Presence of the Genus *Eunectes* (Serpentes, Boidae) in the Neogene of Southwestern Amazonia, Brazil

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Abstract.—The extant genus *Eunectes* was first reported for the Middle Miocene of Colombia, represented by the extinct species *Eunectes stirtoni*. Here, we describe vertebral remains referable to this genus collected in the Neogene Solimões Formation at the Talismã locality, situated on the right-hand bank upstream of the Purus River, in the South of Amazonas State, Brazil. The material consists of isolated mid- and posterior trunk vertebrae characterized by the following combination of features that distinguishes the genus from other Neotropical boids: large size, slightly depressed neural arch, relatively low neural spine, robust and moderately thick zygosphene, with a prominent median tubercle, paracotylar foramen irregularly present, and a strong lateroventral projection of the paradiapophyses on the posterior trunk vertebrae. The presence of *Eunectes* in the Solimões Formation represents the first fossil record of snakes from the southwestern Brazilian Amazonia and supports the origin of this genus in the Miocene or before.

The Neotropical boids, represented by the genera *Boa, Corallus, Epicrates,* and *Eunectes,* constitute a well-supported clade of snakes (Burbrink, 2005; Noonan and Chippindale, 2006). The genus *Eunectes* (Anacondas) includes large semiaquatic snakes that occur in rivers and fresh water lakes, from Venezuela and Colombia to Argentina (Peters and Oreja-Miranda, 1970; Stafford, 1986). Currently, four species are recognized: *Eunectes murinus, Eunectes deschauenseei, Eunectes notaeus,* and *Eunectes beniensis.* Among them, the Green Anaconda, *E. murinus,* has the broadest distribution, occurring in forested environments of Bolivia, Brazil, Colombia, Ecuador, Guiana, French Guiana, Peru, Trinidad, and Venezuela. *Eunectes deschauenseei* (Dark-Spotted Anaconda) lives in the savanna of northeastern Brazil (including Marajó Island) and the coastal regions of French Guiana, whereas *E. notaeus* (Yellow Anaconda) occurs in Mato Grosso State of Brazil and eastern Bolivia to northern Argentina (Henderson et al., 1995). The least known species is *E. beniensis* (Beni Anaconda), restricted to Bolivia (Dirksen, 2002). Despite its broad recent distribution, fossils of the genus *Eunectes* are known only from the Middle Miocene of Colombia and represented by the extinct species *Eunectes stirtoni* (Hoffstetter and Rage, 1977). However, the validity of this species has been questioned (Hecht and La-Duke, 1997).

The aim of this paper is to describe the vertebral remains of snakes referable to the genus *Eunectes* coming from the probable Late Miocene Solimões Formation at the Talismã locality (southwestern Brazilian Amazonia) and to discuss their significance.

Geological Setting and Biochronology.—The vertebral remains were collected at the fossiliferous locality of Talismã (08°48′22″S, 68°48′12″W), situated on the right-hand bank upstream of the Purus River, in Amazonas State, between the mouth of the Iaco River and the municipality of Manuel Urbano, Brazil (Fig. 1A). According to Cozzuol (2006), the section is dominated by fine sediments, mainly silts and clays, with gypsum and calcite veins in the lower part and manganese stains in the upper part, both probably digenetic. The deposits are characterized by massive bedding with no evident lamination. Two fossiliferous levels were found at 1.7 and 7 m above water level (Fig. 1B).

