Fossil snakes (Squamata: Serpentes) from the Tar Pits of Venezuela: Taxonomical, palaeoenvironmental, and palaeobiogeographical implications (#24411)

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Fossil snakes (Squamata: Serpentes) from the Tar Pits of Venezuela: Taxonomical, palaeoenvironmental, and palaeobiogeographical implications

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Background. Tar seep deposits in South America historically are well known for have yielded a rich fossil record of mammals contrasting with just few formal reports of reptiles remains. Here we report a new snake fauna recovered from two tar pits from Venezuela. The fossil remains comes 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). 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), 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 wielded the presence of Boidae, Viperidae, “colubrids”, and the putative oldest South American record of Elapidae. The presence of *Corallus* and *Epicrates* 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

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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 holds

great diversity of carnivores and associated herbivores taxa (Brown et al., 2017). Besides the representative macrovertebrate fauna, these peculiar areas often yields 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 three dimensional preservational status of such specimens allows in many cases, the accurate taxonomical identification of taxa, contributing to precise inferences regarding the palaeoenvironment, palaeotemperature, and palaeobiogeography (LaDuke, 1991a; Friscia et al., 2008; Rincón et al., 2009; Solórzano, Rincón & McDonald, 2015; Holden et al., 2015; Holden et al., 2017).

In America, several tar seep deposits have been discovered since the early 19th century, when the most famous tar pit deposit, Rancho La Brea was discovered in California, United States (Stock, 1930). Subsequently, several deposits throughout the continent were reported from North America, like McKittrick and Carpintera, USA (Stock, 1930; Nowak, 1979); in the Caribbean Las Breas de San Felipe, Cuba (Ituralde–Vinent et al., 2000); and South America: Talara deposit, Peru, Pitch Lake in Trinidad and Tobago, and La Carolina, Ecuador (Hoffstetter, 1952; Wing, 1962). The Venezuelan territory presents several tar pits, where only two has been paleontologically exploited: 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, there are the predominance of reports 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).

A common bias in tar seep deposits is the preferential study of macrovertebrates, usually neglecting the study of small vertebrates, invertebrates and plants (LaDuke, 1991a; Brown et al., 2017). This tendency and preferential collect of macrovertebrates can hampers the whole understanding of the palaeoenvironmental scenario, since these small species can be a good model of inference for palaeoclimatic changings, precise dating of sites, besides, taxonomical studies (Brown et al., 2017; Holden et al., 2015, 2017). In this contribution, we report the fossil snakes from two tar pits from Venezuela, showing its palaeobiogeographical and taxonomical implications for the understanding of the South America squamate diversity during the Neogene/ Quaternary boundary.

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, which one in special 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 deposits of asphalts that were palaeontological exploited in the country (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 have an absolute date that range 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–) into the palaeontological collection of Instituto Venezoelano de Investigacíones Científicas (IVIC), Caracas, Venezuela. The fossils comprises 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

136 based in LaDuke (1991a,b) (Fig. 2B). Measurements were taken with an analogic caliper
137 (0.02 mm) and are expressed in millimetres.
138
139 Fig 2: (A: Anatomical structures; B: Quantitative data)
140
141 **Institutional abbreviations**: **AMNH**, American Museum of Natural History, New York,
142 New York; **MCN.D**, Coleção Didática de Herpetologia, Museu de Ciências Naturais da
143 Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MCN-PV DR**, Seção
144 de Paleontologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio
145 Grande do Sul, Coleção de Paleontologia de Vertebrados, Coleção Didática de Répteis,
146 Porto Alegre, Brazil; **IVIC–OR**, Instituto Venezoelano de Investigaciones Científicas El
147 Breal de Orocual collection; **UFMT**, Coleção da Universidade Federal do Mato Grosso,
148 Mato Grosso, Brazil.
149
150 **Table 1**: Table of the comparative specimens consulted. Museum abbreviations are given
151 in the institutional abbreviations section.
152

153 ## RESULTS

154 SYSTEMATIC PALAEONTOLOGY
155 Serpentes Linnaeus, 1758
156 Alethinophidia Nopcsa, 1923
157 Macrostomata Müller, 1831
158 Boidae Gray, 1825

159 Boinae Gray 1825

160 *Corallus* Daudin, 1803

161 *Corallus* sp.

162 Fig. 3

163

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

165 **Locality and age**: Tar Pit ORS16, El Breal de Orocual, Monagas State, Venezuela. Age
166 estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage
167 (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald,
168 2015).

169 **Description**: The specimen is well preserved. In general view, the vertebra is high, wide
170 and short, having its vertebral centrum smaller than the neural arch width (naw > cl). In
171 anterior view, the zygosphene is thick and ventrodorsally inclined, being about three times
172 wider than the cotyle (zw > ctw). The prezygapophyses are horizontally positioned in
173 relation to the horizontal plane. The prezygapophyseal process is short and extends a
174 little beyond the prezygapophyseal articular facet. The neural canal is subtriangular. The
175 cotyle is rounded, with similar measurements of height and width (ctw ~ cth). The
176 paracotylar fossae are deep and do not show evidences of paracotylar foramina. The
177 paradiapophyses are lateroventrally oriented, showing clear distinction between the dia–
178 and parapophyseal articular facets. The diapophyses have a convex shape, whereas the
179 parapophyses shows triangular morphology.

180 In posterior view, the lateral edges of the neural arch are vaulted and the neural
181 spine rises from its median portion. The zygantrum is almost entirely eroded, however is

possible to note its left edge with a 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 is slightly eroded in its distal tip. The neural spine rises from the anterior margin of the zygosphene roof, being anteroposteriorly short, exceeding from the margin of the neural arch. It is noted that the neural spine invades the posteriormost edge of the neural arch, which forms the spinal blade, described to *B. constrictor* (*sensu* Albino, 2011). The zygosphene articular facets has an oval shape and are 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 is robust, rising ventrally to the cotyle, developing posteroventrally until the proximity of the precondylar constriction.

In ventral view, the vertebral centrum is short and triangular shaped, having a wide anterior edge that becomes slender toward its posterior region. The subcentral fossae are deep and well delimited in the anterior region of the vertebral centra. The haemal keel is large and rises bellow the cotyle, developing anterorposteriorlly 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

205 shape, being longer than wide (prl>prw). The zygosphene roof bears markedly triangular
206 lateral lobes with a distinct slightly convex mid lobe, characterizing the crenate condition
207 (*sensu* Auffenberg, 1963). The interzygapophyseal ridge extends between the pre– to
208 postzygapophysis, being deep. There is a deep posterodorsal notch in the mid portion of
209 the posterior edge of the neural arch, which expose great part of the condyle.
210
211 Fig 3: (*Corallus* plate)
212
213 **Measurements (in millimetres)**: IVIC OR-6113: **cl**. 3.4; **coh**.1.4; **cow**.1.3; **cth**. 0.9;
214 **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;
215 **pr-po**. 4.7; **prl**. 1.6; **prw**. 1.0; **zh**. 0.9; **zw**. 2.9.
216
217 **Identification and comparison**: The specimen IVIC OR–6113 shares with Boidae the
218 combination of the follow vertebral features: broad and vaulted neural arch; well-
219 developed and thick zygosphene; reduced prezygapophyseal process; high neural spine;
220 well delimited and marked precondylar constriction; inclination of the prezygapophyses
221 less than 15º; vertebral centrum short and robust; and presence of haemal keel on
222 midtrunk vertebra (Rage, 1984, 2001; Albino & Carlini, 2008; Hsiou & Albino, 2009; Hsiou
223 et al., 2013). The fossil is clearly distinct from the genera *Eunectes* and *Boa*, due to your
224 comparative reduced size (Hsiou & Albino, 2010), being consistent with the morphology
225 of *Corallus* and *Epicrates*.
226 The described vertebra can be attributed to the genus *Corallus* based in the follow
227 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 intracolunar 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*, once its neural arch is slightly more vaulted than the condition observed in this genus (Rage, 2001).

