New snake remains from the Miocene of northern South America

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We report new snake vertebral remains originating from the late Miocene of south-western Brazilian Amazonia (Solimões Formation) and the middle–late Miocene of Venezuela (Socorro and Urumaco Formations). The Brazilian material was attributed to Boidae (aff. *Epicrates* sp. and *Waincophis* sp.) and to two probably undetermined "Colubridae". The new snake vertebrae from Venezuela are referred to the extant boid *Eunectes* sp.. Known specimens from the middle Miocene of Venezuela (Socorro Formation) are re-evaluated as cf. *Eunectes*. Until now, South American late Miocene squamate records have been reported only from Argentina and Venezuela. We present the first record in the Neogene of Brazil, considerably increasing our knowledge of the South American herpetofauna.

*Key words:* Boidae, "Colubridae", Solimões Formation, Urumaco Formation, Socorro Formation, Brazil, Venezuela

INTRODUCTION

Recent work on squamates from the Miocene of north-ern South America expanded our fossil record and provided new palaeoenvironmental data (Head et al., 2006b; Hsiou & Albino, 2009, Hsiou et al., 2009; Pujos et al., 2009). One of the most relevant South American Neogene vertebrate assemblages is known from Acre and Amazonas states in south-western Brazilian Amazonia, a region characterized by a notable diversity of fossil ver-tebrates collected from several outcrops at road sections and riverbank cuts (Cozzuol, 2006). The palaeoenviron-ments inferred for sites along the Purus, Acre and Juruá rivers include flood plains and lacustrine–paludal systems associated with rivers, grassland and gallery forests (La-trubesse et al., 1997, 2007; Cozzuol, 2006; Aguilera et al., 2008), consistent with a freshwater vertebrate fauna including fishes, crocodilians, turtles, cetaceans and sire-nians (in addition to rodents, xenarthrans, notoungulates and birds; Cozzuol, 2006; Negri et al., 2010). The first report on fossil squamates from this region, an indetermi-nate vertebral fragment of a snake (Paula-Couto, 1970), was followed by the discovery of additional undescribed snake material (Bocquentin et al., 1996; Latrubesse et al., 1997; Souza-Filho, 1998; Negri, 2004). More recently, Hsiou & Albino (2009) described vertebrae of the extant boid *Eunectes*, and Hsiou et al. (2009) recognized lizard remains referable to the extinct teiid *Paradracaena*. In addition, Hsiou et al. (2010) reported new specimens of the probably basal alethinophidian *Colombophis portai*, as well as a new species of this genus, *C. spinosus*. In the present paper, we describe new vertebral remains of macrostomatan snakes referable to the Boidae and "Colu-bridae". Four vertebral remains (UFAC-PV 2962, 5716A, 3483 and 3479) were collected at the locality of Talismã, two vertebrae (UFAC-PV 3245 and 4035) were collected at the locality of Lula, and one vertebra (LPVCZS/003)

was collected on the Upper Juruá River (Fig. 1). Based on the mammal fauna (Latrubesse et al., 1997), the age of the fossils found corresponded to the Huayquerian (late Miocene), possibly reaching the Montehermosan (late Miocene–early Pliocene). Latrubesse et al. (2007), based on palynological data obtained at typical fossiliferous lo-calities, suggested a late Miocene age for the sediments of the Solimões Formation in south-western Brazilian Amazonia.

A further diverse fauna of Miocene vertebrates from northern South America is located in the north-western Falcón State near Urumaco Municipality, Venezuela (Fig. 1), where the Urumaco Formation hosts diverse faunal associations in terrestrial, freshwater, estuarine and ma-rine environments (Sánchez-Villagra & Aguilera, 2006), including cartilaginous and osseous fishes, crocodylo-morphs, turtles and ciconiform birds (Aguilera, 2004; Gaffney et al., 2008; Riff & Aguilera, 2008; Head et al., 2006a; Walsh & Sánchez, 2008). Mammals are repre-sented by marsupials, xenarthrans, cetaceans, sirenians, notoungulates, proteroterids and rodents (Sánchez-Villa-gra & Aguilera, 2006). Head et al. (2006b) described the first records of snakes, belonging to Aniliidae (*Colom-bophis*) and Boidae (gen. et sp. indet.). Here, we report three midtrunk vertebrae from the Urumaco Formation referable to Boidae, and re-evaluate the two Boidae speci-mens described by Head et al. (2006b) from the Socorro Formation. The Urumaco Formation belongs to the late Miocene age, and probably includes a mammal assem-blage between the Chasicoan and Huayquerian South American land mammal ages (8–6 Mya, Díaz de Gam-ero & Linares, 1989; Aguilera, 2004; Sánchez-Villagra & Aguilera, 2006). The boid specimens described by Head et al. (2006b) from the upper member of the Socorro For-mation are considered of middle Miocene age.

