FOSSIL SNAKES FROM THE PALAEOCENE OF SÃO JOSÉ DE ITABORAÍ, BRAZIL. PART II. BOIDAE

by

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ABSTRACT

The middle Palaeocene of São José de Itaboraí (State of Rio de Janeiro, Brazil) has produced a rich and diverse fauna of boid snakes. It comprises six or seven species: *Hechtophis austrinus* gen. et sp. nov., *Corallus priscus* sp. nov., *Waincophis pressulus* sp. nov., *Waincophis cameratus* sp. nov., "Boinae A", and "Boinae B". Moreover, two dentaries might pertain to either *H. austrinus* or "Boinae B", or even represent a distinct taxon. *Hechtophis austrinus* is assigned, with reservation, to the Erycinae. All other taxa are referred to the Boinae. The vertebrae of all taxa have paracotylar foramina, which raises the problem of the apomorphic or plesiomorphic nature of this feature. This fauna also raises the question of the presence of extinct erycine boids in South America, but it does not allow this question to be settled.

RESUME

Le Paléocène moyen de São José de Itaboraí (Etat de Rio de Janeiro, Brésil) a fourni une faune de Boidae riche et variée. Elle comprend six ou sept espèces: *Hechtophis austrinus* gen. et sp. nov., *Corallus priscus* sp. nov., *Waincophis pressulus* sp. nov., *Waincophis cameratus* sp. nov., "Boinae A", and "Boinae B". D'autre part, deux dentaires pourraient appartenir à *H. austrinus* ou au "Boinae B", mais ils pourraient aussi représenter un taxon distinct. *Hechtophis austrinus* est rapporté, avec doute, aux Erycinae alors que tous les autres taxons sont attribués aux Boinae. Les vertèbres de tous les taxons possèdent des foramens paracotyliens, ce qui soulève le problème de la nature, apomorphe ou plésiomorphe, de ce caractère. Cette faune pose également le problème de la présence d'Erycinae fossiles en Amérique du Sud mais ne permet pas de le résoudre.

INTRODUCTION

São José de Itaboraí (hereafter referred to as "Itaboraí"), Brazil, is a middle Palaeocene locality that has yielded a rich and diverse fauna of snakes. The Palaeocene is generally subdivided into two parts only (early and late Palaeocene). However, the use of the informal "middle" Palaeocene better expresses the stratigraphic position of the fauna (Muizon & Brito, 1993; Rage, 1998). According to Marshall *et al.* (1997), the fauna dates between 58.2 and 56.5 million years.

The fauna from Itaboraí apparently includes a mixture of fossils from different fissure fillings that might be of slightly different ages. However, as shown by Marshall *et al.* (1997), the fauna represents a rather short time interval (Rage, 1998).

Madtsoiid and aniliid snakes from the locality have been described (Rage, 1998). They include the madtsoiid *Madtsoia camposi* and the aniliids *Hoffstetterella brasiliensis* and *Coniophis* cf. *C. precedens*. The present article deals with the Boidae from Itaboraí. The third part will include the Tropidophiidae *s.l.*, Booidea *incertae sedis*, and Russellophiidae.

Today, the Boidae represent only a comparatively small part of snakes (less than 5% of the genera and less than 2.5% of the species). But during the early Tertiary (Palaeogene) boids were the dominant group within snakes. The decline of the Boidae began during the Oligocene and since the Miocene the Colubridae have replaced them as the dominant family.

The earliest representatives of the Boidae come from the latest Cretaceous: Maastrichtian (Rage, 1987) or perhaps Campanian (Albino, 2000). At Itaboraí, the Boidae make up an important part of the snake fauna.

The fossils are housed in the Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil. As stated previously (Rage, 1998: 112), it is of interest to keep the names of the collectors and the dates of collections separate because these fossils likely come from different collections; the latter apparently correspond to different fissure fillings the age of which might be slightly different.

REMARKS ON THE SYSTEMATICS OF BOIDAE AND PROBLEMS OF IDENTIFICATION OF ISOLATED REMAINS

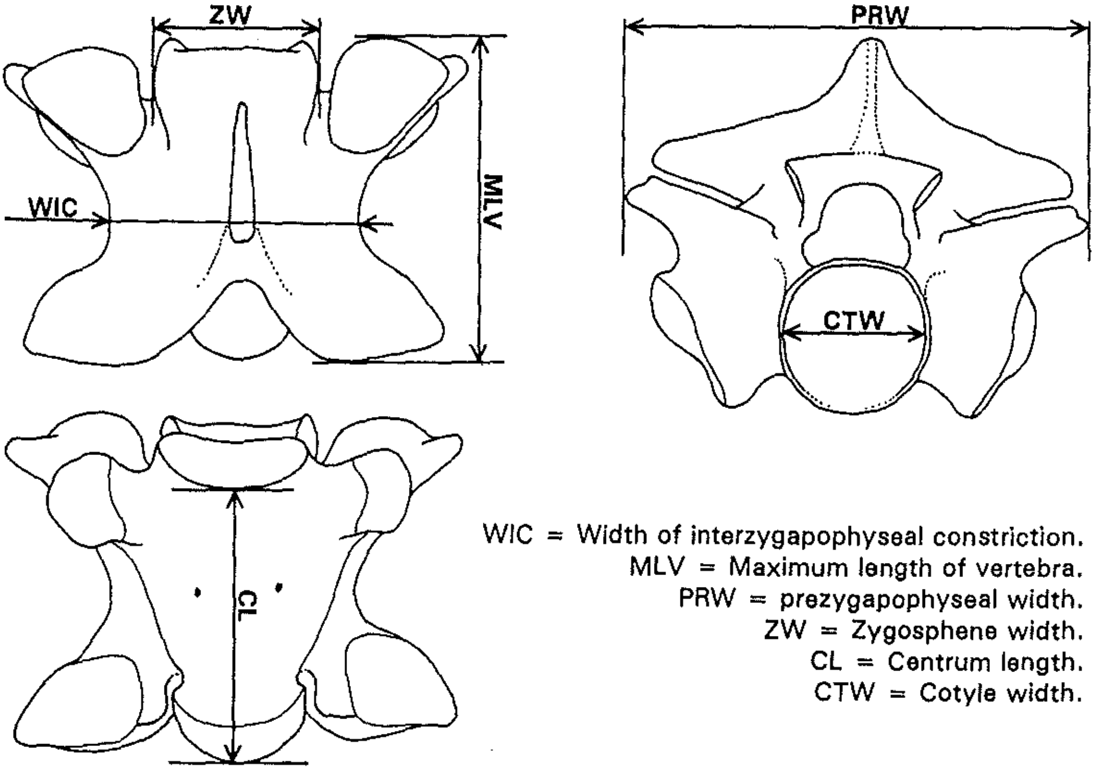
The Boidae, as conceived here, comprise four subfamilies: Boinae, Pythoninae, Erycinae, and Calabariinae. Formerly (Rage, 1984, 1987), I included the Tropidophiidae, Bolyeriidae, and Madtsoiidae in the Boidae; but recent works have shown that these taxa represent independent lineages (McDowell, 1987; Cundall *et al.*, 1993; Scanlon, 1994; Scanlon & Lee, 2000). Within the Boidae, the Erycinae appear to be more closely related to the Boinae than to the Pythoninae (Underwood, 1976; McDowell, 1987; Cundall *et al.*, 1993; Tchernov *et al.*, 2000). However, according to Kluge (1991) and Scanlon & Lee (2000), pythonines and boines are sister groups. On the other hand, the relationships of the enigmatic *Calabaria reinhardti* (only species of the Calabariinae) have been debated. Underwood (1976) placed the genus in a subfamily of its own (Calabariinae), but McDowell (1987) assigned it to the pythonines (Pythonidae for McDowell); finally, Kluge (1993) referred *Calabaria* to the Erycinae, which appears to be credible but cannot be definitely accepted.

Today, pythonines inhabit Africa, Southern Asia, and Australasia whereas boines are present in south and central America up to northern Mexico, Madagascar, and in western Pacific islands. The geographic ranges of pythonines and boines overlap only in Australasia. The Erycinae are found in northern and eastern Africa, southeastern Europe, southern Asia, and westernmost North America. Their range overlaps that of pythonines in Africa and Asia but it is always distinct from that of boines. *Calabaria* occurs only in west Africa.

Fossil boids have been recovered from all continents, except Antarctica. As all snakes, fossil boids are mainly found as isolated vertebrae; therefore, identification of fossils generally rests on such specimens. Except for the Erycinae (see below), trunk vertebrae (mainly those from mid- and posterior trunk regions) are the most useful for purpose of identification. Trunk vertebrae of Boidae are massive and comparatively short and wide; their prezygapophyseal processes are small and their paradiapophyses are weakly subdivided into para-and diapophyseal areas.

Some non-boid snakes have vertebrae with a boid-like overall morphology. This is the case for the Xenopeltidae, Tropidophiidae, and Bolyeriidae (Booidea) and

Madtsoiidae. However, it is possible to distinguish these families on the basis of vertebrae. Bolyeriidae are easily distinguished from Boidae by the presence of a true (i.e. spine-like) hypapophysis on all trunk vertebrae (in Boidae, such hypapophyses are present on anterior trunk vertebrae only). Within Tropidophiidae, only tropidophiines have boid-like vertebrae; but these snakes have trunk vertebrae with deep and squarish haemal keels (often termed "hypapophyses") and very high neural spines. Vertebrae of the two xenopeltid genera differ only slightly from those of the Boidae: in *Xenopeltis* the neural spine has an approximately semicircular outline in lateral view (squarish or hatchet-shaped in Boidae) and in *Loxocemus* the subcentral ridge merges in the parapophyseal part of the paradiapophysis, which results in a peculiar ventro-lateral lamina that does not exist in Boidae (Szyndlar & Böhme, 1996). The vertebrae of the extinct Madtsoiidae differ from those of the Boidae in having parazygantral foramina and in lacking any trace of prezygapophyseal processes.



WIC = Width of interzygapophyseal constriction.
MLV = Maximum length of vertebra.
PRW = prezygapophyseal width.
ZW = Zygosphene width.
CL = Centrum length.
CTW = Cotyle width.

Figure 1.— Measurements used in the present article.

Within Boidae, identification at the genus level is often easy (tabl. 1) but the vertebral morphology is not really characteristic at the subfamily level. The Erycinae are readily identified on the basis of their caudal vertebrae that have a thickened neural spine whose tip is expanded, and (except the living *Lichanura* and extinct *Albaneryx*) are markedly shortened and bear additional processes (Hoffstetter & Rage, 1972; Szyndlar & Schleich, 1994; Szyndlar & Böhme, 1996). Trunk vertebrae of the Erycinae have a depressed neural arch, different from that of living Boinae and Pythoninae. However, of particular relevance here is the fact that Szyndlar & Böhme (1996) shown that the boid *Rottophis atavus*, known by an almost complete specimen from the late Oligocene of Germany, has erycine-like trunk vertebrae but cannot be referred to the Erycinae because of its caudal vertebrae. Consequently, extinct snakes can be confidently referred to the Erycinae only if their caudal vertebrae are known. Trunk vertebrae of *Calabaria* are erycine-like but neural spines are more prominently developed than in Erycinae. Trunk vertebrae of Boinae and Pythoninae display a homogeneous overall morphology. Referral of isolated vertebrae to the Boinae generally rests on the presence of paracotylar foramina (Szyndlar & Schleich, 1993) because such foramina are present in some, but not all, living Boinae and are lacking in all Pythoninae.

Finally, it is clear that referral of a fossil boid snake to a subfamily is uncertain if cranial bones such as palatines or prefrontals are unknown or if it is not an erycine represented by caudal vertebrae.

Measurements work when comparisons are to living species where sample sizes can be large (Auffenberg, 1963; Meylan, 1982; Szyndlar, 1984). But they are more difficult for comparing among fossils which are often damaged (therefore harder to measure) and for which sample sizes are smaller. However, measurements and ratios may help descriptions and comparisons. For this reason, I use a few dimensions (fig. 1) and ratios.

FOSSIL BOIDAE IN SOUTH AMERICA: AN OVERVIEW

A few extinct boids have already been reported from South America. The family was perhaps present as early as the late Cretaceous (Campanian-Maastrichtian) in South America (Argentina: Albino, 1990, 2000). The Palaeocene also yielded some indeterminate boids in Argentina (Albino, 1993) and Bolivia (Rage, 1991).

Eocene localities have produced a richer fauna. The early Eocene of the Gran Barranca Member (Sarmiento Formation, Argentina) furnished *Chubutophis grandis*, a very large Boinae, and perhaps the living genus *Boa* (Albino, 1993). *Waincophis australis*, a boine (see below), was recovered from another early Eocene formation of Argentina, the Cañadón Hondo Formation (Albino, 1987). Moreover, inderterminate boids were found in other early Eocene localities of Argentina (Albino, 1993, 1996a). The Oligocene has yielded only rare indeterminate boids (Albino, 1996a).

Boids are more frequent in the Miocene, although not numerous. In Argentina, the Trelew Member of the Sarmiento Formation, of early Miocene age, produced *Gaimanophis tenuis, Waincophis* sp., and fragmentary remains referred to as "? Erycinae indet." by Albino (1996b), whereas the younger Collón Cura Formation, middle Miocene, yielded *Waincophis australis* (a species that extends back to the early Eocene; Albino, 1993) and an indeterminate Boinae (Albino, 1996b). In the middle Miocene of Colombia, the living genus *Eunectes* is represented by an extinct species, *E. stirtoni* (HOFFSTETTER & RAGE, 1977). Additionally, indeterminate boids were found in other early Miocene localities of Argentina (Albino, 1996a) and in the late Miocene of Venezuela (Estes & Báez, 1985).

Astonishingly, reports of boids from the Pliocene and Pleistocene are very rare, which probably results from insufficient attempts to study localities of that ages. A Boidae (? *Boa*) was identified in the Pliocene of Argentina (Albino, 1992) and only one boid vertebra (indeterminate Boidae) was reported from the Pleistocene of South America (Bolivia; Hoffstetter, 1968).

Itaboraí is an exceptional vertebrate-bearing locality; it has produced the richest and most diverse fauna of boid snakes from South America. Its fauna demonstrates that the rarity of fossil boids in South America is not a true picture.

SYSTEMATIC PALAEONTOLOGY

SERPENTES LINNAEUS, 1758
ALETHINOPHIDIA NOPCSA, 1923
BOIDAE GRAY, 1825

At Itaboraí, the Boidae include at least six species. One of them perhaps belongs to the Erycinae whereas the others are referred to the Boinae. For practical reasons (comparisons), it is necessary to first describe a new taxon the assignement of which is uncertain (? Erycinae).

? **ERYCINAE** BONAPARTE, 1831

Among the species from Itaboraí, a small to medium sized snake is clearly distinct because of the apparent shortness of its vertebrae. It represents a new genus and species.

HECHTOPHIS gen. nov.

Type-species: *Hechtophis austrinus* sp. nov.

Etymology: in honor of Max Hecht, for his contribution to palaeobiology.

Diagnosis: As for the type-species and only known species of the genus.

Hechtophis austrinus sp. nov.