Comparatively, IVIC OR–6113 shares with *Corallus* the ~~neural spine~~ relative size, ~~an~~ anteroposteriorlly elongated condition, and the perpendicular orientation 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 anteroposteriorlly (Hsiou & Albino, 2009).

The zygosphene of IVIC OR–6113 is similar to midtrunk vertebrae present on *Epicrates* and *Corallus*, once they share the crenate condition found on the zygosphene roof in dorsal view. On the other hand, individuals of *Boa* and *Eunectes* shows a thicker and more robust zygosphene built, 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, once the other, possesses a slightly to medium degree of orientation above the horizontal plan (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 specimen is well preserved, showing only a small portion impregnated by sediments. 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 although filled by sediments, has a

297 “trifoliate” morphology in cross-section and its width is similar to the height (ncw ~ nch).
298 The cotyle is rounded (ctw ~ cth) having deep paracotylar fossae with no paracotylar
299 foramina. The paradiapophyses are broad, showing clearly distinction between the
300 parapophyseal articular facets, which is triangular shaped and the diapophyseal articular
301 facet that has a convex morphology.

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

307 In lateral view, the neural spine is long, rising from the posterior edge of the
308 zygosphene. Although broken, the preserved portion of the neural spine indicates a
309 slightly degree of anteroposterior orientation. The articular facets of the zygosphene are
310 oval shaped and oriented dorsolaterally upward. The vertebral centrum of MI–004 is short
311 and delimited by a well marked precondylar constriction. Bellow the precondylar
312 constriction, it noted a long hypapophysis slightly oriented posteriorly, which extends to
313 the edge of the precondylar constriction, not exceeding the posterior rim of the condyle.

314 In ventral view, the vertebral centrum has a marked triangular morphology,
315 showing the anterior region wider than its posterior region. The specimen shows a deep
316 subcentral fossae, with paired subcentral foramina present on each side of the vertebra.
317 A narrow keel develops anteroposteriorlly into the hypapophysis, however not extending
318 beyond the precondylar constriction. The postzygapophyses are broad and displays a
319 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 is a 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).

342 The specimen IVIC MI–004 is attributed to the extant boid *Epicrates* on the basis
343 of the following features: small vertebra that is wide, high and short; vaulted neural arch;
344 deep paracotylar fossae; wide and high neural spine; hypapophysis, which does not
345 exceeds the posterior margin of the condyle; zygosphene showing the crenate
346 morphology; and a well marked triangular vertebral centrum (Teixeira, 2013).
347 Regarding the intracolunar variation, the fossil is recognized as an anterior
348 precloacal vertebra due to the presence of a well developed hypapophysis, which is
349 observed exclusively in this region of the axial skeleton of boids (Rage, 2001); and for the
350 presence of a rounded morphology on the cotyle and condyle (ctw ~ cth) (Teixeira, 2013).
351 The fossil shows comparatively small vertebral size, which is characteristically of
352 boids like *Corallus* and *Epicrates*, being distinct from the great vertebral size of genera as
353 *Boa* and *Eunectes*. The specimen shows a high vertebral size (h), and despite its broken
354 apex of the neural spine, it is higher than individuals of *Corallus* and proportionally
355 *Eunectes*. Comparatively to *Boa*, the neural spine of the fossil is lower, matching only
356 with the size observed in extant individuals of *Epicrates*. IVIC MI–004 exhibits in posterior
357 view a more convexly domed neural arch when compared with anterior precloacal
358 vertebrae of *Eunectes* and *Corallus*, which shows a depressed dorsoventrally
359 morphology.
360 Although broken, the neural spine of IVIC MI–004 is high, and long, divergently
361 from that observed in *Corallus*, which shows a low and shortened anteroposteriorly
362 morphology (Hsiou & Albino, 2009). Specimens of *Boa* exhibits a strong posterior
363 orientation of the neural spine, besides the well marked structures of spinal crest and
364 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*, neither 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), ~~until the date~~, no~~n~~e autapomorphic character of postcranial elements were identified to 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

388 Fig. 5

389

390 **Referred material**: Four nearly complete precloacal vertebrae (IVIC OR–3667; IVIC OR–
391 6124; IVIC OR–2618; IVIC MI–005) and one postcloacal vertebra (IVIC OR–2917).
392 **Localities and Age**: IVIC OR–3667; IVIC OR–6124; IVIC OR–2618: Tar Pit ORS16, El
393 Breal de Orocual, Monagas State, Venezuela. Age estimated to be late Pliocene–early
394 Pleistocene based on the palaeofaunal assemblage (Rincón et al., 2009, Rincón, Prevosti
395 & Parra, 2011; Solórzano, Rincón & McDonald, 2015). IVIC MI–005: Mene de Inciarte
396 Tar pit, Zulia state, Venezuela. Age dated of 25,500±600 ^{14}C years BP (28,456– 30,878
397 cal years BP) and 27,980 ± 370 ^{14}C years BP (31,165–32,843 cal years AP), late
398 Pleistocene (Jull et al., 2004).
399 **Description**: All the specimens are well preserved, showing in some cases eroded
400 structures, and being crusted by sediments. The fossils shares the following common
401 pattern: wide, slender, and long vertebra, with the length of the vertebral centrum greater
402 than the width of the neural arch (cl>naw). In anterior view, the neural spine is high and
403 thin. The zygosphene of the specimens are thin, slender, having a convex edge dorsally.
404 ~~Its width~~ is wider than the cotyle (zw>ctw), and ~~present~~ short articular facets. The neural
405 canal is subtriangular in shape, and inside is possible to note three internal crests that
406 form the trilobated morphology. In some specimens, the neural canal is filled with
407 sediments but is possible by its external outline, to observe the same morphology. The
408 prezygapophyses of the fossils are long and variable regarding the orientation. The
409 specimens IVIC OR–2618, IVIC OR–3667, and IVIC MI–005 shows a slightly inclination
410 of the prezygapophyses above the horizontal plan, whereas, IVIC OR–6124 and IVIC

411 OR–2917 exhibits a higher inclination upward, reaching the mid portion of the neural
412 canal. The prezygapophyseal processes of the specimens are well preserved in IVIC OR–
413 3667 and IVIC OR–6124. They are long and project ventrally beyond the
414 prezygapophyseal articular facets. The cotyle of all vertebrae are rounded with the width
415 similar to the height (ctw ~ cth). The paradiapophyses are anterolaterally oriented with a
416 clear distinction between the dia– to parapophyseal articular facets, where the first is
417 convex and the other concave respectively. IVIC OR–2917 shows the presence of
418 pleurapophyses that is long, slender, and strongly oriented laterally; and the
419 haemapophyses, ventral to the cotyle that is characterized by short and thin processes.
420 In posterior view, the neural arches of all specimens are depressed and in its mid
421 portion rises a high and thin neural spine. The zygantrum is small and deep, and in some
422 preserved specimens there are small paired zygantral foramina. The postzygapophyses
423 of the fossils are variable in orientation: being in IVIC OR–3667, IVIC OR–6124, and IVIC
424 OR–2917 slightly inclined above the horizontal plan; horizontally oriented in IVIC MI–005;
425 and ventrally oriented in IVIC OR–2618. The condyles of all specimens are rounded,
426 showing the height similar or equal to the width (cow ~ coh).
427 In lateral view, the neural spine is high, thin, and anteroposteriorly elongated. Its
428 rises from the posterior edge of the zygosphene, developing until reach the limit of the
429 posterodorsal notch. Only in IVIC OR–2917 is possible to observe paired lateral foramina
430 on each side of the vertebral centrum. The vertebral centrum of all specimens are narrow
431 and elongated, with a moderate precondylar constriction. The condyle is posterodorsally
432 inclined upward. With exception of IVIC OR–2917, all specimens shows on the ventral
433 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 strong 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 ~~until~~ reach the precondylar constriction, ~~do~~ not exceeding the condyle. 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, which ~~rises~~ from the posterior region of the paradiapophyses to the precondylar constriction. 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. In some specimens, the prezygapophyseal process is broken (e.g. IVIC MI–005, IVIC OR–2618, IVIC OR–2917), however is possible to observe an elongated and slender morphology. 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), and not observable in IVIC OR–2917 due to the preservation.

