

The oldest Brazilian snakes from the Cenomanian (early Late Cretaceous)

ANNIE S. HSIU, ADRIANA M. ALBINO, MANUEL A. MEDEIROS, and RONNY A.B. SANTOS



Annie S. Hsiou, Adriana M. Albino, Manuel A. Medeiros, and Ronny A.B. Santos. 2014. The oldest Brazilian snakes from the Cenomanian (early Late Cretaceous). *Acta Palaeontologica Polonica* 59 (3): 635–642.

South American Mesozoic snake diversity is mostly represented by genera from the Cenomanian (*Najash*), Santonian–Campanian (*Dinilysia*), and Campanian–Maastrichtian (*Alamitophis*, *Patagoniophis*, *Rionegrophis*, and *Australophis*) of Patagonia, Argentina. In this paper, we describe a new snake genus and species, *Seismophis septentrionalis*, from the Cenomanian (early Late Cretaceous) of the Alcântara Formation, Maranhão, northeastern Brazil. The new snake comprises a posteriormost trunk vertebra and possibly a poorly preserved midtrunk vertebra. Both vertebrae share small size, zygosphene moderately thick with a rectilinear roof, absence of paracotylar foramina, presence of parazygantral foramina, and strongly marked parasagittal ridges of the neural arch. The new snake is here considered of uncertain systematic affinities, but probably close to the limbed snake *Najash rionegrina*. Although the material is very fragmentary and the systematic assignment is still unresolved, this snake represents the oldest, as well as probably the most primitive snake from Brazil.

Key words: Reptilia, Squamata, Ophidia, snakes, Cretaceous, Alcântara Formation, Brazil.

Anne. S. Hsiou [anniehsiou@ffclrp.usp.br], Departamento de Biologia, FFCLRP, Universidade de São Paulo, Av. Bandeirantes 3900, 14040-901, Ribeirão Preto, SP, Brasil;

Adriana M. Albino [aalbino@mdp.edu.ar], CONICET, Departamento de Biología, Universidad Nacional de Mar del Plata, Funes 3250, 7600 Mar del Plata, Argentina;

Manuel A. Medeiros [manuel.acfredo@ufma.br], Ronny A.B. Santos [rooneysmall@yahoo.com.br], Departamento de Biologia, Centro de Ciências Biológicas e da Saúde, Universidade Federal do Maranhão (UFMA), Avenida dos Portugueses, 1966, Campus Universitário do Bacanga, CEP 65085-580, São Luis, MA, Brasil.

Received 21 August 2012, accepted 4 January 2013, available online 21 January 2013.

Copyright © 2014 A.S. Hsiou et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The Brazilian Mesozoic snake record is scarce and until now limited to Late Cretaceous (Turonian–Santonian) remains from the Adamantina Formation (Bauru Group) of the southeastern region of the country (Bertini and Bonfim-Júnior 1998; Zaher et al. 2003; Candeiro 2007; Fachini and Iori 2009; Fachini and Hsiou 2011). In contrast, the Mesozoic snake record in Argentina is significant and concentrated in the Late Cretaceous of Patagonia. It comprises several remains of primitive snakes, including the limbed form *Najash rionegrina* from the Cenomanian (Apesteguía and Zaher 2006; Zaher et al. 2009; Palci et al. 2013), the medium-sized snake *Dinilysia patagonica* from the Santonian–Campanian (Smith-Woodward 1901; Estes et al. 1970; Hecht 1982; Rage and Albino 1989; Caldwell and Albino 2002; Caldwell and Calvo 2008; Zaher and Scanferla 2012), the diverse Madtsoiidae from the Campanian–Maastrichtian (Albino 1986, 1994,

2000, 2007, 2011a; Martinelli and Forasiepi 2004), and the small “anilioid” *Australophis anilioides* (Gómez et al. 2008). Concerning the Madtsoiidae record, at least three genera are known in the Patagonian Cretaceous: *Alamitophis* (with two species, *A. argentinus* Albino, 1986 and *A. elongatus* Albino, 1994), *Patagoniophis* (*P. parvus* Albino, 1986), and *Rionegrophis* (*R. madtsoioides* Albino, 1986). Moreover, there is a probable Cretaceous madtsoiid from the Maastrichtian of Bolivia (Gayet et al. 2001) as well as probable madtsoiids or boids in the Campanian–Maastrichtian of Argentina (Albino 2000, 2011a).

In a brief communication, Hsiou et al. (2009) documented the presence of two small snake vertebrae from the Cajual Island, Alcântara Formation, early Late Cretaceous (Cenomanian) of Maranhão, northeastern Brazil, and attributed them to Madtsoiidae. Here we formally describe these remains and discuss their affinities, and we reject the previous proposal of Hsiou et al. (2009). As a whole, these new snakes represent the oldest Brazilian snake record.

Institutional abbreviations.— CPHNA-MA VT, Vertebrate Collection of the Centro de Pesquisas de História Natural e Arqueologia do Maranhão, São Luís, Maranhão State, Brazil; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Sección Paleontología de Vertebrados, Buenos Aires, Argentina; MLP, Museo de La Plata, División de Paleontología Vertebrados, La Plata, Argentina; MPCA, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina.

Other abbreviations.—cl, centrum length; cow~coh, condyle width similar to condyle height; ctw~cth, cotyle width similar to cotyle height; naw, neural arch width at interzygapophyseal ridge; pr-po, distance between pre- and postzygapophyses of the same side; pr-pr, distance between prezygapophyses; zw~ctw, zygosphenes width similar to cotyle width.

Geological setting

The snake remains reported here come from the Falésia do Sismo locality (2°28'43.0"S; 44°28'10.3"W) of Cajual Island, Maranhão, northeastern Brazil (Fig. 1A). The fossiliferous locality belongs to the Itapecuru Group, which spreads over a vast area in northern Maranhão, both inland and along the shore, and ranges from Albian to early Cenomanian (Fig. 1B; Pedrão et al. 1993a–c; Rossetti 2001). In the northern border of Maranhão, the Alcântara Formation crops out at the shore exposing fossil-bearing sedimentary transitional sequences at Cajual Island. This region has been considered as part of the São Luís Basin, but a revision undertaken by Góes and Rossetti (2001) considered it contiguous to the southern inland sedimentary successions of the Grajaú basin, forming the São Luís-Grajaú Basin (Rossetti et al. 2001; Rossetti 2003).

