FOSSIL SNAKES FROM THE PALAEOCENE OF SÃO JOSÉ DE ITABORAÍ, BRAZIL.
PART I. MADTSOIIDAE, ANILIIDAE

by

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CONTENTS

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ABSTRACT

The middle Palaeocene of São José de Itaboraí (State of Rio de Janeiro, Brazil) has yielded a very rich and diverse snake fauna which inludes Madtsoiidae, Aniliidae *s.l.*, Boidae, Tropidophiidae *s.l.*, Booidea incertae sedis, and Russellophiidae. The present article (part I) deals with Madtsoiidae and Aniliidae *s.l.* Madtsoiidae are represented by many vertebrae and a few skull bones. They comprise one new species assigned to the genus *Madtsoia* (*M. camposi* sp. nov.). However, the definition of the genus *Madtsoia* is unsatisfactory and the generic allocation might be provisional. A few elements, vertebrae only, belong to the Aniliidae *s.l.* Two taxa are referred to this latter group: *Coniophis* cf. *C. precedens* and *Hoffstetterella brasiliensis* gen. et sp. nov. The forthcoming part II will deal with Boidae.

RESUME

Le Paléocène moyen de São José de Itaboraí (état de Rio de Janeiro, Brésil) a fourni une faune de serpents très riche et diversifiée. Elle comprend des Madtsoiidae, Aniliidae *s.l.*, Boidae, Tropidophiidae *s.l.*, Booidea incertae sedis, et des Russellophiidae. Le présent article représente la première partie de l'ensemble de l'étude des serpents du gisements. Elle se restreint aux Madtsoiidae et aux Aniliidae *s.l.* Les Madtsoiidae sont représentés par de nombreuses vertèbres et quelques os crâniens. La famille comprend une nouvelle espèce qui est attribuée au genre *Madtsoia* (*M. camposi* sp. nov.). Cependant, la définition de ce genre restant imparfaite, cette attribution générique pourrait n'être que provisoire. De rares éléments, uniquement des vertèbres, appartiennent aux Aniliidae *s.l.* Deux taxons représentent ce groupe: *Coniophis* cf. *C. precedens* et *Hoffstetterella brasiliensis* gen. et sp. nov. La seconde partie traitera des Boidae.

INTRODUCTION

South America, appears to have played an important role in the evolutionary history of snakes. Unfortunately, fossil snakes are still rather rare in this continent. However, fissure fillings at São José de Itaboraí, about 25 km east-north-east of Niteroi (state of Rio de Janeiro, Brazil) include many snakes in a rich and diverse vertebrate fauna. This fauna of Palaeocene age represents an important landmark in the history of South American snakes, and also in the history of snakes as a whole.

Numerous vertebrate groups from the locality have already been studied. Marshall *et al.* (1983) and Marshall (1987) gave a list of the mammalian taxa. Alvarenga (1983, 1985) reported on some birds. Price (1955) and Paula Couto (1970) made a partial study of the crocodiles. Paula Couto (1970) and Campos and Broin (1981) briefly reviewed the turtles. Albino (1990) reported a snake (*Coniophis* cf. *C. precedens*) from the locality. Estes (1970) afforded provisional identifications, at the family level, of anurans and lizards from the Palaeocene of Brazil (that is, presumably, from São José de Itaboraí) whereas I gave provisional identifications of snakes (Rage, 1981, 1991, passim). A new genus and species of gymnophionan amphibian and a new species of *Xenopus* (anuran Amphibia) were described by Estes and Wake (1972) and Estes (1975) respectively. Finally, Estes and Báez (1985) provided a list of amphibians and reptiles.

The fauna includes a substantial snake component which is exceptionally interesting because of the great diversity in taxa and the number of specimens. The study of this fauna is based on the collection housed in the Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil. The present study deals with the Madtsoiidae and Aniliidae. Two forthcoming parts will include the Boidae (part II), the Tropidophiidae *s.l.*, Booidea incertae sedis and Russellophiidae (part III).

AGE OF THE FAUNA

The mammal fauna has been generally correlated with the Riochican land mammal age which is defined in Argentina. This land mammal age has been long considered as late Palaeocene in age (Patterson and Pascual, 1972). But it would span the middle and late Palaeocene according to Marshall (1982) and Marshall *et al.* (1983). On the other hand, Paula Couto (1952) coined the name Itaboraian for the Itaboraí fauna, but he did not clearly defined this land mammal age. Subsequently, he regarded the Itaboraian as contemporaneous with the Riochican and he rejected the former name. However, Marshall (1985) resurrected the Itaboraian for the middle Palaeocene, the late Palaeocene corresponding to the Riochican s.s.; Marshall's opinion has been criticized by Soria (1987), Van Valen (1988), Bonaparte (1990) and Bonaparte *et al.* (1993), but Ortiz-Jaureguizar & Pascual (1989) and Marshall and Sempere (1993) held this land mammal age. Anyhow, whatever the name of the mammal age may be, Marshall (1985) regarded the Itaboraí fauna as middle Palaeocene but Sloan (1987) and Van Valen (1988) have favoured a late Palaeocene age.

Apart from these difficulties, which are usual in palaeontology, there may be a more important problem: at Itaboraí, the fauna perhaps includes, to some extent, a mixture of fossils of somewhat different ages which is quite possible in a locality that comprised several fissure infillings. There is no record of which fissures particular specimens came from. Van Valen (1988) has reported an unpublished remark of R. Pascual who suggested that a part of the Itaboraí fossils could be older than the bulk of the fauna. On the other hand, Soria (1987) suggested that some fossils from Itaboraí could be of early Eocene age. Furthermore, Gayet *et al.* (1991) have indicated that a part of the mammals represents the middle Palaeocene but that others could correspond to the late Palaeocene, or even the early Eocene. They have, however, considered this fauna as middle Palaeocene but they have drawn attention to the fact that it may comprise fossils from the late Palaeocene and early Eocene. The revision of this problem by Marshall *et al.* (1997) does not rule out possible mixing of faunas but it shows that the Itaboraí fauna accumulated during a rather short time interval. Itaboraí being near the Atlantic Ocean, Marshall *et al.* have noted that the phreatic level was controlled by the level of the Ocean; they have hypothesized that the deposition of the lacustrine limestones in which the fissures occur and of the overlying limestones took place during marine highstands and that the formation of the karst and the infilling of the fissures occurred during the pronounced drop of the sea-leval between 58.5 and 56.5

Ma which was evidenced by Hacq *et al.* (1987). The opinion of Marshall *et al.* appears logical and judicious; therefore, I admit that the age of the Itaboraí fauna (or faunas) lies between 58.5 and 56.5 Ma, i.e. that it is late Palaeocene if a subdivision in two parts is adopted or middle Palaeocene if the Palaeocene is subdivided into three parts. Here, I adopt the latter subdivision.

It appears from the snake material, that assemblages which come from different collections, i.e. perhaps from different fillings (fossils of different colours, dates of collections, names of collectors) are not always similar. This does not necessarily imply a difference in age but I have kept the names of the collectors and the dates of collections because these differences could indicate different collection sites of different ages within the recognized time span.

KNOWN PALAEOCENE SNAKES OF THE WORLD

The oldest known snakes come from the early Cretaceous of Spain (Rage and Richter, 1994) and from the middle part of the Cretaceous (late Albian and Cenomanian; Cuny *et al.*, 1990; Werner and Rage, 1994) but fossils are not really frequent before the Eocene. Palaeocene localities that have yielded snakes are less numerous than those of late Cretaceous age, but some of them are comparatively rich, only Itaboraí being very rich and diverse.

Apart from Itaboraí, the list of Palaeocene localities of snakes is as follows:

Tiupampa, Bolivia, early Palaeocene, Tiupampan land mammal age (Marshall & Sempere, 1993): numerous vertebrae of Aniliidae and Boidae, some vertebrae of Tropidophiidae *s.l.*, one fragmentary vertebra of a possible madtsoiid (Rage, 1991).

Criadero de Loro, Bolivia, early Palaeocene, Tiupampan land mammal age (Marshall & Sempere, 1993): two vertebrae of a boid (Rage, 1991).

Krebb de Sessao, Niger, (early ?) Palaeocene: rather numerous vertebrae of *Nigerophis mirus* (Nigerophiidae), (Rage, 1975).

Hainin, Belgium, middle Palaeocene (Savage & Russell, 1983): three fragmentary vertebrae and one fragmentary rib. Two of these vertebrae were referred to as cf. *Dunnophis* by Van Dyck (1983); according to the figures, I would regard the three vertebrae as indeterminate alethinophidians.

New Mexico, at least two unnamed localities, USA, middle and late Palaeocene (Puercan and Torrejonian): numerous vertebrae of *Helagras prisciformis* (Boidae), (Gilmore, 1938).

Walbeck, Germany, late middle Palaeocene or early late Palaeocene (Savage & Russell, 1983): undescribed and probably lost snake material (Boidae according to Kuhn, 1940).

Sidi Daoui R.P. 13, Morocco, late (or middle ?) Palaeocene, Thanetian (Cappetta, 1988): one vertebra of an undescribed *Palaeophis* (Palaeophiidae) (unpublished).

Adrar Mgorn, Morocco, late Palaeocene (Gheerbrant *et al.*, 1993): a rather

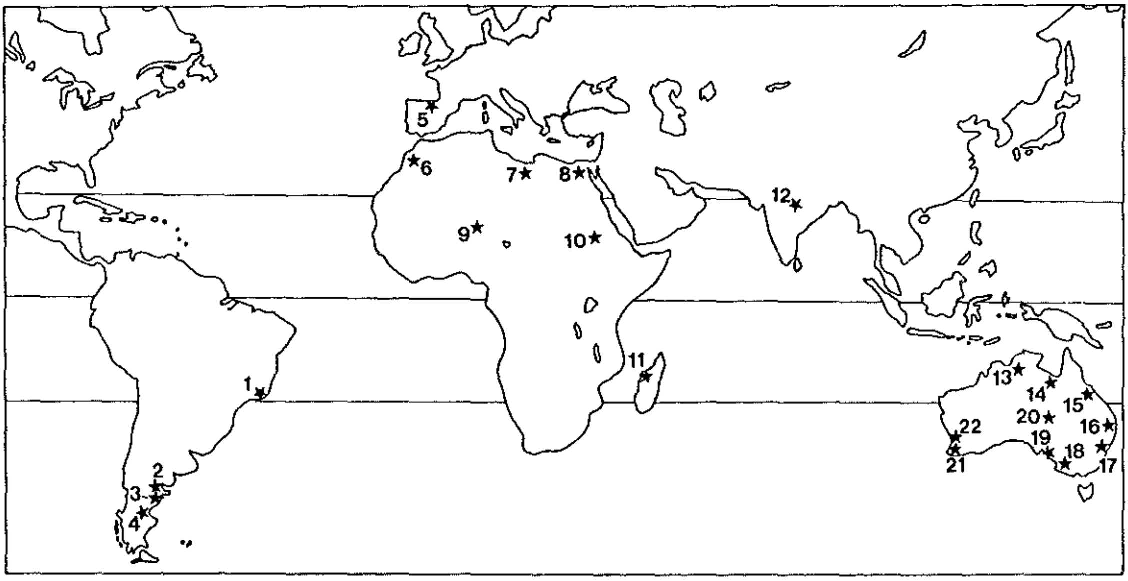

Figure 1.— Geographical distribution of the Madtsoiidae (and possible Madtsoiidae). 1: *Madtsoia camposi* sp. nov.; middle Palaeocene; Itaboraí, Brazil; described in the present article. 2: *Alamitophis argentinus*, *Patagoniophis parvus*, *Rionegrophis madtsoioides*; Campanian or Maastrichtian; Cerro Cuadrado, Argentina; Albino, 1986. 3: *Madtsoia* cf. *M. bai*; late Palaeocene; Pan de Azúcar, Argentina; Hoffstetter, 1959. 4: *Madtsoia* bai; early Eocene; Cañadon Vaca, Argentina; Simpson, 1933. 5: *Madtsoia laurasiae*, *Herensugea caristiorum*; late Campanian or early Maastrichtian; Laño, Spain; Rage, 1996. 6: indeterminate madtsoiid; late Palaeocene; Adrar Mgorn, Morocco; Gheerbrant *et al.*, 1993. 7: *Gigantophis garstini*; late Eocene; Dor et Talha, Libya; Hoffstetter, 1961b. 8: *Gigantophis garstini*; late Eocene; The Fayum, Egypt; Andrews, 1901, 1906. 9: *Madtsoia* aff. *M. madagascariensis*; early Senonian; In Beceten, Niger; Rage, 1981. 10: indeterminate madtsoiid; early late Cretaceous (presumed Cenomanian); Wadi Milk Formation, Sudan; Werner & Rage, 1994. 11: *Madtsoia madagascariensis*; Santonian or Campanian; Berivotra, Madagascar; Hoffstetter, 1961a. 12: possible madtsoiid; Maastrichtian; Takli (= Gitti Khadan), India; Gayet *et al.*, 1985. 13: *Yurlunggur camfieldensis*; middle Miocene; Bullock Creek, Australia; Scanlon, 1992. 14: *Yurlunggur* sp. and *Wonambi* sp.; Oligo-Miocene; Riversleigh, Australia; Scanlon, 1995. 15: *Yurlunggur* sp.; Pleistocene; Wyandotte, Australia; Scanlon, 1995. 16: *Patagoniophis* cf. *P. parvus*, *Alamitophis* cf. *A. argentinus*; early Eocene (or Oligocene ?; Szalay, 1994: 420); Tingamarra, Australia; Scanlon, 1993. 17: *Wonambi naracoortensis*; Pleistocene; Wellington Caves, Australia; Scanlon, 1995. 18: *Wonambi naracoortensis*; Pleistocene; Naracoorte, Australia; Smith, 1976; Barrie, 1990. 19: *Wonambi* cf. *W. naracoortensis* and ? *Yurlunggur* sp.; Pliocene; Curramulka, Australia; Pledge, 1992; Scanlon, 1995. 20: ? *Wonambi* or *Yurlunggur* ; Pliocene; Kanunka, Australia; Scanlon, 1995. 21: *Wonambi naracoortensis*; Pleistocene; Mammoth Cave, Australia; Scanlon, 1995. 22: *Wonambi naracoortensis*; Pleistocene; Koala Cave, Australia; Scanlon, 1995.

diverse, although not rich, fauna comprising an indeterminate scolecophidian, *Coniophis* sp. (Aniliidae *s.l.*), an indeterminate madtsoiid, ? an indeterminate tropidophiid *s.l.* , an indeterminate boid.

