessary to discuss the systematics of the Palaeophiidae.

The Palaeophiidae is an extinct family of snakes that includes two subfamilies: the Palaeophiinae Lydekker, 1888, and the Archaeophiinae Janensch, 1906 (Rage 1983a, 1984). The oldest palaeophiid appears to be an incomplete vertebra from the Cenomanian of Sudan (Rage & Werner 1999). Confirmed palaeophiids are known only from the Maastrichtian to the late Eocene (Rage 1984).

The Archaeophiinae are represented by only two articulated specimens that are rather complete and that represent two taxa: *Archaeophis proavus* Massalongo, 1859 (uppermost lower Eocene of Italy) and *Archaeophis turkmenicus* Tatarinov, 1963 (lower Eocene of Turkmenistan). Tatarinov (1963, 1988) described the latter species and referred it to *Archaeophis* Massalongo, 1859, but it might belong to a distinct, undescribed genus (Rage 1984).

The Palaeophiinae are known only from disarticulated vertebrae and ribs and a few portions of vertebral columns. They range from the Maastrichtian to the late Eocene.

The Palaeophiinae and Archaeophiinae are placed in the same family on the basis of vertebral morphology: vertebrae more or less compressed laterally, tendency toward the reduction of the prezygapophyses, presence of pterapophyses on at least a part of the vertebrae, axis of the cotyle and condyle horizontal or nearly horizontal. Moreover, the cross section of the centrum is triangular in the Archaeophiinae and in juvenile Palaeophiinae, a condition very unusual in snakes.

The vertebrae of Archaeophiinae are more elongate than those of Palaeophiinae. In posterior, and perhaps middle, trunk vertebrae of archaeophiines, the hypapophysis is replaced by a haemal keel, whereas it is present throughout the whole trunk region in palaeophiines (with rare exceptions in posterior trunk vertebrae; see below). In archaeophiines, the paradiapophyses are markedly less developed than in palaeophiines, they do not extend dorsoventrally and also do not project below the level of the ventral face of the centrum. In addition, the plane formed by the prezygapophyses in the archaeophiines is located clearly higher than in palaeophiines.

Only the Palaeophiinae is present in Kutch.

Sub-family PALAEOPHIINAE Lydekker, 1888

Palaeophiinae Lydekker, 1888

Vialovophiidae Nessov, 1984

The vertebrae of the Palaeophiinae have hypapophyses throughout the entire trunk region (only on anterior, ? and middle, trunk vertebrae in the Archaeophiinae), except in *Palaeophis toliapicus* Owen, 1841 (and likely *P. casei* Holman, 1982) in which the hypapophyses of posterior trunk vertebrae are very reduced. The anterior trunk vertebrae have a second, short hypapophysis below the cotyle. Pterapophyses are developed above the postzygapophyses of trunk vertebrae, except on posteriormost ones of

Palaeophis toliapicus and *P. casei* in which they are reduced to a low keel or are absent. The roof of the zygantrum is reduced. The prezygapophyses of the Palaeophiinae are somewhat peculiar: they lack a prezygapophyseal process but the buttress is compressed and it forms an anterolateral ridge that extends from the dorsal border of the diapophysis to the anterolateral tip of the prezygapophysis, just beneath the articular facet (the morphology of the prezygapophyses of the Archaeophiinae is unknown). In the Russellophiidae and Anomalophiidae (Eocene, probably aquatic snakes) and the aquatic Nigerophiidae (Cenomanian-?middle Eocene) the morphology of the prezygapophyses is similar. McDowell (1987) regarded this morphology of the prezygapophyses as a character of systematic significance, but it might represent an adaptation to aquatic life and therefore a feature liable to convergence.

The Palaeophiinae includes snakes of all sizes, from *Palaeophis colossaeus* Rage, 1983 that was perhaps over 9 m (Rage 1983b) to *Palaeophis casei* that was apparently about 0.5 m (Holman 1982).

The palaeophiine species form a morphological series from forms slightly adapted to aquatic life to snakes strongly modified by this mode of life. This series is subdived into two phenotypic genera: *Palaeophis* Owen, 1841, known from the Maastrichtian to the Bartonian, and *Pterosphenus* Lucas, 1899, up to now known from the middle and late Eocene (but see below).

In fact, irrespective of the generic subdivision, three assemblages of species may be distinguished within this series (Rage 1984). It should be noted that the variation within the vertebral column is poorly known in the Palaeophiinae. A thorough revision of the subfamily would probably show that features on which several species are based are only intracolumnar variation. In other words, these species are certainly not all valid. But such a revision is beyond the scope of the present study. The three species assemblages are as follows:

1) Primitive *Palaeophis* grade: species with vertebrae only slightly modified by aquatic life (lateral compression weak, pterapophyses low, prezyg-

apophyses not markedly reduced, paradiapophyses not located very low and not distant from the centrum). This assemblage is composed of several species that are referred to *Palaeophis*: *P. zhylan* (Nessov, 1984) (Thanetian or Ypresian of Kazakhstan), *P. maghrebianus* Arambourg, 1952 (Ypresian of Morocco), *P. virginianus* Lynn, 1934 (Ypresian or Lutetian of the USA), and *P. colossaeus* Rage, 1983 (Lutetian of Mali). *P. africanus* Andrews, 1924 (Lutetian of Nigeria) may be allocated to this assemblage although it shows tendencies toward the morphology of the next assemblage.

Remark: Nessov (1984) described the genus and species *Vialovophis zhylan* and he referred it to a new subfamily, Vialovophiinae, of the Nigerophiidae Rage, 1975. Rage (1987b) suggested that *Vialovophis* is a palaeophiid, and even a synonym of *Palaeophis*. But, Averianov (1997) maintained *Vialovophis* as a distinct genus and he raised the subfamily to family rank (Vialovophiidae Nessov, 1984). The characters on which *Vialovophis* is based are unquestionable features of *Palaeophis*. Only one character, the oblique axis of condyle in posterior trunk vertebrae, might represent a distinctive feature; but it cannot be considered significant because the vertebrae are badly distorted. Averianov (1997) also stressed the fact that the condyle and cotyle are more depressed than in *Palaeophis*, and he used this to characterize the distinction at the family level. It should be noted that this character varies during ontogeny in snakes and it appears to show intracolumnar variation in, at least, *Palaeophis maghrebianus*. In a phylogenetic analysis by Averianov (1997: fig. 8), *Vialovophis* appears as a clade distinct from the Palaeophiidae. But, in addition to the fact that the value of a character matrix based only on isolated vertebrae may be questioned, only three characters in the matrix distinguish *Vialovophis* from *Palaeophis* and *Pterosphenus*: shape of prezygapophyseal facets, anteroposterior length of neural spine, and presence of anterior hypapophyses on anterior trunk vertebrae. As used by Averianov (1997), the first two characters are erroneous, they are similar in *Vialovophis* and *Palaeophis*. The third character

cannot be checked because the vertebra that is considered an anterior trunk (Nessov & Udovitschenko 1984: fig. 19) is certainly not an anterior one: the anteroposterior length of its neural spine shows that it comes from a more posterior region than the holotype, which is a mid-trunk vertebra; in other words, no anterior trunk vertebra is known for *V. zhylan*. In fact, *Vialovophis* cannot be distinguished from *Palaeophis*. Therefore, the species *V. zhylan* is assigned to the latter genus and the family Vialovophiidae is referred to the synonymy of the Palaeophiidae.

2) Advanced *Palaeophis* grade: species that are clearly modified by adaptation to aquatic life (vertebrae laterally compressed, pterapophyses developed, prezygapophyses reduced, paradiapophyses low and distant from the centrum). Several species show this morphology, they are all assigned to *Palaeophis*: *P. casei* Holman, 1982 (Ypresian of the USA), *P. ferganicus* Averianov, 1997 (Ypresian of Kirghizia), *P. littoralis* Cope, 1868 (Ypresian and ?Lutetian of the USA), *P. toliapicus* Owen, 1841 (Ypresian of western Europe), *P. typhaeus* Owen, 1850 (Ypresian and Lutetian of western Europe), *P. grandis* Marsh, 1869 (Lutetian of the USA), *P. tamdy* (Averianov, 1997) (Bartonian of Uzbekistan), *P. nessovi* Averianov, 1997 (Priabonian of Kazakhstan), and *P. udovichenkoi* Averianov, 1997 (Bartonian or Priabonian of Ukraine).