Skeletons of extant and fossil snakes were used for comparisons (see Appendix). Osteological nomenclature,
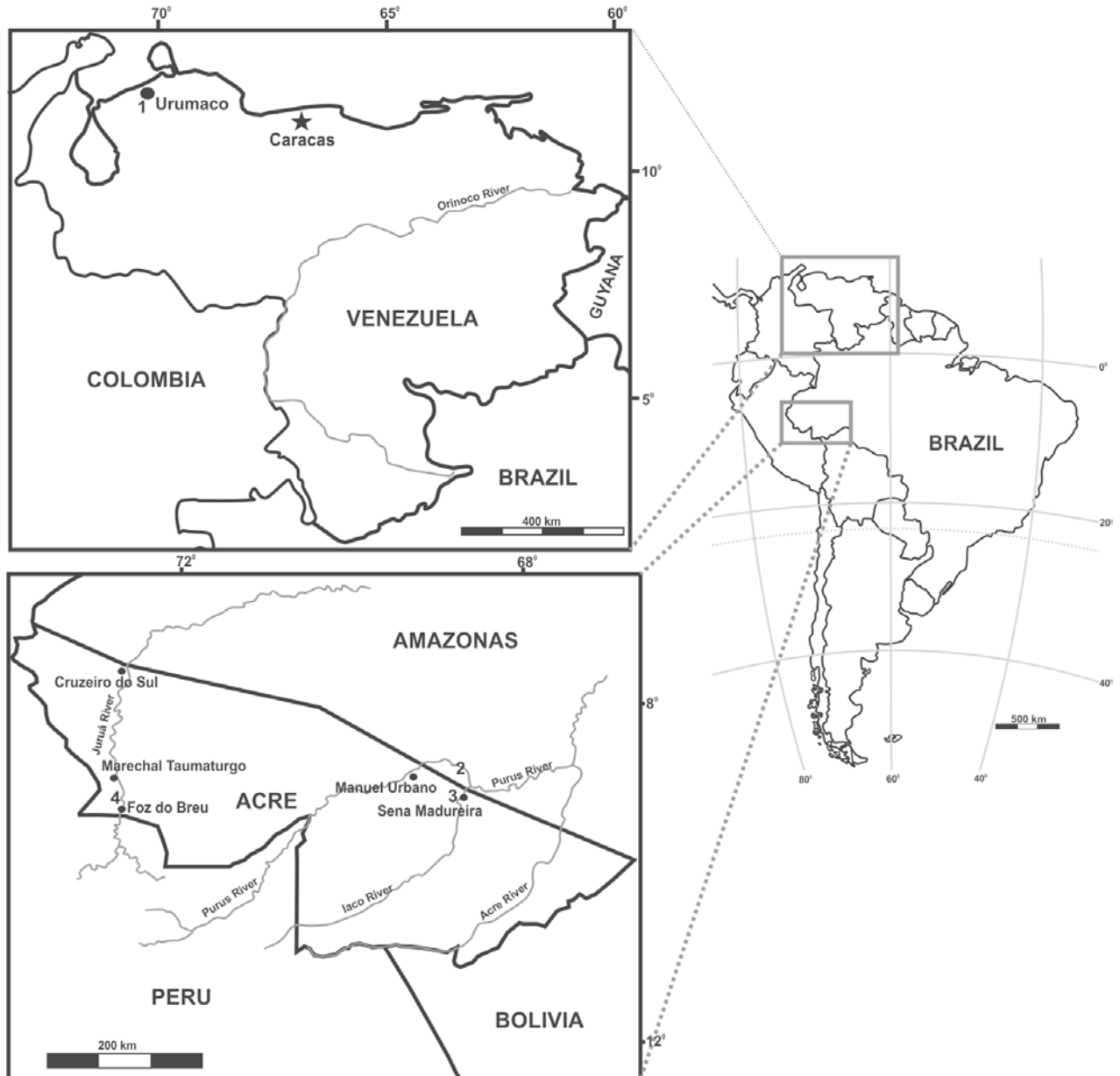
Fig. 1. Location map of the middle–late Miocene fossiliferous localities in northern South America. Top) Urumaco (1); bottom) Talismã (2), Lula (3) and Belford (4).

measurements (in mm) and systematics follow Auffenberg (1963), Hoffstetter & Gasc (1969), Rage (1984), Zaher (1999), Holman (2000) and Lee & Scanlon (2002).

Vertebral measurements and abbreviations

cl, centrum length; coh, condyle height; cow, condyle width; cth, cotyle height; ctw, cotyle width; h, total height of the vertebrae; naw, neural arch width at interzygapophyseal constriction; nch, neural canal height; ncw, neural canal width; nsh, neural spine height; po–po, width across postzygapophyses; pr–pr, width across prezygapophyses; pr–po, distance between pre- and postzygapophyses of the same side; prl, prezygapophyseal facet length; prw, prezygapophyseal facet width; zh, zygosphene thickness; zw, zygosphene width.

Institutional abbreviations

AMU-CURS = Colección Alcaldía de Urumaco, Rodolfo Sánchez, Urumaco, Venezuela; IB = Instituto Butantan, São Paulo, Brazil; LPV/CZS = Coleção de Vertebrados do Laboratório de Paleontologia, Centro Multidisciplinar, Universidade Federal do Acre/Campus Floresta, Cruzeiro do Sul, Brazil; MACN = Museo Argentino de Ciencias Naturales "Bernadino Rivadavia", Buenos Aires, Argentina; MCN.D. = Coleção Didática de Herpetologia, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCN-PV.D. = Coleção Didática de Paleontologia de Vertebrados, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MLP = Museo de La Plata, Argentina; UNMdP-O = Herpetological Collection

of the Universidad Nacional de Mar del Plata, Osteological Section, Argentina; MZUSP = Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; UFAC-PV = Coleção de Paleovertebrados do Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Rio Branco, Brazil; UNEFM-VF = Universidad Nacional Experimental Francisco de Miranda, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Vertebrados Fósiles, Coro, Venezuela.

SYSTEMATIC PALAEONTOLOGY

Serpentes Linnaeus, 1758: Alethinophidia Nopcsa, 1923: Macrostomata Müller, 1831: Boidae Gray, 1825: Boinae Gray, 1825: *Eunectes* Wagler, 1830: *Eunectes* sp. (Fig. 2)

Referred specimens. Three incomplete midtrunk vertebrae, UNEFM-VF 45.

Locality and age. Tío Gregorio locality (11°14'52"N, 70°18'16"W), north of Urumaco Municipality, Falcón State, Venezuela; late Miocene (upper member of the Urumaco Formation).

Description. Most of the remains are incomplete and fragmented, and the description is based on the unique almost completely preserved vertebra. The vertebra is large and robust; it is wide, high and shortened, with the vertebral centrum probably shorter than the neural arch width. In anterior view, a wide and robust zygosphene, bearing fairly long articular facets, is observed. The zygosphene is much wider than the cotyle (zw > ctw) and shows a slightly elevated dorsal edge in the middle. Only the left prezygapophysis is preserved; it is weakly inclined above the horizontal plane. The prezygapophyseal process is preserved; it is short and projects a little beyond the articular facet. The neural canal is triangular. The cotyle is oval, slightly flattened dorsoventrally (ctw > cth). There are no paracotylar foramina on either side of the cotyle. Both paradiapophyses are extremely broken precluding further description; however, they are apparently robust and lateroventrally oriented. In posterior view, although the neural arch roof is broken, it is possible to note that it is slightly depressed. The posterodorsal notch was not preserved. The zygantrum is deep and its roof is thick. The left postzygapophysis is slightly inclined dorsally. The condyle is oval, slightly flattened dorsoventrally in the midtrunk vertebrae (cow > coh). In lateral view, the