The Laje do Coringa bone bed, another fossiliferous locality at Cajual Island, concentrates thousands of fossils in a small area (4 ha), that includes bones, teeth, and plants such as conifers and ferns, revealing Cretaceous coastal forest (Medeiros and Schultz 2002), and a remarkable continental palaeofauna with diverse vertebrate groups including dinosaurs, crocodiles, other reptiles and fishes (Vilas-Bôas and Carvalho 2001; Medeiros and Schultz 2002, 2004; Elias et al. 2007; Medeiros et al. 2007; Pereira and Medeiros 2008; Van-Tomme et al. 2008; Kellner et al. 2011; Lindoso et al. 2012). The Falésia do Sismo locality is a level of the same stratigraphic sequence; just a few hundreds metres from Laje do Coringa and some metres higher in the sedimentary succession.

The Itapecuru deposits lie conformably over Aptian strata of the Codó and Grajaú Formations and are more than 1200 m thick in the coastal area (Rodrigues et al. 1990; Góes and Feijó 1994; Rossetti et al. 2001). The Alcântara Formation comprises layers deposited under a tide and wave dominated environment, conforming to an incised valley fill (Rossetti and Truckenbrodt 1997) and is seen in the coastal cliffs in the southern region of Alcântara.

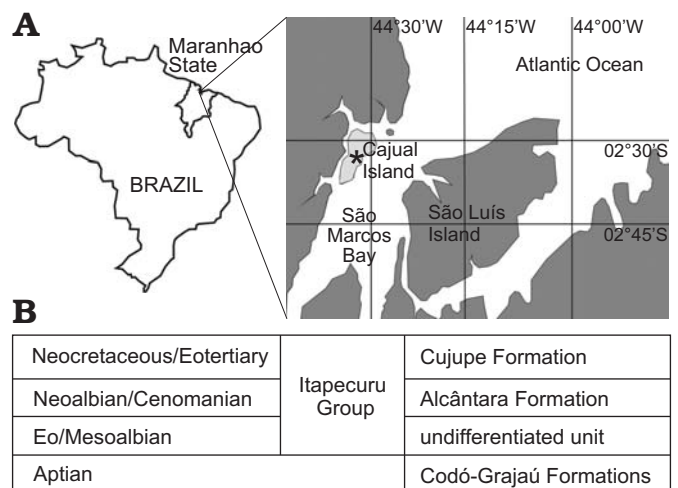


Fig. 1. **A.** Location map of Cajual Island. Asterisk shows Falésia do Sismo locality. **B.** Stratigraphy of São Luís-Grajaú Basin (modified from Rossetti 2001).

Palynological data from layers on São Luís island revealed an early Cenomanian age for the Cretaceous sediments cropping out along the coast, whereas the inland sequences of the Itapecuru Group are considered as Albian (Pedrão et al. 1993a–c). Klein and Ferreira (1979) also attributed a Cenomanian age to the coastal deposits of the Maranhense Gulf, based on bivalves from estuarine facies.

Material and methods

The specimens studied here are stored CPHNA-MA VT, São Luís, Maranhão, Brazil. They were compared with specimens of *Alamitophis argentinus*, *A. elongatus*, *Patagoniophis parvus*, *Rionegrophis madtsoioides*, and *Dinilysia patagonica* (Appendix 1). Data from the literature, as well as figures, of *Alamitophis tingamarra* and *Patagoniophis australiensis* (Scanlon 1993, 2005), *Nanowana godthelpi* (Scanlon 1997), *Herensugea caristorum* (Rage 1996; Rage and Werner 1999), *Najash rionegrina* (Apesteguía and Zaher 2006; Zaher et al. 2009; Palci et al. 2013), and *Dinilysia patagonica* (Rage and Albino 1989; Caldwell and Albino 2002; Scanferla and Canale 2007) were also used. Osteological nomenclature follows Auffenberg (1963), Rage (1984, 1998), Lee and Scanlon (2002), and Scanlon (2005). Systematic arrangement is based on Lee and Scanlon (2002).

Systematic palaeontology

Order Squamata Oppel, 1811

Suborder Ophidia Brongniart, 1800

Genus *Seismophis* nov.

Type species: Seismophis septentrionalis sp. nov.; see below; monotypic.

