

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

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Background. Tar seep deposits in South America historically are well-known for their rich record of fossil mammals, contrasting with only a 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 Orocuál, which comprises an inactive tar seep estimated to be Pliocene/Pleistocene in age; and (b) Mene de Inciarte, an active surface asphalt deposit with an absolute age dating to the late Pleistocene. **Methods.** The taxonomic identity of all specimens was assessed via consultation of the relevant literature and comparison with extant specimens. The taxonomic assignments are supported by detailed anatomical description. **Results.** The Mene de Inciarte snake fauna comprises vertebral remains identified as the genus *Epicrates* sp. (Boidae), indeterminate viperids, and several isolated vertebrae attributable to “Colubridae” (Colubroidea, *sensu* Zaher et al. 2009). Amongst the vertebral assemblage at El Breal de Orocuál, one specimen is assigned to the genus *Corallus* sp. (Boidae), another to cf. *Micrurus* (Elapidae), and several others to “Colubrids” (Colubroides, *sensu* Zaher et al. 2009) and the Viperidae family. **Conclusions.** These new records provide valuable insight into the diversity of snakes in the north of South America during the Neogene/Quaternary boundary. The snake fauna of El Breal de Orocuál and Mene de Inciarte demonstrates the presence of Boidae, Viperidae, “colubrids”, and the oldest South American record of Elapidae. The presence of *Corallus*, *Epicrates*, and viperids corroborates the mosaic palaeoenvironmental conditions of El Breal de Orocuál. The presence of Colubroides within both deposits sheds light on the palaeobiogeographical pattern of caenophidians snake colonization of South America and is consistent with the hypothesis of two episodes of dispersion of Colubroides to the continent.

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2 **taxonomic, palaeoenvironmental, and palaeobiogeographical**
3 **implications for the North of South America during the**
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5

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13

14 **ABSTRACT**

15 **Background.** Tar seep deposits in South America historically are well-known for their
16 rich record of fossil mammals, contrasting with only a few formal reports of reptile
17 remains. Here we report a new snake fauna recovered from two tar pits from
18 Venezuela. The fossil remains come from two localities: (a) El Breal de Orocuá, which
19 comprises an inactive tar seep estimated to be Plio/Pleistocene in age; and (b) Mene de
20 Inciarte, an active surface asphalt deposit with an absolute age dating to the late
21 Pleistocene.

22 **Methods.** The taxonomic identity of all specimens was assessed via consultation of the
23 relevant literature and comparison with extant specimens. The taxonomic assignments
24 are supported by detailed anatomical description.

25 **Results.** The Mene de Inciarte snake fauna comprises vertebral remains identified as
26 the genus *Epicrates* sp. (Boidae), indeterminate viperids, and several isolated vertebrae
27 attributable to “Colubridae” (Colubroidea, *sensu* Zaher et al. 2009). Amongst the
28 vertebral assemblage at El Breal de Orocuá, one specimen is assigned to the genus
29 *Corallus* sp. (Boidae), another to cf. *Micrurus* (Elapidae), and several others to
30 “Colubrids” (Colubroides, *sensu* Zaher et al. 2009) and the Viperidae family.

31 **Conclusions.** These new records provide valuable insight into the diversity of snakes in
32 the north of South America during the Neogene/Quaternary boundary. The snake fauna
33 of El Breal de Orocuá and Mene de Inciarte demonstrates the presence of Boidae,
34 Viperidae, “colubrids”, and the oldest South American record of Elapidae. The presence
35 of *Corallus*, *Epicrates*, and viperids corroborates the mosaic palaeoenvironmental
36 conditions of El Breal de Orocuá. The presence of Colubroides within both deposits
37 sheds light on the palaeobiogeographical pattern of caenophidians snake colonization
38 of South America and is consistent with the hypothesis of two episodes of dispersion of
39 Colubroides to the continent.

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44 **INTRODUCTION**

45 Tar seeps represent a unique taphonomic and preservational context for the recovery of
46 fossils, often providing unparalleled insight into the history of past biotas (LaDuke, 1991a;
47 Friscia et al., 2008; Solórzano, Rincón & McDonald, 2015; Brown et al., 2017). These
48 sites are generally interpreted as entrapment areas, with exemplar deposits, where were
49 recovered mainly mammalian carnivore and associated herbivore taxa (Brown et al.,
50 2017). Besides the representative mammalian fauna, these peculiar deposits also often
51 yield small vertebrates, plants, and invertebrates (e.g. insects) in a lagerstätten-type
52 condition (LaDuke, 1991a; Ward et al., 2005; Friscia et al., 2008; Rincón et al., 2009;
53 Rincón, Prevosti & Parra, 2011; Solórzano et al., 2015; Holden et al., 2015; Holden et al.,
54 2017).

55 The Venezuela contains several tar pits, however, only two have been
56 paleontologically explored: El Breal de Orocuá (Czaplewski, Rincón & Morgan 2005;
57 Rincón 2006; Rincón, White & McDonald, 2008; Rincón et al., 2006, 2009; Rincón,
58 Prevosti & Parra, 2011; Holanda & Rincón, 2012) and Mene de Inciarte (Rincón et al.,
59 2008; Prevosti & Rincón 2007; Steadman, Oswald & Rincón 2015). The majority of
60 reports detailing the palaeodiversity of these deposits have focused on the large
61 mammals, e.g., canids, proboscids, felids, and xenarthrans (Prevosti & Rincón, 2007;
62 Rincón et al., 2006, 2007, 2009; Rincón, Prevosti & Parra, 2011; Holanda & Rincón 2012;
63 Solórzano, Rincón & McDonald, 2015), contrasting with relatively few reports of small
64 vertebrates and reptiles (Brochu & Rincón 2004; Czaplewski, Rincón & Morgan 2005;

65 Fortier & Rincón 2013; Steadman, Oswald & Rincón 2015; Onary-Alves, Hsiou & Rincón,
66 2016).

67 The interval recorded by these deposits covers key geological periods,
68 representing some of the major palaeobiogeographical and palaeoenvironmental
69 transitions within South America. The late Pliocene/ early Pleistocene (El Breal de
70 Orocuá) is chronologically linked with the establishment of the continental connection
71 between the Central and South America continents (Iturralde Vinent & MacPhee, 1999;
72 Coates et al., 2004) and thus the beginning of the Great American Biotic Interchange
73 (GABI) (Pascual, 2006; Woodburne, Cione & Tonni, 2006). On the other hand, the late
74 Pleistocene (Mene de Inciarte) is well-known for the dramatic climatic changes that
75 occurred throughout the globe at this time (Peizhen, Molnar & Downs, 2001). The
76 interaction between these factors shaped the palaeoenvironmental and
77 palaeobiogeographical histories of the groups inhabiting this region (Simpson, 1980;
78 Woodburne, Cione & Tonni, 2006). However, most treatments of this history have been
79 strongly biased towards the mammalian fossil record (Simpson, 1980). In this
80 contribution, we report on the fossil snakes from two tar pits from Venezuela, discussing
81 their palaeobiogeographical and taxonomic implications. This partially fills a crucial gap
82 in the Pliocene fossil snake record, increasing our understanding of squamate diversity
83 during the Neogene/ Quaternary boundary in the North of South America.