Holotype: one mid-trunk vertebra (DGM 1326-R), collected in 1949 by J.S. Carvalho.

Referred material: 71 trunk vertebrae (DGM 1327-R: 1 vertebra; DGM 1328-R: 1 vertebra; DGM 1329a-R: 11 vertebrae; DGM 1329b-R: 1 vertebra; DGM 1329c-R: 1 vertebra; DGM 1329d-R: 10 vertebrae; DGM 1329e-R: 13 vertebrae; DGM 1330a-R: 7

vertebrae; DGM 1330b-R: 7 vertebrae; DGM 1330c-R: 3 vertebrae; DGM 1330d-R: 2 vertebrae; DGM 1330e-R: 14 vertebrae), (collections: 1327-R and 1330a-R by "Price and Campos" in 1968; 1328-R and 1330c-R in 1968 by unknown collector(s); 1329a-R and 1329e-R by "J.S. Carvalho" in 1967; 1329b-R by "J.S. Carvalho, part F.W. Stromer" in 1961; 1329c-R by "J.S. Carvalho and O.S. Santos" in 1953; 1329d-R by "J.S. Carvalho" in 1949; 1330b-R in 1961 by unknown collector(s); 1330d-R in 1949 by unknown collector(s); 1330e-R, date and collector(s) unknown).

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

Horizon: middle Palaeocene.

Etymology: latin *austrinus*, located in, or from the South.

Diagnosis: Boid snake having vertebrae rather similar to those of the living *Lichanura* and extinct *Paraepicrates*, i.e. vertebrae short and wide, with a deep interzygapophyseal constriction, prezygapophyses strongly produced laterally, neural arch not markedly vaulted; differing from *Lichanura* in having a less depressed neural arch that bulges prominently above the zygantrum, less elongate prezygapophyseal facets, and by the constant presence of paracotylar foramina; differing from *Paraepicrates* in having more transversely oriented prezygapophyseal facets, a deeper posterior median notch in the neural arch, and in having paracotylar foramina.

Description of the holotype (fig. 2):

The dimensions of the holotype are as follows (see fig. 1 for abbreviations): PRW: 10.9 mm; MLV: 6.7 mm; ZW: 4.3 mm; CTW: 3.3 mm; CL: 5.5 mm; WIC: 6.6 mm.

In anterior view, the zygosphene is rather wide, not very thick, and its dorsal border is straight. The neural canal is subtriangular and medium sized. The slightly depressed cotyle is narrower than the zygosphene. The prezygapophyses strongly project laterally; their articular surfaces are subhorizontal. The zygapophyseal articular plane is at the level of the lower third of the neural canal height. The prezygapophyseal processes are reduced. The diapophyses moderately protrude laterally. Two paracotylar foramina open in a poorly defined depression on either side of the cotyle. The paradiapophyses do not clearly project below the ventral border of the cotyle.

In dorsal view, the vertebra is short and wide. The interzygapophyseal constriction is deep. The articular facets of the prezygapophyses are ovaloid and their major axis tends to be directed laterally. The anterior border of the zygosphene forms two protruding lateral lobes; between them, it is almost straight but it displays a small median notch. The neural spine is thick and rather short. The posterior median notch in the neural arch is obtuse and not very deep.

In lateral view, both the height and the length of the neural spine appear moderate. The interzygapophyseal ridge is weak and blunt. Lateral foramina are present. The paradiapophysis is massive and not clearly extended dorso-ventrally. The posterior half of the haemal keel is slightly produced ventrally.

In posterior view, the neural arch is moderately vaulted and it markedly bulges above the zygantrum. The posterior face of the neural arch lacks parazygantral foramina. There are two zygantral foramina in each zygantral fossa; one opens in the latero-ventral part of the fossa, very close to the articular facet, the other one lies in the medio-dorsal part of the fossa. The condyle is depressed.

In ventral view, the centrum appears short and it widens anteriorly. The thin and prominent haemal keel reaches the cotylar rim anteriorly. The subcentral ridges are blunt. Small subcentral foramina are present.

Intracolumnar variation:

The anterior trunk vertebrae have a hypapophysis that is laterally compressed. The neural spine is shorter and higher than that of mid-trunk vertebrae. The ventral tip of the paradiapophyses projects below the cotyle rim. Even in the anterior vertebrae, the neural arch is only moderately vaulted and it markedly cambers above the zygantrum. In posterior trunk vertebrae, the haemal keel is wide and its ventral face is smooth and rounded; the keel is markedly wider than in mid-trunk vertebrae (figs 2v, 3v), but this difference is within the range of intracolumnar variation of erycine boids. The ventral face of the centrum is slightly concave on either side of the haemal keel but there are no well-defined grooves. In some posterior trunk vertebrae, the anterior border of the zygosphene forms a median lobe (fig. 3) and the prezygapophyseal processes are more developed than in mid-trunk vertebrae. The ventral border of the paradiapophyses is level with the ventral part of the cotylar rim or slightly above it.

Intraspecific variation:

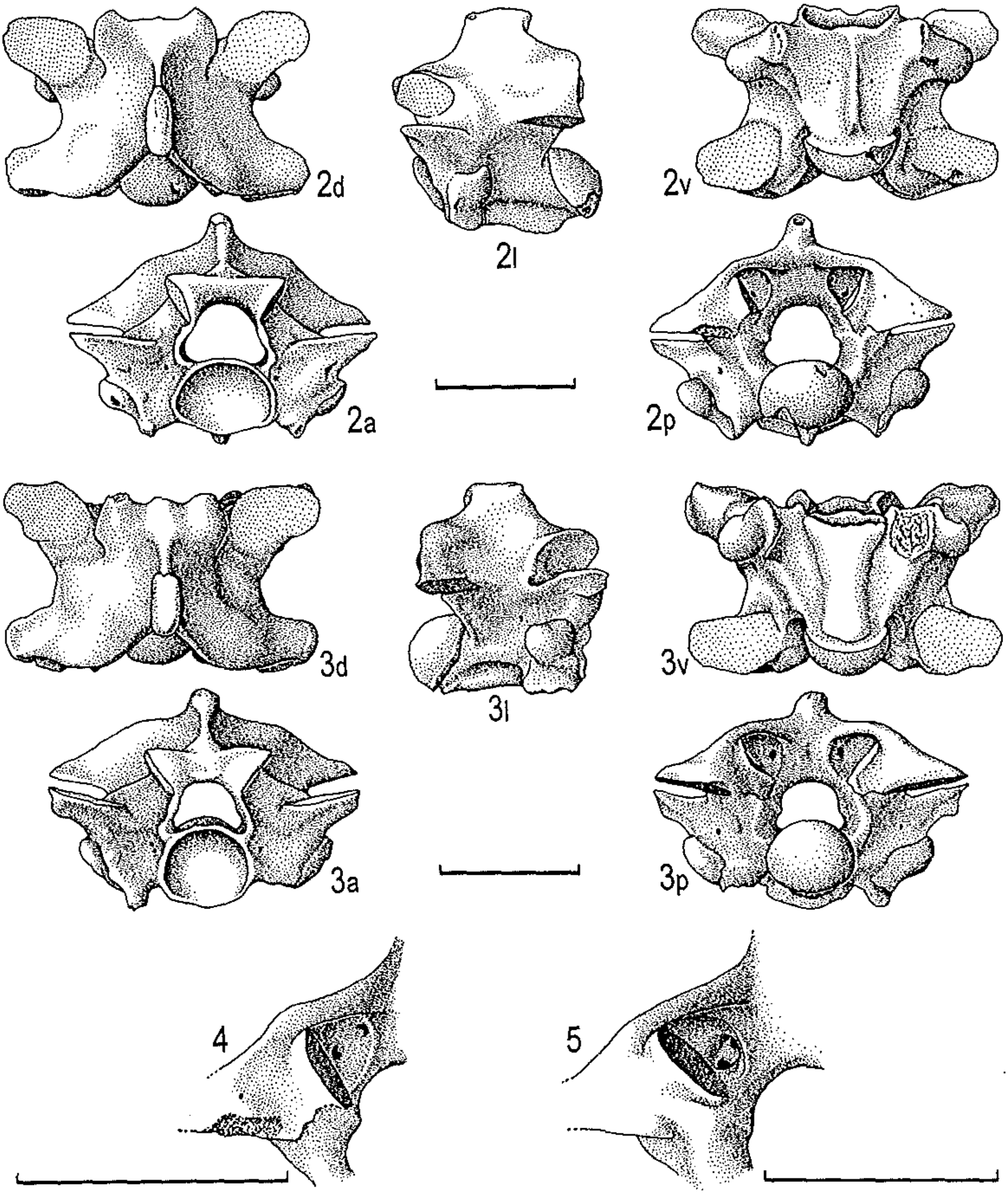
In the largest measurable vertebra, the maximum length (MLV) is 7.8 mm whereas the width of the interzygapophyseal constriction (WIC) attains 8.4 mm. In the smallest vertebra, these dimensions are 4.7 mm and 4.8 mm respectively.

In a few vertebrae, the neural arch does not clearly bulge above the zygantrum. The prezygapophyses are sometimes slightly more slanting than in the holotype. The morphology of the anterior border of the zygosphene is variable. It is generally more or less straight between the lateral lobes; as in the holotype, a small median notch is sometimes present. In some vertebrae, the anterior border is anteriorly convex and in a few it strongly protrudes as a median lobe.

Generally, two zygantral foramina open in each zygantral fossa. They are often distant from one another as in the holotype (fig. 4), but sometimes they are rather closely spaced and they open in a pit located in the bottom of the zygantral fossa (fig. 5). The presence of two foramina in each zygantral fossa is not constant. It was possible to check the number of zygantral foramina on 39 vertebrae: 2 foramina are present in each zygantral fossa in 29 vertebrae; in 6 vertebrae two foramina are present in one fossa and a single foramen opens in the other fossa; in 2 vertebrae there is only one foramen in each fossa (tabl. 2).

Paracotylar foramina are always present but their number varies. In most vertebrae there is one foramen on either side of the cotyle, but in other vertebrae two foramina are present on each side, or two foramina open on one side whereas only one is present on the other side (tabl. 2).

Vertebrae of non-adult individuals display typical juvenile characteristics: neural arch comparatively broader than in adults; cotyle comparatively broader; zygosphene thinner; prezygapophyses less developed and, chiefly, less produced laterally; centrum less widening anteriorly; neural arch gently curved (not bulging) above the zygantrum.



Figures 2-5.— *Hechtophis austrinus* gen. et sp. nov. 2: Holotype, mid-trunk vertebra (DGM 1326-R). 3: posterior trunk vertebra (DGM 1327-R). 4: left part of zygantrum of Holotype, posterior view. 5: left part of zygantrum of DGM 1328-R, posterior view. (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 5mm.

But, unlike most other snakes, non-adults (or at least sub-adults) do not have prezygapophyses more oblique (in dorsal view) than those of adults. As a consequence, in dorsal and ventral views, the outline of vertebrae of non-adult individuals does not significantly differ from that of adults (vertebrae wide and short with a deep interzygapophyseal constriction).

Affinities of *Hechtophis*

Among the characteristics of *Hechtophis*, one of the most striking feature is the conspicuous shortness of the vertebrae. This shortness, coupled with the marked depth of the interzygapophyseal constriction and the transverse dimension of the zygapophyses, gives a characteristic aspect to the vertebrae. Such a morphology is reminiscent of a few boid snakes, namely the living *Lichanura trivirgata* (*Lichanura* is sometimes referred to the synonymy of *Charina*; McDiarmid *et al.*, 1999), and the extinct *Paraepicrates brevispondylus* and "*Paleryx*" *cayluxi*. Furthermore, this peculiar aspect is associated with a non-vaulted neural arch, at least in *Hechtophis*, *Lichanura* and *Paraepicrates*.

The monospecific *Lichanura* is an erycine boid that inhabits western North America. It differs from *Hechtophis* in having more laterally projecting zygapophyses (and, hence, a deeper interzygapophyseal constriction), more elongate prezygapophyseal facets, a markedly more depressed neural arch that does not bulge above the zygantrum, and, when present, only one foramen in each zygantral fossa (in *Lichanura* the presence of paracotylar foramina is irregular and double paracotylar foramina have never been recorded). *Paraepicrates brevispondylus* comes from the early/middle Eocene (Bridgerian) of Wyoming (Hecht, 1959); only the holotype is referred to this species (Kluge, 1988). *Hechtophis* is distinguished from *Paraepicrates* by its clearly deeper posterior median notch in the neural arch, the nearly transverse orientation of the major axis of the zygapophyseal facets (oblique in *Paraepicrates*), the presence of paracotylar foramina, and its smaller condyle and cotyle. "*Paleryx*" *cayluxi* was found in the French "Phosphorites du Quercy" and described by de Stefano (1905) who erroneously referred it to *Paleryx* (Rage, 1984); the precise locality being unknown, its precise geological age remains indeterminate (the "Phosphorites" range from the early/middle Eocene to the early Miocene; Legendre *et al.*, 1992; Sigé *et al.*, 1991). Unfortunately, the material described by de Stefano is lost and this species is known only by the poor original illustrations and description; it does not belong to *Paleryx* (a genus from the European Eocene) but the loss of the fossils prevents the generic allocation of this species. De Stefano's figures show that the prezygapophyses of "*Paleryx*" *cayluxi* were elongate and more projecting laterally than in *Hechtophis*; moreover, the neural arch of the European fossil was apparently more vaulted (which is an important difference) and not bulging above the zygantrum.

Two other boids have very short vertebrae, but they differ distinctly from *Hechtophis*. *Chubutophis grandis* from the early Eocene of Argentina (Albino, 1993) is a large and still poorly known snake. Its vertebrae are high and narrow, and the neural spine is high. Albino (1993) regarded *Chubutophis* as a Boinae, which is probably right. The living *Calabaria* is readily distinguished from *Hechtophis*. Its interzygapophyseal constriction is shallow (because the prezygapophyses are short and oblique in dorsal view), its neural spine is high, and the posterior median notch shallow.

Hecht (1959) stated that *Paraepicrates* is closely related to the living *Epicrates* (Boinae). Kluge (1988) disagreed with the latter opinion and he pointed out that vertebral characters of *Paraepicrates* (presence of a narrow-based neural spine and a shallow median notch) that, according to Hecht, would be *Epicrates*-like features are actually characteristic of *Lichanura*. On the basis of these characteristics and of the overall morphology, Kluge inferred that *Paraepicrates* and *Lichanura* are closely related; he even suggested that these two taxa are congeneric sister species. Kluge appears to be partly accurate. These genera are probably closely related. However, the differences between the two forms overstep intrageneric variation known in boid snakes; consequently, *Paraepicrates* probably represents a distinct genus. The vertebral morphology of *Hechtophis* is more similar to that of *Lichanura* than is that of *Paraepicrates*. However, morphological differences between the species from Itaboraí and *Lichanura* appear to be comparatively important and it does not seem possible to refer the Brazilian fossil to the living genus. However, despite the characters that distinguish these genera, it may be stated that *Hechtophis*, *Paraepicrates*, and *Lichanura* make up an assemblage of likely closely related erycine boid snakes.