The age of the fossils found in the Solimões Formation at Talismã and their relations to other South American fossiliferous localities are controversial because of poorly established correlations between the different stratigraphical levels of the distinct fossiliferous localities where the formation is exposed, which is further complicated by the absence of radiometric datings (Cozzuol, 2006; Latrubesse et al., 2007). According to Latrubesse (1992) and Latrubesse et al. (1997), the mammal fauna of Southwestern Brazilian Amazonia was deemed to correspond to the Huayquerian (Late Miocene) and possibly reached the Montehermosan
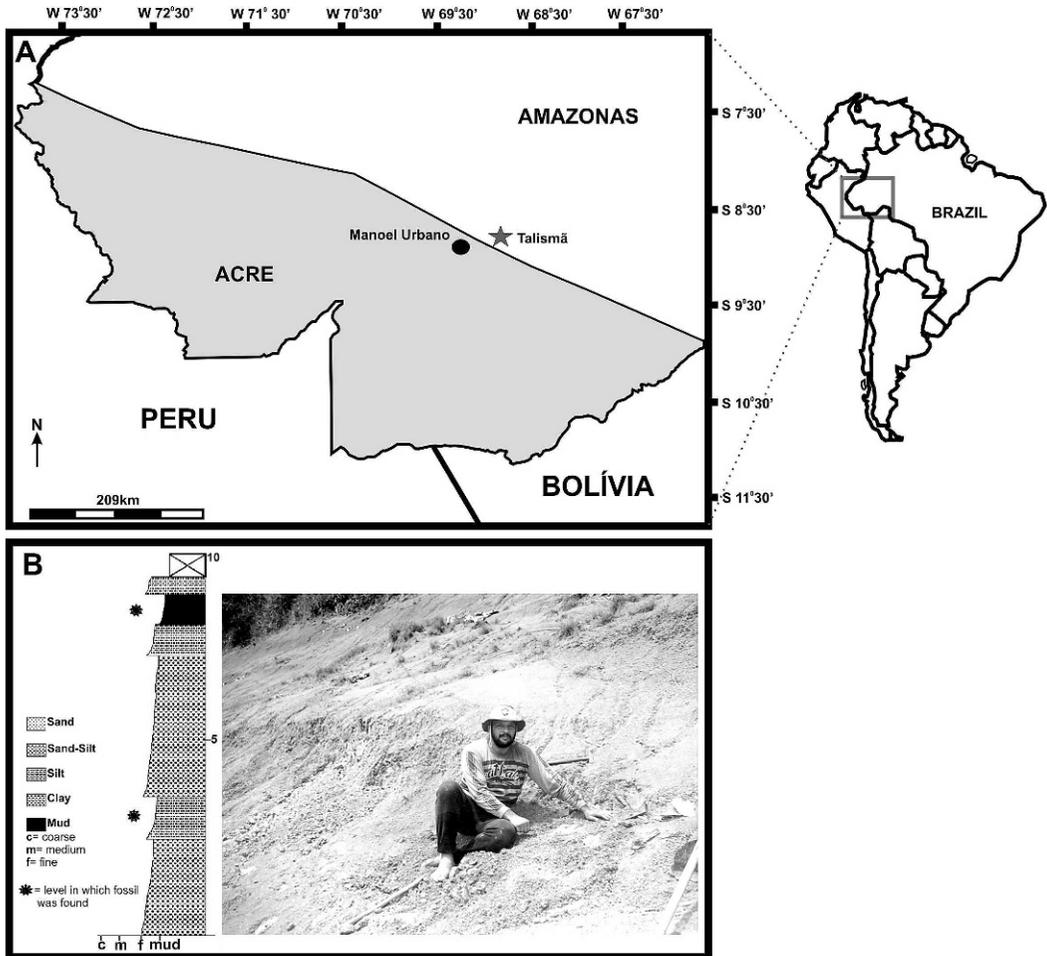
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Fig. 1. Location map (A) and the stratigraphic profile of the fossiliferous locality Talismã (B) (adapted from Cozzuol, 2006; Photo taken from www.ufac.br).

(Late Miocene-Early Pliocene). Based on palynological data obtained in typical fossiliferous localities, Latrubesse et al. (2007) suggested a Late Miocene age for the Solimões Formation. The snake material we studied was collected at the Talismã locality, which is considered by some authors as belonging to the Huayquerian-Montehermosan (Late Miocene/Pliocene) because of the presence of the rodents *Potamarchus murinus* and *Neopliblema horridula* (Santos et al., 1993; Negri, 2004). According to Santos and Negri (1993), the faunal set of xenarthrans (Tardigrada) suggests, on one hand, a probable affinity with the fauna of the Santacrucian Age of Argentina (Early-Middle Miocene) and, on the other, a relation with the Laventan Age of Colombia (Middle Miocene). According to Negri (2004; unpubl. data), the faunistic association of Tardigrada in this locality would indicate an older age, correlatable and close to

the Laventan (13.5–11.8 Ma, Madden et al., 1997). Here, we follow the arguments of Latrubesse et al. (2007) and assume a probable Late Miocene age for the Solimões Formation.

