Fossil snakes (Squamata: Serpentes) from the tar pits of Venezuela: taxonomical, palaeoenvironmental, and palaeobiogeographical implications for the North of South America during the Cenozoic/Quaternary boundary (#24411)

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Fossil snakes (Squamata: Serpentes) from the Tar Pits of Venezuela: taxonomical, palaeoenvironmental, and palaeobiogeographical implications for the North of South America during Cenozoic/Quaternary boundary

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Background. Tar seep deposits in South America historically are well known to have yielded a rich fossil record of mammals contrasting with just few formal reports of reptile remains. Here we report a new snake fauna recovered from two Tar pits from Venezuela. The fossil remains come from two localities: (a) El Breal de Orocual that comprises an inactive tar seep with estimated age in Plio/Pleistocene; and (b) Mene de Inciarte, an active surface asphalt deposit with absolute age of late Pleistocene. **Methods.** In order to provide the most specific assignment of the taxonomic identity of the specimens and a detailed anatomical description, all the analysed fossils were described consulting the relevant literature, besides, the comparison with extant specimens deposited in collections. **Results.** Mene de Inciarte snake fauna comprises vertebral remains assigned to the genus *Epicrates* sp. (Boidae), indeterminate viperids, and several isolated vertebrae attributed to “Colubridae” (Colubroidea, *sensu* Zaher et al. 2009). At El Breal de Orocual one vertebra is assigned to the genus *Corallus* sp. (Boidae), another specimen as cf. *Micrurus* (Elapidae), several attributed to “Colubrids” (Colubroides, *sensu* Zaher et al. 2009), and some vertebrae assigned to the Viperidae family. **Conclusions.** These new records give valuable insights into the diversity of snakes in north of South America during the Neogene/Quaternary boundary. The snake fauna of El Breal de Orocual and Mene de Inciarte reveals the presence of Boidae, Viperidae, “colubrids”, and the putative oldest South American record of Elapidae. The presence of *Corallus*, *Epicrates*, and the viperids together with the previous described *Boa constrictor*, reinforces the mosaic palaeoenvironmental scenario of El Breal de Orocual. The presence of Colubroides at the deposits sheds light in the palaeobiogeographical pattern of colonization of South America and is consistent with the hypothesis of two episodes of dispersion of Colubroides to the

continent.

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ABSTRACT

Background. Tar seep deposits in South America historically are well known to have yielded a rich fossil record of mammals contrasting with just few formal reports of reptile remains. Here we report a new snake fauna recovered from two Tar pits from Venezuela. The fossil remains come from two localities: (a) El Breal de Orocual that comprises an inactive tar seep with estimated age in Plio/Pleistocene; and (b) Mene de Inciarte, an active surface asphalt deposit with absolute age of late Pleistocene.

Methods. In order to provide the most specific assignment of the taxonomic identity of the specimens and a detailed anatomical description, all the analysed fossils were described consulting the relevant literature, besides, the comparison with extant specimens deposited in collections.

Results. Mene de Inciarte snake fauna comprises vertebral remains assigned to the genus *Epicrates* sp. (Boidae), indeterminate viperids, and several isolated vertebrae attributed to “Colubridae” (Colubroidea, *sensu* Zaher et al. 2009). At El Breal de Orocual one vertebra is assigned to the genus *Corallus* sp. (Boidae), another specimen as cf. *Micrurus* (Elapidae), several attributed to “Colubrids” (Colubroides, *sensu* Zaher et al. 2009), and some vertebrae assigned to the Viperidae family.

Conclusions. These new records give valuable insights into the diversity of snakes in north of South America during the Neogene/Quaternary boundary. The snake fauna of El Breal de Orocual and Mene de Inciarte reveals the presence of Boidae, Viperidae, “colubrids”, and the putative oldest South American record of Elapidae. The presence of *Corallus*, *Epicrates*, and the viperids together with the previous described *Boa constrictor*, reinforces the mosaic palaeoenvironmental scenario of El Breal de Orocual. The presence of Colubroides at the deposits sheds light in the palaeobiogeographical pattern of colonization of South America and is consistent with the hypothesis of two episodes of dispersion of Colubroides to the continent.

INTRODUCTION

Tar seeps are considered environments with fossils that suffered unusual and interesting taphonomic conditions of preservation, representing truly pivotal deposits to unravel the past biota (LaDuke, 1991a; Friscia et al., 2008; Solórzano, Rincón & McDonald, 2015; Brown et al., 2017). These sites are usually interpreted as entrapment areas, which hold great diversity of carnivores and associated herbivores taxa (Brown et al., 2017). Besides the representative macrovertebrate fauna, these peculiar areas often yield the preservation of small vertebrates, plants, and invertebrates (*e.g.* insects) in a lagerstätten condition (LaDuke, 1991a; Ward et al., 2005; Friscia et al., 2008; Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano et al., 2015; Holden et al., 2015; Holden et al., 2017).

The Venezuelan territory presents several tar pits, where only two was paleontologically explored: El Breal de Orocual (Czaplewski, Rincón & Morgan 2005; Rincón 2006; Rincón, White & McDonald, 2008; Rincón et al., 2006, 2009; Rincón, Prevosti & Parra, 2011; Holanda & Rincón, 2012), and Mene de Inciarte (Rincón et al., 2008; Prevosti & Rincón 2007; Steadman, Oswald & Rincón 2015). Regarding the recovered palaeodiversity, reports have predominated of large mammals such as canids, proboscids, felids, and xenarthrans (Prevosti & Rincón, 2007; Rincón et al., 2006, 2007, 2009; Rincón, Prevosti & Parra, 2011; Holanda & Rincón 2012; Solórzano, Rincón & McDonald, 2015), contrasting with few reports of small vertebrates and reptiles (Brochu & Rincón 2004; Czaplewski, Rincón & Morgan 2005; Fortier & Rincón 2013; Steadman, Oswald & Rincón 2015; Onary-Alves, Hsiou & Rincón, 2016).

The interval of the studied sites cover key geological periods, which recorded some of the major palaeobiogeographical and palaeoenvironmental transitions in South America. The late Pliocene/ early Pleistocene (El Breal de Orocual) is chronologically related to the establishment of the continental linking between Central and South America continents (Iturralde Vinent & MacPhee, 1999; Coates et al., 2004), besides, the beginning of the Great American Interbiotic Change (GABI) (Pascual, 2006; Woodburne, Cione & Tonni, 2006). In other hand, the late Pleistocene (Mene de Inciarte) is a well know period in which was recorded some drastic climatic changes in the globe (Peizhen, Molnar & Downs, 2001). The interaction between these factors shaped the palaeoenvironmental conditions, reflecting the palaeobiogeographical history of the groups (Simpson, 1980; Woodburne, Cione & Tonni, 2006), though most of the studies were based on the mammalian fossil record (Simpson, 1980). In this contribution, we report the fossil snakes from two Tar pits from Venezuela, showing the palaeobiogeographical and taxonomical implications, filling a Pliocene gap of the snake fossil record, and increasing the understanding of the squamate diversity during the Neogene/ Quaternary boundary on the Northern South America.

GEOLOGICAL SETTINGS

El Breal de Orocual

The recovered fossils of this site comes from an inactive tar seep deposit, located nearly 20 km from Maturín County, Monagas state, north eastern Venezuela (Fig. 1). The locality is emplaced within the Mesa Formation (Hackley et al., 2006; Rincón et al., 2009) and consists in a series of open asphalts fissures, of which one was extensively explored (ORS16 of Solórzano, Rincón & McDonald, 2015; site of this study). The tar pit does not have an absolute age of date, however the Mesa Formation was estimated by thermoluminescence (TL) ranging from ~2 Ma to 0.5 Ma (early to middle Pleistocene; Carbón, Schubert & Vaz, 1992). Alternatively, the recovered vertebrate fossil assemblage of ORS16 strong suggests the age of late Pliocene–early Pleistocene, based on the 30 identified taxa, and, especially due to the occurrence of *Smilodon gracilis* (Carnivora, Felidae) and cf. *Chapalmatherium* (Rodentia, Hydrochoeridae), which are considered characteristically Pliocene/Pleistocene taxa (Rincón et al., 2009; Solórzano et al., 2015). In this sense, here we prefer to retain the Plio–Pleistocene age (~2.6 Ma) for the deposit El Breal de Orocual, due to the previous reported taxa (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Holanda & Rincón, 2012; Solórzano, Rincón & McDonald, 2015), besides geological evidences that ~~can~~ indicate an age of more than 2.0 Ma for the tar pit (see dating issues outlined by Carbón, Schubert & Vaz, 1992; Onary-Alves, Hsiou & Rincón, 2016).

Mene de Inciarte

Mene de Inciarte is an active surface asphalt with production of consolidate sediments and liquid oil (Steadman, Oswald & Rincón, 2015). It is located in Mara County, Zulia state, northwest of Venezuela, about 90 Km from Maracaibo, in the lower hills of Sierra de Perijá (Fig. 1) (Czaplewski, Rincón & Morgan, 2005; Rincón et al., 2008; Steadman, Oswald & Rincón, 2015). Together with El Breal de Orocual constitutes the only two localities, of among a hundred asphalt deposits in the country, to have been explored palaeontologically (Steadman, Oswald & Rincón, 2015; Solórzano, Rincón & McDonald, 2015). Previous geochronological studies of the asphalt seep estimate its formation during the Quaternary due to the flooding of fissures with liquid asphalt (Urbani & Galarraga, 1991) and the relative dating based on the fossil mammal record corroborates the Pleistocene age of the deposit (e.g. pampatheriids, mastodons, equids, and ground sloths) (McDonald, Moody & Rincón, 1999). Currently, the deposit is absolute dated, with age estimated between 25,500±600 14C yr BP (28,456–30,878 cal yr BP) to 27,980 ±

370 14C years BP (31,165–32,843 cal yr BP), based on collagen samples of *Glyptodon clavipes* (Mammalia, Xenarthra) (Jull et al., 2004).

Fig 1: (Maps of the deposits)

MATERIAL & METHODS

Specimens: All recovered specimens consist in vertebral remains that are housed at El Breal de Orocual collection (OR–) or Mene de Inciarte collection (MI–) into the paleontological collection of Instituto Venezoelano de Investigacíones Científicas (IVIC), Caracas, Venezuela. The fossils comprise~~s~~ most precloacal trunk vertebrae, rarely occurring postcloacal specimens. The degree of preservation is variable between the specimens.

Anatomical analysis: In order to provide the most specific assignment of the taxonomic identity of the specimens and an accurate description, all the analysed material were described consulting the relevant literature, besides, comparison with extant specimens from collections (Table 1). The anatomical description follows the terminology of Auffenberg (1963); Hoffstetter & Gasc (1967); Rage (1984, 2001); Lee & Scanlon (2002); Hsiou & Albino (2009); Albino (2011); Hsiou et al. (2014) (Fig.2A). Quantitative data is based on LaDuke (1991a,b) (Fig. 2B). Measurements were taken with an analogic caliper (0.02 mm) and are expressed in millimetres.

Fig 2: (A: Anatomical structures; B: Quantitative data)

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York, New York; **MCN.D**, Coleção Didática de Herpetologia, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MCN-PV DR**, Seção de Paleontologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Coleção de Paleontologia de Vertebrados, Coleção Didática de Répteis, Porto Alegre, Brazil; **IVIC–OR**, Instituto Venezoelano de Investigaciones Científicas El Breal de Orocual collection; **UFMT**, Coleção da Universidade Federal do Mato Grosso, Mato Grosso, Brazil.

Table 1: Table of the comparative specimens consulted. Museum abbreviations are given in the institutional abbreviations section.

RESULTS

SYSTEMATIC PALAEONTOLOGY

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Macrostomata Müller, 1831

Boidae Gray, 1825

Boinae Gray 1825

Corallus Daudin, 1803

Corallus sp.

Fig. 3

Referred material: An isolated posterior precloacal vertebra (IVIC OR–6113).

Locality and age: Tar Pit ORS16, El Breal de Orocual, Monagas State, Venezuela. Age estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald, 2015).

Description: The vertebra is high, wide and short, having its vertebral centrum smaller than the neural arch width (naw > cl). In anterior view, the zygosphene is thick and ventrodorsally inclined, being wider than the cotyle (zw > ctw). The prezygapophyses are horizontally positioned in relation to the horizontal plane. The prezygapophyseal process is short and extends a little beyond the prezygapophyseal articular facet. The neural canal is subtriangular. The cotyle is rounded, with similar measurements of height and width (ctw ~ cth). The paracotylar fossae are deep and do not show evidences of paracotylar foramina. The paradiapophyses are lateroventrally oriented, showing clear distinction between the dia– and parapophyseal articular facets.

In posterior view, the lateral edges of the neural arch are characteristically vaulted. The zygantrum is eroded, however is possible to note the probable zygantral foramen. Next to the correspondent area of the zygantrum, there are small round pits filled with sediments, which here are interpreted as parazygantral foramina (*sensu* Lee & Scanlon, 2002). The postzygapophyses are horizontal oriented in relation to the horizontal plane. The condyle have a marked rounded morphology (cnw ~ cnh).

In lateral view, the neural spine rises from the anterior margin of the zygosphene roof, being anteroposteriorly short, exceeding from the margin of the neural arch. The zygosphene articular facets are oval in shape and dorsolaterally oriented. In each side of the vertebral centrum was observed only one lateral foramina. The vertebral centrum is short and shows a well-marked precondylar constriction. The condyle although distorted, has a slightly dorsal orientation in relation to the horizontal axis of the vertebral centrum. The haemal keel rises ventrally to the cotyle, developing posteroventrally until the proximity of the precondylar constriction.

In ventral view, the vertebral centrum is short and triangular shaped. The subcentral fossae are deep and well delimited in the anterior region of the vertebral centra. The haemal keel is large and develops anteroposteriorly toward the condyle, almost reaching the precondylar constriction. The postzygapohyses are broad and possesses subtriangular morphology.

In dorsal view, the neural arch is slightly wider than long (pr-pr>pr-po). The articular facets of the prezygapophyses are anterolaterally oriented and are subtriangular in shape, and longer than wide (prl>prw). The zygosphene roof bears markedly triangular lateral lobes with a distinct slightly convex mid lobe, characterizing the crenate condition (*sensu* Auffenberg, 1963). The interzygapophyseal ridge extends between the pre– to postzygapophysis, being deep. There is a deep posterodorsal notch in the mid portion of the posterior edge of the neural arch, which expose great part of the condyle.