Remark: Averianov (1997) erected the genus *Nessovophis* to accomodate two species from the Eocene of Central Asia: *N. tamdy* and *N. zhylga*. He assigned this genus to the Nigerophiidae but he did not justify this allocation. The reduced prezygapophyses of *N. tamdy* are not consistent with the Nigerophiidae. Moreover, Averianov stated that the axis of the condyle in *Nessovophis* is oblique, but the illustrations show, at least in *N. tamdy*, that it is horizontal. The very reduced pterapophyses of the mid- and posterior trunk vertebrae of *N. tamdy* do not differ from those of *Palaeophis toliapicus* and *P. casei* as is shown by the neural arch that is shouldered in posterior view. Finally, the hypapophysis of *N. tamdy* appears reminiscent of that of *P. toliapicus* and

P. casei; it is present in mid-trunk vertebrae of *N. tamdy* (regarded as anterior ones by Averianov 1997) and it is replaced by a marked haemal keel in posteriormost trunk vertebrae. Therefore, *Nessovophis tamdy*, the type species of the genus, is referred to *Palaeophis*; it belongs to the same phenotypic assemblage as *P. toliapicus*. "*Nessovophis*" *zhylga* may in fact be a nigerophiid snake.

Palaeophis nessovi Averianov, 1997 is known from a single vertebra. The degree of reduction of its prezygapophyses appears to be similar to that occurring in the second assemblage of *Palaeophis* and in various vertebrae of *Pterosphenus*. The zygosphene is slightly arched dorsally, a feature reminiscent of *Pterosphenus*, but the anterior edge of the neural spine is posterior to the anterior border of the zygosphene. The vertebra is not clearly compressed laterally. This vertebra presents characters of *Palaeophis* and others that might suggest *Pterosphenus*. The status of this species, based on a single specimen, is unclear. It is here provisionally considered valid and retained in *Palaeophis*. If this "species" really belongs to this genus, then it represents the youngest *Palaeophis*.

Averianov (1997) described the species *Palaeophis udovichenskoi*. The vertebrae of this species are markedly compressed laterally and the zygosphene is slightly convex dorsally. These features are reminiscent of *Pterosphenus*. However, the anterior border of the zygosphene is not concave in dorsal view and the vertebrae are elongate, which is not consistent with *Pterosphenus*. The generic status of *P. udovichenskoi* appears to be somewhat doubtful; it is provisionally retained in *Palaeophis*.

3) *Pterosphenus* grade: species that are strongly modified by aquatic life (vertebrae markedly compressed laterally, pterapophyses high, prezygapophyses reduced at least as in the preceding assemblage, paradiapophyses at least as low and distant from the centrum as in the preceding assemblage). Up to now, four species have been described; they are referred to the genus *Pterosphenus* (see discussion below): *Pt. schucherti* Lucas, 1899 (middle and late Eocene of the USA), *Pt. schweinfurthi* (Andrews, 1901) (Priabonian of Egypt and Libya), *Pt. sheppardi* Hoffstetter, 1958 (Priabonian of Ecuador), and *Pt. muruntau* Averianov, 1997 (Bartonian of Uzbekistan).

Finally, it is worth noting that the distinction between the third assemblage (i.e. *Pterophenus*) and the second assemblage (i.e. part of *Palaeophis*) is not more pronounced than that separating the two assemblages of *Palaeophis*. The distinction between *Palaeophis* and *Pterosphenus* is likely artificial, but since it is not possible to establish the interrelationships within palaeophiids, it remains a convenient solution.

Most of the specimens from Kutch do not fully fit this morphological series. They represent a species that shows features more advanced than in the most advanced species referred to *Pterosphenus*, but they also display a *Palaeophis*-like feature. They are, however, referred to *Pterosphenus*. Rare vertebrae represent a second species the vertebrae of which typically correspond to *Pterosphenus*.

Genus *Pterosphenus* Lucas, 1899

Pterosphenus Lucas, 1899: 637, 638, pls 45, 46.

Moeriophis Andrews, 1901: 438-440, fig. 2.

TYPE SPECIES. — *Pterosphenus schucherti* Lucas, 1899, by monotypy.

The inclusion of one of the species from Kutch in *Pterosphenus* leads to a slightly altered diagnosis of the genus proposed by Rage (1984) (see also Rage 1983a; Holman 2000).

EMENDED DIAGNOSIS. — Vertebrae strongly compressed laterally; pterapophyses high; prezygapophyses markedly reduced; paradiapophyses situated low; zygosphene convex dorsally; anterior border of the neural spine close to the anterior border of the zygosphene or originating from the top of the latter border.

THE SPECIES OF *PTEROSPHENUS*
Four species were referred to *Pterosphenus*: *Pt. schucherti*, the type species of the genus, is known from the Priabonian (late Eocene) and the late Lutetian or early Bartonian (middle Eocene) of

the USA. Parmley & Case (1988) reported *Pt. schucherti* from the Yazoo Clay (Louisiana) and they stated that this Formation is early Eocene in age. This is likely a lapsus; the Yazoo Clay is Jacksonian, i.e. Priabonian (late Eocene).

Pt. schweinfurthi (Andrews, 1901) has been found in the Priabonian of Egypt and Libya. Rage (1984) erroneously indicated that the Birket Qarun Formation (Egypt), that produced this species, is late Lutetian (= Biarritzian) in age. Gingerich (1992) has shown that the age of this Formation is Priabonian. The vertebral morphology of *Pt. schweinfurthi* is similar to that of *Pt. schucherti*. According to Rage (1984), *Pt. schweinfurthi* differs from *Pt. schucherti* in having a thicker roof of the zygantrum and shorter pterapophyses. But, in specimens belonging to *Pt. schucherti*, described by Westgate & Ward (1981) and Westgate (1989), the zygantral roof is as thick as that of *Pt. schweinfurthi*. The height of the pterapophyses remains the only feature that distinguishes the two species, but it might represent only intracolumnar variation. *Pt. schweinfurthi* might be a junior synonym of *Pt. schucherti*, but this cannot be demonstrated on the basis of the available material.

Pt. sheppardi Hoffstetter, 1958 comes from the late Eocene (Jacksonian, i.e. Priabonian) of Ecuador. It is represented by a single specimen, i.e. some articulated vertebrae exposed in lateral view; therefore, thorough comparison with other species is not possible. It is distinguished from the above two species by its shorter pterapophyses. This may result from intracolumnar variation and this casts doubts on the validity of the species.

Pterosphenus muruntau Averianov, 1997, from the Bartonian of Uzbekistan, is represented by only two poorly preserved vertebrae. Apart from one feature ("pterapophyses incipient" according to Averianov), the characters cited in the diagnosis of this species are either characters diagnosing the genus *Pterosphenus* or characters connected to ontogeny (neural canal small, external walls of vertebrae relatively thick) or taxonomically non-significant (lateral and pterapophyseal marrow cavities present). The small size of the pterapophyses would be a feature of interest because in other species they are high. But they are broken away in the two known specimens and their remaining bases do not permit inference that they were small or incipient. In summary, these two specimens are too poorly preserved, and this species should be considered a *nomen dubium*.

Pterosphenus kutchensis n. sp.
(Figs 2; 3; 5B)

HOLOTYPE. — 1 trunk vertebra (RUSB 2721-1).

ETYMOLOGY. — From Kutch, name of the District in which is situated the type locality.

TYPE LOCALITY. — HD Pit in Panandhro Mine, Kutch District, India.

REFERRED MATERIAL. — 105 vertebrae: 85 from HD Pit (RUSB 2564-1 to 2564-26; RUSB 2721-2 to 2721-57; RUSB 2784-1 to 2784-3); 20 from Channel Pit (RUSB 2790-1 to 2790-20).

HORIZON. — Naredi Formation, Ypresian, Lower Eocene.

DIAGNOSIS. — *Pterosphenus* that differs from all other snakes in having paradiapophyses that extend further anteroventrally than in any other snake. These paired structures originate from a common base, or may rarely be separated but with their bases closely appressed against each other. Differs from other species in the genus in lacking anterior hypapophyses, in having the anterior edge of the neural spine separated from the anterior border of the zygosphene by a narrow step in most vertebrae, and in having a non-concave anterior border of the zygosphene. Further differs from *Pt. sheppardi* in having higher pterapophyses.

DESCRIPTION OF HOLOTYPE

The holotype (Fig. 2) is a relatively small trunk vertebra, presumably from the mid-trunk region. Its measurements are as follows: length of centrum from cotylar rim to tip of condyle: 8.3 mm; width through prezygapophyses: 6.6 mm; minimum width of interzygapophyseal constriction: 5.4 mm; diameter of cotyle: 4.4 mm; width of zygosphene: 4.7 mm.