MATERIALS AND METHODS

The specimens are satisfactorily preserved and are stored at UFAC (Rio Branco, AC, Brazil). They include three midtrunk vertebrae and one posterior trunk vertebra very well preserved and three incomplete midtrunk vertebrae. Skeletons of extant boids were used for comparisons (Appendix 1). Osteological nomenclature and measurements follow Auffenberg (1963), Hoffstetter and Gasc (1969), Rage (1984), LaDuke (1991a,b), and Lee and Scanlon (2002). Systematic arrangement used is based on Noonan and Chippindale (2005). Measurements are expressed in millimeters.
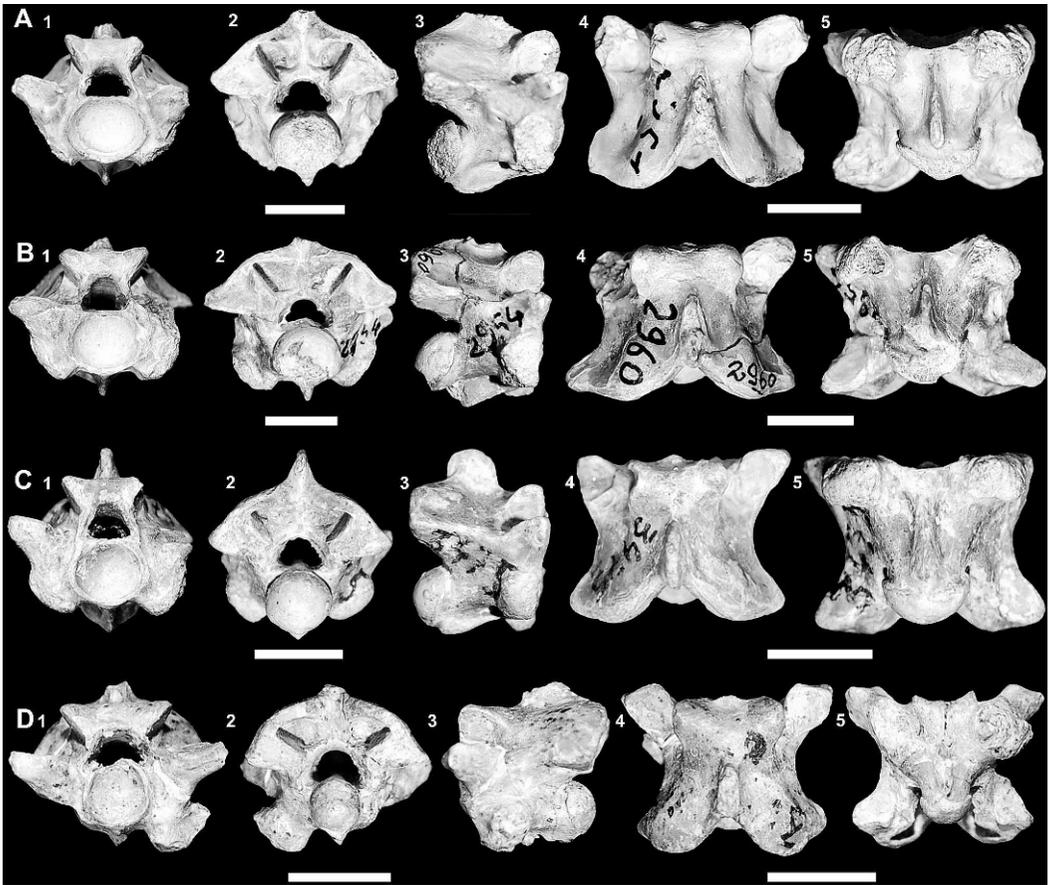
FIG. 2. *Eunectes* sp. Midtrunk vertebrae, UFAC-PV 2951 (A), UFAC-PV 2954/2960 (B), and UFAC-PV 3475 (C); posterior trunk vertebra, UFAC-PV 3476 (D); in (1) anterior, (2) posterior, (3) lateral, (4) dorsal, and (5) ventral views; scale-bars = 10 mm.

Vertebral Measurements.—cl, centrum length; coh, condyle height; cow, condyle width; cth, cotyle height; ctw, cotyle width; h, total high of the vertebrae; naw, neural arch width at inter-zygapophyseal ridge; nch, neural canal height; ncw, neural canal width; nsh, neural spine height; po-po, distance between postzygapophyses; pr-pr, distance between prezygapophyses; pr-po, distance between pre- and postzygapophyses of the same side; prl, prezygapophysis length; prw, prezygapophysis width; zh, zygosphene height; zw, zygosphene width.

Institutional Abbreviations.—HAA, private herpetological collection of Adriana Albino; HASH, private herpetological collection of Annie Schmaltz Hsiou; IB, Instituto Butantan, São Paulo; MCN.D., Didactic Collection of Herpetology, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo; UFAC-PV, Paleovertebrate Collection of the Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Rio Branco.

Systematic Paleontology
Serpentes Linnaeus, 1758
Alethinophidia Nopsca, 1923
Macrostomata Müller, 1831
Booidea Gray, 1825
Boidae Gray, 1825
Eunectes Wagler, 1830
Eunectes sp.
Figure 2

Referred Specimens.—Three almost complete midtrunk vertebrae (UFAC-PV 2951, 2954/2960, 3475) and one almost complete posterior trunk vertebra (UFAC-PV 3476).

Description.—The specimens are very well preserved. In general view, the vertebrae are large and robust. All of the vertebrae are wide, high and short, with a vertebral centrum shorter than the neural arch width (cl < naw). In

anterior view, a wide and robust zygosphene, with fairly long articular facets, is observed. The zygosphene is much wider than the cotyle (zw > ctw) and shows a slightly convex or rectilineous dorsal edge. The prezygapophyses are inclined above the horizontal plane on the midtrunk vertebrae (Fig. 2A–C), and nearly horizontal on the posterior trunk vertebra (Fig. 2D). The prezygapophysial process is well preserved in the posterior vertebra; it is short and stands a little beyond the articular facet (Fig. 2D). The neural canal is triangular and bears three internal crests: one located on the floor and two on the lateral walls, which together produce a trilobated aspect. In the midtrunk vertebrae, the cotyle is oval, slightly flattened dorsoventrally (ctw > cth), whereas it is round in the posterior trunk vertebra (ctw = cth). In only one specimen (UFAC-PV 2954/2960), there is a large pair of paracotylar foramina, one on each side of the cotyle. The paradiapophyses are fragmented hindering further detail; however, they are apparently robust and lateral-ventrally oriented. In the posterior trunk vertebra, a large lateroventral expansion of the paradiapophyses is observed, resembling a large transverse process (Fig. 2D).