Pan de Azúcar, Argentina, late Palaeocene, Riochican *s.l.*: one dentary referred to as *Madtsoia* cf. *M. bai*, Madtsoiidae (Hoffstetter, 1959); see below.

Two other localities could be of Palaeocene age:

Laguna Umayo, Peru, Maastrichtian (Crochet & Sigé, 1993) or early Palaeocene (Marshall & Sempere, 1993): two fragmentary vertebrae of an aniliid snake (Rage, 1981).

Zhylga, Kazakhstan, late Palaeocene or early Eocene: a few vertebrae described as *Vialovophis zhylan* by Nessov and Udovitschenko (1984); this genus is probably a synonym of *Palaeophis* (Palaeophiidae).

Itaboraí yielded the richest, by far, of these Palaeocene snake faunas.

SYSTEMATIC PALAEONTOLOGY

SERPENTES LINNAEUS, 1758

In the most recent classifications, there is an almost general agreement according to which living snakes are distributed in two main groups which are considered as sister groups: Scolecophidia and Alethinophidia (Rieppel, 1988; McDowell, 1987; Rage, 1987; Cundall *et al.*, 1993). Only Dowling and Duellman (1978) are at variance with this classification; they have regarded Scolecophidia as a comparatively minor radiation. Another group, the Cholophidia, comprising fossils more primitive than the Scolecophidia and Alethinophidia could be valid; but its content is highly debatable (McDowell, 1987; Rage & Prasad, 1992). Only alethinophidians occur at Itaboraí.

ALETHINOPHIDIA NOPCSA, 1923

The living Alethinophidia include two main groups: the anilioid assemblage, that is the Anilioidea which are probably paraphyletic (see below), and the Macrostomata (Rieppel, 1988).

The phyletic relationships of various fossil snakes remain questionable and their systematic assignment is not settled. This is the case of the Madtsoiidae which are present in the Itaboraí fauna. Despite the opinion of McDowell (1987) who placed this family in his Cholophidia, the Madtsoiidae are here assigned to the Alethinophidia; but they are perhaps neither Anilioidea nor Macrostomata. They are here considered as Alethinophidia incertae sedis. Apart from the Madtsoiidae, the alethinophidian snakes from Itaboraí belong to the Anilioidea and Macrostomata.

ALETHINOPHIDIA *incertae sedis*

MADTSOIIDAE HOFFSTETTER, 1961

The Madtsoiidae are an extinct family (late Cretaceous-Pleistocene) the members of which are known mainly by vertebrae. Skull bones of only three genera have been found (*Madtsoia*, *Wonambi*, *Yurlunggur*). Consequently, the definition of the family rests on vertebrae. Only one vertebral character may be considered derived without any doubt: the presence, on either side of the zygantrum, of a parazygantral foramen which generally opens in a small fossa (but in *Wonambi* and *Yurlunggur* , this feature seems variable). On the other hand, the vertebrae of madtsoiids display a primitive character: the lack of any salient which could correspond to a prezygapophysial process. Besides, two other features are worth noting: the great width through the diapophyses (which approaches or exceeds the width through the prezygapophyses) and the presence of paracotylar foramina. The phyletic weight of the latter two characters cannot be evaluated.

For a long time, the Madtsoiidae have been placed within the Boidae (Hoffstetter,1961a; Underwood, 1976; Rage, 1984, 1987; Albino, 1986). McDowell (1987) has shown that madtsoiids should be excluded from Boidae. According to Scanlon (1994), the Madtsoiidae could be the sister group of all other alethinophidians exclusive of *Dinilysia* WOODWARD, 1901; despite the fact that this opinion rests on skull bones of Australian madtsoiids only, it may be right.

The family includes ten (or eleven) species allocated to seven (or eight) genera (fig. 1): *Gigantophis garstini* (late Eocene of Egypt and Libya; Andrews, 1906; Hoffstetter, 1961b), *Madtsoia bai* (early Eocene of Argentina; Simpson, 1933), *M. madagascariensis* (Santonian or Campanian of Madagascar; Hoffstetter, 1961a), *M. laurasiae* (late Campanian or early Maastrichtian of Spain; Rage, 1996), and the new species described below, *Herensugea caristiorum* (late Campanian or early Maastrichtian of Spain; Rage, 1996), *Alamitophis argentinus* and *Patagoniophis parvus* (Campanian or Maastrichtian of Argentina; Albino, 1986), *Yurlunggur camfieldensis* (middle Miocene of Australia; Scanlon, 1992), and *Wonambi naracoortensis* (Pleistocene of Australia; Smith, 1976). *Rionegrophis madtsoioides* (Argentina, Campanian or Maastrichtian) is only tentatively referred to the family because of the fragmentary condition of the material (Albino, 1986). Other madtsoiids have been reported but not referred to species or even genera (see fig. 1). *Madtsoia, Gigantophis, Wonambi* and *Yurlunggur* are snakes of large size whereas the other madtsooids are small. *Rionegrophis* is a medium-sized form.

The interrelationships of these genera are still unknown, but it is suspected that the assignment of species to the *Gigantophis-Madtsoia* complex should be reappraised. This was drawn to my attention by M.K. Hecht who has undertaken a study of this problem. Pending publication of his conclusions, I retain the genera *Gigantophis* and *Madtsoia* as previously defined (Hoffstetter, 1961a; Rage, 1984) but it should be kept in mind that the generic allocation of the new species described below may be revised.

MADTSOIA SIMPSON, 1933

Type-species: *Madtsoia bai* SIMPSON, 1933.

The madtsoiid genera, as they are currently recognized, are somewhat poorly defined. The *Madtsoia-Gigantophis* assemblage is distinguished from small ascertained Madtsoiidae (*Alamitophis* , *Patagoniophis* , *Herensugea*) by its large size and shorter vertebrae. It differs from the other large forms, that is the Australian *Wonambi* and *Yurlunggur* , by the almost constant occurrence of one parazygantral foramen located in a small fossa on each side of the zygantrum; the number of foramina is rather variable in the Australian genera. *Madtsoia* is distinguished from *Gigantophis* by its haemal keel which is less distinct from the centrum.

Itaboraí yielded numerous vertebrae, ribs, and few skull bones which belong to a new species of large size.

Madtsoia camposi sp. nov.

Holotype: one mid-trunk vertebra (DGM 1311-R), collected in 1949 by unknown collector(s).

Referred material: 1 palatine (DGM 1313a-R), 1 maxilla (DGM 1313b-R), 1 dentary (DGM 1313c-R), 177 vertebrae, complete or identifiable fragments (DGM 1310a-R/1310i-R, DGM 1314-R, DGM 1315-R, DGM 1316a-R, 1316b-R, DGM 1317a-R, 1317b-R, DGM 1318a-R, DGM 1319-R, DGM 1320a-R, DGM 1320b-R), 36 ribs (DGM 1312a-R, DGM 1312b-R, DGM 1316c-R, DGM 1317c-R, DGM 1317d-R, DGM 1318b-R), (1310a-R/1310i-R, 1315-R, 1320a-R, and 1320b-R: collected in 1949 by unknown collector(s); 1316a-R: collected in 1961 by unknown collector (s); 1312b-R, 1316b-R, and 1316c-R: collected in 1961 by "Julio S. Carvalho and F.W. Sommer"; 1313a-R, 1313b-R, and 1317a-R: collected in 1967 by "col. Luiz A. Gravatá and Sonia Cruz"; 1312a-R, 1317b-R, 1317c-R: collected in 1967 by "Julio S. Carvalho"; 1313c-R, 1318a-R, and 1318b-R: collected in 1968 by "Price and Campos"; 1317d-R: collected in 1967 by "Julio S. Carvalho and students"; 1319-R: date and collectors unknown).

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

Horizon: middle Palaeocene.

Etymology: Dedicated to Diogenes de Almeida Campos, head of the Seção de Paleontologia of the Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.

Diagnosis: *Madtsoia camposi* is a typical large madtsoiid species. It differs from other madtsoiid species, excepting *Herensugea caristiorum* and possibly *Gigantophis garstini*, by its clearly wider zygosphene which is wider than the cotyle (in *G. garstini* the zygosphene width seems variable). The neural spine is lower and comparatively longer than in *M. bai*, *M. madagascariensis*, and in *Wonambi*; it apparently differs from *G. garstini* in the same way, the neural spine of the latter species being poorly known. It is higher than that of *M. laurasiae*, *Yurlunggur* , *Herensugea* , *Patagoniophis* , and apparently *Alamitophis* . As in the other species of *Madtsoia* and in *Patagoniophis parvus*, the haemal keel is shallow and poorly delimited; in other Madtsoiidae, excepting perhaps *Yurlunggur* , it is clearly marked off from the centrum. Beneath the anteromedial corner of the prezygapophysial facet, extends a marked dorsoventral ridge which is lacking in other madtsoiids excepting *Wonambi*. The maxilla bears a strong prefrontal process which rises from the anterior part of the bone. The palatine is provided with a dorsal process; its maxillary process is situated posteriorly. The dentary is short and deep; three mental foramina are present.

Description of the Holotype (fig. 2):

Measurements: Width through the prezygapophyses: 35.2 mm; width of zygosphene: 16.1 mm; transverse diameter of cotyle: 13.7 mm; length of centrum from edge of cotyle to tip of condyle: 17.5 mm.

The holotype is a mid-trunk vertebra which has been selected from rather large

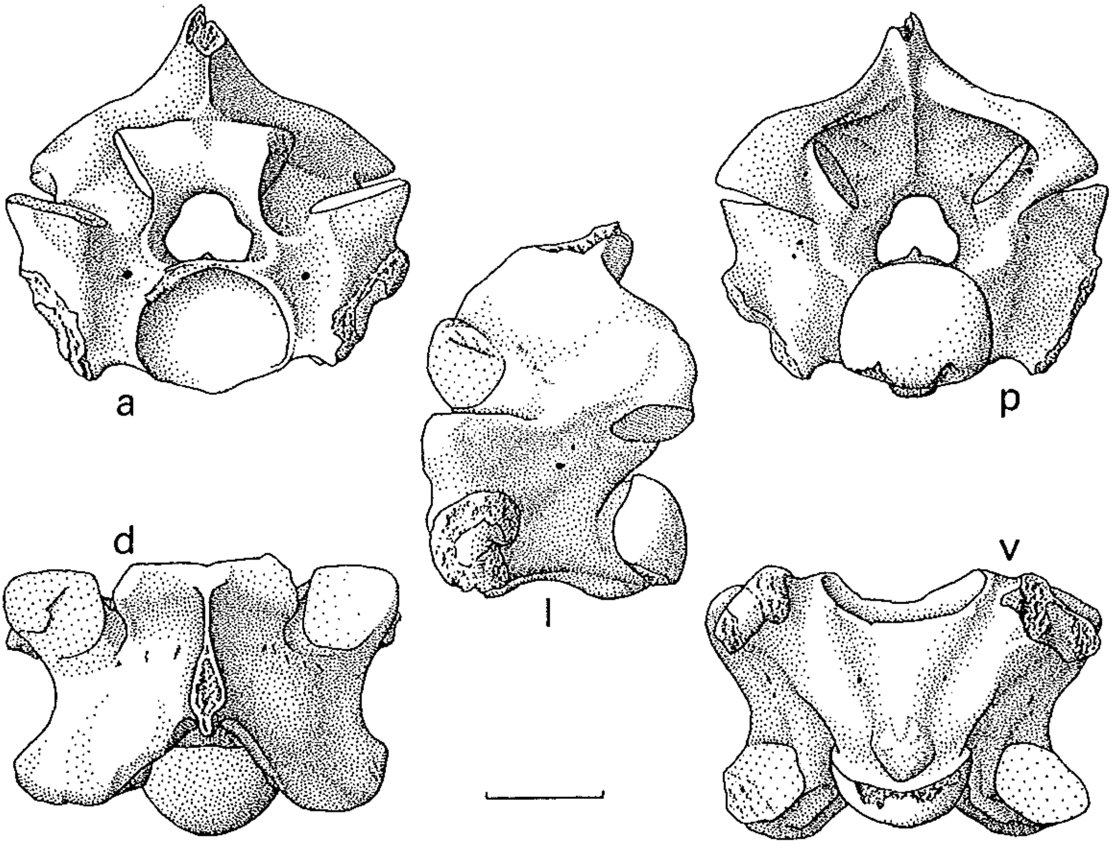

Figure 2.— *Madtsoia camposi* sp. nov., Holotype, mid-trunk vertebra (DGM 1311), (a: anterior view, d: dorsal view, l: left lateral view, p: posterior view, v: ventral view). Scale bar = 1 cm.

vertebrae from the locality. In anterior view, the zygosphene is wider than the cotyle. It is not very thick, which is somewhat surprising in a so large snake. The cotyle appears slightly depressed dorsoventrally. The prezygapophyses do not strongly project laterally; they are clearly inclined upwards (laterally). There is no trace of a salient which could be considered a prezygapophysial process. A marked dorsoventral ridge extends from beneath the anteromedial corner of the prezygapophysial articular facet to the middle part of the anterior limit of the paradiapophysis. The diapophysial part of the paradiapophyses reaches laterally the level of the prezygapophysial tip. On either side of the cotyle, a large paracotylar foramen opens in a high position. The cross section of the neural canal is small and subtrifoliate.