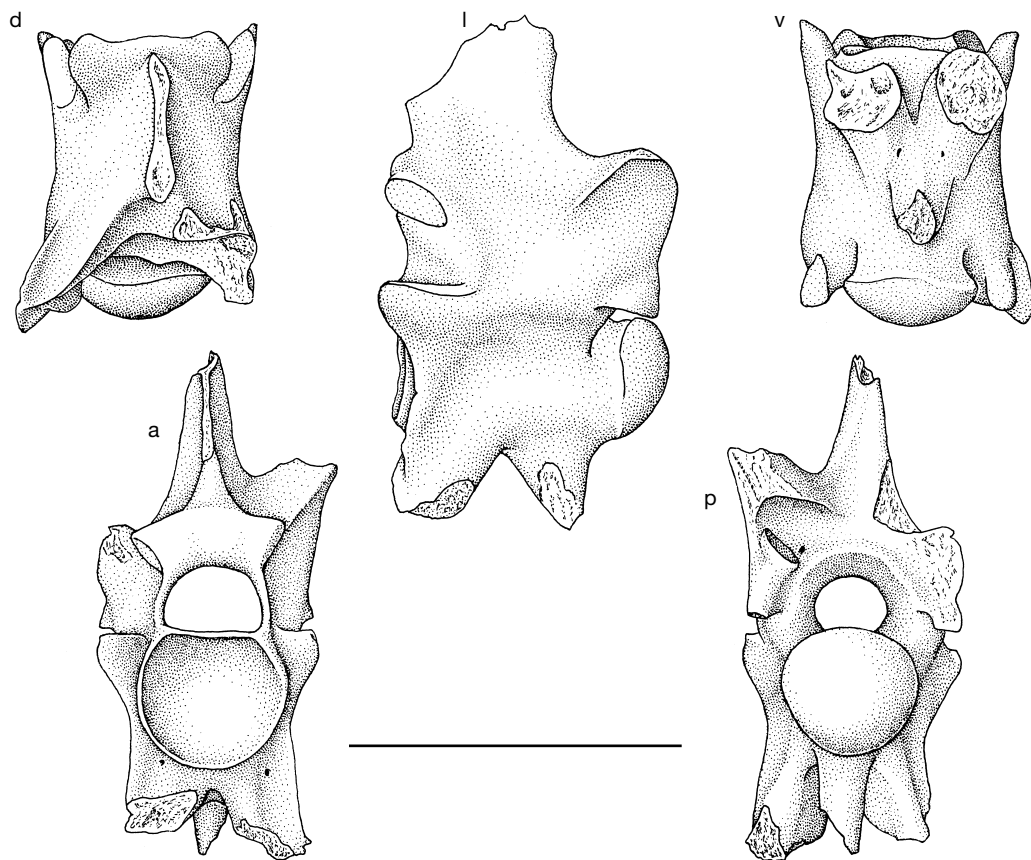In anterior view, the vertebra is markedly compressed laterally and high. The prezygapophyses

F<small>IG</small>. 2. — *Pterosphenus kutchensis* n. sp., holotype, trunk vertebra (RUSB 2721-1), from the Ypresian of Panandhro Mine (HD Pit), in anterior (**a**), dorsal (**d**), left lateral (**l**), posterior (**p**), and ventral (**v**) views. Scale bar: 1 cm.

are very reduced; their articular facets are horizontal and level with the floor of the neural canal. The zygosphene is thick and slightly wider than the cotyle. The dorsal border of the zygosphene is slightly arched dorsally. The base of the anterior edge of the neural spine is rather thick but it narrows dorsally; the dorsal part of the neural spine is broken off. The cotyle is subcircular but its dorsal part is truncated. The neural canal is relatively small. The pterapophyses are damaged but the left one shows that they were high. The paradiapophyses show a very unusual morphology: they are thick, very long (although their distal parts are broken off), and they are not separated from each other in the sagittal plane, i.e. they have a common base. As a result, the vertebra lacks an anterior hypapophysis. The anterior face of each paradiapophysis bears a wide and shallow groove. A small foramen opens in each of these grooves, close to the cotyle. The hypapophysis is compressed laterally. Paracotylar foramina are absent.

In dorsal aspect, the vertebra appears narrow and relatively elongate. The prezygapophyseal articular facets are small, elongate, and directed obliquely, almost anteriorly. On each side, the vertical ridge formed by the prezygapophyseal buttress slightly projects beyond the articular facet. The interzygapophyseal constriction is weakly expressed. The lateral borders of the interzygapophyseal ridges are nearly straight. The

zygosphene comprises two lateral lobes that do not strongly project anteriorly; between them, the anterior border is feebly convex. The neural spine approaches the anterior border of the zygosphene but it does not reach it. The remaining part of the left pterapophysis appears as a low, but well defined keel. The median notch in the posterior border of the neural arch is wide and obtuse, it appears as a broad embayment. As in all palaeophiids, the zygantral roof is reduced.

In lateral view, the vertebra is markedly higher than long, despite the fact that the dorsal part of the neural spine and the ventral parts of the para-diapophyses and hypapophysis are broken off. The height of the neural spine cannot be estimated. The zygosphenal facets are small, ovaloid and oblique. There is no marked interzygapophyseal ridge. The prezygapophysis lacks a prezyg-apophyseal process, but it forms a vertical ridge that extends from the tip of the articular facet to the anterolateral border of the paradiapophysis. The paradiapophysis is directed ventrally and slightly anteriorly. The articular facet for the rib is lacking, but an eroded area on the distal part of the remaining portion might correspond to the dorsal part of the diapophyseal surface. Anyway, at least most of the articular facet was on the missing part, i.e. it occupied a very ventral position, far from the centrum. The incomplete hypapophysis is vertical and not located very posteriorly. The axis of the condyle is horizontal. There is no perceivable lateral foramen.

In posterior view, as in anterior aspect, the laterally compressed morphology is striking. Beneath the pterapophyses the lateral flanks of the neural arch are subvertical. Only the left zygantral foramen appears to be present. The centrum is somewhat triangular in cross-section.

The ventral view displays the unusual position of the paradiapophyses the bases of which are not separated in the sagittal plane. As a consequence of the subtriangular cross-section of the centrum, subcentral ridges are lacking. Anterior to the condyle, the centrum forms a neck that is clearly narrower than the condyle. Two subcentral foramina open between the bases of the hyp-apophysis and paradiapophyses.

OTHER VERTEBRAE AND VARIATION

No caudal vertebrae are known. Two vertebrae each preserve a complete pterapophysis. In lateral aspect, this process appears as a triangular lamina the anterior border of which is sharp. In RUSB 2790-1, the pterapophysis is directed dorsolater-ally (Fig. 3A) whereas in RUSB 2784-1 it is more vertical.

A few vertebrae of juvenile individuals are known (Fig. 3C). They are of interest because they prove that the "large" vertebrae of *Pt. kutchensis* n. sp., that are small for the genus *Pterosphenus*, belong to adults. The vertebrae of juveniles show the features that are usual in all snake families: neural canal relatively wider than in adults, zygosphene and lateral walls of vertebrae thinner, cotyle more depressed dorsoventrally, and zygosphene entire-ly overhanging (i.e. anterior parts of lateral walls of the neural canal not completed).