In posterior view, the neural arch roof is slightly depressed in the midtrunk vertebrae (Fig. 2A–C) and more depressed in the posterior trunk vertebra (Fig. 2D). The posterodorsal notch of the neural arch is quite deep, and the neural spine (only preserved in UFAC-PV 3475) is relatively low, with a vertical crest that is the continuation of the posterior edge of the neural arch. The zygantrum is robust and deep, with the small zygantral foramina located on each side of the vertebra midline. The postzygapophyses are slightly inclined dorsally. The condyle is oval, slightly flattened dorsoventrally in the midtrunk vertebrae (cow > coh) and nearly round in the posterior trunk vertebrae (cow ~ coh).

In lateral view, the neural spine is robust, well developed but relatively low, slightly inclined posteriorly (observed in UFAC-PV 3475, Fig. 2C). It is anteroposteriorly shortened and starts posterior to the roof of the zygosphene. Lateral foramina are present on each side of the neural arch. The centrum is short, showing a well-defined and delimited precondylar constriction. The main axis of the condyle is slightly inclined upward. Ventrally to the condyle, a posteriorly projected haemal keel is observed, which nearly reaches the precondylar constriction.

In dorsal view, the neural arch is wider than long (pr-pr > pr-po) and relatively wider than the total height of the vertebra (pr-pr > h). The articular facets of the prezygapophyses are broad, long (prl > prw) and subtriangular, with its main axis anterolaterally oriented. The anterior edge of the zygosphene is slightly concave but shows a prominent median tubercle anteriorly projected and located just above the neural canal in the midtrunk vertebrae (Fig. 2A–C). In the posterior vertebra, the tubercle resembles a "tongue" that projects anteriorly above the dorsal edge of the neural canal (Fig. 2D). The roof of the neural arch shows a pronounced flexion that starts at the level of the upper angle of each zygantrum up to the basis of the articular facets of the zygosphene. The neural arch presents, on the posterior edge, a deep notch in the middle, beginning at the mentioned flexion. The interzygapophyseal ridge, extending between the prezygapophysis and postzygapophysis on each side of the vertebra, is curved and short but not much constricted.

In ventral view, the vertebral centrum is short (cl < naw) and triangular, wider anteriorly, with subcentral ridges well defined. The haemal keel is well developed longitudinally on the midline of the ventral surface of the centrum. It originates at the ventral edge of the cotyle, becoming more prominent and wider in the midportion of the vertebral centrum. There is a pair of small subcentral foramina, one on each side of the haemal keel. The postzygapophyses show large articular facets with a subtriangular form.

Measurements.—UFAC-PV 2954/2960: naw = 19.5; cl = 14.5; ncw = 6.3; nch = 3.8; cow = 9.5; coh = 7.7; ctw = 9.4; cth = 7.5; po-po = 26.1; pr-po = 17.8; prw = 5.1; prl = 7.4; zw = 12.7; zh = 5. UFAC-PV 2951: naw = 18.4; cl = 13.7; ncw = 6.5; nch = 3.9; cow = 9; coh = 7.4; ctw = 9.1; cth = 8; po-po = 23.2; pr-po = 17; prw = 5.6; prl = 6.7; zw = 10.6; zh = 4. UFAC-PV 3475: h = 19.6; naw = 16.5; cl = 13; ncw = 4.8; nch = 3.2; cow = 7.5; coh = 6.8; ctw = 7.4; cth = 6.5; nsh = 4.1; po-po = 20.5; pr-po = 15.3; prw = 4.3; prl = 6.2; zw = 9.1; zh = 4.2. UFAC-PV 3476: naw = 13.8; cl = 11.5; ncw = 5.5; nch = 2.4; coh = 5; cow 5.5; ctw = 5; cth = 5; po-po = 17.8; pr-pr = 19.2; pr-po = 13.9; prw = 4.2; prl = 5.6; zw = 10.4; zh = 2.9.

cf. *Eunectes* sp.
Figure 3

Referred Specimens.—Three incomplete midtrunk vertebrae (UFAC-PV 2958, 2959, and 3477).

Description.—The specimens UFAC-PV 2958 and 2959 are fragments of nearly complete midtrunk vertebrae. The first specimen is the right side of a precloacal vertebra, and the second, the left side. Neither specimen presents the dorsal portion of the neural arch. In these samples, it is possible to observe the anterolateral orientation of the prezygapophyses and the
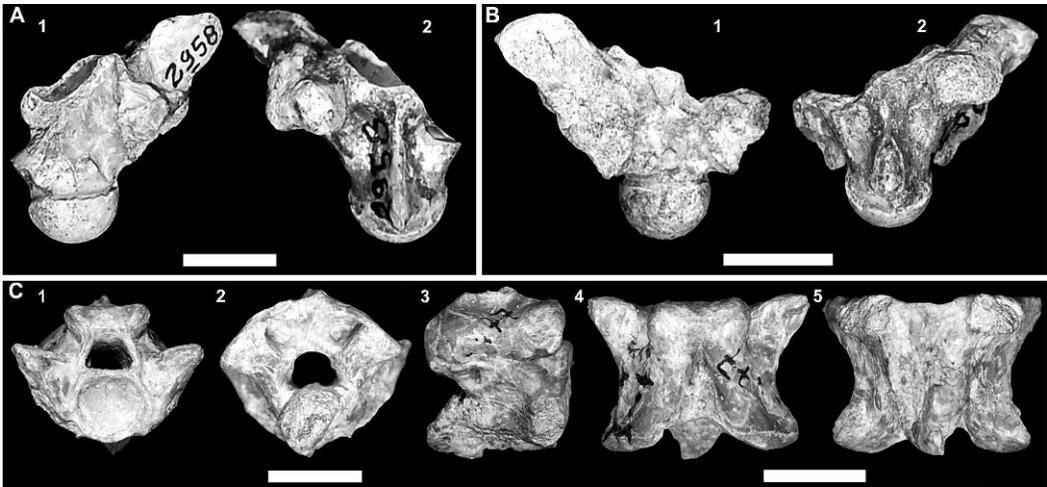
F<small>IG</small>. 3.   cf. *Eunectes* sp. Midtrunk vertebrae, UFAC-PV 2958 (A) in dorsal (1) and ventral (2) views; UFAC-PV 2959 (B) in dorsal (1) and ventral (2) views; and UFAC-PV 3477 (C); in (1) anterior, (2) posterior, (3) lateral, (4) dorsal, and (5) ventral views; scale bars = 10 mm.

