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Source: Journal of Herpetology, 51(3):365-374.
Published By: The Society for the Study of Amphibians and Reptiles

https://doi.org/10.1670/16-031
URL: http://www.bioone.org/doi/full/10.1670/16-031

Journal of Herpetology, Vol. 51, No. 3, 365–374, 2017

The Snake Fossil Record from Brazil

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ABSTRACT.—**Brazilian fossil snakes have had a rich and diverse record since the Late Cretaceous. Here, we provide an overview of the snake fossil record from Brazil, gathering all available data to reconstruct the diversity and distribution of taxa through time. Mesozoic snakes are scarce, represented by the putative ophidian *Tetrapodophis amplectus*, the snake *Seismophis septentrionalis*, and some undescribed material referred to 'Anilioidea.' The Paleocene of São José do Itaboraí holds the richest and most-diverse Brazilian snake fauna composed of several taxa of madtsoids, 'aniloids,' boids, 'booids,' and caenophidians. Fossils from the Brazilian Neogene are reported for the Late Miocene of the Solimões Formation including boids, Colubroides, and an alethinophidian of uncertain relationships, *Colombophis*. Quaternary deposits yield a rich snake fauna represented by extant species such as boids and colubroids. The Brazilian snake fossil record is crucial for understanding issues about the early evolution of snakes and provides valuable insights into paleobiogeography, paleoenvironmental, and morphological studies.**

RESUMO.—**O Brasil possui um registro fossilífero rico e diversificado de serpentes desde o Cretáceo tardio. Neste trabalho nós fornecemos um panorama geral do registro fossilífero de serpentes no território brasileiro, compilando todos os dados disponíveis para reconstruir a diversidade e distribuição dos táxons no decorrer do tempo. Serpentes Mesozoicas são escassas, ocorrendo o possível ofídio de quatro patas *Tetrapodophis amplectus*, a *Seismophis septentrionalis* e alguns materiais ainda não descritos atribuídos a 'Anilioidea'. O Paleoceno de São José do Itaboraí detém a mais rica e diversa fauna de serpentes que é composta por espécies de madtsoideos, 'anilioideos', boídeos, 'booideos' e um cenofídeo. Fósseis do Neógeno são reportados no Mioceno da Bacia do Acre, incluindo boídeos, Colubroides e um aletinofídeo de relações incertas, *Colombophis*. Os depósitos do Quaternário detêm uma rica fauna de serpentes de espécies viventes, como boídeos e um amplo registro de Colubroideos. O registro fossilífero de serpentes brasileiras constitui uma chave crucial para o entendimento de questões sobre a evolução inicial das serpentes, além de, propiciar estudos sobre paleobiogeografia, paleoambiente e morfologia.**

Squamata constitutes the most diversified clade of reptiles today, including nearly 10,000 living species, with snakes representing almost one-third of this diversity (~3,567 spp.) (Uetz and Hošek, 2016). Besides the distribution and diversity of extant snakes, the fossil record is an important key to understanding their biogeography and evolution (Albino, 2011a). Recovered snake remains usually are vertebrae or small skull fragments but rarely complete articulated skeletons (Albino, 2011a). This pattern is because of the nature of the squamate skeleton, which generally is gracile and relatively small, requiring a suitable depositional environment for exceptional preservation (Evans, 2003). The fossil record of snakes usually comes from microvertebrate deposits like ponds, fissures, and cave fillings, but these are often disarticulated or broken remains, complicating the taxonomic assignment of the specimens and in many cases preventing further phylogenetic studies (Evans, 2003).

South America is a crucial region for understanding the origin and early evolution of snakes in Gondwana, with a rich fossil record of stem and extant taxa distributed in several localities with a well-studied and revised literature (Apesteguía and Zaher, 2006; Albino and Brizuela, 2014; Hsiou et al., 2014). In this context, Brazil has an extensive snake record from the Cretaceous (Hsiou et al., 2014; Martill et al., 2015) through the Pleistocene-Holocene, although compared to the modern fauna it still is poorly known. Here we provide an overview of the snake fossil record in Brazil, attempting to gather all the current available data to reconstruct the distribution and diversity of Brazilian fossil snakes through geological time.

MATERIALS AND METHODS

The current revision is based on the literature and uses previous reviews of the South American squamate fossil record as its main guide (Albino, 1996, 2011a; Albino and Brizuela, 2014). The paraphyletic groups throughout the text were denoted in single 'quotes' marks (e.g. 'Anilioids'). The geological time scale follows that established by the International Commission on Stratigraphic Nomenclature v2015/01 (Cohen et al., 2015).

RESULTS AND DISCUSSION

Early Brazilian Snakes.—The Mesozoic fossil record of Brazilian snakes is sparce but tells an important evolutionary story, especially on the origins and ancient lifestyle of Gondwanan snakes. The probable oldest record comes from the Aptian (Early Cretaceous) of the Nova Olinda Member, Crato Formation, Ceará (Martill et al., 2015) (Fig. 1A); it is represented by the single specimen of *Tetrapodophis amplectus*, preserved and articulated on laminated limestone, with part and counterpart (Martill et al., 2015). According to Martill et al. (2015), *Tetrapodophis* shares several osteological features with other snakes, especially among fossorial species. The skull presents a long braincase, a nasal descending lamina, and a typical short rostrum. The bowed mandible morphology has a deep subdental ridge, an intramandibular joint, and hooked unicuspidated teeth. Beyond these cranial characters, *T. amplectus* also was described as possessing >150 precloacal vertebrae with zygantrum-zygosphene articulations and a small tail (low number count of caudal vertebrae).

Moreover, *Tetrapodophis* apparently retains functional fore- and hindlimbs, interpreted as a unique combination among