Fig 3: (*Corallus* plate)

Measurements (in millimetres): IVIC OR-6113: **cl**. 3.4; **coh**.1.4; **cow**.1.3; **cth**. 0.9; **ctw**.1.0; **h**. 5.7; **naw**. 3.6; **nch**. 1.4; **ncw**. 1.2; **nsl**. 2.3; **nsh**. 2.1; **po-po**. 5.3; **pr-pr**. 5.6; **pr-po**. 4.7; **prl**. 1.6; **prw**. 1.0; **zh**. 0.9; **zw**. 2.9.

Identification and comparison: The specimen IVIC OR–6113 shares with Boidae the combination of the following vertebral features: broad and vaulted neural arch; well-developed and thick zygosphene; reduced prezygapophyseal process; high neural spine; well delimited and marked precondylar constriction; inclination of the prezygapophyses less than 15º; vertebral centrum short and robust; and presence of haemal keel on midtrunk vertebra (Rage, 1984, 2001; Albino & Carlini, 2008; Hsiou & Albino, 2009; Hsiou et al., 2013). The fossil is clearly distinct from the genera *Eunectes* and *Boa*, due to its relatively small size (Hsiou & Albino, 2010), being consistent with the morphology of *Corallus* and *Epicrates*.

The described vertebra can be attributed to the genus *Corallus* based on the following vertebral features: reduced vertebral size (naw<10 mm); wide, broad, and vaulted neural arch; prezygapophyses horizontally oriented (~ 180º) in anterior view; crenate morphology of the zygosphene roof in dorsal view; neural spine perpendicular to the vertebral centrum; broad and deep interzygapophyseal ridges; and the presence of parazygantral foramina in shape of small pits (*sensu* Lee & Scanlon, 2002) (Teixeira, 2013).

Regarding the intracolumnar variation of individuals of *Corallus*, the specimen shows the morphology of a posterior midtrunk vertebra, due to the reduced relative size;

long haemal keel; deep subcentral fossae; vertebral centrum very short; cotyle and condyle nearly rounded; and a triangular shaped parapophyseal facet (Teixeira, 2013).

Among the Neotropical Boinae genera the neural arch of IVIC OR–6113 differs substantially from *Boa*, which has a more vaulted condition with a deeper posterodorsal notch (pnl ~ 50% pr-po) (Onary-Alves, Hsiou & Rincón, 2016), and from *Eunectes* that has a depressed dorsoventrally neural arch (Hsiou & Albino, 2009). The fossil specimen also differs from *Epicrates*, in that its neural arch is slightly more vaulted than the condition observed in this genus (Rage, 2001).

Comparatively, IVIC OR–6113 shares with *Corallus* the relative size, an anteroposteriorly elongated condition, and the perpendicular orientation of the neural spine in relation to the vertebral centrum. This morphology matches with posterior precloacal midtrunk vertebrae of individuals of *Corallus*, which were observed in comparative specimens (Teixeira, 2013). In specimens of *Boa* is observed a neural spine stronger oriented anteroposteriorlly and the presence of the spinal blade and laminar crest (*sensu* Albino, 2011). In *Epicrates* it is noted a shorter, higher, and a stronger anteroposteriorlly oriented neural spine (Teixeira, 2013), conditions, which are divergent in comparison to the fossil specimen. The neural spine of *Eunectes*, despite being low as in *Corallus*, it is markedly shortened anteroposteriorly (Hsiou & Albino, 2009).

The zygosphene of IVIC OR–6113 is similar to midtrunk vertebrae present on *Epicrates* and *Corallus*, sharing the crenate condition found on the zygosphene roof in dorsal view in both genera. On the other hand, individuals of *Boa* and *Eunectes* shows a thicker and more robust zygosphene, besides the presence of a median tubercle between the neural canal and the zygosphene in *Eunectes* (Hsiou & Albino, 2009), and a marked concave anterior edge in the zygosphene roof in midtrunk specimens of *Boa* (Albino & Carlini, 2008; Onary-Alves, Hsiou & Rincón, 2016), divergent conditions compared with the fossil.

Concerning the morphology of the prezygapophyses, in anterior view, among the four Neotropical boids genera, the fossil specimen only shares with *Corallus* the condition of horizontal orientation of the prezygapophyses, while the others possess a slight to medium degree of orientation above the horizontal plane (Kluge, 1991; Rage, 2001; Hsiou & Albino, 2013; Teixeira, 2013; Onary-Alves, Hsiou & Rincón, 2016).

There are eight extant species within the genus *Corallus* (Uetz & Hošek 2016): *C. hortulanus* (Linnaeus, 1758); *C. caninus* (Linnaeus, 1758); *C. cookii* (Gray, 1842); *C. batesi* (Gray, 1860); *C. annulatus* (Cope, 1875); *C. ruschenbergerii* (Cope, 1875); *C. grenadensis* (Barbour 1914); *C. blombergi* (Rendahl and Vestergren 1941), and *C. cropanii* (Hoge, 1953). Among the species, only three are currently found in the Venezuela territory (*C. caninus*; *C. hortulanus*; *C. ruschenbergerii*), ~~being~~ just one (*C. ruschenbergerii*) present today in the specific area of the fossiliferous deposit (Rivas et al., 2012). The identification to species is limited due to the lack of autapomorphic features; however, of the three species currently inhabiting the territory, IVIC OR–6113 differs from *C. caninus* that possess a bigger vertebral height (h); the presence of a median tubercle between the neural canal and the zygosphene; and a high neural spine strongly oriented posteriorly. In general, the specimen shares the overall morphology with *C. hortulanus* and *C. ruschenbergerii*, however we prefer to be conservative and attribute the generic identification of *Corallus* sp. to the fossil specimen.

Epicrates Wagler, 1830

Epicrates sp.

Fig. 4

Referred material: An anterior isolated precloacal vertebra (IVIC MI–004)

Locality and Age: Mene de Inciarte Tar pit, Zulia state, Venezuela. Age dated of 25,500±600 ^{14}C years BP (28,456– 30,878 cal years BP) and 27,980 ± 370 ^{14}C years BP (31,165–32,843 cal years AP), late Pleistocene (Jull et al., 2004).

Description: The vertebra is short, robust, wide, and high, possessing a neural arch wider than the centrum length (naw > cl). In anterior view, the zygosphene is thick and wide, having its articular facets laterally oriented. The width of the zygosphene exceeds the width of the cotyle (zw > ctw), and is distinguishable in its median dorsal region, which present a convex prominent border. The prezygapophyses is slightly oriented dorsally above the horizontal axis, and bellow its articular facets, there is a small prezygapophyseal process. The neural canal has a "trifoliate" morphology in cross-section and its width is similar to the height (ncw ~ nch). The cotyle is rounded (ctw ~ cth) having deep paracotylar fossae with no paracotylar foramina. The paradiapophyses are broad, showing clearly distinction between the parapophyseal articular facets.

In posterior view, the neural arch is strongly vaulted. The median region of the zyantrum is not preserved, however it is noted that it is deep, having articular facets laterally oriented that are oval in shape. The postzygapophyses of MI-004 are slightly inclined upward. The condyle is round, with its height similar to the width (cow ~ coh).

In lateral view, the neural spine is long, rising from the posterior edge of the zygosphene. The articular facets of the zygosphene are oval shaped and oriented dorsolaterally upward. The vertebral centrum of MI–004 is short and delimited by a well marked precondylar constriction. Below the precondylar constriction, there is a long hypapophysis, which extends to the edge of the precondylar constriction, not exceeding the posterior rim of the condyle.

In ventral view, the vertebral centrum has a marked triangular morphology. The specimen shows a deep subcentral fossae, with paired subcentral foramina on each side of the vertebra. A narrow keel develops into the hypapophysis, however not extends beyond the precondylar constriction. The postzygapophyses are broad and displays a subtriangular morphology.

In dorsal view, the neural arch is slightly wider than long (pr-pr > pr-po). The articular facets of the prezygapophyses are subtriangular, anterolaterally oriented, and longer than wide (prl > prw). The anterior edge of the zygosphene roof is crenate (*sensu* Auffenberg, 1963), having triangular lateral lobes and an anteriorly projected median lobe. On the neural arch roof there are paired parasagittal ridges (*sensu* Hsiou & Albino, 2010) that extend from the posterior region of the zygosphene until nearly reach the posterior margin of the neural arch. The interzygapophyseal ridge extends between the pre– to postzygapophyses, being short and shallow. The posterodorsal notch is deep and exposes most part of the condyle.

Fig 4: (*Epicrates* plate)

Measurements (in millimetres): IVIC MI–004: **cl**:3.9; **coh**: 1.6; **cow**:2.3; **cth**:2.0; **ctw**:2.1; **h**:9.6; **naw**:4.9; **nch**:1.6; **ncw**:1.9; **nsl**:3.0; **nsh**:2.0; **po–po**:6.8; **pr–pr**:7.1; **pr–po**:5.1; **prl**:2.0; **prw**:1.4; **zh**:1.0; **zw**:3.6.

Identification and comparison: The material here described shares with the four Neotropical boids genera the following features: wide, short and high vertebral built; vaulted neural arch; vertebral centrum shorter than the length of the neural arch; inclination of the prezygapophyses articular facets lower than 15º; presence of a short prezygapophyseal process; deep posterodorsal notch; strong precondylar constriction; presence of paired subcentral foramina; and wide, thick zygosphene (Rage, 2001; Lee & Scanlon, 2002; Szyndlar & Rage, 2003; Hsiou & Albino, 2009).

The specimen IVIC MI–004 is attributed to the extant boid *Epicrates* on the basis of the following features: small vertebra that is wide, high and short; vaulted neural arch; deep paracotylar fossae; wide and high neural spine; hypapophysis, which does not exceeds the posterior margin of the condyle; zygosphene showing the crenate morphology; and a well marked triangular vertebral centrum (Teixeira, 2013).

Regarding the intracolumnar variation, the fossil is recognized as an anterior precloacal vertebra due to the presence of a well developed hypapophysis, which is observed exclusively in this region of the axial skeleton of boids (Rage, 2001); and for the presence of a rounded morphology on the cotyle and condyle (ctw ~ cth) (Teixeira, 2013).

The fossil shows comparatively small vertebral size, which is characteristically of boids like *Corallus* and *Epicrates*, being distinct from the great vertebral size of genera as *Boa* and *Eunectes*. The specimen shows a high vertebral size (h), and despite its broken apex of the neural spine, it is higher than individuals of *Corallus* and proportionally

Eunectes. Comparatively to *Boa*, the neural spine of the fossil is lower, matching only with the size observed in extant individuals of *Epicrates*. IVIC MI–004 exhibits in posterior view a more convexly domed neural arch when compared with anterior precloacal vertebrae of *Eunectes* and *Corallus*, which show~~s~~ a depressed dorsoventrally morphology.

Although broken, the neural spine of IVIC MI–004 is high, and long, divergently from that observed in *Corallus*, which shows a low and shortened anteroposteriorly morphology (Hsiou & Albino, 2009). Specimens of *Boa* exhibit~~s~~ a strong posterior orientation of the neural spine, besides the well marked structures of spinal crest and spinal blade (*sensu* Albino, 2011), morphology that is not present on the fossil specimen. Comparatively with IVIC MI–004, the neural spine of *Eunectes* showing a shorter length and the presence of the spinal crest. Among all the conditions, the neural spine of the fossil specimen shares similar morphology with individuals of *Epicrates*, which is high, short, and moderately oriented posteriorly compared with the aforementioned genera.

IVIC MI–004 shares with *Corallus* and *Epicrates* the crenate morphology of the zygosphene roof (*sensu* Auffenberg, 1963), however as pointed by Hsiou & Albino (2010), this condition is variable concerning the individual and the position of the vertebrae among the axial skeleton. Despite this fact, the crenate zygosphene of the specimen does not resemble the well defined concave morphology of the zygosphene roof found in *Boa*, nor the condition present in *Eunectes*, which possess a median tubercle between the neural canal and the zygosphene (Hsiou & Albino, 2009).

Nowadays in Venezuela, two species of *Epicrates* are distributed under territory: *E. cenchria*, Linnaeus (1758) and *E. maurus*, Gray (1849). Currently, only *E. maurus* is recorded at the site Mene de Inciarte. Between the five continental species of *Epicrates* (Rivera et al., 2011), no autapomorphic character of postcranial elements have been identified as diagnostic to a specific level. Under all listed characters, here we retain the conservative approach and recognize IVIC MI–004 as *Epicrates* sp.

Caenophidia Hoffstetter, 1939

Endoglyptodonta Zaher *et al*., 2009

Colubroides Zaher *et al*., 2009

Colubroidea Oppel, 1811

Indeterminate genera and species

Fig. 5

Referred material: Four nearly complete precloacal vertebrae (IVIC OR–3667; IVIC OR–6124; IVIC OR–2618; IVIC MI–005) and one postcloacal vertebra (IVIC OR–2917).

Localities and Age: IVIC OR–3667; IVIC OR–6124; IVIC OR–2618: Tar Pit ORS16, El Breal de Orocual, Monagas State, Venezuela. Age estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage (Rincón et al., 2009, Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald, 2015). IVIC MI–005: Mene de Inciarte Tar pit, Zulia state, Venezuela. Age dated of 25,500±600 ^{14}C years BP (28,456– 30,878 cal years BP) and 27,980 ± 370 ^{14}C years BP (31,165–32,843 cal years AP), late Pleistocene (Jull et al., 2004).

Description: The fossils share~~s~~ the following common pattern: wide, slender, and long vertebra, with the length of the vertebral centrum greater than the width of the neural arch (cl>naw). In anterior view, the neural spine is high and thin. The zygosphene of the specimens are thin, slender, having a convex edge dorsally. The neural canal is subtriangular in shape, and inside is possible to note three internal crests. The prezygapophyses of the fossils are long and variable regarding the orientation. The specimens IVIC OR–2618, IVIC OR–3667, and IVIC MI–005 shows a slightly inclination of the prezygapophyses above the horizontal plane, whereas, IVIC OR–6124 and IVIC OR–2917 exhibits a higher inclination upward, reaching the mid portion of the neural canal. The prezygapophyseal processes of the specimens are well preserved in IVIC OR–3667 and IVIC OR–6124. They are long and project ventrally beyond the prezygapophyseal articular facets. The cotyles of all vertebrae are rounded with the width similar to the height (ctw ~ cth). The paradiapophyses are anterolaterally oriented with a clear distinction between the dia– to parapophyseal articular facets, where the first is convex and the other concave respectively. IVIC OR–2917 shows the presence of pleurapophyses that is long, slender, and strongly oriented laterally; and the haemapophyses, ventral to the cotyle that is characterized by short and thin processes.