neural spine is broken, but it is robust and slightly inclined posteriorly. It is anteroposteriorly shortened and starts posterior to the roof of the zygosphene. Small 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. Ventral to the condyle, a short posteriorly projecting hypapophysis is observed, which nearly reaches the precondylar constriction. It suggests that the position of the vertebra into the column was between the anterior and middle precloacal region. In dorsal view, the neural arch is wider than it is long (pr–pr > pr–po) and relatively wider than the total height of the vertebra (pr–pr > h). The articular facet of the prezygapophysis is broad, long (prl > prw) and subtriangular, with its main axis anterolaterally oriented. The anterior edge of the zygosphene is concave and shows a prominent median tubercle projecting anteriorly and located just above the neural canal. The interzygapophyseal ridge, well visible on the left side, is curved and short. In ventral view, the vertebral centrum is short and triangular, wider anteriorly, with well defined subcentral ridges. The hypapophysis starts as a keel developing along the midline of the ventral surface of the centrum. It originates from the ventral edge of the cotyle, becoming more prominent and wider in the mid-portion of the vertebral centrum and posteriorly projecting a little below the level of the condyle basis. There is a pair of very small subcentral foramina, one on each side of the hypapophysis. The postzygapophyses show large and subtriangular articular facets.

Measurements. UNEFM–VF 45: cl=16.1; ncw=7.4; nch=4.7; cow=9.4; coh=8.6; ctw=9.4; cth=8.8; pr–po=18.7; prw=6.2; prl=7.9; zw=13.6; zh=5.

Remarks. Fossils of the genus *Eunectes* have been reported from the middle Miocene of Colombia, represented by the extinct species *E. stirtoni* (Hoffstetter & Rage, 1977; questioned by Hecht & LaDuke, 1997, who also described new vertebrae assigned to *Eunectes* sp.). Recently, Hsiou & Albino (2009) reported a new record of this neotropical boine snake from late Miocene southwestern Brazilian Amazonia together with information on vertebral morphology. Here, we describe the first record of late Miocene *Eunectes* from Venezuela. This identification is based on the following features of the vertebrae: large size, slightly depressed neural arch, moderately low neural spine and a robust and moderately thick zy-
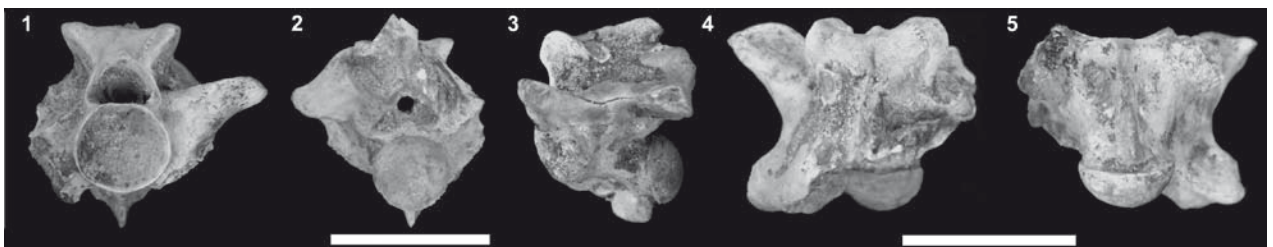
Fig. 2. *Eunectes* sp., UNEFM-VF 45, photograph of a trunk vertebra, probably between the anterior and middle precloacal region of column, in 1) anterior, 2) posterior, 3) lateral, 4) dorsal and 5) ventral views. Scale bars = 20 mm.

gosphene with a prominent median tubercle (Hsiou & Albino, 2009). In addition, Head et al. (2006b, Fig. 1B,C) described two boine vertebral remains (AMU-CURS 155 and 156) from Venezuela (middle Miocene of the Socorro Formation), whose description coincides with the features observed in *Eunectes*: large and robust vertebrae, robust zygosphene with a prominent median tubercle, and although the neural arch has been described as arched, it looks slightly depressed. However, the specimens are deformed and poorly preserved, and we tentatively assign them to cf. *Eunectes*. The record reported here from Venezuela increases the geographical distribution of the genus to northern South America, and supports its origin in the Miocene or before (Hsiou & Albino, 2009).

Epicrates Wagler, 1830; aff. *Epicrates* (Fig. 3)

Referred specimens. Three incomplete trunk vertebrae, UFAC-PV 2962, 5716A and 3483.

Locality and age. Talismã locality (08º48'22"S, 68º48'12"W), on the right bank upstream of the Purus River, Amazonas State, between the mouth of the Iaco River and the municipality of Manuel Urbano, Brazil; late Miocene (Solimões Formation).

Description. The preservation of the vertebrae varies among specimens. Specimen UFAC-PV 2962 is an incomplete vertebra that lacks the right prezygapophysis and the posterior portion of the neural arch, UFAC-PV 5716A does not retain most of the dorsal part of the neural arch and UFAC-PV 3483 is poorly preserved. The specimens are small, relatively robust and high, with short centra. The three vertebrae probably come from the middle of the trunk region, given the presence of a well marked and anteroposteriorly developed haemal keel. Concerning UFAC-PV 2962, the zygosphene is robust and wider than the cotyle (zw > ctw), and, in anterior view, shows a subtle median depression in the dorsal edge between the articular facets (also observed in UFAC-PV 3483). In dorsal view, the anterior edge of the zygosphene of UFAC-PV 2962 and 3483 has an anteriorly projecting median lobe. The articular facets of the zygosphene are dorsolaterally inclined. The prezygapophyses are slightly inclined dorsally, laterally oriented, and display a short prezygapophyseal process. The articular facet of the prezygapophysis is triangular in UFAC-PV 2962, whereas it is subtriangular in UFAC-PV 5716A. The neural canal is subtriangular and bears three internal crests, which together produce a trilobated aspect. The neural spine of UFAC-PV 2962 is mostly broken, only its basis preserved. It is anteroposteriorly short and it seems that it was relatively high. There are small lateral foramina in all specimens.

The centrum is triangular, widened anteriorly and rather narrow. The cotyle and the condyle are slightly wider than high. Two small subcotylar tubercles (Rage, 2001) are present anteriorly on the centrum. There are no paracotylar foramina, and a deep depression on each side of the cotyle. The paradiapophyses are broken, apparently robust and inclined dorsoventrally in UFAC-PV 2962, surpassing the ventral edge of the cotyle. The haemal

keel in UFAC-PV 2962 and 3483, which is well-marked, begins on the ventral edge of the cotyle. It reaches the ventral rim of the condyle in UFAC-PV 2962 and the precondylar constriction in UFAC-PV 3483. Specimen UFAC-PV 5616A shows a well-prominent haemal keel anteroposteriorly developed, that extends up to the precondylar constriction. The subcentral ridges are weakly marked; the subcentral grooves are also shallow, but this is more evident in the middle portion of the centrum, laterally to the haemal keel. There is one pair of subcentral foramina in all specimens.

