FOSSIL SNAKES FROM THE PALAEOCENE OF SÃO JOSÉ DE ITABORAÍ, BRAZIL. PART III. UNGALIOPHIINAE, BOOIDS *INCERTAE SEDIS*, AND CAENOPHIDIA. SUMMARY, UPDATE, AND DISCUSSION OF THE SNAKE FAUNA FROM THE LOCALITY

by

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SUMMARY

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Mots-clés: Serpents, booïdes *incertae sedis*, Ungaliophiinae, "tropidophiidés", Caenophidia, Russellophiidae, Paléocène, Brésil, nouveaux taxons.

Key-words: Snakes, booid-grade *incertae sedis*, Ungaliophiinae, "tropidophiids", Caenophidia, Russellophiidae, Palaeocene, Brazil, new taxa.

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ABSTRACT

Aside from Madtsoiidae, anilioids, and Boidae that were studied previously, the middle Palaeocene of Itaboraí (Brazil) has produced Ungaliophiinae ("tropidophiids"), booid-grade snakes *incertae sedis*, and a possible Russellophiidae (Caenophidia) that are described in the present article. This article is the third and final report on the snakes from the locality. The Ungaliophiinae (*Paraungaliophis pricei* gen. et sp. nov.) are rare whereas the booid-grade snakes *incertae sedis* (*Itaboraiophis depressus* gen. et sp. nov., *Paulacoutophis perplexus* gen. et sp. nov.) are more frequent. A single vertebra is referred to the Russellophiidae (Caenophidia) with reservation. An update of the whole fauna of snakes from Itaboraí is provided. *Hechtophis austrinus* that was tentatively referred to the erycine Boidae is now regarded as a Boidae *incertae sedis*. Most snakes from Itaboraí are known only from the locality. Astonishingly, only the anilioid *Coniophis* cf. *C. precedens* gives possible evidence of interchanges between South and North America. The fauna of snakes from Itaboraí, as well as the other Palaeocene faunas of snakes from South America are distinct from those of the Cretaceous and the Eocene of South America; they appear to be more different from the Cretaceous faunas than from those of the Eocene. The fauna from Itaboraí is the richest and most diverse assemblage of snakes from the Palaeocene worldwide; it shares only a few taxa with other Palaeocene localities.

RESUME

En dehors des Madtsoiidae, anilioïdes et Boidae qui ont déjà été publiés, le Paléocène moyen d'Itaboraí (Brésil) a fourni des Ungaliophiinae ("tropidophiidés"), des serpents *incertae sedis* de grade booïde et un possible Russellophiidae (Caenophidia) qui sont décrits dans le présent article. Il s'agit ici du troisième et dernier article sur les serpents du gisement. Les Ungaliophiinae (*Paraungaliophis pricei* gen. et sp. nov.) sont rares alors que les *incertae sedis* de grade booïde (*Itaboraiophis depressus* gen. et sp. nov., *Paulacoutophis perplexus* gen. et sp. nov.) sont plus fréquents. Une unique vertèbre est attribuée avec quelques doutes aux Russellophiidae (Caenophidia). L'ensemble de la faune de serpents d'Itaboraí est discuté et mis à jour. *Hechtophis austrinus* qui était rapporté avec doutes aux Erycinae (Boidae) est maintenant considéré comme un Boidae *incertae sedis*. La plupart des serpents d'Itaboraí ne sont connus que dans ce gisement. De façon étonnante, seul l'anilioïde *Coniophis* cf. *C. precedens* témoigne de possibles échanges entre Amérique du Sud et du Nord. La faune de serpents d'Itaboraí, tout comme celles des autres gisements paléocènes sud américains, se distingue de celles du Crétacé et de l'Eocène d'Amérique du Sud; ces faunes paléocènes sont plus différentes de celles du Crétacé que de celles de l'Eocène. La faune de serpents d'Itaboraí est la plus riche et la plus diversifiée du Paléocène au niveau mondial; elle ne partage que quelques taxons avec les autres gisements du Paléocène.

INTRODUCTION

Parts of the snake fauna from the middle Palaeocene of São José de Itaboraí (Brazil) were reported in two articles (Rage, 1998, 2001). Rage (1998) detailed the Madtsoiidae and Aniliidae, whereas the second article (Rage, 2001) dealt with the Boidae.

The present article is the third, and final report on this rich and diverse fauna of snakes. It documents the remainder of the booids and the only possible caenophidian from the locality, and it summarizes the snake fauna and examines its significance.

The geological age of São José de Itaboraí (hereafter referred to as "Itaboraí") has until recently been regarded as middle Palaeocene (Muizon & Brito, 1993; Rage, 1998). The fauna from Itaboraí is comprised of fossils from several fissure fillings that are perhaps of slightly different ages (Van Valen, 1988), but, according to Marshall *et al.* (1997), the fauna corresponds to a rather short interval of time, i.e. between 58.2 and 56.5 million years. However, the middle Palaeocene, i.e. the Selandian, would range from 61.7 to 58.7 m.y. according to Gradstein *et al.* (2004). Gelfo *et al.* (2009) suggested an early Eocene age; an opinion that deserves attention, but in this contribution a Palaeocene age is retained (see below).

The fossils are deposited in the Departamento Nacional de Produção Mineral of Rio de Janeiro, Brazil. The names of the collectors and the dates of collection of the fossils are provided because the specimens come from distinct collections; the latter likely correspond to different fissure fillings whose ages are perhaps slightly different.

The used collection acronyms are DGM for the material housed in the Departamento Nacional de Produção Mineral of Rio de Janeiro, Brazil, and MNHN for the specimens curated in the Département Histoire de la Terre, Muséum national d'Histoire naturelle, Paris, France.

Measurements of the vertebrae are defined in Rage (2001: fig. 1).

SYSTEMATIC PALAEONTOLOGY

Booid-grade snakes

Within Alethinophia, booid snakes represent a level of evolution between the anilioid and caenophidian grades, the latter being a clade (Caenophidia) nested within booids. This booid assemblage was long termed Booidea, i.e. Booidea Gray, 1825 (e.g., Albino, 1996a; Holman, 2000; Szyndlar & Rage, 2003), but since the group is paraphyletic this name should be avoided. This assemblage includes several living taxa: the Boidae, Xenopeltidae, Loxocemidae, Bolyeriidae, and the "tropidophiids". The latter group deserves special attention because its systematic structure is debated and it is represented at Itaboraí by at least one species.

Remarks on "tropidophiid" booids

The "tropidophiids" (dwarf boas) were long included in the Boidae, but Underwood (1976) separated them from the latter family. Subsequently, McDowell (1987) distinguished two taxa within this assemblage: the Tropidophiinae (including the living *Tropidophis* and *Trachyboa*) and Ungaliophiinae (for the living *Ungaliophis* and *Exiliboa*). Neither Underwood nor McDowell questioned the monophyly of this group, but Zaher (1994), based on soft anatomy, suggested that "tropidophiids" are polyphyletic, i.e. the Tropidophiinae and Ungaliophiinae are not closely related. Molecular studies have also suggested polyphyly (Vidal & Hedges, 2002; Wilcox *et al.*, 2002; Vidal & David, 2004; Wiens *et al.*, 2008). However, on the basis of anatomy, Lee & Scanlon (2002) and Scanlon (2006) regarded "tropidophiids" as a paraphyletic assemblage. The clear distinction between Tropidophiinae and Ungaliophiinae, whatever their precise relationships, is consistent with vertebral morphology. The vertebrae of these two groups are different from one another. More specifically, the vertebral morphology of ungaliophiines appears to be distinctive within booids, while that of tropidophiines does not clearly differ from the generalized booid (Szyndlar & Böhme, 1996; Szyndlar & Rage, 2003; Szyndlar *et al.*, 2008; and see below). Aside from vertebral morphology, tropidophiines and ungaliophiines are collectively distinguished from other booids, and they differ from each other by the composition of the caudal region (Szyndlar & Böhme, 1996). All caudal vertebrae of ungaliophiines possess haemal keels (instead of the usual paired haemapophyses), while in tropidophiines anterior caudals bear hypapophyses, mid-caudals have paired haemapophyses, and posterior caudals have haemal keels. Therefore, caudal vertebrae appear to be especially useful for identification of both groups. Unfortunately, caudal vertebrae are rare at Itaboraí and none of them unquestionably shows "tropidophiid" characteristics.

On the other hand, despite differences in vertebral morphology and composition of the caudal region, the "tropidophiid assemblage" is distinguished from other booids in having more elongate trunk vertebrae (in fact, mainly narrower, more elongate centra) and depressed neural arches. In addition, some fossil snakes display a combination of features found in both tropidophiines and ungaliophiines. Therefore it is convenient, for at least palaeontological purposes, to retain the term "tropidophiids" (Szyndlar *et al.*, 2008), keeping in mind that it has probably no systematic meaning because it refers to an assemblage that may be para- or polyphyletic.

"Tropidophiids"

Today, "tropidophiid" snakes are restricted to Central America (including Caribbean islands) and northern South America. The Tropidophiinae inhabit northern South America and Caribbean islands while the Ungaliophiinae occur in Central America and northern South America.

Several fossils have been referred to "tropidophiids": *Dunnophis* HECHT, 1959, from the Eocene of North America (Hecht, 1959; Holman, 2000), the Eocene and earliest Oligocene of Europe (Rage, 1984), and perhaps the late Palaeocene of North America (Estes, 1976) and Africa (Augé & Rage, 2006); *Messelophis* BASZIO, 2004, from the middle Eocene of Europe (Baszio, 2004; Schaal & Baszio, 2004); *Platyspondylia* RAGE, 1974 from the Eocene and Oligocene of Europe; *Rottophis* SZYNDLAR & BÖHME, 1996, from the latest Oligocene of Europe; and *Falseryx* SZYNDLAR & RAGE, 2003, from the Oligocene and Miocene of Europe (Szyndlar & Rage, 2003; Szyndlar *et al.*, 2008). None of these genera can be reliably referred to one of the two extant subfamilies; they perhaps represent extinct "tropidophiid" lineages. In addition, McDowell (1987) tentatively referred *Boavus* (implicitly *B. idelmanni* from the middle Eocene of North America) to "tropidophiid" snakes mainly on the basis of cranial characters, but he did not indicate what characters. Wallach & Günther (1998) endorsed McDowell's opinion, but the assignment of this snake to "tropidophiids" is not demonstrated.

Ungaliophiinae MCDOWELL, 1987

Two of the extinct genera referred to "tropidophiids" (*Platyspondylia* and *Messelophis*) were regarded close to ungaliophiines. McDowell (1987) referred *Platyspondylia* to the Ungaliophiinae on the basis of skull bones. The presence of haemapophyses in the caudal region does not seem consistent with this referral (Szyndlar & Rage, 2003; Szyndlar *et al.*, 2008), but this is only a plesiomorphic trait. However, the morphology of trunk vertebrae does not argue for the assignment of *Platyspondylia* to ungaliophiines. Baszio (2004) suggested close relationships between *Messelophis* and the *Ungaliophis*-*Exiliboa* clade, i.e. ungaliophiines. His opinion was mainly based on trunk vertebrae. However, the high number of vertebrae in *Messelophis variatus* argues against assignment to ungaliophiines (Szyndlar *et al.*, 2008) and *Messelophis* remains an enigmatic booid. *Dunnophis* has never been referred to the Ungaliophiinae, but the overall morphology of its trunk vertebrae is somewhat reminiscent of this taxon (Bogert, 1968); however, the presence of haemapophyses on caudal vertebrae casts doubts on such an assignment. Finally, none of the hitherto described extinct "tropidophiid" may be securely assigned to the Ungaliophiinae, but a fossil from Itaboraí appears to be referrable to this subfamily.

Paraungaliophis gen. nov.

Etymology: Greek, *para*, close to, and *Ungaliophis*, the type genus of the subfamily.
Diagnosis: as for the type species and only known species.

Paraungaliophis pricei sp. nov.

1987 *Dunnophis*-like snake: Rage, p. 59.

1991 *Dunnophis*-like snake: Rage, p. 507.

1996b aff. *Dunnophis*: Albino, p. 200.

2003 *Dunnophis*-like snake: Szyndlar and Rage, p. 83.

Holotype: one mid-trunk vertebra (DGM 1365-R), collector(s) and date unknown. **Referred material:** one posterior trunk vertebra (DGM 1366-R), collector(s) and date unknown.

Type locality: Itaboraí, State of Río de Janeiro, Brazil.

Horizon: middle Palaeocene.

Etymology: in honor of Llewellyn I. Price, Brazilian palaeontologist who studied vertebrates from Itaboraí.

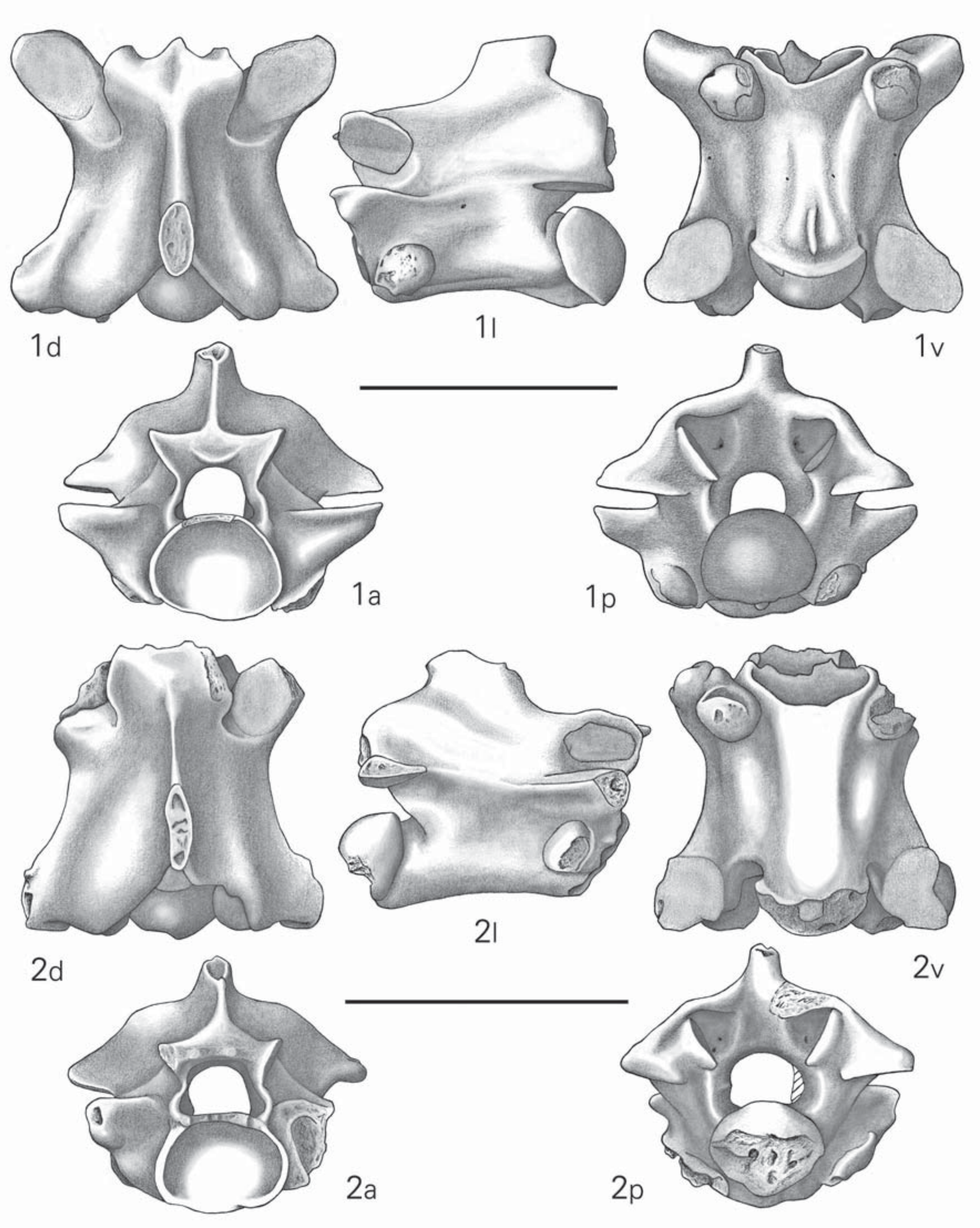
Diagnosis: Referred to the Ungaliophiinae on the basis of the following combination of characters: vertebrae comparatively elongate and narrow, prezygapophyseal processes small, interzygapophyseal and subcentral ridges not well-marked, and haemal keel shallow. Differs from other Ungaliophiinae (*Ungaliophis* and *Exiliboa*) in having a more vaulted neural arch, a stronger central lobe of zygosphene, a shallower interzygapophyseal constriction, and dorsoventrally shorter, hemispherical paradiapophyses. Further differs from *Exiliboa* in having an anteroposteriorly short neural spine, restricted to the posterior part of the neural arch.