84

85 **GEOLOGICAL SETTINGS**

86 **El Breal de Orocuá**

87 The recovered fossil material comes from an inactive Tar seep deposit, located nearly 20
88 km from Maturín County, Monagas state, north eastern Venezuela (Fig. 1). The locality is
89 situated within the Mesa Formation (Hackley et al., 2006; Rincón et al., 2009) and consists
90 of a series of open asphalt fissures, of which one has been extensively explored (ORS16
91 of Solórzano, Rincón & McDonald, 2015; site of this study). The Tar pit has not been
92 dated absolutely; however, the Mesa Formation was estimated by thermoluminescence
93 (TL) to range from ~2 Ma to 0.5 Ma (early to middle Pleistocene; Carbón, Schubert & Vaz,
94 1992). Alternatively, the 30 identified taxa from the ORS16 vertebrate fossil assemblage
95 strongly suggests an age of late Pliocene–early Pleistocene, particularly with respect to
96 the occurrence of *Smilodon gracilis* (Carnivora, Felidae) and cf. *Chapalmatherium*
97 (Rodentia, Hydrochoeridae), which are considered characteristically
98 Pliocene/Pleistocene taxa (Rincón et al., 2009; Solórzano et al., 2015). Therefore, in this
99 contribution we follow the Plio–Pleistocene age (~2.6 Ma) for the El Breal de Orocuál
100 deposit, based on both biostratigraphy (Rincón et al., 2009; Rincón, Prevosti & Parra,
101 2011; Holanda & Rincón, 2012; Solórzano, Rincón & McDonald, 2015) and geological
102 evidence that suggests an age of greater than 2.0 Ma for the Tar pit (see dating issues
103 discussed in Carbón, Schubert & Vaz, 1992).

104

105 **Mene de Inciarte**

106 Mene de Inciarte is an active surface asphalt with production of consolidate sediments
107 and liquid oil (Steadman, Oswald & Rincón, 2015). It is located in Mara County, Zulia
108 state, northwest of Venezuela, about 90 Km from Maracaibo in the lower hills of Sierra de
109 Perijá (Fig. 1) (Czaplewski, Rincón & Morgan, 2005; Rincón et al., 2008; Steadman,

110 Oswald & Rincón, 2015). Previous geochronological studies of the asphalt seep
111 estimated its formation during the Quaternary with reference to the flooding of fissures
112 with liquid asphalt (Urbani & Galarraga, 1991) and relative dating based on the fossil
113 mammal record, the latter suggesting a Pleistocene age for the deposit (e.g.
114 pampatheriids, mastodons, equids, and ground sloths) (McDonald, Moody & Rincón,
115 1999). A more recent absolute date yields an age estimate between $25,500 \pm 600$ 14C yr
116 BP (28,456–30,878 cal yr BP) and $27,980 \pm 370$ 14C years BP (31,165–32,843 cal yr
117 BP), based on collagen samples of *Glyptodon clavipes* (Mammalia, Xenarthra) (Jull et al.,
118 2004).

119

120 Fig 1: (Maps of the deposits)

121

122 MATERIAL & METHODS

123 **Specimens:** All examined specimens consist of vertebral remains that are housed within
124 either the El Breal de Orocuá (OR–) or Mene de Inciarte (MI–) collections of the
125 paleontological collection of Instituto Venezolano de Investigaciones Científicas (IVIC),
126 Caracas, Venezuela. The fossils comprise precloacal trunk vertebrae and rarer
127 postcloacal specimens. The manner of preservation is variable between the specimens.

128

129 **Anatomical analysis:** To provide as accurate a taxonomic assignment as possible, all
130 material was described with reference to the relevant literature as well as comparison
131 with extant specimens outlined in Table 1. The anatomical description follows the
132 terminology of Auffenberg (1963); Hoffstetter & Gasc (1967); Rage (1984, 2001); Lee &

133 Scanlon (2002); Hsiou & Albino (2009); Albino (2011); Hsiou et al. (2014) (Fig.2A).
134 Quantitative data is based on LaDuke (1991a,b) (Fig. 2B). Measurements were taken
135 with an analogic calliper (0.02 mm) and are given in millimetres.

136

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

138

139 **Institutional abbreviations:** **AMNH**, American Museum of Natural History, New York,
140 New York; **MCN.D**, Coleção Didática de Herpetologia, Museu de Ciências Naturais da
141 Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MCN-PV DR**, Seção
142 de Paleontologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio
143 Grande do Sul, Coleção de Paleontologia de Vertebrados, Coleção Didática de Répteis,
144 Porto Alegre, Brazil; **IVIC-OR**, Instituto Venezolano de Investigaciones Científicas El
145 Breal de Orocal collection; **IVIC-MI**, Instituto Venezolano de Investigaciones
146 Científicas Mene de Inciarte collection; **UFMT**, Coleção da Universidade Federal do Mato
147 Grosso, Mato Grosso, Brazil.

148

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

151

152 **RESULTS**

153 SYSTEMATIC PALAEONTOLOGY

154 Serpentes Linnaeus, 1758

155 Alethinophidia Nopcsa, 1923

156 Macrostromata Müller, 1831

157 Boidae Gray, 1825

158 Boinae Gray 1825

159 *Corallus* Daudin, 1803

160 *Corallus* sp.

161 Fig. 3

162

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

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

168 **Description:** The vertebra is dorsoventrally high, mediolaterally wide and
169 anteroposteriorly short, with its vertebral centrum smaller than the neural arch width (naw
170 $> cl$). In anterior view, the zygosphenes are thick and dorsoventrally inclined, being wider
171 than the cotyles ($zw > ctw$). The prezygapophyseal articular facets are oriented parallel to
172 the horizontal plane. The prezygapophyseal process is short and extends beyond the
173 prezygapophyseal articular facet. The neural canal is subtriangular. The cotyle is circular,
174 with similar measurements of height and width ($ctw \sim cth$). The paracotylar fossae are
175 deep and do not show evidence of paracotylar foramina. The paradiapophyses are
176 lateroventrally oriented, showing a clear distinction between the dia- and parapophyseal
177 articular facets.

178 In posterior view, the lateral edges of the neural arch are characteristically vaulted.
179 Although the zygantrum is eroded, the probable zygantral foramen is nonetheless
180 observable as a deep excavation within the zygantral surface. Laterally to the zygantrum,
181 there is a series of small round pits filled with sediment, which here are interpreted as
182 parazygantral foramina (*sensu* Lee & Scanlon, 2002). The postzygapophyses are
183 transversely level with the horizontal plane. The condyle has a marked circular outline
184 morphology (cnw ~ cnh).

185 In lateral view, the neural spine rises from the anterior margin of the zygosphene
186 roof. It is anteroposteriorly short, exceeding from the posterior margin of the neural arch.
187 The zygosphene articular facets are oval and dorsolaterally oriented. Only a single lateral
188 foramen is observable on each side of the centrum. The vertebral centrum is
189 anteroposteriorly short with a well-marked precondylar constriction. The condyle,
190 although distorted, is convex and slightly deflected dorsally. Ventrally, the haemal keel
191 originates at the cotyle, extending posteroventrally until the level of the precondylar
192 constriction.