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DOI: 10.1670/16-031

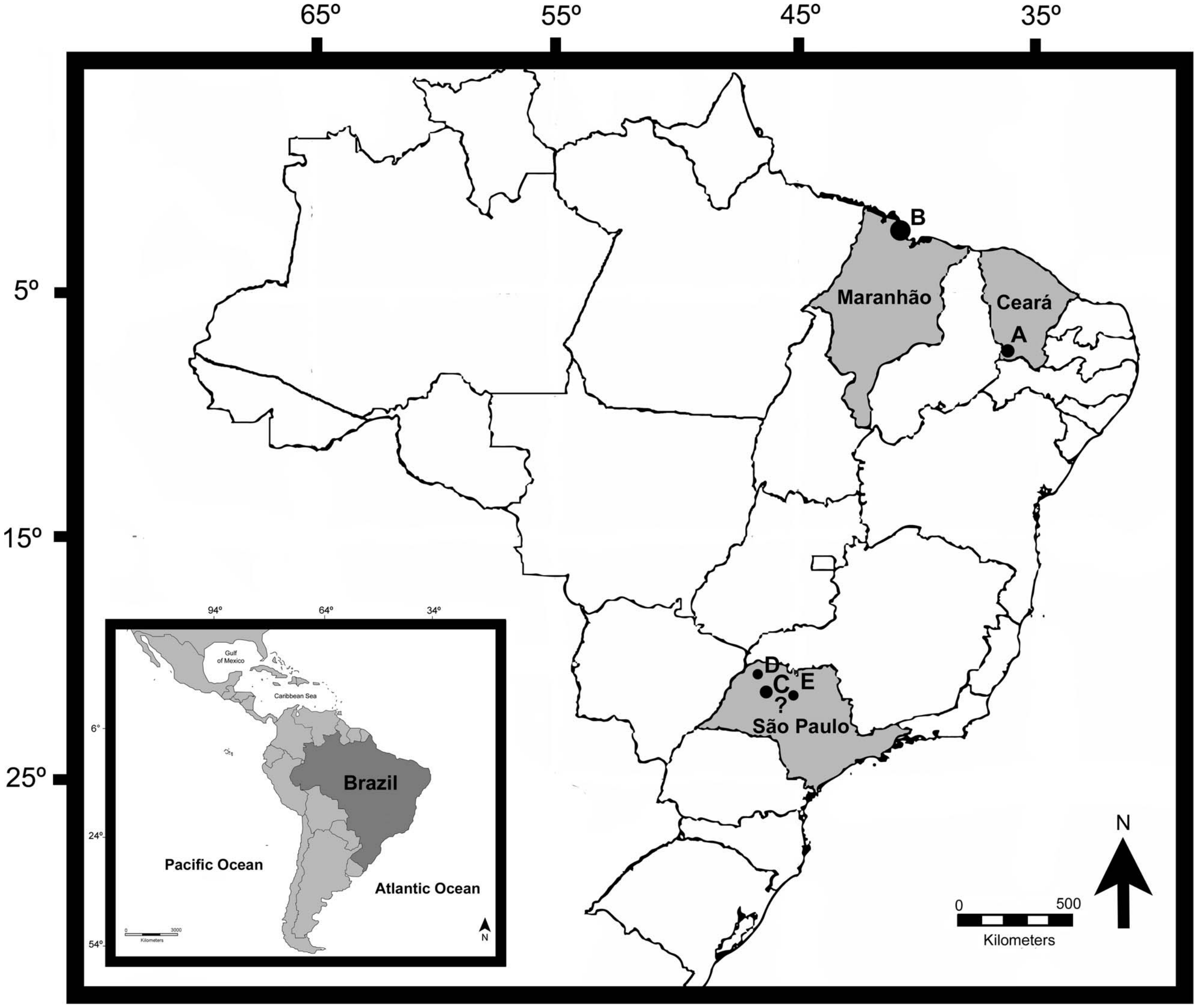

FIG. 1. Distribution of the Mesozoic snakes. (A) *Tetrapodophis amplectus* from Nova Olinda Member, Crato Formation, Ceará State (Martill et al., 2015); (B) *Seismophis septentrionalis* from Falésia do Sismito of Cajual Island, Maranhão State (Hsiou et al., 2014); (C) Indeterminate snake from Adamantina Formation, São Paulo State, the symbol '?' denotes the unknown locality in the state (Bertini and Bonfim-Júnior, 1988); (D) Indeterminate 'Anilioidea' from General Salgado, São Paulo state (Zaher et al., 2003); and (E) Indeterminate 'Anilioidea' from Monte Alto city, Adamantina Formation (Fachini and Iori, 2009; Fachini and Hsiou, 2011).

ophidians. In the phylogenetic analysis performed by Martill et al. (2015), *T. amplectus* emerges as an ophidian sister-group to the North American Cretaceous snake *Coniophis precedens* (Longrich et al., 2012), considered a burrowing fossil snake. This topology strongly suggests a fossorial origin for crown snakes (Tchernov et al., 2000; Apesteguía and Zaher, 2006; Longrich et al., 2012) rather than the alternate marine hypothesis (Caldwell and Lee, 1997; also see Palci et al., 2013). Alternatively, some current studies appointed counter morphological and systematics observations in comparison to the original description, suggesting an alternative interpretation of the specimen, criticizing the proposed affinity (Lee et al., 2016; Caldwell et al., 2016). Some characters, such as enlarged first metapodials, reduced tarsal/carpal ossification, weak girdles, high caudal vertebral count number, long skull, and the absence of intramandibular joint and snake-like teeth, are shared between *Tetrapodophis* and a variety of marine reptiles which possibly approximate the Brazilian fossil with aquatic squamates such as mosasauroids and dolichosaurs (Lee et al., 2016; Caldwell et al., 2016).

Indeed, the evolution of limblessness in tetrapods is a peculiar episode because of its multiple origins (Caldwell, 2003; Brandley et al., 2008; Evans, 2015) and several reversions through the evolution of the group (Cohn and Tickle, 1999; Caldwell, 2003; Brandley et al., 2008; Evans, 2015). Among squamates, trunk elongation often is associated with limb loss, strongly suggesting a linked developmental mechanism (Carroll, 1988; Cohn and Tickle, 1999; Caldwell, 2003). There is a clear threshold between body elongation and limb growth, with no four-limbed modern squamate having more than 70 precloacal vertebrae (Caldwell, 2003; Brandley et al., 2008).

This threshold is potentially broken in the *Tetrapodophis* case, as it retains four functional limbs with more than 150 precloacal vertebrae (Martill et al., 2015; Caldwell et al., 2016). The occurrence of a truly four-limbed snake (e.g., a specimen with Ophidia autapomorphies) in Gondwana possibly sheds light on the origins, ancient lifestyle, and biogeography of stem ophidians; however, the assignment of *Tetrapodophis* as a snake is dubious. Several lineages of squamates have suffered transitions from a lizard-like to snake-like body along their evolutionary history (e.g., dibamids, pygopodids, amphisbaenians, the Cretaceous hind-limbed snake taxa), evidencing the plasticity and the homoplasy degree of these morphological traits such as the elongated trunk body and the presence or absence of limbs (Caldwell, 2003; Brandley et al., 2008). The presence of these intermediate morphologies (e.g., limbless lizards or limbed snakes) is widespread phylogenetically during the evolutionary story of the group, even persisting in crown squamates (Caldwell, 2003; Apesteguía and Zaher, 2006; Brandley et al., 2008; Caldwell et al., 2015). This fact, together with the current reanalysis studies (Lee et al., 2016; Caldwell et al., 2016), hampers a precise assignment of *Tetrapodophis* as a snake. Additionally, evo-devo and paleontological data strongly propose an intrinsic mechanism between the Hox gene expression and regulation pattern to the expansion of the thoracic identity (Cohn and Tickle, 1999; Caldwell, 2003). Generally, this interaction results on the absence of forelimbs together with the axial trunk elongation on the development of the snake-like body plan, although this issue is still in a constant discussion (Cohn and Tickle, 1999; Head and Polly, 2015; Aires et al., 2016; Guerreiro et al., 2016).