It is the assumption that *Hechtophis* is closely related to *Lichanura* that provides evidence of erycine affinities. *Lichanura* and the living *Charina* form the American erycine group (Hoffstetter & Rage, 1972; McDowell, 1987). The non-vaulted neural arch, the neural spine of moderate height, and the wide and not clearly prominent haemal keel of the posterior trunk vertebrae actually represent characteristics of the Erycinae but, as demonstrated by Szyndlar & Böhme (1996), these features can be present also in extinct non-erycine boids (see above). Unfortunately, since the most diagnostic elements of the subfamily (i.e., caudal vertebrae) are not known from Itaboraí, *Hechtophis* may be referred to the Erycinae only with reservation.

cf. *HECHTOPHIS*

In several specimens, the neural arch appears to be more vaulted than in characteristic vertebrae of *Hechtophis*. They might represent extreme variation of that character or, perhaps, even belong to juvenile *Waincophis*. Their referral to *Hechtophis* cannot be definitely demonstrated.

Referred material: 35 trunk vertebrae (DGM 1331a-R: 3 vertebrae; DGM 1331b-R: 11 vertebrae; DGM 1331c-R: 11 vertebrae; DGM 1331d-R: 6 vertebrae; DGM 1331e-R: 4 vertebrae), (collections: 1331b-R by "J.S. Carvalho" in 1949; 1331c-R and 1331d-R by "J.S. Carvalho" in 1967; 1331e-R in 1968 by unknown collector(s); 1331a-R, date and collector(s) unknown).

BOINAE GRAY, 1825

At Itaboraí, the Boinae are diverse; at least five species are present. They represent a significant part of the snake fauna.

CORALLUS DAUDIN, 1803

Up to now, no extinct species has been referred to *Corallus* (Albino, 1996a). Six living species have been recently assigned to the genus: *C. annulatus* (COPE, 1876), *C. caninus* (LINNAEUS, 1758), and *C. hortulanus* (LINNAEUS, 1758); *C. cooki* GRAY, 1842 and *C. ruschenbergeri* (COPE, 1876) are sometimes regarded as species distinct from *C. hortulanus*. Moreover, the rare *Xenoboa cropanii* is sometimes referred to the synonymy of *Corallus* as *C. cropanii* (HOGE, 1953). The genus is restricted to the North of South America, South of Central America, Caribbean islands and Pacific islands of Panama (McDiarmid *et al.*, 1999).

Corallus priscus sp. nov.

1996a aff. *Corallus*: Albino, p. 201.

Holotype: one mid-trunk vertebra (DGM 1332-R), collector(s) and date of collection unknown.

Referred material: 37 trunk vertebrae (DGM 1333-R: 1 vertebra; DGM 1334a-R: 2 vertebrae; DGM 1334b-R: 9 vertebrae; DGM 1334c-R: 1 vertebra; DGM 1335a-R: 1 vertebra; DGM 1335b-R: 1 vertebra; DGM 1335c-R: 1 vertebra; DGM 1335d-R: 21 vertebrae), (collections: 1334a-R by "J.S. Carvalho" in 1949; 1334b-R and 1334c-R by "J.S. Carvalho" in 1967; 1335a-R by "Campos and Silva", date unknown; 1335b-R in 1953, collector(s) unknown; 1335c-R by "Price and Campos" in 1968; 1333-R and 1335d-R, date and collector(s) unknown).

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

Horizon: middle Palaeocene.

Etymology: latin *priscus*, that is extinct.

Diagnosis: Boid snake referred to *Corallus* mainly on the basis of the following combination of characters: zygapophyseal articular facets horizontal, neural arch vaulted, neural spine high. *C. priscus* differs from the living species in having a regularly curved outline of the interzygapophyseal constriction. It is distinguished from *C. hortulanus* and *C. annulatus* by its more vaulted neural arch and its shallower posterior median notch; it differs from *C. caninus* and *C. hortulanus* in having non-constant paracotylar foramina whereas these two living species lack such foramina. Clearly distinguished from *C. cropanii* (assuming the latter species really belongs to *Corallus*) by its horizontal zygapophyseal facets, more vaulted neural arch, less projecting zygapophyses and markedly shallower interzygapophyseal constriction, shallower posterior median notch, and narrower centrum.

Description of the Holotype (fig. 6):

The holotype is a mid-trunk vertebra the dimensions of which are as follows: PRW: 12.8 mm; MLV: 9.7 mm; ZW: 6.5 mm; CTW: 3.8 mm; CL: 6.9 mm; WIC: 9.2 mm.

In anterior view, the dorsal roof of the zygosphene is distinctly concave dorsally.

The zygosphene is markedly wider than the cotyle; the latter appears small and subcircular. The articular facets of the zygapophyses are horizontal and level with the floor of the neural canal. Each prezygapophysis bears a very short prezygapophyseal process that does not project beyond the articular facet located above it. The paradiapophyses do not markedly protrude laterally but they clearly project ventrally below the centrum. Between the cotyle and each diapophysis, a small tubercle projects anteriorly (fig. 6a). On either side, a tiny paracotylar foramen opens in a deep depression. The neural canal is small and subcircular.

In lateral view, the neural spine is high and long. Its anterior border originates on the zygosphene and it forms an anteriorly convex curve. The dorso-ventral extent of the paradiapophyses is rather short. Tiny lateral foramina are present.

In posterior view, the neural arch is highly vaulted and it markedly bulges above the zygantrum. In dorsal view, the vertebra is longer than those of *Hechtophis* ($0.702<MLV/PRW<0.816$). The anterior border of the zygosphene forms a stout median lobe; this lobe is slightly notched anteriorly. The posterior median notch in the neural arch is shallow. The articular facets of the prezygapophyses are broad and rather short; they do not strongly project laterally and their major axis appears to be slightly oblique. The interzygapophyseal constriction is shallow and not squarish. In ventral view, the centrum does not strongly widen anteriorly. The haemal keel is moderately wide.

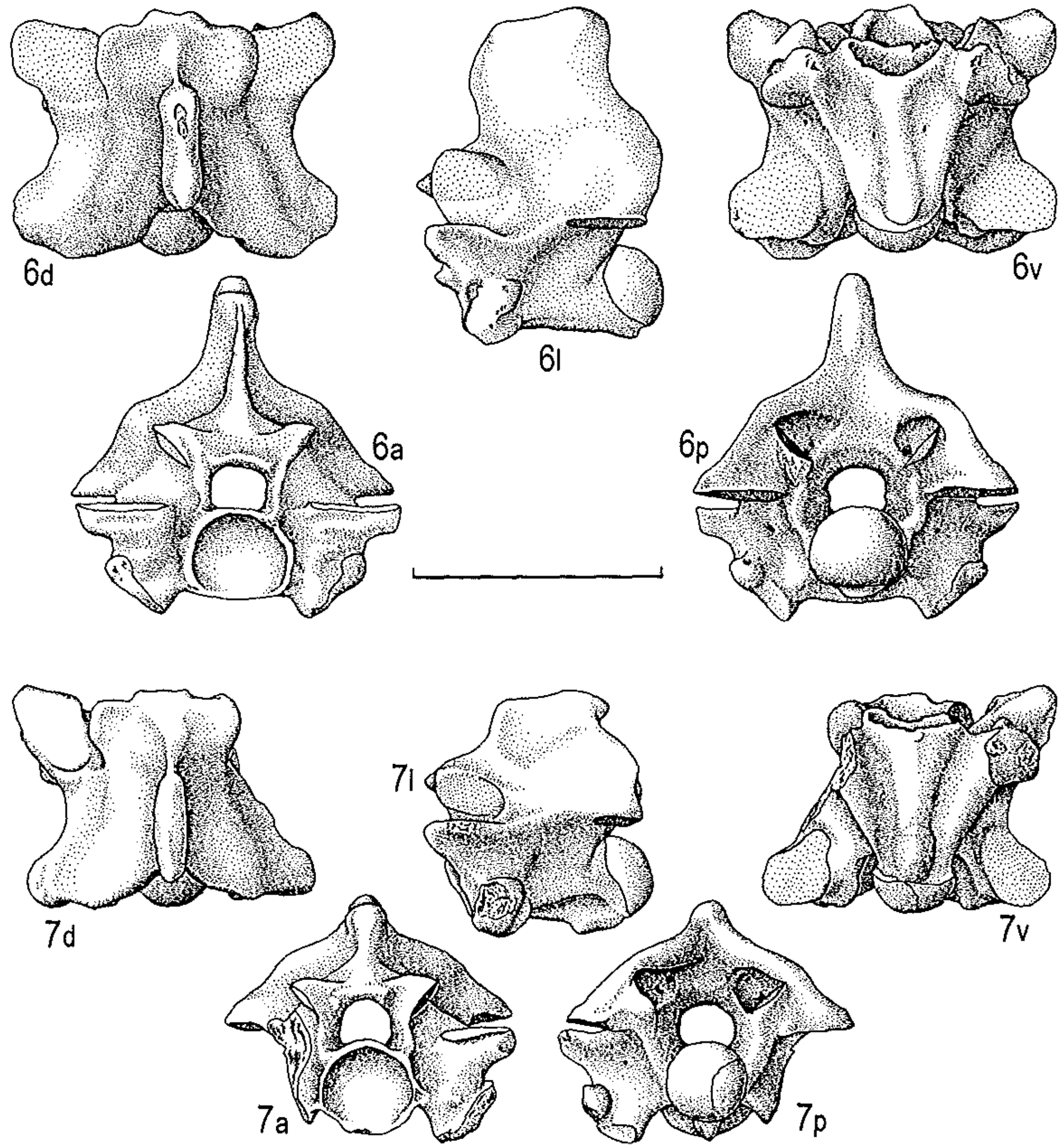
Intracolumnar variation:

No anterior trunk vertebra can be confidently assigned to this species. The morphology of every mid-trunk vertebra is similar to that of the holotype. The posterior trunk vertebrae display the usual variation: the neural arch is less vaulted than in those from the mid-trunk region, their neural spine is lower (especially, in *C. priscus*, the neural spine of posterior trunk vertebrae is clearly lower than that of those in the mid-trunk region) with a straight anterior border, the paradiapophyses are more distant from the centrum, the haemal keel is wider, and, on either side, a wide groove runs along the keel. On the posteriormost trunk vertebrae (fig. 7), the posterior part of the haemal keel is produced ventrally (= cloacal hypapophysis) and the centrum strongly widens anteriorly.

Intraspecific variation:

In the largest vertebra, the maximum length (MLV) is 11.1 mm and the width of interzygapophyseal constriction (WIC) is 12.9 mm. In the smallest vertebra, these dimensions are 5.2 mm and 4.4 mm respectively.

Paracotylar foramina occur irregularly. This feature may be observed on 23 vertebrae: foramina occur bilaterally on ten vertebrae, one is present unilaterally on four vertebrae, and nine vertebrae have no paracotylar foramina (tabl. 2). Such an irregularity has already been noted in living boids (Underwood, 1976). When present, paracotylar foramina are always single (i.e., not double) (tabl. 2). The anterior border of the neural spine is not always curved, it is sometimes straight. On vertebrae smaller than the holotype, the neural spine is thiner and lower (the holotype ranks among the medium sized vertebrae).



Figures 6-7.— *Corallus priscus* sp. nov. 6: Holotype, mid-trunk vertebra (DGM 1332-R). 7: posteriormost trunk vertebra (DGM 1333-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bar = 1cm.

Discussion:

The assignment of this set of vertebrae to the genus *Corallus* rests on the following combination of characters: zygosphene with a strong median lobe and wider than the cotyle, articular facets of prezygapophyses short and horizontal, prezygapophyses not strongly projecting laterally, neural spine high, neural arch highly vaulted, interzygapophyseal constriction shallow. Apart from *Corallus*, no fossil or living boid snake presents such a suite of characters. The vertebral morphology of the extant *Sanzinia*, from Madagascar, seems to be closest. The latter genus differs from *Corallus* mainly by its slightly less vaulted neural arch, the anterior border of its zygosphene that is concave, its deeper posterior median notch in the neural arch, and the slightly more projecting prezygapophyseal processes.

C. priscus is distinguished from the living species of *Corallus* by the regularly curved outline of its interzygapophyseal constriction. This outline is angular, more or less squarish (the bottom being subrectilinear) in *C. caninus* and *C. hortulanus*; *C. annulatus* and *C. cropanii* display an outline intermediate between that of *C. priscus* on one hand, and *C. caninus* and *C. hortulanus* on the other hand. Besides, the neural arch of the fossil species is sligthly more vaulted than in the living *C. hortulanus, C. annulatus*, and *C. cropanii*; it is similar to that of *C. caninus*. The posterior median notch in the neural arch of *C. priscus* and *C. caninus* is less deep than in *C. hortulanus*, *C. annulatus*, and *C. cropanii*. Finally, the non constant presence of paracotylar foramina in the fossil species is somewhat reminiscent of *C. annulatus* and *C. cropanii* in which vertebrae are provided with such foramina; the other species lack paracotylar foramina.

The above listed characters are only differences between the species of *Corallus*; since their polarity remains unknown they are not evidence of relationships within the genus. It would be illusory to search for precise relationships within the genus on the basis of the available material.

cf. *CORALLUS*

Some poorly preserved vertebrae are tentatively assigned to *Corallus* on the basis of their clearly vaulted neural arch.

Referred material: 15 trunk vertebrae (DGM 1336a-R: 7 vertebrae; DGM 1336b-R: 1 vertebra; DGM 1336c-R: 4 vertebrae; DGM 1336d-R: 3 vertebrae), (collections: 1336b-R by "Campos and Silva", date unknown; 1336c-R by "J.S. Carvalho" in 1949; 1336d-R by "J.S. Carvalho" in 1967; 1336a-R, date and collector(s) unknown).

WAINCOPHIS ALBINO, 1987

Up to now, only one species has been referred to the genus *Waincophis*: *W. australis* Albino, 1987, the type species of the genus. The species is based on a single trunk vertebra from the early Eocene (Casamayorian) of Argentina. Subsequently, Albino (1996b) assigned a few incomplete vertebrae from the middle Miocene (Friasian) of Argentina to this species. If the latter specimens really belong to *W. australis*, then this species is, by far, the snake with the longest stratigraphic range (about 40 million years). An indeterminate *Waincophis* was reported from the early Miocene (Colhuehuapian) of Argentina (Albino, 1996b).

W. australis is a small snake, but two markedly larger species from Itaboraí appear to be referrable to the same genus. The assignment of these two species to *Waincophis* leads to the modification of the diagnosis of the genus proposed by Albino (1987). *Waincophis* is not characterized by prominent features that would diagnose it from all other boines, but a combination of characters clearly distinguishes it from other living and extinct genera (tabl. 1a, b, c).

Emended diagnosis: Small to rather large genus showing the generalized overall morphology of a boid. Neural arch not vaulted. Neural spine low. Zygosphene wider or as wide as the cotyle. Prezygapophyseal articular facets lying prominently above the level of the floor of the neural canal and inclined above horizontal. Prezygapophyseal processes reduced. Vertebral centrum short and widened anteriorly. Haemal keel thick and either prominent or flat and wide, depending on the position of the vertebra in the column. Paracotylar foramina present. Paradiapophyses not projecting ventrally beyond the level of the cotyle.