In posterior view, the neural arches of all specimens are depressed and in its mid portion rises a high and thin neural spine. The zygantrum is small and deep, and in some preserved specimens there are small paired zygantral foramina. The postzygapophyses of the fossils are variable in orientation: being in IVIC OR–3667, IVIC OR–6124, and IVIC OR–2917 slightly inclined above the horizontal plan; horizontally oriented in IVIC MI–005; and ventrally oriented in IVIC OR–2618. The condyles of all specimens are rounded, showing the height similar or equal to the width (cow ~ coh).

In lateral view, the neural spine is high, thin, and anteroposteriorly elongated. Its rises from the posterior edge of the zygosphene, developing until reach the limit of the posterodorsal notch. Only in IVIC OR–2917 is possible to observe paired lateral foramina on each side of the vertebral centrum. The vertebral centrum of all specimens are narrow and elongated. The condyle is posterodorsally inclined upward. With exception of IVIC OR–2917, all specimens shows on the ventral region a well developed haemal keel, which extends from the ventral region of the cotyle to the precondylar constriction, do not exceeding the condyle. The subcentral margin of the fossils, with exception of IVIC OR–6124, are strongly developed and well demarked in the entire extension of the vertebrae.

In ventral view, the length of the vertebral centrum exceeds the width of the neural arch (cl > naw). A prominent haemal keel and haemapophyses (in IVIC OR–6124) rises from the ventral region of the cotyle, extending longitudinally reaching the precondylar constriction. In IVIC OR–2618 and IVIC MI–005, can be observed in each side of the haemal keel the presence of paired subcentral foramina. All specimens exhibits the vertebral centrum delimited by marked subcentral groove. The postzygapophyses articular facets shows an oval shape, being posterolaterally oriented in all specimens, with the exception of IVIC MI–005 that shows a lateral orientation.

In dorsal view, the fossils exhibits a similar measurement of width and length (pr–pr ~ pr–po), except IVIC OR–2618 that is wider than long (pr–pr > pr–po).The prezygapophyses articular facets are oval shaped, anterolaterally oriented, slender, and long (prl > prw). A long prezygapophyseal process rises ventrally to the articular facets, being slender, thin, anterolaterally oriented, and particularly elongated in IVIC OR–3667. The zygosphene roof is variable among the specimens, being concave in IVIC OR–3667, straight in IVIC OR–6124, crenate with a median lobe in IVIC MI–005 (*sensu* Auffenberg, 1963). All specimens possesses a thin neural spine, which extends from the posterior region of the zygosphene roof, longitudinally until to reach the limit of the neural arch. The interzygapophyseal constriction is broad, extending from the prezygapophyses to the articular facets of the postzygapophyses. The posterodorsal notch of the neural arch is deep in all specimens, exposing ~~a~~ most ~~part~~ of the cotyle.

Fig 5: (Colubroidea indet. plate)

Measurements (in millimetres): *IVIC OR–3667*: **cl**:6.5; **coh**:2.6; **cow**:3.0; **cth**:2.0; **ctw**:2.5; **naw**:5.6; **nch**:2.6; **ncw**:3.0; **nsl**:5.1; **nsh**:1.9; pr–pr:9.0; **prl**:2.6; **prw**:2.1; **zh**:1.0; **zw**:4.4.

IVIC OR–6124: **cl**:4.9; **coh**:1.7; **cow**:2.1; **cth**:1.4; **ctw**:2.1; **h**:5.0; **naw**:3.5; **nch**:1.4; **ncw**:1.9; **nsl**:3.9; **nsh**:1.0; **po–po**:6.0; **pr–pr**:6.4; **pr-po**:6.6; **prl**:2.1; **prw**:1.1; **zh**:0.5; **zw**:3.0.

IVIC OR–2618: **cl**:8.0; **coh**:3.1; **cow**:3.7; **cth**:3.1; **ctw**:3.1; **naw**:7.1; **nch**:2.1; **ncw**:3.1; **po–po**:10.9; **pr–pr**:13.4; **pr–po**:11.0; **prl**:4.6; **prw**:2.4; **zh**:1.0; **zw**:5.0.

IVIC MI–005: **cl**:6.7; **coh**:2.5; **cow**:2.7; **cth**:2.0; **ctw**:2.2; **h**:7.1; **naw**:3.9; **nch**:2.0; **ncw**:2.2; **nsl**:5.1; **nsh**:1.9; **po–po**:7.3; **pr–po**:8.0; **prl**:2.4; **prw**:1.3; **zh**:0.7; **zw**:3.8.

IVIC OR–2917: **cl**:9.4; **coh**:2.8: **cow**:3.6; **cth**:3.7; **ctw**:3.9; **naw**:5.2; **po–po**:9.8; **pr–pr**:9.6; **pr–po**:11.7.

Identification and Comments: Colubroidea is a monophyletic group supported by several synapomorphic characters that includes cranial and soft tissues; however, none of them belongs to the axial skeleton (Rieppel, 1988; Zaher, 1999; Zaher et al., 2009). Given the current diversity, the group includes about 1853 of the 3596 extant species catalogued (Uetz & Hošek, 2016), representing a well diversified clade with a young evolutionary history (*e.g.* Cenozoic). The fossils here described can be attributed to Colubroidea based in the combination of the following features: gracile, slender and long vertebral build; neural arch longer than wide (cl > naw); thin, gracile, and slender zygosphene morphology; high and thin neural spine; paradiapophyses with clear distinction between the para– to diapophyseal articular facets; and the presence of an elongated prezygapophyseal process (Rage, 1984; Holman, 2000; Albino & Montalvo, 2006).

Traditionally, vertebrae that display the aforementioned features, had been attributed to the generic group "Colubridae". However, "Colubridae" is considered paraphyletic, since most of the previous analyses dealing with the group were made using the phenetical approach (Zaher, 1999), therefore, not representing a clade. Based on this interpretation here we prefer to avoid this generic group for taxonomical assignment.

Among Colubroidea standing out the families Calamariidae, Colubridae (clade *sensu* Zaher et al., 2009), Pseudoxenodontidae, Natricidae, and Dipsadidae (*sensu* Zaher et al., 2009), however no one has given vertebral diagnoses to separate. It is noteworthy that despite the attribution in a generic level of Colubroidea, the fossils specimens show~~s~~ individual variation of combination of vertebral characters, such as divergent orientation of the prezygapophyses, vertebral centrum size, zygosphene morphology, relative size of the prezygapophyseal process, evidencing in this way the possible occurrence of at least four unidentified different taxa under the sample.

Endoglyptodonta Zaher *et al*., 2009

Viperidae Oppel, 1811

Indeterminate genera and species

Fig. 6

Referred material: One almost complete precloacal vertebra (IVIC OR–2617); three partial precloacal vertebrae (IVIC OR–6104; IVIC OR–1760; IVIC OR–3674); and fragment of vertebral centrum (IVIC OR–5544).

Locality and Age: Tar Pit ORS16, El Breal de Orocual, Monagas State, Venezuela. Age estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald, 2015).

Description: In general, the vertebrae are short, high (only observable in IVIC OR–2617), slightly wider than long (pr-pr > pr-po), and possesses the length of the vertebral centrum similar to the width of the neural arch (cl ~ naw). In anterior view, the specimens show a thin zygosphene with a straight dorsal margin. The articular facets of the zygosphene are elliptical in shape and dorsally oriented. The neural canal are trifoliate, and its width is similar to the length (ncw ~ nch). The prezygapophyses are long, slender, and show articular facets, which are strongly inclined above the horizontal plane (~30º). All vertebrae shows a round cotyle, having width similar to the height (ctw ~ cth). Near the cotyle, there are deep paracotylar fossae. The paradiapophyses, despite eroded in some specimens, shows a clear distinction between the dia– to parapophyseal articular facets.

It is noted on the parapophyseal articular facet, small processes well oriented anteroventrally, which exceeds beyond the margin of the cotyle.

In posterior view (only preserved in IVIC OR–2617), the neural arch is slightly depressed and shows a marked triangular shape. The zygantrum is wide and deep. The postzygapophyses are broad and slightly inclined dorsally. The condyle in all specimens are round in outline shape. A long hypapophysis rises ventrally to the condyle, exceeding its distal margin.

In lateral view, only IVIC OR–2617 shows a preserved neural spine that is high, and well developed. The zygosphene articular facets are dorsally oriented and oval in shape. The paradiapophyses are completely preserved only in IVIC OR–6104, being dorsoventrally oriented. On the anteroventral region of the parapophyses, it is distinguishable a large parapophyseal process, which is well developed and strongly oriented anteroventrally. The vertebral centrum bears a prominent and long hypapophysis that despite eroded in IVIC OR–2617, exceed well beyond the posterior margin of the condyle.

In ventral view, the vertebral centrum is narrow and long. The subcentral fossae are shallow in some specimens (*e.g.* IVIC–6104 and IVIC OR–1760), whereas are deeper in others (*e.g.* IVIC OR–2616 and IVIC OR–3674). In all specimens, the fossae are restricted to the anterior region of the vertebral centrum. The subcentral fossae are delimited by well marked subcentral margin. The hypapophysis develops longitudinally to the centrum, being broken in some specimens but clearly surpassing the posterior margin of the condyle. The articular facets of the postzygapophyses are long and shows an elliptical ~~shape~~ outline.

In dorsal view, the neural arch is slightly wider than long (pr-pr > pr-po). The anterior margin of the zygosphene in the specimens IVIC OR–2617 and IVIC OR–6104 are concave, when the specimens IVIC OR–1760 and IVIC OR–3674 exhibits a straight margin. The interzygapophyseal constriction is broad, long, deep, and excavates the neural arch in concave shape. Despite the fact that in some specimens the neural spine is not preserved, it is observable (based in IVIC OR–2617), that the neural spine extends longitudinally from the posterior region of the zygosphene roof, exceeding the posterodorsal notch beyond the neural arch. The prezygapophyseal articular facets are oriented anterolaterally, having a slender, long, and elliptical shape morphology (prl > prw). The posterodorsal notch is deep, exposing great part of the condyle (only preserved in IVIC OR-2617 and IVIC OR–3674).

Fig 6: (Viperidae indet. plate)

Measurements (in millimetres): *IVIC OR-2617*. **cl**:7.0; **cth**:2.1; **ctw**:2.3; **h**:15.4; **naw**:6.0; **nch**:2.0; **ncw**:2.1; **nsl**:4.1; **nsh**:5.0; **po-po**:10.6; **pr-pr**:10.0; **pr-po**:8.0; **prl**:3.0; **prw**:1.5; **zh**:1.0; **zw**:4.8. *IVIC OR-6104*. **cl**:5.8; **cth**:2.7; **ctw**:3.0; **cth**:2.1; **ctw**:2.6; **naw**:5.5; **nch**:1.9; **ncw**:2.0; **pr-pr**:9.4; **prl**:2.3; **prw**:1.8; **zh**:0.8; **zw**:4.0. *IVIC OR-3674*. **cl**:3.2; **cth**:1.1; **ctw**:1.1; **coh**:1.9; **cow**:1.6; **naw**:6.0; **nch**:3.5; **po-po**:5.1; **pr-po**:4.9; **prl**:2.1; **prw**:1.1. *IVIC OR-3674*. **cth**:2.6; **ctw**:2.8; **naw**:6.8; **nch**:1.5; **ncw**:2.1; **prl**:2.5; **prw**:2.8; **zh**:1.4.

Identification and Comments: The analysed fossils share~~s~~ with Colubroidea the following vertebral characters: gracile vertebra, which is longer than wide (pr–po>pr–pr);

thin neural spine; slender zygosphene; presence of short and prominent prezygapophyseal accessory process; and paradiapophyses with clear distinction between the dia– to parapophyszeal articular facets (Rage 1984; Lee & Scanlon 2002; Albino & Montalvo 2006).

The specimens possesses a well-developed hypapophysis, which is considered an apomorphic character found in “Xenodermatinae”, Homalopsinae, “Pseudoxyrhophiinae”, “Boonodontinae”, Elapidae, Viperidae, and Natricinae (Zaher, 1999). Among these groups, IVIC OR–6104 shares within Viperidae the single autapomorphic postcranial character, which is the presence of a well developed parapophyseal process, strongly oriented anteroventrally (Zaher, 1999; Zaher et al., 2009). So far, based in this character, IVIC OR–6104 can be unequivocally assigned to the Viperidae family. Despite the lack of the parapophyseal process, the other specimens can be identified as Viperidae due to the following combination of vertebral characters: vertebra not elongated; slender and straight zygosphene; well-developed hypapophyses; wide and short neural canal; depressed neural arch; postzygapophyses strongly oriented anterolaterally; short prezygapophyseal process; and subcentral fossae restricted to the anterior region of the centrum (Auffenberg, 1963; Rage, 1984; Holman, 2000; Albino & Montalvo, 2006; Head, Sánchez-Villagra & Aguilera, 2006; Hsiou & Albino, 2011).

Concerning the strict taxonomic status, Albino & Montalvo (2006) do not recognizes diagnostic~~s~~ features, neither synapomorphic characters that are informative to identify vertebral remains of Viperidae as genera and species. Among the most common studied genera, Camolez & Zaher (2010) reported subtle differences between *Crotalus* and *Bothrops*, regarding the morphology of the anterior margin of the zygosphene roof and the orientation of the parapophyseal process. Among these features, the anterior margin of the zygosphene roof of *Crotalus* usually tend to present a defined concave mid region morphology, a condition observed in IVIC OR–2617 and IVIC OR–6104.

Currently, six genera of Viperidae are distributed in the Venezuelan territory, which are distributed throughout the country: *Bothrops*, *Crotalus*, *Bothriechis*, *Lachesis*, and *Porthidium*, with 12 valid species (Rivas et al., 2012). Due to the lack of diagnostic vertebral features, as well the poor preservation of the specimens, here we retain the conservative assignment of Viperidae to the specimens.

Endoglyptodonta Zaher et al., 2009
Elapoidea Boie, 1827
Elapidae Boie, 1827
cf. *Micrurus*
Fig. 7

Referred material: One almost complete precloacal vertebra (IVIC OR–2619).

Locality and Age: Tar Pit ORS16, El Breal de Orocual, Monagas State, Venezuela. Age estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald, 2015).