Variation in the trunk vertebrae is minimal. In most vertebrae, as in the holotype, the anterior edge of the neural spine is separated from the anterior border of the zygosphene by a narrow surface; however, in a few vertebrae the top of the anterior border of the zygosphene is prolonged without a break into the anterior edge of the neural spine. The latter condition is seen in other species of *Pterosphenus*. In *Pt. kutchensis* n. sp., the variation of this feature does not appear to be related to the position of vertebrae in the verte-bral column. In some vertebrae, that are more lat-erally compressed than the holotype, the common base of the paradiapophyses is deeper; it appears as a thick process beneath the cotyle (Fig. 3B). It is not possible to determine whether such vertebrae are more anterior or more posterior than those exemplified by the holotype. In a few, damaged vertebrae, it is possible that the com-mon base of the paradiapophyses is very shallow or the paradiapophyses are separated but closely appressed against each other. Zygantral foramina are often lacking whereas their presence is con-stant in non-palaeophiid snakes. But, irrespective of the presence or absence of the usual zygantral foramina, a sagittal foramen sometimes pierces the posterior wall of the neural arch between the two zygantral fossae, below the neural spine. This
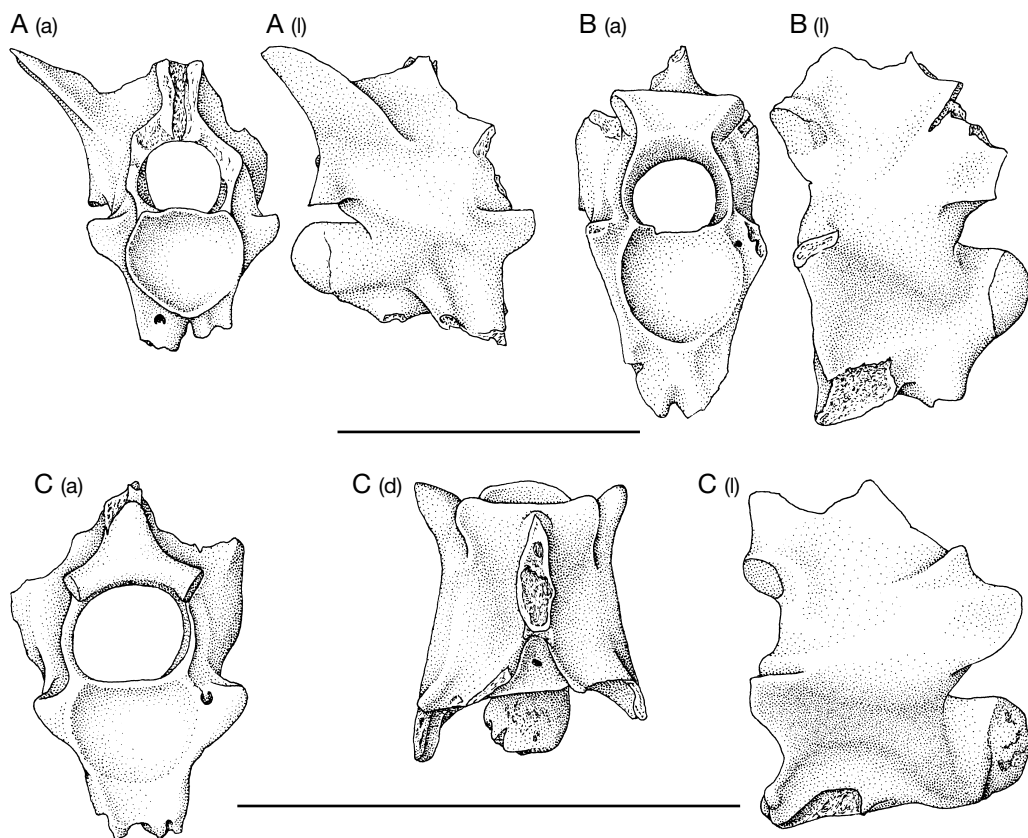
FIG. 3. — *Pterosphenus kutchensis* n. sp. from the Ypresian of Panandhro Mine; **A**, trunk vertebra (RUSB 2790-1) in which a pterapophysis is complete and the paradiapophyses are separated (or their common base is very shallow?), Channel Pit; **B**, trunk vertebra (RUSB 2721-2) showing a very deep common base of the paradiapophyses, HD Pit; **C**, trunk vertebra (RUSB 2790-2) of a juvenile individual, Channel pit. Anterior (**a**), dorsal (**d**), and lateral (**l**) views. Scale bars: 1 cm.

condition of the zygantral foramina seems common in Palaeophiidae. Paracotylar, lateral, and subcentral foramina are rarely and irregularly present. The foramen that opens in the anterior groove of each paradiapophysis, close to the cotyle, is nearly always present.

The size ranges from juveniles (centrum length: about 4.3 mm) to largest adults (centrum length: 10.5 mm).

COMMENTS

This snake poses a peculiar problem. The long paradiapophyses are more or less reminiscent of pleurapophyses, i.e. processes present only in caudal vertebrae. Since, on the available vertebrae, paradiapophyseal articular facets are not obser-

vable we are led to conclude that either these facets were on the distal parts of the paradiapophyses that are always broken off (which is quite possible because the facets are borne by spongy bone) or that the processes are pleurapophyses. But, if these processes are pleurapophyses, then all vertebrae come from the caudal region, which is not possible. Caudal vertebrae are, by far, more rarely found than vertebrae from the trunk region. Moreover, these vertebrae do not come from a single individual; they have been found in two sites (HD Pit and Channel Pit) and the vertebrae are of different sizes. Besides, caudal vertebrae of *Palaeophis* are known, and as in nearly all snakes they have typical pleurapophyses and paired haemapophyses (Rage 1983a). The verte-

brae of *Pt. kutchensis* n. sp. lack the latter processes but they have all a hypapophysis. The caudal vertebrae of nearly all snakes have paired haemapophyses; they are replaced by a haemal keel in a very few snakes (Szyndlar & Böhme 1996). In the caudal region, hypapophyses occur only in the anterior caudal vertebrae of two living genera; moreover, they appear as deep keels rather than true hypapophyses (Szyndlar & Rage 2003). Consequently, the presence of true hypapophyses on all vertebrae demonstrates that they come from the trunk region. Caudal vertebrae of *Pt. kutchensis* n. sp. have not been found.

These vertebrae show characteristic features of the Palaeophiinae, more especially of the genus *Pterosphenus* (see above).

They differ from all other species of *Pterosphenus* in having a non-concave anterior border of the zygosphene in dorsal aspect and longer, deeper paradiapophyses. Moreover, the two paradiapophyses originate from a common base, or at least (in a few vertebrae) the bases of the two paradiapophyses are perhaps very narrowly separated, which is unique in snakes. This condition plus the marked ventral orientation of the paradiapophyses and the narrowness of the vertebrae lead to a reduction of the width but it increases the depth of the animal. This certainly corresponds to a very strong adaptation to aquatic life. This lateral compression is stronger in *Pt. kutchensis* n. sp. than in other species of *Pterosphenus*; therefore, as far as this feature is concerned, *Pt. kutchensis* n. sp. appears to be the most advanced palaeophiid. As a consequence of the position of the paradiapophyses, the anterior hypapophysis that is characteristic of other species of *Pterosphenus* is absent in *Pt. kutchensis* n. sp. In addition, in most vertebrae of *Pt. kutchensis* n. sp. there is a step between the anterior border of the zygosphene and the base of the anterior edge of the neural spine. This character recalls *Palaeophis* although the step is clearly narrower than in the latter genus. This step does not occur in the other species of *Pterosphenus*. This feature probably represents a plesiomorphic state within palaeophiids.

It may be added that the pterapophyses of *Pt. kutchensis* n. sp. are higher than those of *Pt. shep-*

pardi, but this difference might be a result of intracolumnar variation. Finally, it should be noted that *Pt. kutchensis* n. sp. is the smallest and one of the two earliest species of *Pterosphenus*.

Pterosphenus biswasi n. sp.
(Figs 4; 5A)

HOLOTYPE. — 1 trunk vertebra (RUSB 2784-4).

ETYMOLOGY. — Named for Dr. S. K. Biswas, in recognition of his work on the geology of Kutch.

TYPE LOCALITY. — HD Pit in Panandhro Mine, Kutch District, India.

REFERRED MATERIAL. — 2 vertebrae: 1 from HD Pit (RUSB 2565-1) and 1 from Channel Pit (RUSB 2790-21).

HORIZON. — Naredi Formation, Ypresian, Lower Eocene.

DIAGNOSIS. — Species of *Pterosphenus* distinguished from *Pt. schucherti*, *Pt. schweinfurthi*, and *Pt. muruntau* by its markedly less deeply concave anterior border of the zygosphene. Differs from *Pt. schucherti* and *Pt. schweinfurti* in having the zygapophyseal plane located slightly higher. Differs from *Pt. sheppardi* by its longer and more oblique paradiapophyses, and the anteroposteriorly longer basis of its hypapophysis. Distinguished from *Pt. kutchensis* n. sp. by its less laterally compressed vertebrae, the concave anterior border of its zygosphene, its markedly shorter paradiapophyses, separated bases of the paradiapophyses, and the presence of an anterior hypapophysis.

DESCRIPTION OF HOLOTYPE
The holotype is a large, massive trunk (presumably mid-trunk) vertebra (Fig. 4). The measurements are as follows: length of centrum from cotylar rim to tip of condyle: 18.9 mm; width through prezygapophyses: 19.7 mm; width of interzygapophyseal constriction: 18.2 mm; diameter of cotyle: 12.8 mm; width of zygosphene: 13.2 mm.