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 shows vertebral diagnosis that separates one group for another. It is noteworthy that despite the attribution in a generic level of Colubroidea, the fossils specimens shows 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.

503

504 Endoglyptodonta Zaher *et al*., 2009

505 Viperidae Oppel, 1811

506 Indeterminate genera and species

507 Fig. 6

508

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

512 **Locality and Age**: Tar Pit ORS16, El Breal de Orocual, Monagas State, Venezuela. Age
513 estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage
514 (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald,
515 2015).

516 **Description**: Most of the vertebrae are eroded and incomplete. In general, the vertebrae
517 are short, high (only observable in IVIC OR–2617), slightly wider than long (pr-pr > pr-
518 po), and possesses the length of the vertebral centrum similar to the width of the neural
519 arch (cl ~ naw). In anterior view, the specimens show a thin zygosphene with a straight
520 dorsal margin. The articular facets of the zygosphene are elliptical in shape and dorsally
521 oriented. The neural canal have a trilobated morphology, and its width is similar to the
522 length (ncw ~ nch). The prezygapophyses are long, slender, and show articular facets,
523 which are strongly inclined above the horizontal plane (~30º). All vertebrae shows a round
524 cotyle, having width similar to the height (ctw ~ cth). Near the cotyle, there are deep
525 paracotylar fossae; however, it is not observable paracotylar foramina, probably due to

526 the preservation. The paradiapophyses, despite eroded in some specimens, shows a
527 clear distinction between the dia– to parapophyseal articular facets, being the first convex
528 and oriented posterolaterally, and the second, convex and slightly oriented
529 anterolaterally. It is noted on the parapophyseal articular facet, small processes well
530 oriented anteroventrally, which exceeds beyond the margin of the cotyle.

531 In posterior view (only preserved in IVIC OR–2617), the neural arch is slightly
532 depressed and shows a marked triangular shape. The zygantrum is wide and deep, does
533 not presenting none foramina due the preservation of the specimens. The
534 postzygapophyses are broad and slightly inclined dorsally. The condyle in all specimens
535 are round in outline shape. A long hypapophysis rises ventrally to the condyle, exceeding
536 its distal margin.

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

546 In ventral view, the vertebral centrum is narrow and long. The subcentral fossae
547 are shallow in some specimens (*e.g.* IVIC–6104 and IVIC OR–1760), whereas are deeper
548 in others (*e.g.* IVIC OR–2616 and IVIC OR–3674). In all specimens, the fossae are

549 restricted to the anterior region of the vertebral centrum. The subcentral fossae are
550 delimited by well marked subcentral margin, which extends from the posterior region of
551 the paradiapophyses to the mid lateral region of the hypapophysis. The hypapophysis
552 develops longitudinally to the centrum, being broken in some specimens but clearly
553 surpassing the posterior margin of the condyle. The articular facets of the
554 postzygapophyses are long and shows an elliptical shape outline.

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

566

567 Fig 6: (Viperidae indet. plate)

568

569 **Measurements (in millimetres)**: *IVIC OR-2617*. **cl**:7.0; **cth**:2.1; **ctw**:2.3; **h**:15.4;
570 **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;
571 **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;

572 **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*.
573 **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;
574 **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;
575 **prw**:2.8; **zh**:1.4.

576 **Identification and Comments:** The analysed fossils shares with Colubroidea the
577 following vertebral characters: gracile vertebra, which is longer than wide (pr–po>pr–pr);
578 thin neural spine; slender zygosphene; presence of short and prominent
579 prezygapophyseal accessory process; and paradiapophyses with clear distinction
580 between the dia– to parapophyszeal articular facets (Rage 1984; Lee & Scanlon 2002;
581 Albino & Montalvo 2006).

582 The specimens possesses a well-developed hypapophysis, which is considered
583 an apomorphic character found in “Xenodermatinae”, Homalopsinae,
584 “Pseudoxyrhophiinae”, “Boonodontinae”, Elapidae, Viperidae, and Natricinae (Zaher,
585 1999). Among these groups, IVIC OR–6104 shares within Viperidae the single
586 autapomorphic postcranial character, which is the presence of a well developed
587 parapophyseal process, strongly oriented anteroventrally (Zaher, 1999; Zaher et al.,
588 2009). So far, based in this character, IVIC OR–6104 can be unequivocally assigned to
589 the Viperidae family. Despite the lack of the parapophyseal process, the other specimens
590 can be identified as Viperidae due to the following combination of vertebral characters:
591 vertebra not elongated; slender and straight zygosphene; well-developed hypapophyses;
592 wide and short neural canal; depressed neural arch; postzygapophyses strongly oriented
593 anterolaterally; short prezygapophyseal process; and subcentral fossae restrict 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 diagnostics 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 is 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 specimen is partially preserved, showing the mid dorsal region of the neural spine partially eroded, the left postzygapophysis entirely broken, and the right prezygapophysis fragmented. 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 trilobated 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 which, the first is prominent, convex, and lateroventrally positioned, whereas the second, is slightly concave in shape.

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 poorly preserved but 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 possess a distinction between its articular facets and exhibits 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 diapophyzeal articular facets of the paradiapophyses, which are convex in shape and lateroposteriorlly oriented. The

662 interzygapophyseal constriction is long and broad, extending from the base of the
663 prezygapophysis to the postzygapophysis, being relatively shallow. The neural spine is
664 thin, rising from the posterior region of the zygosphene roof developing longitudinally until
665 reach the contact with the posterodorsal notch. The postzygapophyses are slightly
666 anterolaterally oriented, exposing a small portion of its articular facets. The posterodorsal
667 notch is deep and excavates in the mid region of the neural arch.
668
669 Fig 7: (cf. *Micrurus* plate)
670
671 **Measurements (in millimetres)**: *IVIC OR-2619*. **cl**:5.9; **coh**:2.0; **cow**:2.2; **cth**:1.6;
672 **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;
673 **zh**:0.7; **zw**:3.7.
674 **Identification and Comments**: The diagnosis within Elapidae genera is based on cranial
675 characters (*e.g.* the morphology of the proteroglyph condition of the maxilla), as well as,
676 morphological traits associated with the venom glands (Underwood & Kochva, 1993;
677 Zaher, 1999), do not being reported yet a single autapomorphic diagnostic postcranial
678 character in genera/ species level. Currently, Venezuelan territory host two genera of
679 elapids: *Micrurus* and *Leptomicrurus* (Rivas et al., 2012), occurring at the fossiliferous site
680 two species of *Micrurus*: *M*. *dissoleucus* Cope, 1860 and *M*. *isozonus* Cope, 1860.
681 Among the comparative osteological material accessed for this study, IVIC OR–
682 2619 shares with the genus *Micrurus* the following vertebral characters: gracile vertebra
683 with a depressed neural arch; oval shaped cotyle (ctw > cth); slender and elongated pre–
684 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 none diagnostic either indicative set of vertebral traits that can be use to a precise assignment.