Waincophis pressulus sp. nov.

1990 Boinae indet.: Albino, p. 338-340, fig. 1C, D.

Holotype: one mid-trunk vertebra (DGM 1337-R), collector(s) and date of collection unknown.

Referred material: 34 trunk vertebrae (DGM 1338-R: 1 vertebra; DGM 1339-R: 1 vertebra; DGM 1340a-R: 3 vertebrae; DGM 1340b-R: 4 vertebrae; DGM 1340c-R: 4 vertebrae; DGM 1341a-R: 2 articulated vertebrae; DGM 1341b-R: 1 vertebra; DGM 1341c-R: 4 vertebrae; DGM 1341d-R: 13 vertebrae; DGM 1341e-R: 1 vertebra), (collections: 1338-R and 1341c-R by "Price and Campos" in 1968; 1339-R and 1340b-R by "J.S. Carvalho" in 1949; 1340a-R by "J.S. Carvalho" in 1967; 1340c-R by "J.S. Carvalho and O.S. Santos" in 1953; 1341a-R in 1968 by unknown collector(s); 1341b-R in 1953 by unknown collector(s); 1341d-R and 1341e-R, date and collector(s) unknown).

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

Horizon: middle Palaeocene.

Etymology: latin *pressulus*, somewhat flattened; refers to the morphology of the neural arch.

Diagnosis: Species markedly larger than the type species, *W. australis*. Differs from the latter species by its shorter and more depressed vertebrae, comparatively narrower zygosphene, broader centrum, clearly depressed cotyle and condyle, smaller neural canal, neural spine comprising a thick posterior portion and a thin anterior part, and by the presence of a strong median lobe on the anterior border of the zygosphene (at least in mid-trunk vertebrae).

Description of the Holotype (fig. 8):

The basic measurements of the holotype are as follows: MLV: 11.2 mm; ZW: 7 mm; CTW: 7.1 mm; WIC: 11.4 mm.

The holotype is the largest vertebra. It is massive, strongly built, and depressed. In anterior view, the zygosphene is moderately thick and its roof is concave dorsally. A strong, although incomplete, median lobe stands out against the bulk of the zygosphene. The cotyle is markedly depressed and its width is similar to that of the zygosphene. The relatively small section of the neural canal shows a somewhat subtriangular outline. The prezygapophyseal facets are short, moderately inclined above the horizontal, and they lie distinctly above the level of the floor of the neural canal (above half the height of the neural canal; their lateral extremities are level with the top of the canal). The prezygapophyses do not strongly project laterally; they bear a very small prezygapophyseal process. The paradiapophyses do not strongly protrude laterally but, as a result of the shortness of the prezygapophyseal facets, they approach the prezygapophyseal tip. The ventral border of the paradiapophyses lies slightly above the ventralmost part of the cotylar rim. A single paracotylar foramen, recessed in a fossa, opens on either side of the cotyle on a level with the floor of the neural canal. Moreover, on the right side only, there is a foramen that occupies the position of a parazygosphenial foramen.

In dorsal view, the vertebra is short, wide, and the interzygapophyseal constriction rather shallow. The prezygapophyseal facets are short and their major axis is clearly oblique. The anterior border of the zygosphene forms three lobes (that are poorly preserved); the median one strongly protrudes (the nearly undamaged zygosphene of a mid-trunk vertebra is illustrated fig. 9). The long neural spine comprises two parts, a thick posterior one and a thin anterior one. The posterior median notch in the neural arch is rather deep.

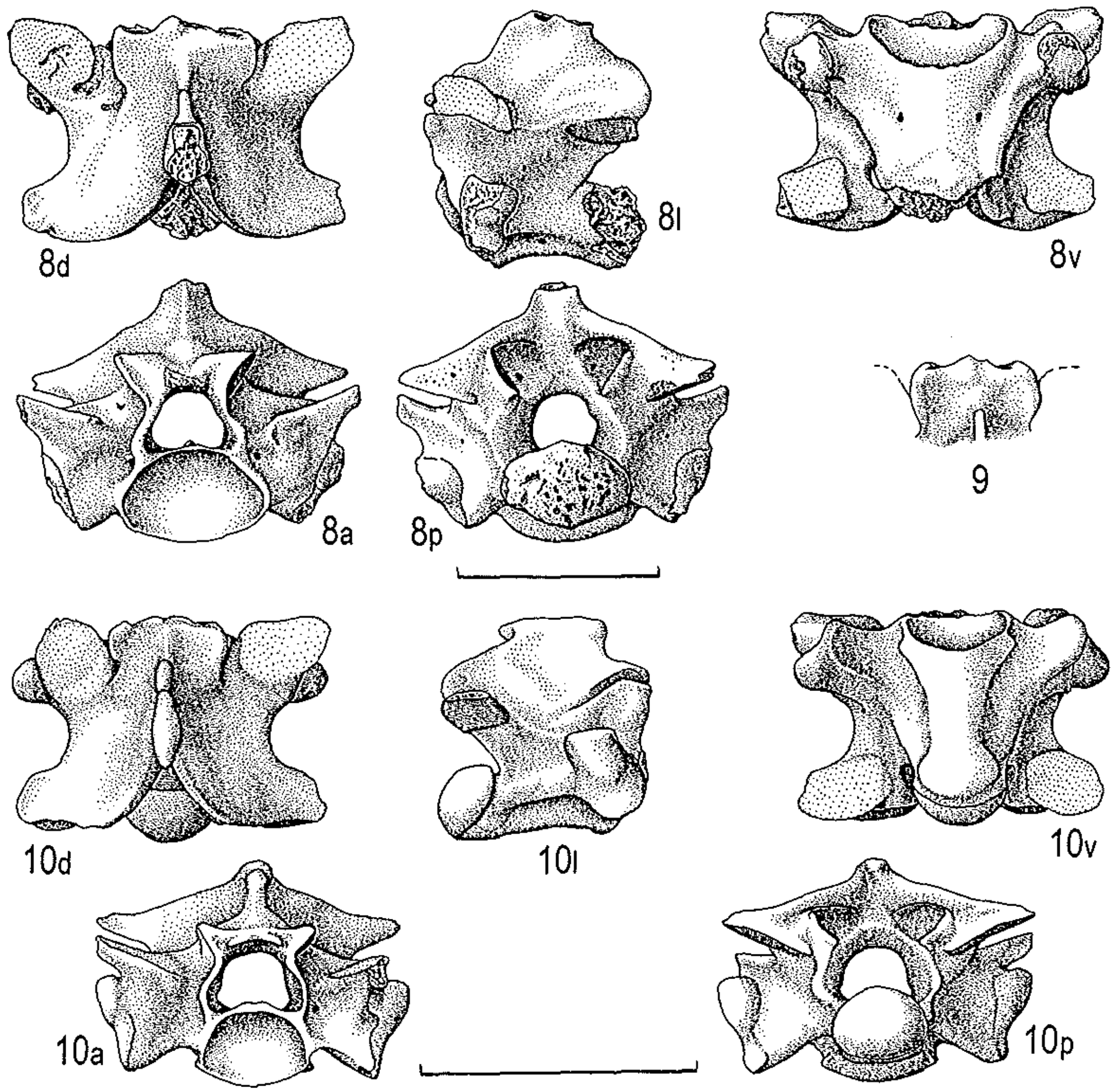
In lateral view, the neural spine appears long and low. The interzygapophyseal ridge is quite prominent and rather sharp. A lateral foramen is present. The paradiapophysis is massive and moderately elongate dorso-ventrally. The ventral border of the haemal keel is arched upward.

In posterior view, the neural arch is depressed and slightly bulging above the zygantrum. The posterior face of the neural arch lacks parazygantral foramina but several scattered foramina are present there. The condyle is strongly depressed.

In ventral view, the centrum is short and it strongly widens anteriorly. Much of the ventral face is occupied by the wide, transversely rounded, haemal keel. The subcentral ridges are rounded and not well-defined. Subcentral foramina are present.

Intracolumnar variation:

No anterior vertebra can be confidently referred to *W. pressulus*. In the most anterior available vertebrae, the posterior part of the haemal keel is more or less strongly produced ventrally; but even in these vertebrae, the anterior part of the keel remains wide and blunt. Mid-trunk vertebrae are illustrated by the holotype. Posterior trunk vertebrae display usual variations (fig. 10). They are more depressed than those from the mid-trunk; especially, their neural arch is strongly flattened. The neural spine appears longer and lower than in mid-trunk vertebrae. As is characteristic of most snakes, the paradiapophyses of posterior trunk vertebrae are more distant from the centrum; in *W. pressulus*, they project as far laterally as the prezygapophyseal extremities located above them or they even slightly overstep them. The medial lobe of the zygosphenial anterior border is wider and less protruding (or lacking) than that of mid-trunk vertebrae. Ventrally, the paradiapophyseal extremities lie above the level of the ventral part of the cotylar rim. The haemal keel is wide and clearly distinct from the centrum; on either side, a groove runs along it.



Figures 8-10.— *Waincophis pressulus* sp. nov. 8: Holotype, mid-trunk vertebra (DGM 1337-R). 9: nearly undamaged zygosphene of a mid-trunk vertebra (DGM 1341e-R), dorsal view. 10: posterior trunk vertebra (DGM 1338-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 1cm.

Intraspecific variation:

The maximum length (MLV) of the largest vertebra is 11.2 mm while the width of its interzygapophyseal constriction (WIC) is 11.4 mm. In the smallest vertebra, these measurements are 6.6 mm and 6.4 mm respectively.

All vertebrae are short; the ratio MLV/PRW ranges between 0.614 and 0.708, i.e. it is only slightly different from that in *Hechtophis*. The posterior thick and anterior thin parts of the neural spine remain generally distinct but, in some specimens (chiefly in posterior trunk vertebrae), the anterior portion is thickened too. It is worth mentioning that even juvenile specimens have a neural spine made up by thick posterior and thin anterior parts. In a few vertebrae, the zygosphene is slightly wider than the cotyle. The prezygapophyseal facets are subtriangular to ovaloid in outline. The constancy of paracotylar foramina cannot be ascertained but their occasional absence seems to be an artifact of fossilization (for example, the illustrated posterior trunk vertebra lacks one paracotylar foramen as well as the two lateral foramina). The number of paracotylar foramina is somewhat variable. Generally, a single foramen opens on each side, but in two vertebrae there is a double foramen on one side and a single foramen on the other side, and in one vertebra, a foramen is present unilaterally. In each zygantral fossa, there is almost always only one zygantral foramen; variation is rare (tabl. 2). Tiny foramina occasionally open on the posterior border of the neural arch. They are not recessed in fossae and they cannot be considered parazygantral foramina. Foramina occupying the position of parazygosphenial foramen are rare: there is one foramen on either side in two vertebrae, and one foramen is present on one side in two vertebrae (including the holotype).

Discussion:

Waincophis pressulus is clearly larger than the type species, *W. australis*; it is twice the size of the latter species. Moreover, the vertebrae of *W. pressulus* are shorter and more depressed (therefore less narrow in anterior or posterior view). The zygosphene is narrower and thicker. The section of the neural canal appears smaller and less high. The condyle and cotyle are notably depressed whereas they are almost circular in *W. australis*. The centrum is clearly broader. In mid-trunk vertebrae, the median lobe of the zygosphene is more distinct and it strongly protrudes in *W. pressulus*. Moreover, in most vertebrae the zygosphene is comparatively thicker than that of *W. australis*. Above the zygantrum, the neural arch slightly bulges in *W. pressulus* whereas it is not affected by the zygantral cavities in the type species. The neural spine of *W. australis* is unknown on the holotype but it is preserved in specimens from the Miocene; it is low, thin, and anteroposteriorly long (Albino, 1996b). In lateral aspect, the neural spine of *W. pressulus* is not clearly different from that of *W. australis*; but, in dorsal view, it comprises a thick posterior part anteriorly prolonged by a thinner portion. In *W. australis*, the neural spine is uniformly thin. Moreover, although this cannot be definitely ascertained, the posterior median notch in the neural arch of *W. pressulus* appears to be more acute than that of *W. australis*.

As noted above, *W. pressulus* differs from *W. australis* by its markedly larger size (about twice). On the other hand, several of the characters that distinguish *W. pressulus* from the type species appear to be size-related: shorter vertebrae, thicker zygosphene, smaller section of the neural canal, and broader centrum. However, *W. pressulus* is a species clearly distinct from *W. australis*.

Waincophis cf. *W. pressulus*

Some vertebrae that are not well preserved cannot be referred to *W. pressulus* without reservation.

Referred material: 14 trunk vertebrae (DGM 1342a-R: 7 vertebrae; DGM 1342b-R: 2 vertebrae; DGM 1342c-R: 1 vertebra; DGM 1342d-R: 3 vertebrae; DGM 1342e-R: 1

vertebra), (collections: 1342b-R by "J.S. Carvalho and O.S. Santos" in 1953; 1342c-R by "J.S. Carvalho" in 1967; 1342d-R by "J.S. Carvalho" in 1949; 1342e-R by "Price and Campos" in 1968; 1342a-R, date and collector(s) unknown).

Waincophis cameratus sp. nov.

Holotype: one mid-trunk vertebra (DGM 1343-R), collector(s) and date of collection unknown.

Referred material: 48 trunk vertebrae (DGM 1344-R: 1 vertebra; DGM 1345a-R: 3 vertebrae; DGM 1345b-R: 5 vertebrae; DGM 1345c-R: 1 vertebra; DGM 1346a-R: 21 vertebrae; DGM 1346b-R: 17 vertebrae), (collections: 1345a-R by "J.S. Carvalho" in 1967; 1345b-R by "J.S. Carvalho and O.S. Santos" in 1953; 1345c-R by "J.S. Carvalho" in 1949; 1346a-R in 1968, by unknown collector(s); 1344-R and 1346b-R, date and collector(s) unknown).

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

Horizon: middle Palaeocene.

Etymology: latin *cameratus*, vaulted; in reference to the neural arch that is less depressed than in the other species from the locality.

Diagnosis: Large species, size similar to that of *W. pressulus*. *Waincophis cameratus* differs from *W. australis* and *W. pressulus* by its less depressed vertebrae and antero-posteriorly shorter neural spine. Moreover, it is distinguished from the type species, *W. australis*, in having shorter vertebrae, a comparatively thicker zygosphene, a broader centrum, depressed cotyle and condyle, and a smaller neural canal. Besides, *Waincophis cameratus* differs from *W. pressulus* in having a less depressed (but non-vaulted) neural arch, a neural spine comprising only a thick part, and in having a less protruding median lobe of zygosphene in mid-trunk vertebrae.

Description of the Holotype (fig. 11):

The holotype is a rather large, massive, strongly built, and non-depressed mid-trunk vertebra. The basic measurements of this vertebra are as follows: PRW: 17.7 mm; ZW: 7.3 mm; CTW: 6.2 mm; MLV: 11.2 mm; CL: 8.7 mm; WIC: 12.7 mm.