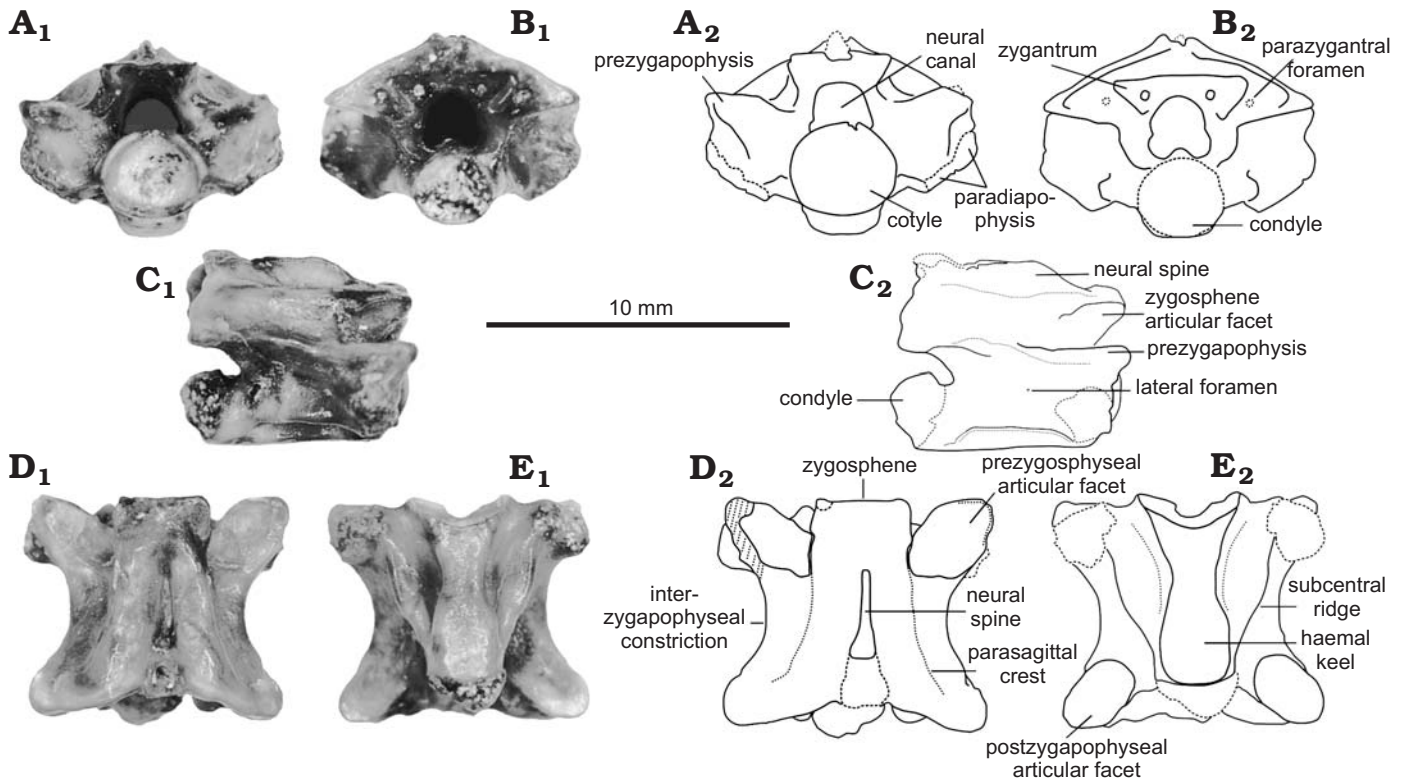


Fig. 2. Trunk vertebra of the snake *Seismophis septentrionalis* gen et sp. nov. (CPHNA-MA VT 1221) from the Cenomanian (early Late Cretaceous) of Falésia do Sismo, Cajual Island, Maranhão, northeastern Brazil. Photographs (A₁–E₁) and explanatory drawings (A₂–E₂), in anterior (A), posterior (B), lateral (C), dorsal (D), and ventral (E) views.

Etymology: From the Greek *seism*, earthquake, in allusion to the type locality Falésia do Sismo at Cajual Island; and *ophis*, snake.

Seismophis septentrionalis sp. nov.

Fig. 2.

Etymology: From Latin *septentrionalis*, from the north, northern, referring to the type locality, which is the northernmost region of Maranhão.

Holotype: CPHNA-MA VT-1221, almost complete posterior trunk vertebra.

Type locality: Falésia do Sismo (2°28'43.0"S; 44°28'10.3"W) of Cajual Island, Maranhão, northeastern Brazil.

Type horizon: Cenomanian (early Late Cretaceous), Alcântara Formation, Itapecuru Group, São Luis-Grajaú Basin (Góes and Rossetti 2001).

Diagnosis.—Snake characterized by low and rather long vertebrae with the following combination of character states: zygosphene moderately thick with a rectilinear roof; strongly marked parasagittal ridges of the neural arch; parazygantral foramina present; deep interzygapophyseal constriction; low, long, and anteroposteriorly elongate neural spine; prezygapophyseal process absent; paracotylar foramina absent; centrum broader anteriorly than posteriorly, with well-defined and sinuous subcentral ridges; and well-defined, broad, and flattened haemal keel.

Description.—The holotype is a posteriormost trunk vertebra as evidenced by the deep subcentral grooves, and also because it displays prominent lateroventral expansions of the paradiapophyseal facets. In general, it is a very small and

delicate vertebra, low, longer than wide, with the centrum somewhat longer than the neural arch width ($cl > naw$), and depressed, wider than the long neural arch ($pr-pr > pr-po$). The vertebra lacks the distal end of the neural spine, and the condyle, and both paradiapophyses are eroded.

In anterior view, a wide and moderately thick zygosphene with short articular facets is seen. The width of the zygosphene is almost equal to the transverse diameter of the cotyle ($zw \approx ctw$) and shows a rectilinear roof that is not elevated in the middle. The prezygapophyses are somewhat inclined above the horizontal plane, but do not reach the level of the zygosphene. There is no evidence of prezygapophyseal processes. The cotyle is nearly circular ($ctw \sim cth$) and there are no paracotylar foramina, only a deep fossa on each side of the cotyle. Paradiapophyses are lateroventrally expanded, where the diapophyses almost reach the prezygapophyseal tip. Although eroded, the paradiapophyses do not seem to have reached the cotylar rim ventrally.

In dorsal view, the articular facets of the prezygapophyses are broad and subtriangular, with the main axis anterolaterally oriented. The roof of the neural arch shows a strong pronounced ridge joining the lateral edge of the zygosphene and the posteromedial margin of the postzygapophysis on each side of the neural spine. The neural spine is anteroposteriorly elongate and extends all along the roof of the neural arch, but its distal end is broken. Anteriorly it looks as a thin keel, but it is posteriorly enlarged as a robust tubercle. The posterodorsal notch of the neural arch is weakly defined and