DISCUSSION

The Venezuelan snake fossil record is still scarce when compared to other South America localities (*e.g.* Argentina, Brazil, Colombia). The oldest and single Mesozoic record comes from the Cenomanian (early late Cretaceous) of the La Luna Formation (Albino, Carrillo–Briceño & Neenan, 2016). The material comprises isolated and articulated precloacal vertebrae of the taxon *Lunaophis aquaticus* Albino, Carrillo–Briceño & Neenan (2016). Due to its peculiar morphology and the marine depositional environment that the fossil was found, the specimen was interpreted as a marine snake with no affinity with any stem/crown snake group (Albino, Carrillo–Briceño & Neenan, 2016). Among the Cenozoic, most of the fossil record comes from the Socorro Formation (middle Miocene) and the Urumaco Formation (late Miocene) (Head, Sánchez–Villagra & Aguilera, 2006). For the Socorro Formation, Head, Sánchez–Villagra & Aguilera (2006) preliminarily identified some isolated precloacal vertebrae as *Colombophis* cf. *C. portai* and an indeterminate Boinae, which were subsequently reinterpreted as the alethinophidian of uncertain affinities *Colombophis spinosus* (Hsiou, Albino & Ferigolo, 2010) and *Eunectes*

708 sp. (Hsiou & Albino, 2010) respectively. The same is seen in the Urumaco Formation
709 when first was reported the presence of an indeterminate Boinae (Head, Sánchez–
710 Villagra & Aguilera, 2006), which after the reappraisal of Hsiou & Albino (2010) was
711 assigned to the genus *Eunectes*. Recently, Onary–Alves, Hsiou & Rincón (2016) reported
712 the presence of *Boa constrictor* from the El Breal de Orocual, uncovering the
713 northernmost record of a fossil belonging to the species for South America. The youngest
714 snake record comes from the late Pleistocene of Cucuruchu gravels, where Head,
715 Sánchez–Villagra & Aguilera (2006) identified based in an isolated precloacal vertebra,
716 an indeterminate Viperidae.

717 The boids reported here corroborates the palaeoenvironmental condition that were
718 previously interpreted for the Northern of South America based in studies of the
719 palaeofaunal mammal assemblage, which suggests the predominance of a dry savanna
720 crossed by fragmentary forests with the dominance of humid-climate species of plants
721 (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald,
722 2015). Although *Corallus* and *Epicrates* currently being widespread boids genera across
723 the South American territory (Henderson, 1995), some species within these genera can
724 persist only in suitable microclimate and microenvironment, especially concerning the
725 forest exclusive species (Rodrigues, 2005; Carvajal–Cogollo & Urbina–Cardona, 2015).
726 Most of species of *Corallus* and *Epicrates* can be characterized to demand specific forest
727 environment to establish viable population (Henderson et al., 1995), and a major change
728 in the microclimate can thread these genera, even leading to the local extinction
729 (Rodrigues, 2005; Carvajal–Cogollo & Urbina–Cardona, 2015). The recovered *Corallus*
730 vertebra of El Breal de Orocual reaffirms the presence of forests region with a suitable

731 environment for boids at the Plio–Pleistocene, like attested previous studies (Onary–
732 Alves, Hsiou & Rincón, 2016). Furthermore, the today occurrence of *Corallus* and
733 *Epicrates* at the Venezuelan Llanos (Rivas et al., 2012), given the presence of the late
734 Pleistocene *Epicrates* here reported, suggests that none great climatic environmental
735 change affected the North of South America since the Plio-Pleistocene until today, since
736 these small boids are susceptible to abrupt environmental changes. Additionally, the
737 recovered Colubroides (*sensu* Zaher, 2009), such as the "colubrids" (Colubroidea), and
738 especially the viperids reinforces the presence of savanna components mixed with the
739 humid regions of forests during the Plio-Pleistocene of El Breal de Orocual, since some
740 species of colubrids and viperids occupies open–areas and are well-known to live in dry
741 environments (*e.g*. *Crotalus* sp.).
742 Regarding the Colubroides (*sensu* Zaher et al., 2009), an interesting
743 biogeographical question centre in its origins and entrance in South America (Fig. 8). The
744 oldest records of "Colubridae" in America, comes from the late Eocene of Georgia, North
745 America (Fig. 8A) (Parmley & Holman, 2003), whereas they are dated only during the
746 early Miocene in South America (Fig. 8B) (Colhuehuiapianense South America Land
747 Mammal Age, SALMA) (Albino, 1996b). This record together with the presence of the
748 South American Viperidae remains for the late Miocene of the Cerro Azul Formation (Fig.
749 8C) (Huayquerian SALMA) (Verzi et al., 2004; Albino & Montalvo 2006), evidences that
750 the dispersion of Colubroides from North America to South America, occurred prior to
751 major continental events like the uplifting of the Panama Isthmus and the great American
752 biotic interchange (GABI) (Albino & Montalvo, 2006; O'Dea et al., 2016). The dispersion
753 can be hypostatized probable by the aquatic crossing of a series of island complex in the

754 Central America during the Miocene (Fig. 8D) (Hoffstetter, 1967; Cadle & Greene, 1993;
755 Albino, 1996b).

756 Based in the Venezuelan record of Viperidae to the late Pleistocene collectively
757 with the snake faunal analysis, Head, Sánchez–Villagra & Aguilera (2006) suggested that
758 the Colubroides could be reached in South America in two distinct episodes during the
759 Neogene. Indeed, the snakes here described corroborate the aforementioned hypothesis
760 in which the first entrance of colubrids and viperids occurred at least in the early Miocene,
761 with species reaching to the Southernmost region of the South American continent
762 (Albino, 1996b; Albino & Montalvo, 2006), and the second entrance possibly during the
763 Pliocene/Pleistocene boundary (Fig. 8E). The recovered fauna of Plio/Pleistocene
764 “colubrids” and viperids at El Breal de Orocual, jointly with a suitable route after the
765 complete uplift of the Panama Isthmus (O’Dea et al., 2016), supports the hypothesis of
766 the second entrance of Colubroides in South America. Additionally, studies in molecular
767 divergence date (Wüster et al., 2002, 2005) suggests a similar pattern in which viperids
768 like *Bothrops*, *Lachesis*, and *Bothriechis* could be reached and diversified in South
769 America before the total closure of the Panama Isthmus (*e.g.* the early Miocene records
770 of Argentina, Albino, 1989; Albino, 1996b; Albino & Montalvo, 2006), whereas some
771 genera like *Crotallus* and *Porthidium* are estimated to be late dispersers, after the total
772 uplift of the Panama Isthmus (*e.g.* the Venezuelan Plio/Pleistocene records of “colubrids”
773 and viperids and the late Pleistocene viperids, Head, Sánchez–Villagra & Aguilera 2006
774 Fig. 8F).

775 The recovered viperids fossils of El Breal de Orocual are spatial and
776 chronologically consistently with the estimated entrance of the genus *Crotalus* for the

777 continent (Wüster et al., 2002, 2005). Regarding the described material, the specimens
778 IVIC OR–6104 and IVIC OR–2617 shows no significate morphological distinction with the
779 comparative osteological material analysed of *Crotalus* (*see appendix*). These specimens
780 shares with the genus *Crotalus* the distinct characteristic in possess a concave anterior
781 edge of the zygosphene roof, which is argued to be exclusive of the genus (Camolez &
782 Zaher, 2010). However, since no reliable synapomorphic character are present beyond
783 the family level, here we preferred to retain the conservative approach for the
784 identification. Despite the generic assignment of the Colubroides material, the specimens
785 shows a great potential for future biogeographical studies, especially the aforementioned
786 viperids. However, only refined taxonomical identifications can be assertive and provide
787 conclusive patterns of “colubrids” and viperids dispersion to the South America based in
788 the fossil record.