Description: The vertebra is gracile, low, and long, possessing the vertebral centrum longer than the width of the neural arch (cl > naw). In anterior view, the zygosphene is gracile, slim, and wider than the cotyle (zw > ctw), exhibiting a convex shape dorsally oriented. The neural canal of the specimen is trifoliate and is as wide as high (ncw ~ nch). The prezygapophyses are short and slightly oriented above the horizontal plane. The only preserved prezygapophyseal process is ventrally located to the right prezygapophysis, being elongated and well developed. The cotyle of the specimen have an oval shape, being slightly flattened dorsoventrally, and possessing the width greater than the height (ctw > cth). The paradiapophyses are clearly divergent regarding the dia– to parapophyseal articular facets.

In posterior view, the neural arch is depressed. The neural spine is low and in its mid region is possible to note a deep sulcus excavated by the posterodorsal notch of the neural arch. The zygantrum is deep and wide. The postzygapophyses are slightly oriented lateroventrally. The condyle is round with the height similar to its wide (cow ~ coh). Beneath the condyle, there is a hypapophysis that slightly exceeds its ventral margin.

In lateral view, the neural spine is very low, straight, anteroposteriorlly elongated, possessing a slope toward the posterior region of the neural arch. The articular facet of the zygosphene is anterolaterally oriented and elliptical in shape. The paradiapophyses exhibit~~s~~ a slightly anterolateral orientation. The vertebral centrum is long, and bears a weakly marked precondylar constriction. Ventral to the centrum, the hypapophysis is slender, strongly oriented posteriorly, and despite not showing the distal region preserved, probably extend out the posterior margin of the condyle.

In ventral view, the vertebral centrum is long and narrow (cl > naw), having a shallow subcentral fossae, which are delimited by strong marked subcentral margins. The hypapophysis extends longitudinally from the ventral margin of the cotyle to the mid region of the vertebral centrum, do not exceeding the precondylar constriction. The postzygapophyseal articular facets are long and elliptical in shape.

In dorsal view, the vertebral centrum have the width equal to its length (pr–pr = pr–po). The zygosphene roof exhibit triangular shaped lateral edges with a straight mid region. The prezygapophyseal articular facets are elliptical in shape, slender (prl > prw), and exhibits an anterolateral orientation. A poorly preserved and elongated prezygapophyseal process is located ventrally to the right prezygapophyseal articular facet, possessing a transverse orientation in relation to the prezygapophysis. It is noted ventrally to the prezygapophyses, the diapophyseal articular facets of the paradiapophyses, which are convex in shape and lateroposteriorly oriented. The interzygapophyseal constriction is long and broad, extending from the base of the prezygapophysis to the postzygapophysis, being relatively shallow. The neural spine is thin, rising from the posterior region of the zygosphene roof developing longitudinally until reach the contact with the posterodorsal notch. The postzygapophyses are slightly anterolaterally oriented, exposing a small portion of its articular facets. The posterodorsal notch is deep and excavates in the mid region of the neural arch.

Fig 7: (cf. *Micrurus* plate)

Measurements (in millimetres): *IVIC OR-2619*. **cl**:5.9; **coh**:2.0; **cow**:2.2; **cth**:1.6; **ctw**:2.1; **naw**:3.6; **nch**:1.9; **ncw**:2.0; **po-po**:6.7; **pr-pr**:6.8; **pr-po**:6.8; **prl**:2.0; **prw**:0.9; **zh**:0.7; **zw**:3.7.

Identification and Comments: The diagnosis within Elapidae genera is based on cranial characters (*e.g.* the morphology of the proteroglyph condition of the maxilla), as well as, morphological traits associated with the venom glands (Underwood & Kochva, 1993; Zaher, 1999), do not being reported yet a single autapomorphic diagnostic postcranial character in genera/ species level. Currently, Venezuelan territory host two genera of elapids: *Micrurus* and *Leptomicrurus* (Rivas et al., 2012), occurring at the fossiliferous site two species of *Micrurus*: *M. dissoleucus* Cope, 1860 and *M. isozonus* Cope, 1860.

Among the comparative osteological material accessed for this study, IVIC OR–2619 shares with the genus *Micrurus* the following vertebral characters: gracile vertebra with a depressed neural arch; oval shaped cotyle (ctw > cth); slender and elongated pre– and postzygapophyseal articular facets; in lateral view, thin and very low neural spine possessing a straight dorsal edge that develops into a slope posteriorly to the neural arch; and thin hypapophysis which is strongly compressed anteroposteriorlly (Auffenberg, 1963; Holman, 1977). Due to the poor preservation of the specimen, as well the lack of formal studies concerning the postcranial osteology within Elapidae, here we prefer to retain the conservative taxonomic attribution of IVIV OR–2619 as cf. *Micrurus*, sharing the overall morphology with vertebrae of individuals of the modern genus, but lacking either diagnostic or indicative traits that can be used for precise assignment.

DISCUSSION

The Venezuelan snake fossil record is still scarce when compared to other South America localities (*e.g.* Argentina, Brazil, Colombia). Among the Cenozoic, the Socorro Formation (middle Miocene) provided records of the alethinophidian of uncertain affinities *Colombophis* and the boid *Eunectes* (Head, Sánchez–Villagra & Aguilera, 2006 after Hsiou, Albino & Ferigolo, 2010; Hsiou & Albino, 2010), whereas in the Urumaco Formation (middle Miocene) it was only found remains of *Eunectes* (Head, Sánchez–Villagra & Aguilera, 2006 after Hsiou & Albino, 2010). Recently, Onary-Alves, Hsiou & Rincón (2016) reported the presence of *Boa constrictor* from the El Breal de Orocual, uncovering the single record for the here studied locality. The youngest record comes from the late Pleistocene of Cucuruchu gravels, where Head, Sánchez–Villagra & Aguilera (2006) identified an indeterminate Viperidae. Although limited, these punctual records when gathered and scrutinized can give direct insights about palaeoenvironmental and palaeobiogeography of snakes during the Cenozoic/ Quaternary in South America.

The palaeoenvironmental conditions interpreted for the North~~ern~~ of South America is strictly based on studies concerning the palaeofaunal mammal assemblage, which strongly suggests the predominance of a dry savanna crossed by fragmentary forests, rivers, and patches of gallery forest, with the occurrence of humid-climate species of plants (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald, 2015). The snakes recovered from the Tar Pits deposits corroborate the interpretation of the mosaic environmental scenario composed of small forests, arid regions, and the occurrence of rivers, analogous to the modern Venezuelan Llanos (Rincón et al., 2007; Rincón et al., 2009; Rincón, Prevosti & Parra, 2011). Although

Corallus and *Epicrates* currently ~~being~~ widespread boid~~s~~ genera across the South American territory (Henderson, 1995), some species within these genera can persist only in suitable microclimate and microenvironment, especially ~~concerning~~ the forest exclusive species (Rodrigues, 2005; Carvajal–Cogollo & Urbina–Cardona, 2015). Most ~~of~~ species of *Corallus* and *Epicrates* can be characterized to demand specific forest environment to establish viable population (Henderson et al., 1995), and a major change in the microclimate can threaten these genera, even leading to ~~the~~ local extinction (Rodrigues, 2005; Carvajal–Cogollo & Urbina–Cardona, 2015). The recovered *Corallus* vertebra of El Breal de Orocual reaffirms the presence of forest regions with adequate environment (*i.e.* humidity and temperature) for boids at the Plio–Pleistocene, and increases the boid diversity, which was only restricted to the occurrence of *Boa constrictor* (Onary-Alves, Hsiou & Rincón, 2016). The recovered Colubroides (*sensu* Zaher, 2009), such as the "colubrids" (Colubroidea), and especially the viperids corroborate the presence of savanna dry components mixed with the humid regions of forests, since some species of colubrids and viperids occupies open areas and are well-known to live in dry environments (*e.g. Crotalus* sp.). Nowadays, all these snakes, *Corallus*, *Epicrates*, "colubrids" and viperids are present in the Venezuelan Llanos (Rivas et al., 2012), and the records of *Corallus*, "colubrids", and Viperidae during the Plio/Pleistocene, together with the presence of *Epicrates*, "colubrids", and Viperidae in the Late Pleistocene, suggest that the palaeoenvironment, despite the climatic fluctuations, could persisted in some degree throughout this time interval.

Regarding the Colubroides (*sensu* Zaher et al., 2009), an interesting biogeographical question centre in its origins and entrance in South America (Fig. 8). The state of art concerning the studies of palaeobiogeography of the group suggest two episodes of dispersion from ~~the~~ North America to South America, the first dated back to the uplift of the Panama Isthmus (Albino & Montalvo, 2006; Hoffstetter, 1967; Cadle & Greene, 1993; Albino, 1996b) and the second attesting another episode during the Plio/Pleistocene (Wüster et al., 2002, 2005; Head, Sánchez–Villagra & Aguilera 2006). The oldest records of “Colubridae” in America, comes from the late Eocene of Georgia, North America (Fig. 8A) (Parmley & Holman, 2003), whereas they are dated only during the early Miocene in South America (Fig. 8B) (Albino, 1996b). This early Miocene record together with the late Miocene records of Viperidae from Argentina and “Colubroids” from Brazil (Fig. 8C) (Verzi et al., 2004; Albino & Montalvo 2006), evidences that the first great dispersion of Colubroides, occurred prior to major continental events like the uplifting of the Panama Isthmus and the great American biotic interchange (GABI) (Albino & Montalvo, 2006; O’Dea et al., 2016). This dispersion can be explained probable by the aquatic crossing of a series of island complex in the Central America during the Miocene (Fig. 8D) (Hoffstetter, 1967; Cadle & Greene, 1993; Albino, 1996b).

Based on the Venezuelan record of Viperidae of the late Pleistocene, Head, Sánchez–Villagra & Aguilera (2006) suggested that the Colubroides could be reached in South America in two distinct episodes during the Neogene. Indeed, the snakes here described corroborate the aforementioned hypothesis reinforcing the hypothesis of the second entrance during the Pliocene/Pleistocene boundary (Fig. 8E). The recovered fauna of Plio/Pleistocene “colubrids” and viperids at El Breal de Orocual, jointly with a suitable route after the complete uplift of the Panama Isthmus (O’Dea et al., 2016), supports the hypothesis of the second entrance of Colubroides in South America.

Additionally, studies in molecular divergence date (Wüster et al., 2002, 2005) suggests a similar pattern in which viperids like *Bothrops*, *Lachesis*, and *Bothriechis* could have reached and diversified in South America before the total closure of the Panama Isthmus (*e.g.* the early Miocene records of Argentina, Albino, 1989; Albino, 1996b; Albino & Montalvo, 2006), whereas some genera like *Crotal~~l~~us* and *Porthidium* are estimated to be late dispersers, after the total uplift of the Panama Isthmus (*e.g.* the Venezuelan Plio/Pleistocene records of "colubrids" and viperids and the late Pleistocene viperids, Head, Sánchez–Villagra & Aguilera 2006 Fig. 8F). The recovered viperids fossils of El Breal de Orocual are spatial and chronologically consistentl~~y~~ with the estimated entrance of the genus *Crotalus* to the continent (Wüster et al., 2002, 2005). Regarding the described material, the specimens IVIC OR–6104 and IVIC OR–2617 show~~s~~ no significant morphological distinction with the comparative osteological material analysed of *Crotalus* (*see appendix*). These specimens share~~s~~ with the genus *Crotalus* the distinct characteristic in possess a concave anterior edge of the zygosphene roof, which is argued to be exclusive for the genus (Camolez & Zaher, 2010). However, since no reliable synapomorphic~~s~~ characters are present beyond the family level, here we preferred to retain the conservative approach for the identification. Despite the generic assignment of the Colubroides material, the specimens shows a great potential for future biogeographical studies, especially regarding the aforementioned viperids. However, only refined taxonomical identifications can be assertive and provide conclusive patterns of "colubrids" and viperids dispersion to the South America based in the fossil record.

The extant species of "coral snakes" are currently represented in America by the genus *Micruroides* and *Micrurus* and in Asia by the genus *Sinomicrurus* (Lee et al., 2016).

In the scope of the fossil record, remains of “coral-snakes” are very scarce and geologically young (~16 to 13 Ma) (Holman, 1977), representing an observation, which is concordant with the time calibrated phylogeny of the group that estimates the rise of the lineage in ~30 Ma. (Lee et al., 2016). South American records are restricted to the Quaternary of Brazil, represented by some cranial remains attributed to *Micrurus corallinus*, and vertebrae assigned to *Micrurus* sp. (Camolez & Zaher, 2010). The North American territory have some occurrences, like the oldest fossil record of the group from the late Barstovian North American Land Mammal Age of Nebraska (middle Miocene) (Holman, 1977), and some material attributed to *Micrurus fulvius* and *Micrurus* cf. *M*. *fulvius* for the Pleistocene of Florida (Auffenberg, 1963). Records dated from the middle Miocene of Europe show~~s~~ the occurrence of the extinct species *Micrurus gallicus*, *Micrurus* cf. *M*. *gallicus*, and an indeterminate *Micrurus* vertebral material (Rage & Holman, 1984; Venczel, 2001; Ivanov & Böhme, 2011). Indeed, the palaeobiogeographical history of the genus *Micrurus* is somewhat complex and the scarcity of studies concerning the anatomy of the axial skeleton of the genus hampers the identification of fossil material in a specific level, preventing further inferences about biological events in ~~the~~ deep time (Head, Mahlow & Müller, 2016). Although the listed factors restrict the knowledge of the biogeography of the genus *Micrurus*, Rage & Holman (1984) based on the fossil record inferred a North American origin of the genus, followed by an early Miocene dispersion to Asia, eventually reaching Europe. The South American continent is estimated to be colonized by *Micrurus* after the complete uplift of the Panama Isthmus (~2.8 Ma.) (O’Dea et al., 2016), probably by events of dispersion caused by the decrease of the average temperature on higher latitudes in North America (Rage &

Holman, 1984). The herein described putative cf. *Micrurus* is spatial-temporally consistent with the hypothesis of a South American colonization of “coral-snakes” during the Plio/Pleistocene (Fig. 8G), representing an interesting record that can bring valuable insights for the biogeography of the group.