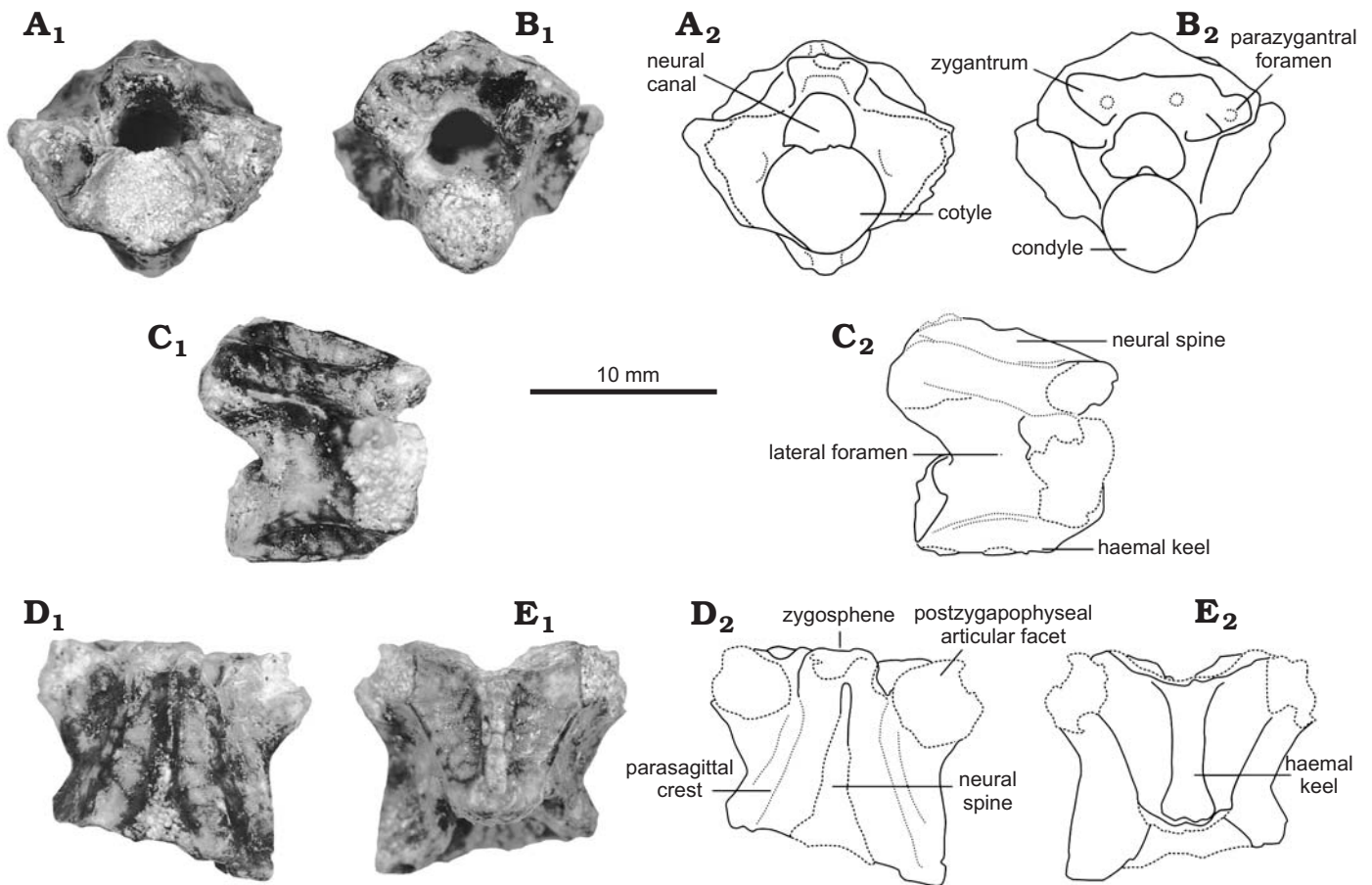


Fig. 3. Midtrunk vertebra of the snake cf. *Seismophis septentrionalis* sp. nov. (CPHNA-MA VT 1222), from the Cenomanian (early Late Cretaceous) of Falésia do Simito, Cajual Island, Maranhão, northeastern Brazil. Photographs (A₁–E₁) and explanatory drawings (A₂–E₂), in anterior (A), posterior (B), lateral (C), dorsal (D), and ventral (E) views.

shallow, without a clearly defined median bay (Rage 1996). The interzygapophyseal ridges are long, strongly salient and curved.

In posterior view, the neural arch roof is depressed, with the two halves inclined but not vaulted. The zygantrum is deep, with small zygantral foramina. Small parazygantral foramina are present in shallow depressions lateral to the zygantrum, one on each side. The postzygapophyses are slightly inclined dorsally. The condyle is nearly circular (cow~coh), with the main axis slightly inclined upward. In lateral view, the centrum is longer than the neural arch, and the vertebra looks depressed. The neural spine is low and elongate anteroposteriorly. The subcentral ridges are narrow and well defined. Small lateral foramina are present on each lateral wall of the neural arch.

In ventral view, the centrum is elongate and widens anteriorly. The well-marked subcentral ridges are sinuous and diverge anteriorly. The haemal keel is clearly defined laterally by deep subcentral grooves. It is flattened, very wide, and occupies much of the ventral surface of the centrum. It originates at the ventral edge of the cotyle and becomes more prominent in the mid-portion of the centrum. From there on, it widens significantly, almost reaching the same width of the condyle. Posteriorly, it reaches the precondylar

constriction, which is moderately marked. There is a pair of small subcentral foramina, one on each side, hidden on the lateral surface of the haemal keel. The postzygapophyses show broad subtriangular articular facets.

cf. *Seismophis septentrionalis* sp. nov.

Fig. 3.

Referred material.—CPHNA-MA VT-1222, incomplete midtrunk vertebra from the same locality of *Seismophis septentrionalis* sp. nov. exposed at the Falésia do Simito (2°28'43.0"S; 44°8'10.3"W) of Cajual Island, Maranhão, northeastern Brazil; Cenomanian (early Late Cretaceous), Alcântara Formation, Itapecuru Group, São Luis-Grajaú Basin (Góes and Rossetti 2001).

Description.—The material is an incomplete isolated vertebra poorly preserved, lacking most of the prezygapophyses, part of the anterior edge of the zygosphene, the distal end of the neural spine, both paradiapophyses, much of the condyle, and much of the posterior portion of the neural arch. For this reason, measurements and ratios are not used in the description. In general, the vertebra is small, relatively robust, short, wide and moderately high, with the centrum probably shorter than the neural arch width ($cl < naw$). In anterior

view, although very fragmented, the zygosphene is narrow and moderately thick, apparently narrower than the cotyle ($zw < ctw$) and probably bearing a flat roof that is not elevated in the middle. Although broken, the prezygapophyses are nearly horizontalized, and it is not possible to observe if they carried prezygapophyseal processes. The neural canal is triangular and small. The cotyle is slightly wider than high, and there are no paracotylar foramina, only a deep fossa on each side of the cotyle. The paradiapophyses are fragmented, hindering further detail; however, they were apparently well developed and lateroventrally oriented, with the dorsal portion (diapophysis) almost reaching the prezygapophyseal articular surface, and the parapophysis probably not surpassing the ventral rim of the cotyle.

In posterior view, the neural arch is vaulted, with the roof clearly arched. The zygantrum is deep, with small zygantral foramina. There is one parazygantral foramen lateral to the right zygantral facet of the zygantrum. The posterior face of the neural arch is broken on the left side making impossible to verify the presence of this foramen. The condyle is eroded, nearly circular ($cow \sim coh$). In lateral view, the centrum is shorter than the neural arch. In this view, the neural spine is obliquely oriented because the neural arch becomes higher posteriorly. Small lateral foramina are present on each lateral wall of the neural arch. From this view, the interzygapophyseal ridges look rather inclined anteroposteriorly.

In dorsal view, the neural arch is apparently wider than long ($pr-pr > pr-po$). The prezygapophyseal facets are oval and anterolaterally oriented. The neural spine was apparently thicker posteriorly than anteriorly, although its posterior part is broken. It is low, starting posterior to the zygosphene and extending all along the roof of the neural arch. The roof of the neural arch shows a strongly pronounced ridge joining the lateral edge of the zygosphene and the posteromedial margin of the postzygapophysis on each side of the neural spine. Although the interzygapophyseal constriction is quite deformed, it looks somewhat deep. In ventral view, the centrum is strongly triangular in outline and broader anteriorly than posteriorly with marked and straight subcentral ridges. The precondylar constriction is moderately marked. The haemal keel is well defined, thick, and slightly prominent from the ventral surface of the centrum.