193 In ventral view, the centrum is anteroposteriorly short and triangular shaped. The
194 subcentral fossae are deep and well-delimited in the anterior region of the centra. The
195 postzygapophyses are broad and possesses subtriangular morphology.

196 In dorsal view, the neural arch is slightly wider than long (pr-pr>pr-po). The articular
197 facets of the prezygapophyses are anterolaterally oriented, subtriangular in shape, and
198 longer than wide (prl>prw). The zygosphene roof bears markedly triangular lateral lobes
199 with a distinct slightly convex mid lobe, typifying the crenate condition (*sensu* Auffenberg,
200 1963). A deep interzygapophyseal ridge extends between the pre- and

201 postzygapophysis. There is a deep posterodorsal notch in the mid portion of the posterior
202 edge of the neural arch, which exposes a large part of the condyle.

203

204 Fig 3: (*Corallus* plate)

205

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

209

210 **Identification and comparison:** The specimen IVIC OR–6113 shares with Boidae the
211 following vertebral features: dorsoventrally broad and vaulted neural arch; a well-
212 developed and thick zygosphene; reduced prezygapophyseal process; high neural spine;
213 well-defined precondylar constriction; inclination of the prezygapophyses less than 15°;
214 vertebral centrum anteroposteriorly short; and presence of a haemal keel on midtrunk
215 vertebrae (Rage, 1984, 2001; Albino & Carlini, 2008; Hsiou & Albino, 2009; Hsiou et al.,
216 2013).

217 Among Neotropical Boinae genera, IVIC OR–6113 can be distinguished from
218 *Eunectes* and *Boa* primarily with respect to its smaller absolute size (Hsiou & Albino,
219 2010). *Boa* also differs substantially in its more vaulted condition with a deeper
220 posterodorsal notch (posterodorsal notch length ~ 50% pr-po) (Onary-Alves, Hsiou &
221 Rincón, 2016), whereas *Eunectes* displays a relatively depressed dorsoventrally neural
222 arch (Hsiou & Albino, 2009).

223 IVIC OR–6113 can be attributed to the genus *Corallus* based on the following
224 features: reduced absolute vertebral size ($naw < 10$ mm); wide, broad, and vaulted neural
225 arch; prezygapophyses horizontally oriented ($\sim 180^\circ$) in anterior view; crenate
226 morphology of the zygosphene roof in dorsal view; neural spine perpendicular to the
227 vertebral centrum; deep interzygapophyseal ridges; and the presence of small, pit-shaped
228 parazygantral foramina (*sensu* Lee & Scanlon, 2002) (Teixeira, 2013).

229 With respect to intracolumnar variation, the specimen is consistent with the
230 morphology of posterior midtrunk vertebrae, as supported by the reduced vertebral
231 relative size ($pr-po < 5$ mm); long haemal keel; deep subcentral fossae; very short vertebral
232 centrum; cotyle and condyle relatively circular shaped in outline; and a triangular shaped
233 parapophyseal facet (Teixeira, 2013).

234 IVIC OR–6113 shares with posterior precloacal midtrunk vertebrae of the
235 comparative specimens of *Corallus* (Table 1), the absolute vertebral size ($pr-po < 5$ mm);
236 its anteroposteriorly elongated proportions; and the perpendicular orientation of the neural
237 spine in relation to the vertebral centrum. In *Boa* the neural spine is oriented at a stronger
238 dorsoventrally angle in addition to possessing both a spinal blade and laminar crest
239 (*sensu* Albino, 2011). In contrast, *Epicrates* has high dorsoventrally neural spine
240 (Teixeira, 2013). The neural spine of *Eunectes*, despite being low as in *Corallus*, it is
241 markedly shortened anteroposteriorly (Hsiou & Albino, 2009).

242 The zygosphene of IVIC OR–6113 is similar to the midtrunk vertebrae of *Epicrates*
243 and *Corallus*, which also exhibit a crenate morphology. In contrast, *Boa* and *Eunectes*
244 have a dorsoventrally thicker zygosphene, in addition to the presence of a median

245 tubercle in *Eunectes* (Hsiou & Albino, 2009) and a markedly concave zygosphene anterior
246 edge in *Boa* (Albino & Carlini, 2008; Onary-Alves, Hsiou & Rincón, 2016).

247 Finally, IVIC OR–6113 shares exclusively with *Corallus* horizontally oriented
248 prezygapophyseal facets, whereas in the other Neotropical boid genera these processes
249 are slightly-to-modestly inclined relative to the horizontal plane (Kluge, 1991; Rage, 2001;
250 Hsiou & Albino, 2013; Teixeira, 2013; Onary-Alves, Hsiou & Rincón, 2016).

251 There are eight extant species within the genus *Corallus* (Uetz & Hošek 2016): *C.*
252 *hortulanus* (Linnaeus, 1758); *C. caninus* (Linnaeus, 1758); *C. cookii* (Gray, 1842); *C.*
253 *batesi* (Gray, 1860); *C. annulatus* (Cope, 1875); *C. ruschenbergerii* (Cope, 1875); *C.*
254 *grenadensis* (Barbour 1914); *C. blombergi* (Rendahl and Vestergren 1941), and *C.*
255 *cropanii* (Hoge, 1953). Among these species, three are currently found within Venezuela
256 (*C. caninus*; *C. hortulanus*; *C. ruschenbergerii*), with only *C. ruschenbergerii* present in
257 the area containing the fossiliferous deposit (Rivas et al., 2012). The lack of
258 autapomorphic features limits a species-level identification for IVIC OR–6113. However,
259 of the three species currently inhabiting the territory, *C. caninus* can be distinguished from
260 IVIC OR–6113 with respect to its greater absolute dorsoventrally vertebral height (h);
261 presence of a median tubercle on the zygosphene. In general morphology, IVIC OR–
262 6113 shares a close similarity with *C. hortulanus* and *C. ruschenbergerii*, however, we
263 conservatively prefer to restrict taxonomic assignment of the fossil specimen to *Corallus*
264 sp. for the time being.

265

266 *Epicrates* Wagler, 1830

267 *Epicrates* sp.

268 Fig. 4

269

270 **Referred material:** An anterior isolated precloacal vertebra (IVIC MI-004)

271 **Locality and Age:** Mene de Inciarte Tar pit, Zulia state, Venezuela. Dated to 25,500±600

272 ¹⁴C years BP (28,456– 30,878 cal years BP) and 27,980 ± 370 ¹⁴C years BP (31,165–

273 32,843 cal years AP), late Pleistocene (Jull et al., 2004).

274 **Description:** The vertebra is anteroposteriorly short, mediolaterally wide ($naw > cl$), and

275 dorsoventrally high. In anterior view, the zygosphene dorsoventrally thick, with its articular

276 facets laterally oriented. The width of the zygosphene exceeds the width of the cotyle (zw

277 $> ctw$), with its median dorsal region present as a prominent convex border. The

278 prezygapophyses are oriented slightly dorsally above the horizontal axis of the centrum.

279 A small prezygapophyseal process is located below their articular facets. The neural

280 canal has a “trifoliate” morphology in cross-section with its width subequal to its height

281 ($ncw \sim nch$). The cotyle is circular shaped in outline ($ctw \sim cth$) and displays deep

282 paracotylar fossae but no paracotylar foramina. The paradiapophyses are broad and

283 show a clear distinction between the dia- and parapophyseal articular facets.