Description of the holotype (fig. 1):

Measurements (in mm). Width across the prezygapophyses (PRW): 6.4; total length from prezygapophysis to postzygapophysis (MLV): 5.7; length of centrum (CL): 4.4; width of zygosphene (ZW): 2.7; width of cotyle (CTW): 2.4; width of interzygapophyseal constriction (WIC): 3.9.

The holotype is a massively built and relatively elongate mid-trunk vertebra. In anterior view, it is wider than high. The cotyle is relatively large and slightly depressed. Its width is similar to that of the zygosphene. The thickness of the zygosphene is moderate. The zygosphenal roof is concave dorsally and it slopes anteriorly; consequently, it grows thiner anteriorly and the median lobe appears to be produced by the ventral part of the roof. The neural canal is comparatively small. The prezygapophyseal facets are horizontal and they lie at a low level, i.e. at the level of the floor of the neural canal. The prezygapophyseal processes are present but they are very reduced. The vertebra lacks paracotylar fossae but deep grooves separate the cotyle from the prezygapophyseal buttresses. In the bottom of the right groove there are perhaps two foramina, but this cannot be confirmed.

In dorsal aspect, the interzygapophyseal constriction appears shallow and obtuse. It is asymmetrical, its maximum depth being located very anteriorly. The prezygapophyseal facets are oval and their major axis is oblique. The prezygapophyseal processes do not project beyond the facets. The anterior border of the zygosphene forms three strongly projecting lobes. The central lobe is narrow, acute, and projects slightly farther anteriorly than the lateral lobes. The posterior median notch deeply indents the neural arch. The neural spine is restricted to the posterior part of the neural arch. It is prolonged anteriorly by a blunt keel that reaches the posterior area of the zygosphene, but the thick dorsal border of the neural spine is very short anteroposteriorly (it represents less than one fifth of the vertebral length). The neural arch markedly bulges above the zygantrum and the resulting convexities clearly extend anteriorly.



Figures 1-2.— *Paraungaliophis pricei* gen. et sp. nov. 1: Holotype, mid-trunk vertebra (DGM 1365-R). 2: posterior trunk vertebra (DGM 1366-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 5 mm.

In lateral view, the vertebral morphology appears to be somewhat peculiar. The vertebra is relatively elongate, without well-marked interzygapophyseal ridges, and the neural spine is short anteroposteriorly, confined to the posterior part of the neural arch, and moderately high. The anterior border of the neural spine arises gently from the neural arch and is nearly vertical in its dorsal part. The posterior border of the neural spine barely overhangs posteriorly. The zygosphenal facets are large. The paradiapophyses are more or less tubercular and small; more specifically, they do not clearly extend dorsoventrally. Although their articular surfaces are more or less damaged, it may be inferred that they lack any trace of division into dia- and parapophyseal areas. Subcentral ridges are hardly apparent. Only the posterior part of the haemal keel projects ventrally. Lateral foramina are present.

In posterior view, the neural arch is vaulted and it swells out markedly above the zygantrum. The neural spine is rather thick. There is one zygantral foramen on each side. Parazygantral foramina are lacking. The condyle is comparatively large.

In ventral view, the centrum is narrow, elongate and it does not widen anteriorly. The vertebra lacks clear subcentral ridges; as a result, the centrum is poorly limited laterally. The haemal keel is poorly marked off from the centrum; it widens posteriorly. In its wide posterior part, the keel produces a shallow sagittal ridge that projects ventrally. There are no subcentral grooves. Tiny subcentral foramina are present.

Posterior trunk vertebra (fig. 2):

Nearly all differences that distinguish the posterior trunk vertebra DGM 1366-R from the mid-trunk vertebra (holotype) fall within the range of usual intracolumnar variation. The neural arch is less vaulted, but it remains clearly upswept above the zygantrum. Although slightly longer anteroposteriorly than in the holotype, the neural spine remains short. Its dorsal part is broken, consequently its height cannot be evaluated. Wide, shallow, and poorly defined subcentral grooves are present in the anterior part of the centrum. The haemal keel is wider than in the holotype; anteriorly, it is almost flat and relatively well-limited by the subcentral grooves, but posteriorly it is weakly salient and poorly limited. The posterior trunk vertebra lacks the small sagittal ridge that is present on the posterior part of the haemal keel of the holotype. The anterior border of the zygosphene is damaged, but it may be inferred that the three lobes were present, as in the holotype. The lateral lobes were apparently less salient but, as judged from its remaining base, the central lobe was certainly strong. The vertebra lacks paracotylar and parazygantral foramina.

Discussion:

The vertebral morphology of *Paraungaliophis* is very peculiar, which allows description of a new taxon despite limited material. The vertebrae are relatively elongate, the centrum is narrow and elongate, the interzygapophyseal ridges are weak, the subcentral ridges are practically absent, and the neural spine is short anteroposteriorly and restricted to the posterior part of the neural arch. This combination of characters occurs only in ungaliophiine "tropidophiids" and in the Nigerophiidae.

The Nigerophiidae are extinct, highly aquatic snakes known from the mid-Cretaceous to the Palaeocene, perhaps the middle Eocene (Rage & Werner, 1999). They include *Nigerophis mirus* from the Palaeocene of Niger and *Nubianophis afaahus* from the Cenomanian of Sudan. Moreover, three other snakes may belong to the

Nigerophiidae: *Indophis sahnii* (Maastrichtian of India), *Woutersophis novus* (middle Eocene of Belgium), and "*Nessovophis*" *zhylga* (early Eocene of Kazakhstan; Averianov, 1997; Rage *et al*., 2003). In addition, LaDuke (2002) reported an "undescribed genus and species of nigerophiid" from the latest Cretaceous of Madagascar. These snakes differ from *Paraungaliophis* in having vertebrae more or less compressed laterally and by their peculiar prezygapophyses. In confirmed, and also in possible nigerophiids, as in various other aquatic snakes, the prezygapophyses lack prezygapophyseal processes, but each prezygapophyseal buttress is compressed anteroposteriorly and forms a subvertical ridge that stretches from the dorsal limit of the paradiapophysis to the lateral extremity of the prezygapophyseal facet. Confirmed nigerophiids (i.e, *Nigerophis* and *Nubianophis*) and *Indophis* further differ from *Paraungaliophis* in having the zygapophyseal plane lying at a high level (markedly above the floor of the neural canal); consequently, their neural arch occupies a high position. In confirmed nigerophiids, the posterior part of the haemal keel is clearly deflected ventrally, contrary to that of *Paraungaliophis*. In *Indophis* and *Woutersophis*, the interzygapophyseal and subcentral ridges are relatively marked, which distinguishes them from *Paraungaliophis*. The latter genus further differs from "*Nessovophis*" *zhylga* in having a distinct, markedly higher neural spine. Thus, *Paraungaliophis* clearly differs from the Nigerophiidae.

The vertebral morphology of *Paraungaliophis* compares favorably with that of the Ungaliophiinae. Vertebrae of ungaliophiine "tropidophiids" are very characteristic; they are relatively elongate and narrow, with small prezygapophyseal processes and weak to hardly marked interzygapophyseal and subcentral ridges, and the haemal keels are shallow. They clearly differ from the vertebrae of the Tropidophiinae that display a typical booid pattern (i.e., vertebrae shorter and wider) and have deep, blade-like haemal keels (Szyndlar & Rage, 2003; Szyndlar *et al*., 2008). Such a marked difference in vertebral morphology would be surprising, although not impossible, if the traditional Tropidophiidae form a clade, but, as discussed above, this assemblage may be either para- or polyphyletic.

Whatever the precise relationships of the Ungaliophiinae, the vertebral morphology of *Paraungaliophis* is consistent only with that of this subfamily and I refer it to this group because of the combination of characters given above.

Paraungaliophis differs from all other ungaliophiines in having a strong central lobe of the zygosphene, a more vaulted neural arch, and paradiapophyses very short dorsoventrally. The paradiapophyses appear to be more or less hemispherical, without any trace of division between dia- and parapophyseal areas. This morphology may occur in juvenile snakes, but the two vertebrae assigned to *Paraungaliophis* do not belong to juveniles. They are well-ossified; more specifically, the lateral walls of the vertebral canal, below the zygosphenal facets, are completed, and the roof of the zygantrum is thick. Such hemispherical paradiapophyses are also present in lizards and scolecophidian snakes, which would argue for the primitive nature of this morphology. If that be the case, then this character would represent a reversal in *Paraungaliophis*. The latter genus further differs from the living ungaliophiines by its shallower interzygapophyseal constriction. In addition, *Paraungaliophis* is distinguished from *Exiliboa* in having neural spines clearly shorter anteroposteriorly: the anterior border of the neural spines of the fossil is shifted markedly behind the zygosphene. The morphology of the neural spines of *Paraungaliophis* is reminiscent of *Ungaliophis*.

The absence of caudal vertebrae hinders a fully reliable assignment of *Paraungaliophis* to the Ungaliophiinae, but the peculiar vertebral morphology is so similar to that of the living *Ungaliophis* that this referral does not appear to be questionable.

cf. ***Paraungaliophis pricei***

Referred material: one poorly preserved posterior (posteriormost ?) trunk vertebra (DGM 1377-R), collected by "Price and Campos" in 1968.

Description and discussion:

DGM 1377-R is a poorly preserved vertebra that shows the overall morphology of *Paraungaliophis pricei*. It differs from the two vertebrae referred to the latter species in having marked (but damaged) subcentral grooves and an anteroposteriorly longer neural spine. The presence of conspicuous subcentral grooves suggests that this vertebra comes from the posteriormost trunk region. The length of the neural spine also is a character consistent with the posteriormost region of the trunk, but in this vertebra the neural spine is markedly longer than that of the two other vertebrae. Therefore, DGM 1377-R cannot be confidently assigned to this species, it is referred to as cf. *Paraungaliophis pricei*.

Booids *incertae sedis*

Itaboraiophis gen. nov.

Etymology: from the name of the fossiliferous locality.

Diagnosis: as for the type species and only known species.

Itaboraiophis depressus sp. nov.

Holotype: one mid-trunk vertebra (DGM 1357-R), collected by J.S. Carvalho and O.S. Santos in 1953.

Referred material: ten trunk vertebrae (DGM 1358-R to 1362-R; DGM 1363a, b-R; DGM 1364a, b, c-R), (collections: DGM 1358-R and 1360-R by "J.S. Carvalho and O.S. Santos" in 1953; DGM 1359-R and 1362-R by "Campos and Silva" in 1968; DGM 1364a, b, c-R by "J.S. Carvalho" in 1967; DGM 1363a, b in 1961 by unknown collector(s); DGM 1361 by "Campos and Silva", date unknown).

Type locality: Itaboraí, State of Río de Janeiro, Brazil.

Horizon: middle Palaeocene.

Etymology: latin *depressus*, low, depressed, in reference to the strongly depressed neural arch.

Diagnosis: A distinctive booid snake that differs from other fossil and extant taxa in the group, except the living *Loxocemus* and the extinct *Cadurcoboa*, by the following combination of characters: vertebrae not elongate, neural spine high, neural arch strongly depressed, and mid- and posterior trunk vertebrae devoid of hypapophyses or deep haemal keels. Differs from *Loxocemus* in having narrower vertebrae and centra, anterior border of neural spines inclined posteriorly, and in lacking coalescence of posterior part of parapophysis with subcentral ridge. Distinguished from *Cadurcoboa* by its more depressed neural arch, more oblique prezygapophyseal facets in both dorsal and anterior views, shallower interzygapophyseal constriction, and inclined anterior border of neural spine. Further differs from *Loxocemus*, *Cadurcoboa*, and most other booids in having posterodorsal expansions of the diapophyses and by the markedly dorsal location of the subcentral ridges.