In this sense, *Tetrapodophis* can really represent a snake fossil; however, in the present moment we prefer to recognize it as a putative ophidian. Only additional robust morphological reappraisal of the specimen can help to elucidate the systematic affinities of the fossil and avoid misinterpretation. In this case, a comprehensive anatomical description of the specimen is required because the set of derived characters appointed by Martill et al. (2015) as snake autapomorphies are somewhat questionable and the specimen was poorly described. Additional tools and methodologies, such as micro-tomography scan images and a robust phylogenetic reanalysis, can elucidate the systematics of this enigmatic fossil.

Another pertinent question concerning *Tetrapodophis* is about the obscure provenance and acquisition of the specimen. The authors do not provide a precise origin of the fossil, comparing the sediments of the rock matrix to infer the provenance from Crato Formation (see Martill et al., 2015; Supplementary Data). In addition to this case, innumerous other occurrences involving fossil trafficking from the Crato Formation were reported. Under the legislation of Brazil, federal laws protect the mineralogical materials (including fossils), and prospection without permission is considered a crime. Due to the problematic scenario, as members of Sociedade Brasileira de Paleontologia (Brazilian Society of Paleontology), here we reaffirm and draw attention to the issue about fossil trafficking in Brazil (see Langer et al., 2012).

An important and unquestionable Mesozoic snake is *Seismophis septentrionalis* (Hsiou et al., 2014), described from vertebral remains (Fig. 2A). It holds a unique combination of vertebral characters that distinguishes it from any known extant or extinct taxa (Hsiou et al., 2014). The fossil comes from Falésia do Sismito, Cajual Island, Maranhão, northeastern Brazil (Cenomanian, Early Late Cretaceous) (Fig. 1B).

The systematic affinities of *Seismophis* are still uncertain because of the poor preservation of the fossils and the limited phylogenetic information based only on vertebrae. The specimens retain a set of plesiomorphic characters such as the higher level of inclination of the prezygapophysis, the absence of a prezygapophyseal process, and the shallow posterodorsal notch. These plesiomorphic conditions are shared between the Brazilian fossil, the hind-limbed *Najash*, and the Patagonian snake *Dinilysia* (Rage and Albino, 1989; Zaher et al., 2009a; Hsiou et al., 2014).

In spite of these primitive conditions, *Seismophis* also shows derived conditions such as the presence of paired parazygantral foramina (seen in Madtsoiidae; Lee and Scanlon, 2002; Wilson et al., 2010) and the presence of parasagittal ridges that strongly resemble the laminar crest present in boids such as *Boa*, *Eunectes*, and *Chubutophis* (Albino, 2011b; Hsiou et al., 2014; Onary-Alves et al., 2016). Even with its phylogenetic affinities not defined, the combination of derived and plesiomorphic conditions on this taxon makes the fossil an interesting taxon to be investigated to interpret the early snake evolution, especially when compared with the Argentinean Cretaceous snake taxa (Hsiou et al., 2014).

The Late Cretaceous (Turonian-Santonian) Adamantina Formation, Bauru Group, contains records of snake vertebrae from several localities in São Paulo State, but the materials are still undescribed. Bertini and Bonfim-Júnior (1998) briefly reported the occurrence of isolated vertebra attributed to an indeterminate snake from the Adamantina Formation, São Paulo, unknown site (Fig. 1C). In General Salgado, Zaher et al. (2003) reported the presence of articulated midtrunk vertebrae attributed to an indeterminate 'Anilioidea' based on vertebral morphology (Fig. 1D). The material reportedly can represent a new taxon, differing from previous described fossils and extant taxa; however, it is still undescribed. Later, Fachini and Iori (2009) followed by Fachini and Hsiou (2011) provided the first record of an 'anilioid' snake for the Monte Alto region (Fig. 1E). Morphological features are similar to those of the material reported by Zaher et al. (2003) and, likewise, remain undescribed.

The Rich and Diverse Paleogene Snake Fauna.—The Paleogene of Brazil has a rich and diverse snake fauna restricted to the Paleocene of São José do Itaboraí, Rio de Janeiro (Rage, 1998, 2001, 2008). These remains come from different fissure fillings that unfortunately have confused the age of the deposits. There is temporal reworking and no record of the provenance of each specimen. Some authors consider the locality as Middle Paleocene (Muizon and Brito, 1993; Rage, 1998) with only minor variation in age (Van Valen, 1988); however, others authors suggest Early Eocene age (Gayet et al., 1991; Gelfo et al., 2009). Here we adopt the position of Rage (1998), accepting a Middle Paleocene age for the São José do Itaboraí deposits.

Itaboraí represents the most diverse deposit with fossil squamates in South America (Carvalho, 2001). Regarding the snake record, Madtsoiidae, 'Aniliidae,' Boidae, 'booids,' and a single caenophidian were recorded (Albino, 1990; Rage, 1998, 2001, 2008).

Madtsoiidae represents an extinct family of snakes known from the Late Cretaceous to the Pleistocene (Scanlon and Lee, 2000). The only genus recorded in the Brazilian Paleocene is *Madtsoia*, represented by a single species: *M. camposi* (Fig. 2B, 3A) (Rage, 1998). Within the worldwide diversity of Madtsoiidae, *M. camposi* retains a unique combination of vertebral features that, together with the mandibular traits, support the validity of this taxon (Rage, 1998). Although phylogenies based only on vertebral features are unusual, Madtsoiidae is considered a monophyletic group and *M. camposi* belongs to a clade with medium-to-large taxa, together with the Australian *Wonambi* and *Yulunggur*, the European *Gigantophis* and *Menarana*, and the Indian *Sanajeh* (for systematic review see Vasile et al., 2013:fig. 5A,B).