Discussion

The holotype of *Seismophis septentrionalis* gen. et sp. nov. (CPHNA-MA VT-1221) shares with CPHNA-MA VT-1222 the small size, zygosphene moderately thick with a rectilinear roof, absence of paracotylar foramina, presence of parazygantral foramina, and strongly marked parasagittal crests on the neural arch. The morphological similarities and subtle differences among the studied vertebrae could be attributed to intracolumnar or intraspecific variation, suggesting they represent the same taxa. However, the poor preservation of the specimen CPHNA-MA VT-1222 prevents a clear com-

parison of all characters, and so it is not possible to be sure. It is noteworthy that the locality where these vertebrae were collected, represents one of the few bone-beds from Brazil and has yielded hundreds of isolated elements, some probably reworked from previous deposits (Medeiros and Schultz 2002; Van Tomme et al. 2008; Kellner et al. 2009, 2011). For this reason, we establish that these vertebrae do not belong to the same individual. Most of the differences between both vertebrae are considered intracolumnar variation due to a more anterior position of the vertebra CPHNA-MA VT-1222 in the column, and others represent possible intraspecific variations. First, their proportions are different: the specimen CPHNA-MA VT-1222 is a higher than long vertebra, whereas the holotype of *Seismophis* is longer than high, showing a more depressed general aspect, and a longer neural arch and vertebral centrum than in CPHNA-MA VT-1222. In the holotype, the prezygapophyses are inclined above the horizontal plane, differing from the midtrunk vertebra CPHNA-MA VT-1222, where they are almost horizontal. The neural spine of the *Seismophis* holotype is low and anteroposteriorly elongate, keeping the same height all along the neural arch, unlike CPHNA-MA VT-1222, in which it is obliquely developed anteroposteriorly, and looks higher posteriorly than anteriorly. The interzygapophyseal ridge of the holotype is long and straight in lateral view. It looks curved in dorsal view because the constriction is strong. In ventral view, the subcentral ridges are sinuous in the holotype, but straight in CPHNA-MA VT-1222. Also, the haemal keel of *Seismophis*'s holotype is much broader and flattened than in CPHNA-MA VT-1222.

Isolated snake vertebrae are very common in Mesozoic and Cenozoic deposits with vertebrate remains, and difficulties involved in vertebral identification have been widely recognized (LaDuke 1991). In this way, many fossil taxa are described based on a single vertebra because several vertebral characters can be sufficiently applicable to distinguish one taxon from another. In the last years, efforts to understand the origins and evolution of snakes resulted in several phylogenetic studies that include important vertebral characters previously seen only in morphological studies. As consequence, since then, some workers have tried to employ these vertebral characters in the study of isolated snake vertebrae in an attempt to define their phylogenetic affinities (e.g., Scanlon 2005; Albino and Montalvo 2006; Hsiou et al. 2010). In this context, both vertebrae described here display a unique combination of character states that distinguishes them from other known fossil and extant snakes. The absence of paracotylar foramina in the *Seismophis* holotype and CPHNA-MA VT-1222, as well as in *Najash* vertebrae (according to Zaher et al. 2009), distinguishes these genera from madtsoiids, where the foramina are always present (Rage 1998; Scanlon 2005). Paracotylar foramina are usually present in *Dinilysia* (Rage and Albino 1989) and always present in advanced Macrostromata. The absence of this foramen is considered a primitive condition (Wilson et al. 2010). Traditionally considered an apomorphy of Madtsoiidae (Albino 1986, 2007; Rage 1984, 1987,

1998; Scanlon 1992, 2005), the presence of large, paired parazygantral foramina noted in the *Seismophis* holotype, CPHNA-MA VT-1222, *Najash* specimens (see MCPA 397, Zaher et al. 2009; Palci et al. 2013), and Madtsoiidae (non-small specimens) is considered a derived condition (Lee and Scanlon 2002; Wilson et al. 2010). The parasagittal ridges of the neural arch observed in the holotype of *Seismophis* and CPHNA-MA VT-1222 are similar to the laminar crest described in precloacal vertebrae of *Boa constrictor* (Albino 2011b). This crest has also been observed in large madtsoiids (*Madtsoia* and *Yurlunggur*), and in large extant and extinct boids (*Eunectes* and *Chubutophis*). This morphology could be related with complex epaxial muscle insertions, which are responsible for constriction (Jayne 1982). Nevertheless, the strong development of these ridges in the holotype of *Seismophis* and CPHNA-MA VT-1222, connecting the lateral edge of zygosphene and the postero-medial margin of the postzygapophysis is an outstanding character that, together with the absence of paracotylar foramina and presence of parazygantral foramina constitute a combination of character states resembling these vertebrae with some vertebral remains of *Najash* (see Zaher et al. 2009; Palci et al. 2013). Moreover, the presence of parasagittal ridges of the neural arch combined with the prominent and sharp subcentral ridges are features only present in the *Seismophis* holotype and CPHNA-MA VT-1222.

The holotype of *Seismophis* shares with *Najash* (see MCPA 397; Zaher et al. 2009) the absence of prezygapophyseal process, but this condition cannot be evaluated in the specimen CPHNA-MA VT-1222, because of poor preservation of the prezygapophyses. The absence of prezygapophyseal processes is interpreted as a plesiomorphic condition, seen in several primitive fossil snakes, including *Najash* and Madtsoiidae (Lee and Scanlon 2002; Rieppel et al. 2002; Scanlon 2006; Zaher et al. 2009; Wilson et al. 2010; LaDuke et al. 2010). The holotype of *Seismophis* has a shallow posterodorsal notch in the neural arch, exposing part of the condyle in dorsal view. This feature is similar to that observed in *Najash* (MCPA 397; Zaher et al. 2009) and also in *Dinilyisia* (Rage and Albino 1989; Apesteguía and Zaher 2006; Zaher et al. 2009), and it is interpreted as a plesiomorphic condition among snakes (Lee and Scanlon 2002; Wilson et al. 2010). The deep V-shaped embayment exposing much of the centrum in front of the condyle is a derived condition observed in madtsoiids and alethinophidians. It is not possible to evaluate this character in the CPHNA-MA VT-1222 midtrunk vertebra. The width between the diapophyses that approaches the width between the prezygapophyses is a plesiomorphic condition (Apesteguía and Zaher 2006; Wilson et al. 2010) seen in the *Seismophis* holotype and also described for posterior trunk vertebrae of *Najash* (MCPA 397; Zaher et al. 2009) and Madtsoiidae.