In dorsal view, the vertebra is markedly shorter than wide. The prezygapophysial facets are short and somewhat reduced; the anteromedial part of their outline is clearly angulate. As a result of the weak lateral projection of the zygapophyses, the interzygapophysial constriction is shallow. The anterior border of the zygosphene is subrectilinear and hardly indented by a tiny median notch. The anterior edge of the neural spine originates near the anterior border of the zygosphene. The neural spine does not show two clearly distinct parts, i.e. a lamellar anterior constituent and a thick posterior part. Such a structure occurs in various snakes (including madtsoiids), but in the species from Itaboraí, the neural spine regularly grows thinner anteriorly. Barely posterior to the zygosphene, a line of tiny pits extends on each side from the base of the neural spine toward the prezygapophysis; the pits are more conspicuous on the right side. The posterior median notch in the neural arch is wide and deep.

In posterior view, the neural arch is moderately vaulted. The neural spine is thick. A parazygantral foramen opens on each side of the zygantrum; in this specimen, the fossae which contain these foramina are rather badly defined. The condyle is slightly depressed dorsoventrally.

In lateral view, the neural spine as a whole slopes backward, but the lowermost part of its anterior edge is subvertical whilst the remaining part of this edge markedly slants backward (it is more inclined than the posterior edge). The neural spine is rather high; its top is damaged, but a comparison with other vertebrae shows that the highest point which remains approximately indicates the actual height. The interzygapophysial ridge is short, thick and curved anterodorsally. The condyle is moderately oblique. The paradiapophyses are massive and kidney-shaped; there is no clear distinction between dia- and parapophysial areas. On each side of the vertebra, two lateral foramina are present. The posterior part of the haemal keel bulges ventrally.

In ventral view, the short centrum widens strongly anteriorly. The subcentral ridges are clearly marked but they are not salient. The wide haemal keel is poorly delimited laterally; its ventral part is blunt. Anteriorly, the haemal keel reaches the cotyle; posteriorly, it ends before the condyle. The posterior part of the haemal keel appears as a rather well limited rhombic area which bears a weak radial ornamentation; such ornamentation also appears in some vertebrae of *Madtsoia madagascariensis* (Hoffstetter, 1961a). Two small subcentral foramina are present.

Anterior trunk vertebrae (fig. 3):

The anterior trunk vertebrae differ from mid-trunk ones (exemplified by the holotype) in ways which are usual in snakes. In anterior vertebrae the zygosphene is clearly wider than in the mid-trunk ones and it is arched dorsally. The major axis of its articular facets is oriented more or less anteroposteriorly (in lateral view) whereas it is clearly oblique in mid- and posterior trunk vertebrae. The paradiapophyses are more distant from the centrum and they face more ventrally. The prezygapophyses are more reduced; their articular facets are narrow and their main axis tends to parallel the vertebral axis. The interzygapophysial constriction is very shallow. The neural spine is higher than in mid-trunk vertebrae (fig. 8); its anterior edge originates more posteriorly than in the latter vertebrae. The neural arch is more vaulted. The posterior median notch in the neural arch is not so deep. The ventral face of the centrum is more elongated and narrower. A more or less laterally compressed hypapophysis is present.

Mid-trunk vertebrae (fig. 4):

The characteristics of mid-trunk vertebrae are those of the holotype. Nevertheless, some variations affect the haemal keel. The keel of certain vertebrae lack the rhombic area with a radial ornamentation (fig. 4v). In some other vertebrae, the posterior part of the haemal keel forms two swellings separated by a shallow sagittal depression. Such swellings, considered as ligamentous insertions (Hoffstetter, 1961a), also occur in *M. bai* and *M. madagascariensis*. In *Yurlunggur* and *Wonambi*, the posterior part of the haemal keel is also divided into two lateral prominences, but it is morphologically different (Scanlon, 1992; Smith, 1976).

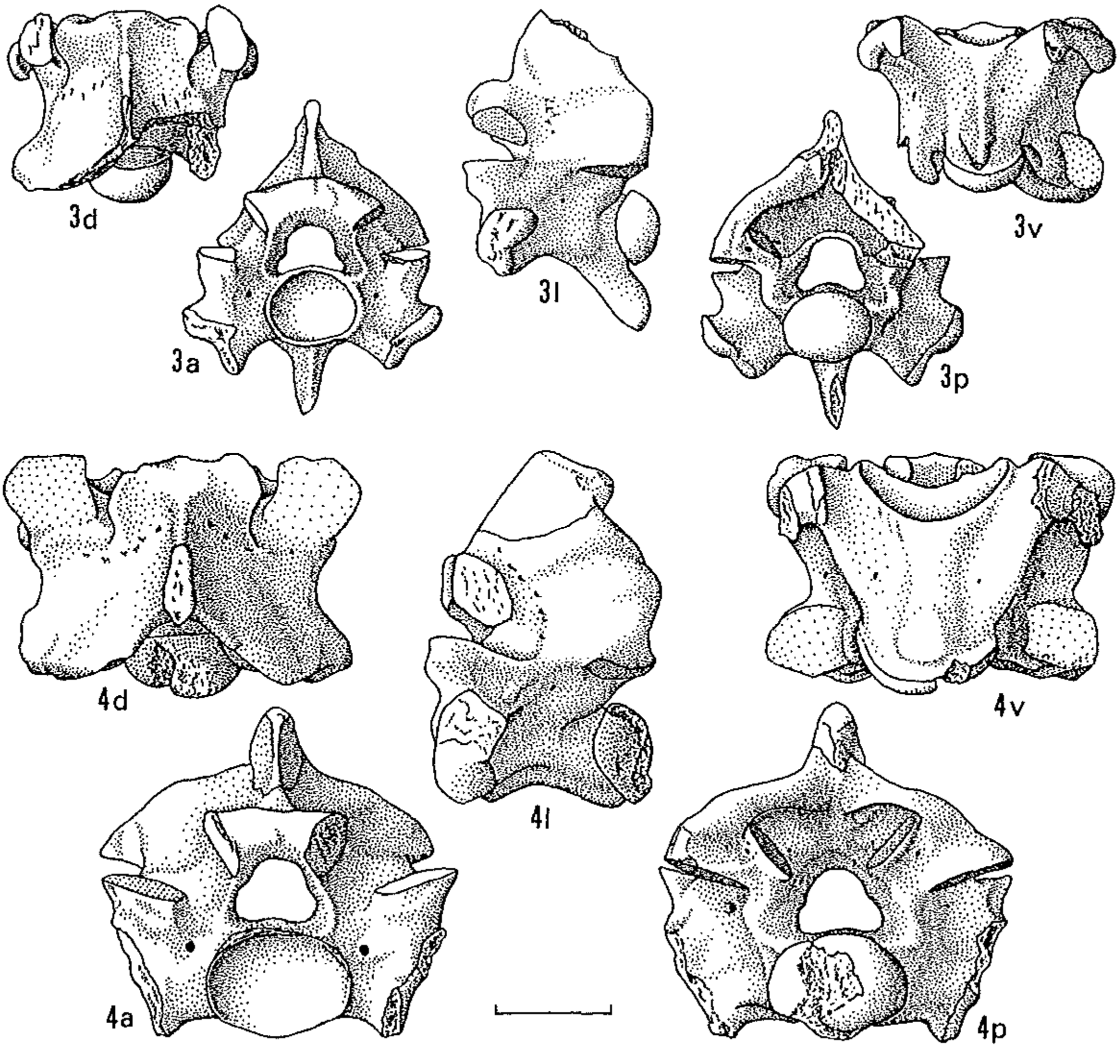

Figure 3-4.— *Madtsoia camposi* sp. nov. 3: anterior trunk vertebra (DGM 1310a). 4: mid-trunk vertebra (DGM 1310b). (a: anterior view, d: dorsal view, l: left lateral view, p: posterior view, v: ventral view). Scale bar = 1 cm.

Posterior trunk vertebrae (fig. 5):

Posterior trunk vertebrae are mainly characterized by the very strong lateral extension of the paradiapophyses; the diapophysial part projects prominently beyond the tip of the prezygapophyses. The neural spine is lower than that of the mid-trunk

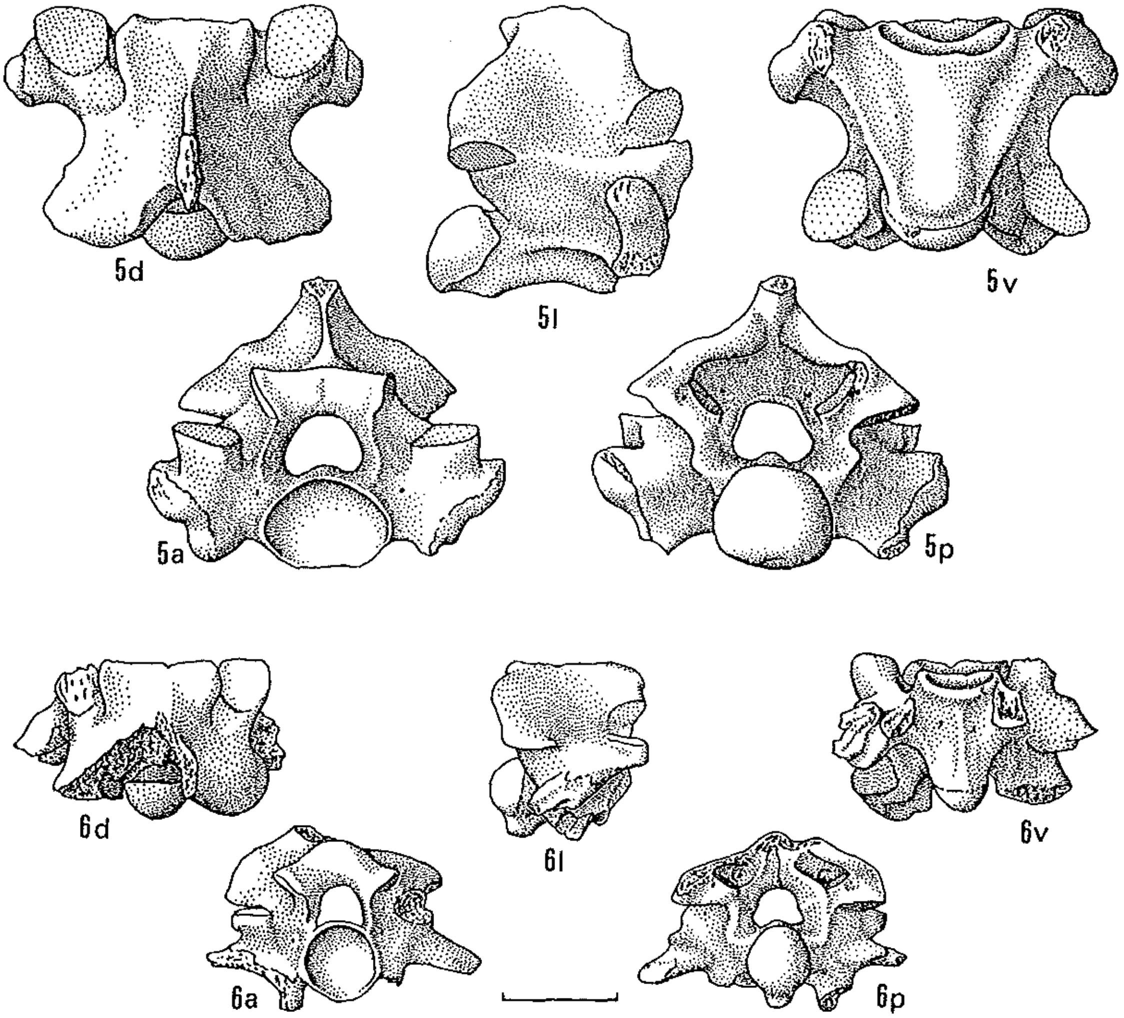

Figure 5-6.— *Madtsoia camposi* sp. nov. 5: posterior trunk vertebra (DGM 1310c). 6: anterior caudal vertebra (DGM 1310d). (a: anterior view, d: dorsal view, l: right lateral view, p: posterior view, v: ventral view). Scale bar = 1 cm.

vertebrae. In snakes, the neural arch is usually more depressed in posterior trunk vertebrae than in mid-trunk ones; but, in *M. camposi*, the posterior trunk vertebrae retain a neural arch approximately as vaulted as in mid-trunk vertebrae, excepting perhaps in the posteriormost ones in which the neural arch seems more depressed. The haemal keel of posteriormost trunk vertebrae is rather clearly delimited laterally owing to the presence of concavities which separate it, on either side, from the subcentral ridges. Such concavities are characteristic of posterior trunk vertebrae of most snakes.