In anterior view, the zygosphene is rather thick and wider than the cotyle; its roof is concave dorsally. The section of the neural canal is small and it displays a subtrifoliate outline. The cotyle is not depressed but its ventral part is truncate. The prezygapophyseal facets are short and moderately inclined. The level of these facets lies prominently above that of the floor of the neural canal (above half the height of the neural canal); their lateral tips are level with the top of the canal. The prezygapophyses are not markedly produced laterally; they are provided with very small prezygapophyseal processes. The paradiapophyses do not strongly project laterally; however, because of the rather weak lateral projection of the prezygapophyses, they laterally approach the vertical level of the prezygapophyseal extremity. The ventral tip of the paradiapophyses is even with the ventral part of the cotylar rim. Two paracotylar foramina are present in a depression on either side of the cotyle; they are level with the floor of the neural canal.

In dorsal view, the vertebra appears distinctly wider than long. The prezygapophyseal facets are short; their postero-lateral border is more or less rectilinear, which gives a subtriangular shape to the facets. The major axis of these facets is oblique. As a consequence of the shortness of the prezygapophyseal facets, the interzygapophyseal constriction is rather shallow. The anterior border of the zygosphene forms three lobes that weakly project anteriorly. The neural spine is short (less than half the length of the neural arch) and thick; it lacks a thin anterior part. The posterior median notch deeply indents the posterior border of the neural arch.

In lateral view, the neural spine is low and short. The interzygapophyseal ridge is fairly prominent but blunt. The paradiapophysis appears rather elongate dorso-ventrally. A lateral foramen is present. The sulcus for the costal ligament that runs along the anterior border of the paradiapophysis forms a deep groove. The haemal keel is slightly produced ventrally in the posterior half of the centrum.

In posterior view, the neural arch is moderately vaulted and it barely bulges above the zygantrum. Parazygantral foramina are lacking. There is only one foramen in each zygantral fossa. The ventral part of the condyle is truncate.

In ventral view, the centrum markedly widens anteriorly; its ventral face is sub-plane and it is delimited by subcentral ridges that are distinct but not prominent. The haemal keel, of moderate width, is prominent, mainly in the posterior part of the centrum. Subcentral foramina are present.

Intracolumnar variation:

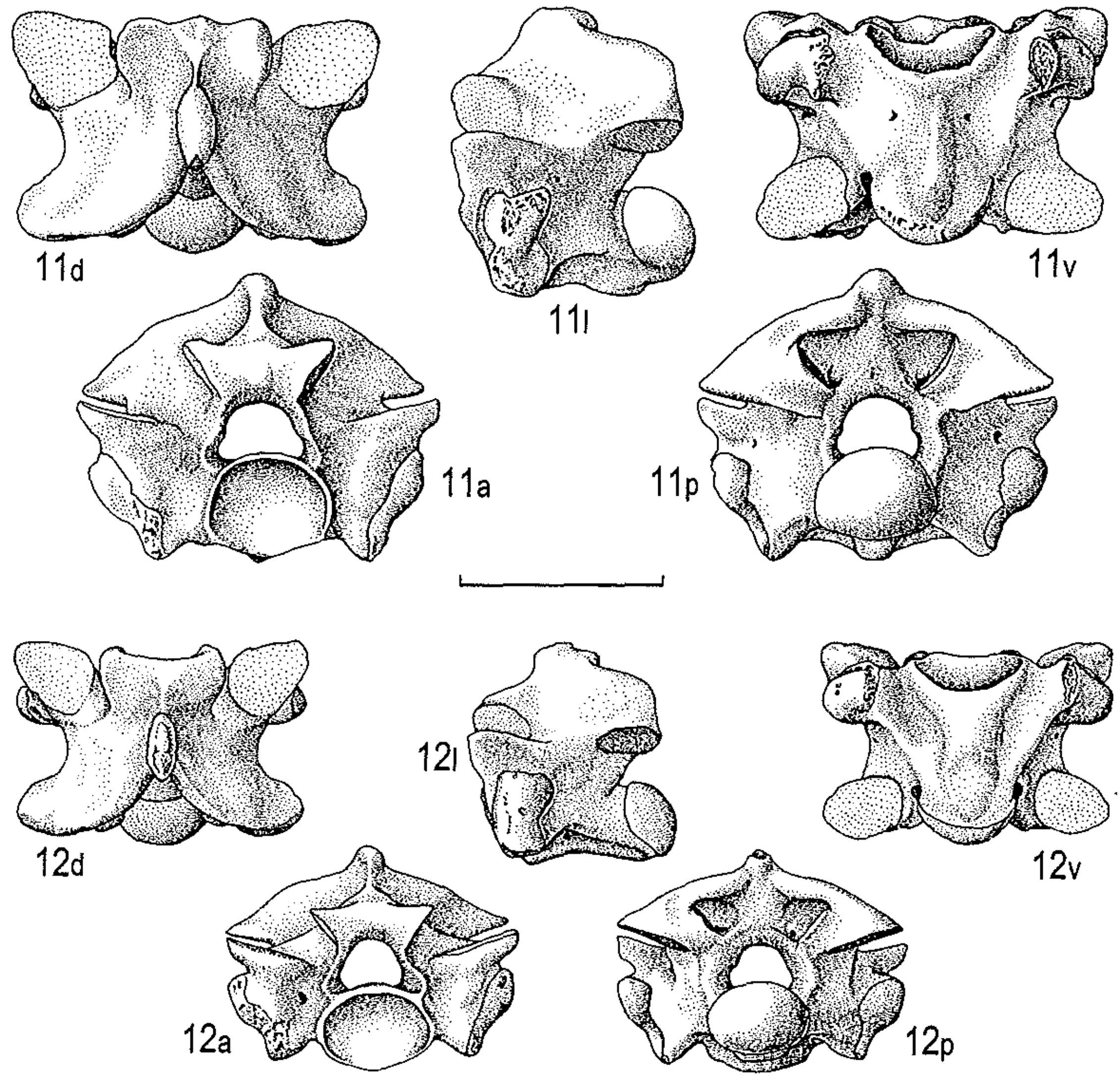
Anterior trunk vertebrae are known; they bear a hypapophysis. In these vertebrae, the neural spine and the neural canal are higher and the neural arch is more vaulted than in mid-trunk vertebrae. The prezygapophyseal facets are ovaloid whereas they are subtriangular in mid- and posterior trunk vertebrae. Mid-trunk vertebrae are exemplified by the holotype. The anterior border of their zygosphene bears generally three lobes (as in the holotype) but the median one is absent in several specimens.

In posterior trunk vertebrae (fig. 12), the neural arch is slightly less vaulted than in the mid-trunk region; generally, it does not camber above the zygantrum. The shape of the neural spine remains similar to that of mid-trunk vertebrae. The median lobe of the zygosphene is absent, consequently the anterior border of the zygosphene is either straight or slightly concave. The diapophyseal part of the paradiapophyses, in posterior trunk vertebrae, strongly projects laterally; it reaches, and may even slightly project beyond the lateral tip of the prezygapophyses. Generally, the ventral extremities of the paradiapophyses are slightly above the ventralmost part of the cotyle. On posterior trunk vertebrae, the haemal keel is wide and hardly salient. The cotyle and condyle are dorso-ventrally depressed but their ventral part is not truncate.

Intraspecific variation:

The size varies considerably. The holotype is the largest measurable vertebra, but it is not the largest specimen. In the holotype, the maximum length (MLV) attains 11.2 mm and the width of the interzygapophyseal constriction (WIC) is 12.7. In the smallest vertebra, these dimensions are 6.2 mm and 6.6 mm respectively.

As in *W. pressulus*, all vertebrae are short; MLV/PRW is similar to that in the latter species (it ranges between 0.610 and 0.709). The shape of the cotyle varies largely in mid-trunk vertebrae; it is either truncate ventrally, or depressed, or even nearly circular. Intraspecific variation affects mainly foramina. Generally, only one paracotylar foramen opens on either side of the cotyle but variations are rather important (tabl. 2). It should be noted that the holotype displays double paracotylar foramina on both sides, which is not the most frequent condition in the species. The number of zygantral foramina is also variable; the most frequent condition is the presence of one foramen in each zygantral fossa (tabl. 2). The occurrence of foramina on the posterior border of the neural arch, lateral to the zygantrum, is exceptional. In one vertebra only, there is a foramen that opens unilaterally in the position of a parazygosphenial foramen.



Figures 11-12.— *Waincophis cameratus* sp. nov. 11: Holotype, mid-trunk vertebra (DGM 1343-R). 12: posterior trunk vertebra (DGM 1344-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bar = 1cm.

Discussion:

Waincophis cameratus clearly differs from *W. australis*, i.e. the type species; it is apparently morphologically closer to *W. pressulus*. *W. cameratus* may be distinguished from both *W. australis* and *W. pressulus* by its less depressed vertebrae and its antero-posteriorly shorter neural spine. Moreover, *W. cameratus* differs from *W. australis* by its shorter vertebrae, broader centrum, smaller neural canal, and depressed or ventrally truncate cotyle. As in *W. pressulus*, some of these features are size-related. *W. cameratus* is markedly larger than *W. australis*, its size is similar to that of *W. pressulus*. The zygosphene is comparatively narrower than that of *W. australis*, but slightly wider than that of *W. pressulus*; it is thicker than in *W. pressulus* and markedly thicker than that of *W. australis*. In mid-trunk vertebrae, the median lobe of the zygosphene does not strongly project anteriorly. The neural spine does not comprise an anterior thin portion, which clearly distinguishes *W. cameratus* from *W. pressulus*. In mid- and posterior trunk vertebrae of *W. cameratus*, the prezygapophyseal facets are subtriangular (their shape varies in anterior trunk vertebrae), whereas they are subtriangular to oval in *W. pressulus*, and oval in *W. australis* (but the latter species is known by only a few specimens).

Waincophis cf. *W. cameratus*

A few poorly preserved vertebrae of *Waincophis* are tentatively referred to *W. cameratus* on the basis of their non-depressed neural arch.

Referred material: 5 trunk vertebrae (DGM 1347a-R: 3 vertebrae; DGM 1347b-R: 1 vertebra; DGM 1347c-R: 1 vertebra), (collections: 1347a-R by "Price, Campos, and Silva" in 1968; 1347c in 1949 by unknown collector(s); 1347b, date and collector(s) unknown).

Waincophis sp.

Incomplete vertebrae belong to *Waincophis*, but their state of preservation do not permit assignment at species level.

Referred material: 58 trunk vertebrae (DGM 1348a-R: 14 vertebrae; DGM 1348b-R: 3 vertebrae; DGM 1348c-R: 10 vertebrae; DGM 1349a-R: 4 vertebrae; DGM 1349b-R: 2 vertebrae; DGM 1349c-R: 5 vertebrae; DGM 1349d-R: 1 vertebra; DGM 1349e-R: 1 vertebra; DGM 1349f-R: 18 vertebrae), (collections: 1348a-R by "J.S. Carvalho" in 1949; 1348b-R by "J.S. Carvalho and O.S. Santos" in 1953; 1348c-R by "J.S. Carvalho" in 1967; 1349a-R by "Price, Campos and Silva" in 1968; 1349b-R by "Price and Campos" in 1968; 1349c-R in 1968 by unknown collector(s); 1349d-R by "Campos and Silva", date unknown; 1349e by "col. L.A. Gravatá and Sonia Cruz" in 1967; 1349f-R, date and collector(s) unknown).

cf. *Waincophis*

Dentaries (fig. 13)

Referred material: 2 dentaries (DGM 1350-R and DGM 1351-R), (collections: 1350-R by "col. L.A. Gravatá and Sonia Cruz" in 1967; 1351-R by "J.S. Carvalho" in 1967).

Two rather large dentaries are very similar. DGM 1350-R is the more complete of the two. Its posterior part is lacking (bone broken through the 11th alveolus) but its anterior extremity is well preserved. Only the anteriormost part of the notch that housed the compound bone is preserved, which means that the missing part of the dentary was probably relatively long. The specimen bears 10 complete tooth alveoli. In lateral aspect, the dentary is deep. The dorsal edge is convex dorsally and the ventral edge is convex ventrally (but it is damaged in its posterior part). Anteriorly, the dentary tapers and forms a peculiar extremity (triangular and unusually symmetrical in lateral view; fig. 13m, l). The large mental foramen opens below the 4th alveolus. A weak imprint shows that the anterior process of the compound bone reached the level of the 9th alveolus. In medial view, the Meckelian groove appears widely open; it only slightly narrows anteriorly. It opens ventromedially for most of its length, but, at its anterior extremity it is open ventrally only. The groove is sharply defined dorsally below the two anterior alveoli, but posteriorly its dorsal limit is indistinct. In dorsal view, the dentary curves smoothly medially. In ventral view, the anterior part of the Meckelian groove is visible; it is shallow and clearly limited anteriorly (fig. 13v).

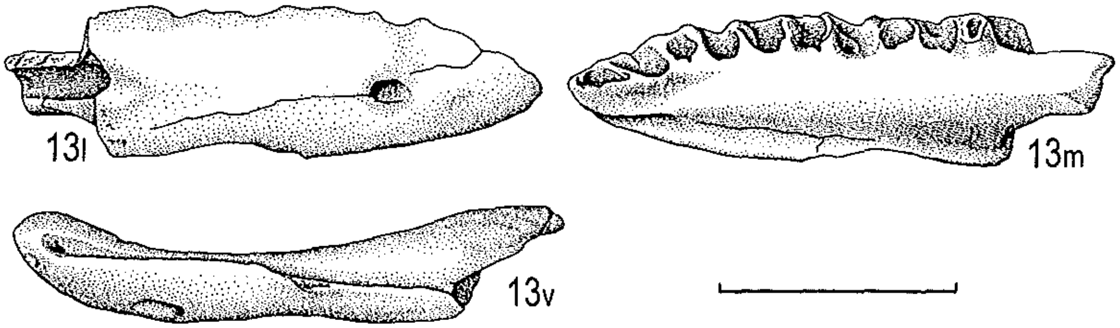


Figure 13.— cf. *Waincophis*. Right dentary (DGM 1350-R). (l: lateral view, m: medial view, v: ventral view). Scale bar = 1cm.

These dentaries differ from those of the Madtsoiidae (Rage, 1998) in having only one mental foramen. McDowell (1975) has shown that in the Pythoninae the Meckelian cartilage extends anteriorly beyond the dentary and reaches the skin; in the Boinae, and Erycinae (Erycini, a tribe of the Boinae, according to McDowell), the anterior tip of this cartilage is limited by the dentary. This results in two distinct morphologies of the dentary: in the Pythoninae, the Meckelian groove opens anteriorly whereas in the Boinae and Erycinae the groove has an anterior limit defined by bone. DGM 1350-R and DGM 1351-R display the condition known in both Boinae and Erycinae. The latter condition *a priori* represents the derived state (the groove is open at its tip in lizards) although it is present in at least one madtsoiid snake (*Madtsoia* cf. *bai*; Rage, 1998: 127). Scanlon & Lee (2000) regarded the anteriorly limited condition as derived. Unfortunately, this feature only permits to distinguish Pythoninae from Boinae and Erycinae, but there is no difference between the two latter subfamilies. However, in the locality, the rather large size of DGM 1350-R and DGM 1351-R is consistent with *Waincophis*. These dentaries are too large to represent the other boid genera recognized from vertebrae. Consequently, they are tentatively referred to *Waincophis*.