The zygapophyses of the holotype of *Seismophis* are well inclined above the horizontal plane, as in *Najash* (between 20–30° to the horizontal plane; see Zaher et al. 2009: 16). Among primitive snakes, *Dinilyisia* also usually has this

plesiomorphic condition (Lee and Scanlon 2002) frequently reaching the level of the zygosphene (Rage and Albino 1989), so that the inclination of the zygapophyses observed in the holotype of *Seismophis* and *Najash* is interpreted as an intermediate condition (Lee and Scanlon 2002). On the other hand, the zygapophyses of the CPHNA-MA VT-1222 midtrunk vertebra are almost horizontal in anterior view, relating to its location in the column or a minor variation. Also, the *Seismophis* holotype and posterior vertebrae of *Najash* share a very depressed neural arch in posterior view (see MCPA 397; Zaher et al. 2009: fig. 09), contrasting with the more elevated neural arch of the midtrunk vertebra CPHNA-MA VT-1222.

In spite of the strong resemblances between *Seismophis* and *Najash* in many characters, *Seismophis* has a low but well developed neural spine, with the same height all along the roof of the neural arch. On the contrary the neural spine is reduced to a low crest mostly restricted to the posterior half of the neural arch in *Najash* (see MCPA 397; Zaher et al. 2009: fig. 09). In addition, the holotype of *Seismophis* is significantly smaller than *Najash*, it has a comparatively longer neural arch and centrum, and the paradiapophyses are in a higher position, not surpassing the ventral edge of the cotyle as in *Najash* vertebrae. Thus, it clearly represents a new and distinctive genus from the South American Late Cretaceous.

Conclusions

Together, the new snake vertebrae described here represent the oldest Brazilian records of the group. The identification of a new genus and species (*Seismophis septentrionalis* gen. et sp. nov.) probably related to one of the most primitive snakes, *Najash*, corroborates the assumption that South America has been a relevant territory in the origin and early diversification of snakes since the early Late Cretaceous (Albino 2007).

Acknowledgements

We thank Alejandro Kramarz (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina), Marcelo Reguero, Eduardo Tonni, and Lucas Pommi (all Museo de La Plata, La Plata, Argentina) for their assistance and help during visits to palaeontological collections in March 2008 and the Universidade Federal do Maranhão (UFMA), Secretaria de Estado da Cultura do Estado do Maranhão (SECMA), Fundação de Amparo à Pesquisa e ao Desenvolvimento Científico e Tecnológico do Maranhão (FAPEMA), and PETROBRAS for financial support. ASH would like to thank the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for financial support (process n° 2011/14080-0), and also Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the Postdoctoral Fellowship (process n° 150803/2010-9) during her studies at Museu de Ciências Naturais da FZB/RS. AMA thanks CONICET (PIP N° 112-200901-00176) for financial support. The authors also thank Max C. Langer and Felipe C. Montefeltro (both Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Brazil) for language revision and critical reading of the manuscript. We are

thankful for the useful comments and critical suggestions provided by the editor, Michael J. Benton (University of Bristol, UK), and the three reviewers, Jean Claude Rage (Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements, Département Histoire de la Terre, Muséum National d'Histoire Naturelle, Paris, France), John Scanlon (Ecoscape, North Fremantle, Western Australia), and Zbigniew Szyndlar (Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Department of Vertebrate Zoology, Cracow, Poland).