284 In posterior view, the neural arch is strongly vaulted. The median region of the

285 zyantrum is not preserved. The postzygapophyses of MI-004 are slightly inclined upward.

286 The condyle is circular in shape ($cow \sim coh$).

287 In lateral view, the neural spine is anteroposteriorly long, rising from the posterior

288 edge of the zygosphene. The articular facets of the zygosphene are oval shaped and

289 oriented dorsolaterally. The vertebral centrum of MI-004 is anteroposteriorly short and

290 delimited by a well-marked precondylar constriction. Below the precondylar constriction

291 there is a long hypapophysis which extends to the edge of the precondylar constriction,
292 not exceeding beyond the posterior rim of the condyle.

293 In ventral view, the centrum has a marked triangular morphology tapering towards
294 the precondylar constriction. The specimen possesses two deep subcentral fossae, with
295 associated subcentral foramina excavating its interior on each side of the vertebra. A
296 narrow midline keel rises from the base of the cotyle and develops posteriorly into the
297 hypapophysis, however this process does not extend beyond the precondylar
298 constriction. The postzygapophyses are broad ($p_{zw} > p_{zl}$) and display a subtriangular
299 morphology.

300 In dorsal view, the neural arch is slightly wider than long ($pr-pr > pr-po$). The
301 articular facets of the prezygapophyses are subtriangular, anterolaterally oriented, and
302 longer than wide ($prl > prw$). The anterior edge of the zygosphenic roof is crenate (*sensu*
303 Auffenberg, 1963), bearing triangular lateral lobes and an anteriorly projected median
304 lobe. Paired parasagittal ridges (*sensu* Hsiou & Albino, 2010) extend along the roof of the
305 neural arch from the posterior region of the zygosphenic, nearly reaching the posterior
306 margin of the neural arch. A shallow interzygapophyseal ridge extends between the pre-
307 and postzygapophyses.

308

309

310 Fig 4: (*Epicrates* plate)

311

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

315

316 **Identification and comparison:** The specimen described above shares with the four
317 Neotropical boid genera the following features: anterior precloacal vertebrae that are
318 mediolaterally wide, dorsoventrally short, and dorsoventrally high relative to other aniliids
319 and macrostomatans families; a vaulted neural arch; vertebral centrum shorter than the
320 length of the neural arch; dorsolaterally inclination of the prezygapophysis articular facets
321 lower than 15°; presence of a short prezygapophyseal process; deep posterodorsal
322 notch; strong precondylar constriction; presence of paired subcentral foramina; and a
323 mediolaterally wide and dorsoventrally thick zygosphene (Rage, 2001; Lee & Scanlon,
324 2002; Szyndlar & Rage, 2003; Hsiou & Albino, 2009).

325 IVIC MI-004 is attributed to the extant boid *Epicrates* based on the following
326 features: small absolute size of the vertebra ($h < 10$ mm); vaulted neural arch; deep
327 paracotylar fossae; dorsoventrally high neural spine; hypapophysis which does not
328 exceed the posterior margin of the condyle; crenate zygosphene; and a centrum with a
329 strong triangular outline in ventral (Teixeira, 2013).

330 With respect to intracolumnar variation, the fossil is interpreted as an anterior
331 precloacal vertebra due to the presence of a well-developed hypapophysis, a feature
332 observed exclusively in this region of the axial skeleton of boids (Rage, 2001); and the
333 circular outline morphology of the cotyle and condyle ($ctw \sim cth$) (Teixeira, 2013).

334 The fossil is small in absolute size ($h < 10$ mm), which is characteristic of the
335 vertebrae of boids like *Corallus* and *Epicrates*, being distinct from the comparatively great
336 vertebral size of genera as *Boa* and *Eunectes*. The vertebral height (h) of IVIC MI–004,
337 despite the broken apex of its neural spine, is proportionally greater (i.e. considering the
338 ratio between the neural spine size and the centrum length) than in individuals of *Corallus*
339 and *Eunectes*. In contrast to *Boa*, the neural spine of IVIC MI–004 is relatively lower,
340 being more similar in general size to *Epicrates*. In posterior view, IVIC MI–004 exhibits a
341 more convexly domed neural arch compared to anterior precloacal vertebrae of *Eunectes*
342 and *Corallus*, which exhibit a more dorsoventrally depressed morphology.

343 Although broken, the neural spine of IVIC MI–004 is dorsoventrally high and
344 mediolaterally long, contrasting with *Corallus* which bears a low and mediolaterally
345 shortened neural spine (Hsiou & Albino, 2009). The neural spine of *Boa*, in addition to
346 bearing a well-delineated spinal crest and spinal blade (*sensu* Albino, 2011), exhibits a
347 strong posterior orientation, both features that are absent in the fossil specimen.

348 IVIC MI–004 shares with *Corallus* and *Epicrates* the crenate morphology of the
349 zygosphene roof (*sensu* Auffenberg, 1963); however, as pointed by Hsiou & Albino
350 (2010), this condition is variable with respect to both the individual and the position of the
351 vertebra along the axial skeleton. Nonetheless, the crenate zygosphene of IVIC MI–004
352 does not resemble the well-developed concave morphology of the zygosphene roof seen
353 in *Boa*, nor the condition present in *Eunectes*, which possesses a median tubercle
354 between the neural canal and the zygosphene (Hsiou & Albino, 2009).

355 Currently, two species of *Epicrates* are registered in Venezuela: *E. cenchria*,
356 Linnaeus (1758) and *E. maurus*, Gray (1849), of which only the distribution of *E. maurus*

357 encompasses the Mene de Inciarte site. No autapomorphic characters of the postcranial
358 elements have been identified as diagnostic to the specific level among the five
359 continental species of *Epicrates* (Rivera et al., 2011). We therefore maintain a
360 conservative approach and recognize IVIC MI-004 as *Epicrates* sp.

361 Caenophidia Hoffstetter, 1939

362 Endoglyptodonta Zaher *et al.*, 2009

363 Colubroides Zaher *et al.*, 2009

364 Colubroidea Opperl, 1811

365 Indeterminate genera and species

366 Fig. 5

367

368 **Referred material:** Four nearly complete precloacal vertebrae (IVIC OR-3667; IVIC OR-
369 6124; IVIC OR-2618; IVIC MI-005) and one postcloacal vertebra (IVIC OR-2917).

370 **Localities and Age:** IVIC OR-3667; IVIC OR-6124; IVIC OR-2618: Tar Pit ORS16, El
371 Breal de Orocual, Monagas State, Venezuela. Estimated to be late Pliocene-early
372 Pleistocene in age based on the palaeofaunal assemblage (Rincón et al., 2009, Rincón,
373 Prevosti & Parra, 2011; Solórzano, Rincón & McDonald, 2015). IVIC MI-005: Mene de
374 Inciarte Tar pit, Zulia state, Venezuela. Dated to 25,500±600 ¹⁴C years BP (28,456-
375 30,878 cal years BP) and 27,980 ± 370 ¹⁴C years BP (31,165-32,843 cal years AP), late
376 Pleistocene (Jull et al., 2004).