CONCLUSIONS

The Venezuelan snake fossil record is becoming increasingly uncovered and this report contributes to our knowledge about the Cenozoic squamate fossils from South America as a whole. The snake fauna of these Tar pits shows the presence of Boidae, Viperidae, “colubrids”, and the putative oldest South American record of Elapidae. The presence of *Corallus*, *Epicrates*, and viperids together with the previous described *Boa constrictor*, reinforces the mosaic palaeoenvironmental scenario of El Breal de Orocual, composed of forest areas mixed with savannah components and dry environments. The recovered Colubroides (*sensu* Zaher et al. 2009) remains are consistent with the hypothesis of a second episode of dispersion and colonization of Colubroides into the South America, after the total uplift of the Panama Isthmus, especially with the occurrence of the putative fossils of *Crotalus* and cf. *Micurus*. All the described fossils are potentially significant to reveal specific palaeobiogeographic and palaeoenvironmental patterns and constitute an important preliminary step. However only the identification at lower taxonomical level can provide further information for more likely inferences. In this sense, additional analyses and the use of new methodologies, such as three–dimensional morphometrics, and the exhaustive anatomical analysis of the postcranial material, especially of Colubroides constitute a crucial and a future perspective in our research.

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REFERENCES

Albino AM, 1989. Primer registro de Colubroidea (Reptilia: Serpentes) de Argentina (Edad Montehermosense s.l., Plioceno). *Ameghiniana* **25**:281–287.

Albino AM. 1996a. The South America Fossil Squamata (Reptilia: Lepidosauria). *Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie* **30**:185-202.

Albino AM. 1996b. Snakes from the Miocene of Patagonia (Argentina) Part II: the Colubroidea. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **200**: 353–360.

Albino AM, Carlini A. 2008. First record of *Boa constrictor* (Serpentes, Boidae) in the Quaternary of South America. *Journal of Herpetology* **42**: 82–88.

Albino AM, Montalvo CL. 2006. Snakes from the Cerro Azul Formation (Upper Miocene), central Argentina, with a review of fossil viperids from South America. *Journal of Vertebrate Paleontology* **26**: 581–587.

Albino AM. 2011. Morfologia vertebral de *Boa constrictor* (Serpentes: Boidae) y la validez del gênero mioceno *Pseudoepicrates* Auffenberg, 1923. *Ameghiniana* **48**: 53–62.

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

Barbour T. 1914. A Contribution to the Zoögeography of the West Indies, with Especial Reference to Amphibians and Reptiles. *Memoirs of the Museum of Comparative Zoölogy* **44**: 205-359.

Brochu CA, Rincón AD. 2004. A Gavialoid Crocodylian from the lower Miocene of Venezuela. *Special Papers in Palaeontology* **71**: 61-79.

Brown C, Curd E, Anthony F. 2017. An actualistic experiment to determine skeletonization and disarticulation in the La Brea Tar Seeps. *Palaios* **32**: 119-124.

Cadle JE, Greene HW. 1993. Phylogenetic patterns, biogeography and the ecological structure of Neotropical snake assemblages. In: R.E. Ricklefes, and D. Schluter (Eds), *Species diversity in ecological communities. Historical and geographical perspectives*. Chicago, University of Chicago Press, 281-293.

Camolez T., Zaher H. 2010. Levantamento, identificacão e descrição da fauna de Squamata do Quaternário Brasileiro (Lepidosauria). *Arquivos de Zoologia, Museu de Zoologia da Universidade de São Paulo* **41**: 1–96.

Carbón J, Schubert C, Vaz, JE. 1992. Caracterización y edades termoluminiscentes de los sedimentos de la Formacion Mesa, en dos localidades del sur de Anzoategui (Venezuela). *Acta Científica Venezolana* **43**: 387–391.

Carvajal-Cogollo JE, Urbina-Cardona NU. 2015. Ecological grouping and edge effects in tropical dry forest: reptile-microenvironment relationships. *Biodiversity & Conservation* **24**: 1109-1130.

Cope ED. 1860. Supplement to "A catalogue of the venomous serpents in the Museum of the Academy of Natural Sciences of Philadelphia, with notes on the families, genera, and species.". *Proceedings of the Academy of Natural Sciences of Philadelphia* **1860**: 72-74.

Cope ED. 1875. On the Batrachia and Reptilia of Costa Rica with notes on the herpetology and ichthyology of Nicaragua and Peru. *Journal of the Academy of Natural Sciences of Philadelphia N.S.* **8**: 93-183.

Czaplewski NJ, Rincón AD, Morgan GS. 2005. Fossil Bat (Mammalia: Chiroptera) Remains from Inciarte Tar Pit, Sierra de Perijá, Venezuela. *Caribbean Journal of Science* **41**:768-781.

Daudin FM. 1803. *Histoire Naturelle, Générale et Particulière des Reptiles*. F. Dufart, Paris, 439 pp.

Fortier DC, Rincón AD. 2013. Pleistocene crocodylians from Venezuela, and the description of a new species of *Caiman*. *Quaternary Research* **305**: 141-148.

Friscia AR, Valkenburgh BV, Spencer L, Harris J. 2008. Chronology and spatial distribution of large mammal bones in Pit 91, Rancho La Brea. *Palaios* **23**: 35-42.

Gray JE. 1842. Synopsis of the species of prehensile-tailed snakes, or family Boidae. *Zoological Miscellany* **2**: 41-46.

Gray JE. 1849. *Catalogue of the specimens of snakes in the collection of the British Museum*. Edward Newman, London, i-xv; 125p.

Gray JE. 1860. Description of a new genus of Boidae discovered by Mr. Bates on the Upper Amazon. *The Annals and magazine of natural history; zoology, botany, and geology* **6**: 131-132.

Gray JE. 1825. A synopsis of the genera of Reptilia and Amphibia. *Annals of Philosophy* **10**: 193–217.

Hackley PC, Urbani F, Karlsen AW, Garrity CP. 2006. *Mapa Geologico de Venezuela a Escala 1:750,000*. Available online at https://pubs.er.usgs.gov/publication/ofr20061109 (accessed 3 July 2017).

Head JJ, Sanchéz-Villagra MR, Aguilera OA. 2006. Fossil snakes from the Neogene of Venezuela (Falcón State). *Journal of Systematic Palaeontology* **4**: 233–240.

Head JJ, Mahlow K, Müller J. 2016. Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidea, Colubridae. *Palaeontologia Electronica* **19.2.2FC**: 1-21.

Henderson RW, Waller T, Micucci P, Puorto G, Bourgeois RW. 1995. Ecological correlates and patterns in the distribution of Neotropical Boines (Serpentes: Boidae): a preliminary assessment. *Herpetological Natural History* **3**: 15–27.

Hoffstetter R, Gasc J. 1969. Vertebrate and ribs of modern reptiles. *In*:. C. Gans, A. D'A. Bellairs, and T. Parsons, (Eds), *Biology of Reptilia*. Academic Press, London, 201–310.

Hoffstetter R. 1967. Remarques sur les dates d´ implantation des différents groupes de Serpents terrestres en Amérique du Sud. *Comptes Rendues Sommaire des Séances de la Société Géologique de France* **3**: 93–94.

Hoffstetter R, Rage, JC. 1977. Le gisement de vertébrés miocènes de La Venta (Colombie) et sa faune de serpents. *Annales de Paléontologie (Vertébrés)* **63**:161–190.

Hoge AR. 1953. A new genus and species of Boinae from Brazil, *Xenoboa cropanii*, gen. nov., sp. nov. *Memórias do Instituto Butantan* **25**: 27-31.

Holanda EC, Rincón AD. 2012. Tapirs from the Pleistocene of Venezuela. *Acta Palaeontologica Polonica* **57**: 463–473.

Holden AR, Erwin DM, Schick KN, Gross J. 2015. Late Pleistocene galls from the La Brea Tar Pits and their implications for cynipine wasp and native plant distribution in southern California. *Quaternary Research* **84**: 358-367.

Holden AR, Southon JR, Will K, Kirby ME, Aalbu RL, Markey MJ. 2017. A 50,000 year insect record from Rancho La Brea, Southern California: Insights into past climate and fossil deposition. *Quaternary Science Reviews* **168**: 123-136.

Hollman JA. 1977. Upper Miocene Snakes (Reptilia, Serpentes) from Southeastern Nebraska. *Journal of Herpetology* **11**: 323-335.

Holman JA. 2000. *Fossil Snakes of North America*. Indiana University Press, Bloomington, Indiana, 357 pp.

Hsiou AS, Albino AM, Ferigolo J. 2010. Reappraisal of the South American Miocene snakes of the genus *Colombophis*, with description of a new species. *Acta Palaeontologica Polonica* **55**: 365–379.

Hsiou AS, Albino AM. 2009. Presence of the genus *Eunectes* (Serpentes, Boidae) in the Neogene of Southwestern Amazonia, Brazil. *Journal of Herpetology* **43**: 612–619.

Hsiou AS, Albino AM. 2010. New snake remains from the Miocene of northern South America. *Herpetological Journal* **20**: 249–259.

Hsiou AS, Albino AM, Medeiros MA, Santos RAB. 2014. The oldest Brazilian snakes from the Cenomanian (early Late Cretaceous). *Acta Paleontologica Polonica* **59**: 635–642.

Hsiou AS, Albino AM. 2011. First record of Viperidae snakes from the Pleistocene of southwestern Brazilian Amazonia. *Alcheringa* **35**: 389–395.

Hsiou AS, Winck GR, Schubert BW, Ávilla L. 2013. On the presence of *Eunectes murinus* (Squamata, Serpentes) from the late Pleistocene of northern Brazil. *Revista Brasileira de Paleontologia* **16**: 77–82.

Iturralde-Vinent MA, MacPhee RDE, Díaz-Franco S, Rojas-Consuegra R., Suárez W., Lomba A. 2000. Las Breas de San Felipe, a Quaternary fossiliferous asphalt seep near Martí (Matanzas Province, Cuba). *Caribbean Journal of Science* **36**:300–313.

Ivanov M, Böhme M. 2011. Snakes from Griesbeckerzell (Langhian, Early Badenian), North Alpine Foreland Basin (Germany), with comments on the evolution of snake faunas in Central Europe during the Miocene Climatic Optimum. *Geodiversitas* **33**: 411-449.

Jull AJT, Iturralde-Vinent M, O'Malley JM, MacPhee RDE, McDonald HG, Martin PS, Moody J, Rincón AD. 2004. Radiocarbon dating of extinct fauna in the Americas recovered from tar pits. *Nuclear Instruments and Methods in Physics Research B* **224**: 668–671.

Kluge AG. 1991. Boine snake phylogeny and research cycles. *Miscellaneous publications (University of Michigan. Museum of Zoology)* **178**: 1-58.

LaDuke TC. 1991a. The fossil snakes of Pit 91, Rancho La Brea, California. *Contributions in Science* **424**:1–28.

LaDuke TC. 1991b. *Morphometric Variability of the Precaudal Vertebrae of Thamnophis sirtalis sirtalis (Serpentes: Colubridae), and Implications for the Interpretation of the Fossil Record*. Ph.D. thesis, City University of New York, New York.

Lee MSY, Scanlon JD. 2002. Snake phylogeny based on osteology, soft anatomy and ecology. *Biological Reviews of the Cambridge Philosophical Society* **77**: 333–401.

Lee MSY, Sanders KL, King B, Palci A. 2016. Diversification rates and phenotypic evolution in venomous snakes (Elapidae). *Royal Society Open Science* **3**:150277. DOI: http://dx.doi.org/10.1098/rsos.150277.

Linnaeus C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentii Salvii, Holmiae, 824 p.

McDonald GH, **Moody JM**, **Rincón AD**. 1999. Preliminary report on Pleistocene vertebrates from asphalt deposits in the Maracaibo basin, Venezuela. *Congreso Internacional–Evolución Neotropical del Cenozoico, 19-22 May, La Paz-Bolivia. Programa y Resúmenes*, p. 27.

Müller J. 1831. Beiträge zur Anatomie und Naturgeschichte der Amphibien. *Zeitschrift für Physiologie* **4**: 190–275.

Nopcsa F. 1923. *Eidolosaurus* und *Pachyophis*, Zwei neue Neocom Reptilien. *Palaeontographica* **55**: 97–154.

O'Dea A, Lessios HA, Coates AG, Eytan RI, Restrepo-Moreno SA, Cione AL, Collins LS, De Queiroz A, Farris DW, Norris RD, Stallard RF, Woodburne MO, Aguilera O, Aubry MP, Berggren WA, Budd AF, Cozzuol MA, Coppard SE, Duque-Caro H, Finnegan S, Gasparini GM, Grossman EL, Johnson KG, Keigwin LD, Knowlton N, Leigh EG, Leonard-Pingel JS, Marko PB, Pyenson ND,, Rachello-Dolmen PG, Soibelzon E, Soibelzon L, Todd JA, Vermeji GJ, Jacson JBC. 2016. Formation of the Isthmus of Panama. *Science Advances* **2**:e1600883. DOI: 10.1126/sciadv.1600883

Onary-Alves SY, Hsiou AS, Rincón AD. 2016. The northernmost South American fossil record of *Boa constrictor* (Boidae, Boinae) from Plio–Pleistocene of El Breal de Orocual (Venezuela). *Alcheringa* **41**: 1–8. DOI: http://dx.doi.org/10.1080/03115518.2016.1180031

Parmley D, Holman JA. 2003. *Nebraskophis* Holman from the late Eocene of Georgia (USA), the oldest known North American colubrid snake. *Acta Zoologica Cracoviensia* **46**: 1–8.

Prevosti FJ, Rincón AD. 2007. A new fossil canid assemblage from the Late Pleistocene of northern South America: The canids of the Inciarte Asphalt Pit (Zulia, Venezuela), fossil record and biogeography. *Journal of Paleontology* **81**: 1053–1065.

Pyron RA, Burbrink FT, Wiens JJ. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* **13**: 1-53.

Rage JC. 1984. Part 11 Serpentes. *In*: M. Wellnhofer, (Ed.), *Encyclopedia of Paleoherpetology*. Gustav Fischer Verlag, New York, USA, 1–79.

Rage JC. 2001. Fossil snakes from the Paleocene of São José de Itaboraí. Brazil. Part II. Boidae. *Paleovertebrata* **30**: 111–150.

Rendahl H, Vestergren G. 1941. Notes on Colombian snakes. *Arkiv för Zoologi 33A [1940]* **5**: 1-16.

Rieppel O. 1988. A review of the origin of snakes. *Evolutionary Biology* **22**: 37-130.

Rincón AD, White RS, McDonald G. 2008. Late Pleistocene cingulates (Mammalia: Xenarthra) from Mene de Inciarte tar pits, Sierra de Perijá, western Venezuela. *Journal of Vertebrate Paleontology* **28**: 197–207.