789 The extant species of “coral snakes” are currently found in America represented
790 by the genus *Micruroides* and *Micrurus* and in Asia by the genus *Sinomicrurus* (Lee et
791 al., 2016). The relationship of these genera are controversial, in some analyses
792 *Sinomicrurus* and *Micrurus* emerges as a sister group, being this total clade, sister group
793 to the North American *Micruroides* (Pyron et al., 2013), whereas in another scenario,
794 *Micruroides* and *Micrurus* are recovered as a sister group, with the total clade sister group
795 to the Asian *Sinomicrurus* (Lee et al., 2016). In the scope of the fossil record, remains of
796 “coral-snakes” are very scarce and geologically young (~16 to 13 Ma) (Holman, 1977),
797 representing an observation, which is concordant with the time calibrated phylogeny of
798 the group that estimates the rise of the lineage in ~30 Ma. (Lee et al., 2016). South
799 American records are restricted to the Quaternary of Brazil, represented by some cranial

remains attributed to *Micrurus corallinus*, and precloacal vertebrae assigned to *Micrurus* sp. (Camolez & Zaher, 2010). The North American territory wields some occurrences, like the oldest fossil record of the group that comes from the late Basrstovian 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 region (Auffenberg, 1963). Records dated from the middle Miocene of Europe shows 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, as well as, the Caenophidia as whole, 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 in the fossil record inferred a North American origin of the genusfollowed by an early Miocene dispersion to Asia, until reach the 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 El Breal de Orocual and Mene de Inciarte wielded the presence of Boidae, Viperidae, “colubrids”, and the putative oldest South American record of Elapidae. The presence of *Corallus* and *Epicrates* together with the previous described *Boa constrictor*, reinforces the mosaic palaeoenvironmental scenario of El Breal de Orocual, composed of forest areas mixed with savanna components and dry environments. Furthermore, the records of *Corallus* since the Plio-Pleistocene, the presence of *Epicrates* in late Pleistocene, and the current occurrences of these two genera in North South America, suggest that none episode of great climatic change occurred within this interval, since these genera demands special conditions of temperature and microenvironment to survive. 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

845 postcranial material, especially of Colubroides constitute a crucial and a future
846 perspective in our research.

847

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855

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FIGURES CAPTIONS

Fig. 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.

Fig. 2A. Isolated midtrunk vertebra of *Boa constrictor* (MCN.D. 344) showing the anatomical nomenclature herein adopted. 2B. 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.

Fig. 3A. Isolated posterior precloacal vertebra attributed to *Corallus* sp. (IVIC OR–6113). 3B. 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 3.

Fig. 4A. Anterior precloacal vertebra attributed to *Epicrates* sp. (IVIC MI–004). 5B. 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 3.

1231 Fig. 5. Isolated vertebral remains attributed to Colubroidea. 6A. IVIC OR–3667; 6B. IVIC
1232 OR–6124; 6C. IVIC OR–2618; 6D. IVIC MI–005; and 6E.IVIC OR–2917. Abbreviations:
1233 hae, haemapophysis; pl, pleurapophysis.
1234
1235 Fig. 6. Isolated vertebral remains attributed to Viperidae. 6A. IVIC OR–2617; 6B.
1236 schematic drawing of IVIC OR–2617; 6C. IVIC OR–6104; 7D. schematic drawing of IVIC
1237 OR–6104; 6E. IVIC OR–1760; 6F. schematic drawing of IVIC OR–1760. Abbreviations
1238 present in figure 3.
1239
1240 Fig. 7A. Isolated precloacal vertebra (IVIC OR–2619) identified as cf. *Micrurus*. 7B.
1241 schematic drawing of IVIC OR–2619; 7C. comparative material of precloacal vertebra of
1242 *Micrurus lemniscatus* diutius (AMNH 78969). Abbreviations in figure 3.
1243
1244 Fig. 8 (A-G). Representative maps of (1) Eocene; (2) Miocene; and (3) Pleistocene of
1245 America evidencing the fossil record of Colubroides during the space and time. Arrows
1246 indicate the dispersion of the snakes. Palaeomaps based in the reconstructions from
1247 PALEOMAP Project (Scotese 2010).

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

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2 **Table 1**: Table of the comparative specimens consulted. Museum abbreviations are given

3 in the institutional abbreviations section.

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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.

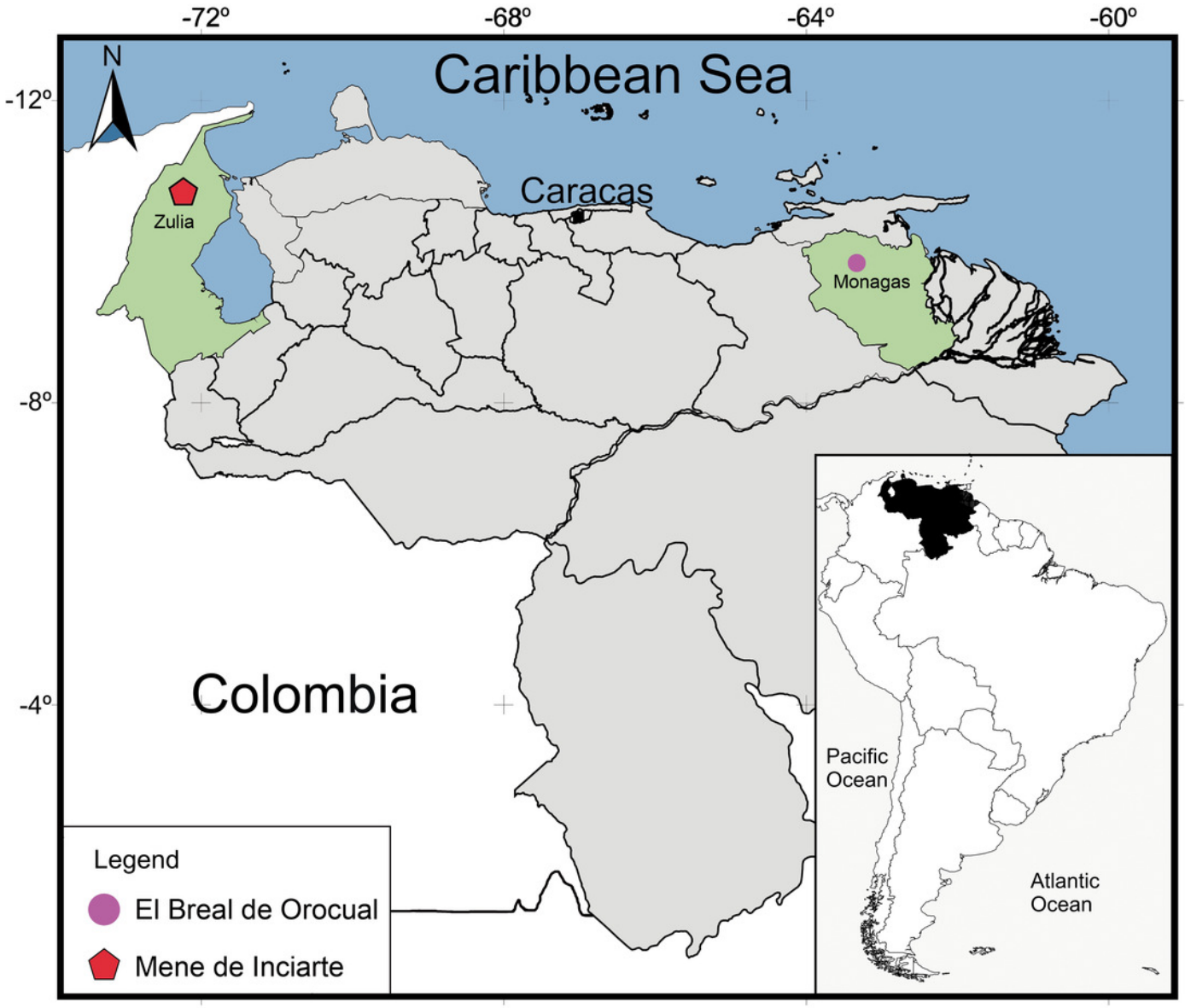

Figure 2

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

2A. Isolated midtrunk vertebra of *Boa constrictor* (MCN.D. 344) showing the anatomical nomenclature herein adopted. 2B. 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.