Measurements. UFAC-PV 2962: cl=7; ncw=3.4; nch=2.7; cow=4.6; coh=4; ctw=4.4; cth=4; prw=2.8; prl=4.5; zw=6.2; zh=1.7. UFAC-PV 5617A: cl=6.3; cow=4.7; coh=4.2; ctw=4.5; cth=3.9; prw=2.7; prl=4.

Remarks. The taxonomic assignment of the specimens described above is based on the following combination of vertebral characters shared with the genera of extant neotropical boines: robust, high, short and wide vertebrae; although only the basis is preserved, the neural spine is apparently well developed; relatively thick zygosphene; low inclination of the articular facet of the prezygapophysis (less than 15º); short prezygapophyseal process; vertebral centrum short; marked precondylar constriction; haemal keel well developed in the mid-trunk vertebrae instead of a hypapophysis; and presence of subcentral and lateral foramina (Rage, 2001; Lee & Scanlon, 2002; Szyndlar & Rage, 2003; Albino & Carlini, 2008).

Within the neotropical boines, these trunk vertebrae are similar to samples from individuals of the genera *Epicrates* and *Corallus*, differing from *Eunectes* and *Boa* in their smaller size. In addition, they differ from *Boa*, *Corallus annulatus* and *C. cropanii* in the absence of paracotylar foramina (Kluge, 1991; Rage, 2001; Albino & Carlini, 2008). The zygosphenes of the fossils, as well as those of *Eunectes*, *Epicrates* and *Corallus*, are distinctively wider and thinner than in *Boa*, and have a median tubercle in the middle, contrasting with the thicker and "V-shaped" zygosphene of *Boa* (Albino & Carlini, 2008). The anterior edge of the zygosphene of the fossil specimens shows a prominent and wide median lobe. This feature is present along the vertebral column only in the extant genera *Epicrates* and *Corallus*, whereas *Eunectes* has a zygosphene with a conspicuous median tubercle that projects anteriorly, between the dorsal edge and the neural canal (Hsiou & Albino, 2009). According to Camolez (2006), *Epicrates* presents an anterior lobe on the anterior edge of the zygosphene in dorsal view, whereas *Corallus* shows a "crenate" zygosphene as defined by Auffenberg (1963). However, these morphologies are very similar in both genera, and could be interpreted as the same morphology. In *Corallus* (*C. hortulanus*), the median lobe of the zygosphene seems to be more convex and small, and the shape is not homogeneous along the column. Some regions of the column do not show this feature, the border of the zygosphene being more rectilinear or even with only a small median prominence. *Epicrates* (*E. cenchria*, *E. crassus*, *E. assizi* and *E. alvarezi*) also shows differences in the shape of the anterior edge of the
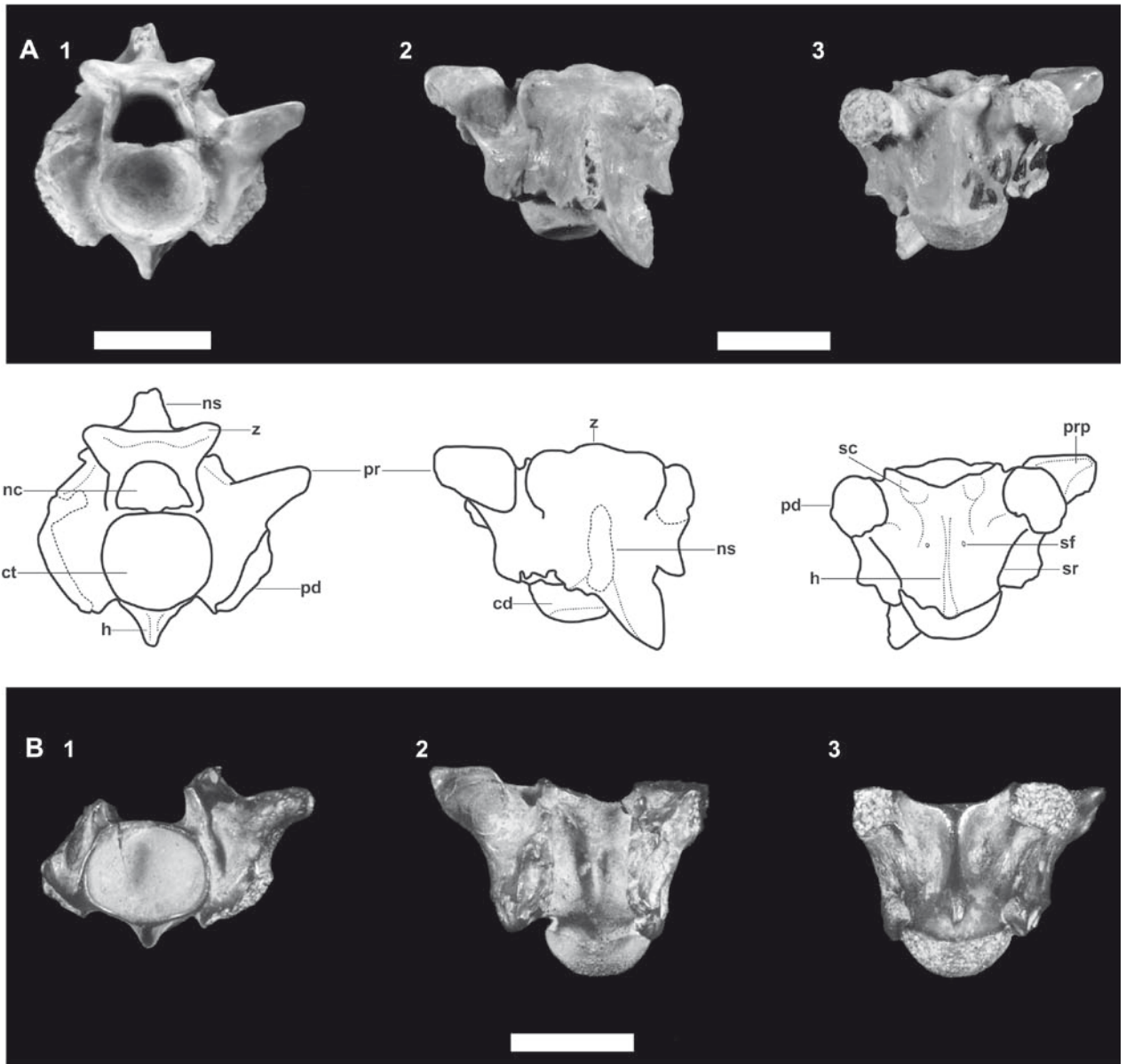
Fig. 3. aff. *Epicrates*, A) UFAC-PV 2962 and B) UFAC-PV 5616A, photographs of midtrunk vertebrae and schematic drawings, in 1) anterior, 2) dorsal and 3) ventral views. Scale bars = 5 mm. Osteological abbreviations: ct, cotyle; cd, condyle; h, haemal keel; nc, neural canal; ns, neural spine; pd, paradiapophyses; pr, prezygapophysis; prp, prezygapophyseal process; sc, subcotylar tubercle; sf, subcentral foramen; sr, subcentral ridge; z, zygosphene.