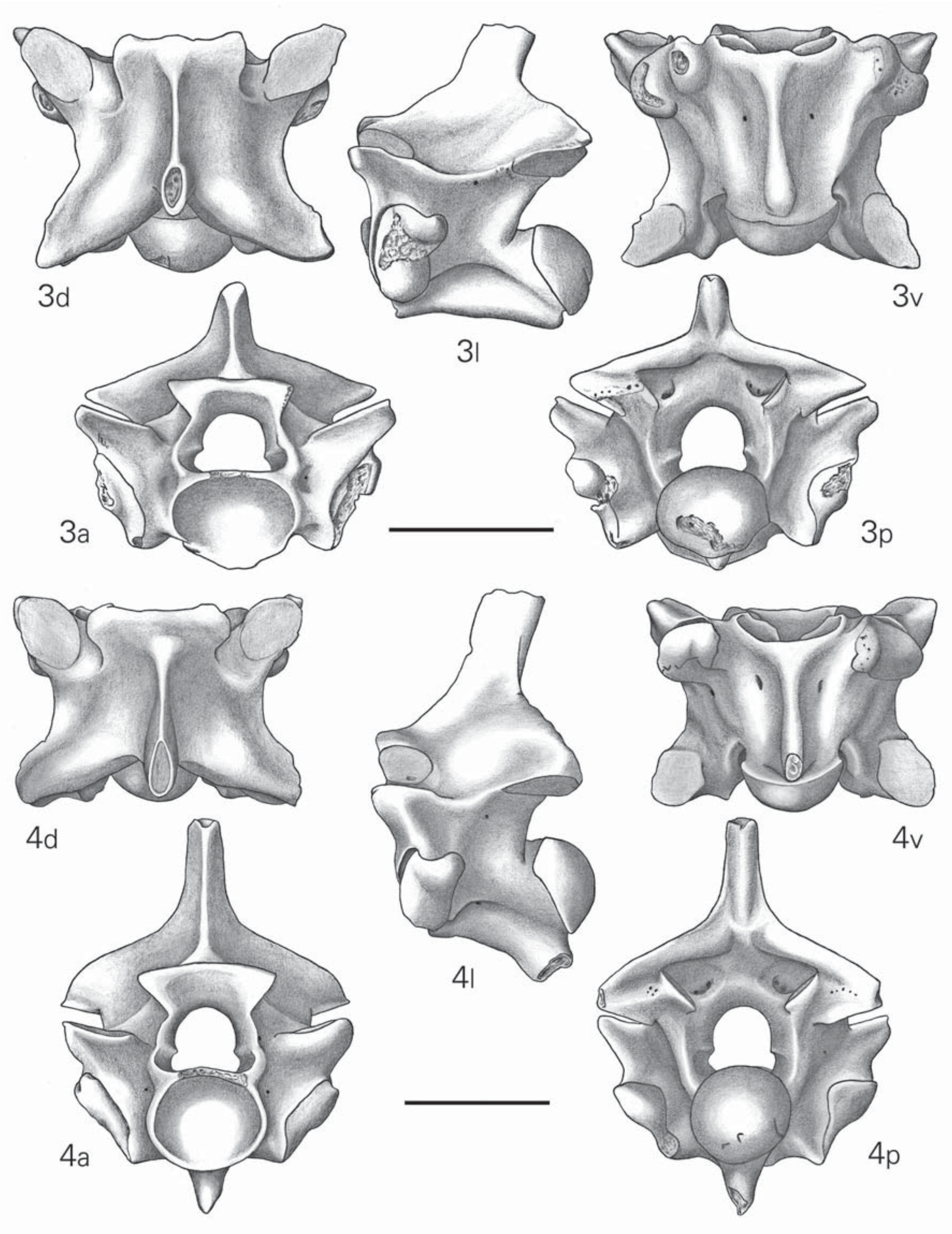
Description of the Holotype (fig. 3):

Measurements (in mm). Width across the prezygapophyses (PRW): 10.2; total length from prezygapophysis to postzygapophysis (MLV): 7.5; length of centrum (CL): 6.1; width of zygosphene (ZW): 3.9; width of cotyle (CTW): 3.6; width of interzygapophyseal constriction (WIC): 6.1.

In anterior view, the markedly oblique prezygapophyseal facets appear as the main characteristic; the medial limit of the facets lies well above the floor of the neural canal (at about half the height of the neural canal) whereas their lateral extremities are above the roof of the canal. The zygosphene is thin and about as wide as the cotyle. The neural canal is rather large. The upper part of the cotyle is truncate; as a result this articular cavity appears more or less depressed. The paradiapophyses do not markedly project laterally. Only one tiny paracotylar foramen is present (on the left side).

In dorsal view, the vertebra is wider than long. The prezygapophyseal articular facets are somewhat elongate and oval, their major axis is oblique. The interzygapophyseal constriction is shallow and obtuse. The prezygapophyseal processes project slightly beyond the articular facets. The posterior median notch is shallow and it forms an obtuse angle. The anterior border of the zygosphene is provided with three lobes that barely protrude anteriorly. The base of the neural spine is long; anteriorly, it originates on the roof of the zygosphene. The dorsal border of the neural spine is not swollen.

In lateral view, the neural spine is high and inclined posteriorly; it overhangs the posterior median notch. Anteriorly, the neural spine begins on the zygosphenal roof as a gently slanting ridge, but it rises steeply at the anteroposterior midpoint of the neural arch. The prezygapophyseal processes are compressed anteroposteriorly. A strong, prominent interzygapophyseal ridge connects pre- and postzygapophyses. The paradiapophyses clearly stretch dorsoventrally. The diapophyses markedly extend posterodorsally; they do not appear to be clearly separated from the parapophyses. The subcentral ridges run very dorsally with regard to the haemal keel and they are arched dorsally. The haemal keel is rather deeply produced ventrally. Lateral foramina are present.



Figures 3-4.— *Itaboraiophis depressus* gen. et sp. nov. 3: Holotype, mid-trunk vertebra (DGM 1357-R). 4: anterior trunk vertebra (DGM 1358-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 5 mm.

In posterior aspect, the neural arch is strongly depressed. Parazygantral foramina are lacking. There are two zygantral foramina in the right fossa, but only one is present on the left side.

In ventral view, the centrum is short and poorly limited laterally. Although subcentral ridges are marked in lateral aspect, they appear to be weak in ventral view. The ventral surface of the centrum widens anteriorly and it bears a narrow and rather distinct haemal keel. Subcentral foramina are present.

Intracolumnar variation:

Anterior trunk vertebrae are narrower and higher than those from the mid-trunk region; they are provided with a hypapophysis that is not clearly flattened laterally (fig. 4). As is usual, the neural arch is less depressed that those of mid-trunk vertebrae. However, it is astonishingly depressed for the anterior trunk region. The neural spine is very high and short anteroposteriorly. Mid-trunk vertebrae are illustrated by the holotype.

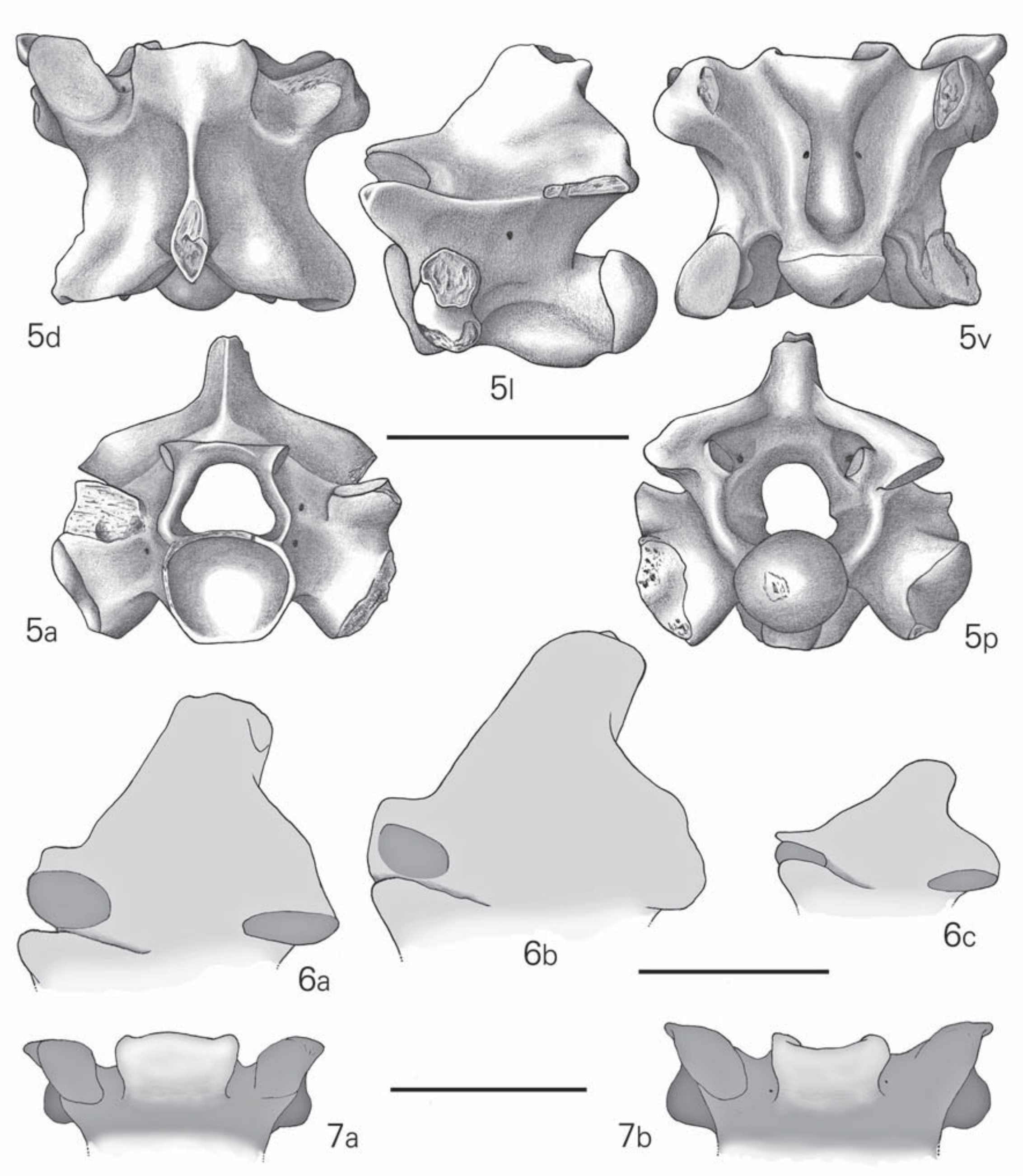
In the posterior trunk region, normal variation affects the vertebrae. They differ from those of more anterior regions in having marked subcentral grooves on either side of the haemal keel, a wider haemal keel, a lower neural spine (nevertheless, it remains comparatively high), and paradiapophyses more distant from the centrum (fig. 5a, p). In addition, the posterior expansion of the diapophyses appears to be either reduced or absent. Usually, in the posterior trunk region the neural arch is more depressed than that of mid-trunk vertebrae. However, in *Itaboraiophis*, the neural arch is very depressed in the mid-trunk region and, consequently, in posterior trunk vertebrae it displays a similar degree of flattening.

Intraspecific variation:

In the largest vertebra (DGM 1363b-R), the width across prezygapophyses (PRW) reaches 12 mm and the length between pre-and postzygapophyses (MLV) is 8.4 mm. In the smallest measurable specimen (DGM 1360-R), these dimensions are 7.3 mm and 5.5 mm respectively.

Itaboraiophis depressus exhibits a rather important intraspecific variability. In various vertebrae, the incline of the neural spine at the anteroposterior midpoint of the neural arch is often less abrupt than in the holotype; the anterior border of the neural spine may be even practically straight (fig. 6). The dorsal border of the neural spine is not swollen except in DGM 1364b-R in which a weak thickening appears. Several vertebrae lack the medial lobe of the zygosphene; in such cases, the zygosphenal border is either slightly convex or slightly concave between the lateral lobes (fig. 7). In the largest vertebrae, the zygosphene is narrower than the cotyle and thicker than that of smaller vertebrae. The posterodorsal extension of the paradiapophyses shows some variation; it is never more extended than in the holotype. Except in the anterior trunk vertebra DGM 1363a-R, the interzygapophyseal ridges are salient and often sharp.

Paracotylar foramina are always tiny. They appear irregularly, either on each side or on one side only. No vertebra has a double foramen in both zygantral fossae, but a double foramen is present on one side in two vertebrae. It should be noted that on one of the largest vertebrae (DGM 1362-R) and on one posterior trunk vertebra (DGM 1359-R; fig. 5a,d), parazygosphenal foramina are present. Such foramina are very rarely present in snakes; they occur in recent Acrochordidae, and in the extinct *Palaeophis colossaeus* (Palaeophiidae; Eocene) and *Pouitella* (lapparentophiid grade; Cenomanian). But these foramina may occur irregularly on rare occasion in other



Figures 5-7.— *Itaboraiophis depressus* gen. et sp. nov. 5: posterior trunk vertebra (DGM 1359-R) (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). 6: variation of neural spine (a: anterior/mid-trunk vertebra DGM 1362-R, b: anterior/mid-trunk vertebra DGM 1363b-R, c: mid/posterior trunk vertebra DGM 1360-R). 7: variation of zygosphene (a: mid/posterior trunk vertebra DGM 1360-R, b: mid-trunk vertebra DGM 1364b-R). Scale bars = 5 mm.

snakes, including in the taxon described below.

Discussion:

The vertebrae of *Itaboraiophis depressus* display the booid-like pattern that characterizes booids and the Madtsoiidae. They are short and wide, not lightly built, and the paradiapophyses are only weakly divided into dia- and parapophyseal areas. *Itaboraiophis* cannot be assigned to the Madtsoiidae because its vertebrae lack parazygantral foramina and are provided with prezygapophyseal processes. The overall morphology of the vertebrae of *Itaboraiophis* is consistent with that of the booids, but the ungaliophiine "tropidophiids". In the latter group, the vertebrae are elongate (or, at least, the centrum is narrow and elongate).

The combination of a high neural spine with a strongly depressed neural arch is quite unusual among booid snakes. It is known only in some tropidophiine "tropidophiids", the boine *Candoia aspera* (Molucca and Pacific islands), the loxocemid *Loxocemus* (Central America), and to a lesser extent in the enigmatic booid *Calabaria* (Africa), as well as in the extinct *Cadurcoboa* (late Eocene of Europe) and *Geringophis* (Oligocene and Miocene of North America). Holman (1982, 2000) referred *Geringophis* to the erycine Boidae, but this assignement was questioned by Szyndlar & Rage (2003). The relationships of *Geringophis* within the booids remain unknown. Rage (1978, 1984) regarded *Cadurcoboa* as a Boidae *incertae sedis*, but at that time the Boidae included taxa that are today regarded as distinct families. *Cadurcoboa* should be more appropriately regarded a booid *incertae sedis*.

Tropidophiines and *Candoia* may be discarded from comparisons because they are characterized by trunk vertebrae bearing hypapophyses or deep lamellar haemal keels (the latter often termed hypapophyses). *Itaboraiophis* is easily distinguished from *Loxocemus* whose vertebrae are clearly wider and have centra more widening anteriorly, broader articular zygapophyseal facets, neural spines with vertical anterior borders, and lamellar posterior parts of the parapophyses that merge in the subcentral ridges. *Calabaria* clearly differs from *Itaboraiophis* in having vertebrae wider and more depressed, zygapophyseal facets directed almost transversely, paradiapophyses less extended dorsoventrally, and subcentral ridges located more ventrally.

Vertebrae of *Itaboraiophis* differ from those of *Geringophis* in being less elongate, in having a more flattened neural arch, a more inclined anterior border of neural spine, and by its zygapophyses that are apparently more inclined on the horizontal.