In anterior view, the vertebra is clearly compressed laterally and high. The prezygapophyses are small; their articular facets are slightly inclined above the horizontal and they lie slightly above the level of the floor of the neural canal. The zygosphene is thick and hardly wider than the cotyle; its dorsal border forms the base
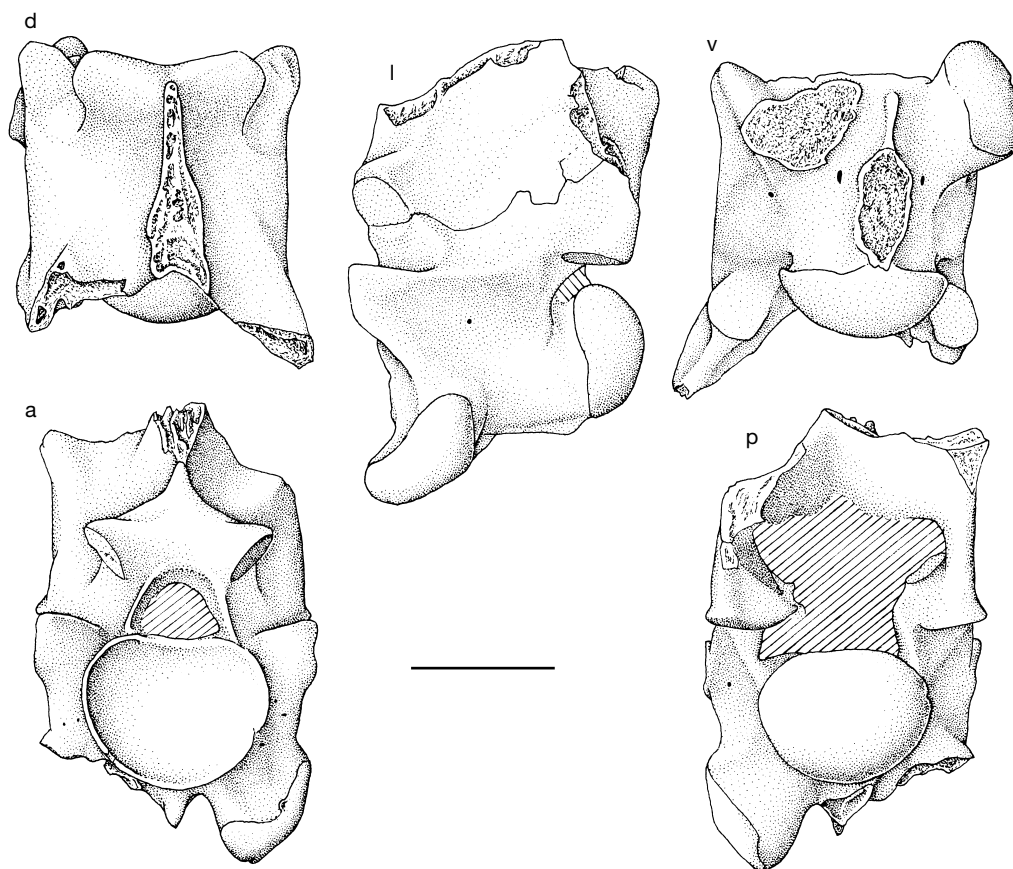
FIG. 4. — *Pterosphenus biswasi* n. sp., holotype, trunk vertebra (RUSB 2784-4), in anterior (**a**), dorsal (**d**), left lateral (**l**), posterior (**p**), and ventral (**v**) views, Ypresian of Panandhro Mine (HD Pit). Scale bar: 1 cm.

of the anterior edge of the neural spine, which gives a subtriangular shape to the frontal aspect of the zygosphene. The cotyle appears to be slightly depressed dorsoventrally and its dorsal part is truncated. The section of the neural canal is small, markedly narrower than the zygosphene and cotyle. The pterapophyses are incomplete; the base of the right one shows that they were high. The paradiapophyses are situated low and distant from the centrum. Below the cotyle, a space that represents about one third the diameter of the cotyle, separates the bases of the paradiapophyses. A small anterior hypapophysis is present beneath the cotyle, between the paradiapophyses. The vertebra lacks para-cotylar foramina but irregular small foramina open in the anterior face of the prezygapophyseal buttresses.

In dorsal aspect, the vertebra appears to be more or less squarish, not clearly longer than wide. The prezygapophyseal facets are small, not elongate, and directed more anteriorly than laterally. The interzygapophyseal constriction is hardly expressed. The lateral borders of the interzygapophyseal ridges are slightly convex laterally. The zygosphene does not form clearly defined lateral lobes; its anterior border is weakly concave. Anteriorly, the neural spine reaches the anterior face of the zygosphene; it grows thicker posteriorly. The basal parts of the pterapophyses

that are preserved form blunt, poorly defined keels. The median notch in the posterior border of the neural arch is shallow and obtuse, but its bottom is clearly triangular. The roof of the zygantrum is not extended.

In lateral view, the vertebra is short and high. The neural spine and the hypapophysis are broken off. The zygosphenal facet is small, subcircular, and directed more dorsally than anteriorly. The interzygapophyseal ridge is strong and prominent. The anterolateral ridge of the prezygapophyseal buttress originates on the anterodorsal margin of the paradiapophysis. The articular facet of the paradiapophysis is elongate and markedly oblique (about 45° from the vertical); there is no distinction between the dia- and parapophyseal areas. The axis of the condyle is horizontal. A small lateral foramen opens below the interzygapophyseal ridge.

In posterior view, the lateral flanks of the neural arch are vertical. The cotyle is slightly depressed. The area of zygantral foramina is obscured by matrix.

In ventral view, the centrum appears cylindrical. It lacks subcentral ridges. The base of the hypapophysis is elongate. Posteriorly, it reaches the condyle; anteriorly, it is prolonged by a thin keel the anterior part of which forms the anterior hypapophysis. Elongate subcentral foramina are present.

OTHER SPECIMENS AND VARIATION

Only two other specimens are available. One large vertebra (RUSB 2565-1) is very worn; a smaller vertebra (RUSB 2790-21) is damaged. They are referred to *Pt. biswasi* n. sp. on the basis of markedly separated bases of paradiapophyses (i.e. they clearly differ from *Pt. kutchensis* n. sp. from the same locality), slightly concave anterior border of zygosphene, and an anterior hypapophysis below the cotyle (the latter feature cannot be checked in RUSB 2565-1). In both vertebrae, as in the holotype, the anterior edge of the neural spine is continuous with the anterior face of the zygosphene; as a result, the latter face is subtriangular. The presence or absence of foramina is not verifiable in these two specimens.
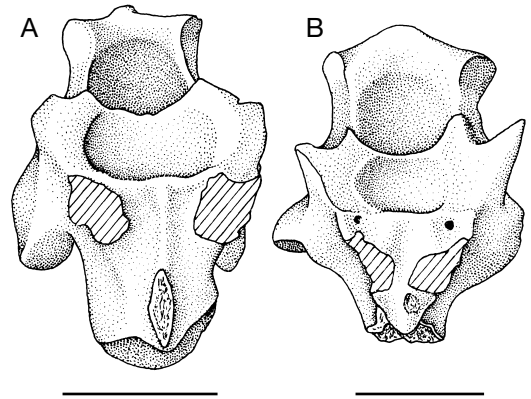

FIG. 5. — Comparison between *Pterosphenus biswasi* n. sp. and *Pt. kutchensis* n. sp., trunk vertebrae of similar sizes in antero-ventral views; **A**, *Pt. biswasi* n. sp., the bases (hatched areas) of the paradiapophyses (broken off) are markedly separated (RUSB 2790-21); **B**, *Pt. kutchensis* n. sp., the paradiapophyses (broken off; hatched areas) originate from a common base (RUSB 2790-3). Both vertebrae from Channel Pit. Scale bars: 5 mm.

COMMENTS

A problem arises from the fact that there are two species at Panandhro Mine, a small and a large one. Therefore, it may be argued that the palaeophiid described above as *Pt. kutchensis* n. sp. is only represented by juvenile individuals of *Pt. biswasi* n. sp. However, as shown above, the vertebrae referred to *Pt. kutchensis* n. sp. include some juveniles but mainly adult specimens. Moreover, at least one of the characters that distinguish the two species cannot be interpreted as an ontogenetic change: the paradiapophyses originate from a common base in *Pt. kutchensis* n. sp. whereas the bases are markedly separated in *Pt. biswasi* n. sp. as in all other snakes. Such an ontogenetic change has never been reported. In addition, vertebrae of similar size belonging to these two species (i.e. a large vertebra of *Pt. kutchensis* n. sp. and a small one of *Pt. biswasi* n. sp.) display the conditions of the paradiapophyses typical for these two species: the paradiapophyses arise from a single base in the large vertebra of *Pt. kutchensis* n. sp. while the bases of the two paradiapophyses are clearly separated on the vertebra of similar size belonging to *Pt. biswasi* n. sp. (Fig. 5). This clearly demonstrates that this difference is not of ontogenetic nature and that there are two distinct species.