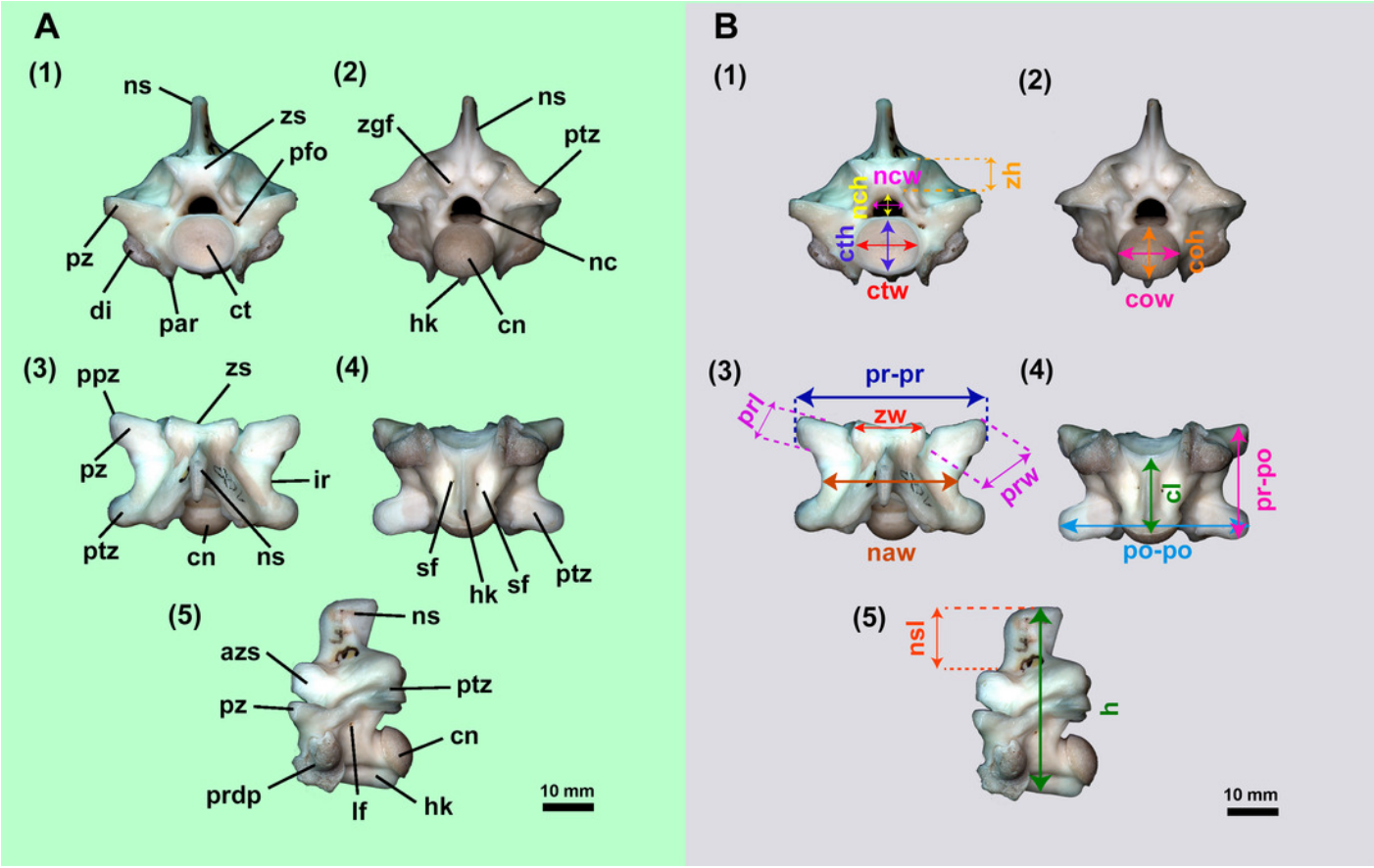
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Figure 3

Fossil specimen IVIC OR–6113

3A. Isolated posterior precloacal vertebra attributed to *Corallus* sp. (IVIC OR–6113). 3B. 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 3.

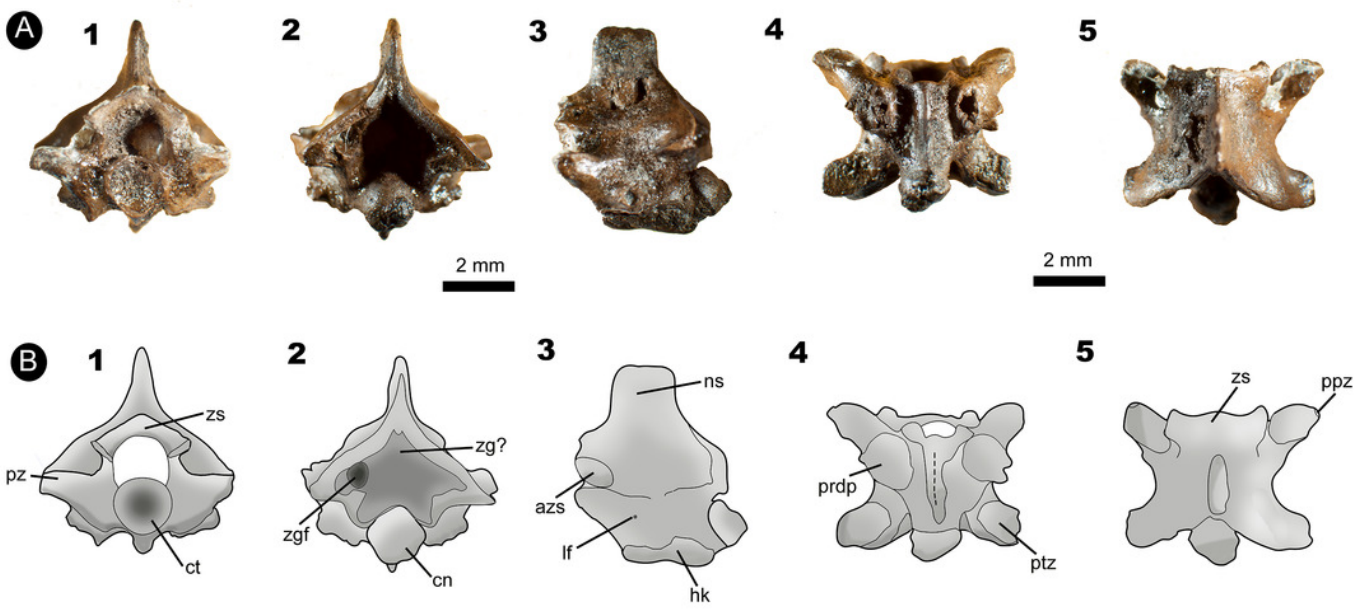

Figure 4

Fossil specimen of IVIC MI–004

4A. Anterior precloacal vertebra attributed to *Epicrates* sp. (IVIC MI–004). 5B. 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 3.