presence of a short prezygapophysial process (more visible on the ventral surface of the articular facet). The paradiapophyses are quite fragmented and lateroventrally oriented. The vertebral centrum is short and anteriorly broadened, with a well-developed and thin haemal keel on the ventral surface. The condyle is large and slightly flattened dorsoventrally. The specimen UFAC-PV 3477 is rather fragmented and, because of the depressed aspect of the neural arch from a posterior view, seems to be a vertebra of the posterior trunk region. The poor preservation and fragmentation of the material allow us only a tentative assignation to the genus *Eunectes*.

Measurements.—UFAC-PV 2958: cl = 17.3; cow = 10.4; coh = 9; prw = 7.1; prl = 9.8. UFAC-PV 2959: cl = 14.8; cow = 8.8; coh = 7; prw = 6.7; prl = 8.5. UFAC-PV 3477: h = 17.3; naw = 15.9; cl = 14.1; ncw = 5.4; nch = 3.5; ctw = 7.4; cth = 6.2; po-po = 19.4; pr-pr = 21.4; pr-po = 14.4; prw = 4.3; prl = 5.9; zgw = 9.9; zh = 4.1.

Comparisons and Comments on the Characters.— The material described in this paper shares the following combination of vertebral characters with the genera of Neotropical boids: very robust, high, short, and wide vertebrae; neural arch not strongly depressed; neural spine well developed; posterior edge of neural arch with a marked notch; robust zygosphene; low inclination of the articular facet of the prezygapophysis (less than 15°); short prezygapophyseal process; vertebral centrum shorter than the width of the neural arch; delimited precondylar constriction; haemal keel in the vertebrae of the midtrunk region instead of a hypapophysis; presence of subcentral, lateral and paracotylar foramina (Rage, 2001;

Lee and Scanlon, 2002; Szyndlar and Rage, 2003; Albino and Carlini, 2008).

The vertebrae are assigned to the extant genus *Eunectes* on the basis of the following features: large size; slightly depressed neural arch; moderately low neural spine; robust and moderately thick zygosphene with a prominent median tubercle; paracotylar foramen irregularly present; and a strong lateroventral orientation of the paradiapophyses on the posterior trunk vertebrae.

Within the Neotropical boids, the midtrunk vertebrae are similar to samples of midsized individuals of the genera *Eunectes* and *Boa*, differing from the smaller size of *Corallus* and *Epicrates*. In *Eunectes* and *Corallus*, as in the fossils, the midtrunk vertebrae are usually lower than in *Boa* and *Epicrates.*

The neural arch of the fossil material and *Eunectes* is slightly depressed on the midtrunk vertebrae, differing from the condition in *Boa* and *Corallus* (except *Corallus cropanii*), which have a high neural arch, and in *Epicrates*, which shows an intermediate condition (Rage, 2001; pers. obs.).

The midtrunk vertebrae of the fossil material show a lower neural spine than in *Boa* and *Epicrates*. Rage (2001) argues that the neural spine is high in *Boa*, *Corallus cropanii*, *Epicrates,* and *Eunectes,* but less high in other *Corallus* species. These conclusions do not coincide with our observations of the osteological material (Appendix 1) where vertebrae of *Eunectes* have a proportionally low neural spine. This character seems to be variable among species and specimens. Nevertheless, the neural spine of *Corallus* is anteroposteriorly elongated, whereas it is shortened in the fossils as in *Eunectes*.

The zygosphene of *Eunectes*, *Epicrates,* and *Corallus* are distinctively wider and thinner than in *Boa*, but *Eunectes* shows a more robust zygosphene than the other two genera (Camolez, 2006; pers. obs.). According to Albino and Carlini (2008), *Boa constrictor* shows a very thick and robust zygosphene, different from that of the other genera. The zygosphene of the fossil material is wide and moderately thick, resembling the condition in *Eunectes*. Another feature in the zygosphene is a conspicuous median tubercle that projects anteriorly, between the dorsal edge and the neural canal, on the midtrunk vertebrae of the fossil material and *Eunectes*. In the fossil posterior trunk vertebra, this tubercle is tongue-shaped, projecting above the dorsal edge of the neural canal, as in posterior trunk vertebrae of extant specimens of *Eunectes*. The anterior edge of the zygosphene in the vertebrae of *Boa* shows a **V**-shaped notch in dorsal view, or it is often concave, without any trace of a median tubercle (Albino and Carlini, 2008). According to Camolez (2006), *Epicrates* presents an anterior blade on the zygosphene, whereas *Corallus* shows a ''crenate'' zygosphene, as that described by Auffenberg (1963).