Pt. biswasi n. sp. is easily distinguished from *Pt. kutchensis* n. sp. Apart from its larger size and separate bases of paradiapophyses, it differs from *Pt. kutchensis* n. sp. in having an anterior hypapophysis, less laterally compressed vertebrae, shorter paradiapophyses, and a concave anterior border of zygosphene.

The distinction between *Pt. biswasi* n. sp. and the other species of *Pterosphenus* is less marked. It differs from all other species in having a shallow concave anterior border of zygosphene, while it is deeply concave, even notched, in *Pt. schucherti*, *Pt. schweinfurthi*, and *Pt. muruntau* (not observable in *Pt. sheppardi*). *Pt. biswasi* n. sp. further differs from *Pt. schucherti* and *Pt. schweinfurthi* by its zygapophyseal plane that is located slightly higher (mainly shown by the postzygapophyseal facets) and from *Pt. sheppardi* by its more elongate and more oblique paradiapophyses, and the anteroposteriorly longer base of its hypapophysis.

Pterosphenus sp.

REFERRED MATERIAL. — 15 vertebrae: 8 from HD Pit (RUSB 2721-58, 2721-59; RUSB 2564-27 to 2564-31; RUSB 2784-5) and 7 from Channel Pit (RUSB 2790-22 to 2790-28).

These vertebrae are too damaged to be allocated at species level. But their referral to *Pterosphenus* is unquestionable.

COMMENTS ON THE PALAEOPHIIDAE FROM KUTCH

Thus far, the earliest *Pterosphenus* (*Pt. schucherti*) has been reported from the middle Eocene (Westgate 1989), more precisely the late Lutetian or early Bartonian (Westgate pers. comm.), of the USA. Therefore, the two species of *Pterosphenus* from Panandhro Mine antedate the North American species.

Although *Pt. kutchensis* n. sp., one of the two species from Panandhro Mine, is one of the two earliest species of *Pterosphenus*, it is the most advanced palaeophiid species as far as adaptation to aquatic life is concerned.

It appears to be somewhat peculiar and rather different from the other known species of *Pterosphenus*. It appears to be more strongly adapted to aquatic life, i.e. it is more advanced than other species of *Pterosphenus* in being deeper and more laterally flattened. But it is less advanced than the other species of *Pterosphenus* in having a space between the anterior face of the zygosphene and the anterior edge of the neural spine in most vertebrae, which is the condition retained in *Palaeophis*. In addition, the anterior border of the zygosphene is not concave in *Pt. kutchensis* n. sp. In other species of *Pterosphenus* the anterior border of the zygosphene is concave and, except in *Pt. biswasi* n. sp., it is even notched. The zygosphene is notched in lizards and in most early snakes; consequently, the notched zygosphene would represent the plesiomorphic state. Therefore, *Pt. kutchensis* n. sp. likely represents a distinct lineage of *Pterosphenus*. Finally, the recovery of the genus *Pterosphenus* from the early Eocene necessitates a change in our views on the evolution of the Palaeophiinae. It was suggested that the palaeophiines evolved from "primitive" *Palaeophis* to *Pterosphenus*, through "advanced" *Palaeophis* (Janensch 1906). Hoffstetter (1958) showed that this over-simplified view was wrong and he implicitly inferred that *Palaeophis* is a paraphyletic assemblage, stem group of *Pterosphenus*. The discovery of a very derived *Pterosphenus* from the early Eocene strongly supports Hoffstetter's opinion.

Family ?MADTSOIIDAE Hoffstetter, 1961 or BOIDAE Gray, 1825

The Madtsoiidae and Boidae are two clearly distinct families. Madtsoiids are basal snakes (Scanlon & Lee 2000) whereas boids are living snakes that may be considered "relatively advanced". Although the two families are phylogenetically clearly distinct, their vertebrae show a similar overall morphology. The referral of well preserved vertebrae at family level is easy, but the assignment may be doubtful when the vertebrae are damaged, which is the case of the fossils from Panandhro Mine.
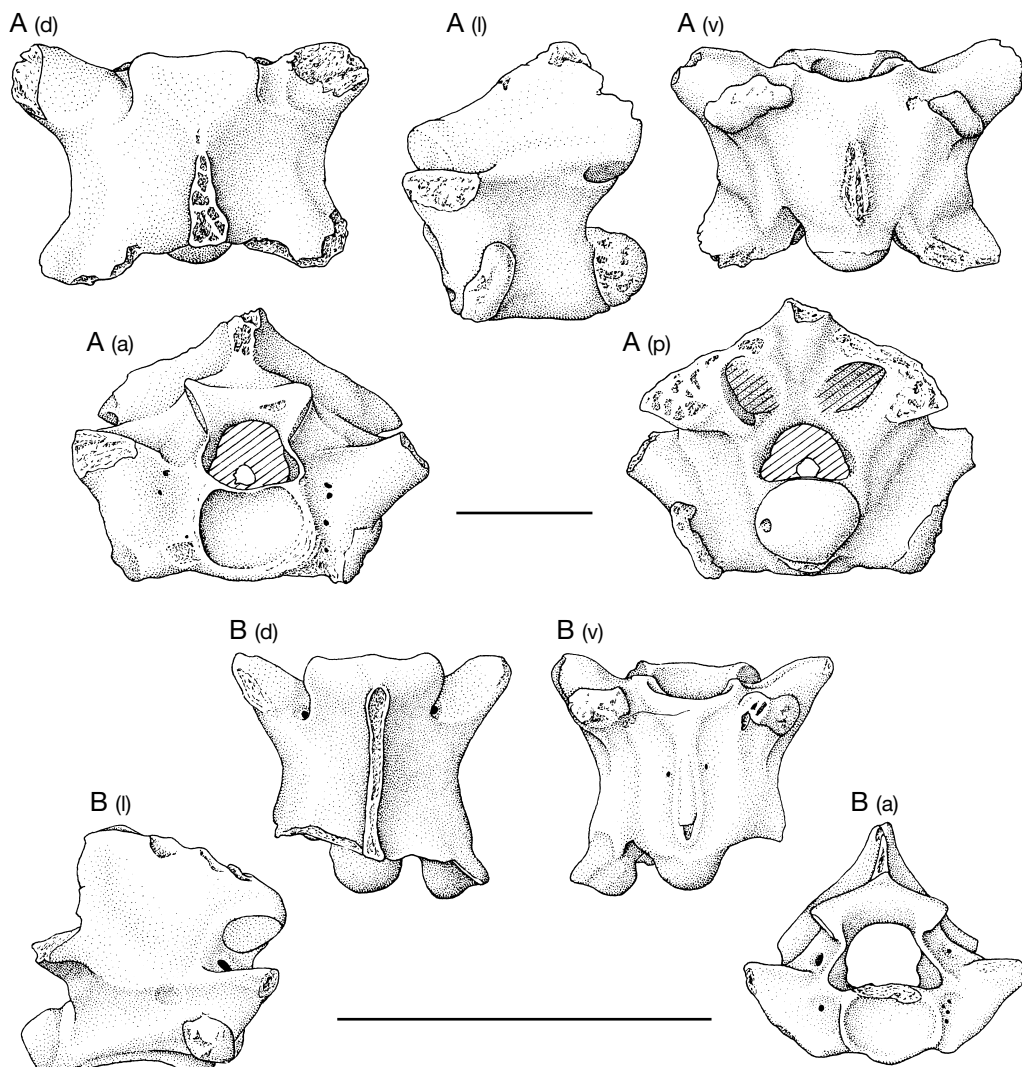
FIG. 6. — **A**, Madtsoiidae or Boidae, trunk vertebra (RUSB 2784-6), Ypresian of Panandhro Mine (HD Pit); **B**, Colubroidea, family indeterminate, trunk vertebra (RUSB 2790-29), Ypresian of Panandhro Mine (Channel Pit). Anterior (**a**), dorsal (**d**), lateral (**l**), posterior (**p**), and ventral (**v**) views. Scale bars: 1 cm.

Indeterminate genus
(Fig. 6A)

REFERRED MATERIAL. — 2 vertebrae (RUSB 2784-6 and 2784-7) from HD Pit.

DESCRIPTION
RUSB 2784-6 is a large mid-trunk vertebra (length of centrum from cotylar lip to tip of condyle: 13.6 mm; minimum width of interzygapophyseal constriction: 18.2 mm; width of zygosphene: 9.1 mm). The neural spine and lateral parts of prezygapophyses are broken off while the paradiapophyses and the posterior border of the neural arch are eroded.