377 **Description:** The fossils share the following common pattern: vertebrae with the length
378 of the vertebral centrum greater than the width of the neural arch ($cl > naw$). In anterior
379 view, the neural spine is dorsoventrally high and mediolaterally thin. The zygosphenes of

380 the specimens is dorsoventrally slender, with a convex dorsal edge. The neural canal is
381 subtriangular in shape with a tapering dorsal apex. Internally, three well-developed crests
382 extend anteroposteriorly towards the posterior margin of the neural canal. The
383 prezygapophyses vary in orientation among the specimens. IVIC OR–2618, IVIC OR–
384 3667, and IVIC MI–005 show a slight dorsolaterally inclination of the prezygapophyses
385 above the horizontal plane, whereas IVIC OR–6124 and IVIC OR–2917 exhibit a higher
386 dorsolaterally angle of inclination, reaching the mid portion of the neural canal. The the
387 prezygapophyses are well preserved in IVIC OR–3667 and IVIC OR–6124, the main body
388 of these processes are dorsoventrally elongate and extend well ventrally below their
389 articular facets. The cotyles of all vertebrae are rounded with subequal width to height
390 ratios ($ctw \sim cth$). The paradiapophyses are anterolaterally oriented with a clear distinction
391 between the articular facets. The pleurapophyses of IVIC OR–2917 are dorsoventrally
392 long, mediolaterally slender, and strongly oriented ventrolaterally. The haemapophysis is
393 positioned ventral to the cotyle and are characterized by dorsoventrally thin processes
394 that extend a short distance along the sagittal axis of the element.

395 In posterior view, the neural arches of all specimens are dorsoventrally depressed.
396 The zygantrum mediolaterally shortened and deep with some specimens (e.g., IVIC OR–
397 6124, IVIC OR–2618) exhibiting small paired zygantral foramina. The postzygapophyses
398 articular facets are variable in orientation: being inclined slightly dorsolaterally in IVIC
399 OR–3667, IVIC OR–6124, and IVIC OR–2917; horizontally oriented in IVIC MI–005; and
400 dorsoventrally oriented in IVIC OR–2618. The condyles of all specimens are circular in
401 outline, with a height similar or equal to the width ($cow \sim coh$).

402 In lateral view, the neural spine is dorsoventrally high, mediolaterally thin, and
403 anteroposteriorly elongated. Its rises from the posterior edge of the zygosphene,
404 extending until the posterodorsal notch. Paired lateral foramina are observable on each
405 side of the vertebral centrum only in IVIC OR–2917. The vertebral centra of all specimens
406 are anteroposteriorly elongated. The condyle is posterodorsally inclined. With the
407 exception of IVIC OR–2917, all specimens bear a well-developed haemal keel on ventral
408 surface of the centrum, which does not extend beyond the condyle.

409 In ventral view, a prominent haemal keel and haemapophysis (in IVIC OR–6124)
410 rise from the ventral border of the cotyle, extending longitudinally and reaching the
411 precondylar constriction. In IVIC OR–2618 and IVIC MI–005 paired subcentral foramina
412 can be observed on each side of the haemal keel. A marked subcentral groove excavates
413 the mid portion of the centrum of all specimens. The postzygapophyseal articular facets
414 are oval in shape and posterolaterally oriented in all specimens, except for IVIC MI–005
415 that shows a lateral orientation.

416 In dorsal view, the fossils are as wide mediolaterally as they are anteroventrally
417 long ($pr-pr \sim pr-po$), except for IVIC OR–2618 which is wider than long ($pr-pr > pr-po$).
418 The prezygapophyseal articular facets are oval shaped ($prl > prw$) and anterolaterally
419 oriented. An anterolaterally oriented prezygapophyseal process rises ventrally to the the
420 articular facets. This process is particularly anterolaterally elongated in IVIC OR–3667.
421 The zygosphene roof is variable among the specimens, being concave in IVIC OR–3667,
422 straight in IVIC OR–6124, and crenate with a median lobe in IVIC MI–005 (*sensu*
423 Auffenberg, 1963). All specimens possess a mediolaterally thin neural spine, which
424 extends longitudinally until the posterior edge of the neural arch. The interzygapophyseal

425 constriction is anteroposteriorly long, extending from the prezygapophyses to the articular
426 facets of the postzygapophyses. The posterodorsal notch of the neural arch is deep in all
427 specimens, exposing most of the cotyle.

428

429 Fig 5: (Colubroidea indet. plate)

430

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

434 *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;
435 **ncw**:1.9; **nsi**: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;
436 **zw**:3.0.

437 *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;
438 **po-po**:10.9; **pr-pr**:13.4; **pr-po**:11.0; **prl**:4.6; **prw**:2.4; **zh**:1.0; **zw**:5.0.

439 *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;
440 **ncw**:2.2; **nsi**: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.

441 *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-**
442 **pr**:9.6; **pr-po**:11.7.

443

444 **Identification and Comments:** Colubroidea is a monophyletic group supported by
445 several synapomorphic features that includes both cranial and soft tissue characters;
446 however, none of them relate to the axial skeleton (Rieppel, 1988; Zaher, 1999; Zaher et
447 al., 2009). The group currently includes about 1853 of the 3596 catalogued extant snake

448 species (Uetz & Hošek, 2016), representing a well-diversified clade with a young
449 evolutionary history (*i.e.* Cenozoic). The fossils described above can be attributed to
450 Colubroidea based on the following combination of features: anteroposteriorly elongated
451 vertebral morphology; neural arch longer than wide ($cl > naw$); extremely dorsoventrally
452 slender zygosphenes ($zh \leq 1mm$); dorsoventrally high neural spine; paradiapophyses with
453 a clear distinction between their articular facets; and the presence of an anterolaterally
454 elongated prezygapophyseal process (Rage, 1984; Holman, 2000; Albino & Montalvo,
455 2006).

456 Traditionally, vertebrae that display the above features have been attributed to the
457 generic group “Colubridae”. However, “Colubridae” is considered paraphyletic, with most
458 previous analyses dealing with the group conducted using phenetic methods (Zaher,
459 1999) and therefore not representing a clade (*i.e.*, a “natural” group) in the modern sense.
460 For this reason, we prefer to avoid assigning anything to this generic group.

461 Among Colubroidea, some families are well studied, such as Calamariidae,
462 Colubridae (clade *sensu* Zaher et al., 2009), Pseudoxenodontidae, Natricidae, and
463 Dipsadidae (*sensu* Zaher et al., 2009). However, none of these groups have diagnoses
464 pertaining to vertebral anatomy. It is worth noting, however, the variation in character
465 combinations among the individual fossils, suggesting the possible occurrence of at least
466 four different unidentified colubroidean taxa within the sample.

467

468 Endoglyptodonta Zaher *et al.*, 2009

469 Viperidae Opperl, 1811

470 Indeterminate genera and species

471 Fig. 6

472

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

476 **Locality and Age:** Tar Pit ORS16, El Breal de Orocuál, Monagas State, Venezuela. Age
477 estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage
478 (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald,
479 2015).