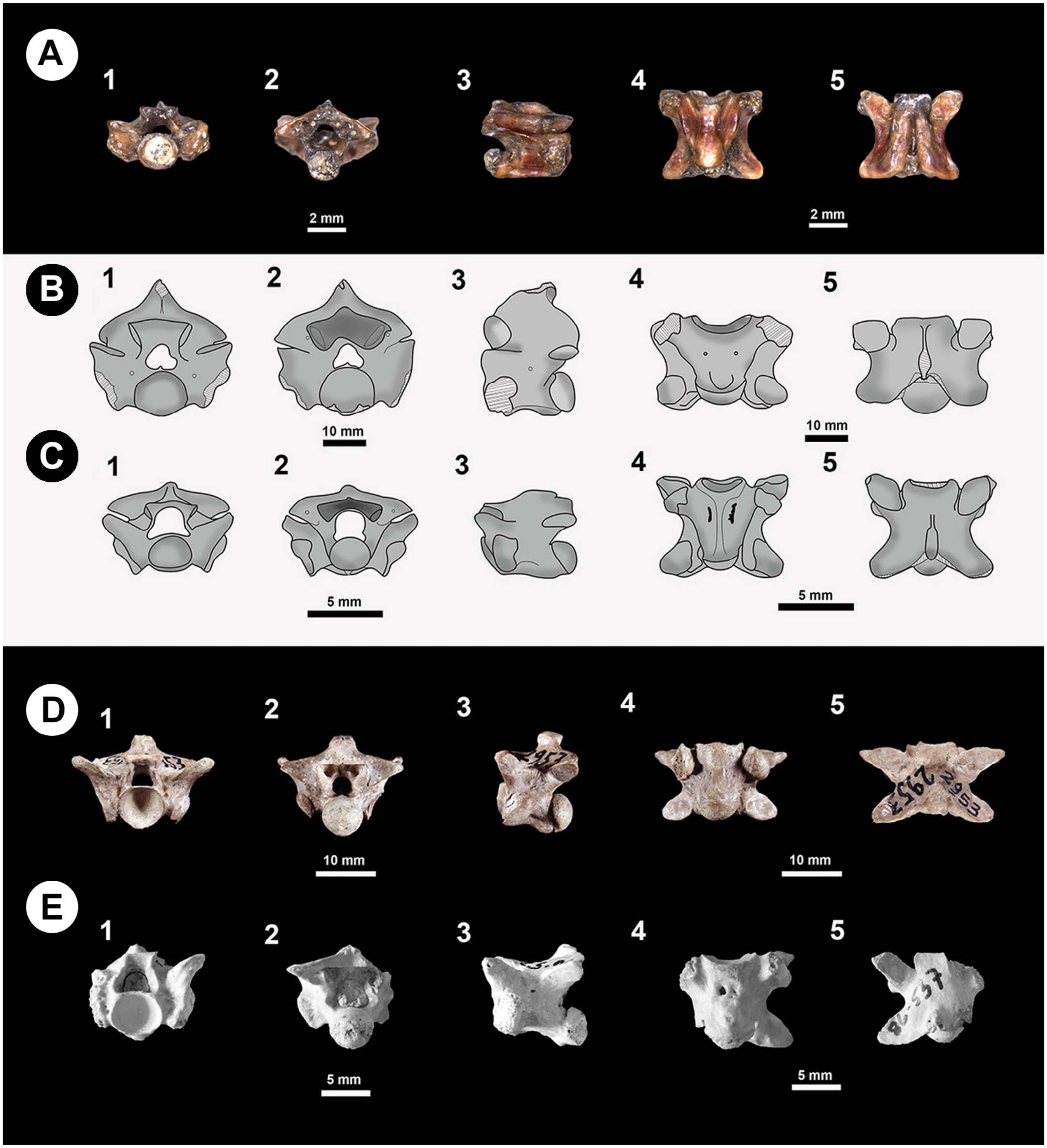

FIG. 2. Main fossil snakes species from Brazil showing the typical preservation found in the country, isolated precloacal vertebrae. (A) *Seismophis septentrionalis*; (B) schematic drawing of *Madtsoia camposi* (modified from Rage, 1988); (C) schematic drawing of *Hoffstetterella brasiliensis* (modified from Rage, 1988); (D) *Colombophis spinosus* (modified from Hsiou et al., 2010); and (E) *Colombophis portai* (modified from Hsiou et al., 2010). In (1) anterior; (2) posterior; (3) lateral; (4) ventral; and (5) dorsal views.

Traditionally, 'Anilioidea' is considered a clade sister group to all Macrostomata (Rage, 1984; Lee and Scanlon, 2002). Some studies support the group as a clade (Rieppel, 1988; Kluge, 1991), but current analyses accept them as paraphyletic (Tchernov et al., 2000; Lee and Scanlon, 2002; Reeder et al., 2015). The Paleocene of São José de Itaboraí bears two snakes initially attributed to 'Aniliidae': *Coniophis* cf. *C. precedens* (Fig. 3B) and *Hoffstetterella brasiliensis* (Albino, 1990; Rage, 1998) (Fig. 3C). Both taxa display the overall vertebral morphology that allows their assignment to 'Aniliidae,' but these are symplesiomorphic characters that hamper a precise diagnosis for the group (Rage, 1998).