In anterior view, the vertebra is wide and depressed. The zygosphene is rather thick and its

roof is slightly concave dorsally. It is slightly wider than the neural canal and cotyle. Because its rim is damaged, it is not possible to state whether the cotyle was depressed or circular. The articular facets of the prezygapophyses are inclined. Beneath the facets, the remaining parts of the prezygapophyses are thick. The paradiapophyses are worn but it may be inferred that they probably faced laterally. Three paracotylar foramina open on each side.

In dorsal view, the interzygapophyseal constriction is shallow. The shape of the prezygapophyseal facets cannot be determined. The anterior border of the zygosphene is nearly straight. The neural spine is anteroposteriorly short. Its sloping anterior edge progressively widens anteriorly; it reaches the roof of the zygosphene with which it forms a subtriangular surface. The neural spine is thickened posteriorly. The precise shape of the posterior median notch cannot be determined but it was shallow and very obtuse.

In lateral aspect, the vertebra is short and high. The anterior edge of the neural spine is markedly inclined. The interzygapophyseal ridges are prominent but not sharp. The paradiapophyses are anteroposteriorly narrow. The subcentral ridges are weakly marked.

In posterior view, the neural arch is moderately vaulted. The state of preservation of its posterior border does not permit to establish whether parazygantral foramina are present.

In ventral view, the centrum widens anteriorly. It is limited by poorly developed subcentral ridges that slightly arch posterolaterally. The haemal keel is damaged but it was not wide.

RUSB 2784-7 is a damaged posterior trunk vertebra. It mainly differs from RUSB 2784-6 in having a wider, more prominent, and more clearly limited haemal keel. On either side, a rather deep subcentral groove runs between the haemal keel and subcentral ridge. The latter ridges are better developed and the centrum widens less anteriorly than in the mid-trunk vertebra. These differences between the two vertebrae represent usual variation that distinguishes mid- from posterior trunk vertebrae in snakes. At least two foramina are present on each side of the cotyle.

COMMENTS

The vertebrae from HD Pit are short, wide, and massively built. This vertebral morphology is characteristic of the Boidae and Madtsoiidae. Vertebrae of Madtsoiidae differ from those of the Boidae in having parazygantral foramina (a derived feature) and in lacking any trace of prezygapophyseal processes (plesiomorphic state). Moreover, the paradiapophyses of madtsoiids strongly project laterally; they approach, or even project beyond the level of the lateral extremity of the prezygapophyseal facets, which is not the case in boids, except in posteriormost trunk vertebrae of rare taxa. In addition, madtsoiids have paracotylar foramina (often, two on each side) while, in the Boidae such foramina occur only in various Boinae; in the latter subfamily, the paracotylar foramina are not double, except in a few vertebrae of three species from the Palaeocene of Brazil (Rage 2001) and in *Bavarioboa hermi* from the Miocene of Germany (Szyndlar & Schleich 1993). The polarity of the two latter features (protruding paradiapophyses, presence of paracotylar foramina) is unknown.

Unfortunately, in the fossils from HD Pit, the posterior face of the neural arch is damaged and the lateral extremities of the prezygapophyses are lacking; consequently, it is not possible to state whether parazygantral foramina and prezygapophyseal processes are present. In RUSB 2784-6 three paracotylar foramina are present whereas at least two are observable in RUSB 2784-7, which appears to be more consistent with madtsoiids than with boids. The morphology of the centrum of the posterior trunk vertebra (RUSB 2784-7) is similar to that of various species of *Madtsoia*; more specifically, the wide and clearly limited haemal keel resembles that of *M. madagascariensis* (pers. obs.) from the ?Maastrichtian (Rogers *et al.* 2000) of Madagascar and of *M. camposi* from the Palaeocene of Brazil (Rage 1998). On the other hand, the remaining parts of the paradiapophyses show that they probably did not markedly protrude laterally, which argues against assignment to madtsoiids but is consistent with the boid vertebral morphology. Moreover, the prezygapophyses clearly projected laterally as in various boids; in madtsoiids they are less elongated.

Finally, it does not seem possible to confidently refer these vertebrae to one of these two families. The Madtsoiidae range from the mid-Cretaceous to the Pleistocene (Rage & Werner 1999). However, post-Eocene madtsoiids are known only in Australia (Scanlon 1995, 1997). They primarily inhabited Gondwanan regions. The earliest Boidae come from the latest Cretaceous (Campanian-Maastrichtian) of Europe, and South and North America (Rage 1984; Albino 2000). In Asia, aside from the possible boid from the Ypresian of Panandhro Mine, the oldest representative of the family was recovered from the early-middle Eocene of Pakistan (Rage 1987a). The Boidae probably originated in a Gondwanan region, but as early as the Eocene they were widely distributed on Laurasian continents.

Super-family COLUBROIDEA Oppel, 1811

The Colubroidea are regarded as the most advanced snakes. They comprise four living (Colubridae, Atractaspididae Günther, 1858, Elapidae, Viperidae Gray, 1825) and two extinct (Anomalophiidae, Russellophiidae) families. The Russellophiidae are known from the mid-Cretaceous (Cenomanian) to the late Eocene (Rage & Werner 1999) whereas the Anomalophiidae are restricted to the early Eocene. Besides, colubroids without family reference were reported from the Cenomanian of Sudan (Colubroidea *incertae sedis*; Rage & Werner 1999), the late early Eocene of France (Colubroidea *incertae sedis*; Augé *et al*. 1997), and the late Eocene of Britain (*Vectophis wardi* Rage & Ford, 1980; *Headonophis harrisoni* Holman, 1993). The earliest member of a living family is a Colubridae from the late Eocene of Thailand (Rage *et al.* 1992). In the Ypresian of Panandhro Mine, the Colubroidea are represented by a single vertebra whose assignment is not possible at family level.

Indeterminate family
(Fig. 6B)

REFERRED MATERIAL. — 1 trunk vertebra (RUSB 2790-29) from Channel Pit.

DESCRIPTION

The vertebra probably comes from the mid-trunk region. The posterior part of the neural arch, the neural spine, tips of prezygapophyses, and paradiapophyses are damaged. The vertebra is not heavily built and it is comparatively elongate (length of centrum from cotylar rim to tip of condyle: 5.1 mm; width of zygosphene: 3.6 mm; minimum width of interzygapophyseal constriction: 4.6 mm). In anterior aspect, the vertebra appears wide and relatively lightly built. The zygosphene is wide, moderately thick, and its roof is slightly arched dorsally. The neural canal is comparatively broad. The cotyle is rather small and depressed dorsoventrally. The zygapophyseal facets are nearly horizontal; they lie above the floor of the neural canal. The tip of each prezygapophysis is damaged, but the thickness of the remaining lateral part suggests that prezygapophyseal processes were present. The paradiapophyses are eroded, but it may be inferred that they faced lateroventrally. On the right side, a foramen opens in the position of a paracotylar foramen, but on the left side four foramina are present in the "paracotylar area". The fact that four foramina are present on one side does not permit to definitely regard these foramina as homologous to paracotylar foramina, but this cannot be rejected. On either side, a large parazygosphenial foramen opens in a deep fossa located between the zygosphenial and prezygapophyseal facets.

In dorsal view, the prezygapophyseal facets are elongate and oblique. The interzygapophyseal constriction is shallow. The zygosphene is wide; its anterior border is trilobate but the lobes project only weakly anteriorly. On each side, the large parazygosphenial foramen is visible. Anteriorly, the neural spine reaches the roof of the zygosphene but it does not approach the anterior border.

In lateral view, the vertebra is approximately as high as long. The zygosphenial facets are broad. The damaged lateral tips of the prezygapophyses suggest that prezygapophyseal processes were present but this cannot be definitely confirmed. The interzygapophyseal ridges are sharply defined. On each side, below the interzygapophyseal ridge

is a large and deep fossa; on the right side, matrix obscures the bottom of the fossa, but on the left side the fossa contains the lateral foramen. The paradiapophyses are small, not more elongate dorsoventrally than anteroposteriorly. The subcentral ridges are well developed. Like the ventral border of the haemal keel, they are slightly arched dorsally. The axis of the condyle appears to be slightly oblique.

In ventral view, the centrum is narrow and limited by parallel subcentral ridges; its ventral surface is flat. The haemal keel is not strongly defined; it is narrow and moderately prominent. Two subcentral foramina are present.

The damaged posterior face of the vertebra shows that the neural arch was vaulted. Parazygantral foramina are absent.

COMMENTS

The relatively light build and elongation of the vertebra, as well as the narrowness of the centrum show that this specimen belongs to the Colubroidea.