480 **Description:** In general, the vertebrae are relatively dorsoventrally high (only observable
481 in IVIC OR–2617), slightly wider than long ($pr-pr > pr-po$) and have a centrum length
482 similar to the width of the neural arch ($cl \sim naw$). In anterior view, the specimens bear a
483 dorsoventrally thin zygosphene with a straight dorsal margin. The articular facets of the
484 zygosphene are elliptical in outline and dorsally oriented. The neural canal is trifoliate with
485 a subequal width to length ratio ($ncw \sim nch$). The articular facets of the anteroposteriorly
486 elongate prezygapophyses are dorsolaterally inclined relative to the horizontal plane at
487 an angle of $\sim 30^\circ$. The cotyles of all vertebrae are circular in outline, having a similar width
488 to height ratio ($ctw \sim cth$). Deep paracotylar fossae excavate the laterally the cotyle. The
489 paradiapophyses, although eroded in some specimens, show a clear distinction between
490 the articular facets. The parapophyseal processes is small, anteroventrally oriented and
491 extend beyond the margin of the cotyle.

492 In posterior view (only preserved in IVIC OR–2617), the neural arch has a
493 triangular outline with a shallowly concave posterior surface. The zygantrum is

494 mediolaterally wide and deep in depth. The postzygapophyses articular facets are
495 mediolaterally broad ($p_{zw} > p_{zl}$) and inclined slightly dorsally. In all specimens the condyle
496 is circular in outline. A long dorsoventrally hypapophysis rises ventrally from the condyle,
497 exceeding its ventral margin.

498 Only IVIC OR–2617 preserves a neural spine. In lateral view it is well developed
499 and dorsoventrally high. The zygosphene articular facets of all specimens are oval and
500 dorsally oriented. The paradiapophyses are completely preserved only in IVIC OR–6104,
501 being dorsoventrally oriented. A large parapophyseal process is observable in the
502 anteroventral region of the parapophysis, being well developed and strongly oriented
503 anteroventrally. The centrum bears a prominent and anteroposterioly elongated
504 hypapophysis which in IVIC OR–2617 exceeds well beyond the posterior margin of the
505 condyle.

506 In ventral view, the vertebral centrum is mediolaterally narrow and
507 anteroposteriorly long. The subcentral fossae are variable in expression, being shallow in
508 some specimens (*e.g.* IVIC–6104, IVIC OR–1760), and deep in others (*e.g.* IVIC OR–
509 2616, IVIC OR–3674). In all specimens, the fossae are restricted to the anterior region of
510 the vertebral centrum. The subcentral fossae are delimited by a well-marked subcentral
511 margin. The hypapophysis develops longitudinally to the centrum, being broken in some
512 specimens but clearly surpassing the posterior margin of the condyle. The articular facets
513 of the postzygapophyses are anteroposteriorly long ($p_{zl} > p_{zw}$) and elliptical in outline.

514 In dorsal view, the anterior margin of the zygosphene in IVIC OR–2617 and IVIC
515 OR–6104 is concave, whereas IVIC OR–1760 and IVIC OR–3674 exhibit a straight
516 margin. The interzygapophyseal constriction is anteroposteriorly long and concave in

517 shape. The neural spine of IVIC OR–2617) extends longitudinally along the dorsal
518 surface of the arch, terminating posterior to the posterior margin of the posterodorsal
519 notch. The prezygapophyseal articular facets are elongate ellipses ($prl > prw$), and
520 oriented anterolaterally. The posterodorsal notch is deep, exposing a large portion of the
521 condyle (only preserved in IVIC OR-2617 and IVIC OR–3674).

522

523 Fig 6: (Viperidae indet. plate)

524

525 **Measurements (in millimetres):** *IVIC OR-2617*. **cl:**7.0; **cth:**2.1; **ctw:**2.3; **h:**15.4;
526 **naw:**6.0; **nch:**2.0; **ncw:**2.1; **nsi:**4.1; **nsh:**5.0; **po-po:**10.6; **pr-pr:**10.0; **pr-po:**8.0; **prl:**3.0;
527 **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;
528 **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*.
529 **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;
530 **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;
531 **prw:**2.8; **zh:**1.4.

532

533 **Identification and Comments:** The specimens share with Colubroidea the following
534 vertebral characters: gracile vertebrae which are longer than wide ($pr-po > pr-pr$);
535 mediolaterally thin neural spine; dorsoventrally slender zygosphenes; presence of
536 prominent accessory prezygapophyseal processes; and paradiapophyses with a clear
537 distinction between the dia- and parapophyseal articular facets (Rage 1984; Lee &
538 Scanlon 2002; Albino & Montalvo 2006).

539 The specimens possess a well-developed hypapophysis, which is considered an
540 apomorphic character of “Xenodermatinae”, Homalopsinae, “Pseudoxyrhophiinae”,
541 “Boonodontinae”, Elapidae, Viperidae, and Natricinae (Zaher, 1999). Among these
542 groups, IVIC OR–6104 shares with Viperidae a single autapomorphic postcranial
543 character: the presence of a well-developed, strongly anteroventrally oriented
544 parapophyseal process (Zaher, 1999; Zaher et al., 2009). Based on this character, IVIC
545 OR–6104 is unequivocally assigned to the Viperidae family. Despite the lack of the
546 parapophyseal process, the other specimens can be identified as Viperidae due to the
547 following combination of vertebral characters: a not well-elongated anteroposteriorly
548 vertebrae (e.g. compared to Colubridae clade *sensu* Zaher et al. 2009); slender and
549 straight zygosphene; well-developed hypapophyses; dorsoventrally depressed neural
550 arch; postzygapophyses processes strongly oriented anterolaterally; anteroposteriorly
551 short prezygapophyseal process; and subcentral fossae restricted to the anterior region
552 of the centrum (Auffenberg, 1963; Rage, 1984; Holman, 2000; Albino & Montalvo, 2006;
553 Head, Sánchez-Villagra & Aguilera, 2006; Hsiou & Albino, 2011).

554 With respect to the taxonomic identity of the specimens, Albino & Montalvo (2006)
555 do not recognize any diagnostic vertebral characters of Viperidae that are informative at
556 either a the generic or specific level. Among the most common studied genera, Camolez
557 & Zaher (2010) reported subtle differences between *Crotalus* and *Bothrops*, mainly
558 regarding the morphology of the anterior margin of the zygosphene roof and the
559 orientation of the parapophyseal processes. Among these features, the anterior margin
560 of the zygosphene roof of *Crotalus* is generally strongly concave in its mid-region, a
561 condition observed in IVIC OR–2617 and IVIC OR–6104.

562 Currently, six genera of Viperidae are distributed throughout Venezuela: *Bothrops*,
563 *Crotalus*, *Bothriechis*, *Lachesis*, and *Porthidium*, representing 12 valid species (Rivas et
564 al., 2012). Due to the lack of diagnostic vertebral features, as well the poor preservation
565 of the specimens, here we restrict assignment of the specimens to Viperidae indet.

566

567 Endoglyptodonta Zaher et al., 2009

568 Elapoidea Boie, 1827

569 Elapidae Boie, 1827

570 cf. *Micrurus*

571 Fig. 7

572

573 **Referred material:** One almost complete preloacal vertebra (IVIC OR–2619).

574 **Locality and Age:** Tar Pit ORS16, El Breal de Orocuá, Monagas State, Venezuela. Age
575 estimated to be late Pliocene–early Pleistocene based on the palaeofaunal assemblage
576 (Rincón et al., 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald,
577 2015).