The relative length of the centrum and the proportions of the prezygapophyseal surfaces observed in the fossil specimens and *Eunectes* also distinguishes them from *Boa*, which has a shorter centrum and longer prezygapophysis than the other genera (Albino and Carlini, 2008). The fossil posterior trunk vertebra shows a larger lateroventral expansion of the paradiapophyses, resembling a large transverse process, as observed in posterior vertebrae of extant specimens of *Eunectes* through direct comparisons (Appendix 1).

According to Kluge (1991), the presence of paracotylar foramina on both sides of the cotyle is a derived character state, shared, within Neotropical boids, by *Boa* and some species of *Corallus*. However, it was also observed in one fossil specimen here studied (UFAC-PV 2954/2960) and in two extant specimens of *E. murinus* (MCN.D. 306 and 342). The presence of this foramen in extant specimens of *E. murinus* is irregular; often they only appear on one side of the cotyle, rarely a pair, although the presence of one pair on each side of the cotyle has also been observed. The fossil vertebrae are distinguished from *Boa*, *Corallus annulatus*, and *C. cropanii* because in these genera the foramina are always present (Kluge, 1991; Rage, 2001; Albino and Carlini, 2008). The polarity of this foramen is controversial (Kluge, 1991; Rage, 2001) but its presence in one fossil specimen studied here represents a similarity with the species *E. murinus.*

According to Camolez (2006), the species of *Eunectes* do not show differences in the morphology of the precloacal vertebrae, although some differences are noticeable in the caudal vertebrae. Unfortunately, no postcloacal vertebrae have been preserved among the fossils, making their identification to the species level impossible at the moment, apart from the similarity in the presence of paracotylar foramina in one specimen as in *E. murinus*. Additionally, there are distinctions in the body dimensions of the extant species that can be compared with the studied fossils. The extant species of *Eunectes* stand out for being large snakes, among which, *E. murinus* is considered one of the largest snake known, with individuals reaching 11.4 m (Pope, 1961, 1962; Rivas, 1999). *Eunectes murinus* (usually 3 m for males and 6 m for females, Waller and Micucci, 1993; Rivas and Burghardt, 2001) is much larger than *E. notaeus* (generally 3 m for females) and *E. deschauenseei* (2 m in length) (Waller and Micucci, 1993). According to our observations, the vertebral fossil material shows a similar size to vertebrae belonging to midsized individuals of the species *E. murinus.*

Fossils of the genus *Eunectes* have only been reported from the Middle Miocene of La Venta (Colombia), represented by the extinct species *E. stirtoni* Hoffstetter and Rage, 1977. The material was described based on a right prootic and an incomplete basisphenoid. According to Hoffstetter and Rage (1977), they are distinct in morphology from extant *E. murinus*. The authors also assigned an incomplete series of vertebrae associated with the holotype to *E. stirtoni*, without providing a formal description. Later, Hecht and LaDuke (1997) examined these vertebrae and questioned the allocation to the genus *Eunectes*. They argued that the size and shape, and other characters, do not match with the vertebral morphology of *Eunectes*, but they did not provide a discussion of these features. These authors also assume as *Eunectes* sp. a series of eight fragmented presumably posterior trunk vertebrae from La Venta that have a very protuberant paradiapophyses; nevertheless, the composite drawing provided by the authors does not show the projected paradiapohyses as in the posterior vertebra of the Solimões Formation studied in this paper.

DISCUSSION

The extant species of *Eunectes* are adapted to a semiaquatic lifestyle, living in rivers, lakes, lagoons, swamps, temporary pools, and flooded forests (Strimple, 1993). They have morphological adaptations consistent with the lifestyle: dorsal nostrils and eyes fairly close to each other on the top of the head, relatively small eye

diameter, and narrower ventral scales (Scartozzoni, 2005). The aquatic habit arose only once among the Neotropical boids, in the snakes of the genus *Eunectes*, despite the great diversity of habits found in other genera (Murphy and Henderson, 1997). This statement could support the hypothesis proposed by Latrubesse et al. (1997, 2007) that a large fluvial megafan complex would be present in the Late Miocene of the Solimões Formation. The environment proposed for the region is suggested by the presence of vertebrate fauna (rodents, crocodiles, turtles, and freshwater fish) and palynological data that indicate open areas and forest galleries along rivers, swamps, and shallow lakes that would be subject to variation in the water level in a seasonal dry-humid tropical climate (Latrubesse et al., 2007).