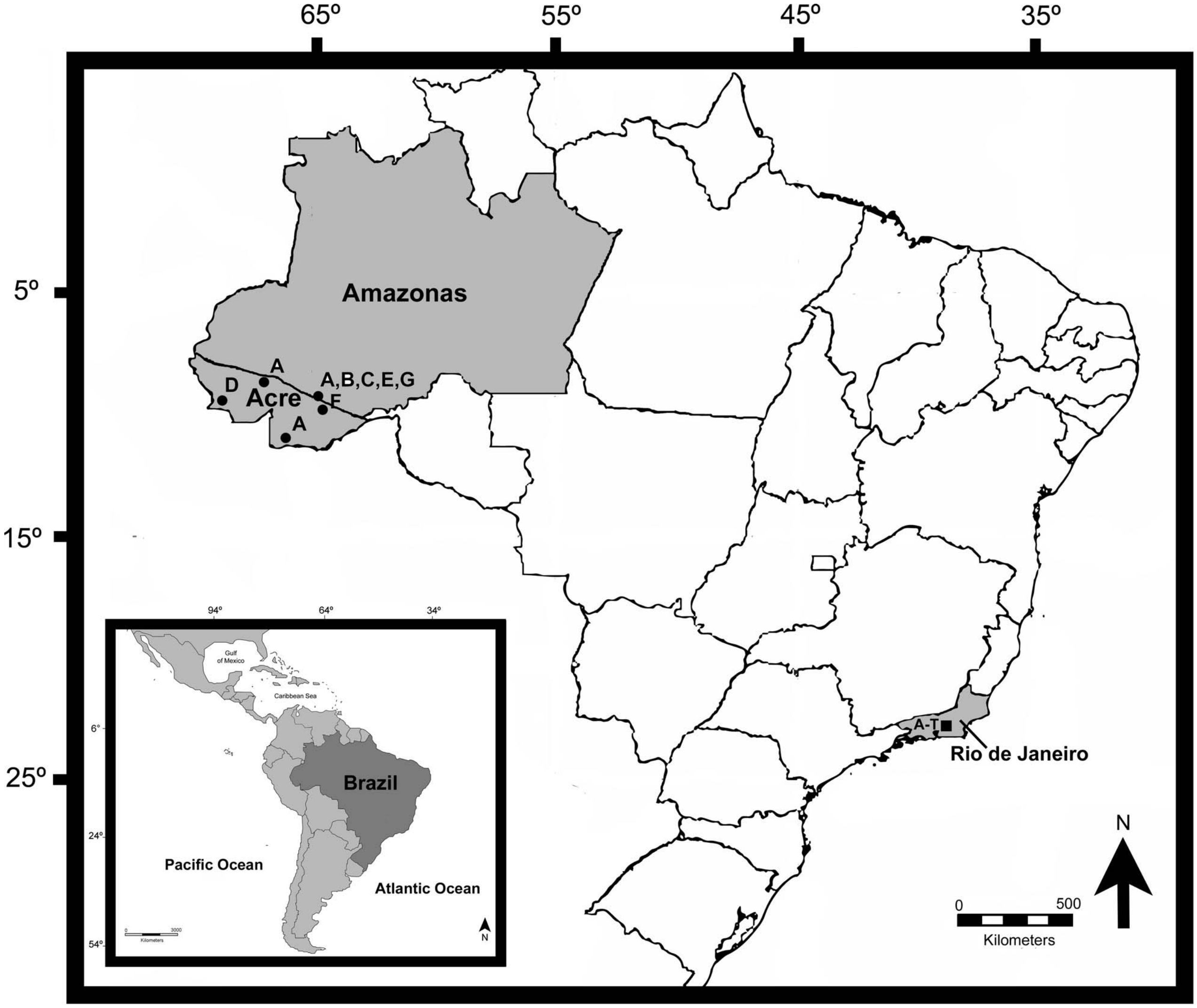

FIG. 3. Distribution of the Paleogene snakes (square symbol). All material comes from the Middle Paleocene of São José do Itaboraí, Rio de Janeiro. (A) *Madtsoia camposi* (Rage, 1998); (B) *Coniophis* cf *C. precedens* (Rage, 1998); (C) *Hoffstetterella brasiliensis* (Rage, 1998); (D) *Hechtophis austrinus* (Rage, 2001); (E) cf. *Hechtophis* (Rage, 2001); (F) *Corallus pricus* (Rage, 2001); (G) cf. *Corallus* (Rage, 2001); (H) *Waincophis pressulus* (Rage, 2001); (I) *Waincophis cameratus* (Rage, 2001); (J) cf. *W. pressulus* (Rage, 2001); (K) cf. *W. cameratus* (Rage, 2001); (L) cf. *Waincophis* (Rage, 2001); (M) Boinae A (Rage, 2001); (N) Boinae B (Rage, 2001); (O) Indeterminate boine (Rage, 2001); (P) *Paraungaliophis pricei* (Rage, 2008); (Q) cf. *Paraungaliophis* (Rage, 2008); (R) *Itaboraiophis depressus* (Rage, 2008); (S) *Paulacoutophis perplexus* (Rage, 2008); and (T) ?Russellophiidae (Rage, 2008). Distribution of the Neogene snakes (circle symbol).All material comes from the Late Miocene of Solimões Formation. (A) *Colombophis portai* from the Morro do Careca and Patos, Acre State; Talismã locality, Amazonas state locality (Hsiou et al., 2010); (B) *Colombophis spinosus* from Talismã locality, Purus River, Amazonas State (Hsiou et al., 2010); (C) aff. *Epicrates* from Talismã locality, Purus River, Amazonas State (Hsiou and Albino, 2010); (D) *Waincophis* sp. from Belford locality, Upper Juruá River, Belford site (Hsiou and Albino, 2010); (E) *Eunectes* sp. from Talismã locality, Purus River, Amazonas State (Hsiou and Albino. 2009); (F) Indeterminate 'Colubridae' A from Lula locality near Sena Madureira city, Amazonas State (Hsiou and Albino, 2010); and (G) Indeterminate 'Colubridae' B from Talismã locality, Purus River, Amazonas State (Hsiou and Albino, 2010).

The Brazilian specimens of *Coniophis* show a vertebral morphology similar to the North American species, but no autapomorphic features support the assignment of the fossil to the species *C. precedens* (Rage, 1998). Additionally, Longrich et al. (2012), based on new fossils attributed to the genus (with skull elements), proposes a phylogenetic hypothesis that recognized the genus *Coniophis* as a stem-snake. This fact made unclear the placement of the genus within 'Aniliidae' which consequently affected the taxonomic identity of the Brazilian putative *Coniophis* cf. *C. precedens*.

The single record of 'Aniliidae' from the Middle Paleocene of São José do Itaboraí is *Hoffstetterella brasiliensis* (Fig. 2C) (Rage, 1998). The specimen consists of vertebral remains with the typical 'anilioid' morphology. Nevertheless, diagnostic features make it divergent from all known fossil and extant species (Rage, 1998). The dubious phylogenetic relations of 'Aniliidae,' especially regarding the fossil taxa, make inferring the systematic position of *H. brasiliensis* difficult. Accordingly, a review of all *Hoffsteterella* material has potential to show unexpected results, as in the cases of *Coniophis* (Longrich et al., 2012) and *Colombophis* (Hsiou et al., 2010).