578 **Description:** The vertebra is relatively anteroposteriorly elongate, with a centrum length
579 greater than the width of the neural arch ($cl > naw$). In anterior view, the zygosphenes are
580 convex shaped, being dorsoventrally slender and mediolaterally wider than the cotyle (zw
581 $> ctw$). The neural canal is trifoliate and as wide as it is high ($ncw \sim nch$). The
582 prezygapophyses are short and oriented slightly above the horizontal plane. The only
583 preserved prezygapophyseal process is anteroposteriorly elongated and located ventral
584 to the right prezygapophysis. The cotyle is slightly flattened dorsoventrally such that the

585 width is greater than the height ($ctw > cth$). The paradiapophyses show a clear distinction
586 between the dia- and parapophyseal articular facets.

587 In posterior view the neural arch is dorsoventrally depressed. The neural spine is
588 dorsoventrally low with its mid-region excavated by the posterodorsal notch to form a
589 deep sulcus. The postzygapophyses are oriented slightly lateroventrally. The condyle is
590 round with the height similar to its width ($cow \sim coh$). The hypapophysis is dorsoventrally
591 shortened and located beneath the condyle, slightly exceeding its ventral margin.

592 In lateral view, the neural spine is very low, dorsally straight, anteroposteriorly
593 elongated, and sloping towards the posterior region of the neural arch. The articular facet
594 of the zygosphenes is anterolaterally oriented and elliptical in shape. The paradiapophyses
595 exhibit a slight anterolateral orientation. The centrum is anteroposteriorly elongated and
596 displays a weakly developed precondylar constriction. Ventral to the centrum, the
597 hypapophysis is mediolaterally slender with a strong posterior orientation and, despite the
598 distal region not being preserved, probably extended beyond the posterior margin of the
599 condyle.

600 In ventral view, the centrum is long and narrow ($cl > naw$), bearing shallow
601 subcentral fossae which are delimited by marked subcentral margins. The hypapophysis
602 extends longitudinally from the ventral margin of the cotyle to the mid region of the
603 centrum, not exceeding the posterior margin of the precondylar constriction. The
604 postzygapophyseal articular facets are elliptical in shape.

605 In dorsal view, the centrum has a width equal to its length ($pr-pr = pr-po$). The
606 zygosphenes possess anterolaterally tapering lateral edges and a non-crenate mid
607 region (i.e. straight anterior edge). The prezygapophyseal articular facets are elliptical in

608 outline (prl > prw) and orientated anterolaterally. A poorly preserved prezygapophyseal
609 process is located ventral to the right prezygapophyseal articular facet, being
610 mediolaterally elongate and transversely orientated relative to the prezygapophysis.
611 Located ventral to the prezygapophyses, the diapophyseal articular facets of the
612 paradiapophyses are convex in shape and lateroposteriorly oriented. The
613 interzygapophyseal constriction is anteroposteriorly long, extending from the base of the
614 prezygapophysis to the postzygapophysis, being relatively shallow. The neural spine is
615 mediolaterally thin, rising from the posterior region of the zygosphenic roof and extending
616 longitudinally to contact the posterodorsal notch. The postzygapophyses articular facets
617 are slightly anterolaterally oriented.

618

619 Fig 7: (cf. *Micrurus* plate)

620

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

624

625 **Identification and Comments:** Diagnostic features for Elapidae pertain mainly to cranial
626 characters (e.g. the morphology of the proteroglyph condition of the maxilla), in addition
627 to morphological traits associated with the venom glands (Underwood & Kochva, 1993;
628 Zaher, 1999). No autapomorphic postcranial features have been reported at
629 genus/species level. Venezuela currently has two recognised genera of elapids: *Micrurus*

630 and *Leptomicrosaurus* (Rivas et al., 2012), with two species of *Micrurus* previously reported
631 at the fossiliferous site: *M. dissoleucus* Cope, 1860 and *M. isozonus* Cope, 1860.

632 Among the comparative osteological material accessed for this study, IVIC OR–
633 2619 shares with the genus *Micrurus* the following vertebral characters: gracile vertebrae
634 with a dorsoventrally depressed neural arch; oval shaped cotyle ($ctw > cth$);
635 anteroposteriorly elongated pre– and postzygapophyseal articular facets ($pri, pzi > prw,$
636 pzw); mediolaterally thin and very dorsoventrally low neural spine in lateral view,
637 possessing a straight dorsal edge that develops into a slope anteriorly to the posterior
638 margin of the neural arch; and thin hypapophysis which is strongly compressed
639 anteroposteriorly (Auffenberg, 1963; Holman, 1977). Due to the poor preservation of the
640 specimen, as well the lack of formal studies concerning the postcranial osteology of
641 Elapidae, here we prefer to restrict taxonomic attribution of IVIC OR–2619 to cf. *Micrurus*,
642 sharing an overall vertebral morphology with the modern genus, but lacking either
643 diagnostic or indicative traits that can be used for more precise assignment.

644

645 **DISCUSSION**

646 The Venezuelan snake fossil record is still scarce when compared to other South America
647 countries (e.g. Argentina, Brazil, Colombia). With respect to Cenozoic strata, the Socorro
648 Formation (middle Miocene) preserves *Colombophis* (Alethinophidia, *incertae sedis*), and
649 the boid *Eunectes* (Head, Sánchez–Villagra & Aguilera, 2006 after Hsiou, Albino &
650 Ferigolo, 2010; Hsiou & Albino, 2010), whereas only *Eunectes* has been reported as
651 coming from the Urumaco Formation (middle Miocene), (Head, Sánchez–Villagra &
652 Aguilera, 2006 after Hsiou & Albino, 2010). Recently, Onary-Alves, Hsiou & Rincón (2016)

653 reported the presence of *Boa constrictor* from the El Breal de Orocuál, representing the
654 single fossil snake record for that locality. The youngest record comes from the late
655 Pleistocene of the Cucuruchu gravels, where Head, Sánchez–Villagra & Aguilera (2006)
656 identified an indeterminate Viperidae. Although fragmentary, such occurrences provide
657 direct insight into the palaeoenvironmental and palaeobiogeographic histories of snakes
658 during the Cenozoic/ Quaternary in South America.