Presence of the semiaquatic *Eunectes* in the Solimões Formation represents the first fossil record of snakes from southwestern Brazilian Amazonia. It would indicate a general ecological similarity with the Miocene fauna of La Venta (Colombia), extending the distribution of the genus toward the southeast. It also would indicate at least some similarity between the Miocene faunas of Talismã (Brazil), La Venta (Colombia), and Socorro and Urumaco (Venezuela). Although the fossils of boids found in the Socorro and Urumaco areas may not be assigned to the generic level (Head et al., 2006), the presence of these kind of snakes in the Miocene faunas of Brazil, Colombia, and Venezuela would demonstrate that the boids were broadly distributed in northern South America as early as the Middle and Late Miocene.

Recent phylogenetic analyses based on molecular data of Neotropical boids, conclude that *Eunectes* and *Epicrates* form a strongly supported clade (Burbrink, 2005; Noonan and Chippindale, 2006). According to Noonan and Chippindale (2006), *Epicrates* is recovered as paraphyletic with respect to *Eunectes*, suggesting that the Caribbean *Epicrates* are the sister group to *Eunectes* + South American *Epicrates* clade. The molecular data sets are consistent with Caribbean dispersal of *Epicrates* prior to the divergence between the representatives of South American *Epicrates* and *Eunectes* (Noonan and Chippindale, 2006). The authors propose that after the isolation of South America at the end of the Late Cretaceous (or Paleocene, Gayet et al., 1992), the Neotropical boids underwent little diversification until the invasion of the Caribbean at the beginning of the Oligocene, where the connectivity of what today represents the Greater Antilles reached its peak. If this hypothesis is correct, the divergence of the genus *Eunectes* from the South American *Epicrates* may have occurred immediately after that dispersal event. The earliest fossil record from the Middle and Late Miocene of northern South America is congruent with this supposition and corroborates the probable origin of the genus as early as the Miocene.

LITERATURE CITED

ALBINO, A. M., AND A. A. CARLINI. 2008. First record of *Boa constrictor* (Serpentes, Boidae) in the Quaternary of South America. Journal of Herpetology 42:82–88.

AUFFENBERG, W. 1963. The fossil snakes of Florida. Tulane Studies in Zoology 10:131–216.

BURBRINK, F. T. 2005. Inferring the phylogenetic position of *Boa constrictor* among the Boinae. Molecular Phylogenetics and Evolution 34:167–180.

CAMOLEZ, T. 2006. Levantamento, identificação e descrição da fauna de Squamata do Quaternário brasileiro (Lepidosauria). Unpubl. master's thesis, Universidade de São Paulo, São Paulo, Brazil.

COZZUOL, M. A. 2006. The Acre vertebrate fauna: age, diversity, and geography. Journal of South American Earth Sciences 21:185–203.

DIRKSEN, L. 2002. Anakondas. Natur und Tier Verlag., Münster, Germany.

GAYET, M., J. C. RAGE, T. SEMPERE, AND P. Y. GAGNIER. 1992. Modalités des échanges de vertebras continentaux entre l'Amérique Du Nord ET l'Amérique du Sud au Crétacé supérieur et au Paléocène. Bulletin de La Societe Geologique de France 6:781–791.

HEAD, J. J., M. R. SANCHEZ-VILLAGRA, AND O. A. AGUILERA. 2006. Fossil snakes from the Neogene of Venezuela (Falcón State). Journal of Systematic Palaeontology 3:233–240.

HECHT, M. K., AND T. C. LADUKE. 1997. Limbless tetrapods. *In* R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics—The Miocene Fauna of La Venta, Colombia, pp. 95–99. Smithsonian Institution Press, Washington, DC.

HENDERSON, R. W., T. W. P. MICUCCI, G. PUORTO, AND R. W. BOURGEOIS. 1995. Ecological correlates and patterns in the distribution of Neotropical boines (Serpentes: Boidae): a preliminary assessment. Hepertological Natural History 3:15–27.

HOFFSTETTER, R., AND J. P. GASC. 1969. Vertebrate and ribs of modern reptiles. *In* C. Gans, A. D'a. Bellairs, and T. S. Parsons (eds.), Biology of the Reptilia—Morphology A, pp. 201–310. Academic Press, London.

HOFFSTETTER, R., AND J. C. RAGE. 1977. Le gisement de vertébrés miocènes de La Venta (Colombie) et sa faune de serpents. Annales de Paléontologie (Vertébrés) 63:161–190.

KLUGE, A. G. 1991. Boine snake phylogeny and research cycles. Miscellaneous Publications Museum of Zoology, University of Michigan 178:1–58.

LADUKE, T. C. 1991a. Morphometric Variability of the Precaudal Vertebrae of *Thamnophis sirtalis sirtalis* (Serpentes: Colubridae), and Implications for the Interpretation of the Fossil Record. Unpubl. Ph.D. diss., City University of New York, New York.

———. 1991b. The fossil snakes of Pit 91, Rancho La Brea, California. Contributions in Science 424:1–28.

LATRUBESSE, E. M. 1992. El Cuaternario fluvial de la cuenca del Purus en el Estado de Acre, Brasil. Unpubl. Ph.D. diss., Universidade Nacional de San Luis, San Luis, Argentina.

LATRUBESSE, E. M., J. BOCQUENTIN, C. R. SANTOS, AND C. G. RAMONELL. 1997. Paleoenvironmental model for the late Cenozoic southwestern Amazonia: paleontology and geology. Acta Amazonica 27:103–118.