Itaboraiophis is clearly distinguished from *Cadurcoboa* by a suite of characters. In *Itaboraiophis* the neural arch is more depressed, the zygapophyses are more oblique in dorsal view and more inclined on the horizontal, the interzygapophyseal constriction is less deep, and the anterior border of the neural spine is inclined posteriorly (vertical in *Cadurcoboa*).

Therefore, comparisons show that *Itaboraiophis* is a distinct taxon, but they do not disclose its relationships. The association of a high neural spine with a depressed neural arch in non-elongate vertebrae suggests relationships with the Tropidophiinae. Although *Itaboraiophis* lacks hypapophyses or deep lamellar haemal keels throughout the trunk region, it compares best with the latter taxon. The presence of hypapophyses or deep haemal keels probably represents a derived state, therefore *Itaboraiophis* cannot be excluded from tropidophiines on the basis of this feature; but such an assignment cannot be confirmed. On the other hand, the specific association of characters of *Itaboraiophis* does not permit exclusion of boid affinities, although it seldom occurs in this family. Unfortunately, caudal vertebrae (that may afford important information, see above) are rare at Itaboraí; none of them can be assigned to *Itaboraiophis*.

Finally, as is the case for other extinct booids that have a high neural spine and a depressed neural arch, *Itaboraiophis* is referred to booid *incertae sedis*, it being understood that, within this paraphyletic assemblage, it cannot belong to the ungaliophiine "tropidophiids" (because of its overall vertebral morphology) or erycine Boidae (because of its high neural spine).

Paulacoutophis gen. nov.

Etymology: named in honor of the late Brazilian palaeontologist Carlos de Paula Couto.

Diagnosis: as for the type species and only known species.

Paulacoutophis perplexus sp. nov.

Holotype: one mid-trunk vertebra (DGM 1367-R), collected in 1968 by unknown collector(s).

Referred material: ten trunk vertebrae (DGM 1368-R to 1372-R; DGM 1373a, b-R; DGM 1374a, b, c-R) and one cloacal or anterior caudal vertebra (DGM 1375-R), (collections: DGM 1368-R and 1373a, b-R by "J.S. Carvalho" in 1949; DGM 1370-R by "J.S. Carvalho" in 1967; DGM 1371-R by "Sonia Cruz" in 1966; 1372-R in 1968 by unknown collector(s); 1369-R, 1374a, b, c-R, and 1375-R, date(s) and collector(s) unknown).

Type locality: Itaboraí, State of Río de Janeiro, Brazil.

Horizon: middle Palaeocene.

Etymology: latin *perplexus*, puzzling, uncertain, in reference to the unclear relationships of the taxon.

Diagnosis: Snake with vertebrae of booid type but differing from all other booids, except *Itaboraiophis depressus*, in having irregular parazygosphenal foramina. Further differs from all booids but *Xenopeltis*, *Huberophis*, *Rottophis*, and *Paraplatyspondylia* in having, in mid- and posterior trunk regions, neural spines with an anterior border clearly slanting posterodorsally, the anterior border joining the dorsal border at a widely obtuse angle. Further distinguished from *Itaboraiophis* by its more weakly depressed neural arch, not dorsoventrally elongate paradiapophyses, and more ventrally located subcentral ridges. Further distinguished from *Xenopeltis* in having vertebrae not markedly depressed, a distinct posterior border of neural spine, and a posterior expansion of diapophyses in anterior and mid-trunk regions; from *Huberophis* in having a deeper interzygapophyseal constriction, narrower centrum, more marked subcentral ridges, and posterior expansions of diapophyses; from *Rottophis* by its wider zygosphene and posterior expansions of diapophyses; and from *Paraplatyspondylia* in having a wider zygosphene, wider centrum, more marked subcentral ridges, and stronger prezygapophyseal processes.

Description of the Holotype (fig. 8):

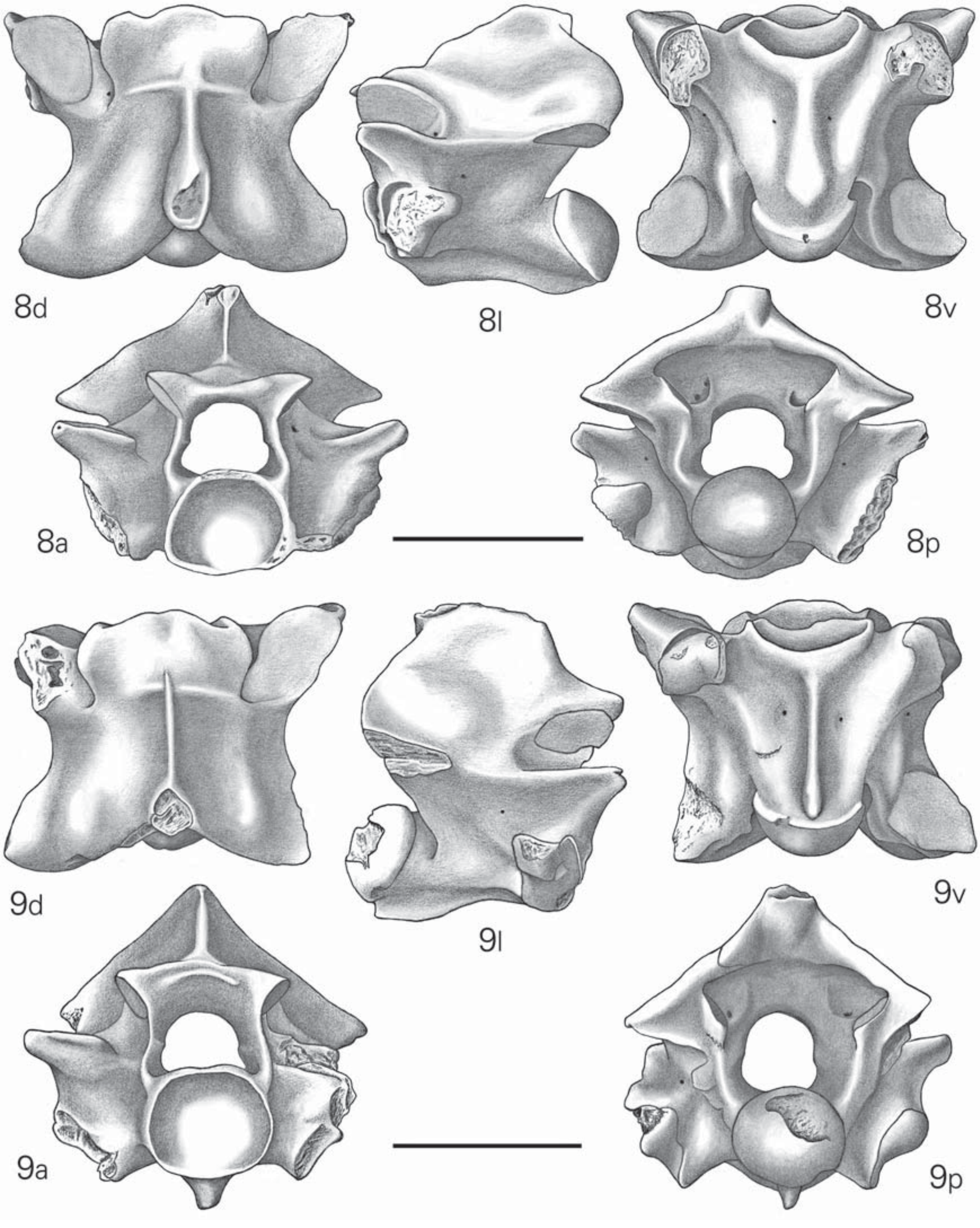
Measurements (in mm). Width across the prezygapophyses (PRW): 9.2; total length from prezygapophysis to postzygapophysis (MLV): 6.9; length of centrum (CL): 5.3; width of zygosphene (ZW): 4.4; width of interzygapophyseal constriction (WIC): 5.6.

The holotype is a mid-trunk vertebra that displays the typical booid morphology: it is massive, clearly wider than long, and its prezygapophyseal processes are small. In anterior view, the vertebra appears to be slightly depressed. The zygosphene is wider than the cotyle; it is comparatively thin and its roof is concave dorsally. The cotyle is not depressed. The section of the neural canal is medium-sized. The prezygapophyseal facets are moderately inclined; the level of the facets lies markedly above the floor of the neural canal. The prezygapophyses are not strongly produced laterally. The prezygapophyseal processes are short but well-marked. The paradiapophyses do not markedly protrude laterally; they are not well-preserved, but judging from the remaining part on the right side, the ventral extremity of the paradiapophysis did not project beyond the level of the cotyle ventrally. The vertebra lacks paracotylar foramina.

In dorsal view, the width and relative shortness of the vertebra are clearly apparent. The interzygapophyseal constriction is well-marked. The zygosphene is wide and its anterior border forms three rounded lobes that do not strongly project anteriorly. The zygosphene is limited posteriorly by a marked transverse ridge. The prezygapophyseal facets are oval, short, with an oblique major axis. The prezygapophyseal processes slightly project beyond the facets. The posterior median notch is not deep. The neural spine reaches the base of the zygosphene anteriorly. It is comprised of a posterior rather thick part and a thinner anterior portion. On either side of the neural spine, a broad, rounded bulge in the posterior part of the neural arch corresponds to the roof of the zygantrum. On the left side only, a parazygosphenal foramen is present.

In lateral view, the neural spine is relatively low. Its anterior border rises from the posterior limit of the zygosphene steeply at first, but then gently for most of its length; it joins the thick posterior part whose dorsal border is approximately horizontal. The paradiapophyses are poorly preserved; the dorsal part of the diapophysis markedly extends posteriorly. The sulcus for the costal ligament that bounds the anterodorsal part of the paradiapophysis forms a deep groove. The interzygapophyseal ridge is marked but not very salient. The subcentral ridges are poorly expressed in lateral view. Lateral foramina are present.

In posterior view, the neural arch is comparatively depressed. The neural spine is low and thick. Two zygantral foramina are present on the left side, but only one occurs on the right side. Parazygantral foramina are lacking.



Figures 8-9.— *Paulacoutophis perplexus* gen. et sp. nov. 8: Holotype, mid-trunk vertebra (DGM 1367-R). 9: anterior trunk vertebra (DGM 1368-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 5 mm.

In ventral view, the centrum appears to be comparatively narrow, but it clearly widens anteriorly. The ventral surface is limited by blunt, but relatively well-marked subcentral ridges. The haemal keel is broad and blunt. On either side of the keel, the ventral surface is flat.

Intracolumnar variation:

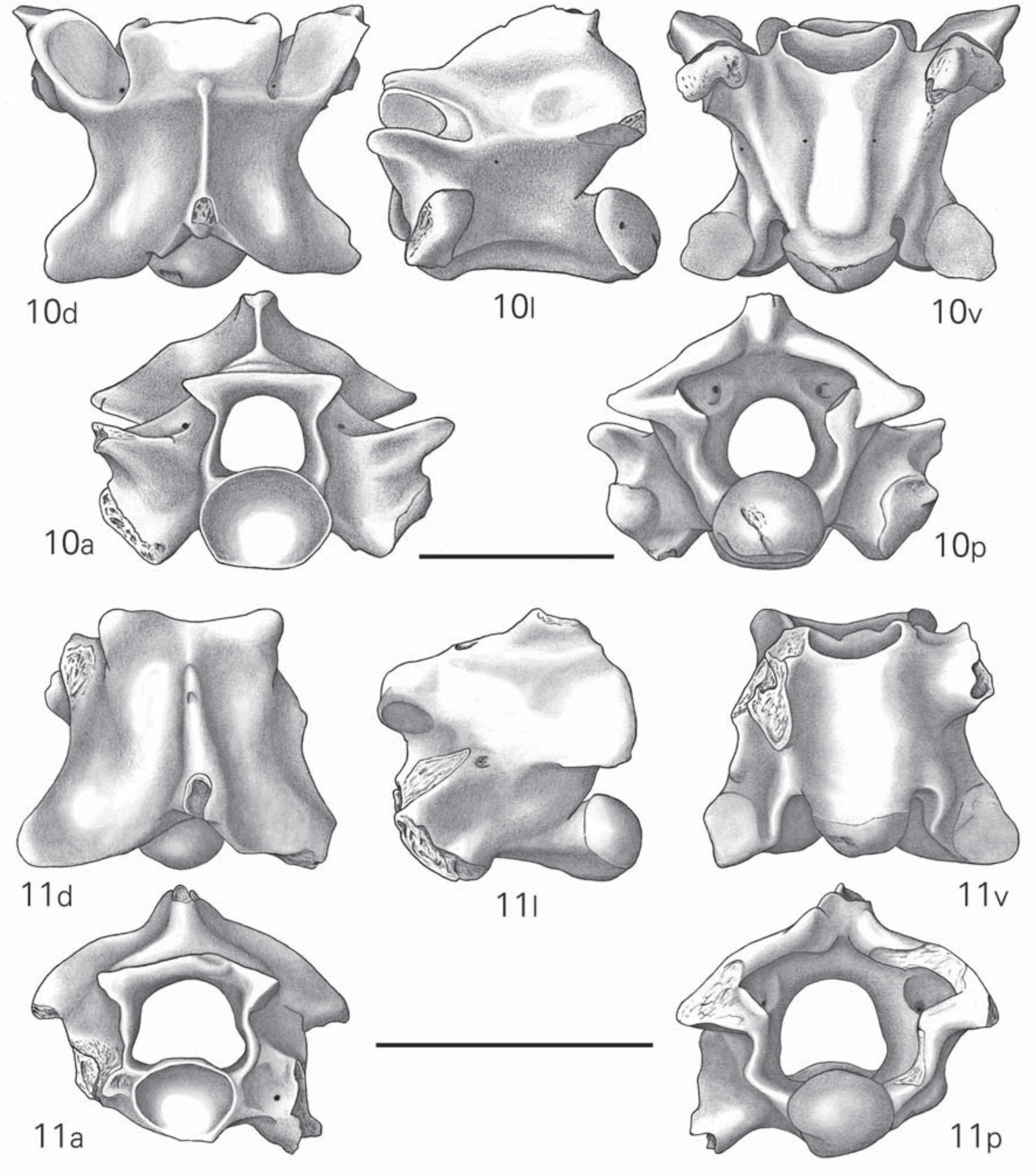
The anterior trunk region is represented by only one vertebra (fig. 9) that comes from the posterior part of this portion, but it cannot be excluded that this specimen is from the transition between the anterior and middle regions. It lacks a typical hypapophysis but a deep, thin haemal keel is present; the posterior part of the keel projects ventrally. Other usual differences distinguish this vertebra from those of more posterior portions of the column: its paradiapophyses are situated more distantly from the centrum (a feature that reappears in the posterior trunk vertebrae), its neural arch is more vaulted, and its centrum less widens anteriorly. However, these differences are not strongly marked, which is not surprising since this vertebra was not clearly anterior to the mid-trunk region. This vertebra further differs from those of the mid-trunk region in having a more vertical anterior border of the neural spine (which renders the neural spine boid-like), a shallower posterior median notch in the neural arch, and a tiny median notch in the median lobe of the zygosphene.