Caudal vertebrae (fig. 6):

On the anterior caudal vertebrae (= posterior cloacal vertebrae) lymphapophyses supersede paradiapophyses and a short cloacal hypapophysis is present. The cotyle is not dorsoventrally depressed but it is circular, or even laterally compressed. Apart from these differences, the overall morphology is rather similar to that of posterior trunk vertebrae. In posterior caudal vertebrae, pleurapophyses take the place of lymphapophyses as is usual in snakes. Haemapophyses are present. These vertebrae are narrower than anterior caudal ones and their neural arch is more vaulted than in the latter. Parazygantral foramina are present in anterior and posterior caudal vertebrae.

Intraspecific variations:

The line of pits which extends on each side of the neural arch just posterior to the zygosphene is present on numerous vertebrae. The dorsal part of the line can be located more posteriorly; this posterior position is frequent in anterior vertebrae (fig. 3a, d) but very rare in other ones. When present, the pits are often more conspicuous than on the holotype; they can take on the shape of short and shallow grooves oriented anteroposteriorly. Apparently, such pits, or grooves, are known only in *Madtsoia camposi*. They quite probably represent the insertion of the m. interarcualis (Gasc, 1967 and pers. comm.). The dorsoventral edge which extends beneath the anteromedial corner of the prezygapophysial facet can be sharp. In some vertebrae, the anterior edge of the neural spine is not subdivided into a subvertical lowermost part and a slanting upper part; it slopes backward as a whole. On the larger vertebrae, the zygosphene is very thick and it approaches the morphology known in *M. bai*, *M. madagascariensis*, *Yurlunggur* , and *Wonambi*; however, it remains wider than in the latter taxa. The anterior border of the zygosphene is almost always subrectilinear. Nevertheless, it may be very weakly crenate (sensu Auffenberg, 1963) and, in anterior vertebrae, a median lobe can rather protrude (fig. 3d); in a few cases, a small median notch indents it. Among the largest vertebrae, rare specimens have a zygosphene with a slightly concave border; but this concavity always remains more shallow than in the other species of *Madtsoia*.

In an anterior vertebra (DGM 1320a-R) and a posterior one (DGM 1320b-R), both collected in 1949 by unknown collector(s), the neural spine is clearly higher than in the other vertebrae (fig. 9). This characteristic is the only significant one which makes these two vertebrae distinct from the others; it is considered as an intraspecific variation. Generally, one parazygantral foramen is present on each side. This is the general condition in madtsoiids, excepting the Australian genera (*Yurlunggur* , *Wonambi*) in which there are frequently two or more foramina on each side. In *M. camposi*, variations are as follows (number of foramina on one side/number of foramina on the other side): 2/2 in one vertebra, 2/1 in six vertebrae, 0/1 in one vertebra, 1/1 in the other vertebrae. In Madtsoiidae, paracotylar foramina are present: generally two on each side in *M. bai*, *M. madagascariensis* and *Gigantophis*, apparently only one on either side in *M. laurasiae*, one on each side in *Herensugea* and *Wonambi*, and several on either side in *Yurlunggur* ; the number appears variable, one or two, in the rare known vertebrae of *Alamitophis* , *Patagoniophis* , and *Rionegrophis*. In *M. camposi* there is only one foramen on either side in most vertebrae (2/2 in one vertebra, 2/1 in five vertebrae, 1/0 in one vertebra, 0/0 in one vertebra, 1/1 in the other vertebrae). Lateral foramina are either single or double.

Some vertebrae of juvenile individuals are available (fig. 7). The juvenile traits are similar to those of practically all snakes: cotyle and condyle markedly depressed dorsoventrally, cross section of neural canal broad, position of zygapophysial plane high, zygosphene thin. On these juvenile vertebrae referred to *M. camposi*, parazygantral and paracotylar foramina are present.

Posterior trunk vertebrae (fig. 5):

In the largest vertebra (a mid-trunk one: DGM 1314), the centrum attains, at least, a length of 19.7 mm (the condyle is worn), and the width through prezygapophyses is, at least, 46.7 mm (the tip of the right prezygapophysis is broken off). This vertebra represents a snake probably 5 to 6 m long. The very large vertebrae are wider and shorter than smaller ones which is typical in snakes.

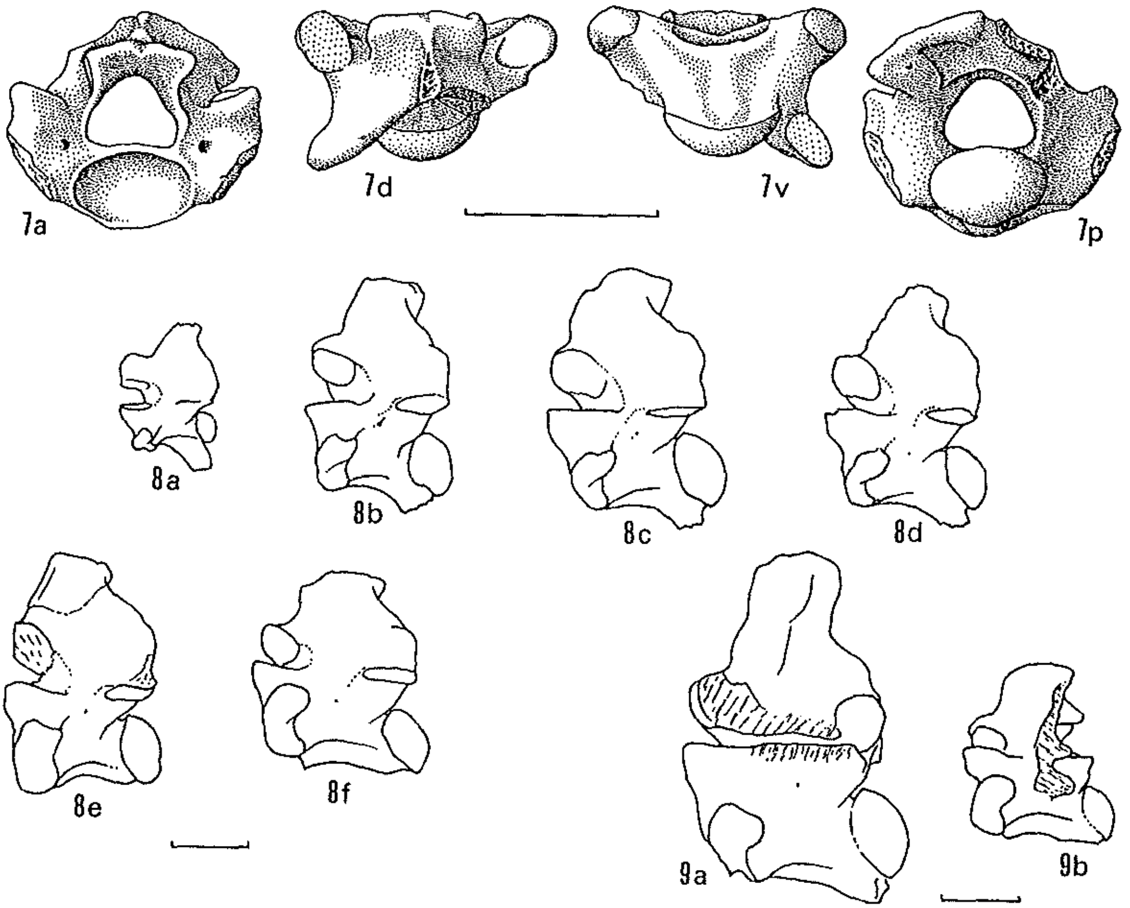

Figure 7-9.— *Madtsoia camposi* sp. nov. 7: trunk vertebra of a juvenile individual (DGM 1310i), (a: anterior view, d: dorsal view, p: posterior view, v: ventral view). 8: variations of trunk vertebrae in lateral view (a-d: anterior trunk vertebrae, e: mid-trunk vertebra, f: posterior trunk vertebra), (a: DGM 1310e, b: DGM 1310g, c: DGM 1310h, d: DGM 1310f, e: DGM 1310b, f: DGM 1310c). 9: Extreme variations in the height of the neural spine (a: anterior trunk vertebra, DGM 1320a; b: posterior trunk vertebra, DGM 1320b). Scale bars = 1cm.

Ribs (figs. 10, 11):

Among the snake ribs from Itaboraí, two morphologies are distinguished. In one set of ribs, the dorsal articular facet is markedly more laterally situated than the ventral facet, and the latter facet clearly projects anteriorly. This set of ribs includes the largest ones, the size of which is consistent with that of *M. camposi*; they are assigned to this species. In the other ribs, the dorsal articular facet is not clearly located laterally with regard to the ventral one, and this latter facet does not project anteriorly. None of these ribs displays a size consistent with the madtsoiids from the locality. Most of them, perhaps all, belong to Boidae.

The articular extremity of the ribs referred to *M. camposi* is about twice as wide dorsoventrally as anteroposteriorly; the surface of the dorsal facet is approximately equal to that of the ventral one. The dorsal facet is markedly concave. It lies clearly more laterally than the ventral one, which is also the condition in *Dinilysia* from the late Cretaceous (Rage & Albino, 1989: fig. 1D). The ventral facet is flat or slightly convex and it protrudes anteriorly. A well developed posterodorsal process (tuber costae) is present. These features occur in all ribs assigned to *M. camposi* whatever their size. Within this species, the large ribs differ from the small ones by only two characters. The tuber costae of large ribs is stout (its length is unknown) whereas it appears thinner, in medial view, in small ribs. Moreover, in the smallest ribs, there is a tiny ridge ventral to the articular head; it vanishes in medium sized and large ribs. This ridge is well developped in *Dinilysia*.

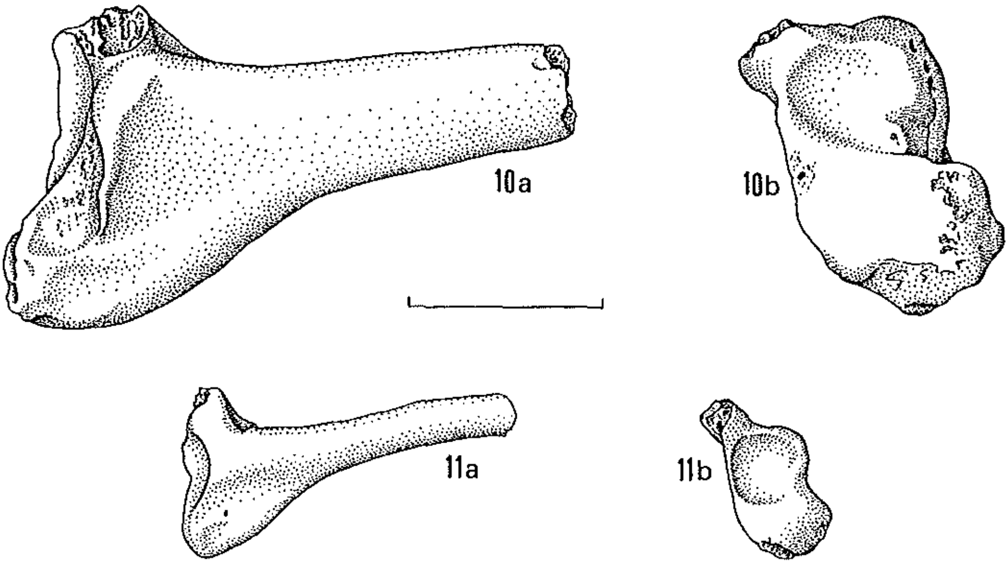

Figure 10-11.— *Madtsoia camposi* sp. nov., ribs. 10: left rib of a large individual (DGM 1312b). 11: left rib of a small individual (DGM 1312a). (a: anterior view, b: medial view). Scale bar = 1 cm.