Vertebrae

Several vertebrae are generally poorly preserved and most of them represent juvenile specimens. The generic allocation cannot be definitely demonstrated.

Referred material: 34 trunk vertebrae (DGM 1352a-R: 2 vertebrae; DGM 1352b-R: 5 vertebrae; DGM 1352c-R: 1 vertebra; DGM 1352d-R: 3 vertebrae; DGM 1352e-R: 18 vertebrae; DGM 1352f-R: 5 vertebrae), (1352a-R by "Price and Campos" in 1968; 1352c-R in 1961, collector(s) unknown; 1352d-R by "J.S. Carvalho and O.S. Santos" in 1953; 1352e-R by "J.S. Carvalho" in 1949; 1352f-R by "J.S. Carvalho" in 1967; 1352b-R, date and collector(s) unknown).

Comparisons between *Waincophis* and other Boidae

Waincophis displays the typical vertebral morphology of the Boidae. It does not show traits that would sharply distinguish it from all other boids, but the combination of characters that characterizes it demonstrates that it is distinct from all living and other extinct genera of Boidae.

Waincophis cannot be referred to the Pythoninae. The vertebrae of pythons are not depressed, their neural arch is vaulted, and they never have paracotylar foramina.

Because of their depressed overall morphology, non-vaulted neural arch, and low neural spine, the vertebrae of *Waincophis* are consistent with those of the Erycinae. But, as noticed above (see discussion about *Hechtophis*), trunk vertebrae with such an overall morphology can be present in non-erycine boids. This is unquestionably demonstrated by *Rottophis atavus* from the late Oligocene of Germany. This snake has erycine-like trunk vertebrae but its caudal vertebrae do not display the complex morphology that characterizes the Erycinae. According to Szyndlar & Böhme (1996), *Rottophis* either belongs to the Boinae or to a boid lineage of its own; but, in a "note added in the proof" they conclude that this genus is closely related to the Tropidophiinae. Szyndlar (1997) confirmed the latter opinion. On the other hand, although the overall vertebral morphology of *Waincophis* is consistent with that of Erycinae, the vertebrae of this genus do not show close resemblance to any ascertained member of the subfamily. Finally, because of the almost constant presence of paracotylar foramina and because of the large size of two of its species, the referral of *Waincophis* to the Erycinae does not appear to be supported.

characters taxa	height of vertebra	length/width ratio of vertebra	neural arch	neural spine	interzygapophyseal constriction	paracotylar foramina	prezygapophyses in anterior aspect	prezygapophyseal facets	paradiapophyses	centrum	posterior median notch in neural arch
Waincophis	**depressed**	**short**	**moderately to strongly depressed**	**low**	**shallow**	**present**	**clearly above floor of neural canal and inclined**	**rather short**	**not projecting beyond ventral border of cotyle**	**short and broad**	**rather deep and acute**
Boa	not depressed	*similar*	vaulted	clearly higher	*similar*	*similar*	*similar*	more elongated	project more ventrally	narrower	more obtuse
Xenoboa	less depressed	*similar*	*similar*	clearly higher	deeper	*similar*	nearly level nearly horizontal	more elongated	project more ventrally	*similar*	*similar*
Corallus	less depressed	clearly longer	vaulted	higher	*similar*	absent (*part*)	level with floor horizontal	*similar*	project more ventrally	longer and narrower	shallower
Epicrates	not depressed	*similar*	less depressed	clearly higher	deep	absent	*similar*	*similar*	project more ventrally	narrower	shallower
Eunectes	*similar*	*similar*	*similar*	clearly higher	*similar*	absent	*similar*	*similar*	project more ventrally	longer and narrower	*similar*
Sanzinia	*similar*	*similar*	*similar*	clearly higher	deeper	accidentally present	horizontal	more elongated	project more ventrally	narrower	shallower
Acrantophis	not depressed	*similar*	less depressed	clearly higher	*similar*	accidentally present	horizontal	*similar*	project more ventrally	narrower	more obtuse
Candoia	not depressed	clearly longer	*similar*	higher	deeper	*similar*	level with floor horizontal	*similar*	project more ventrally	narrower	shallower and more obtuse
Calabaria	*similar*	*similar*	*similar*	higher	*similar*	absent	*similar*	*similar*	project slightly more ventrally	*similar*	shallower and obtuse

Table 1a.— Comparisons between *Waincophis*, living Boinae, and *Calabaria* ("*similar*" means "similar to *Waincophis*").

characters / taxa	height of vertebra	length/width ratio of vertebra	neural arch	neural spine	interzygapophyseal constriction	paracotylar foramina	prezygapophyses in anterior aspect	prezygapophyseal facets	paradiapophyses	centrum	posterior median notch in neural arch
Waincophis	**depressed**	**short**	**moderately to strongly depressed**	**low**	**shallow**	**present**	**clearly above floor of neural canal and inclined**	**rather short**	**not projecting beyond ventral border of cotyle**	**short and broad**	**rather deep and acute**
Chubutophis	not depressed	*similar*	vaulted	clearly higher	*similar*	*similar*	? inclined	*similar*	?	?	?
Bavarioboa	less depressed	*similar*	*similar*	slightly higher	deeper	*similar*	*similar*	*similar*	project more ventrally	*similar*	*similar*
Palaeopython	not depressed	longer (*part*)	vaulted (*part*)	higher	deeper	absent	*similar*	more elongated	project more ventrally	*similar*	*similar*
Pseudoepicrates	*similar*	*similar*	*similar*	clearly higher	deeper	*similar*	*similar*	more elongated	*similar*	*similar*	more obtuse
Cheilophis	*similar*	clearly longer	*similar*	slightly higher	*similar*	absent	almost horizontal	*similar*	project more ventrally	longer and narrower	*similar*
Paleryx	not depressed	longer	?	higher	? deeper	absent	*similar*	*similar*	project more ventrally	longer and narrower	shallow and obtuse
Anilioides	*similar*	? longer	*similar*	?	deeper	?	*similar*	*similar*	*similar*	longer and narrower	more obtuse
Boavus	not depressed	longer	vaulted	clearly higher	*similar*	absent	*similar*	?	project more ventrally	narrower	?
Dawsonophis	?	longer	?	?	*similar*	? absent	*similar*	?	? project more ventrally	narrower	more obtuse
Sanjuanophis	not depressed	longer	vaulted	high	*similar*	?	*similar*	?	?	?	?
Tallahataophis	less depressed	longer	vaulted	? higher	*similar*	? absent	*similar*	*similar*	?	?	*similar*

Table 1b.— Comparisons between *Waincophis*, extinct Boinae, extinct presumed Boinae, and North American Boidae *incertae sedis* ("*similar*" means "similar to *Waincophis*").

characters / taxa	height of vertebra	length/width ratio of vertebra	neural arch	neural spine	interzygapophyseal constriction	paracotylar foramina	prezygapophyses in anterior aspect	prezygapophyseal facets	paradiapophyses	centrum	posterior median notch in neural arch
Waincophis	**depressed**	**short**	**moderately to strongly depressed**	**low**	**shallow**	**present**	**clearly above floor of neural canal and inclined**	**rather short**	**not projecting beyond ventral border of cotyle**	**short and broad**	**rather deep and acute**
Cadurcoboa	*similar*	*similar*	*similar*	clearly higher	deeper	absent	*similar*	*similar*	project more ventrally	longer and narrower	more obtuse
Hordleophis	not depressed	longer	less depressed	clearly higher	*similar*	absent	*similar*	*similar*	project more ventrally	longer and narrower	shallow and more obtuse
Plesiotortrix	not depressed	longer	vaulted	?	*similar*	absent	*similar*	?	*similar*	narrower	more obtuse
Rottophis	not depressed	longer	*similar*	*similar*	*similar*	absent	*similar*	more elongated	project more ventrally	narrower	shallow and obtuse
Totlandophis	less depressed	longer	*similar*	*similar*	*similar*	absent	*similar*	*similar*	project more ventrally ?	longer and narrower	*similar*
Paraepicrates	*similar*	*similar*	*similar*	*similar*	deeper	absent	*similar*	more elongated	*similar*	*similar*	shallow and obtuse
Hechtophis	*similar*	*similar*	*similar*	*similar*	deeper	*similar*	*similar*	*similar*	project more ventrally	*similar*	more obtuse
Gaimanophis	*similar*	longer	*similar*	?	*similar*	absent	*similar*	*similar*	*similar*	*similar*	more obtuse
Helagras	?	longer	*similar*	? higher	?	?	*similar*	?	? project more ventrally	longer and narrower	shallow and obtuse
Huberophis	less depressed	longer	*similar*	*similar*	*similar*	absent	*similar*	? more elongated	?	longer and narrower	*similar*
Geringophis	less depressed	longer	*similar*	higher	*similar*	absent	*similar*	? more elongated	*similar*	narrower	*similar*
Lithophis	?	?	?	?	?	absent	level with floor horizontal	*similar*	?	narrower	?
Tregophis	less depressed	longer	*similar*	?	deeper	absent	*similar*	*similar*	?	*similar*	?

Table 1c.— Comparisons between *Waincophis*, extinct European Boidae *incertae sedis*, and non-ascertained Erycinae ("*similar*" means "similar to *Waincophis*").

Consequently, *Waincophis* should be compared with the Boinae (extinct and living), *Calabaria*, and various extinct genera the relationships of which are unknown or highly doubtful within the Boidae. The Boinae comprise eight living genera (*Boa*, *Xenoboa*, *Corallus*, *Epicrates*, *Eunectes*, *Sanzinia*, *Acrantophis*, and *Candoia*). In addition, I regard four genera as extinct Boinae: *Chubutophis* (early Eocene; Albino, 1993) in south America, *Pseudoepicrates* (early Miocene; Auffenberg, 1963) in North America, *Bavarioboa* (late Oligocene?-Miocene; Szyndlar, 1998) and *Palaeopython* (Eocene-? Oligocene; Rage, 1984) in Europe. Moreover, the North American *Cheilophis* (early Eocene; Holman, 2000) and the European *Paleryx* (Palaeocene?-Eocene; Rage, 1984), that is perhaps close to *Palaeopython*, might belong to the Boinae. Boid genera of unknown relationships include fossils formerly referred to the Erycinae and several taxa that cannot be referred to one of the boid subfamilies. As noted above, trunk vertebrae alone cannot confirm referral to the Erycinae, but several American genera for which the caudal vertebrae are unknown have been assigned or tentatively referred to this subfamily (Rage, 1984; Albino, 1996b; Holman, 2000). These genera are: *Geringophis* (early Oligocene-middle Miocene), *Helagras* (early Palaeocene-early Oligocene), *Huberophis* (middle Eocene), *Lithophis* (early/middle Eocene), and *Tregophis* (middle/late Miocene) in North America (Holman, 2000), and, apart from *Waincophis*, *Gaimanophis* (early Miocene) in South America (Albino, 1996b). These genera cannot be definitely discarded from the Erycinae, but their assignment to this subfamily appears to be doubtful. It should be noted that, among the American extinct genera that were assigned to the Erycinae, only *Calamagras* (early/middle Eocene-middle Miocene) and *Pterygoboa* (early and middle Miocene) are known by trunk and characteristic caudal vertebrae (Holman, 2000); therefore, these two genera, along with *Ogmophis* (probable synonym of *Calamagras*; Rage, 1984) are confirmed Erycinae. Furthermore, *Paraepicrates* (early/middle Eocene of North America) and *Hechtophis* (the present study) cannot be definitely regarded as Erycinae; therefore, they should be included in the comparisons. The other genera of unknown subfamily reference (i.e., Boidae *incertae sedis*) are as follows: *Anilioides* (late Oligocene-early Miocene; Holman, 2000), *Boavus* (Eocene-early Oligocene; Holman, 2000), *Dawsonophis* (middle Eocene; Holman, 2000), *Sanjuanophis* (early Eocene; Sullivan & Lucas, 1988), and *Tallahataophis* (early Eocene; Holman, 2000) in North America; *Cadurcoboa* (late Eocene; Rage, 1984), *Hordleophis* (late Eocene; Holman, 1996), *Plesiotortrix* (Eocene or Oligocene; Rage, 1984), *Rottophis* (late Oligocene; Szyndlar & Böhme, 1996), and *Totlandophis* (late Eocene; Holman & Harrison, 1998) in Europe.

The main morphological differences between *Waincophis* on one hand, and the Boinae, *Calabaria*, and the above mentioned extinct genera on the other hand are given in tables 1a, b, c. These comparisons show that *Waincophis* is a distinct genus.

Affinities of *Waincophis*

Albino (1987) first assigned *Waincophis* to an indeterminate boid subfamily. Later, Szyndlar & Schleich (1993) referred the genus to the Boinae because of the presence of paracotylar foramina. The opinion of Szyndlar and Schleich escaped the attention of Albino who, subsequently, tentatively assigned *Waincophis* to the Erycinae

(Albino, 1996b). According to Albino, the tentative referral to the Erycinae rested on the small size of the vertebrae, the depressed condition of the neural arch, and the low neural spine. It should be noted that, at that time, *Waincophis* comprised only *W. australis*, that is a small species. The assignment of the rather large *W. pressulus* and *W. cameratus* to the genus renders the size character worthless. As noticed by Albino (1996b), the morphology of the neural arch and neural spine may result from convergence due to similar mode of life (fossorial or secretive). Moreover, she emphasized the fact that the assignment to the Erycinae could not be ascertained because of the absence of characteristic caudal vertebrae in the locality that yielded *W. australis*. Finally, as shown above (see "Comparisons"), *Waincophis* does not appear to be referrable to the Erycinae.

On the other hand, *Waincophis* cannot be referred to the Pythoninae (see above "Comparisons"). Moreover, although not strongly different from *Calabaria*, several features of *Waincophis* (tabl. 1a) argue against close relationships between these two snakes.

No character of *Waincophis* prevents referral to the Boinae. The vertebral morphology of boines is not as homogeneous as that of pythonines; the vertebrae of some of them are depressed and have a neural arch that is not clearly vaulted. Moreover, paracotylar foramina occur in various boine species. In other words, the vertebral morphology of *Waincophis* is consistent with that of several boine genera (tabl. 1a, b). Only two features distinguish *Waincophis* from all living boine genera: in the fossil genus the neural spine is lower and the paradiapophyses do not project beyond the ventral border of the cotyle. These two characters cannot exclude the assignment of *Waincophis* to the Boinae. Obviously, since the polarity of vertebral characters cannot be unambiguously demonstrated, only shared combinations of characters may be used in the search for relationships, which leaves some uncertainty. Consequently, I assign *Waincophis* to the Boinae with some reservation.

Indeterminate BOINAE

Two vertebrae cannot be referred to the members of the Boidae described above. They represent two distinct taxa. Both taxa are likely new, at least at species level, but the specimens are not complete enough to be name-bearers. These two snakes probably belong to the Boinae.

"BOINAE A"

Referred material: one mid-trunk vertebra (DGM 1353-R), date of collection and collector(s) unknown.