LATRUBESSE, E. M., S. A. F. SILVA, M. A. COZZUOL, AND M. L. ABSY. 2007. Late Miocene continental sedimentation in southwestern Amazonia and its regional significance: biotic and geological evidence. Journal of South American Earth Sciences 23:61–80.

LEE, M. S. Y., AND J. D. SCANLON. 2002. Snake phylogeny based on osteology, soft anatomy and ecology. Biological Reviews 77:333–401.

MADDEN, R. H., J. GUERRERO, R. F. KAY, J. J. FLYNN, C. C. SWISHER III, AND A. WALTON. 1997. The Laventan Stage and Age. *In* R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics—The Miocene Fauna of La Venta, Colombia, pp. 499–519. Smithsonian Institution Press, Washington, DC.

MURPHY, J. C., AND R. W. HENDERSON. 1997. Tales of Giants Snakes: A Historical Natural History of Anacondas and Pythons. Krieger Publishing, Malabar, FL.

NEGRI, F. R. 2004. Os Tardigrada (Mammalia, Xenarthra) do Neógeno, Amazônia Sul-Ocidental, Brasil. Unpubl. Ph.D. diss., Pontifícia Universidade Católica do Rio Grande do Sul, Brasil.

NOONAN, B. P., AND P. T. CHIPPINDALE. 2006. Dispersal and vicariance: the complex evolutionary history of boid snakes. Molecular Phylogenetics and Evolution 40:347–358.

PETERS, J. A., AND B. OREJAS-MIRANDA. 1970. Catologue of the Neotropical Squamata. Part II. Lizards and Amphisbaenians. Smithsonian Institution Press, London.

POPE, C. H. 1961. The Giant Snakes. Alfred A. Knopf, New York.

———. 1962. The six giants. Two boas and four pythons of the tropics are the longest of all existing land animals. Natural History 71:21–27.

RAGE, J. C. 1984. Handbuch der Paleoherpetologie, Part 11, Serpentes. Gustav Fisher Verlag, Stuttgart, Germany.

———. 2001. Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part II. Boidae. Palaeovertebrata 30:111–150.

RIVAS, J. A. 1999. The Life History of the Green Anaconda (*Eunectes murinus*), with Emphasis on Its Reproductive Biology. Unpubl. Ph.D. diss., University of Tennessee, Knoxville.

RIVAS, J. A., AND G. M. BURGHARDT. 2001. Understanding sexual size dimorphism in snakes: wearing the snake's shoes. Animal Behaviour 62:F1–F6.

SANTOS, J. C. R., AND F. R. NEGRI. 1993. Sobre alguns Tardigrada (Edentata, Mammalia) da localidade fossilífera Talismã (Fm. Solimões), Amazônia Sul-Ocidental Brasileira. In Congresso Brasileiro de Paleontologia and Simpósio Paleontológico do Cone Sul, 13 and 1. Boletim de Resumos, São Leopoldo, Brasil.

SANTOS, J. C. R., G. DE LULLIS, AND G. SILVA. 1993. Novos achados de *Urumacotherium* Bocquentin-Villanueva, 1984 (Edentata, Tardigrada) no Huayquer-iense-Montehermosense do Estado do Acre, Brasil. Ameghiniana 30:340–341.

SCARTOZZONI, R. R. 2005. Morfologia de serpentes aquáticas neotropicais: um estudo comparativo. Unpubl. master's thesis, Universidade de São Paulo, São Paulo, Brasil.

STAFFORD, P. J. 1986. Pythons and boas. T.F.H Publications Ltd., London.

STRIMPLE, P. D. 1993. Overview of the natural history of the Green Anaconda (*Eunectes muirnus*). Herpetological Natural History 1:25–35.

SZYNDLAR, Z., AND J. C. RAGE. 2003. Non-erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals. Polish Academy of Science, Kraków, Poland.

WALLER, T., AND P. A. MICUCCI. 1993. Estado Actual del Conocimiento de la Biología, Comercio y Conservación de las Boas Neotropicales: Géneros *Boa* L. (1758) y *Eunectes* Wagler (1830) (Reptilia: Serpentes: Boidae). Informe Traffic Sudamerica, Secretaría de CITES, Argentina.

APPENDIX 1

Comparative Material Examined in This Study

Boa constrictor constrictor, HASH 02, MCN.D. 335-343-344-347-351; *Boa constrictor*, HAA 13-14-15-16-19-25; *Corallus caninus*, IB 46900, MZUSP 14426; *Corallus hortulanus*, MZUSP 13853-13855-13050; *Epicrates cenchria*, IB 23052, MZUSP 13888; *Epicrates cenchria alvarezi*, HAA 01-06; *Epicrates cenchria assisi*, IB 49335; *Epicrates cenchria crassus*, IB 52174; *Eunectes deschauenseei*, IB 17642, MPEG 18019; *Eunectes murinus*, HASH 01, IB 19795, MCN.D. 306-316-319-342, MPEG 16443, MZUSP 2501; *Eunectes notaeus*, HAA 18, IB 7540, IB 17014, MZUSP 8303.