Apart from *M. camposi*, ribs are known in *M. bai*, *Wonambi*, *Yurlunggur* and in the Australian representatives of *Patagoniophis* and *Alamitophis* . The comparatively lateral position of the dorsal facet is known only in *M. bai* and *M. camposi*. Besides, contrary to *M. camposi*, in *M. bai* the dorsal facet protrudes anteriorly (= anterodorsal process; Scanlon, 1993) as in one of the small madtsoiids from the Australian Eocene (either *Patagoniophis* or *Alamitophis* ; Scanlon, 1993). In *M. camposi*, the ventral facet projects anteriorly, which seems to be unique among Madtsoiidae.

Maxilla (fig. 12):

The anterior part of a left maxilla is attributed to *M. camposi* on the basis of its large size and of a primitive character unknown in the other large snakes (i.e., Boidae) present in the locality. Two tooth sockets and the bases of two teeth remain. The subacrodont implantation of the teeth corroborates the referral to snakes. No striations are present on the tooth bases. This maxilla is characterized by the presence of a strong ascending process (= prefrontal process) the dorsal and posterior parts of which are broken off. It rises on the anterior part of the maxilla. On the medial face, a wide and shallow groove runs along the anterodorsal border of the process but it does not reach the anterior tip of the bone. It probably corresponds to an articular surface for the prefrontal which, thus, apparently extended far anteriorly as in the living *Xenopeltis*. Two large foramina open on the lateral face. Anteriorly, on the medial face, the maxilla does not bear a small process as in *Anilius* and *Xenopeltis*. In these two living snakes, this process comes into contact with the septomaxilla.

Among living snakes, the prefrontal process is known only in primitive forms: Aniliidae *s.l.*, Uropeltidae, and as a reduced dorsal rise, in *Loxocemus*. The maxilla of three fossil snakes bears such a process: *Dinilysia patagonica* (Dinilysiidae; Estes *et al.*, 1970), "*Archaeophis*" *turkmenicus* (Palaeophiidae from the early Eocene; Rage, 1984; Tatarinov, 1988), and *Wonambi naracoortensis* (Madtsoiidae from the Pleistocene; Barrie, 1990). But it should be stressed that the maxillae of other primitive fossil snakes remain unknown. The prefrontal process of the maxilla is well developped in lizards and amphisbaenians. It is therefore considered a primitive feature in snakes.

Palatine (fig. 13):

One left palatine is known; its posteriormost part is lacking. The morphology appears somewhat unusual. An anterior dentigerous process is present. It bears eight teeth or tooth-sockets. The posterior two thirds of the bone extend dorsally as a subtriangular dorsal process which is slightly deflected medially. The posterior half of the dorsal border of this process slopes posteroventrally and it strongly extends laterally; thus, is formed a rather broad plate which slopes posteroventrally too. The latter plate probably contacted the maxilla and represents the maxillary process of other alethinophidians. Anterodorsally to the maxillary process, the dorsal edge of the dorsal process is bordered, on its lateral side, by a short and narrow lamina (laterodorsal lamina). Between the dorsalmost part of the dorsal process and the laterodorsal lamina, a groove runs anteroposteriorly (dorsolateral groove). On the medial face of the dorsal process, a ridge (dorsomedial ridge) runs anteroposteriorly at about the same level as the laterodorsal lamina. A very shallow recess occurs ventrally to the posterior part of the maxillary process and laterally to the dentigerous part; it could correspond to an articular area for the pterygoid, which would indicate that only a very short part of the bone is wanting posteriorly. Such a complex of processes, laminae and ridges is unknown in other snakes.

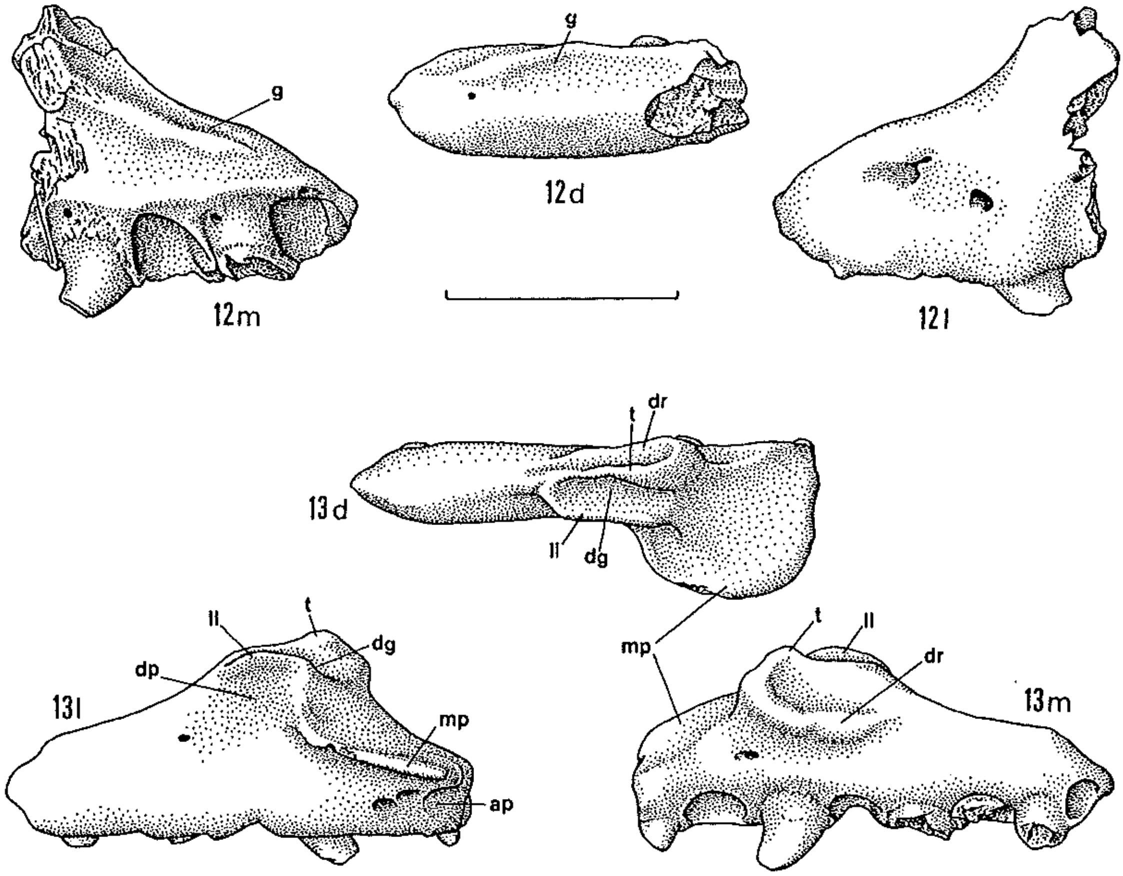

Figure 12-13.— *Madtsoia camposi* sp. nov. 12: left maxilla, DGM 1313b (d: dorsal view, l: lateral view, m: medial view), (g: groove). 13: left palatine, DGM 1313a (d: dorsal view, l: lateral view, m: medial view), (ap: ? articular area for pterygoid, dp: dorsal process, dr: dorsomedial ridge, dg: dorsolateral groove, ll: laterodorsal lamina, mp: maxillary process, t: top of dorsal process). Scale bar = 1 cm.

Assuming that only a short posterior part of this palatine is broken off, the maxillary process occupied a posterior position. Its plate-like morphology is approached in *Dinilysia* (Dinilysiidae, late Cretaceous), *Lichanura* and *Charina* (living Boidae); however, in the latter two genera the anteroposterior dimension of this process remains smaller than the transversal one. Besides, in *Dinilysia* the maxillary process originates on the anteriormost part of the bone (which is also its position in scolecophidians and lizards). In the palatine of *M. camposi*, there is no maxillary foramen for the maxillaris nerve (V2). Such a foramen occurs in *Anomochilus* (Cundall & Rossman, 1993), *Cylindrophis* (Aniliidae *s.l.*), Uropeltidae s.s., *Xenopeltis*, *Loxocemus*, Bolyeriidae, *Dinilysia*, certain Tropidophiidae, pythonine Boidae and Acrochordidae. Excepting in Uropeltidae, this foramen perforates the base of the maxillary process; in the Uropeltidae s.s., the foramen occupies a very dorsal position. When the maxillary foramen is lacking, it is replaced by a notch which indents the anterodorsal border of the junction between the maxillary process and the lateral wall of the palatine. In various snakes (Boinae, Erycinae), this notch becomes so wide that it practically vanishes. This latter condition seems to be that in *Madtsoia* unless the maxillaris nerve passed in the groove bounded by the laterodorsal lamina and the dorsalmost part of the dorsal process. However, this latter possibility may be apparently ruled out; the maxillaris nerve should run markedly anteroventrally in this area whereas the groove tends to be oriented slightly anterodorsally. The palatine of *Madtsoia* lacks a medial process (= choanal process) but it is not impossible that the dorsal border of the dorsal process is broken off; in such a case, it could have been the base of a medial process.

Apart from *M. camposi*, among Madtsoiidae the palatine is known only in *Wonambi* (Barrie, 1990). It differs from that of *Madtsoia* by, at least, the anterior position of the maxillary process. It bears a wide choanal process which is reminiscent of that of Tropidophiidae; concerning this feature, no comparison can be made between the two genera (see above). The condition of the maxillary foramen is unknown in *Wonambi*.

The enclosure of the maxillaris nerve by the palatine is generally considered a primitive feature (McDowell, 1975: 17; Underwood, 1976: 161). But Underwood and Stimson (1990) have reversed the polarity. However, their opinion rests on a partly wrong basis; they have stated that the foramen is never enclosed in lizards. It is indeed not easy to establish whether the opening of the maxillaris foramen as a notch is a primitive or a derived state. Nevertheless, an enclosed foramen being known in *Dinilysia*, *Cylindrophis*, uropeltids, *Xenopeltis* and *Loxocemus*, this condition could be the primitive state in snakes. The rise of the dorsal part (dorsal process) of the palatine is known in primitive alethinophidian snakes: *Dinilysia* (Estes *et al.*, 1970: fig. 3a,b), *Anilius*, *Cylindrophis*, *Loxocemus*. Therefore this feature may be considered plesiomorphic. The anteroposterior extension of the maxillary process, the presence of a laterodorsal lamina which laterally limits a dorsal groove, and the presence of a dorsomedial ridge are peculiar features which could be specialisations of *Madtsoia*.

Dentary (fig. 14):

A large left dentary is referred to *M. camposi*. Its posteriormost part is broken off and its anterior tip is slightly damaged. It is comparatively short and deep and it bears 10 tooth sites. On the lateral face three mental foramina open in a more or less depressed line which slightly slopes down anteriorly; the two anterior foramina are larger than the posterior one. The deep incisure which housed the surangular displays subparallel borders; its anterior extremity is situated beneath the eighth tooth. On the medial face, the wide Meckelian groove runs up to the anterior extremity of the bone; unfortunately, its anterior part being slightly damaged, it is not possible to state whether the groove was closed or not at its tip (but a dentary from Pan de Azúcar demonstrates that in *Madtsoia* the Meckelian groove was closed by the dentary at its tip; see below).

Hoffstetter (1959) referred to *Madtsoia* (as *Madtsoia* cf. *bai*) a dentary which comes from the late Palaeocene of Pan de Azúcar (Argentina; Báez and Gasparini, 1979), a locality named Gaiman by Hoffstetter. At that time, no dentary of madtsoiid snake was reported. Although this bone was isolated, Hoffstetter assigned it to *Madtsoia* on the basis of its boid overall morphology (madtsoiids were then included in the Boidae), its size, and the stratigraphic and geographic source. This generic allocation is corroborated by the Itaboraí dentary which is practically identical. The two dentaries show the same overall morphology. The disposition of the mental foramina is identical and, especially, the two anterior foramina are larger than the third one in both specimens

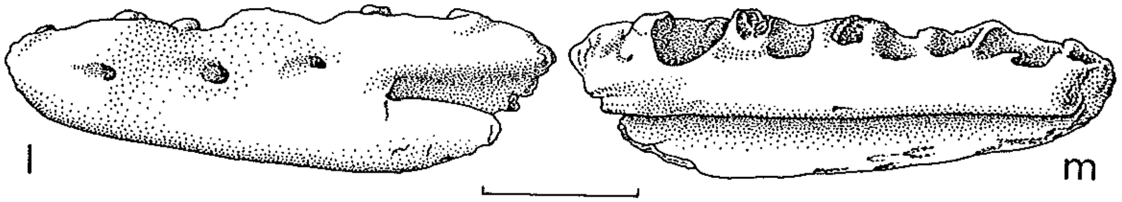

Figure 14.— *Madtsoia camposi* sp. nov., left dentary, DGM 1313c (l: lateral view, m: medial view). Scale bar = 1 cm.