Description (fig. 14):

The vertebra is massive and large (PRW: 20.9 mm; MLV: 14.2 mm). Its size is similar to that of the largest vertebrae of *Waincophis* (non-measurable vertebrae of *W. cameratus*). A pathological outgrowth developed on the right side of the neural arch. In anterior view, the zygosphene is thick and hardly wider than the cotyle. The cotyle is depressed. The neural canal shows a trifoliate section. The prezygapophyseal facets lie above the floor of the neural canal and they are moderately inclined; the prezygapophyses are short and thick. The very short prezygapophyseal processes hardly project beyond the articular facets. The diapophyseal part of the paradiapophysis is broad; it does not prominently protrude laterally. The paradiapophyses markedly project ventrally beyond the ventral border of the cotyle. Tiny paracotylar foramina open on either side of the cotyle (two on the right side).

In dorsal aspect, the vertebra does not appear to be clearly short. The interzygapophyseal constriction is moderately deep (it cannot be measured). The prezygapophyseal facets are short and oblique. The anterior border of the zygosphene lacks a median lobe. The neural spine is thick. The posterior median notch in the neural arch is deep and rather obtuse. In lateral view, the neural spine is high. It displays a peculiar morphology: its anterior border is beveled; the lower fourth of the anterior border is vertical, the remaining part is inclined posteriorly, parallel to the posterior border. The paradiapophyses are very broad. The ventral border of the haemal keel is straight. In posterior view, the neural arch is moderately vaulted. The vertebra lacks parazygantral foramina. In ventral view, the centrum is somewhat narrow. The straight and well-defined subcentral ridges moderately diverge anteriorly. The haemal keel is deep and narrow. Two large subcentral foramina are present; large foramina are frequent in Scolecophidia, but in Alethinophidia such a size is unusual and it appears to be pathological.

Discussion:

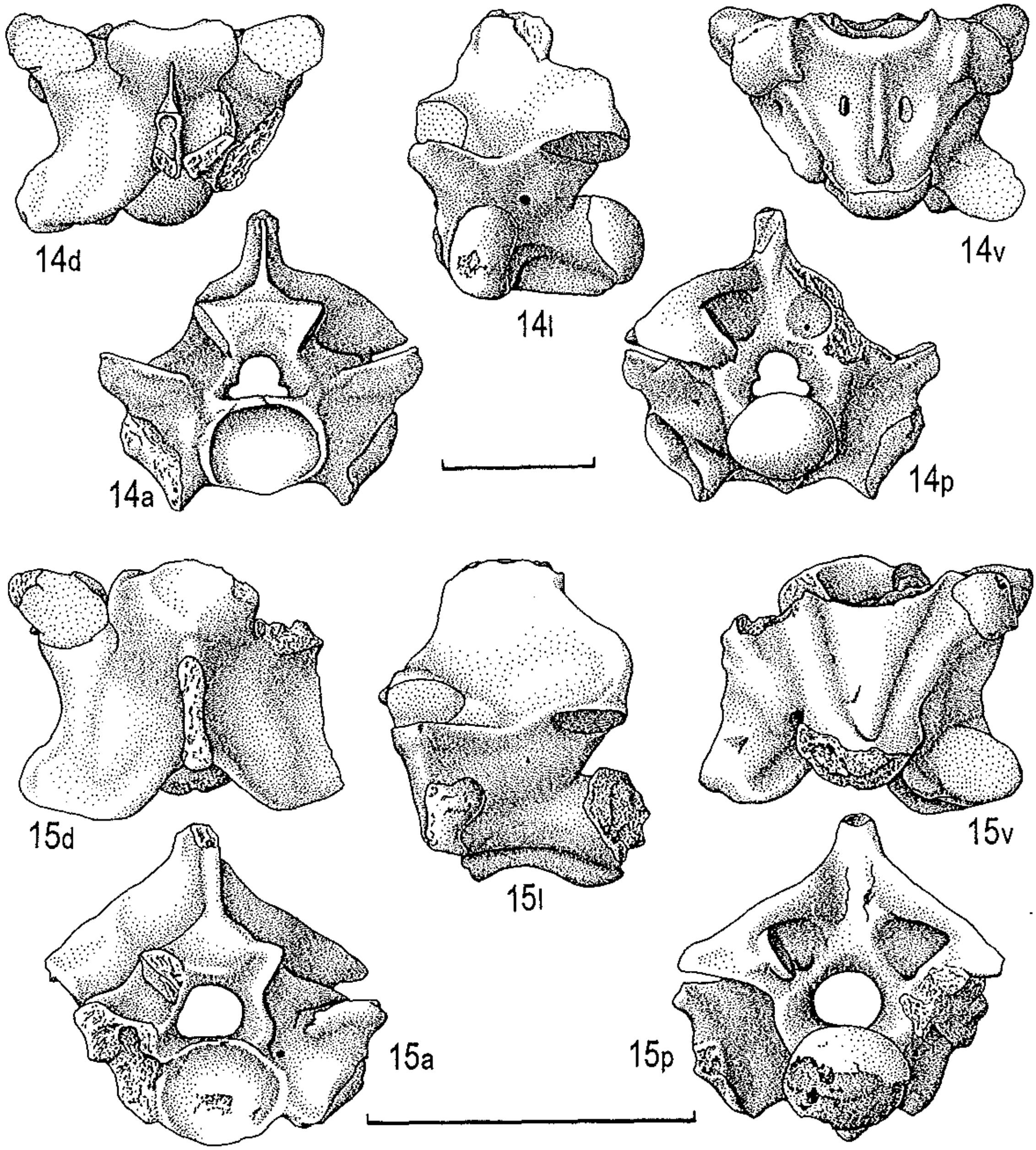
"Boinae A" clearly differs from the other Boidae of Itaboraí. It differs from *Hechtophis* in having longer and less depressed vertebrae, a less depressed neural arch, a higher neural spine, prezygapophyseal facets inclined above horizontal, a shallower interzygapophyseal constriction, and a thicker zygosphene. "Boinae A" differs from *Corallus* mainly by its more dorsal zygapophyseal plane (lying above the level of the floor of the neural canal), non-horizontal prezygapophyseal facets, its much less vaulted neural arch, lower neural spine, comparatively narrower zygosphene, and the absence of a median lobe on the zygosphene. It is distinguished from *Waincophis* by its higher neural spine, narrower centrum with more distinct subcentral ridges, clearly narrower haemal keel, and paradiapophyses projecting more ventrally.

The combination of a narrow and well delimited centrum with a high neural spine and a non-depressed neural arch is vaguely reminiscent of *Sanjuanophis* from the early Eocene of North America (Sullivan & Lucas, 1988). However, the latter genus has more oblique prezygapophyseal facets (in dorsal aspect), a shallower interzygapophyseal constriction, a more highly vaulted neural arch, and the anterior border of its neural spine forms an anterodorsally directed curve.

Finally, the vertebra of "Boinae A" is rather similar to those of the boine *Palaeopython cadurcensis* from the Eocene of Europe. Specifically, the shape of the neural spine is similar in these two snakes. However, in the European species the vertical part of the anterior border is longer (Rage 1988a: fig. 18*l*). Moreover, vertebrae of *P. cadurcensis* lack paracotylar foramina, their zygosphene is wider than the cotyle (as wide as the cotyle at Itaboraí), and their centrum is wider. But the overall morphology of the snake from Itaboraí does not conspicuously differ from that of *P.*

cadurcensis.

It is not possible to infer from a single vertebra that this snake from Itaboraí is related to a European species. However, such relationships between South American taxa and fossils from the Paleogene of Europe have been already disclosed in various Vertebrate groups (Rage, 1988b, 1999).



Figures 14-15.— Indeterminate Boinae. 14: "Boinae A", mid-trunk vertebra (DGM 1353-R). 15: "Boinae B", mid-trunk vertebra (DGM 1354-R). (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 1cm.

The vaulted neural arch and high neural spine precludes "Boinae A" from membership in the Erycinae. The absence of shortening of the vertebra and the vaulted neural arch are inconsistent with a referral to the Calabariinae. On the other hand, because of the presence of paracotylar foramina, "Boinae A" cannot be referred to the Pythoninae. Finally, no character precludes assignment to the Boinae.

"BOINAE B"

Referred material: one mid-trunk vertebra (DGM 1954-R), collected by "Price, Campos and Silva" in 1968.

Description (fig. 15):

The vertebra of "Boinae B" is not depressed, comparatively long and narrow. It is smaller than that of "Boinae A". The maximum length (MLV) is 7.9 mm and the width of interzygapophyseal constriction (WIC) is 7.7 mm.

In anterior view, the zygosphene is approximately as wide as the cotyle and moderately thick; its roof is dorsally concave. The cotyle appears to be slightly depressed. The prezygapophyses and paradiapophyses are damaged. The plane of the prezygapophyseal facets is above the floor of the neural canal and the facets were apparently inclined. Paracotylar foramina are present (one on each side ?). In dorsal view, the vertebra is relatively narrow and not shortened. The interzygapophyseal constriction is shallow. The anterior border of the zygosphene forms a median lobe that was seemingly wide. The neural spine is moderately thick. The posterior median notch in the neural arch is rather deep and obtuse. In lateral view, the neural spine is anteroposteriorly long; it appears comparatively high but its posterior border is short because the posterior part of the neural arch dorsally reaches a high level. The paradiapophyses are not broad. The posterior part of the haemal keel is deflected ventrally. In posterior view, the neural arch is narrow and vaulted; it does not swell out above the zygantrum and its posterodorsal borders are straight. Parazygantral foramina are absent. In ventral view, the centrum is short and narrow; the subcentral ridges are indistinct. A groove occurs on either side of the haemal keel, which shows that this vertebra comes from the posterior part of the trunk region. The ventral face of the haemal keel is rounded.

Discussion:

The vertebra of "Boinae B" differs prominently from those of *Hechtophis*; it is not depressed, it is narrower and longer, its neural arch is vaulted, and its interzygapophyseal constriction is shallower. It differs from *Corallus* in having a more dorsal zygapophyseal plane, the neural arch not bulging above the zygantrum, a lower neural spine, and the zygosphene not wider than the cotyle. The vertebra of "Boinae B" is distinguished from those of *Waincophis* in being non-depressed, longer and narrower, and in having a vaulted neural arch. "Boinae B" differs from "Boinae A" by having the combination of the following characters: longer and comparatively narrower vertebra, lower and anteroposteriorly longer neural spine the anterior border of which does not show an angulation, neural arch more vaulted and not swelling out above the zygantrum.

The vertebra of "Boinae B" is reminiscent of only *Boavus*, a snake from the Eocene-early Oligocene of North America. Specifically, the narrowness of the vaulted neural arch, and the posterodorsal borders of which are straight, point to *B. occidentalis* from the early/middle Eocene (Gilmore, 1938), the type species of the genus. Further similarities are the narrow centrum, poorly defined subcentral ridges, and comparatively small paradiapophyses. The neural spine of "Boinae B" is lower than that of known specimens of *B. occidentalis,* but this probably results from the fact that the vertebra fom Itaboraí comes from a more posterior part of the vertebral column. The presence of paracotylar foramina in "Boinae B" is the only significant difference; however, it does not preclude assignment to the same genus. Here, *Boavus* is not regarded as an ascertained Boinae because this referral cannot be demonstrated; this snake is poorly known and lacks paracotylar foramina. But it should be noted that, if the presence of paracotylar foramina represents a feature that supports referral to the Boinae, the absence of these foramina cannot argue against assignment to the latter subfamily. Similarities between "Boinae B" and *Boavus* are perhaps only of phenetic nature but relationships between these two snakes cannot be definitely discarded, which hints that *Boavus* might be a member of the Boinae.

As in the case of "Boinae A", the referral of "Boinae B" to the Boinae rests on the fact that it cannot be referred to another subfamily of Boidae and that no character prevents its assignment to that subfamily. "Boinae B" cannot be assigned to the Erycinae because of its vaulted neural arch and relatively high neural spine. Besides, the vertebra from Itaboraí markedly differs from those of Calabariinae that are short, depressed, and have a depressed neural arch. The presence of paracotylar foramina prevents referral to the Pythoninae.

Indeterminate BOIDAE

Referred material: two dentaries (DGM 1355-R: one rather complete dentary; DGM 1356-R: anteriormost part of a dentary), (collections: 1355-R by "J.S. Carvalho" in 1949; 1356-R by unknown collector(s) in 1953).

These two dentaries (fig. 16) are smaller and less robust in build than those referred to as cf. *Waincophis* on the basis of size (see above). The most complete specimen (DGM 1355-R) lacks the posterior parts of the dentigerous process and posteroventral process. The dentary curves slightly medially. Fourteen teeth or tooth-sockets are present. In lateral view, the dorsal border is nearly straight while the ventral edge is convex ventrally. Anteriorly, the bone does not strongly taper in lateral aspect. The mental foramen is located beneath the 5th tooth position. The notch that housed the anterior process of the compound bone is narrow. As in the dentaries referred to as cf. *Waincophis*, the compound bone reached the 9th tooth anteriorly. In medial view, the Meckelian groove is comparatively broad and it narrows anteriorly; it mainly opens medially. Dorsally, the groove is well defined through its whole length. Anteriorly, the Meckelian groove is distinctly limited by a low, but well-defined crest that slightly protrudes anteroventrally. The tip of the groove is unusually close to the anterior extremity of the bone.

DGM 1355-R and 1356-R show the derived condition that characterizes the Boinae and Erycinae, i.e. the tip of the Meckelian groove is anteriorly limited. Unfortunately, no feature of the dentary permits one to distinguish boines from erycines. The size of these two dentaries is consistent with all taxa of the locality, except *Waincophis* and "Boinae A" that are clearly larger. On the other hand, assuming that the dentary of *Corallus priscus* was approximately similar to those of the living species of the genus, DGM 1355-R and 1356-R cannot be referred to this species (the fossils are less deep and the anterior tip of their Meckelian groove is located markedly more anteriorly than in *Corallus*). Consequently, the two dentaries might belong to either *Hechtophis* (a possible Erycinae), or to "Boinae B", or even to another taxon not represented by vertebrae in the locality. Therefore, DGM 1355-R and 1356-R are only referred to as indeterminate Boidae, it being understood that they cannot represent pythonine boids.

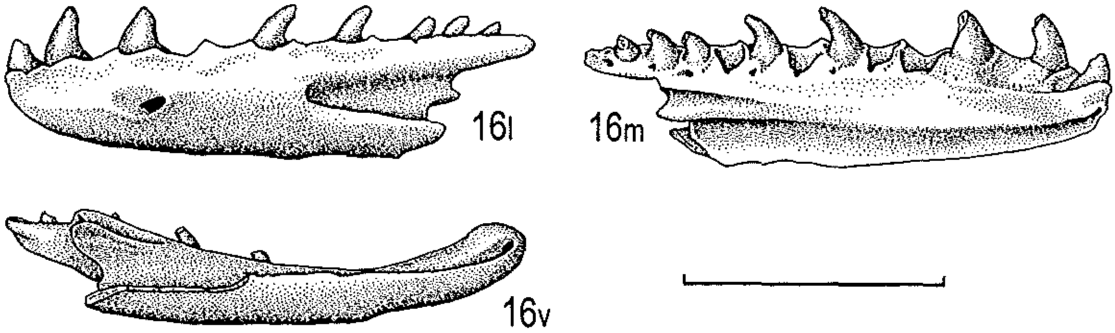


Figure 16.— Indeterminate Boidae. Left dentary (DGM 1355-R). (l: lateral view, m: medial view, v: ventral view). Scale bar = 1cm.