zygosphene, a character that is more constant along the column (pers. obs.). Almost all specimens of *Epicrates* show a protruding and large median lobe on the anterior edge of zygosphene along the column. The exception is *E. assizi*, which displays a concave anterior edge on some midtrunk vertebrae (pers. obs.). On the basis of this feature, a probable relationship of the fossil specimens with both *Epicrates* and *Corallus* is suggested. However, the inclination of the prezygapophyses in UFAC-PV 2962, 3483 and 5716A suggests more affinities with *Epicrates*. In *Corallus*, the prezygapophyses are horizontal in anterior view (Rage, 2001; pers. obs.), whereas they are relatively more inclined above the horizontal plane in *Epicrates*. In conclusion, the fossil material described

here can be tentatively attributed to aff. *Epicrates*. If the identification is correct, this represents the earliest fossil record of the genus, corroborating the molecular data that postulates the probable origin of the genus as early as the Miocene (Noonan & Chipindale, 2006; Hsiou & Albino, 2009).

Waincophis Albino, 1987; *Waincophis* sp. (Fig. 4)

Referred specimens. One incomplete trunk vertebra, LPVCZS/003.

Locality and age. Belford locality, Upper Juruá River, shore at the Belford site (09⁰11'10.0"S, 72⁰42'31.6"W),

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located between Marechal Taumaturgo and Foz do Breu areas, Acre State, Brazil; late Miocene (Solimões Formation).

Description. The specimen does not preserve the left prezygapophysis or either of the paradiapophyses, and displays an incomplete neural spine. The vertebra is small and lightly built, wide, low and short, with a centrum shorter than the neural arch width (cl < naw). In anterior view, a wide and very thin zygosphene with small articular facets (only the right side is preserved) is observed. The zygosphene is wider than the cotyle (zw > ctw) and arched dorsally. The right prezygapophysis is inclined above the horizontal plane, from the level of the floor of the neural canal. The prezygapophyseal process, although broken, was apparently small. The neural canal is subtriangular, large and high, with three internal crests, which together produce a trilobated aspect. The cotyle is nearly circular (ctw ~ cth). There is one paracotylar foramen on the right side of the cotyle (presence of a foramen on the other side cannot be checked because the left side is broken away). The paradiapophyses are not preserved; however, judging from their outline, they were apparently small, dorsoventrally inclined, and probably slightly surpassing the ventral edge of the cotyle. In posterior view, the neural roof is depressed, showing a well-marked posterior median notch. The neural spine is broken, but it is possible to observe that its base is wider posteriorly than anteriorly. The zygantrum is small and deep. The postzygapophyses are subtriangular and slightly inclined dorsally. The condyle is nearly circular (cow ~ coh). In lateral view, the neural spine is mostly broken. It seems to have been long, probably low and thin or blade-like, starting posterior to the roof of the zygosphene. Lateral foramina are present on each side of the neural arch. In ventral view, the centrum is shorter than the width of the neural arch (cl < naw), and bears a well-defined and prominent haemal keel, which reaches the precondylar constriction. The subcentral grooves are quite deep, and the subcentral ridges are poorly evident and diverge anteriorly. In

dorsal view, the neural arch is shorter than long (pr–po < po–po). The articular facets of the prezygapophyses are slender, longer than broad (prl > prw) and subtriangular, with the main axis anterolaterally oriented. The anterior edge of the zygosphene is missing; however, it was apparently straight. The posterior median notch is well marked, but moderately deep. The neural spine shows a posterior base wider than the anterior base. The interzygapophyseal ridge is well defined and short. In ventral view, the centrum is rather triangular, quite wider anteriorly than posteriorly. The haemal keel occupies all of the centrum extension, and it is well defined, relatively thin and well prominent. The subcentral grooves are relatively deep anteroposteriorly. There is one subcentral foramen, located on the left side of the haemal keel.

Measurements. cl=6.4; naw=6; ncw=3.1; nch=2.2; cow=3.4; coh=3; ctw=3.3; cth=3; po–po=9.2; pr–po=7.9; prw=2; prl=2.9; zw=4.9; zh=0.8.