(the only difference is that the posterior foramen is relatively smaller in the Argentinian dentary). Finally, the anterior end of the surangular incisure is located beneath the eighth tooth as in *M. camposi*. It is of interest to note that in the dentary from Argentina, the anterior extremity of which is not damaged, the Meckelian groove is closed anteriorly at tip. When the dentary from Pan de Azúcar was referred to as *Madtsoia* cf. *bai* by Hoffstetter (1959), *M. bai* was the only known species of *Madtsoia*. The dentary of *M. camposi* is so similar to that from Pan de Azúcar that the specific assignment of the latter may be questioned. The only difference is the size, the dentary of *M. camposi* being markedly smaller (distance from the anterior tip of the dentary to the anterior extremity of the surangular incisure: 41 mm in the Argentinian specimen, 25.4 mm in *M. camposi*) but this cannot be considered a character of specific value. The dentary from Pan de Azúcar could belong to a form closer to *M. camposi* than to *M. bai*, or even to *M. camposi*. However, no dentary from the type locality of *M. bai* being known, a thorough discussion of this question would be pointless.

The presence of three mental foramina on the dentary is a primitive character. Snakes have only one foramen or very rarely two; several foramina (more than three) generally occur in lizards and amphisbaenians. The shortening of the dentary appears as a derived feature (Hoffstetter, 1959). Similarly, the anterior closure of the Meckelian groove is probably a derived characteristic (Underwood, 1976).

Discussion:

The overall vertebral morphology of *Madtsoia camposi* is similar to that of the other large Madtsoiidae: *Madtsoia* bai, *M. madagascariensis*, *M. laurasiae*, *Gigantophis garstini*, *Yurlunggur camfieldensis*, and *Wonambi naracoortensis*. The vertebrae display a feature, the presence of parazygantral foramina, which is considered a synapomorphy of Madtsoiidae, although *Yurlunggur* and *Wonambi* show some variations.

The neural spine of *M. camposi* is lower and longer than that of the other large madtsoiids excepting *M. laurasiae* and *Yurlunggur* , and with some doubts concerning *Gigantophis* in which it is poorly known. In *M. laurasiae*, *Herensugea* , *Yurlunggur* , *Patagoniophis* , and apparently in *Alamitophis* , the neural spine is lower than in *M. camposi*. The prezygapophysial articular facets of *M. camposi*, as those of *M. bai* and *Gigantophis*, are rather small; in the other large forms they are elongated obliquely (only *M. laurasiae*) or transversely whereas in small madtsoiids they are either obliquely elongated or unknown. The marked angulation of the anteromedial part of the prezygapophyses occurs only in *M. camposi* and *Wonambi*. In *M. camposi* the zygosphene is clearly wider than in the other madtsoiid species excepting *Gigantophis* (in which the width seems variable) and *Herensugea* . The zygosphene of *M. camposi* is also comparatively thinner than that of other large madtsoiids excepting *M. laurasiae*; in the other species it is very thick as is usual in snakes of large size. As in the other three species of *Madtsoia* and in the small *Patagoniophis parvus*, the haemal keel of *M. camposi* is low and weakly marked off from the centrum; in other madtsoiids, it is more clearly delimited. In the posterior trunk vertebrae of *M. camposi*, *M. bai*, and *Wonambi*, the paradiapophyses are very prominent laterally; the diapophysial part markedly projects beyond the tip of the prezygapophysis. In *M. madagascariensis*, and apparently in *M. laurasiae*, *Herensugea* and *Yurlunggur* the lateral protrusion of the paradiapophyses is less pronounced. *Gigantophis* is represented by only few vertebrae and intracolumnar variation remains badly known; strongly projecting paradiapophyses were perhaps present on posterior or posteriormost trunk vertebrae of this genus but this is not established. Posterior trunk vertebrae of small species (excepting *Herensugea*) are not available and comparisons are not possible with respect to this feature. I do not consider the presence of lines of pits on the neural arch as a specific character, because their absence in the other species could result from coarser preservational conditions.

The dorsal articular facet of the ribs is situated laterally with regard to the ventral one; this condition occurs elsewhere only in *M. bai*. The anterior protrusion of the ventral facet is unique within Madtsoiidae.

Among Madtsoiidae, the dentary, maxilla, and palatine are known only in *Madtsoia* and *Wonambi*. The dentary of *Madtsoia* differs from that of *Wonambi* by the presence of three mental foramina whereas one only is seen in the Australian genus. Besides, the dentary of *Wonambi* appears less shortened than that of *Madtsoia*; it has 15 teeth anterior to the incisure for the surangular (Barrie, 1990) whereas the tip of this incisure is situated beneath the eighth tooth in *Madtsoia*. In both genera, the maxilla is provided with a well developed prefrontal process; this process rises near the anterior extremity in *M. camposi* whereas it is located more posteriorly, at one-third from the anterior tip in *Wonambi* (Barrie 1990). As mentioned above, the maxillary process of the palatine is located posteriorly in *M. camposi*; in *Wonambi*, this process is situated anteriorly.

M. camposi appears as a clearly distinct species, but its generic allocation might be questioned. This uncertainty rests on the fact that *Madtsoia* and *Gigantophis* should be redefined or perhaps synonymized.

M. camposi probably comes from several fissures of Itaboraí which are perhaps not coeval. This indicates that it may have been present over an extended period of time and makes it likely that it was common.

Finally, it should be noted that some pronounced differences distinguish *Madtsoia* from the Australian *Wonambi*, the best known madtsoiid. The presence of a rather large bilateral and well defined parazygantral foramen is not constant in *Wonambi*. Only one mental foramen is present on the dentary of the Australian fossil, as in practically all living snakes. Besides, the palatines of both genera are prominently different; this bone is boid-like in *Madtsoia* whilst the anterior position of the maxillary process in *Wonambi* seems peculiar (primitive because reminiscent of that of lizards and *Dinilysia*?). The rather marked difference between the two forms, which are geographically widely separated, is consistent with a long independant history of the two lineages, that is an ancient separation. Madtsoiidae probably represent a rather wide and primarily Gondwanan radiation, only a few representatives of which are apparently known at present.

ANILIOIDEA FITZINGER, 1826

The Anilioidea represent a primitive assemblage which comprises snakes traditionally included in the Aniliidae and Uropeltidae. To these families, McDowell (1975, 1987) added the Loxocemidae and Xenopeltidae. However, it is generally accepted that Xenopeltidae and Loxocemidae are booid lineages (Underwood 1976; Rieppel, 1979; Rage, 1984, 1987) or more closely related to booids than to anilioids (Kluge, 1991). The Anilioidea, as they are recognized here (i.e. Loxocemidae and Xenopeltidae excluded), consist of three very primitive living snakes (*Anilius*, *Cylindrophis*, *Anomochilus*) plus the specialized uropeltids. I more or less questioned the monophyly of anilioids (Rage, 1984, 1987) but Rieppel (1988) and Kluge (1991) hypothesized that Anilioidea are monophyletic. Nevertheless, Cundall *et al.* (1993) considered they are paraphyletic. At present, my own conviction is that Anilioidea are paraphyletic, but their precise phyletic structure cannot be considered as definitely established. Within Anilioidea, the traditional classification corresponds to a phenetic subdivision into Aniliidae (the three primitive living genera) and Uropeltidae. This classification was challenged by McDowell (1975, 1987) who has recognized a close relationship between *Cylindrophis* (and *Anomochilus*) and uropeltids. As a consequence, he classified both *Cylindrophis* and *Anomochilus* with the uropeltids in the family Uropeltidae, whereas his Aniliidae comprise only *Anilius*. According to Cundall *et al.* (1993), the Uropeltidae of McDowell would be paraphyletic, consequently they split the anilioid complex into four families: Anomochilidae, Uropeltidae, Cylindrophiidae, and Aniliidae. In view of this uncertainty, I provisionally maintain here the traditional classification, it being understood that both Anilioidea and Aniliidae (that is Aniliidae sensu lato) are probably paraphyletic and could represent the stem group of Macrostomata.

ANILIIDAE FITZINGER, 1826

The Aniliidae include snakes which are probably the most primitive. Today, they inhabit northern South America (*Anilius*) and southeastern Asia (*Cylindrophis*, *Anomochilus*). The oldest known Aniliidae could be fossils from the early late Cretaceous (presumed Cenomanian) of Sudan (Werner & Rage, 1994). Four fossil genera have been described and assigned to the family: *Coniophis*, late Cretaceous to latest Eocene, known in North and South America, Europe, and Africa (Rage, 1987;

Gheerbrant *et al.*, 1993); *Eoanilius*, late Eocene to early Miocene, from Western Europe (Szyndlar & Schleich, 1993); *Colombophis*, from the middle Miocene of South America (Hoffstetter and Rage, 1977); *Michauxophis*, from the late Pliocene of Western Europe (Bailon, 1988). Two aniliids are present at Itaboraí.

CONIOPHIS MARSH, 1892

Type-species: *Coniophis precedens* MARSH, 1892.

Coniophis is a small snake known only by vertebrae which display primitive features: very short prezygapophysial processes, absence of a posterior median notch in the neural arch, neural arch not markedly rising above the zygapophysial plane, massiveness of the vertebrae. The primitive state of most features makes it difficult to establish the relationships of the genus; as a consequence, its family affinities have been disputed. Marsh (1892) recognized the ophidian nature of *Coniophis* but he made no attempt at a more precise assignment. Gilmore (1938) regarded it as a snake "of unknown family reference". Hoffstetter (1955) placed *Coniophis* in its own family, the Coniophiidae. Hecht (1959) allocated the genus to the Aniliidae; the latter opinion has been subsequently endorsed by Holman (1979a, b) and Rage (1984, 1987). But Hecht (1982) suggested that *Coniophis* is perhaps the closest relative of *Dinilysia*, the phyletic relationships of which are controversial (Rage, 1977; Rieppel, 1979; Hecht, 1982), and that it could be allocated to the Dinilysiidae. Hecht's opinion rests mainly on the lack of a posterior median notch in the neural arch; but this character is known in other snakes which are neither Dinilysiidae nor Aniliidae (Rage & Prasad, 1992). Moreover, the posterior border of the neural arch of *Anilius* forms a shallow embayment (? an incipient median notch) which is not really different from that of *Coniophis precedens*. Besides, the vertebrae of *Dinilysia* have a well developed neural spine and their centrum prominently widens anteriorly (Rage & Albino, 1989). *Coniophis* has a very reduced neural spine and its centrum tends to remains narrow. These two characteristics fit the aniliid morphology and are inconsistent with that of *Dinilysia*. Albino (1990) already noticed differences between these two genera. Despite the fact that McDowell (1987) provisionally assigned *Coniophis* to the Dinilysiidae, I tentatively retain it in the Aniliidae. Obviously, the assignment of *Coniophis* is based only on overall similarity, all features liable to analysis being of plesiomorphic nature. But overall similarity is not devoid of significance; it is based on continuously variable characters which cannot be readily described (because of their non-discrete nature) and, therefore, which escape rigorous analysis. It should be taken into account, more especially when it is the only available evidence.

On the other hand, it may be wondered whether the set of snakes allocated to *Coniophis* corresponds to the range of variation of a single genus. For example, *C. precedens*, with short prezygapophyses, clearly differs from C. *carinatus* the prezygapophyses of which strongly project laterally. The vertebral morphology of *Coniophis* apparently represents the most primitive morphology that may be expected in alethinophidians (or perhaps an intermediate morphology between scolecophidians and alethinophidians). Therefore, *Coniophis* could be a paraphyletic assemblage which would be the stem group of the other Aniliidae, these latter being possibly the stem group of Macrostomata as suggested above. Pending a revision of this genus, I hold this assemblage in one genus, *Coniophis*, which can be defined as follows (Rage, 1984, modified): posterior border of neural arch without a median notch (a shallow embayment is generally present), centrum only slightly widened anteriorly, main axis of zygapophysial articular facets oblique, neural spine much reduced, haemal keel distinct. Four species were described, all from North America: *C. cosgriffi*, from the Campanian (Armstrong-Ziegler, 1978); *C. precedens*, from the Maastrichtian (Marsh, 1892); C. *carinatus* and *C. platycarinatus* , both from the Bridgerian (late early or early middle Eocene) (Hecht, 1959). Other *Coniophis* were reported, but without specific determination: late Palaeocene and early Eocene of Northern Africa (Gheerbrant, 1987; Gheerbrant *et al.*, 1993), late Eocene of the U.S.A. (Holman, 1979b), and late Eocene of France (Rage, 1988a). This genus was erroneously reported (because of an error of mine) from the Palaeocene of Tiupampa (Bolivia), formerly regarded as Maastrichtian, by de Muizon *et al.* (1983, tab. I, as *Coniophys* [sic]). In fact, additional material has demonstrated that the aniliid from Tiupampa is not *Coniophis* (Rage, 1991).

Coniophis occurs at Itaboraí where it is rare. In a work founded on material housed in the Museum of La Plata, Albino (1990) has reported the presence of *Coniophis* cf. *C. precedens* at Itaboraí. Only one vertebra from the collection of the Departamento Nacional de Produção Mineral is referred to *Coniophis* , it corroborates Albino's opinion.

***Coniophis* cf. *C. precedens* MARSH, 1892**

1990 *Coniophis* cf. *C. precedens* MARSH, 1892: Albino, pp. 337-338, fig. 1A,B.