The Paleocene of São José do Itaboraí has a rich boid fossil record that can help unravel questions about morphology, systematics, and paleobiogeography of the group. Almost all specimens belong to the subfamily Boinae (sensu Kluge, 1991; Rage, 2001), but *Hechtophis austrinus* (Fig. 3D–E) was initially attributed to Erycinae (Rage, 2001). Usually, the assignment to this subfamily is based on postcloacal vertebral features such as short additional processes and a thickened neural spine

FIG. 4. Distribution of the Quaternary snakes. (A) *Eunectes murinus* from Gruta do Urso, Tocantins (Hsiou et al., 2013) and Lapa dos Brejões, Morro do Chapéu, Bahia (Camolez and Zaher, 2010); (B) *Eunectes* sp. from Buraco do Japonês, Bonito city, Mato Grosso do Sul (Camolez and Zaher, 2010); (C) *Boa constrictor* from Caverna Carneiro, Goiás state; Morro do chapéu, Bahia state, and Lapa do Santo, Lapa das Boleiras, and Lapa do Boquete, Minas Gerais state (Camolez and Zaher, 2010); (D) *Epicrates cenchria* from Lapa do Santo, Lapa das Boleiras, and Lapa do Boquete from Minas Gerais (Camolez and Zaher, 2010); (E) cf. *Epicrates* from speological province of Ubajara, Ceará (Hsiou and Albino, 2010); (F) *Corallus* cf. *C. hortullanus* from Caverna Carneiro, Goiás and Lapa do Boquete, Minas Gerais state (Camolez and Zaher, 2010); (G) *Chironius* sp. from Gruta Cuvieri, Lapa do Santo and Lapa das Boleiras, Minas Gerais states (Camolez and Zaher, 2010); (H) *Tantilla* sp. from Abismo Ponta de Flecha, Iporanga city, São Paulo state (Camolez and Zaher, 2010); (I) cf. *Pseustes sulphureus* from Gruta Cuvieri, Matozinhos city, Minas Gerais state (Camolez and Zaher, 2010); (J) cf. *Mastigodryas bifossatus* from Caverna Carneiro, Goiás state, Lapa dos Brejões, Bahia state, and Lapa do Santo, Minas Gerais state (Camolez and Zaher, 2010); (K) Indeterminated 'Colubridae' from Abismo Ponta de Flecha, Iporanga, São Paulo state and Lapa do Santos, Matozinhos, Minas Gerais state (Camolez and Zaher, 2010); (L) *Helicops leopardinus* from Lapa das Boleiras, Matozinhos, Minas Gerais state (Camolez and Zaher, 2010); (M) cf. *Philodryas* from Lapa do Santo, Matozinhos, Minas Gerais state (Camolez and Zaher, 2010); (N) Indeterminate Pseudoboini from Caverna Nossa Senhora Aparecida, Goiás state and Abismo Ponta de Flecha, Iporanga, São Paulo (Camolez and Zaher, 2010); (O) Indeterminate Xenodontinae from Abismo Ponta de Flecha, Iporanga, São Paulo state and Lapa do Santo, Matozinhos, Mina Gerais state (Camolez and Zaher, 2010); (P) Indeterminate Dipsadinae from Caverna Nossa Senhora de Aparecida, Goiás state (Camolez and Zaher, 2010); (Q) *Micrurus corallinus* from Abismo Ponta de Flecha, Iporanga, São Paulo state (Camolez and Zaher, 2010); (R) *Micrurus* sp. from Abismo Ponta de Flecha, Iporanga, São Paulo state (Camolez and Zaher, 2010); (S) *Bothrops* sp. from speleological province of Ubajara, Ceará state and Caverna Carneiro, Goiás state, Lapa do Santo and Lapa do Boquete, Minas Gerais state (Camolez and Zaher, 2010); (T) *Crotallus durissus* from Lapa dos Brejões, Bahia state and Lapa do Santo, Lapa do Boquete from Minas Gerais state (Camolez and Zaher, 2010); and (U) Indeterminate Viperidae from Mississippi locality/Estirão do Mississipi, Upper Juruá river, Acre state (Hsiou and Albino, 2011).

with expanded tips (Hofstetter and Rage, 1972). The marked shortness of the specimens, together with the absence of additional diagnostic traits on the postcloacal vertebrae, led Rage (2001) to assign the species to Erycinae. Yet, a subsequent reappraisal of the holotype and comparisons with the extant genus *Epicrates* showed that the relation of *Hechtophis* is controversial, as the genus shares features with *Epicrates* and no characteristic appears to be exclusive. Accordingly, *H. austrinus* was attributed to Boidae incertae sedis (Rage, 2008).

As for the Boinae remains, there are five or six described species including the extant genus *Corallus* (Rage, 2001). Its record in the Middle Paleocene of São José do Itaboraí is considered the oldest for an extant boid (Head, 2015). Although the fossil shows the morphology of *Corallus*, it has sufficient autapomorphies to be considered a species distinct from all