Remarks. LPVCZS/003 may be clearly attributed to *Waincophis* because the midtrunk vertebra is small and exhibits the following features: depressed neural arch with a probably low, thin and long neural spine; thin zygosphene, wider than the cotyle; slanting prezygapophyses; reduced prezygapophyseal process; relatively large and subtriangular neural canal; short and anteriorly widened vertebral centrum; relatively thick and prominent haemal keel; paracotylar foramina present; and small paradiapophyses (Albino, 1987, 1996a; Rage, 2001). At present, there are three species of *Waincophis* described from the Caenozoic of South America. The type species, *W. australis*, is from the mid to late Eocene (Gelfo et al., 2009) of Argentina, previously assigned to the early Eocene (Albino, 1987), whereas other records of the genus (*Waincophis* sp.) are from the early and middle Miocene of the same country (Albino, 1996a,b). There are two other species of *Waincophis* recorded for the early Eocene (Gelfo et al., 2009) of Brazil that were previously considered middle Palaeocene in age (Rage, 2001). They are *W. pressulus*
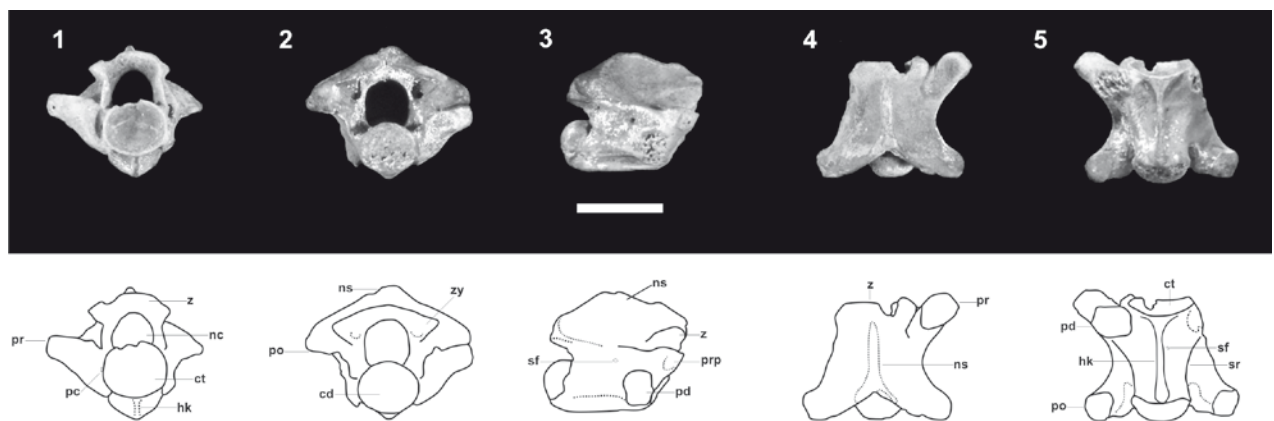
Fig. 4. *Waincophis* sp., LPV/CZS 03, photograph of midtrunk vertebra and schematic drawing, in 1) anterior, 2) posterior, 3) lateral, 4) dorsal and 5) ventral views. Scale bars = 5 mm. Osteological abbreviations: ct, cotyle; cd, condyle; hk, haemal keel; nc, neural canal; ns, neural spine; pc, paracotylar foramen; pd, paradiapophyses; po, postzygapophyses; pr, prezygapophysis; prp, prezygapophyseal process; sf, subcentral foramen; sr, subcentral ridge; z, zygosphene; zy, zygantrum.

and *W. cameratus* (Rage, 2001). The affinities of *Wain-cophis* were discussed by Rage (2001), who gives new information about the genus. In previous works, Albino (1987) allocated *Waincophis* as a Boidae of undetermined subfamily; later, she tentatively assigned the genus to the Erycinae (Albino, 1996a,b) based on the small size of the vertebrae, the presence of a depressed neural arch and the low neural spine. Until that moment, *Waincophis* was represented only by the type species. Subsequently, Rage (2001) described the other two species of the genus, and rediagnosed *Waincophis*. For this author, *Waincophis* has a typical vertebral morphology of the Boidae but it has unique morphological characters that distinguish it from all other living Boidae genera. Some arguments by Rage (2001) contrast with the Erycinae morphology, but the absence of caudal vertebrae raises difficulties for the Erycinae attribution (see Rage, 2001 for more discussion). However, Rage (2001) agrees with Albino's (1996a) assumption that the vertebral morphology of *Waincophis* may have resulted from convergence due to a similar lifestyle (fossorial or secretive).

Colubroidea Oppel, 1811; "Colubridae" Oppel, 1811; gen et sp. indet. (Fig. 5)

Referred specimens. Three almost complete trunk vertebrae, UFAC-PV 3245, 3479 and 4035.

Locality and age. One vertebra (UFAC-PV 3479) was recovered from the Talismã locality, Purus River, Amazonas State, and two vertebrae (UFAC-PV 3245 and 4035) belong to Lula locality (09°01'21.6"S, 68°48'29.5"W), near the municipality of Sena Madureira, along the BR-364 road, Acre State. Both localities are in the late Miocene south-western Brazilian Amazonia (Solimões Formation).

Description. The specimens are very well preserved, although UFAC-PV 3479 lacks the posterior portion of the neural arch. The vertebrae are thin and elongated. UFAC-PV 3245 and 4035 are wide, high and elongated, with a vertebral centrum longer than the neural arch width (cl > naw). In anterior view, the zygosphene is very thin, having short articular facets. In general, the zygosphene is much wider than the cotyle (zw > ctw) and shows a slightly convex or rectilineous dorsal edge or even a median elevation such as in specimen UFAC-PV 3479. The prezygapophyses of UFAC-PV 3245 and 4035 are weakly inclined above the horizontal plane, and nearly horizontal in UFAC-PV 3479, where they are positioned at the level of the floor of the neural canal. The prezygapophyseal process is well developed in UFAC-PV 3245 and 4035. It is very long and projects beyond the articular facet. Due to the fragmentation of UFAC-PV 3479, the prezygapophyseal process cannot be seen well, but it appears to be shorter than in the previous specimens. The neural canal is subtriangular and bears three internal crests, which together produce a trilobated aspect. The cotyle is circular or nearly circular in all specimens (ctw ~ cth). In only one specimen (UFAC-PV 3245) is there a small pair of paracotylar foramina, one foramen on each side of the cotyle. The paradiapophyses are hardly divided into two articular

facets; they are relatively large and ventrolaterally orientated. The diapophysis is more prominent and convex, whereas the parapophysis is strongly concave. In posterior view, the neural arch roof is depressed but the neural spine is high. The posterodorsal notch of the neural arch is deep. Above the posterodorsal notch, the neural spine basis is very large and robust. The zygantrum is small and deep, with small zygantral foramina located on each side of the vertebral midline. The postzygapophyses are slightly inclined dorsally, and there is a well-developed epizygapophyseal spine projecting above the postzygapophyseal articular facet. The condyle is round or nearly circular (cow ~ coh).

In lateral view, the neural spine is thin and high. It is anteroposteriorly elongated in all the extension and starts posterior to the roof of the zygosphene. Lateral foramina are present on each side of the neural arch in UFAC-PV 3245 and 4035. The centra are elongated and narrow, showing a moderate precondylar constriction. The main axis of the condyle is posterodorsally directed. Ventrally, there is a well-developed haemal keel in all specimens that ends at the precondylar constriction. The subcentral ridges are relatively well marked in all extension of the centra.