Referred material: one posterior trunk vertebra (DGM 1322-R).

Description

The morphology of the vertebra (fig. 15) is quite similar to that of the ones described by Albino (1990), that is only one species of *Coniophis* is present at Itaboraí. Albino rightly recognized that this fossil is closer to *C. precedens* than to the other described specis of *Coniophis*. Her opinion was based on the following combination of features which characterizes both *C. precedens* and the fossil from Itaboraí: zygapophyses weakly slanting above the horizontal, neural spine very reduced, zygantral mounds lacking, and haemal keel not reaching the condyle. To these characteristics, it may be added that in these two fossil forms, the main axis of the prezygapophyses is clearly oblique (which is also reminiscent of *C. cosgriffi*) whereas in C. *carinatus* and *C. platycarinatus* the prezygapophyses project more laterally.

No marked difference distinguishes *C. precedens* from the Itaboraí *Coniophis*. The holotype of *C. precedens*, which has a comparatively vaulted neural arch, is a rather anterior trunk vertebra whereas the known vertebrae from Itaboraí are more posterior trunk vertebrae. This accounts for the more depressed neural arch in the latter vertebrae. The fossils from Itaboraí could be, perhaps, referred to *C. precedens* but the original description and the Hecht (1959)'s revision bear on the holotype only. As a result, the intracolumnar variation of *C. precedens* is unknown and can be only inferred. A redescription of the species, based on specimens from the area of the type locality (i.e., "Peterson Quarry", Wyoming, in the type area of the Lance Formation) is necessary but, until such a revision is made, it seems best that the fossils from Itaboraí are referred to as *Coniophis* cf. *C. precedens*.

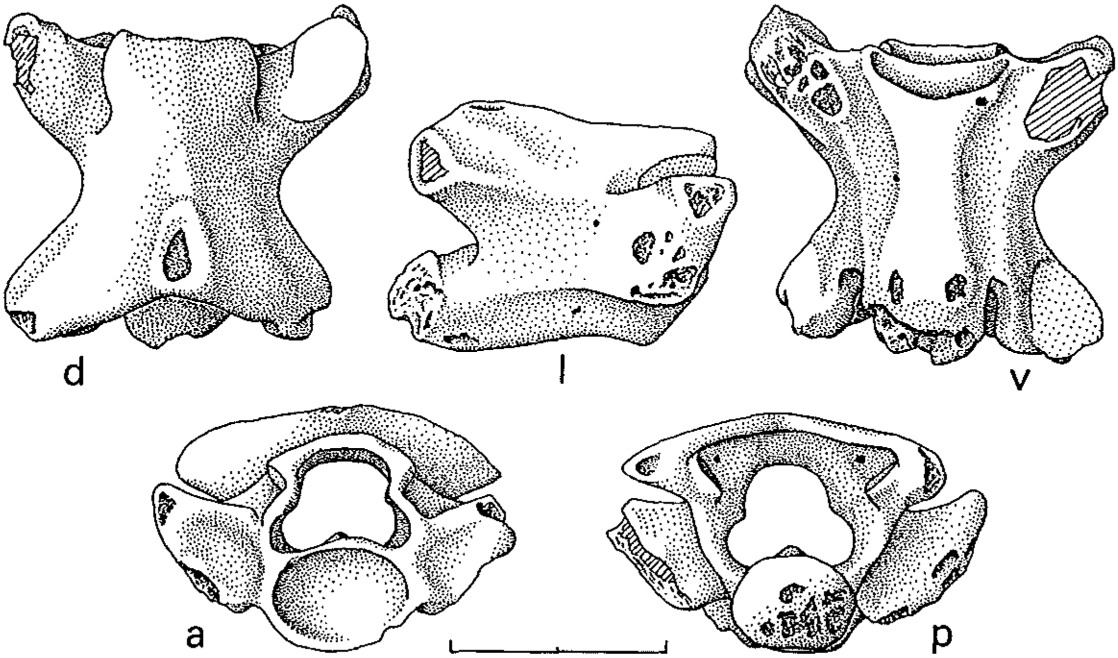

Figure 15.— *Coniophis* cf. *C. precedens*, posterior trunk vertebra, DGM 1322, (a: anterior view, d: dorsal view, l: right lateral view, p: posterior view, v: ventral view). Scale bar = 2 mm.

Discussion

Whatever the precise specific status of the Itaboraí *Coniophis* may be, it is close to *C. precedens* from the Lancian (late Maastrichtian) of North America. Such relationships are consistent with the existence of a land route between South and North America during the late Cretaceous-Palaeocene interval (Rage, 1978, 1988b; Gingerich, 1985; Bonaparte, 1986; Gayet *et al.*, 1992; Marshall & Sempere, 1993). Although the North American form is older than the Itaboraí one, the dispersal probably occurred in a South-North direction (Rage, 1981).

HOFFSTETTERELLA gen. nov.

Type-species: *Hoffstetterella brasiliensis* sp. nov.

Etymology: In honour of Robert Hoffstetter for his contribution to both the palaeontology of South America and palaeoherpetology.

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

Hoffstetterella brasiliensis sp. nov.

Holotype: one mid-trunk vertebra (DGM 1323-R) collected in 1968 by "Price and Campos".

Referred material: 7 vertebrae (DGM 1324a-R, DGM 1324b-R, DGM 1325-R) all collected in 1968 by "Price and Campos".

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

Horizon: middle Palaeocene.

Etymology: From the geographic origin.

Diagnosis: The vertebrae show the typical overall aniliid morphology but they differ from those of all other aniliids by their higher neural spine, the posteromedial extension of the articular area of their diapophyses, the tendency of subcentral foramina to form slits, and the presence of small subcotylar tubercles in mid- and posterior trunk vertebrae. They differ from other Aniliidae, except *Eoanilius*, by the deeper median notch in the posterior border of the neural arch.

Description of the Holotype (fig. 16):

The holotype is a mid-trunk vertebra which has the following measurements: Width through prezygapophyses: 5.3 mm; horizontal diameter of cotyle: 1.7 mm; width of zygosphene: 1.8 mm; length of centrum from ventral rim of cotyle to tip of condyle: 3.2 mm.

In anterior view, the vertebra appears depressed. The zygosphene is thin, slightly arched dorsally, and hardly wider than the cotyle. The neural canal is rather broad. The prezygapophyses are prominently inclined above the horizontal; a tiny and hardly projecting prezygapophysial process is present. The paradiapophyses face mainly laterally. The diapophysial part is salient but its lateral tip is flat or even slightly concave. The parapophysial part is concave. This vertebra lacks paracotylar foramina.

In dorsal view, the vertebra is shorter than wide. The articular facets of the prezygapophyses appear approximately ovaloid; their main axis is clearly oblique. The prezygapophysial processes project anterolaterally slightly beyond the facets. The interzygapophysial constriction is not very deep, nevertheless it is well marked. The anterior border of the zygosphene is damaged; but in other mid-trunk vertebrae, the zygosphene forms a subrectilinear border flanked by two small lateral lobes (fig. 17). The neural spine does not reach the zygosphene; its top is rather thick. A shallow and very obtuse angled bay indents the posterior border of the neural arch.

In posterior view, the neural arch is very depressed; the neural spine is thick and very low. The diapophysial articular surface slightly extends posteromedially. A small foramen opens on either side of the zygantrum; contrary to the parazygantral foramina of madtsoiids, these two foramina are not located in fossae. The roof of the zygantrum is rather thick.

In lateral view, the low and rather long neural spine occupies about half the length of the neural arch. Its anterior edge rises behind the zygosphene and it gently slopes posteriorly. The interzygapophysial ridges are not salient. The condyle is clearly oblique. The paradiapophyses are rather elongate dorsoventrally and the diapophysial areas slightly extend posteriorly. The diapophysial articular surface is weakly separated from the parapophysial one. The subcentral ridges arch dorsally. The haemal keel is rather deep; the posterior part of its ventral edge is straight and horizontal. One lateral foramen is present on each side.

In ventral view, the centrum anteriorly widens moderately; it is rather well delimited by the subcentral ridges. Anteriorly, the haemal keel does not reach the cotyle; it is narrow and poorly delimited laterally. The cotyle rim markedly projects anteriorly. Two small subcotylar tubercles are present. Oddly, each subcentral foramen appears as a long and irregular slit oriented anteroposteriorly.

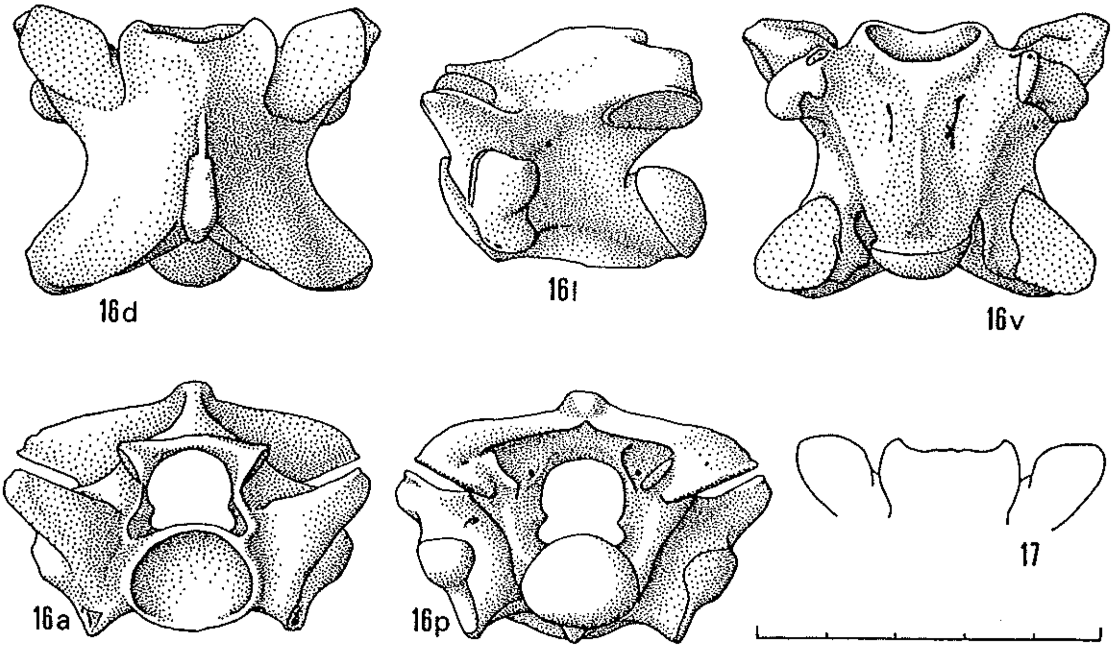

Figure 16-17.— *Hoffstetterella brasiliensis* gen. nov., sp. nov. 16: Holotype, mid-trunk vertebra, DGM 1323 (a: anterior view, d: dorsal view, l: left lateral view, p: posterior view, v: ventral view). 17: morphology of the anterior border of an undamaged zygosphene illustrated by another mid-trunk vertebra. Scale bar = 5 mm.

Anterior trunk vertebrae (fig. 18):

One anterior trunk vertebra is available (DGM 1324a-R). It displays the usual characters of such vertebrae. It is less depressed than mid-trunk vertebrae. The neural spine is shorter and higher than in the latter vertebrae. It slants backwards and it is composed of two parts: a thick columnar part posteriorly and a thinner laminar one anteriorly. The zygosphene clearly arches dorsally (the morphology of its anterior part is unknown). The zypapophyses are less slanting than those of mid-trunk vertebrae. As in mid-trunk vertebrae, the diapophysial area clearly stretches posteromedially. The neural arch is slightly more vaulted than in these latter vertebrae. The posterior median notch in the posterior border of the neural arch seems slighly shallower. The cotyle rim does not strongly project anteriorly; it lacks subcotylar tubercles. A hypapophysis was present but it is broken off; it is not possible to state whether it was an elongate apophysis as in *Cylindrophis*, or a deep and squarish lamina as in *Anilius*. A tiny foramen is located on the left side of the posterior border of the neural arch but the right side lacks foramina. The right subcentral foramen opens in the bottom of an oblique slit. On the left side, the subcentral foramen lies in a small and slightly elongate depression; another depression occurs more anteriorly (it is not possible to settle whether this depression contains a foramen).

Posterior trunk vertebrae (fig. 19):

Two posterior trunk vertebrae are known. As usual, posterior trunk vertebrae are more depressed than mid-trunk ones. The anterior border of the zygosphene forms a wide lobe which weakly projects anteriorly, whereas the two lateral lobes are more reduced than in the anterior and mid-trunk vertebrae. The neural arch is more depressed than that of mid-trunk vertebrae. The posterior median notch is deeper than in more anterior vertebrae. The zygapophyses slant above the horizontal. The haemal keel is shallow and wide; its ventral surface is rounded. On each side, a shallow depression bounds it. The paradiapophyses are more distant from the centrum than in the other vertebrae and ventral spaces separate them from the cotyle; as in vertebrae from other parts of the trunk, the diapophysial articular area extends posteromedially. Weakly developed subcotylar tubercles are present. The cotyle rim clearly projects anteriorly. The posterior border of the neural arch lacks foramina. The subcentral foramina are "normal", that is they do not appear as slits and they do not open in slits either.