Vertebrae from the mid-trunk region are illustrated by the holotype. Posterior trunk vertebrae differ from those of the mid-trunk region by their laterally more distant paradiapophyses, their slightly more projecting prezygapophyseal processes, their slightly wider centrum, wider haemal keel, and less projecting median lobe of zygosphene; in addition, the dorsal part of the diapophyses does not extend posteriorly and subcentral grooves are present (fig. 10).

One cloacal or anterior caudal vertebra is available (fig. 11). Only the base of one of the ventrolateral processes is preserved on the left side. Therefore, it is not possible to determine whether the processes were lymphapophyses (forked) or pleurapophyses (not forked). Lymphapophyses occur in cloacal vertebrae (termed anterior caudals in various studies) whereas pleurapophyses are present in the caudal region (i.e. middle and posterior caudal regions in various studies) (Szyndlar & Rage, 2003). The vertebra is assigned to *Paulacoutophis* on the basis of having a wide zygosphene, and a neural spine and degree of vaulting of neural arch similar to those of trunk vertebrae. The most striking feature of this vertebra is the smooth ventral surface of the centrum that lacks haemapophyses or a haemal keel.

Intraspecific variation:

The few available vertebrae do not display important variation. The maximum length (MLV) of the largest vertebra (DGM 1370-R) is 7.2 mm and the width of its interzygapophyseal constriction (WIC) is 5.6 mm. In the smallest vertebra (DGM 1372-R) these dimensions are 5.3 mm and 4 mm respectively. The most striking variation occurs in a posterior trunk vertebra (DGM 1373a-R) in which the anterior border of the neural spine rises abruptly. Moreover, the length of the posterior extension of the diapophyses shows variation. The transverse ridge that forms the posterior limit of the zygosphene roof may be strongly or weakly marked; several vertebrae lack it. Only DGM 1375-R displays a paracotylar foramen (on the left side, the other side being broken away). Parazygosphenal foramina may be present (bilaterally in four vertebrae, unilaterally in two vertebrae) or absent (five vertebrae); the character cannot be checked in one vertebra.



Figures 10-11.— *Paulacoutophis perplexus* gen. et sp. nov. 10: posterior trunk vertebra (DGM 1369-R). 11: cloacal or anterior caudal vertebra (DGM 1375-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 5 mm.

Discussion:

As for *Itaboraiophis*, and for the same reasons (see above), *Paulacoutophis* may be referred to the non-ungaliophiine booids. *Paulacoutophis* differs from all other booids, but *Itaboraiophis depressus*, in having irregular parazygosphenal foramina. It is distinguished from almost all other booids by its peculiar neural spine in mid- and posterior trunk regions. In almost all booids, the neural spine of trunk vertebrae has well-defined anterior, dorsal, and posterior borders; the angles between the anterior and dorsal borders on one hand, and between the dorsal and posterior borders on the other hand are close to right angles. In the mid- and posterior trunk regions of *Paulacoutophis*, the anterior border is markedly slanting dorsoposteriorly and it joins the dorsal border at a very obtuse angle (figs 8, 10). Among booids, aside from *Paulacoutophis*, exceptions are the living *Xenopeltis*, and the extinct *Huberophis*, *Rottophis*, and *Paraplatyspondylia*.

Apart from the morphology of the neural spine, *Paulacoutophis* further differs from other booids, excepting the Boidae, by various features. It clearly differs from the Bolyeriidae in lacking hypapophyses in the mid- and posterior trunk regions. It is distinguished from *Loxocemus* in lacking the posterior extension of the parapophyses that merges with the subcentral ridges. It differs from the Tropidophiinae in having a low neural spine and in lacking deep, blade-like haemal keels. Finally, only the Boidae do not show differences other than the morphology of the neural spine and presence of parazygosphenal foramina.

Itaboraiophis differs from *Paulacoutophis* by the morphology of its neural spine, its strongly depressed neural arch, the dorsoventral elongation of its paradiapophyses, an the dorsal position of its subcentral ridges.

The living *Xenopeltis*, only representative of the Xenopeltidae, displays a neural spine that is more or less reminiscent of *Paulacoutophis*. However, in the mid- and posterior trunk vertebrae of *Xenopeltis* the dorsal border of the neural spine merges with the posterior border of the neural arch, i.e. the neural spine does not have a posterior border. In addition, the overall vertebral morphology of *Xenopeltis* is markedly different from that of *Paulacoutophis* (more specifically, the vertebrae of *Xenopeltis* are clearly depressed) and in *Xenopeltis* there is no posterior expansions of diapophyses.

Huberophis is a booid from the late Eocene of North America, known by a single vertebra. It was referred to the erycine booids (Holman, 1977, 2000), but Szyndlar & Rage (2003) questioned this assignment. The neural spine of this poorly known snake somewhat recalls that of *Paulacoutophis*, but several characters clearly distinguish *Huberophis* from the latter. *Paulacoutophis* has a more marked interzygapophyseal constriction, a narrower centrum, more prominent subcentral ridges, and posterior expansions of diapophyses.

Rottophis from the latest Oligocene of Europe appears to be related to the Tropidophiinae (Szyndlar & Rage, 2003; Szyndlar *et al.*, 2008). However, although represented by several more or less complete skeletons, its relationships remain somewhat uncertain. In the middle trunk region of *Rottophis*, the anterior border of the neural spine is markedly inclined and the neural spine more or less resembles that of mid- and posterior trunk vertebrae of *Paulacoutophis*. However, the horizontal dorsal border is clearly longer in *Rottophis*. In addition, *Rottophis* has a narrower zygosphene and a deeper, thinner haemal keel, a comparatively smaller cotyle, and it lacks the posterior expansion of the diapophyses.

Paraplatyspondylia was described by Holman & Harrison (1998) from a level (MP 17) of southern England that has been generally referred to the late Eocene, but that should be more appropriately regarded late middle Eocene (Cavelier & Pomerol, 1983). Holman & Harrison (1998) referred *Paraplatyspondylia* to as Boidae *incertae sedis*. However, they suggested affinities between *Paraplatyspondylia* and *Platyspondylia* and they hint at relationships of both snakes with erycine Boidae. Yet, *Platyspondylia*, was generally regarded as a "Tropidophiidae". Whatever the precise assignment of *Paraplatyspondylia*, this snake is a booid whose neural spine is somewhat similar to that of *Paulacoutophis*. But *Paraplatyspondylia* differs from the latter by its narrower zygosphene, narrower centrum that is poorly limited laterally, and by its more reduced prezygapophyseal processes (the presence or absence of a posterior expansion of the diapophysis cannot be checked in this snake).

It should be noted incidentally that the neural spine of *Paulacoutophis* is somewhat similar also to that of an unnamed snake from the Cretaceous (Campanian-Maastrichtian) of Argentina that was regarded a snake *incertae sedis* by Albino (2000). This snake is known by a single trunk vertebra. But, aside from the neural spine, the vertebra from Argentina differs clearly from *Paulacoutophis*. Contrary to the latter, it does not display the booid type; it is more elongate, with narrower and very shallow interzygapophyseal constriction, and it has larger condyle and cotyle.

In summary, as shown above, vertebrae of *Paulacoutophis* may be easily distinguished from those of all taxa of booids, but the Boidae, on the basis of several morphological differences. *Paulacoutophis* differs from the Boidae by its neural spine and the irregular presence of parazygosphenal foramina. Referral of *Paulacoutophis* to the Boidae cannot be definitely discarded on the basis of the morphology of the neural spine, but the latter is so different from that of confirmed Boidae that an assignment to this family appears to be questionable, which is consistent with the irregular presence of parazygosphenal foramina. Unfortunately, the only cloacal or anterior caudal (DGM 1975-R) belonging to *Paulacoutophis* does not afford information because its precise position in the column cannot be determined. Consequently, I regard *Paulacoutophis* as a booid *incertae sedis*.

Caenophidia HOFFSTETTER, 1939

? **Russellophiidae** RAGE, 1978

Indeterminate genus and species

Referred material: one posteriormost trunk vertebra (DGM 1376-R), collected in 1961 by unknown collector(s).

Description (fig. 12):

DGM 1376-R is a small posteriormost trunk vertebra that lacks the left prezygapophysis and paradiapophysis. Its measurements are as follows (in mm): total length from prezygapophysis to postzygapophysis (MLV): 4.7; length of centrum (CL): 3.6; width of zygosphene (ZW): 3.1; width of cotyle (CTW): 1.8.

In anterior aspect, the vertebra is comparatively high, but the zygapophyseal plane is approximately level with the floor of the neural canal. The preserved prezygapophyseal facet is inclined below the horizontal, i.e. it shows an orientation that is quite unusual in snakes: it faces slightly dorsolaterally. A reduced, or incipient prezygapophyseal process is present; its tip is worn. The zygosphene is wide, comparatively thin, and its roof slightly arches dorsally. The cross-section of the neural canal seems more or less squarrish. The cotyle is circular, clearly narrower than the zygosphene but as wide as the neural canal. The vertebra lacks paracotylar foramina and marked paracotylar fossae. As is typical for posteriormost trunk vertebrae, the paradiapophysis is distant from the centrum and its articular facet faces rather ventrally.

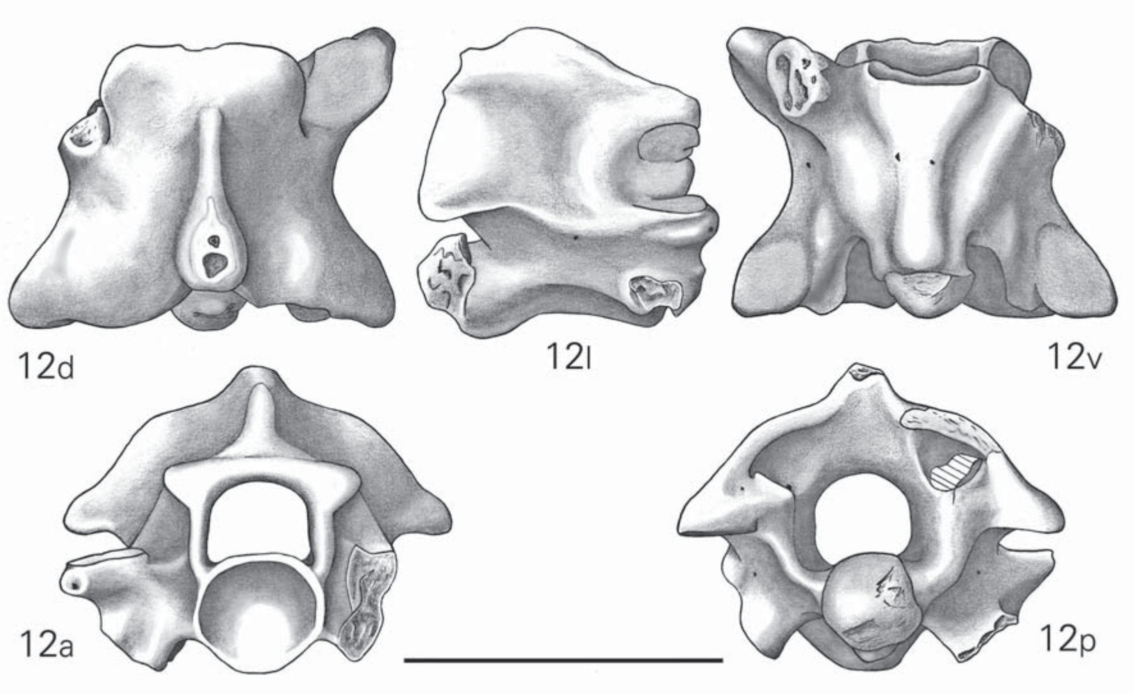


Figure 12.— ? Russellophiidae, indeterminate genus and species, posteriormost trunk vertebra (DGM 1376-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bar = 5 mm.

In dorsal view, the vertebra is clearly shorter than wide, with a rather shallow interzygapophyseal constriction. The zygosphene is wide and it has rounded lateral borders whereas its anterior edge is more or less straight. The major axis of the prezygapophyseal facet is clearly oblique. A shallow posterior median notch indents the neural arch. The neural spine is thick posteriorly and it becomes thinner anteriorly; its anterior border reaches the posterior part of the zygosphene.

In lateral view, the vertebra is high and rather short. The neural spine is long anteroposteriorly and low; its anterior border originates from the posterior part of the zygosphenal roof and it rises gently. The articular facet of the zygosphene is short anteroposteriorly. The paradiapophyses are damaged and the shape of their articular surfaces cannot be observed. The top of the paradiapophysis is located close to the prezygapophyseal process. The well-marked subcentral ridges arch dorsally. The haemal keel is deep and its posterior part is strongly deflected ventrally.

The posterior view is striking. The neural arch is very vaulted and wide, with a comparatively thin zygantral roof. The postzygapophyseal facets face slightly medioventrally. The cotyle is small.

In ventral view, the centrum markedly widens anteriorly; well-marked subcentral ridges bound the ventral face. Deep and wide subcentral grooves are present. Because of these subcentral grooves, the haemal keel appears clearly marked off from the centrum. The keel is hardly constricted in its middle part.

Discussion:

This vertebra comes from the posteriormost region of the trunk, which complicates comparisons because vertebrae from this region differ from those of more anterior parts of the vertebral column. More specifically, they are often shortened and their neural arch is less vaulted.

Despite this position in the column, DGM 1376-R has a vaulted neural arch, which means that the arch was probably very vaulted in more anterior vertebrae. The combination of the strong vaulting of the neural arch and of the peculiar orientation of the zygapophyseal facets (below the horizontal) suggests the Russellophiidae. Such an assignment is supported by the relatively small cotyle and condyle and by the wide and thin zygosphene, i.e. two features characteristic of *Russellophis tenuis*.

However, differences occur between DGM 1376-R and typical vertebrae of russellophiids. Trunk vertebrae of russellophiids (except posteriormost trunk vertebrae) are elongate, have a narrow centrum, compressed prezygapophyseal buttresses (each buttress forms an anterolateral vertical ridge), and lack prezygapophyseal processes. The shortening of DGM 1376-R and the resulting widening of its centrum are the consequences of the position of the vertebra in the vertebral column. No posteriormost trunk vertebra belonging to russellophiids has been described, but such a vertebra is available from the early Eocene (Ypresian) of Condé-en-Brie (France), the type locality of *Russellophis tenuis*. This vertebra (MNHN, CB 1604) is shortened and its centrum is widened anteriorly as in DGM 1376-R.