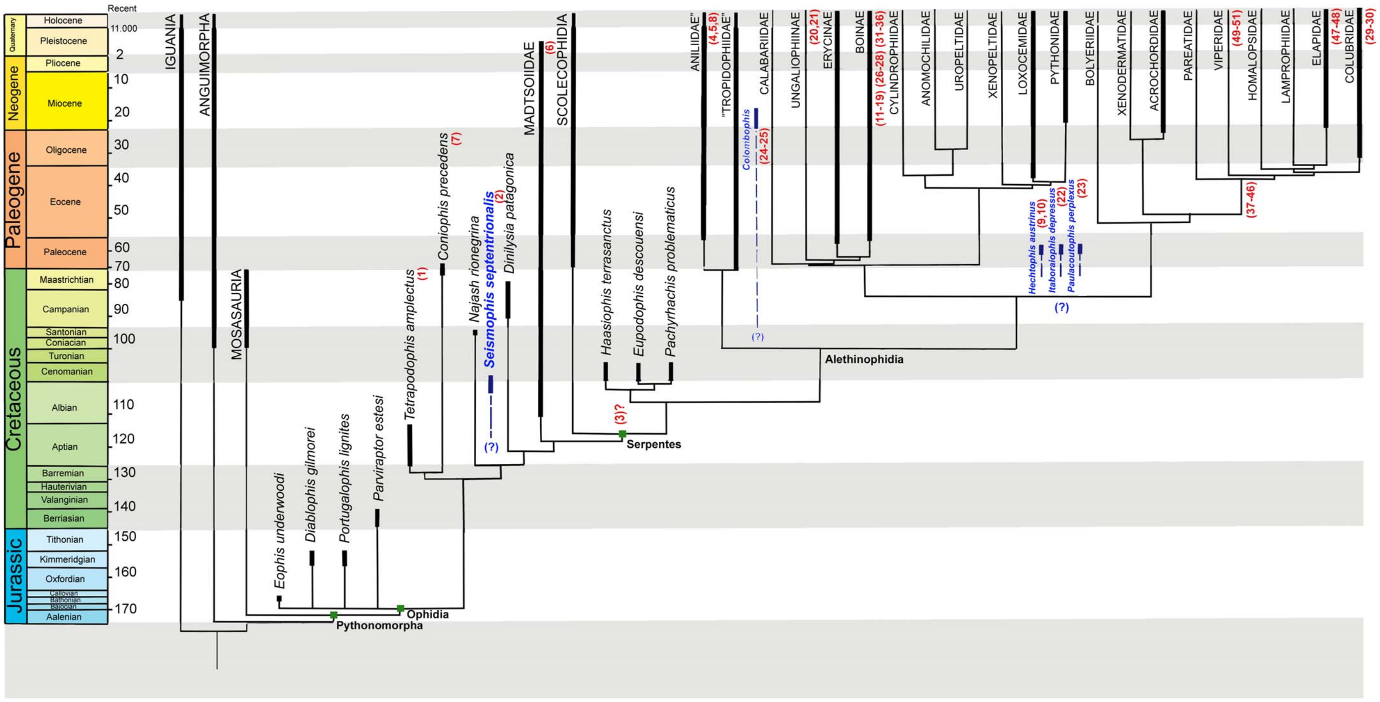

FIG. 5. Fossil snakes from Brazil plotted into the phylogenetic hypothesis of Martill et al. (2015) (Modified from Martill et al., 2015). Dashed lines indicate the dubious relationships based only on vertebral morphology. (1) *Tetrapodophis amplectus*; (2) *Seismophis septentrionalis*; (3) Indeterminate snake; (4) Indeterminate 'Anilioidea'; (5) Indeterminate 'Anilioidea'; (6) *Madtsoia camposi*; (7) *Coniophis* cf *C. precedens*; (8) *Hoffstetterella brasiliensis*; (9) *Hechtophis austrinus* (10) cf. *Hechtophis*; (11) *Corallus pricus*; (12) cf. *Corallus*; (13) *Waincophis pressulus*; (14) *Waincophis cameratus*; (15) cf. *W. pressulus*; (16) cf. *W. cameratus*; (17) cf. *Waincophis*; (18) Boinae A; (19) Boinae B; (20) *Paraungaliophis pricei*; (21) cf. *Paraungaliophis*; (22) *Itaboraiophis depressus*; (23) *Paulacoutophis perplexus*; (24) *Colombophis portai*; (25) *Colombophis spinosus*; (26) aff. *Epicrates*; (27) *Waincophis* sp.; (28) *Eunectes* sp.; (29) Indeterminate 'Colubridae' A; (30) Indeterminate 'Colubridae' B; (31) *Eunectes murinus*; (32) *Eunectes* sp.; (33) *Boa constrictor*; (34) *Epicrates cenchria*; (35) cf. *Epicrates*; (36) *Corallus* cf. *C. hortullanus*; (37) *Chironius* sp. (38) *Tantilla* sp.; (39) cf. *Pseustes sulphureus*; (40) cf. *Mastigodryas bifossatus*; (41) Indeterminate 'Colubridae'; (42) *Helicops leopardinus*; (43) cf. *Philodryas*; (44) Indeterminate Pseudoboini; (45) Indeterminate Xenodontinae; (46) Indeterminate Dipsadinae; (47) *Micrurus corallinus*; (48) *Micrurus* sp.; (49) *Bothrops* sp.; (50) *Crotallus durissus*; and (51) Indeterminate Viperidae.

extant forms and was described as *Corallus priscus* (Rage, 2001) (Fig. 3F–G). This early Paleogene Brazilian taxon is a crucial component of evolutionary studies of Neotropical boines, as its occurrence constrains the divergence of the clade at ± 50 million years (Ma) (Head, 2015).

The genus *Waincophis* was attributed to Boinae based on the overall morphology (Rage, 2001), although there is no formal phylogenetic study of the taxon. The material attributed to *Waincophis* is diverse and abundant, comprising two species (*W. pressulus* and *W. cameratus*), plus additional material tentatively attributed to the latter species (Rage, 2001) (Fig. 3H–L). The systematic relation of *Waincophis* is still unclear, but Rage (2001) reviewed its vertebral morphology and proposed a Boinae affinity. The proposal has little support but still is followed by some authors (Hsiou et al., 2010).

Indeterminate boines also are known from the São José do Itaboraí deposits but, in the absence of additional vertebral information, were not assigned to a given Boinae genus and species (Boinae A and Boinae B; Fig. 3M–N) (Rage, 2001). These fossils bear features that distinguish them at the specific level from all other boines from Itaboraí, but the low number of specimens prevents a certain identification (Rage, 2001). Finally, another indeterminate boine (Fig. 3O) was described based on dentary material, but the lack of diagnostic features hampers refining its taxonomic identity (Rage, 2001).

The "advanced snakes," a group of macrostomatans with dubious relationships that comprise ungaliophiines, 'tropidophiids,' bolyeriines, and caenophidians (sensu Kluge, 1991; Lee and Scanlon, 2002), are represented in São José do Itaboraí by *Paraungaliophis pricei* (Fig. 3P–Q) described from vertebral materials (Rage, 2008). The snakes *Itaboraiophis depressus* (Fig. 3R) and *Paulacoutophis perplexus* (Fig. 3S) also represent advanced snakes (=Booids-grade, sensu Rage, 2008), but these are of non-ungaliophiinae advanced snakes as the vertebrae retain 'booid' features (sensu Rage, 2008). Yet, the absence of ungaliophiine/'tropidophiid" characters (Rage, 2008) allowed the allocation of these taxa as Booid-grade incertae sedis, representing Middle Paleocene snakes of uncertain affinities (Rage, 2008).

There is only a single record of a caenophidian in Itaboraí represented by a posteriormost midtrunk vertebra (Rage, 2008). The fossil was dubiously recognized as ?Russellophiidae (Fig. 3T) based on the combination of vertebral features that resembles the taxon *Russellophis tenuis* Rage, 1975 from the early Eocene (Ypresian) of Condé-en-Brie (France) (Rage, 2008). The fragile attribution is because of the possible intervertebral differences of the specimen, as no posterior-most vertebrae of russellophiids were described and the available comparative material consists in midtrunk specimens (e.g., *R. crassus*, *R. tenuis*, and *Krebsophis tobanus*) (Rage, 2008). The precise taxonomic assignment made by Rage (2008), if confirmed as belonging to rusellophiids, will represent the first record of a member of Russellophiidae in America, expanding the paleobiogeographical range of the family (Rage, 2008).