Rincón AD. 2006. A first record of the Pleistocene saber-toothed cat *Smilodon populator* Lund, 1842 (Carnivora: Felidae: Machairodontinae) from Venezuela. *Ameghiniana* **43**: 499–501.

Rincón AD. 2011. New remains of *Mixotoxodon larensis* Van Frank 1957 (Mammalia: Notoungulata) from Mene de Inciarte tar pit, North-Western Venezuela. *Interciencia* **36**: 894-899.

Rincón AD, Prevosti FJ, Parra GE. 2011. New saber-toothed cat records (Felidae: Machairodontinae) for the Pleistocene of Venezuela, and the Great American Biotic Interchange. *Journal of Vertebrate Paleontology* **31**: 468–478.

Rincón AD, Parra G, Prevosti FJ, Alberdi MT. Bell CJ. 2009. A preliminary assessment of the mammalian fauna from the Pliocene–Pleistocene El Breal de Orocual locality, Monaga State, Venezuela. *In*: B. Albright (Ed.) *Papers on Geology, Vertebrate Paleontology and Biostratigraphy, in honor of Mike O. Woodburne, Bulletin of the Museum of Northern Arizona* **65**: 593–620.

Rincón AD, Alberdi MT, Prado JL. 2006. Nuevo registro de *Equus* (*Amerhippus*) *santaeelenae* (Mammalia, Perissodactyla) del pozo de asfalto de Inciarte (Pleistoceno Superior), estado Zulia, Venezuela. *Ameghiniana* **43**:529–538.

Rincón AD, Parra GE, Prevosti FJ, Alberdi MT, Bell CJ. 2009. A preliminary assessment of the mammalian fauna from the Pliocene–Pleistocene El Breal de Orocual locality, Monagas State, Venezuela. *In*: L.B. Albright, (Ed.) *Papers on Geology,* *Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin* **64**: 593–620.

Rivas GA, Molina CR, Ugueto GN, Barros TR, Barrioamorós CL, Kok PJR. 2012. Reptiles of Venezuela: an updated and commented checklist. *Zootaxa* **3111**: 1–64.

Riveira PC, Di Cola V, Martinéz JJ, Gardenal CN, Chiaraviglio M. 2011. Species Delimitation in the Continental Forms of the Genus *Epicrates* (Serpentes, Boidae) Integrating Phylogenetics and Environmental Niche Models. *PLoS ONE* **6**:e22199.

Rodrigues MT. 2005. The Conservation of Brazilian Reptiles: Challenges for a Megadiverse Country. *Conservation Biology* **19**: 659-664.

Scotese C.R. 2010*.* *PALEOMAP Project*. Avaliable at http://www.scotese.com/Default.htm

Solórzano A, Rincón AD, McDonald HG. 2015. A new mammal assemblage from the Late Pleistocene El Breal de Orocual, northeast of Venezuela. *In*: J.M. Harris (Ed.), La Brea and Beyond: The Paleontology of Asphalt-Preserved Biotas. *Science Series, Natural History Museum of Los Angeles County* **42**: 125–150.

Steadman DW, Oswald JA, Rincón AD. 2015. The diversity and biogeography of late Pleistocene birds from the lowland Neotropics. *Quaternary Research* **83**: 555-564.

Szyndlar Z, Rage JC. 2003. *Non-erycine Booidea from the Oligocene and Miocene of Europe*. Institute of Systematics and Evolution of Animals, Polish Academy of Science, Kraków, Poland, 109 pp.

Teixeira G. 2013. *Anatomia comparada dos Boinae (Serpentes, Boidae) sul-americanos: uma abordagem osteológica para fins aplicativos na paleontologia de vertebrados*. Monograph, Universidade de São Paulo, Ribeirão Preto, 88 p.

Uetz P, Hošek J. 2016. *The reptile database*. Available online at: http://reptile-database.reptarium.cz/ (accessed 7 August 2017).

Underwood GL, Kochva E. 1993. On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). *Zoological Journal of the Linnean Society* **107**: 3-64.

Urbani F, Galarraga F. 1991. Inventario de menes de la Sierra de Perijá. Univ. Central Venezuela. *Facult. Ingeniería. Esc. Geol., Minas y Geofís. Informe interno* 1-80.

Venczel M. 2001. Anurans and squamates from the Lower Pliocene (MN 14) Osztramos 1 locality (Northern Hungary). *Fragmenta Palaeontologica Hungarica* **19**: 79-90.

Verzi DH, Deschamps CM, Montalvo CL. 2004. Bioestratigrafía y biocronología del Mioceno Tardío en Argentina central. *Ameghiniana* **41**(**4**, Suplemento):21R.

Ward JK, Harris JM, Cerling TE, Wiedenhoeft A, Lott MJ, Dearing MD, Coltrain JB, Ehleringer JR. 2005. Carbon starvation in glacial trees recovered from La Brea tar pits, southern California. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 690-694.

Wüster W, Ferguson JE, Quijada-Mascareñas JA, Pook CE, Salomão MG, Thorpe RS. 2005. Tracing an invasion: landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotalus durissus*). *Molecular Ecology* **14**: 1095–1108.

Wüster W, Salomão MG, Quijada-Mascareñas JA, Thorpe RS, B.B.B.S.P. 2002. Origins and evolution of the South American pitviper fauna: evidence from mitochondrial DNA sequence analysis. *In*: G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (Eds.). *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah, 111–128.

Zaher H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History* **240**: 1–168.

Zaher H, Grazziotin FG, Cadle JE, Murphy RW, Moura-Leite JC. Bonatto SL. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on

South American xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia, Museu de Zoologia da Universidade de São Paulo* **49**:115–153.

Table 1(on next page)

Table of the comparative specimens consulted.

Museum abbreviations are given in the institutional abbreviations section.

Taxon	Group	Museum and specimen number
Boa constrictor imperator	Boidae	AMNH R 155261, AMNH R 155257, AMNH R 77590, AMNH R 74737, AMNH R 57472
Boa constrictor	Boidae	AMNH R 57467, AMNH R 57476, AMNH R 131475, AMNH R 75478, AMNH R 141144, AMNH R 7204, AMNH R 75267, AMNH R 7118, MCN.D, 333, MCN.D 335, MCN.D 343, MCN.D 344, MCN.D 347, MCN.D 351
Corallus caninus	Boidae	AMNH R 57788, AMNH R 73347, AMNH R 57816, AMNH R 155265, AMNH R 169154, AMNH R 155260, AMNH R 73347, AMNH R 155264, AMNH R 139338, AMNH R 155263, AMNH R 57816
Crotallus durissus	Viperidae	AMNH 56455, AMNH 744442
Crotallus durissus terrificus	Viperidae	AMNH 77027
Clelia clelia	Colubroidea	AMNH 57797
Bothrops atrox	Viperidae	AMNH 29885
Bothrops bilineatus	Viperidae	AMNH R 140856
Corallus cf. *C. caninus*	Boidae	AMNH R 57804
Corallus annulatus	Boidae	AMNH R 114496
Corallus batesi	Boidae	UFMT-R 05362
Drymarchon corais couperi	Colubroidea	AMNH R 155299
Eunectes murinus	Boidae	AMNH 57474, MCN.D 306, MCN.D 316, MCN.D 319, MCN.D 342
Epicrates crassus	Boidae	MCN-PV DR 0003
Epicrates striatus	Boidae	AMNH R 140542
Epicrates striatus striatus	Boidae	AMNH R 155262
Epicrates striatus strigilatus	Boidae	AMNH 155259, AMNH R 70263, AMNH R 155259
Epicrates striatus fosteri	Boidae	AMNH R 77633, AMNH R 77057
Corallus cropanii	Boidae	AMNH R 92997
Corallus hortulanus cookii	Boidae	AMNH R 141098, AMNH R 74832, AMNH R 7812,

		AMNH R 75740, AMNH R 57809
Corallus hortulanus	Boidae	AMNH 104528, AMNH R 57786, MCN-PV DR 0001, UFMT 02389, UFMT 02398
Chironius carinatus	Colubroidea	AMNH 82841
Dipsas indica	Colubroidea	AMNH 53780
Drymoluber dichrous	Colubroidea	AMNH 55847
Dendrophidian nucale	Colubroidea	AMNH 138461
Erythrolamprus mimus micrurus	Colubroidea	AMNH 109828
Erythrolamprus bizona	Colubroidea	AMNH 90018
Epicrates angulifer	Boidae	AMNH R 77596, AMNH R 114497
Epicrates cenchria	Boidae	AMNH R 114716, AMNH R 57473, AMNH R 71153, AMNH R 75796, AMNH R 75795, MCN-PV DR 0002
Epicrates inornatus	Boidae	AMNH 70023
Helicops angulatus	Colubroidea	AMNH R 139137, AMNH R 155310, AMNH R 56031
Hydrodynastes bicinctus	Colubroidea	AMNH 60822
Hydrodynastes gigas	Colubroidea	AMNH 57956
Mastigodryas boddaerti boddaerti	Colubroidea	AMNH R 8675
Micrurus spixi obscurus	Elapidae	AMNH 74813
Micrurus lemniscatus diutius	Elapidae	AMNH 78969
Pseustes poecilonotus	Colubroidea	AMNH 85309
Ninia atrata	Colubroidea	AMNH R 75825
Oxybelis aeneus	Colubroidea	AMNH R 155359
Oxyrhopus petola	Colubroidea	AMNH 77649
Oxyrhopus trigeminus	Colubroidea	AMNH 85969
Urotheca multilineata	Colubroidea	AMNH R 98288
Spillotes pullatus	Colubroidea	AMNH R-155390
Xenodon rhabdocephalus	Colubroidea	AMNH 70257
Xenodon severus	Colubroidea	AMNH 35997, AMNH R 76573

Table 1: Table of the comparative specimens consulted. Museum abbreviations are given in the institutional abbreviations section.

Figure 1

Geographical map of Venezuela showing the relative position of the deposits where the snake remains were found

El Breal de Orocual (Plio/ Pleistocene), in pink dot, and Mene de Inciarte (upper Pleistocene) in red pentagon. (Map drawing by Ascanio Rincón and minor edits by Silvio Onary).

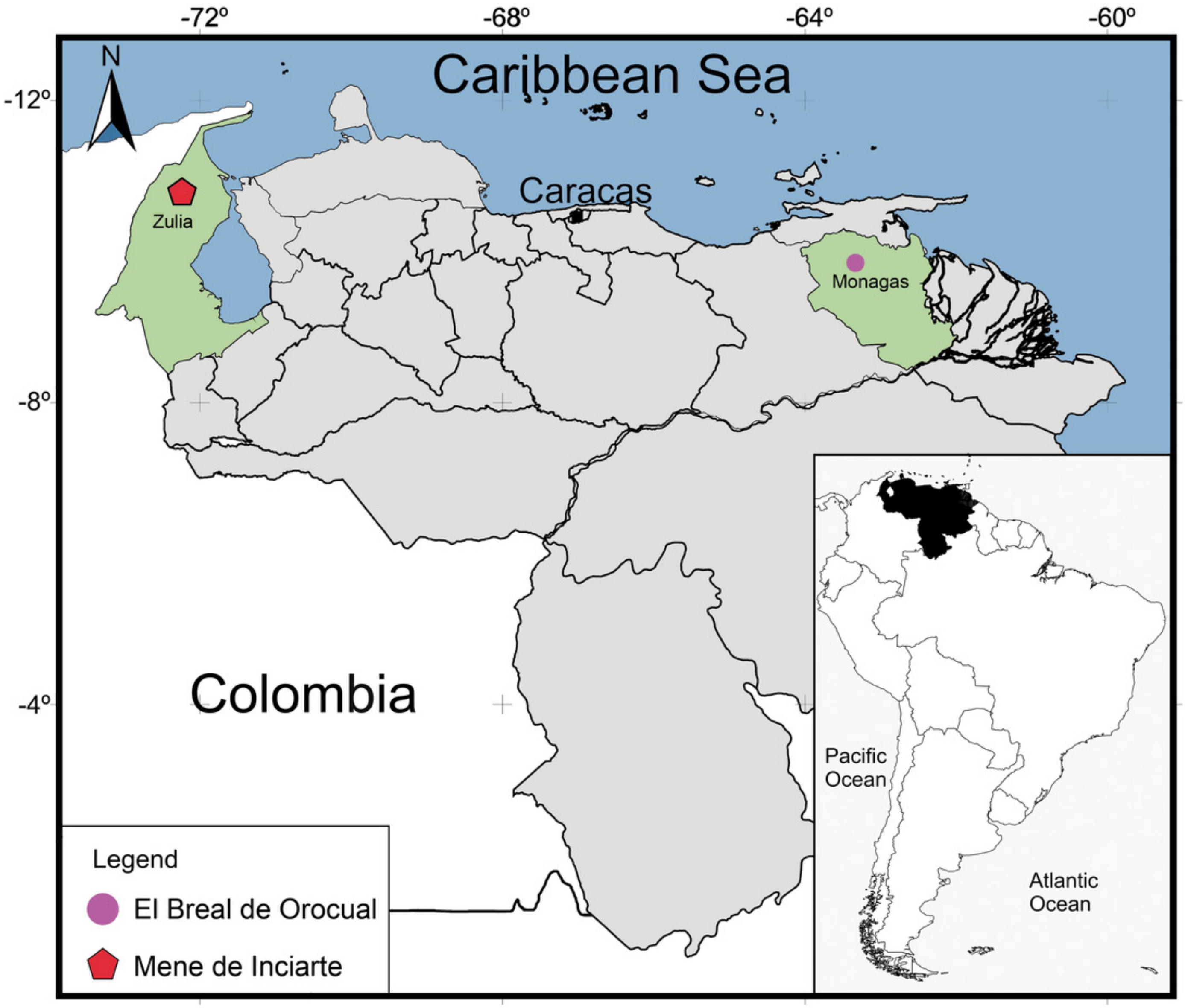
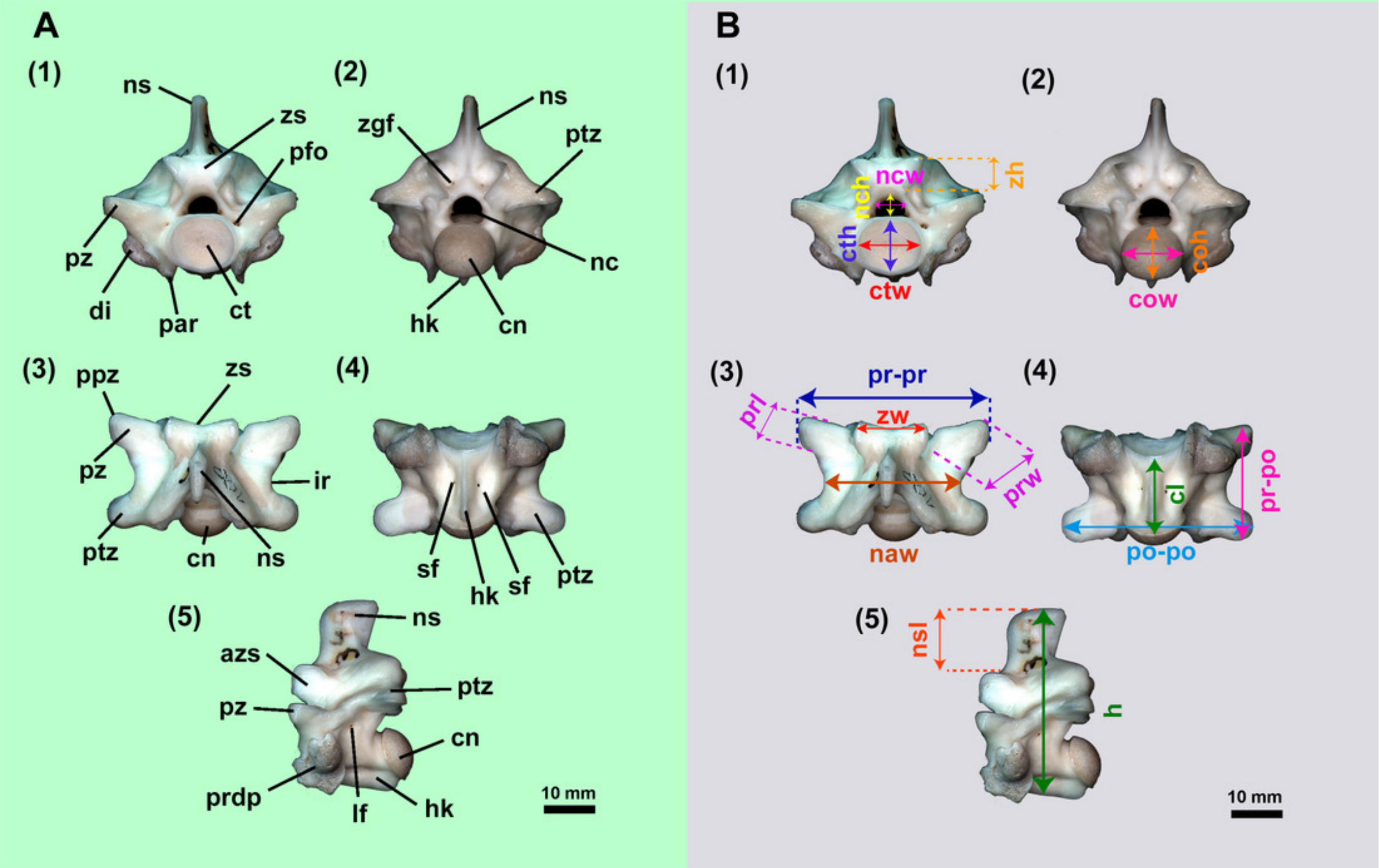