Other differences between DGM 1376-R and typical vertebrae of russellophiids are the presence of a small prezygapophyseal process and the absence of compression of the prezygapophyseal buttress (i.e., absence of a vertical ridge) in the fossil from Itaboraí. In typical vertebrae of russellophiids the vertical ridge resulting from the compression of the prezygapophyseal buttress runs up to the lateral tip of the prezygapophysis and a prezygapophyseal process is consequently lacking. However, in MNHN CB 1604, the same change as in DGM 1376-R occurs with regards to more anterior vertebrae: a small prezygapophyseal process is present whereas the buttress is not compressed. This may be related to the fact that, in various snakes, the morphology of the prezygapophyses of the last trunk vertebrae is altered, prezygapophyseal processes being stronger than those of more anterior vertebrae.

Finally, no character argues against assignment to the Russellophiidae, but in view of the nature of the material, referral of DGM 1376-R to this family cannot be accepted definitely.

The Russellophiidae includes three species: *Russellophis tenuis* from the early Eocene of western Europe (Rage & Augé, 1993; Holman *et al*., 2006), *Russellophis crassus* from the early Eocene of India (Rage *et al*., 2008), and *Krebsophis thobanus* from the early late Cretaceous (Cenomanian) of Sudan (Rage & Werner, 1999). In addition, indeterminate russellophiids were reported from the earliest to the late middle (formerly regarded late Eocene) Eocene of western Europe (Godinot *et al*., 1978; Nel *et al*., 1999; Holman *et al*., 2006; Rage, 2006). If the referral of the fossil from Itaboraí to the Russellophiidae is confirmed, then it represents the first member of this family from the Americas.

Conclusion

Aside from Madtsoiidae, Aniliidae s.l., and Boidae that were reported previously (Rage, 1998, 2001), the middle Palaeocene of Itaboraí has yielded an ungaliophiine, two booids whose precise referral remains unknown, and a possible russellophiid.

Paraungaliophis pricei is a new taxon (new genus and species) that is assigned to the Ungaliophiinae ("tropidophiids") on the basis of its overall vertebral morphology. The latter is so peculiar that this referral is reliable despite limited material. Today, the Ungaliophiinae are restricted to Central America and northern South America, but if the extinct *Platyspondylia*, *Dunnophis* and *Messellophis* really belong to this group (which was suggested but is not confirmed), then the ungaliophiines were present in North America, Europe, and perhaps Africa during the Palaeogene. Anyway, *Paraungaliophis* has been found outside of the present geographical range of ungaliophiines.

Two other snakes, *Itaboraiophis depressus* and *Paulacoutophis perplexus* represent new taxa (new genera and species) and they are referred to as *incertae sedis* within booids. *Itaboraiophis* is reminiscent of tropidophiine "tropidophiids" but this assignment cannot be confirmed; moreover, referral to the Boidae cannot be definitely discarded. *Paulacoutophis* might be a Boidae, but its peculiar neural spine and the irregular presence of parazygosphenal foramina cast doubts on such an assignment.

A distinctive snake, represented by a single vertebra, is tentatively referred to the Russellophiidae that is regarded a basal family of Caenophidia (i.e., advanced snakes). Nearly all vertebrae of russellophiids show a typical combination of characters and identification at family level is easy. Unfortunately, the only vertebra from Itaboraí is from the posteriormost part of the trunk region, which renders identification somewhat uncertain. The assignment to the Russellophiidae cannot be made without reservation. If the referral is accurate, then this fossil is the only russellophiid from the Americas. Elsewhere, the family occurs in the late Cretaceous of Africa and the Palaeogene of Europe and Asia.

The vertebral morphology of *Paraungaliophis*, *Itaboraiophis*, and *Paulacoutophis* does not display morphological adaptations that could point to a peculiar mode of life (arboreal, fossorial, aquatic). Russellophiids include snakes that were more or less aquatic (*Russellophis*) or whose mode of life is unknown (*Krebsophis*). Finally, no palaeoenvironmental inference can be drawn from these snakes.

THE SNAKE FAUNA FROM ITABORAÍ: SUMMARY, UPDATE, AND DISCUSSION

Composition of the fauna:

The middle Palaeocene of Itaboraí has produced the richest and most diverse fauna of extinct snakes from South America and this is the most diverse snake fauna from the Palaeocene of the world. The fauna consists of the following taxa:

Stem snakes
  Madtsoiidae HOFFSTETTER, 1961
      Madtsoia camposi RAGE, 1998
Alethinophidia NOPCSA, 1923
  Anilioid-grade snakes
      Coniophis cf. *C. precedens* MARSH, 1892
      Hoffstetterella brasiliensis RAGE, 1998
      cf. *Hoffstetterella brasiliensis*
  Booid-grade snakes
    Boidae GRAY, 182
      Boinae GRAY, 1825
        Corallus priscus RAGE, 2001
        Waincophis pressulus RAGE, 2001
        Waincophis cf. *W. pressulus*
        Waincophis cameratus RAGE, 2001
        Waincophis cf. *W. cameratus*
        cf. *Waincophis*
      Indeterminate Boinae
        Boinae A
        Boinae B
      Boidae *incertae sedis*
        Hechtophis austrinus RAGE, 2001
    "Tropidophiids"
      Ungaliophiinae McDOWELL, 1987
        Paraungaliophis pricei gen. et sp. nov.
    Booid-grade snakes *incertae sedis*

Itaboraiophis depressus gen. et sp. nov.
Paulacoutophis perplexus gen. et sp. nov.
Caenophidia HOFFSTETTER, 1939
? Russellophiidae RAGE, 1978
Indeterminate genus and species

All identified species, but perhaps one, are known only from Itaboraí. The only possible exception is *Coniophis precedens* that occurs in the late Maatrichtian (Lancian) of North America; however, the presence of the species at Itaboraí cannot be confirmed (*Coniophis* cf. *C. precedens*; Albino, 1990; Rage, 1998).

I previously regarded the Madtsoiidae as members of the alethinophidians (Rage, 1998), but it has been demonstrated that they originated before the Alethinophidia-Scolecophidia dichotomy (Scanlon, 2006; Scanlon & Lee, 2000). They represent an old radiation that originated in Gondwana. Madtsoiids are frequent components of the Cretaceous and early Cainozoic faunas of Gondwanan continents. At Itaboraí, they are represented by a single species, *Madtsoia camposi*.

Coniophis and *Hoffstetterella* were allocated to the Aniliidae, it being understood that this taxon was regarded as probably paraphyletic (Rage, 1998). Recent studies based on morphology and anatomy argued for the paraphyly of aniliids (Lee & Scanlon, 2002; Scanlon, 2006). Molecular phylogenies have confirmed paraphyly or even suggested polyphyly (Vidal & Hedges, 2002; Vidal *et al.*, 2007). If this assemblage is not monophyletic, the name Aniliidae should apply only to the South American lineage represented by the extant *Anilius*. Because of a few characters, *Hoffstetterella* appears to be more similar to *Anilius* than to any other member of the anilioid-grade (i.e. "anilioids"), but this similarity is perhaps not evidence of close relationships (Rage, 1998). *Hoffstetterella* cannot be reliably referred to the Aniliidae sensu stricto.

Coniophis raises a peculiar problem. This "genus" is based only on plesiomorphic vertebral characters, mainly the lack of a median notch in the posterior border of the neural arch. Consequently, most fossil snakes lacking this notch have been referred to this snake genus. *Coniophis* appears to be a "waste basket" to which were ascribed basal alethinophidians, and even perhaps snakes that precede the Alethinophidia-Scolecophidia dichotomy. If they are really basal alethinophidians, then these snakes belong to the anilioid grade, but their precise relationships cannot be established. Whatever the composition of this "genus", *Coniophis precedens* (the species that is likely present at Itaboraí) is the type species. Therefore, the name *Coniophis* may be used without reservation for the fossil from Itaboraí.

The Boidae was the dominant and most diverse family at Itaboraí as in almost all terrestrial faunas from the Palaeogene of the world. They include several Boinae and a boid *incertae sedis*. The latter snake, *Hechtophis austrinus*, was tentatively referred to the Erycinae (Rage, 2001). However, in view of the lack of caudal vertebrae, this assignment cannot be confirmed. In addition, since the description of *Hechtophis* I have understood that the morphology of the trunk vertebrae of the extant boine *Epicrates* is not very different from that of *Hechtophis*. More specifically, the combination of the markedly short vertebrae, conspicuous depth of the interzygapophyseal constriction, non-vaulted condition of the neural arch, and almost transverse orientation of the zygapophyseal facets led to regard *Hechtophis* as close to the extant erycine *Lichanura*. However, this combination of characters appears to be present also in *Epicrates*; therefore, the relationships of *Hechtophis* within the Boidae should be reappraised. For now, I regard it as a Boidae *incertae sedis*.

The other snakes from Itaboraí are described in the present article. Among them, only *Paraungaliophis* may be assigned with confidence to a taxon of the family group. It is referred to the Ungaliophiinae, a typical Central/South American taxon whose relationships within the booid paraphyletic complex are discussed. *Itaboraiophis* and *Paulacoutophis* are referred to the booid assemblage within which they are regarded *incertae sedis*. Aside from supra-generic taxa that are still extant, several extinct groups probably represented the booids during the Cainozoic (and Cretaceous ?). *Itaboraiophis* and *Paulacoutophis* perhaps belonged to one or two of such extinct lineages.

Finally, caenophidians are perhaps present at Itaboraí, a single vertebra being referred with reservation to the russellophiids. Thus far, this family was reported only from the Cretaceous and Paleogene of the Old World.

The presence of Boinae, and even the presence of at least one extant genus (*Corallus*), show that these taxa were distinct as early as the middle Palaeocene (Albino, 1993; Rage, 2001). The same conclusion may be drawn about the Ungaliophiinae.

Palaeoenvironment:

Among the species from Itaboraí, *Corallus priscus* was probably arboreal as are the living members of the genus. *Coniophis* and *Hoffstetterella* may be regarded as secretive and/or fossorial as all snakes of the anilioid-grade and as suggested by their vertebral morphology. The russellophiid, assuming this snake really belongs to this family, may have been more or less aquatic. The other snakes do not show morphological traits that indicate a precise mode of life. Finally, this fauna does not provide clear information about the environment.

Palaeobiogeographical aspects:

The presence of both Boinae and Ungaliophiinae in this Palaeocene fauna is reminiscent of present tropical America.

Contrary to the Boinae and Ungaliophiinae, the Russellophiidae (if the referral is accurate) recalls the Palaeogene and Cretaceous of the Old World.

The presence of *Madtsoia*, that is a member of the *Madtsoia*-*Gigantophis* assemblage, perhaps denotes West-Gondwanan (i.e., South America plus Africa) affinities. *Madtsoia* is known from the Palaeocene and Eocene of South America, the late Cretaceous of Africa, and the latest Cretaceous of Madagascar. From Africa, it reached southernmost Europe where it occurs in the latest Cretaceous (Rage, 1996). Since *Madtsoia* is still unknown from the Cretaceous of South America (from which different madtsoiids are known; Albino, 1996b), its presence in the Palaeocene of the latter continent cannot be definitely regarded as the result of vicariance.

Dispersal between Africa and South America cannot be ruled out (Rage, 1981). It is well established that the Cretaceous and the Palaeocene were periods of interchanges between South and North America (Gayet *et al.*, 1992). Surprisingly, at Itaboraí only *Coniophis* cf. *C. precedens* may represent an evidence of such interchanges, but the direction of its dispersal is unknown. The other taxa from Itaboraí may be autochthonous, except probably the russellophiid (if the identification is accurate) whose earliest representative was found in the Cenomanian of Africa (Rage & Werner, 1999).

Comparisons with other Palaeocene faunas:

Snake faunas from the Palaeocene are rare and generally poor. Apart from Itaboraí, only Tiupampa (early Palaeocene) in South America (Bolivia), a locality ("CM Loc 517"; late Palaeocene) in North America (USA), and Adrar Mgorn 1 (late Palaeocene) in Africa (Morocco) have yielded relatively diverse faunas. Most of the other Palaeocene localities have produced only one taxon.

The early Palaeocene of Tiupampa yielded several unnamed snakes: an anilioid, two boids, a madtsoiid or boid, and a "tropidophiid" (Rage, 1991). The anilioid is not *Hoffstetterella* and the two boids differ from those of Itaboraí. The single vertebra from Tiupampa that represents either a madtsoiid or a boid cannot be compared with snakes from Itaboraí because of its incompleteness. The "tropidophiid" from Tiupampa is represented by four vertebrae largely covered by matrix. The parts of the vertebrae that are observable suggest that this snake may be *Paraungaliophis*; unfortunately, this cannot be confirmed. Muizon & Brito (1993) noted differences between the faunas of mammals from Tiupampa and Itaboraí. Faunas of marsupials are somewhat similar in the two localities while placentals are different. They suggested that this results from the fact that, coming from North America, marsupials entered South America before the placentals. Tiupampa includes immigrant marsupials, the descendants of which are present at Itaboraí, whereas the immigration of placentals took place after the fauna of Tiupampa was formed. This assumption appears to be logical as far as mammals are concerned, but it cannot account for the differences between the faunas of snakes of the two localities. At Itaboraí and Tiupampa, there is no evidence of snakes of North American origin, except perhaps *Coniophis* cf. *C. precedens* at Itaboraí; if the species *C. precedens* is really present at Itaboraí, then it dispersed between the two continents but the direction of the dispersal is unknown. The differences between the faunas of snakes from Itaboraí and Tiupampa may be the result of different environments.

The other South American localities of Palaeocene age produced snakes that differ from those of Itaboraí: an indeterminate Boidae from the early Palaeocene of Criadero de Loro (Bolivia; Rage, 1991), an indeterminate Madtsoiidae and an indeterminate Boidae from the middle Palaeocene of Las Flores (Argentina; Albino, 1993), *Madtsoia* cf. *M. bai* from the middle/late Palaeocene of Pan de Azucar (Gaiman, Argentina; Hoffstetter, 1959), the Boidae *Titanoboa cerrejonensis* from the middle/late Palaeocene of Cerrejón Coal Mine (Colombia; Head *et al.*, 2009), ? *Madtsoia* from the late Palaeocene of Cerro Piatnizky-Cañadón Hondo (Argentina; Albino, 1993), an indeterminate Boidae from the late Palaeocene of Mina Aguilar (Argentina; Albino, 1989), and an anilioid somewhat similar to *Coniophis* from the late Palaeocene (Sigé *et al.*, 2004) of Laguna Umayo (Peru; Rage, 1981).