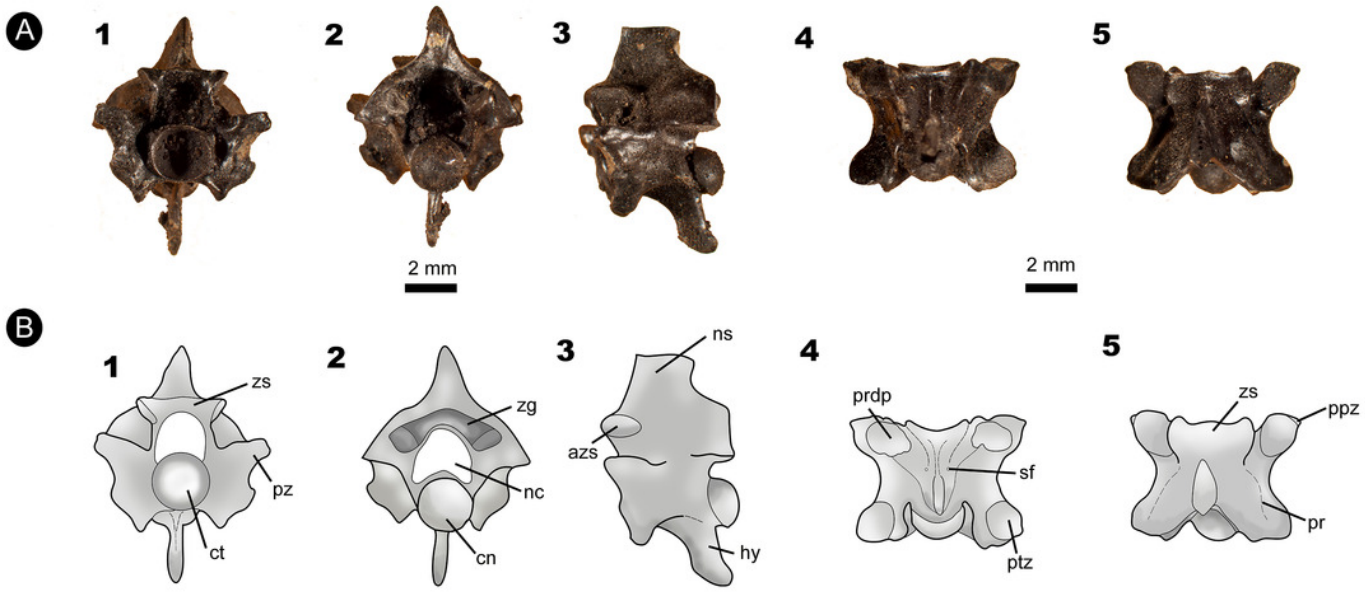

Figure 5

Isolated vertebral remains attributed to Colubroidea.

5A. IVIC OR–3667; 5B. IVIC OR–6124; 5C. IVIC OR–2618; 5D. IVIC MI–005; and 5E.IVIC OR–2917. Abbreviations: hae, haemapophysis; pl, pleurapophysis.

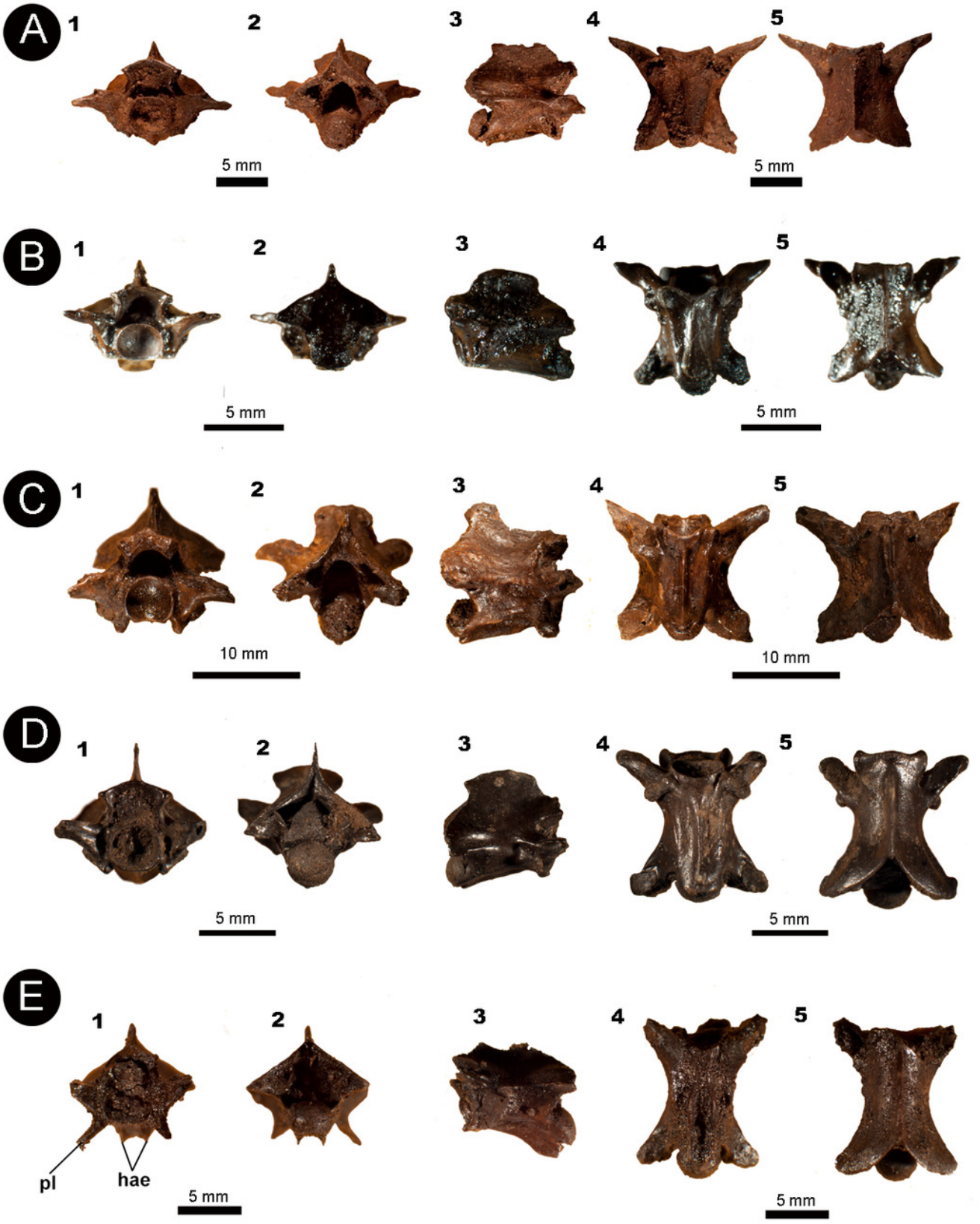
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Figure 6

. Isolated vertebral remains attributed to Viperidae.

6A. IVIC OR–2617; 6B. schematic drawing of IVIC OR–2617; 6C. IVIC OR–6104; 7D. schematic drawing of IVIC OR–6104; 6E. IVIC OR–1760; 6F. schematic drawing of IVIC OR–1760. Abbreviations present in figure 3.