References

- Albino, A.M. 1986. Nuevos Boidae Madtsoiinae en el Cretácico tardío de Patagonia (Formación Los Alamitos, Río Negro, Argentina). *Abstracts (Actas) of the 4th Congreso Argentino de Paleontología y Bioestratigrafía* 2: 15–21.
- Albino, A.M. 1994. Una nueva serpiente (Reptilia) en el Cretácico Superior de Patagonia, Argentina. *Pesquisas* 2: 58–63.
- Albino, A.M. 2000. New record of snakes from the Cretaceous of Patagonia (Argentina). *Geodiversitas* 22: 247–253.
- Albino, A.M. 2007. Lepidosauria. In: Z. Gasparini, L. Salgado, and R.A. Coria (eds.), *Patagonian Mesozoic Reptiles*, 87–115. Indiana University Press, Indiana.
- Albino, A.M. 2011a. Evolution of Squamata reptiles in Patagonia based on the fossil record. *Biological Journal of the Linnean Society* 103: 441–457.
- Albino, A.M. 2011b. Morfología vertebral de *Boa constrictor* (Serpentes: Boidae) y la validez del género Mioceno *Pseudoepicrates* Auffenberg, 1923. *Ameghiniana* 48: 53–62.
- Albino, A.M. and Montalvo, C.L. 2006. Snakes from the Cerro Azul Formation (Upper Miocene), central Argentina, with a review of fossil viperids from South America. *Journal of Vertebrate Paleontology* 26: 581–587.
- Apesteiguá, S. and Zaher, H. 2006. A Cretaceous terrestrial snake with robust hindlimbs and a sacrum. *Nature* 440: 1037–1040.
- Auffenberg, W. 1963. The fossil snakes of Florida. *Tulane Studies in Zoology* 10: 131–216.
- Bertini, R.J. and Bonfim-Júnior, F.C. 1998. Os lacertílios fósseis do Brasil. *Abstracts (Anais) of the 50th Congresso Brasileiro de Geologia* 450–450. Belo Horizonte, Minas Gerais State, Brazil.
- Caldwell, M.W. and Albino, A.M. 2002. Exceptionally preserved skeletons of the Cretaceous snake *Dinilysia patagonica* Woodward, 1901. *Journal of Vertebrate Paleontology* 22: 861–866.
- Caldwell, M.W. and Calvo, J. 2008. Details of a new skull and articulated cervical column of *Dinilysia patagonica* Woodward, 1901. *Journal of Vertebrate Paleontology* 28: 349–362.
- Candeiro, C.R.A. 2007. Paleogeographic distribution of the terrestrial squamate reptiles from the Cretaceous of Brazil. *Bioscience Journal* 23: 65–74.
- Elias, F.A., Bertini, R.J., and Medeiros, M.A. 2007. Pterosaur teeth from the Laje do Coringa, middle Cretaceous, São Luís-Grajaú Basin, Maranhão, northern-northeastern Brazil. *Revista Brasileira de Geociências* 37: 1–9.
- Estes, R., Frazzetta, T.H., and Williams, E.E. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward: Part 1. Cranial morphology. *Bulletin of the Museum of Comparative Zoology* 140: 25–74.
- Fachini, T.S. and Iori, F.V. 2009. Primeiro registro fóssil de Squamata na região do município de Monte Alto, Estado de São Paulo (Bacia Bauru, Cretáceo Superior). *Abstracts (Livro de Resumos) of the 21st Congresso Brasileiro de Paleontologia* 172–172.
- Fachini, T.S. and Hsiou, A.S. 2011. Presence of an “anioid” snake from the Late Cretaceous of Adamantina Formation, Brazil. *Abstracts of the 4th Congreso Latinoamericano de Paleontología de Vertebrados*, 13–13.
- Gayet, M., Marshall, L.G., Sempere, T., Meunier, F.J., Capetta, H., and Rage, J.C. 2001. Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). *Biostratigraphic, palaeoecologic and palaeobiogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology*, 169: 39–68.
- Góes, A.M.O. and Feijó, F.J. 1994. A Bacia do Parnaíba. *Boletim de Geociências da Petrobras* 8: 57–67.
- Góes, A.M.O. and Rossetti, D.F. 2001. Gênese da Bacia de São Luís-Grajaú. Meio Norte do Brasil. In: D.F. Rossetti, A.M. Góes, and W. Truckenbrodt (eds.), *O Cretáceo na Bacia de São Luís-Grajaú*, 15–29. Museu Paraense Emílio Goeldi, Belém.
- Gómez, R.O., Báez, A.M., and Rougier, G.W. 2008. An anioid snake from the Upper Cretaceous of northern Patagonia. *Cretaceous Research* 29: 481–488.
- Hecht, M. 1982. The vertebral morphology of the Cretaceous snake, *Dinilysia patagonica* Woodward. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1982: 523–532.
- Hsiou, A.S., Santos, R.A.B., and Medeiros, M.A. 2009. First record of Madtsoiidae (Serpentes) from the Middle Cretaceous (Albian–Early Cenomanian) of Brazil. *Abstracts (Livro de Resumos) of the 21st Congresso Brasileiro de Paleontologia*, 90–90.
- Hsiou, A.S., Albino, A.M., and Ferigolo, J. 2010. Reappraisal of the South American Miocene snakes of the genus *Colombophis*, with description of a new species. *Acta Palaeontologica Polonica* 55: 365–379.
- Jayne, B.C. 1982. Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. *Journal of Morphology* 172: 83–96.
- Kellner, A.W.A., Pinheiro A.E.P., Azevedo, S.A.K., Henriques, D.D.R., Carvalho, L.B., and Oliveira, G. 2009. A new crocodyliform from the Alcântara Formation (Cenomanian), Cajual Island, Brazil. *Zootaxa* 2030: 49–58.
- Kellner A.W.A., Azevedo, S.A.K., Machado, E.B., Carvalho, L.B., and Henriques, D.D.R. 2011. A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. *Anais da Academia Brasileira de Ciências* 83: 99–108.
- Klein, V. de C. and Ferreira, C.S. 1979. Paleontologia e Estratigrafia de uma fácies estuarina da Formação Itapecuru, Estado do Maranhão. *Anais da Academia Brasileira de Ciências* 51: 523–533.
- LaDuke, T.C. 1991. The fossil snakes of Pit 91, Rancho La Brea, California. *Contributions in Science, Natural History Museum of Los Angeles County* 424: 1–28.
- LaDuke, T.C., Krause, D.W., Scanlon, J.D., and Kley, N.J. 2010. A Late Cretaceous (Maastrichtian) snake assemblage from the Maevarano Formation, Mahajanga Basin, Madagascar. *Journal of Vertebrate Paleontology* 30: 109–138.
- Lee, M.S.Y. and Scanlon, J.D. 2002. Snake phylogeny based on osteology, soft anatomy and ecology. *Biological Reviews* 77: 333–401.
- Lindoso, R.M., Medeiros, M.A., Carvalho, I. de S., and Marinho, T. da S. 2012. *Masiakasaurus*-like theropod teeth from the Alcântara Formation, São Luís Basin (Cenomanian), northeastern Brazil. *Cretaceous Research* 36: 119–124.
- Martinelli, A.G. and Forasiepi, A.M. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 6: 257–305.
- Medeiros, M.A. and Schultz, C.L. 2002. A fauna dinossauriana da Laje do Coringa, Cretáceo Médio do Nordeste do Brasil. *Arquivos do Museu Nacional* 60: 155–162.
- Medeiros, M.A. and Schultz, C.L. 2004. *Rayososaurus* (Sauropoda, Diplodocoidea) no meso-Cretáceo do Norte-Nordeste Brasileiro. *Revista Brasileira de Paleontologia* 7: 255–279.
- Medeiros, M.A., Freire, P.C., Pereira, A.A., Santos, R.A.B., Lindoso, R.M., Coelho, A.F.A., Passos, E.B., and Sousa, E. 2007. Another African dinosaur recorded in the Eocenomanian of Brazil and a revision on the paleofauna of the Laje do Coringa site. In: I.S. Carvalho, R.C.T. Cassab, C.S. Schwanke, M.A. Carvalho, A.C.S. Fernandes, M.A.C. Rodrigues, M.S.S. Carvalho, M. Arai, and M.E.Q. Oliveira (eds.), *Paleontologia: Cenários de Vida, Volume 1*, 413–423. Interciência, Rio de Janeiro.