Figure 2

Isolated midtrunk vertebra of *Boa constrictor* evidencing the anatomical traits and quantitative data here analysed

A. Isolated midtrunk vertebra of *Boa constrictor* (MCN.D. 344) showing the anatomical nomenclature herein adopted. B. same vertebra evidencing the quantitative measurements adopted in this study. Based in LaDuke (1991a,b). In (1) anterior, (2) posterior, (3) dorsal, (4) ventral, and (5) lateral views. Scale bar: 10 mm. Abbreviations: azs, articular facet of zygosphene; cl, centrum length; cn, condyle; coh, condyle height; cow, condyle width; ct, cotyle; cth, cotyle height; ctw, cotyle width; di, diapophysis; h, total height of vertebra; hk, haemal keel; ir, interzygapophyseal ridge; lf, lateral foramen; naw, neural arch width; nc, neural canal; nch, neural canal height; ncw, neural canal width; ns, neural spine; nsl, neural spine length; par, parapophysis; pfo, paracotylar foramen; po-po, distance between postzygapophyses; ppz, parapophyseal process; prdp, paradiapophysis; prl, prezygapophysis length; pr-po, distance between prezygapophyses and postzygapophyses of the same side; pr-pr, pr–pr, distance between prezygapophyses; prw, prezygapophysis width; ptz, postzygapophisis; pz, prezygapophysis; sf, subcentral foramen; zgf, zygantral foramen; zh, zygosphene height; zw, zygosphene width. (Photography source: Silvio Onary)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(4)
sf
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sf
ptz
(5)
ns
azs
ptz
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cn
prdp
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hk
10 mm
B
(1)
zh
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(3)
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prw
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(4)
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pr-po
po-po
(5)
nsl
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10 mm

Figure 3

Fossil specimen IVIC OR–6113

A. Isolated posterior precloacal vertebra attributed to *Corallus* sp. (IVIC OR–6113). B. Schematic drawing of the specimen evidencing its anatomical structures. In (1) anterior, (2) posterior, (3) lateral, (4) ventral, and (5) dorsal views. Abbreviations in figure 2. (Photography and outline drawing source: Silvio Onary)

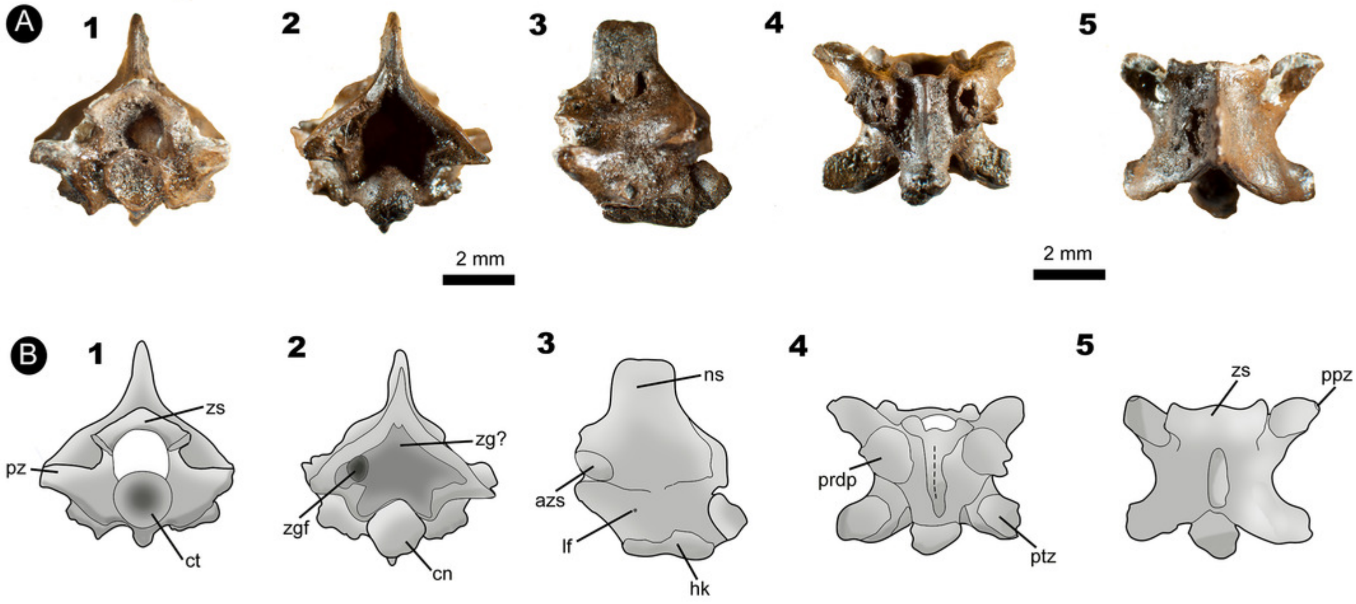


Figure 4

Fossil specimen of IVIC MI–004

A. Anterior precloacal vertebra attributed to *Epicrates* sp. (IVIC MI–004). B. Schematic drawing of the specimen evidencing the anatomical structures. Abbreviations in the relevant section. In (1) anterior, (2) posterior, (3) lateral, (4) ventral, and (5) dorsal views. Abbreviations in figure 2. (Photography and outline drawing source: Silvio Onary)

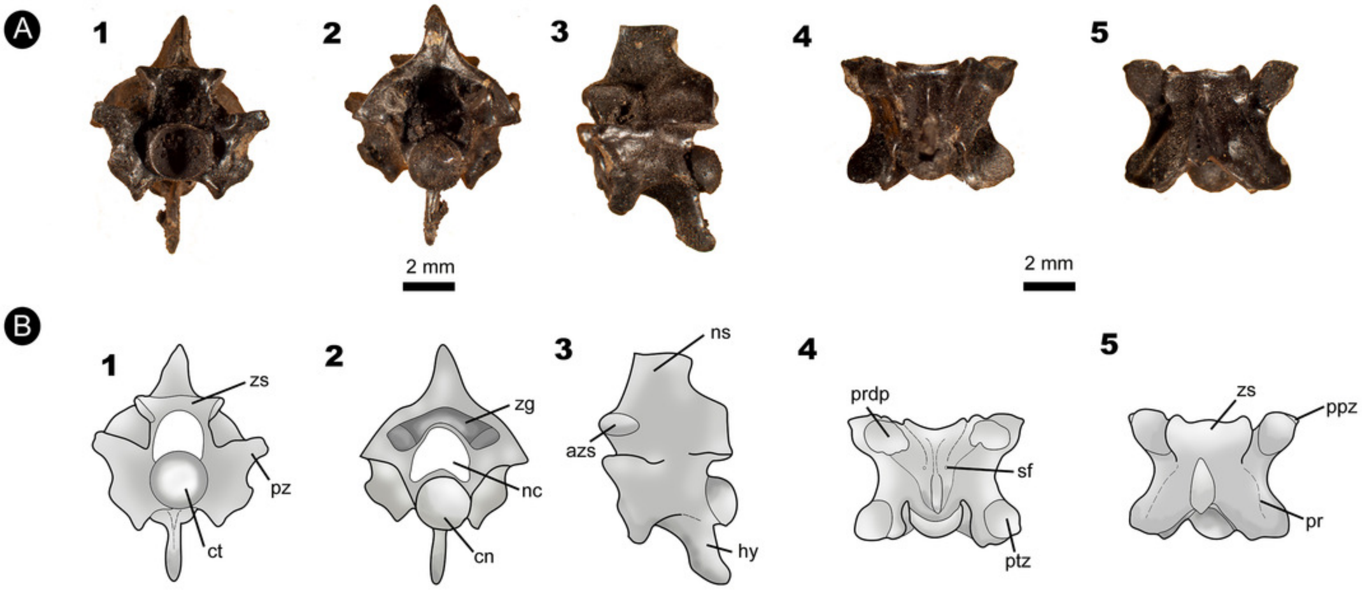
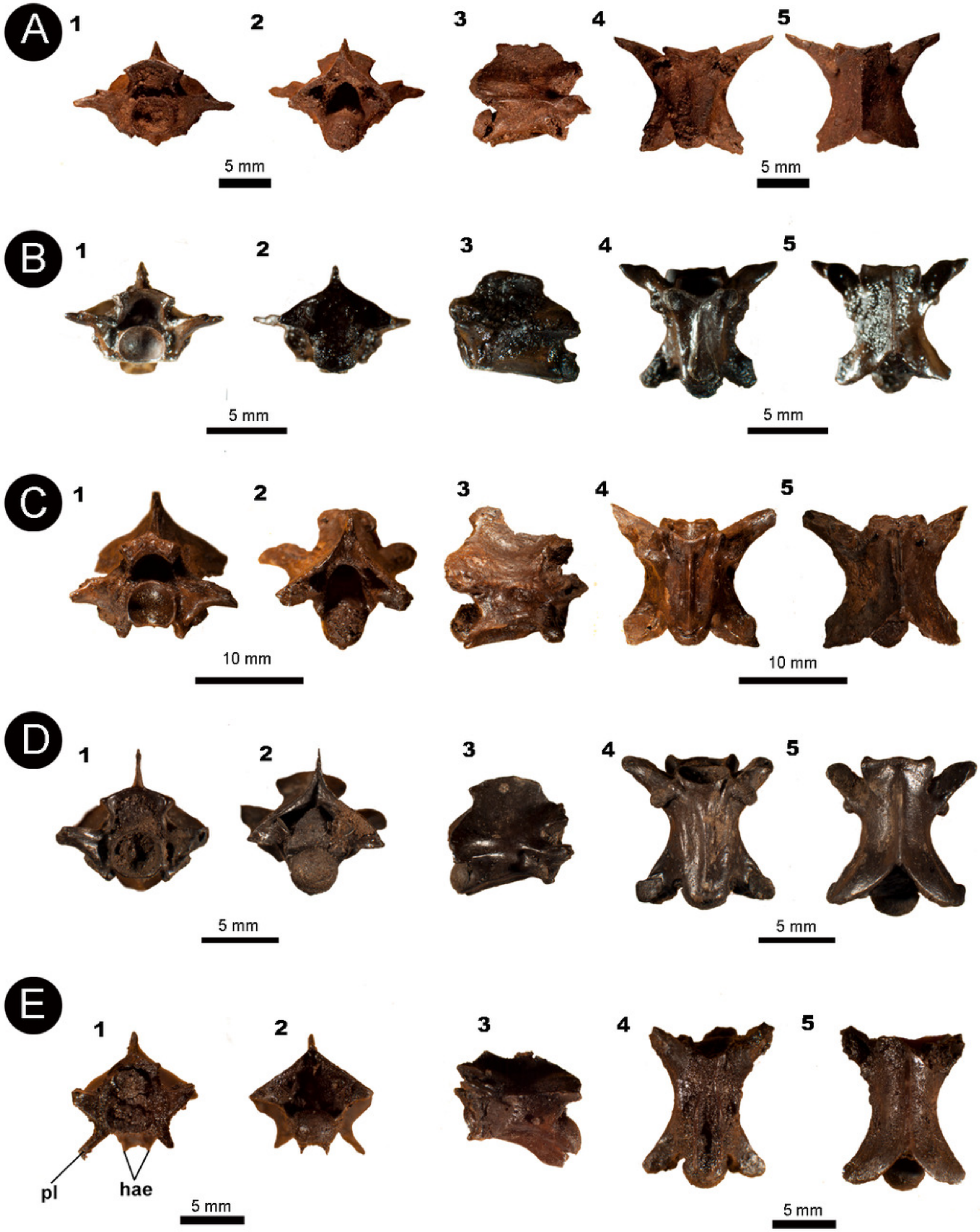


Figure 5

Isolated vertebral remains attributed to Colubroidea.