Variations:

Within this small set of vertebrae, variations affect only foramina. In three vertebrae only, the subcentral foramina are normal. In three other vertebrae, these foramina appear as slits (or open in slits) and in two vertebrae they tend to form slits. Foramina occur on the posterior border of the neural arch in three vertebrae: bilaterally in two of them (including the holotype), unilaterally in one vertebra.

Discussion:

Hoffstetterella brasiliensis is allocated to the Aniliidae *s.l.* on the basis of the following combination of characters: vertebrae depressed and not elongated, neural arch very depressed, neural spine low, zygapophyses prominently inclined, prezygapophysial processes very short, median notch in the posterior border of the neural arch shallow, and centrum not markedly widened anteriorly.

Nevertheless, two features are not fully consistent with this referral. Although shallow, the posterior median notch is deeper than in other aniliids, excepting *Eoanilius*; moreover, although low, the neural spine is higher than that of other Aniliidae. These two characteristics are somewhat reminiscent of alethinophidians more advanced than anilioids, that is Macrostomata. However, despite these two features, I refer (with little reservation) *Hoffstetterella brasiliensis* to the Aniliidae. The vertebral morphology does not seem consistent with any other group.

Two characters of *H. brasiliensis* appear to be unique, at least within aniliids: the posteromedial stretching of the articular area of the diapophyses, and the tendency of

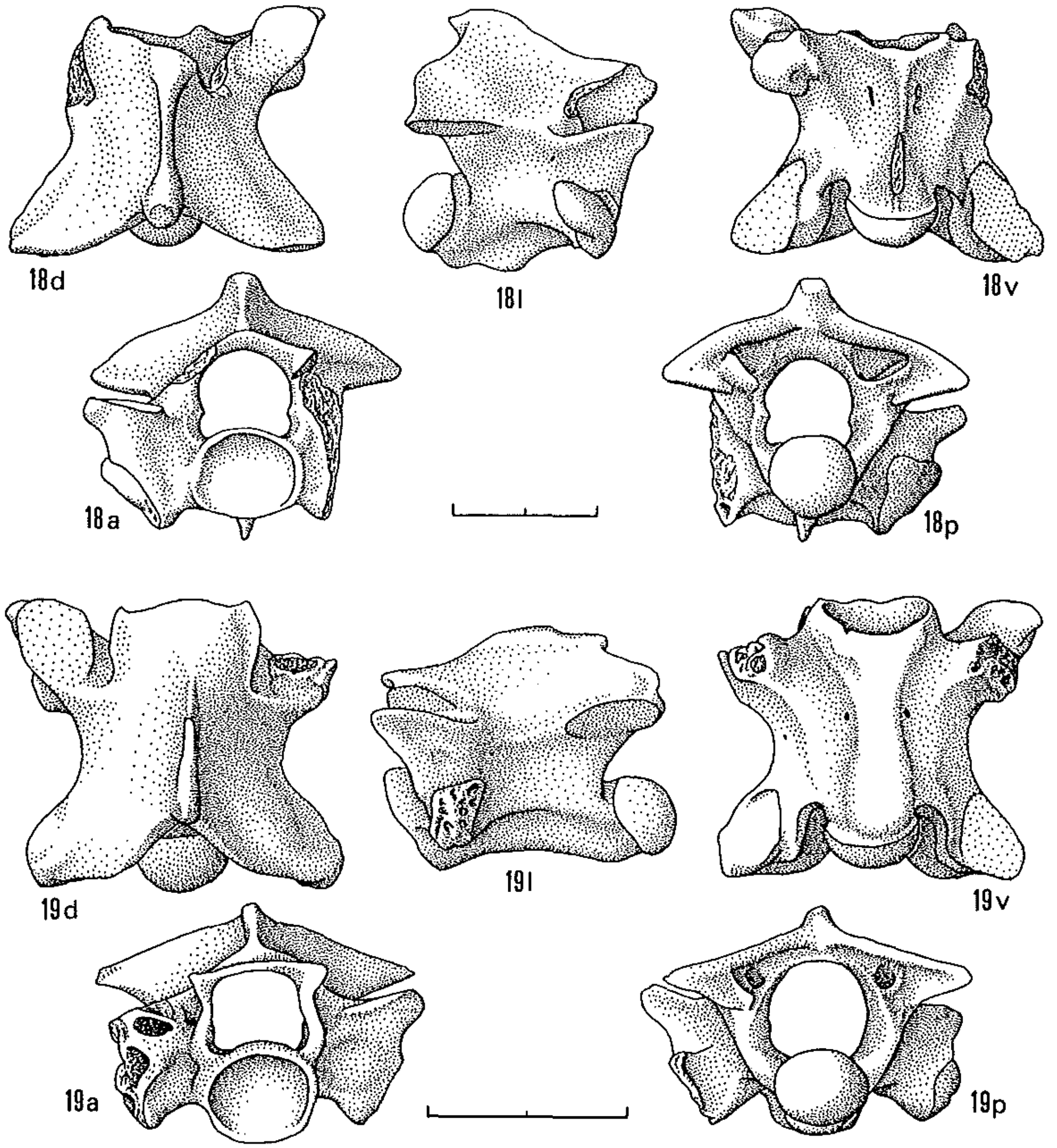

Figure 18-19.— *Hoffstetterella brasiliensis* gen. et sp. nov. 18: anterior trunk vertebra, DGM 1324a. 19: posterior trunk vertebra, DGM 1324b. (a: anterior view, d: dorsal view, l: lateral view, p: posterior view, v: ventral view). Scale bars = 2 mm.

subcentral foramina to form slits.

Apart from *Hoffstetterella*, among aniliids small subcotylar tubercles are seen only on posterior trunk vertebrae of *Anilius* (they occur on mid- and posterior trunk vertebrae in *Hoffstetterella*). The neural spine is markedly longer than that of *Cylindrophis*, *Colombophis*, *Michauxophis*, *Coniophis precedens*, and *C.*

platycarinatus in which it appears as a posterior tubercle. Its length is more or less reminiscent of *Anilius*, *Eoanilius*, and *Coniophis carinatus* but it is higher than that of these three taxa. As mentioned above, the posterior median notch in the neural arch is deeper than that of the other Aniliidae, excepting *Eoanilius*. The shallowness of the interzygapophysial constriction is similar to that of *Eoanilius* only; it is deeper in the other aniliids. The prezygapophyses of *Hoffstetterella* project less laterally than those of *Anilius*, *Cylindrophis*, *Colombophis*, and *Coniophis carinatus* ; they are more inclined above the horizontal than in *Anilius* and *Michauxophis*. The main axis of their articular facets is oriented more anteriorly than in *Anilius*, *Cylindrophis*, *Michauxophis*, *Coniophis carinatus* , and *C. platycarinatus* . The centrum widens anteriorly more than in other aniliids, except perhaps in *Coniophis carinatus* . The vertebrae as a whole are less depressed than those of *Anilius* and *Cylindrophis* but they are more depressed than those of *Eoanilius*. The neural canal is broader than that of *Anilius*, *Cylindrophis*, and *Colombophis*. The anterior protrusion of the cotyle rim occurs elsewhere only in *Michauxophis* and *Coniophis carinatus* . The dia- and parapophysial areas are slightly distinct from one another, this condition is known in *Cylindrophis* and *Michauxophis*; in *Eoanilius*, *Coniophis platycarinatus* and *C. precedens*, the distinction is barely recognisable whilst it is absent in other aniliids.

From this array of differences, *Hoffstetterella* appears clearly distinct among Aniliidae. On the whole, despite some features which are reminiscent of *Eoanilius*, it seems most similar to *Anilius* because of the length of the neural spine and the presence of subcotylar tubercles, but mainly because of its overall morphology.

cf. ***Hoffstetterella brasiliensis***

Referred material: one vertebra (DGM 1321-R), collected in 1968 by "Price and Campos".

One tiny vertebra is referred, with reservation, to *Hoffstetterella brasiliensis* (fig. 20). It displays the overall morphology of aniliids, but it differs from vertebrae of *Coniophis* and *Hoffstetterella* by juvenile features, more specifically the smaller size and the more depressed cotyle and condyle. This vertebra is fragmentary, which does not permit thorough comparisons. The tentative assignment to *H. brasiliensis* is based on the strong anterior protrusion of the cotyle rim.

CONCLUSION

Fossil aniliids are not numerous, but they appear comparatively frequently in South America where fossil snakes are still somewhat scanty. The oldest South American aniliid could be a small form (perhaps *Coniophis*) from Laguna Umayo (Rage, 1981, 1991). This Peruvian locality is either of Maastrichtian or early Palaeocene age (see above: "Known palaeocene snakes of the World"). An aniliid of ascertained early palaeocene age is known at Tiupampa (Bolivia); this fossil is still undescribed (Rage, 1991). An unusually large aniliid (*Colombophis portai*) was recovered from the middle Miocene (Friasian) of La Venta, Colombia (Hoffstetter & Rage, 1977). With the addition of *Coniophis* cf. *C. precedens* and *Hoffstetterella brasiliensis* from the middle Palaeocene of Itaboraí, the South American record of aniliids is the most diverse.

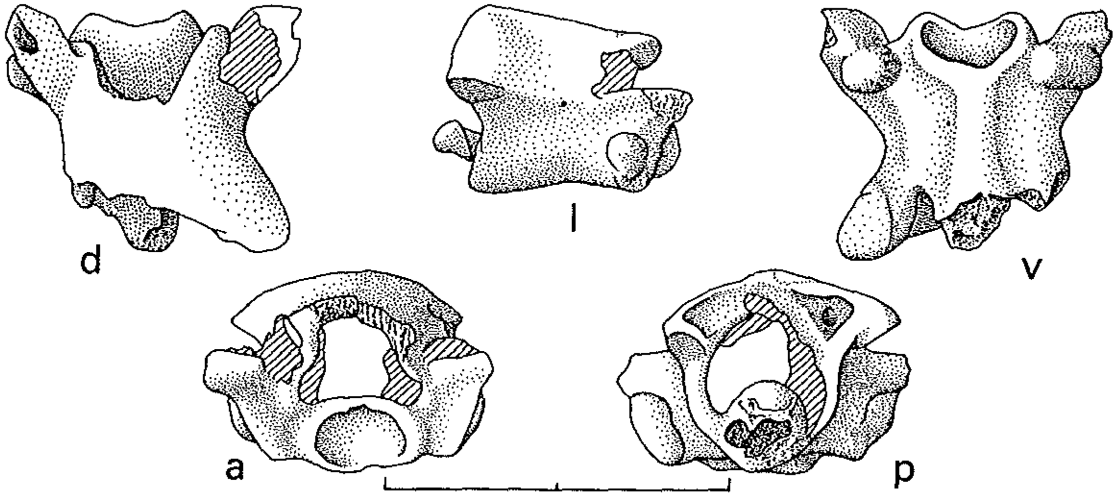

Figure 20.— cf. *Hoffstetterella brasiliensis*, trunk vertebra of a juvenile individual, DGM 1321 (a: anterior view, d: dorsal view, l: right lateral view, p: posterior view, v: ventral view). Scale bar = 2 mm.

CONCLUDING REMARKS

The Madtsoiidae and Aniliidae, studied in the present article, represent only a small part of the snake fauna from the Palaeocene of São José de Itaboraí. Therefore, to draw information about the palaeoecology of the locality from them only could be misleading. It may be only indicated that all living Aniliidae are fossorial or secretive snakes. The depressed vertebrae of *Coniophis* and *Hoffstetterella* fit such habits. The remains of *Madtsoia* lack features which could disclose a peculiar mode of life.

As far as the geological age is concerned, *Madtsoia camposi* and *Hoffstetterella brasiliensis*, which are known only in the locality, cannot afford information. The identification of *Coniophis* at the specific level cannot be ascertained. It appears to be close to *Coniophis precedens* from the late Maastrichtian of North America. This is not inconsistent with the middle Palaeocene age suggested by mammals.

Finally, because the Madtsoiidae are by far primarily Gondwanan, *Madtsoia* gives a Gondwanan pattern to the fauna. The presence of *Coniophis* corroborates the existence of a land connection between South and North America by latest Cretaceous/Palaeocene times.

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Note added in proof:

After this article was accepted for publication, J.D. Scanlon described a new genus with two small species (*Nanowana godthelpi* and *N. schrenki*) from lower Miocene beds at Riversleigh, Australia. They should be added to *Yurlunggur* sp. and *Wonambi* sp. from the Oligo-Miocene of the same locality (fig. 1, this paper). The maxillae, palatines, dentaries, and vertebrae referred to these two small species clearly differ from those of *Madtsoia camposi* [Scanlon, J.D., 1997.- *Nanowana* gen. nov., small madtsoiid snakes from the Miocene of Riversleigh: sympatric species with divergently specialised dentition. *Mem. Qd. Mus.*, 41 (2): 393-412].