- Palci, A., Caldwell, M.W., and Albino, A.M. 2013. Emended diagnosis and phylogenetic relationships of the Upper Cretaceous fossil snake *Najash rionegrina* Apesteguía and Zaher, 2006. *Journal of Vertebrate Paleontology* 33: 131–140.
- Pedraza, E., Arai, M., Barrilari, I.M.R., and Carvalho, I.S. 1993a. *Análise palinológica de uma amostra de superfície de Querru (Formação Itapecuru)*, Município de Itapecuru Mirim-MA. 11 pp. Relatório Técnico Petrobras, CENPES, Rio de Janeiro.
- Pedraza, E., Arai, M., Carvalho, I.S., and Ferreira, C.S. 1993b. *Palinómorfos de sedimentos albianos (Formação Itapecuru) da Bacia do Paranaíba*. 13 pp. Relatório Técnico Petrobras, CENPES, Rio de Janeiro.
- Pedraza, E., Arai, M., Carvalho, I.S., and Santos, M.H.B. 1993c. *Palinómorfos da Formação Itapecuru – análise palinológica de uma amostra de superfície da Ponta do Farol, São Luís-MA*. 10 pp. Relatório Técnico Petrobras, CENPES, Rio de Janeiro.
- Pereira, A.A. and Medeiros, M.A. 2008. A new Sclerorhynchiform (Elasmobranchii) from the middle Cretaceous of Brazil. *Revista Brasileira de Paleontologia* 11: 207–212.
- Rage, J.C. 1984. *Encyclopaedia of Paleoherpology, Part II, Serpentes*. 80 pp. Gustav Fischer Verlag, Stuttgart.
- Rage, J.C. 1987. Fossil history. In: R.A. Seigel, J.T.C. Collins, and S.S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, 57–76. MacMillan, New York.
- Rage, J.C. 1996. Les Madtsoiidae (Reptilia, Serpentes) du Crétacé supérieur d'Europe: témoins gondwaniens d'une dispersion trans-thésienne. *Comptes Rendus de l'Académie des Sciences, Paris, Série IIa* 322: 603–608.
- Rage, J.C. 1998. Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part I. Madtsoiidae, Aniliidae. *Palaeovertebrata* 27: 109–144.
- Rage, J.C. and Albino, A.M. 1989. *Dinilysia patagonica* (Reptilia, Serpentes): matériel vertébral additionnel du Crétacé supérieur d'Argentine. Étude complémentaire des vertèbres, variations intraspécifiques et intracolumnaires. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1989: 433–447.
- Rage, J.C. and Werner, C. 1999. Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: The earliest snake assemblage. *Palaeontologia Africana* 35: 85–110.
- Rieppel, O., Kluge, A.G., and Zaher, H. 2002. Testing the phylogenetic relationships of the Pleistocene snake *Wonambi naracoortensis* Smith. *Journal of Vertebrate Paleontology* 22: 812–829.
- Rodrigues, T.L. das N., Lovato, O.G., and Caye, B.R. 1990. Contribuição à estratigrafia da Folha de São Luís (AS. 23-Z-A)/MA. *Abstracts (Anais) of the 36th Congresso Brasileiro de Geologia* 1: 124–135.
- Rossetti, D.F. 2001. Arquitetura deposicional da Bacia de São Luís-Grajaú. In: D.F. Rossetti, A.M. Góes, and W. Truckenbrodt (eds.), *O Cretáceo na Bacia de São Luís-Grajaú*, 31–46. Museu Paraense Emílio Goeldi, Belém.
- Rossetti, D.F. 2003. Bacia de São Luís-Grajaú. *Boletim da Fundação Paleontológica Phoenix* 58: 1–9.
- Rossetti, D.F. and Truckenbrodt, W. 1997. Revisão estratigráfica para os depósitos do Albiano-Terciário Inferior (?) na bacia de São Luís (MA), norte do Brasil. *Boletim do Museu Paraense Emílio Goeldi (Série Ciências da Terra)* 9: 29–41.
- Rossetti, D.F., Góes, A.M., and Arai, M. 2001. A passagem Aptiano-Albiano na Bacia Grajaú, MA. In: D.F. Rossetti, A.M. Góes, and W. Truckenbrodt (eds.), *O Cretáceo na Bacia de São Luís-Grajaú*, 101–117. Museu Paraense Emílio Goeldi, Belém.
- Scanferla, C.A. and Canale, J.I. 2007. The youngest record of the Cretaceous snake genus *Dinilysia* (Squamata, Serpentes). *South American Journal of Herpetology* 2: 76–81.
- Scanlon, J.D. 1992. A new large madtsoiid snake from the Miocene of the Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 9: 49–60.
- Scanlon J.D. 1993. Madtsoiid snakes from the Eocene Tingamarra Fauna of eastern Queensland. *Kaupia* 3: 3–8.
- Scanlon, J.D. 1997. *Nanowana* gen. nov., small madtsoiid snakes from the Miocene of Riversleigh: sympatric species with divergently specialised dentition. *Memoirs of the Queensland Museum* 41: 393–412.
- Scanlon, J.D. 2005. Australia's oldest known snakes: *Patagoniophis*, *Alamitophis*, and cf. *Madtsoia* (Squamata: Madtsoiidae) from the Eocene of Queensland. *Memoirs of the Queensland Museum* 51: 215–235.
- Scanlon, J.D. 2006. Skull of the large non-macrostromatan snake *Yurlungur* from the Australian Oligo-Miocene. *Nature* 439: 839–842.
- Smith-Woodward, A. 1901. On some extinct reptiles from Patagonia of the genera *Miolania*, *Dinilysia*, and *Genyodectes*. *Proceedings of the Zoological Society of London* 1901: 169–184.
- Van-Tomme, M.P.A., Medeiros, M.A., and Machado, E.B. 2008. On an enigmatic theropod tibia from the Alcântara Formation (Late Cretaceous, Early Cenomanian) of Maranhão, NE Brasil. In: *6th Simpósio Brasileiro de Paleontologia de Vertebrados, 28th–30th, May, Boletim de Resumos*, 199–200. FFCLRP/USP, Ribeirão Preto.
- Vilas-Bôas, I.C.C. and Carvalho, I.S. 2001. Répteis marinhos (Mosasauria e Plesiosauria) do Cretáceo Superior da Bacia de São Luís (Maranhão, Brasil). In: D.F. Rossetti, A.M. Góes, and W. Truckenbrodt (eds.), *O Cretáceo na Bacia de São Luís-Grajaú*, 223–233. Museu Paraense Emílio Goeldi, Belém.
- Wilson, J.A., Mohabey, D.M., Peters, S.E., and Head, J.J., 2010. Predation upon hatchling dinosaurs by a new snake from the Late Cretaceous of India. *PLoS Biol* 8: e1000322.
- Zaher, H., Langer, M.C., Fara, E., Carvalho, I.S., and Arruda, J.T. 2003. A mais antiga serpente (Anilioidea) brasileira: Cretáceo Superior do Grupo Bauru, General Salgado, SP. *Paleontologia em Destaque (Boletim Informativo da Sociedade Brasileira de Paleontologia)* 18: 50.
- Zaher, H., Apesteguía, S., and Scanferla, C.A. 2009. The anatomy of the upper cretaceous snake *Najash rionegrina* Apesteguía and Zaher, 2006, and the evolution of limblessness in snakes. *Zoological Journal of the Linnean Society* 156: 801–826.
- Zaher, H. and Scanferla, C.A. 2012. The skull of the Upper Cretaceous snake *Dinilysia patagonica* Smith-Woodward, 1901, and its phylogenetic position revisited. *Zoological Journal of the Linnean Society* 164: 194–238.

Appendix 1

- Alamitophis argentinus*, MACN-RN 27, 28, and 38;
Alamitophis elongatus, MLP 88-III-31-1;
Alamitophis sp., MLP 88-III-31-12;
Rionegrophis madtsoioides, MACN-RN 32;
Patagoniophis parvus, MACN-RN 33, 34, and 35;
Dinilysia patagonica, MACN-RN 26, MACN-RN 976, 1017, and 1019; MLP 26-410, MLP 79-II-27-2 to 7, MLP 79-II-27-8 to 17.