In dorsal view, the neural arch of UFAC-PV 3245 and 4035 is slightly wider than long (pr–pr ~ pr–po). The articular facets of the prezygapophyses are slender (prl > prw) and oval. The prezygapophyses of UFAC-PV 3245 and 4035 are anterolaterally orientated and have long and robust prezygapophyseal processes, which, although partially broken, are curved laterally and projecting well beyond the limits of the articular facets. In UFAC-PV 3479 the prezygapophyses are more laterally orientated than in the previous specimens described, and carry an apparently shorter prezygapophyseal process. The anterior edge of the zygosphene in UFAC-PV 3245 and 4035 shows a slightly "crenate" shape in the middle portion of the zygosphene. In specimen UFAC-PV 3479, the anterior edge of the zygosphene is very irregular in dorsal view, displaying several small lobes, being very similar to the "notched crenate zygosphene" *sensu* Auffenberg (1963). The interzygapophyseal constriction is well marked and deep in UFAC-PV 3245 and 4035, whereas it is apparently shorter in UFAC-PV 3479. In ventral view, the centra are elongate (cl > naw) and narrow, rather wider anteriorly, with subcentral ridges well-defined. The haemal keel is well developed on the whole ventral surface of the centra. It originates at the ventral edge of the cotyle, and is prominent and slender in UFAC-PV 3479 and 4035, whereas it is more flattened and robust in UFAC-PV 3245. There is a pair of small subcentral foramina, one foramen on each side of the haemal keel. The postzygapophyses show slender articular facets with an oval form, posterolaterally orientated.

Measurements. UFAC-PV 3245: naw=8.7; cl=9.8; ncw=3.6; nch=2.6; cow=4.7; coh=3.8; ctw=4.5; cth=3.9; po–po=13.7; pr–pr=13.7; pr–po=12.2; prw=2.3; prl=3.9; zw=7; zh=1.5. UFAC–PV 3479: naw=4.8; cl=6.4; ncw=2.2; nch=1.7; cow=2.3; coh=2.4; ctw=2.4; cth=2.1; pr–pr=8.1; prw=1.8; prl=2.4; zw=4.4; zh=0.7. UFAC-PV

4035: h=12; naw=6.9; cl=9.2; ncw=3.1; nch=2.7; cow=4; coh=3.4; ctw=3.8; cth=3.2; nsh=4.7; po–po=11.2; pr–pr=11.4; pr–po=11; prw=2; prl=3.5; zw=5.5; zh=1.3.

Remarks. The Colubroidea is a monophyletic group of snakes supported by at least seven synapomorphies, none from the postcranium (Rieppel, 1988; Zaher, 1999). Based only on vertebral morphology, the colubroids are traditionally identified by the following combination of characters: delicate vertebrae, longer than wide; thin zygosphene, neural spine thin and slender; paradiapophyses differentiated; paracotylar foramina usually present; and prezygapophyseal processes well developed (Rage, 1984; Holman, 2000; Albino & Montalvo, 2006). These characters are found in the fossil material described here. As far as postcranial characters are concerned, according to Lee & Scanlon (2002), colubroids can be recognized by the following combination of derived states, some of which are present in the fossil specimens: condyle round in posterior outline; condyle facing posteriorly or posterodorsally; precondylar constriction moderate; prezygapophyseal processes small to prominent; zygapophyses not strongly inclined medially from horizontal (i.e. less than 30^0); and ventral surface of centrum bearing a single median haemal keel or hypapophysis. Regarding the well-developed hypapophyses on mid-posterior trunk vertebrae, this varies among colubroids, being a derived condition observed in "boonontines", "xenodermatines", "pseudoxyrhophiines", homalopsines, natricines, elapids and viperids, whereas the primitive condition of very reduced or absent hypapophyses occurs in atractaspidids, most colubrines, xenodontines, dipsadines, pareatines and calamariines (Zaher, 1999; Albino & Montalvo, 2006). Except for the Elapidae, Atractaspididae and Viperidae, all other colubroids are grouped in the family "Colubridae," which currently cannot be diagnosed by any unambiguous synapomorphy (Zaher, 1999; Albino & Montalvo, 2006). Thus, due to the presence of a haemal keel instead of a well-developed hypapophysis on the ventral surface of the centrum, the vertebrae described here are assigned to the "Colubridae". There are some differences between the fossil specimens described here. Specimens UFAC-PV 3245 and 4035 exhibit a distinct prezygapophyseal morphology with respect to UFAC-PV 3479. In addition, the prezygapophyses of UFAC-PV 3245 and 4035 are more inclined dorsally and anterolaterally directed, whereas they are positioned close to the horizontal plane and laterally oriented in UFAC-PV 3479. Furthermore, the prezygapophyseal process of UFAC-PV 3245 and 4035 is more elongated and prominent than in UFAC-PV 3479, the latter being apparently shorter and robust. The anterior edge of the zygosphene in dorsal view shows a "crenate" shape in specimens UFAC-PV 3245 and 4035, whereas it exhibits four lobes, giving a very irregular form to its anterior edge, in UFAC-PV 3479. Although not a very obvious feature, the interzygapophyseal constriction in the first two specimens is deeper, whereas it is shallower in the latter. Thus, UFAC-PV 3245 and 4035
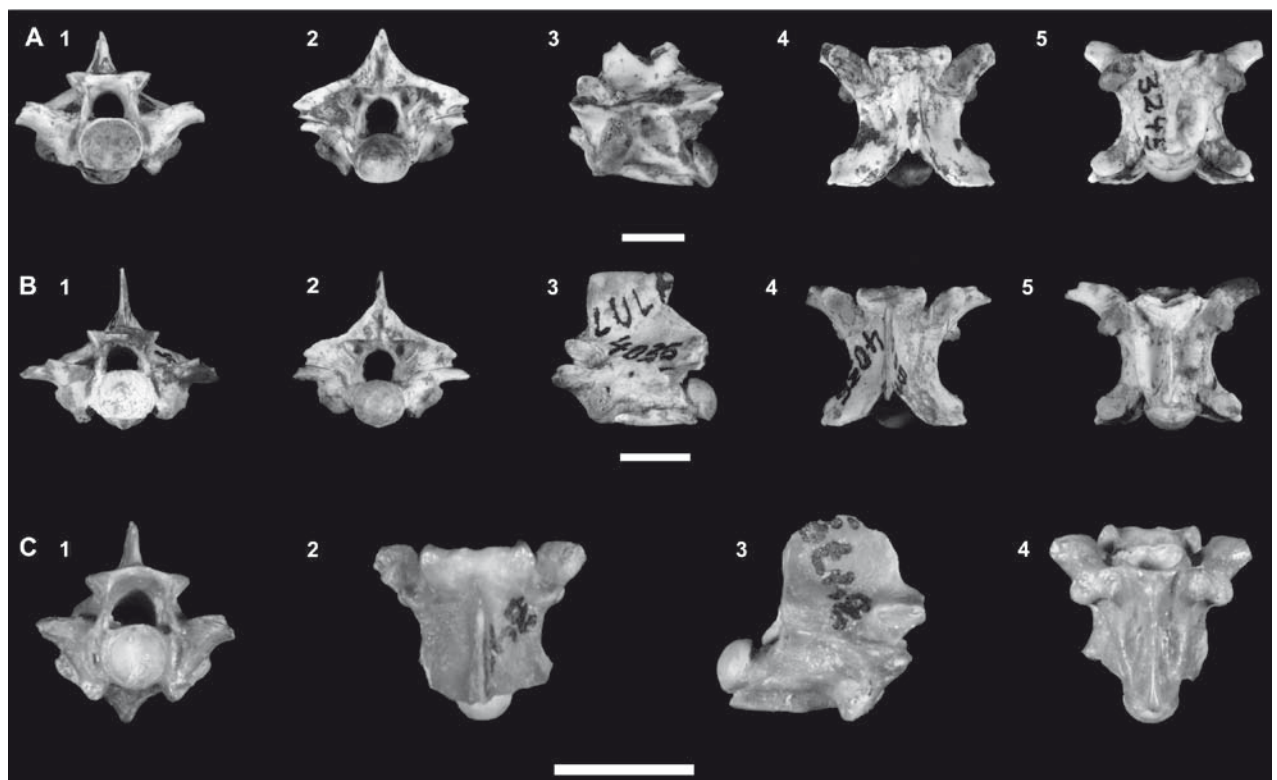
Fig. 5. "Colubridae" indeterminate genus and species, photographs of midtrunk vertebrae. A) UFAC-PV 3245 and B) 4035 in 1) anterior, 2) posterior, 3) lateral, 4) dorsal and 5) ventral views; and C) UFAC-PV 3479 in 1) anterior, 2) dorsal, 3) lateral and 4) ventral views. Scale bars = 5mm.