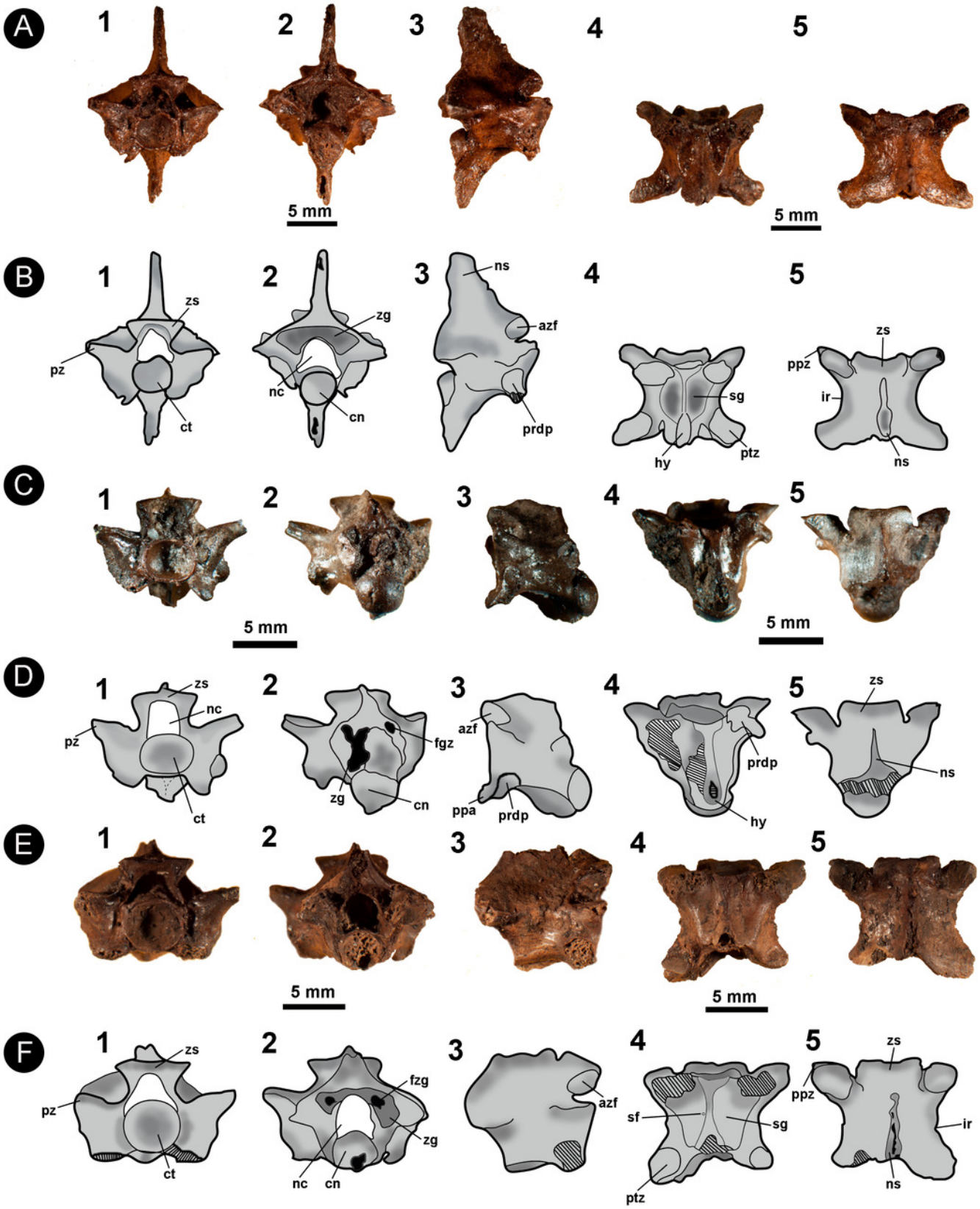
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Figure 7

Fossil specimen of IVIC OR–2619

Isolated precloacal vertebra (IVIC OR–2619) identified as cf. *Micrurus*. 7B. schematic drawing of IVIC OR–2619; 7C. comparative material of precloacal vertebra of *Micrurus lemniscatus* diutius (AMNH 78969). Abbreviations in figure 3.

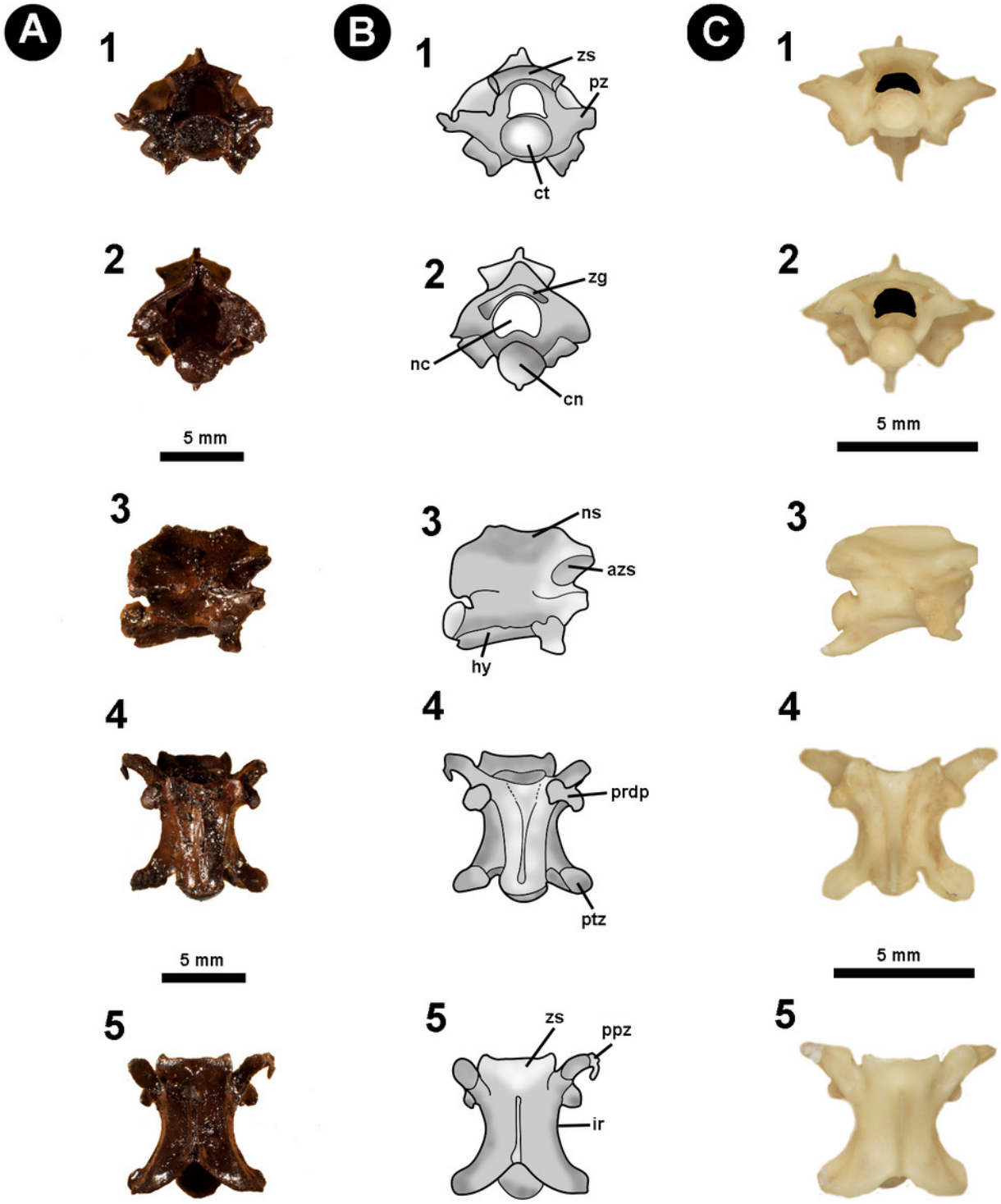
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Figure 8

8 (A-G). Representative maps of (1) Eocene; (2) Miocene; and (3) Pleistocene of America evidencing the fossil record of Colubroides during the space and time. Arrows indicate the dispersion of the snakes. Palaeomaps based in the reconstructions from PALEO