The presence of parazygosphenial foramina in RUSB 2790-29 makes it possible to distinguish it from all other colubroids, but it should be noted that the significance of these foramina is unknown. Such foramina are present in *Pouitella* Rage, 1988, a basal snake of unknown family reference from the Cenomanian (Rage 1988), *Palaeophis colossaeus*, a palaeophiid from the Lutetian (Rage 1983b), and in the Acrochordidae, a living family (Hoffstetter & Gayrard 1964). These foramina are also known in a mosasauroid lizard from the Cenomanian (Rage & Néraudeau in press). The presence of parazygosphenial foramina in an early colubroid appears to be consistent with their presence in acrochordids that are the sister group to colubroids; these foramina probably represent a plesiomorphic state within Colubroidea.

The presence of foramina in the paracotylar region permits us to distinguish RUSB 2790-29 from other colubroids that do not belong to recent families, except *Headonophis* Holman, 1993 that has paracotylar foramina.

The absence of compressed buttresses of the prezygapophyses forming a vertical ridge on either side of the vertebra, demonstrates that RUSB 2790-29 cannot be referred to the Russellophiidae or Anomalophiidae. Moreover, the weak inclination of the zygapophyseal facets is like that of nearly all other snakes (i.e. dorsomedial), whereas in russellophiids they face dorsolaterally. The vertebra from Panandhro Mine further differs from those of the Anomalophiidae in being more lightly built.

Apart from the presence of the foramina discussed above (parazygosphenial and ?paracotylar foramina), RUSB 2790-29 clearly differs from the colubroids from the Cenomanian of Sudan and from the early Eocene of France in having a much more vaulted neural arch, and from the vertebrae of *Vectophis* Rage & Ford, 1980 in being markedly more elongate.

On the whole, RUSB 2790-29 clearly resembles modern colubroids belonging to the Colubridae and Elapidae, although in the latter family hypapophyses are present on trunk vertebrae. The overall morphology of the vertebra is clearly reminiscent of that of Colubridae. The vertebral differences between colubroids belonging to modern families and Cretaceous-Eocene fossils are the presence of prezygapophyseal processes and of subdivided paradiapophyseal areas in modern forms. Moreover, recent colubroids have paracotylar foramina, whereas the foramina are absent in Eocene and pre-Eocene forms, except *Headonophis*. Unfortunately, it does not appear possible to state whether the foramina that open on either side of the cotyle of RUSB 2790-29 are true paracotylar foramina. The paradiapophyses are eroded and one cannot determine whether the articular surfaces were subdivided into para- and diapophyseal areas. Finally, from the form of lateral tip of the prezygapophyses, it is strongly suspected that prezygapophyseal processes were present, but this cannot be definitely confirmed. The presence of prezygapophyseal processes would represent a derived character that, along with the presence of possible paracotylar foramina, might suggest that this vertebra belong to the colubrid lineage; if this is right, RUSB 2790-29 would represent the earliest member of this group. Unfortunately, the state of preservation of

the specimen does not permit us to refer it to the Colubridae.

Whatever the precise taxonomic position of RUSB 2790-29 within the colubroids, it represents a "modern" snake within the present fauna. In fact, its close resemblance to the modern Colubridae might lead to the suspicion that the vertebra belongs to a recent snake that became mixed with specimens from the fossiliferous bed. However, the specimen is mineralized and it shows the same color as most of the palaeophiid vertebrae from the site; in addition, parts are worn and polished in such a manner that this specimen cannot be a bone of a recent individual. Therefore, RUSB 2790-29 really represents a colubroid from the early Eocene.

This specimen represents a new genus and species, but this single and incomplete vertebra cannot be a name-bearer of a new taxon. Consequently, this new colubroid snake remains unnamed.

CONCLUSIONS

The Eocene of Panandhro Mine has produced a rich fauna of snakes that is largely dominated by palaeophiids. The presence of the snake *Pterosphenus* would argue for a middle or late Eocene age, but the early Eocene age suggested by foraminifera (for the correlative units in the Naredi formation) appears more likely at present. The fauna includes Palaeophiidae (*Pterosphenus kutchensis* n. sp. and *Pt. biswasi* n. sp.), a snake that is either a Madtsoiidae or a Boidae, represented by an indeterminate genus and species, and an indeterminate family of Colubroidea. The Palaeophiidae are represented by 124 vertebrae, while two vertebrae are referred to the madtsoiid or boid snake, and only one belongs to the Colubroidea.

Within palaeophiids, *Pterophenus kutchensis* n. sp., a small species, markedly outnumbers the large *Pt. biswasi* n. sp. (106 vertebrae to 3). *Pt. biswasi* n. sp. is a typical *Pterosphenus* that does not call for particular comments. But *Pt. kutchensis* n. sp. is a peculiar species that shows a unique feature, i.e. the two paradiapophyses originate from a common base, or, in a few specimens, there is perhaps not a common base but the base of each paradiapophysis is closely appressed against the base of the opposite paradiapophysis. These two species are the first palaeophiids reported from India.

The presence of Madtsoiidae in India remains doubtful. The specimens from the Ypresian of Kutch, as the specimen from the Maastrichtian of Takli (= Gitti Khadan) (Gayet *et al.* 1985), are the only fossils from India that might be referred to madtsoiids. Unfortunately, their state of preservation does not permit a secure referral. If they do not belong to the Madtsoiidae, then they represent Boidae. In the latter case, the vertebrae from Panandhro Mine might represent the earliest Boidae from Asia.

The colubroid from Channel Pit is the first pre-Neogene representative of the group reported from India.

It should be noted that, assuming that the Ypresian age is well established, *Pt. kutchensis* n. sp. and *Pt. biswasi* n. sp. represent the earliest members of *Pterosphenus* (see above). This is somewhat astonishing since *Pt. kutchensis* n. sp. is more strongly adapted to aquatic life than the species from the late Eocene. Previously, it was supposed that this adaptation more or less progressively developed in the palaeophiines to culminate in the late Eocene *Pterosphenus*. *Pt. kutchensis* n. sp. probably corresponds to a divergent lineage of *Pterosphenus*, unfortunately the available material does not permit a phylogenetic analysis within the group.

Pterosphenus was a snake highly adapted to aquatic life. Its vertebrae are tall and narrow, and the ribs are weakly curved; as a result, the body was laterally compressed. Such a body form is known only in highly aquatic snakes: living laticaudine and hydrophiine Elapidae, and extinct bipedal snakes from the mid-Cretaceous. In addition, the paradiapophyses (i.e. the articulations for ribs) are displaced ventrally; consequently, the centre of gravity is also shifted ventrally, which certainly improved trim and maneuverability in water. Unfortunately, these anatomical characteristics

do not suggest whether these snakes lived in marine or freshwater (or both).

According to Westgate & Gee (1990), *Pt. schucherti* from the middle Eocene of Texas lived in brackish and freshwater, close to or in an estuarine mangrove, under tropical conditions. The same species has also been found in open marine deposits from the late Eocene (Westgate 2001). The Birket Qarun and Qasr el Sagha Formations of Egypt that yielded *Pt. schweinfurthi* also correspond to brackish and/or shallow marine coastal environments (lagoon, delta front, mangrove) (Gingerich 1992). From this, it appears that *Pterosphenus* lived in marine, brackish, and freshwater, close to the coasts. Mangrove areas were perhaps especially favourable to this snakes. The mode of life of the species of *Pterosphenus* might have been similar to that of the living *Acrochordus granulatus* (Acrochordidae) that is highly adapted to salt water (Dunson & Dunson 1973) and lives in marine water, along the coasts, but may enter rivers and lakes (McDowell 1979).

The vertebrae of the colubroid and madtsoiid or boid found at Panandhro Mine do not display any adaptation to aquatic life (which does not mean that they were unable to temporarily enter water). They are probably allochthonous terrestrial snakes within the fauna of Panandhro Mine. From a palaeobiogeographic point of view, only the Madtsoiidae are significant (if madtsoiids are present at Panandhro Mine). This family is essentially Gondwanan. Out of Gondwanan areas they are known only from Spain (Rage 1996, 1999) and southern France (Sigé *et al.* 1997). Unfortunately, the presence of this family in India is still doubtful. During the Eocene, boids were likely nearly cosmopolitan and they provide no palaeobiogeographical information if the subfamily is not identified. *Pterosphenus* was probably widely distributed as a consequence of its aquatic mode of life. It is known in the early Eocene of India, while it is present in the middle Eocene of North America, and in the late Eocene of Africa, North and South America. The question arises whether this distribution is significant as far as the geographic origin and dispersal of the genus are concerned. In our present state of

knowledge, no conclusion can be drawn because too few localities bearing *Pterosphenus* are known.

Acknowledgements

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