In Africa, the richest Palaeocene locality (Adrar Mgorn 1, Morocco) produced a fauna of late Palaeocene age: an indeterminate madtsoiid, an indeterminate scolecophidian, the anilioid *Coniophis* sp., a possible Boidae, and a "tropidophiid" that might be *Dunnophis* (cf. *Dunnophis*) (Augé & Rage, 2006). At least three taxa are common with Itaboraí: The Madtsoiidae, *Coniophis*, and "tropidophiids"; to them should be perhaps added the Boidae. However, apart from the perhaps polyphyletic *Coniophis*, there is no taxon in common at genus or species level. Only two other snake bearing localities are of Palaeocene age in Africa; they each yielded one highly aquatic snake: the nigerophiid *Nigerophis mirus* from the (?) early Palaeocene of Krebb de Sessao (Niger; Rage, 1975) and *Palaeophis* sp. from the late (or middle ?) Palaeocene of Sidi Daoui R.P. 13 (Morocco; Rage, 1998).

In North America, the Boidae *Helagras prisciformis* was found in the early Palaeocene of New Mexico (Sullivan & Lucas, 1986; Holman, 2000); it was regarded as an erycine, but this referral cannot be confirmed (Rage 2001; Szyndlar & Rage, 2003). The middle Palaeocene of Medicine Rocks (Montana) yielded *Coniophis* sp. and cf. *Dunnophis* (Estes, 1976). *Palaeophis* sp., known from a single vertebra, was reported from the late Palaeocene of South Carolina by Erickson (1998). The richest assemblage was recovered from the late Palaeocene of the locality "CM Loc. 517" (Mississipi), but it includes only highly aquatic snakes: *Tuscahomaophis leggetti*, that likely belongs to the palaeophiid-nigerophiid assemblage, and the palaeophiids *Palaeophis casei*, *P. littoralis*, and *P. virginianus* (Holman & Case, 1992; Holman, 2000). Therefore, only the rather widely distributed "genus" *Coniophis* is common to the Palaeocene of Itaboraí and North America.

The Palaeocene of Europe has yielded very rare snakes: an indeterminate scolecophidian and an indeterminate Boidae from the middle Palaeocene of Hainin (Belgium; Folie, 2006) and an indeterminate Boidae (a fragmentary skull bone only) from the middle/late Palaeocene of Walbeck (Germany; Kuhn, 1940; Szyndlar & Böhme, 1993).

In Asia, only one locality bearing snakes (Zhylga 1a, Kazakhstan) may be of Palaeocene age; it is referred either to the latest Palaeocene or early Eocene. It produced the palaeophiid *Palaeophis zhylan* (Averianov, 1997; Rage *et al*., 2003).

As seen in this short review, Palaeocene faunas are generally poor and have little diversity. Itaboraí appears as an exception and it shares only a few taxa with other faunas. However, it should be noted that Gelfo et al. (2009) suggested that the Itaboraí faunas may be of early Eocene age. On a world scale, the diversity of the snakes from Itaboraí is indeed more consistent with an early Eocene than with a Palaeocene age. Nevertheless, although Gelfo *et al.*"s opinion is worth considering, the traditional view (i.e., Palaeocene age) is retained here pending further stratigraphic studies because, in the South American context, snakes do not provide reliable biostratigraphic information.

Faunas of snakes from late Cretaceous-Eocene interval in South America:

At family level, four taxa of snakes have been reported from the Cretaceous of South America: Dinilysiidae, Madtsoiidae, anilioids and, with reservation, Boidae. Aside from these snakes, *Najash rionegrina* was regarded as the representative of a distinct lineage by Apesteguía & Zaher (2006) (but see below) and an unnamed snake was referred to as *incertae sedis*.

The Dinilysiidae are basal snakes known only from the late Cretaceous of Argentina. Most of them were recovered from the Bajo de la Carpa Formation (Caldwell & Albino, 2001, 2002; Albino, 2007) whose precise geological age was debated. It was referred to the Campanian, with reservation, by Uliana & Dellapé (1981), whereas Bonaparte (1991) suggested an age as old as the Coniacian; however, Leanza *et al.* (2004) assigned it a Santonian age, which may be provisionally accepted. A few other specimens were recovered from the Anacleto Formation that is referred to the early Campanian (Albino, 2007). Moreover, a part of the specimens allocated to the late Turonian *Najash rionegrina* (see below) appears to belong to a dinilysiid.

The Madtsoiidae from the South American Cretaceous are distinct from those of the Tertiary of this continent. They are all small snakes and almost all of them come from the Campanian-early Maastrichtian of Argentina: *Rionegrophis madtsoioides*, *Patagoniophis parvus*, *Alamitophis argentinus*, and *A. elongatus* (Albino, 1986, 1987a, 1994, 1996); however, a part of the late Turonian specimens described as *Najash rionegrina* likely belongs to madtsoiids (see below). A small indeterminate snake that is probably a madtsoiid was reported from the Maastrichtian of Pajcha Pata, Bolivia (Gayet *et al.*, 2001).

Two anilioids are known from the Cretaceous of South America. *Australophis anilioides*, from the late Campanian-early Maastrichtian of Argentina, is morphologically closer to South American forms than to other anilioids (Gómez *et al.*, 2008). Assignment of this snake to the Aniliidae sensu stricto may be considered. An indeterminate anilioid snake was reported from the late Cretaceous of Brazil by Zaher *et al.* (2003). It comes from beds that are regarded Turonian-Santonian in age (Candeiro *et al.*, 2006). As briefly described, the fossil comprises vertebrae and ribs; however, according to E. Fara (pers. com.) a quadrate bone is also present. This fossil remains undescribed and its referral to the anilioids cannot be accepted without reservation.

Boidae were reported, with some reservation, from the Campanian-Maastrichtian of Argentina (Albino, 1996, 2000, 2007). They are represented by poorly preserved specimens and referral to the Boidae cannot be definitely confirmed.

An unnamed snake from the Campanian-Maastrichtian of Argentina displays a peculiar vertebral morphology; it was regarded a snake *incertae sedis* by Albino (2000). It clearly differs from all snakes known from the Tertiary.

Finally, *Najash rionegrina*, from the late Cretaceous of Argentina, poses a peculiar problem. It was regarded as the most basal snake by Apesteguía & Zaher (2006), which was questioned by Caldwell & Calvo (2008). The material comprises a specimen (the holotype) made up of a portion of vertebral column (including the sacral region) plus elements of the pelvic girdle and incomplete hindlimbs, and other, non-associated specimens: another portion of vertebral column plus a fragment of mandible, a posterior braincase, and some disarticulated cranial bones and vertebrae. However, the braincase appears to belong to a snake very close to the dinilysiid *Dinilysia* as rightly noticed by Caldwell (2007) and Caldwell & Calvo (2008), while the vertebrae show a combination of features that is unique to madtsoiids (presence of parazygantral foramina, absence of any trace of prezygapophyseal processes, diapophyses projecting beyond the prezygapophyses laterally) and is different from that of the dinilysiids in which parazygantral foramina are lacking, tiny prezygapophyseal processes are present, and prezygapophyses are elongate and project markedly beyond the diapophyses. According to Apesteguía & Zaher (2006), additional undescribed vertebrae are associated to the braincase. It would be valuable to establish if these vertebrae are consistent with those that are associated with the pelvic girdle and hindlimbs. Unfortunately, Zaher et al. (2009) did not consider them in their recent study. For the time being, it is uncertain that the braincase on one hand and the sections of vertebral column, pelvic girdle and hindlimbs on the other hand belong to a single taxon. Apesteguía & Zaher (2006) assigned a Cenomanian-Turonian age to this fossil, but Caldwell (2007) referred it to the late Turonian. In fact, the specimens described as *Najash rionegrina* might show that the Dinilysiidae and Madtsoiidae were present as early as the late Turonian in South America, and that madtsoiids, or at least one madtsoiid had hindlimbs.

During the Palaeocene, South American faunas comprised madtsoiids, anilioids, boids, ungaliophiine "tropidophiids", and perhaps russellophiids. In addition, snakes *incertae sedis* belonging to the booid grade were also present. These taxa are all represented at Itaboraí. Therefore, in South America, only the Madtsoiidae are unquestionably found in common in the faunas from the Cretaceous and Palaeocene (mainly Itaboraí). Within madtsoiids, the taxa from the Cretaceous differ from those of the Palaeocene. The Cretaceous madtsoiids are small and none of them belongs to *Madtsoia*. On the contrary, at Itaboraí the madtsoiid is large and it is assigned to *Madtsoia*. Boids and an anilioid taxon are perhaps also common to the Cretaceous and Palaeocene, but this cannot be confirmed.

The faunas of Eocene snakes are poor in South America. All fossils, but one, come from the early Eocene (Casamayoran) of Argentina. The early Eocene produced only madtsoiids and boids. The madtsoiids include *Madtsoia bai* from Cañadón Vaca (Simpson, 1933) and an indeterminate form (? *Madtsoia* sp.) from Great Barranca (Albino, 1993). The boids are represented by *Waincophis australis* from Rocas Gemelas-Cañadón Hondo (Albino, 1987b), *Chubutophis grandis* from Valle Hermoso (Albino, 1993), and indeterminate Boidae from Great Barranca, Estancia Pampa Grande, and Aguada de Batistín (Albino, 1993). The only Eocene snake that does not come from the Casamayoran of Argentina is the highly aquatic *Pterosphenus sheppardi* (Palaeophiidae) from the late Eocene of Ecuador (Hoffstetter, 1958).

Aside from the aquatic snake *Pterosphenus*, the poor Eocene faunas differ from that of Itaboraí by the presence of the peculiar boid *Chubutophis*. The other identified genera, i.e. *Madtsoia* and *Waincophis*, are common to Itaboraí and the Eocene; however, the species are different. The differences between the fauna from Itaboraí (plus those from the South American Palaeocene as a whole) and those from the Eocene appear to be less marked than the differences that distinguish the snakes from the Palaeocene from those of the Cretaceous in South America. However, these comparisons are likely partly biased because the rich fauna from Itaboraí likely results from very favourable conditions of fossilization, whereas the conditions were probably not so good in most of the other localities.

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REFERENCES

ALBINO, A.M., 1986. — Nuevos Boidae Madtsoiinae en el Cretácico tardío de Patagonia (Formación Los Alamitos, Río Negro, Argentina). *IV Congr. Argentino Paleontol. Bioestratigr.*, Actas **2**: 15-21, Mendoza.

ALBINO, A.M., 1987a. — The late Cretaceous fauna of los Alamitos, Patagonia, Argentina; Part V - The ophidians. In: Bonaparte, J.F. (ed.), The late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. *Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia", Paleontol.*, **3**: 141-145.

ALBINO, A.M., 1987b. — Un nuevo Boidae (Reptilia: Serpentes) del Eoceno temprano de la Provincia del Chubut, Argentina. *Ameghiniana*, **24**: 61-66.

ALBINO, A.M., 1989. — Noticia preliminar sobre el más antiguo Boinae (Serpentes: Boidae) de Argentina (Formacíon Mealla, Edad Riochiquense, Provincia de Jujuy). *Ameghiniana*, **26**: 237.

ALBINO, A.M., 1990. — Las Serpientes de São José de Itaboraí (edad Itaboraiense, Paleoceno medio), Brasil. *Ameghiniana*, **27**: 337-342.

ALBINO, A.M., 1993. — Snakes from the Paleocene and Eocene of Patagonia (Argentina): Paleoecology and coevolution with mammals. *Historical Biology*, **7**: 51-69.

ALBINO, A.M., 1994. — Una nuova serpiente (Reptilia) en el Cretacico superior de Patagonia, Argentina. *Pesquisas,* **21**: 58-63.

ALBINO, A.M., 1996a. — Snakes from the Miocene of Patagonia (Argentina). Part I: The Booidea. *N. Jb. Geol. Paläont., Abh.*, **199**: 417-434.

ALBINO, A.M., 1996b. — The South American fossil Squamata (Reptilia: Lepidosauria). In: ARRATIA, G. (ed.), Contributions of Southern South America to Vertebrate Paleontology. *Münchner Geowiss. Abh.*, A, **30**: 185-202.

ALBINO, A.M., 2000. — New record of snakes from the Cretaceous of Patagonia (Argentina). *Geodiversitas*, **22**: 247-253.

ALBINO, A.M., 2007. — Lepidosauromorpha. In: GASPARINI, Z., SALGADO, L. & CORIA, R.A. (eds), Patagonian Mesozoic Reptiles. Indiana University Press, Bloomington and Indianapolis: 87-115.

APESTEGUÍA, S. & ZAHER, H., 2006. — A Cretaceous terrestrial snake with robust hindlimbs and a sacrum. *Nature*, **440**: 1037-1040.

AUGÉ, M. & RAGE, J.C., 2006. — Herpetofaunas from the Upper Paleocene and Lower Eocene of Morocco. *Ann. Paléontol.*, **92**: 235-253.

AVERIANOV, A.O., 1997. — Paleogene sea snakes from the eastern part of the Tethys. *Russian J.*

Herpetol., **4**: 128-142.

BASZIO, S., 2004. — *Messelophis variatus* n.gen. n.sp. from the Eocene of Messel: a tropidopheine snake with affinities to Erycinae (Boidae). In: HABERSETZER, J. & SCHAAL, S. (eds), Current Geological and Paleontological Research in the Messel Formation. *Cour. Forsch.-Inst. Senckenberg*, **252**: 47-66.

BOGERT, C.M., 1968. — A new genus and species of dwarf Boa from southern Mexico. *Amer. Mus. Nov.*, **2354**: 1-38.

BONAPARTE, J.F., 1991. — Los vertebrados fósiles de la Formación Río Colorado de Neuquén y cercanías, Cretácico Superior, Argentina. *Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia", Paleontol.*, **4**: 12-123.

CALDWELL, M.W., 2007. — Snake phylogeny, origins, and evolution. In: ANDERSON, J.S. & SUES, H.D. (eds), Major transitions in Vertebrate evolution. Indiana University Press, Bloomington and Indianapolis: 253-302.

CALDWELL, M.W. & ALBINO, A.M., 2001. — Palaeoenvironment and palaeoecology of three Cretaceous snakes: *Pachyophis, Pachyrhachis*, and *Dinilysia*. *Acta Palaeontol. Pol.*, **46**: 203-218.

CALDWELL, M.W. & ALBINO, A.M., 2002. — Exceptionally preserved skeletons of the Cretaceous snake *Dinilysia patagonica* Woodward, 1901. *J. Vert. Paleont.*, **22**: 861-866.

CALDWELL, M.W. & CALVO, J., 2008. — Details of a new skull and articulated cervical column of *Dinilysia patagonica* Woodward, 1901. *J. Vert. Paleont.*, **28**: 349-362.

CANDEIRO, C.R.A., MARTINELLI, A.G., AVILLA, L.S. & RICH, T.H., 2006. — Tetrapods from the Upper Cretaceous (Turonian-Maastrichtian) Bauru Group of Brazil: a reappraisal. *Cretaceous Res.*, **27**: 923-946.