CONCLUSIONS

The middle Palaeocene of Itaboraí has yielded a rich and taxonomically diverse fauna of boid snakes. It comprises six or seven species: *Hechtophis austrinus* gen. et sp. nov., *Corallus priscus* sp. nov., *Waincophis pressulus* sp. nov., *W. cameratus* sp. nov., "Boinae A", "Boinae B", and an indeterminate boid. The latter snake, known only by dentaries, may either belong to *Hechtophis austrinus,* or "Boinae B", or represent a distinct taxon.

Hechtophis is referred to the Erycinae on the basis of the close resemblance of its trunk vertebrae to those of the living erycine *Lichanura*. However, since no caudal vertebrae are available, this referral cannot be definitely confirmed. All other taxa are referred to the Boinae; this assignment rests mainly on the presence of paracotylar foramina. Dentaries, at least those that appear to be referrable to *Waincophis*, lend additional support to the referral to Boinae.

The subfamily Boinae was therefore a separate phylogenetic entity as early as the middle Palaeocene (ca. 58.5-56.5 million years) and it was already present and diverse in South America at that time. The extant South American genus *Corallus* was already present, which corroborates the possible presence of the living genus *Boa* in the early Eocene of Patagonia (Albino, 1993). It may be inferred that extant boine lineages originated early in the Tertiary or, more probably, in the late Cretaceous. Futhermore, the fauna of boids from Itaboraí provides interesting information on paracotylar foramina and it revives the problem of Erycinae (? presence of extinct Erycinae in South America; see below).

Remarks on paracotylar foramina:

In living snakes, paracotylar foramina occur in Colubroidea (i.e., the presumed most derived snakes), Acrochordoidea and Bolyeriidae. They are occasionally present in the Boidae and Tropidophiidae. Anilioidea and Scolecophidia lack such foramina. In other words, paracotylar foramina are known only in "non-primitive" Alethinophidia, whereas they are absent in "primitive" Alethinophidia (Anilioidea) and in Scolecophidia (the sister group of Alethinophidia). From this systematic distribution, it has been generally inferred that the presence of paracotylar foramina represents the derived condition (e.g., Kluge, 1991; Szyndlar & Schleich, 1993; Szyndlar & Böhme, 1996). Therefore, it is astonishing to find paracotylar foramina in most of the oldest snakes: *Lapparentophis*, *Simoliophis* (both from the Cenomanian and/or perhaps the late Albian), *Podophis* (a bipedal snake from the Cenomanian; Rage & Escuillié, 2000), and *Dinilysia* from the ? Coniacian-Santonian (Rage & Albino, 1989). Furthermore, paracotylar foramina are also known in the Madtsoiidae (Cenomanian-Pleistocene) that probably represent a basal lineage of snakes (Scanlon & Lee, 2000). The presence of paracotylar foramina in these snakes raises doubts about the polarity of this character. Surprisingly, all representatives of the Boidae from Itaboraí have paracotylar foramina.

Moreover, these foramina are often double, which is unusual in boids. The presence of paracotylar foramina in all these boids, that rank among the oldest representatives of the family, does not clarify the question of the polarity of this feature.

Paracotylar foramina					
Number of foramina (one side/other side)	0/0	1/0	1/1	2/1	2/2
Hechtophis austrinus	0 vertebra	1 vertebra	23 vertebrae	8 vertebrae	8 vertebrae
Corallus priscus	9 vertebrae	4 vertebrae	10 vertebrae	0 vertebra	0 vertebra
Waincophis pressulus	1 vertebra	1 vertebra	10 vertebrae	2 vertebrae	1 vertebra
Waincophis cameratus	1 vertebra	6 vertebrae	18 vertebrae	7 vertebrae	3 vertebrae
Zygantral foramina					
Number of foramina (one side/other side)	0/0	1/0	1/1	2/1	2/2
Hechtophis austrinus	0 vertebra	0 vertebra	2 vertebrae	6 vertebrae	29 vertebrae
Corallus priscus	0 vertebra	0 vertebra	3 vertebrae	10 vertebrae	22 vertebrae
Waincophis pressulus	0 vertebra	0 vertebra	16 vertebrae	2 vertebrae	2 vertebrae
Waincophis cameratus	0 vertebra	0 vertebra	19 vertebrae	10 vertebrae	3 vertebrae

Table 2.— Variations in the number of paracotylar and zygantral foramina.

It does not seem possible to state whether the presence of paracotylar foramina is apomorphic or plesiomorphic in the Boidae and/or snakes as a whole.

Extinct erycine boids in South America ?

Living erycine snakes inhabit the Old World and North America. *Eryx* (*Gongylophis* included) is present in Asia, Europe, and Africa, whereas *Lichanura* and *Charina* occur in western North America. *Calabaria*, that is a member of the erycine clade according to Kluge (1993), is an African snake.

Thus far, the earliest possible erycines are fossils from the late Cretaceous (without more precision) of Patagonia reported by Albino (1996a) and one vertebra from the Maastrichtian Hell Creek Formation of North America (Estes *et al.*, 1969; Rage, 1987). Unfortunately, caudal vertebrae of these fossils are unknown. The earliest confirmed Erycinae is *Calamagras gallicus* (for which a caudal vertebra is known; Rage, 1977) from the European early Eocene.

Today, South America lacks erycine snakes, but Albino tentatively referred some fossils from South America to the Erycinae: undescribed remains from the late Cretaceous (Albino, 1996a), *Waincophis australis* from the Eocene-Miocene (Albino, 1987, 1996b), *Gaimanophis tenuis, Waincophis* sp., and perhaps an indeterminate form from the Miocene (Albino, 1996b). Unfortunately, these fossils are represented only by trunk vertebrae, which cannot secure allocation to the Erycinae as shown by Szyndlar & Böhme (1996). Albino (1996b), herself, emphasized this uncertainty. It should be noted that, assuming that the referral of *W. pressulus* and *W. cameratus* to *Waincophis* is accurate, then this genus (including *W. australis*) cannot pertain to the Erycinae (see above). On the other hand, *Hechtophis* represents an additional possible erycine from South America (see above). Therefore, in South America the subfamily Erycinae might be represented by the above-mentioned undescribed fossils from the late Cretaceous (Albino, 1996a), *Hechtophis austrinus* from the middle Palaeocene (the present work), *Gaimanophis tenuis* and perhaps the indeterminate form from the early Miocene (Albino, 1996b). But, since these fossils are represented only by trunk vertebrae, assignment to the Erycinae remains doubtful. Even *Hechtophis*, the trunk vertebrae of which so closely resemble those of the living *Lichanura*, cannot be referred to the Erycinae without reservation. Obviously, an absence (i.e., absence of caudal vertebrae) in the locality is not a definite proof. Consequently, from the evidence at hand, the possibility that Erycinae could have been present in South America cannot be definitely substantiated, nor may it be ruled out.

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BIBLIOGRAPHY

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

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

ALBINO, A.M., 1992.— Primer registro de un Boidae (Reptilia: Serpentes) en el Plioceno de la Provincia de Buenos Aires, Argentina. *Pesquisas*, **19**: 106-109.

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

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

AUFFENBERG, W., 1963.— The fossil snakes of Florida. *Tulane Stud. Zool.*, **10**: 131-216.

CUNDALL, D., WALLACH, V. & ROSSMAN, D.A., 1993.— The systematic relationships of the snake genus *Anomochilus*. *Zool. J. Linn. Soc.*, **109**: 275-299.

ESTES, R. & BÁEZ, A.M., 1985.— Herpetofauna of North and South America during the late Cretaceous and Cenozoic: evidence for interchange? *In*: STEHLI, F.G. & WEBB, S.D. (eds), The great American biotic interchange. Plenum Press, New York, pp. 139-197.

ESTES, R., BERBERIAN, P. & MESZOELY, C.A.M., 1969.— Lower vertebrates from the late Cretaceous Hell Creek Formation, McCone County, Montana. *Breviora*, **337**: 1-33.

GILMORE, C.W., 1938.— Fossil snakes of North America. *Geol. Soc. Amer.*, spec. pap., **9**:1-96.

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., 1968.— Ñuapua, un gisement de vertébrés pléistocènes dans le Chaco Bolivien. *Bull. Mus. nat. Hist. nat.*, **40**: 823-836.

HOFFSTETTER, R. & RAGE, J.C., 1972.— Les Erycinae fossiles de France (Serpentes, Boidae). Compréhension et histoire de la sous-famille. *Ann. paléontol. (Vertébrés)*, **58**: 81-124.

HOFFSTETTER, R. & RAGE, J.C.,1977.— Le gisement de vertébrés miocènes de La Venta (Colombie) et sa faune de serpents. *Ann. Paléontol.*, **63**: 161-190.

HOLMAN, J.A., 1996.— A new genus of diminutive boid snake from the Upper Eocene of Hordle Cliff, Hampshire, England. *Tertiary Res.*, **17**: 11-13.

HOLMAN, J.A., 2000.— Fossil snakes of North America. Origin, evolution, distribution, paleoecology. Indiana University Press, Bloomington and Indianapolis, xi +357 p.

HOLMAN, J.A., & HARRISON, D.L., 1998.— A new genus of small boid snake from the Upper Eocene of Hordle Cliff, Hampshire, England. *Acta zool. cracov.*, **41**: 29-33.

KLUGE, A.G., 1988.— Relationships of the Cenozoic boine snakes *Paraepicrates* and *Pseudoepicrates*. *J. Vertebr. Paleontol.*, **8**: 229-230.

KLUGE, A.G., 1991.— Boine snake phylogeny and research cycles. *Miscell. Publ. Mus. Zool., Univ. Michigan*, 178: 1-58.

KLUGE, A.G., 1993.— *Calabaria* and the phylogeny of erycine snakes. *Zool. J. Linn. Soc.*, **107**: 293-351.

LEGENDRE, S., MARANDAT, B., SIGÉ, B., CROCHET, J.-Y., GODINOT, M., HARTENBERGER, J.-L., SUDRE, J., VIANEY-LIAUD, M., MURATET, B. & ASTRUC, J.G., 1992.— La faune de mammifères de Vielase (phosphorites du Quercy, Sud de la France): preuve paléontologique d'une karstification du Quercy dès l'Eocène inférieur. *N. Jb. Geol. Paläont. Mh.*, **7**: 414-428.

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

McDIARMID, R.W., CAMPBELL, J.A. & TOURÉ, T.A., 1999.— Snake species of the World. Vol. 1. Herpetologists' League, Washington D.C., 511 p.

McDOWELL, S.B., 1975.— A catalogue of the snakes of New Guinea and the Solomons...Part. II. Anilioidea and Pythoninae. *J. Herpetol.*, **9**: 1-80.

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

MEYLAN, P.A., 1982.— The squamate reptiles of the Inglis IA Fauna (Irvingtonian: Citrus County, Florida). *Bull. Florida State Mus., Biol. Sci.*, **27**: 1-85.

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

RAGE, J.C., 1977.— An Erycine snake (Boidae) of the genus *Calamagras* from the French Lower Eocene, with comments on the phylogeny of the Erycinae. *Herpetologica*, **33**: 459-463.

RAGE, J.C., 1984.— Serpentes. *In*: WELLNHOFER, P. (ed.), Handbuch der Paläoherpetologie, part 11. Gustav Fischer Verlag, Stuttgart, xii + 80 p.

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, pp. 51-76.

RAGE, J.C., 1988a.— Le gisement du Bretou (phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de Vertébrés de l'Eocène supérieur. I. Amphibiens et Reptiles. *Palaeontographica*, A, **205**: 3-27.

RAGE, J.C., 1988b.— Gondwana, Tethys and terrestrial Vertebrates during the Mesozoic and Cainozoic. *In*: AUDLEY-CHARLES, M.G. & HALLAM, A. (eds), Gondwana and Tethys. *Geol. Soc. special paper* n° 37: 235-273.

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. Técnica YPFB*, **12**: 503-508.

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., 1999.— Faunes à affinités sud-américaines dans le Paléogène d'Europe: état de la question. Allons-nous vers une nouvelle interprétation? *Bull. Soc. géol. Fr.*, **170**: 951-954.

RAGE, J.C. & ALBINO, A.M., 1989.— *Dinilysia patagonica* (Reptilia, Serpentes): matériel vertébral additionnel du Crétacé supérieur d'Argentine. Etude complémentaire des vertèbres, variations intraspécifiques et intracolumnaires. *N. Jb. Geol. Paläont. Mh.*, **7**: 433-447.

RAGE, J.C. & ESCUILLIÉ, F., 2000.— Un nouveau serpent bipède du Cénomanien (Crétacé). Implications phylétiques. *C.R. Acad. Sci. Paris*, IIa, **330**: 513-520.

SCANLON, J.D., 1994.— The phylogenetic position of the Madtsoiidae (Serpentes). 2nd World Congr. Herpetology, Adelaide, Abstract vol.: 230-231.

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

SIGÉ, B., AGUILAR, J.P., MARANDAT, B. & ASTRUC, J.G., 1991.— Extension au Miocène inférieur des remplissages phosphatés du Quercy. La faune de vertébrés de Crémat (Lot, France). *Geobios*, **24**: 497-502.

STEFANO, G. de, 1905.— Appunti sui Batraci e sui Rettili del Quercy appartenenti alla collezione Rossignol. III. Coccodrilli - Serpenti - Tartarughe. *Boll. Soc. Geol. Ital.*, **24**: 17-63.

SULLIVAN, R.M. & LUCAS, S.G., 1988.— Fossil Squamata from the San José Formation, early Eocene, San Juan Basin, New Mexico. *J. Paleont.*, **62**: 631-639.

SZYNDLAR, Z., 1984.— Fossil snakes from Poland. *Acta Zool. Cracov.*, **28**: 1-156.

SZYNDLAR, Z., 1997.— A review of the fossil snakes (Reptilia, Serpentes) described by Hermann von Meyer. *N. Jb. Geol. Paläont. Abh.*, **203**: 211-219.

SZYNDLAR, Z., 1998.— Vertebrates from the early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria). *Ann. Naturhist. Mus. Wien*, **99 A**: 31-38.

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. & SCHLEICH, H.H., 1993.— Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern Germany. *Stuttgarter Beitr. Naturk.*, B, **192**: 1-47.

SZYNDLAR, Z. & SCHLEICH, H.H., 1994.— Two species of the genus *Eryx* (Serpentes; Boidae; Erycinae) from the Spanish Neogene with comments on the past distribution of the genus in Europe. *Amphibia-Reptilia*, **15**: 233-248.

TCHERNOV, E., RIEPPEL, O., ZAHER, H., POLCYN, M.J. & JACOBS, L.J., 2000.— A fossil snake with limbs. *Science*, **287**: 2010-2012.

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. Academic Press, London.