A. IVIC OR–3667; B. IVIC OR–6124; C. IVIC OR–2618; D. IVIC MI–005; and E. IVIC OR–2917. Abbreviations: hae, haemapophysis; pl, pleurapophysis. (Photography source: Silvio Onary)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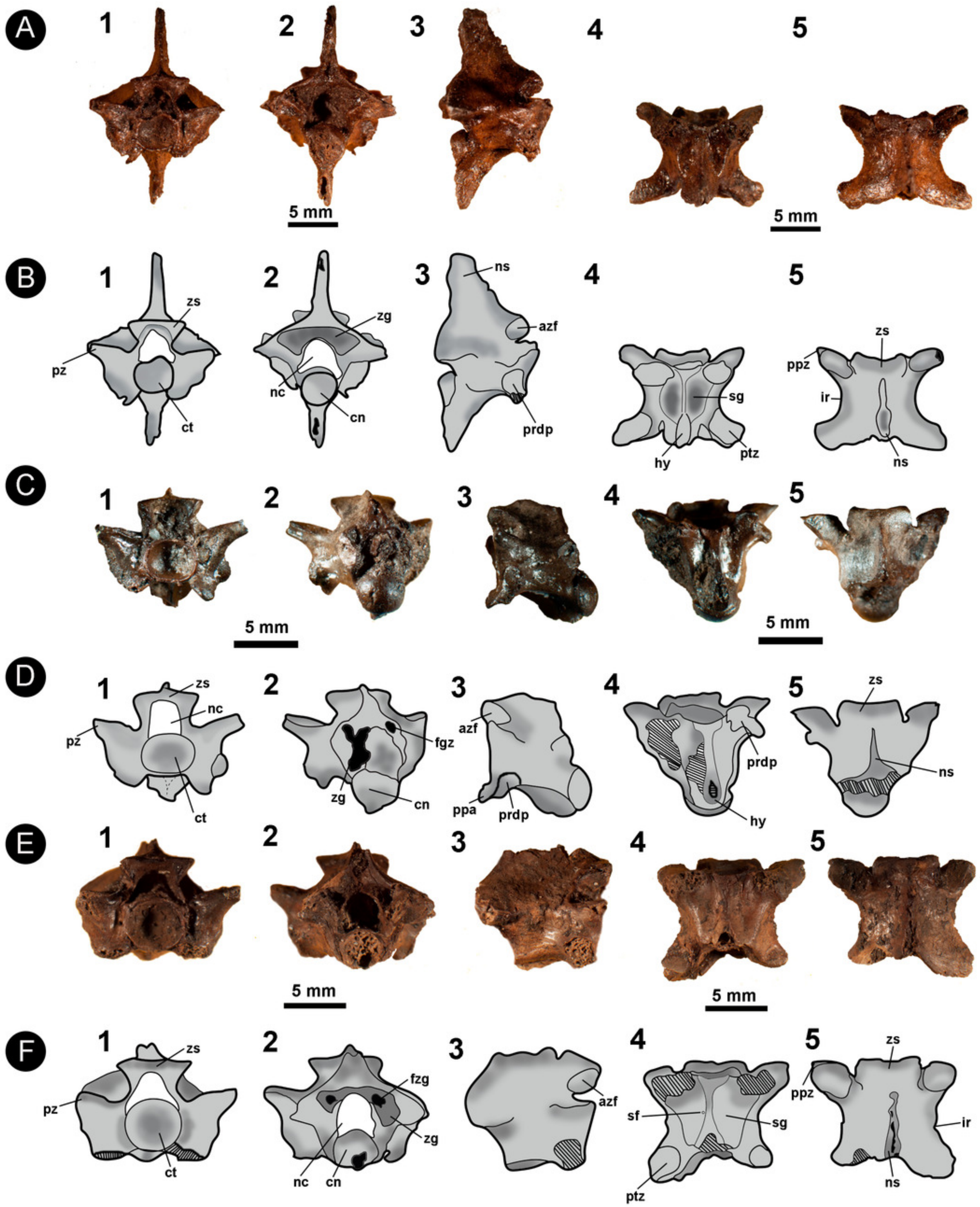
3
4
5
5 mm
5 mm
E
1
2
3
4
5
pl
hae
5 mm
5 mm

Figure 6

Isolated vertebral remains attributed to Viperidae.

A. IVIC OR–2617; B. schematic drawing of IVIC OR–2617; C. IVIC OR–6104; D. schematic drawing of IVIC OR–6104; E. IVIC OR–1760; F. schematic drawing of IVIC OR–1760. Abbreviations present in figure 2. (Photography and outline drawing source: Silvio Onary)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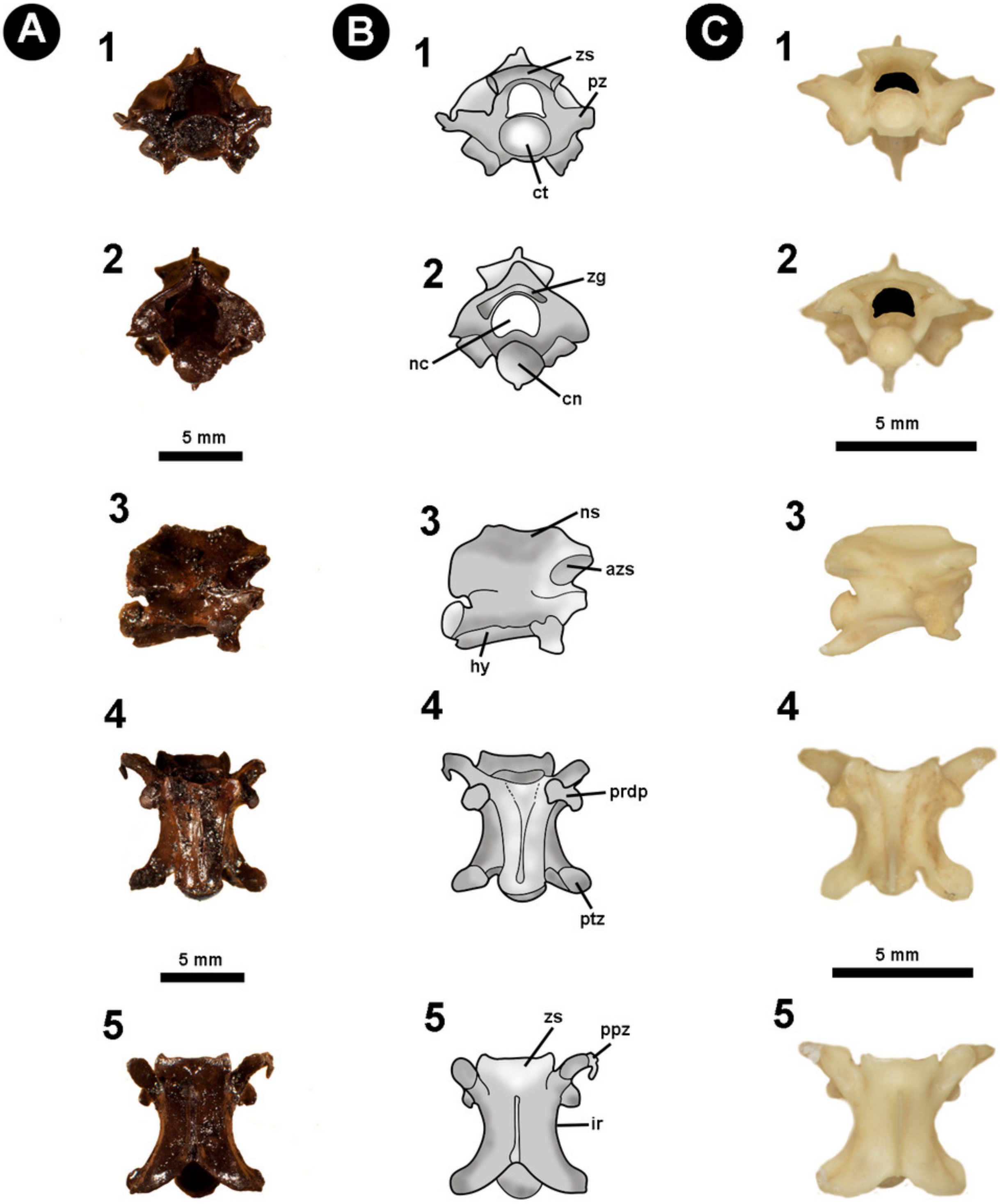
ir
ns

Figure 7

Fossil specimen of IVIC OR–2619

Isolated precloacal vertebra (IVIC OR–2619) identified as cf. *Micrurus*. B. schematic drawing of IVIC OR–2619; C. comparative material of precloacal vertebra of *Micrurus lemniscatus* diutius (AMNH 78969). Abbreviations in figure 2. (Photography and outline drawing source: Silvio Onary)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B
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zs
pz
ct
2
zg
nc
cn
3
ns
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hy
4
prdp
ptz
5
zs
ppz
ir
C
1
2
5 mm
3
4
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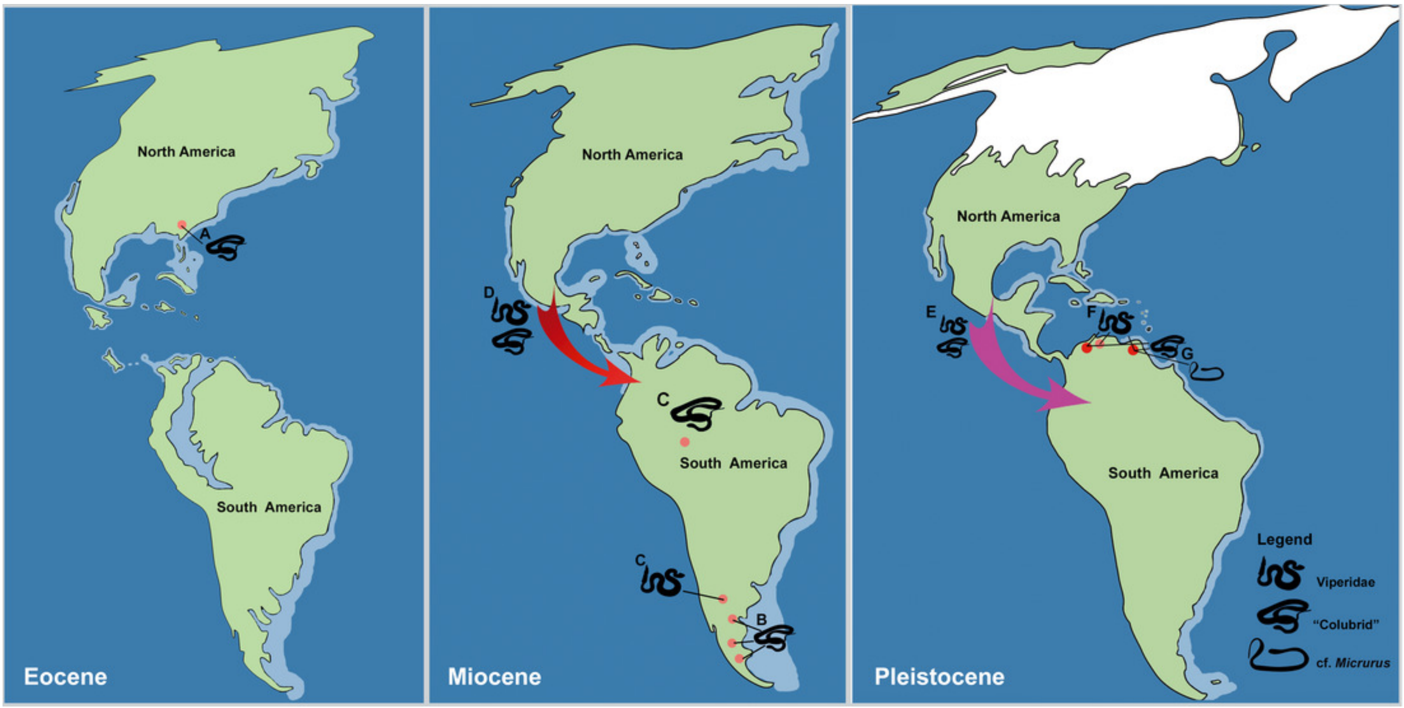
5

Figure 8

The historical biogeography of Colubroides (sensu Zaher et al. 2009) throughout the American continent during the Eocene to Pleistocene, based on the fossil record.

(A) The oldest American “Colubridae” recorded from the late Eocene of Georgia, North America (Parmley & Holman, 2003); (B) “Colubridae” record from the early Miocene of Argentina, South America (Colhuehuiapianense South America Land Mammal Age, SALMA) (Albino, 1996b); (C) Viperidae remains from the late Miocene of Cerro Azul Formation (Huayquerian SALMA), Argentina (Albino & Montalvo, 2006) and the "Colubridae" record from the late Miocene of Amazonia, Brazil (Hsiou & Albino, 2010); (D) First entrance of Colubroides from North America to South America by dispersion via Central American island complex during the Miocene (Hoffstetter, 1967; Cadle & Greene, 1993; Albino, 1996b); (E) Second event of dispersion of Colubroides from North America to South America during the Plio/Pleistocene (Head, Sánchez–Villagra & Aguilera, 2006); (F) Viperidae remains from Cucuruchu gravels, late Pleistocene of Venezuela (Head, Sánchez–Villagra & Aguilera, 2006); and (G) The herein described record of cf. *Micrurus* (Elapoidea, Elapidae), which is the putative oldest South American record of Elapidae, supporting the hypothesis of establishment of the genus in the South American continent at least ~2.1 Ma, after the complete uplift of the Panama Isthmus (Rage & Holman, 1984). From the left to the right: representative maps of Eocene; Miocene; and Pleistocene of America. Red arrows denote the first episode of dispersion and pink arrow denote the second event of dispersion. Palaeomaps based in the reconstructions from PALEOMAP Project (Scotese 2010). (Drawing provided by Silvio Onary)


North America
A
South America
Eocene
North America
D
C
South America
C
B
Miocene
North America
E
F
G
South America
Legend
Viperidae
"Colubrid"
cf. *Micrurus*
Pleistocene