CAVELIER, C. & POMEROL, C., 1983. — Echelle de corrélation stratigraphique du Paléogène. Stratotypes, étages standards, biozones, chimiozones et anomalies magnétiques. *Géol. France*, **3**: 261-262.

ERICKSON, B.R., 1998. — A palaeophid snake from the late Paleocene of South Carolina. In: SANDERS, A.E. (ed.), Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, USA. *Trans. Amer. Phil. Soc.*, **88**: 215-220.

ESTES, R., 1976. — Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. *J. Paleont.*, **50**: 500-520.

FOLIE, A., 2006. — Evolution des amphibiens et squamates de la transition Crétacé-Paléogène en Europe: les faunes du Maastrichtien du Bassin de Hateg (Roumanie) et du Paléocène du Bassin de Mons (Belgique). PhD Thesis, Université Libre de Bruxelles, 274 p.

GAYET, M., MARSHALL, L.G., SEMPERE, T., MEUNIER, F.J., CAPPETTA, H. & RAGE, J.C., 2001. — Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, **169**: 39-68.

GAYET, M., RAGE, J.C., SEMPERE, T. & GAGNIER, P.Y., 1992.- Modalités des échanges de vertébrés continentaux entre l'Amérique du Nord et l'Amérique du Sud au Crétacé supérieur et au Paléocène. *Bull. Soc. géol. Fr.*, **163**: 781-791.

GELFO, J.N., GOIN, F.J., WOODBURNE, M.O. & MUIZON, C. DE, 2009. — Biochronological relationships of the earliest South American Paleogene mammalian faunas. *Palaeontology*, **52**: 251-269.

GODINOT, M., BROIN, F. de, BUFFETAUT, E., RAGE, J.C. & RUSSELL, D.E., 1978. — Dormaal: une des plus anciennes faunes éocènes d'Europe. *C. R. Acad. Sc. Paris*, D, **287**: 1273-1276.

GÓMEZ, R.O., BÁEZ, A.M. & ROUGIER, G.W., 2008. — An anilioid snake from the Upper Cretaceous of northern Patagonia. *Cretaceous Res.*, **29**: 481-488.

GRADSTEIN, F.M., OGG, J.G. & SMITH, A.G., 2005. — A Geologic Timescale 2004. Cambridge University Press, Cambridge.

HEAD, J.J., BLOCH, J.I., HASTINGS, A.K., BOURQUE, J.R., CADENA, E.A., HERRERA, F.A., POLLY, P.D. & JARAMILLO, C.A., 2009. — Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature*, **457**: 715-718.

HECHT, M.K., 1959. — Amphibians and Reptiles. In: McGREW, P.O. (ed.), The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. *Bull. Amer. Mus. Nat. Hist.,***117**: 130-146.

HOFFSTETTER, R., 1958. — Un serpent marin du genre *Pterosphenus* (*Pt. sheppardi* nov. sp.) dans l'Eocène supérieur de l'Equateur (Amérique du Sud). *Bull. Soc. géol. Fr.*, **8**: 45-50.

HOFFSTETTER, R., 1959. — Un dentaire de *Madtsoia* (serpent géant du Paléocène de Patagonie). *Bull. Mus. natn. Hist. nat.*, **31**: 379-386.

HOLMAN, J.A., 1977. — Upper Eocene snakes (Reptilia, Serpentes) from Georgia. *J. Herpetol.*, **11**: 141-145.

HOLMAN, J.A., 1982. — *Geringophis* (Serpentes: Boidae) from the middle Oligocene of Nebraska. *Herpetologica*, **38**: 489-492.

HOLMAN, J.A., 2000. — Fossil snakes of North America. Indiana University Press, Bloomington and Indianapolis.

HOLMAN, J.A. & CASE, G.R., 1992. — A puzzling new snake (Reptilia: Serpentes) from the late Paleocene of Mississipi. *Ann. Carnegie Mus.*, **61**: 197-205.

HOLMAN, J.A. & HARRISON, D.L., 1998. — A new genus of snake (Serpentes: Boidae) from the Upper Eocene of Hordle Cliff, Hampshire, England. *Acta zool. cracov.*, **41**: 23-27.

HOLMAN, J.A., HARRISON, D.L. & WARD, D.J., 2006. — Late Eocene snakes from the Headon Hill Formation, southern England. *Cainozoic Res.*, **5**: 51-62.

KUHN, O., 1940. — Crocodilier- und Squamatenreste aus dem oberen Paleocän von Walbeck. *Zentr. Mineral. Geol Paläont.*, B, **1**: 21-25.

LADUKE, T.C., 2002. — Fossil snake assemblage from the Upper Cretaceous of Madagascar. *J. Vert. Paleont.*, **22** (3, suppl.): 76A-77A.

LEANZA, H.A., APESTEGUIA, S., NOVAS, F.E. & DE LA FUENTE, M.S., 2004. — Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Res.*, **25**: 61-87.

LEE, M.S.Y. & SCANLON, J.D., 2002. — Snake phylogeny based on osteology, soft anatomy and ecology. *Biol. Rev.,* **77**: 333-401.

MARSHALL, L.G., SEMPERE, T. & BUTLER, R.F., 1997. — Chronostratigraphy of the Mammal-bearing Paleocene of South America. *J. South Amer. Earth Sc.*, **10**: 49-70.

MCDOWELL, S.B., 1987. — Systematics. In: SEIGEL, R.A., COLLINS, J.T. & NOVAK, S.S. (eds), Snakes. Ecology, and evolutionary biology. McMillan, New York: 3-50.

MUIZON, C. & BRITO, I.M., 1993. — Le bassin calcaire de São José de Itaboraí (Rio de Janeiro, Brésil): ses relations fauniques avec le site de Tiupampa (Cochamba, Bolivie). *Ann. Paléontol.*, **79**: 233-268.

NEL, A., de PLÖEG, G., DEJAX, J., DUTHEIL, D., FRANCESCHI, D. DE, GHEERBRANT, E., GODINOT, M., HERVET, S., MENIER, J.J., AUGÉ, M., BIGNOT, G., CAVAGNETTO, C., DUFFAUD, S., GAUDANT, J., HUA, S., JOSSANG, A., LAPPARENT de BROIN, F. DE, POZZI, J.P., PAICHELER, J.C., BEUCHET, F. & RAGE, J.C., 1999. — Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Eocène basal, MP7) : Le Quesnoy (Oise, France). *C.*

R. Acad. Sc. Paris, **329**: 65-72.

RAGE, J.C., 1975. — Un serpent du Paléocène du Niger. Etude préliminaire sur l'origine des Caenophidiens (Reptilia, Serpentes). *C. R. Acad. Sc. Paris*, D, **281**: 515-518.

RAGE, J.C., 1978. — La poche à phosphates de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. 5 - Squamates. *Palaeovertebrata*, **8**: 201-215.

RAGE, J.C., 1981. — Les continents péri-atlantiques au Crétacé supérieur: migrations des faunes continentales et problèmes paléogéographiques. *Cretaceous Res.*, **2**: 65-84.

RAGE, J.C., 1984. — Serpentes. Handbuch der Paläoherpetologie, part 11. Gustav Fischer Verlag, Stuttgart.

RAGE, J.C., 1987. — Fossil History. In: SEIGEL, R.A., COLLINS, J.T. & NOVAK, S.S. (eds), Snakes. Ecology, and evolutionary biology. McMillan, New York: 51-76.

RAGE, J.C., 1991. — Squamate Reptiles from the early Paleocene of Tiupampa area (Santa Lucía Formation), Bolivia. In: SUAREZ SORUCO, R. (ed.), Fosiles y Facies de Bolivia., Vol. I - Vertebrados. *Rev. Técn. Yacim. Petrol. Fisc. Bolivianos*, **12**: 503-508.

RAGE, J.C., 1996. — Les Madtsoiidae (Reptilia, Serpentes) du Crétacé supérieur d'Europe: témoins gondwaniens d'une dispersion transtéthysienne. *C.R. Acad. Sci. Paris*, IIa, **322**: 603-608.

RAGE, J.C., 1998. — Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part I. Madtsoiidae, Aniliidae. *Palaeovertebrata*, **27**: 109-144.

RAGE, J.C., 2001. — Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part II. Boidae. *Palaeovertebrata*, **30**: 111-150.

RAGE, J.C., 2006. — The lower vertebrates from the Eocene and Oligocene of the Phosphorites du Quercy (France): an overview. In: PÉLISSIÉ, T. & SIGÉ, B. (eds), 30 millions d'années de biodiversité dynamique dans le paléokarst du Quercy, "Journées Bernard Gèze". Strata, **13**: 161-173.

RAGE, J.C. & AUGE, M., 1993. — Squamates from the Cainozoic of the Western part of Europe. A review. *Rev. Paléobiol.*, **vol. sp. 7**: 199-216.

RAGE, J.C., BAJPAI, S., THEWISSEN, J.G.M. & TIWARI, B.N., 2003. — Early Eocene snakes from Kutch, Western India, with a review of the Palaeophiidae. *Geodiversitas*, **25**: 695-716.

RAGE, J.C., FOLIE, A., RANA, R.S., SINGH, H., ROSE, K. D. & SMITH, T., 2008. — A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India. *Acta Palaeontol. Pol.*, **53**: 391-403.

RAGE, J.C. & WERNER, C., 1999. — Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: the earliest snake assemblage. *Palaeont. afr.*, **35**: 85-110.

SCANLON, J.D., 2006. — Skull of the large non-macrostomatan snake *Yurlunggur* from the Australian Oligo-Miocene. *Nature*, **439**: 839-842.

SCANLON, J.D. & LEE, M.S.Y., 2000. — The Pleistocene serpent *Wonambi* and the early evolution of snakes. *Nature*, **403**: 416-420.

SCHAAL, S. & BASZIO, S., 2004. — *Messelophis ermannorum* n.sp., eine neue Zwergboa (Serpentes: Boidae: Tropidopheinae) aus dem Mittel-Eozän von Messel. In: HABERSETZER, J. & SCHAAL, S. (eds), Current Geological and Paleontological Research in the Messel Formation. *Cour. Forsch.-Inst. Senckenberg*, **252**: 67-77.

SIGÉ, B., SEMPERE, T., BUTLER, R.F., MARSHALL, L.G. & CROCHET, J.Y., 2004. — Age and stratigraphic reassessment of the fossil-bearing Laguna Umayo red mudstone unit, SE Peru, from regional stratigraphy, fossil record and paleomagnetism. *Geobios*, **37**: 771-794.

SIMPSON, G.G., 1933. — A new fossil snake from the *Notostylops* beds of Patagonia. *Bull. Amer. Mus. Nat. Hist.*, **67**: 1-22.

SULLIVAN, R.M. & LUCAS, S.G., 1986. — Annotated list of lower Vertebrates from the Paleocene

Nacimiento Formation (Puercan-Torrejonian), San Juan Basin, New Mexico. *J. Herpetol.*, **20**: 202-209.

SZYNDLAR, Z. & BÖHME, W., 1993. — Die fossilen Schlangen Deutschlands: Geschichte der faunen und ihrer Erforschung. *Mertensiella*, **3**: 381-431.

SZYNDLAR, Z. & BÖHME, W., 1996. — Redescription of *Tropidonotus atavus* von Meyer, 1855 from the upper Oligocene of Rott (Germany) and its allocation to *Rottophis* gen. nov. (Serpentes, Boidae). *Palaeontographica*, A, **240**: 145-161.

SZYNDLAR, Z. & RAGE, J.C., 2003. — Non-erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals, Cracow.

SZYNDLAR, Z., SMITH, R. & RAGE, J.C., 2008. — A new dwarf boa (Serpentes, Booidea, "Tropidophiidae") from the Early Oligocene of Belgium: a case of the isolation of Western European snake faunas. *Zool. J. Linn. Soc.*, **152**: 393-406.

ULIANA, M.A. & DELLAPÉ, D.A., 1981. — Estratigrafía y evolución paleoambiantal de la sucesión maestrichtiana-eoterciaria del engolfamiento neuquino (Patagonia septentrional). Actas VIII Congr. Geol. Argentino, San Luis, **3**: 673-711.

UNDERWOOD, G., 1976. — A systematic analysis of boid snakes. In: BELLAIRS, A. d'A. & COX, C.B. (eds), Morphology and biology of reptiles. *Linn. Soc. Symp. Ser.*, **3**: 151-175.

VAN VALEN, L., 1988. — Paleocene dinosaurs or Cretaceous ungalutes in South America? *Evol. Monographs*, **10**: 1-79.

VIDAL, N. & DAVID, P., 2004. — New insights into the early history of snakes inferred from two nuclear genes. *Mol. Phyl. Evol.*, **31**: 783-787.

VIDAL, N., DELMAS, A.S. & HEDGES, S.B., 2007. — The higher-level relationships of alethinophidian snakes inferred from seven nuclear and mitochondrial genes. In: HENDERSON, R.W. & POWELL, R. (eds), Biology of the Boas and Pythons. Eagle Mountain Publ., Eagle Montain, Utah: 27-33.

VIDAL, N. & HEDGES, S.B., 2002. — Higher-level relationships of snakes inferred from four nuclear and mitochondrial genes. *C.R. Biologies*, **325**: 977-985.

WALLACH, V. & GÜNTHER, R., 1998. — Visceral anatomy of the Malaysian snake genus *Xenophidion*, including a cladistic analysis and allocation to a new family (Serpentes: Xenophidiidae). *Amphibia-Reptilia*, **19**: 385-405.

WIENS, J.J., KUCZYNSKI, C.A., SMITH, S.A., MULCAHY, D.G., SITES, J.W. Jr, TOWNSEND, T.M. & REEDER, T.W., 2008. — Branch lengths, support, and congruence: testing the phylogenetic approach with 20 nuclear loci in snakes. *Syst. Biol.*, **57**: 420-431.

WILCOX, T.P., ZWICKL, D.J., HEATH, T.A. & HILLIS, D.M., 2002. — Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Mol. Phyl. Evol.*, **25**: 361-371.

ZAHER, H., 1994. — Les Tropidopheoidea (Serpentes; Alethinophidia) sont-ils réellement monophylétiques? Arguments en faveur de leur polyphylétisme. *C.R. Acad. Sci. Paris, Sc. Vie*, **317**: 471-478.

ZAHER, H., APESTEGUÍA, S. & SCANFERLA, C.A ., 2009. — The anatomy of the upper Cretaceous snake *Najash rionegrina* Apesteguía & Zaher, 2006, and the evolution of limblessness in snakes. *Zool. J. Linn. Soc.*, **156**: 801-826.

ZAHER, H.D., LANGER, M.C., FARA, E., CARVALHO, I.S. & ARRUDA, J.T., 2003. — A mais antigua serpente (Anilioidea) brasileira: Cretáceo Superior do Grupo Bauru, General Salgado, SP. *Paleont. Destaque*, **44**: 52.