probably belong to the same taxa, and UFAC-PV 3479 probably belongs to a distinct taxon due to the differences noted above and its reduced size.

DISCUSSION

In this paper we report snake remains from late Miocene south-western Brazilian Amazonia, attributed to Boidae (*Waincophis* sp. and aff. *Epicrates*) and undetermined "Colubridae". In addition, we confirm the record of *Eunectes* in the late Miocene of Venezuela, constituting the northernmost known distribution of this genus in Miocene times. The records from south-western Brazilian Amazonia, such as *Waincophis* (this paper), *Eunectes* (Hsiou & Albino, 2009) and *Colombophis* (Hsiou et al., 2010), extend the distribution of these taxa towards the southeast. They also imply the survival of *Waincophis* and *Colombophis* until the late Miocene. As for aff. *Epicrates*, if this identification is correct, it represents the oldest record of the genus. The "colubrid" remains described here also represent the oldest record of this group in the Neogene of Brazil.

The late Miocene of Brazil constitutes one of the most diverse Caenozoic squamate faunas known in South America. This fauna has yielded remains of teiid lizards (Hsiou et al., 2009), boid and "colubrid" snakes (Hsiou & Albino, 2009; this paper), and a probable basal alethinophidian snake (*Colombophis*, Hsiou et al., 2010). As a whole, these reports represent the first record of squamates in the late Miocene of south-western Brazilian Amazonia and the earliest record of squamates in the Neogene of Brazil. Until now, South American late Miocene squamate records were only known from Argentina (Albino et al., 2006; Albino & Montalvo, 2006) and Venezuela (Head et al., 2006b). The new squamate fauna from the late Miocene of Brazil considerably increases our knowledge of the South American Neogene herpetofauna.

The squamate association from late Miocene south-western Brazilian Amazonia demonstrates ecological similarities among the Miocene faunas of northern South America (e.g. La Venta fauna of Colombia, Urumaco region of Venezuela), and evidence exists for the presence of similar fossil squamates in south-western Brazilian Amazonia, supported by the presence of the boid snake *Eunectes* and the teiid lizard *Paradracaena* (Hsiou & Albino, 2009; Hsiou et al., 2009), as well as the presence of *Colombophis* in the three regions (Hsiou et al., 2010). The predominance of tropical faunal elements and associated environments (Kay & Madden, 1997; Latrubesse et al., 1997, 2007; Aguilera, 2004; Sánchez-Villagra & Aguilera, 2006) matches the presumed lifestyle of lizards and snakes recorded from these regions.

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APPENDIX

Comparative material examined in this study

Boa constrictor constrictor, MCN.D. 335–343–344–347–351; *B. c. occidentalis*, UNMdP–O 44–45–46–47–49–50; *Crotalus durissus* MCP-AN 057; *Corallus caninus*, IB 46900, MZUSP 14426; *C. hortulanus*, MZUSP 13853–13855–13050, MCN-PV.DR. 0001; *Epicrates cenchria*, IB 23052, MZUSP 13888, MCN-PV.DR. 0002; *Epicrates alvarezi*, UNMdP-O 42–43; *Epicrates assizi*, IB 49335; *Epicrates crassus*, IB 52174, MCN-PV.DR. 0003; *Eunectes deschauenseei*, IB 17642; *Eunectes murinus*, IB 19795, MCN.D. 306–316–319–342, MZUSP 2501; *Eunectes notaeus*, UNMdP-O 48, IB 7540, IB 17014, MZUSP 8303; *Gaimanophis tenuis*, MACN-CH 997–2, 997–3, 997–4, 1000–1, 1001–1, 1001–2, 1004–1, 1004–2, 1004–3, 1005–2, 1006; *Waincophis* sp., MACN-CH 998–1, 999–1, 999–2, 1003–2, 1002–3; *Waincophis australis*, MACN-CH 1008, MLP 91-IV-1-127, 92-XI-21-8 a,b, MLP 90-II-20-17, 91-IX-1-73.