Neogene Fossil Snakes.—Snake remains from the Brazilian Neogene are concentrated in the Late Miocene of the Solimões Formation, southwestern Amazonia, and are represented mainly by extant species with the exception of the extinct *Colombophis*

(Fig. 2C–D). *Colombophis* was originally described from *Colombophis portai*, from the Middle Miocene of Colombia, and allocated into the 'Aniliidae' (Hoffsteter and Rage, 1977; Hecth and LaDuke, 1997). This review identified the presence of *C. portai* (Fig. 3A) as well as a second species of *Colombophis*, *C. spinosus* (Fig. 3B), also showing morphological evidence that recognizes this genus as aletinophidian of uncertain affinity. According to Hsiou et al. (2010), *C. spinosus* shares vertebral features with the stem-snake *Dinilysia patagonica* (Albino and Caldwell, 2003), suggesting a semiburrowing or semiaquatic lifestyle, shedding light on the paleoenvironmental interpretation of the Solimões Formation (Hsiou et al., 2010). If studied under a more nesting systematics approach, this taxon could help understand alethinophidian evolution.

Boines comprise three taxa from the Late Miocene of southwestern Brazilian Amazonia: aff. *Epicrates*, *Waincophis* sp., and *Eunectes* sp. (Fig. 3C–E) (Hsiou and Albino, 2009, 2010). The presence of aff. *Epicrates* in the Late Miocene of Solimões Formation could represent the earliest record of the genus, corroborating molecular studies that estimated the origins of the clade in the Early Miocene or before (Noonan and Chippindale, 2006).

Hsiou and Albino (2010) described two indeterminate 'Colubridae' based on isolated vertebral material (Fig. 3F–G). A major problem within the systematics of Colubroidea (sensu Zaher et al., 2009b) is the absence of postcranial synapomorphies and the lack of diagnostic vertebral features among 'Colubridae' (Zaher, 1999), hampering the precise taxonomic assignment of 'colubrid' fossils. The Solimões Formation material shares a typical 'colubrid' vertebral morphology, but only an extensive comparative study can refine the taxonomic status of these specimens.

Overview of Quaternary Fossil Snakes.—The Brazilian Quaternary fossil record of snakes is rich and diverse and mainly registered in karstic systems (Fig. 4) (Camolez and Zaher, 2010; Hsiou and Albino, 2011; Hsiou et al., 2012, 2013). An extensive work of Camolez and Zaher (2010) dealt with most of the recovered fossils represented by boines, viperids, elapids, and 'colubrids.' Other additional reports complement the survey (Hsiou and Albino, 2011; Hsiou et al., 2012, 2013). These specimens represent mainly extant species identified from fragmentary vertebrae and/or cranial remains and often associated with archaeological sites.

The Quaternary Boinae record comprises four current Neotropical genera: *Eunectes*, *Boa*, *Corallus*, and *Epicrates* (Camolez and Zaher, 2010; Hsiou and Albino, 2011; Hsiou et al., 2012, 2013). On other hand, several Colubroides (sensu Zaher et al., 2009b) were discovered in Pleistocene gravels, and the materials are well diversified including the groups Colubroidea, Elapoidae, and Viperidae (sensu Zaher et al., 2009b).

Among Colubroidea, several specimens of Colubridae (sensu Zaher et al., 2009b) were recovered such as *Chironius* sp., *Tantilla* sp., cf. *Pseustes sulphureus*, and cf. *Mastigodryas bifossatus* (Camolez and Zaher, 2010). Dipsadidae is represented by *Helicops leopardinus*, cf. *Philodryas*, and indeterminate vertebral remains attributed to Pseudoboini, Xenodontinae, and Dipsadinae (Camolez and Zaher, 2010).

The fossil record of Elapoidae is restricted to Elapidae and represented by the species *Micrurus corallinus* and an isolated midtrunk vertebra of *Micrurus* sp. (Camolez and Zaher, 2010). Finally, Viperidae is recorded based on some vertebral remains attributed to *Bothrops* sp. and *Crotalus durissus* (Camolez and Zaher, 2010; Hsiou et al., 2012), with only a single record of an indeterminate Viperidae from the late Pleistocene of the Amazon (Hsiou and Albino, 2011).

The presence of fossil snakes on karstic systems is related to the propitious environment for fossilization, once these sites represent true "natural traps." Additionally, the great diversity of Quaternary Colubroides remains is consistent with the fossil record, showing the decline of boids since the Oligocene, followed by the diversification of Colubroides starting in the Miocene (Albino and Montalvo, 2006) and reaching the apex in the Neogene/Quaternary (Rage, 1998).

CONCLUSIONS

This overview compiles the main occurrences of fossil snakes in Brazil (Fig. 5). The presence of stem taxa is important to understand questions about snake origins in Gondwana; however, the assignment of *Tetrapodophis* as a snake remains uncertain because of the poor morphological understanding of the specimen. The richness and abundance of snakes in Paleogene sites bring morphological data that can help understand snake evolution. Neogene deposits provide a valuable fossil record for understanding paleoenvironmental changes, especially regarding the ancient territory of the Amazon rainforest. Fossils of extinct snakes can help in understanding the presence and its implications of alethinophidians of uncertain relationships in the late Miocene of Amazonia. Quaternary deposits yield rich records of the modern fauna that can give insights about the current diversity of snakes and about paleoenvironmental changes during the Pleistocene-Holocene boundary. Despite these records, the snake fauna of Brazil retains three major temporal gaps corresponding to the Eocene, Oligocene, and Pliocene (Fig. 5). Most of the fossil snake record is biased by the nature of the preservation, thus hampering precise phylogenetic inferences. Yet, they are valuable to better understand the biogeography, paleoenvironment, and morphology of fossil snakes and also can provide phylogenetic interpretations.

Acknowledgments.—We thank the Brazilian agencies Fundação de Amparo à Pesquisa do Estado de São Paulo (grant to ASH, FAPESP Process n. 2011/14080-0) and Coordenação de Aperfeioamento de Pessoal de Nível Superior (grant to SYOA and TSF, CAPES Master Science Fellowship) for their financial support. We are deeply grateful to the reviewer M.W. Caldwell and the anonymous reviewer 2 for their valuable insights and help to improve the manuscript, to M.C. Langer (FFCLRP/USP), F. Burbrink (AMNH) for critical reading, suggestions, and language revision of the early version of the manuscript, and to the associate editor and co-editor (T. Doan) of the *Journal of Herpetology* who helped us in the submission and revision process. Our special thanks to T. Simões (University of Alberta, Canada) and S. Apesteguía (Universidade Maimónides, Argentina) for the invitation to contribute to this special issue of the *Journal of Herpetology*.

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Accepted: 1 March 2017.

Supplementary Data

Supplementary data associated with this article can be found online at http://dx.doi.org/10.1670/16-031