659 The palaeoenvironmental conditions for the North of South America has primarily
660 been inferred with reference to the palaeofaunal mammal assemblage, which strongly
661 suggests the predominance of dry savanna crossed by fragmentary forests, rivers, and
662 patches of gallery forest comprised of humid–climate species of plants (Rincón et al.,
663 2009; Rincón, Prevosti & Parra, 2011; Solórzano, Rincón & McDonald, 2015). The tar pit
664 snakes corroborate the interpretation of a mosaic environmental scenario composed of
665 small forests, arid regions, and rivers, analogous to the modern Venezuelan Llanos
666 (Rincón et al., 2007; Rincón et al., 2009; Rincón, Prevosti & Parra, 2011). Although the
667 boid genera *Corallus* and *Epicrates* are currently widespread across South America
668 (Henderson, 1995), some species within these genera can persist only in suitable
669 microclimatic and microenvironmental conditions, particularly forest-exclusive species
670 (Rodrigues, 2005; Carvajal–Cogollo & Urbina–Cardona, 2015). Most species of *Corallus*
671 and *Epicrates* require specific forested environments to establish a viable population
672 (Henderson et al., 1995), and a major change in the microclimate can threaten these
673 genera, even leading to local extinction (Rodrigues, 2005; Carvajal–Cogollo & Urbina–
674 Cardona, 2015). The presence of *Corallus* in El Breal de Orocuál, in addition to increasing
675 the known boid palaeodiversity, supports the existence of forest regions with adequate

676 environmental conditions (*i.e.* humidity and temperature) for habitation by boids during
677 the Plio–Pleistocene. Moreover, the presence of Colubroides (*sensu* Zaher, 2009), such
678 as the “colubrids” (Colubroidea) and especially the viperids, corroborate the existence of
679 dry savanna components mixed with humid forested regions, since some colubrid and
680 viperid species inhabit open areas and are well-known to live in dry environments (*e.g.*
681 *Crotalus* sp.). Nowadays, *Corallus* and *Epicrates* are present in the Venezuelan Llanos
682 (Rivas et al., 2012), and the record of *Corallus* during the Plio/Pleistocene, together with
683 the presence of *Epicrates* in the Late Pleistocene, suggests that, despite climatic
684 fluctuations, the palaeoenvironment was amenable to habitation by, boids throughout this
685 time interval.

686 Regarding Colubroides (*sensu* Zaher et al., 2009), an interesting biogeographical
687 question pertains to the group’s origins and entrance into South America (Fig. 8A–C).
688 Current palaeobiogeographical studies of the group suggest two episodes of dispersion
689 from North America to South America, the first dating back to the uplift of the Panama
690 Isthmus (Albino & Montalvo, 2006; Hoffstetter, 1967; Cadle & Greene, 1993; Albino,
691 1996b), with a second episode thought to have occurred during the Plio/Pleistocene
692 (Wüster et al., 2002, 2005; Head, Sánchez–Villagra & Aguilera 2006). The oldest record
693 of “Colubridae” in the Americas come from the late Eocene of Georgia, North America
694 (Fig. 8A) (Parmley & Holman, 2003), whereas the oldest South American occurrence
695 dates to the early Miocene of Argentina (Fig. 8B) (Albino, 1996b). This early Miocene
696 record, together with the late Miocene records of Viperidae from Argentina and
697 “Colubroids” from Brazil (Fig. 8B) (Verzi et al., 2004; Albino & Montalvo 2006), suggests
698 that the first great dispersion of Colubroides occurred prior to major continental events

699 such as the uplifting of the Panama Isthmus and the GABI (Albino & Montalvo, 2006;
700 O’Dea et al., 2016). This dispersion can likely be explained via the aquatic crossing of a
701 series of island complexes within Central America during the Miocene (Fig. 8B)
702 (Hoffstetter, 1967; Cadle & Greene, 1993; Albino, 1996b).

703 Based on the Venezuelan record of Viperidae in the late Pleistocene, Head,
704 Sánchez–Villagra & Aguilera (2006) suggested that Colubroides could also have reached
705 South America during a later episode of the Neogene, mainly based on the Cucuruchu
706 gravels record. Indeed, the combination of the Colubroides specimens described here,
707 the fauna of Plio/Pleistocene “colubrids” and viperids at El Breal de Orocuál, and the
708 presence of a suitable colonisation route after the complete uplift of the Panama Isthmus
709 (O’Dea et al., 2016), supports the hypothesis of a second entrance of Colubroides into
710 South America at the Pliocene/Pleistocene boundary (Fig. 8C). Additionally, studies in
711 the timing of molecular divergence (Wüster et al., 2002, 2005) suggest a similar pattern
712 in which viperids like *Bothrops*, *Lachesis*, and *Bothriechis* could have reached and
713 diversified in South America before the total closure of the Panama Isthmus (e.g. the early
714 Miocene records of Argentina, Albino, 1989; Albino, 1996b; Albino & Montalvo, 2006). In
715 contrast genera such as *Crotalus* and *Porthidium* are thought to be late dispersers, only
716 reaching South America after the complete uplift of the Panama Isthmus (e.g. the
717 Venezuelan Plio/Pleistocene records of “colubrids” and viperids and the late Pleistocene
718 viperids; Head, Sánchez–Villagra & Aguilera 2006 Fig. 8C). The viperid fossils of El Breal
719 de Orocuál are geographically and chronologically consistent with this later estimated
720 entrance of *Crotalus* onto the continent (Wüster et al., 2002, 2005). With respect to the
721 described material, IVIC OR–6104 and IVIC OR–2617 bear no significant morphological

722 distinction from extant comparative material of *Crotalus* (Table 1). These specimens
723 share with *Crotalus* the distinct characteristic of a concave anterior edge of the
724 zygosphene roof, which is argued to be exclusive to the genus (Camolez & Zaher, 2010).
725 Despite the generic assignment of these Colubroides specimens, the material
726 nonetheless indicates great potential for future palaeobiogeographical investigations,
727 especially with respect to the history of viperids on the continent.

728 The extant species of “coral snakes” are currently represented in the Americas by
729 the genera *Micruroides* and *Micrurus* and in Asia by the genus *Sinomicrurus* (Lee et al.,
730 2016). Fossil remains of “coral-snakes” are very scarce and geologically young (~16 to
731 13 Ma) (Holman, 1977). This is concordant with the time calibrated phylogeny of the
732 group, which estimates the divergence of the lineage at ~30 Ma. (Lee et al., 2016). South
733 American records are restricted to the Quaternary of Brazil and are represented by cranial
734 remains attributed to *Micrurus corallinus* and vertebrae assigned to *Micrurus* sp.
735 (Camolez & Zaher, 2010). North America preserves the oldest fossil record of the group
736 from the late Barstovian North American Land Mammal Age of Nebraska (middle
737 Miocene) (Holman, 1977), whereas material attributed to *Micrurus fulvius* and *Micrurus*
738 cf. *M. fulvius* is known from the Pleistocene of Florida (Auffenberg, 1963). Records dating
739 to the middle Miocene of Europe demonstrate the presence of the extinct *Micrurus*
740 *gallicus* and *Micrurus* cf. *M. gallicus*, as well as indeterminate *Micrurus* vertebral material
741 (Rage & Holman, 1984; Venczel, 2001; Ivanov & Böhme, 2011). However, the
742 palaeobiogeographical history of the genus *Micrurus* is somewhat complex and the
743 scarcity of studies pertaining to axial skeleton anatomy hampers the identification of fossil
744 material to a specific level, preventing further inferences about the palaeobiological past

745 of the group (Head, Mahlow & Müller, 2016). Although this also impacts on our knowledge
746 of the palaeobiogeography of *Micrurus*, Rage & Holman (1984), based on the fossil
747 record, inferred a North American origin of the genus, followed by an early Miocene
748 dispersion to Asia before eventually reaching Europe. The South American continent is
749 estimated to have been colonized by *Micrurus* following the complete uplift of the Panama
750 Isthmus (~2.8 Ma.) (O’Dea et al., 2016), with dispersion potentially related to decreasing
751 average temperatures within the higher latitudes of North America (Rage & Holman,
752 1984). The putative cf. *Micrurus* described herein is geographically and temporally
753 consistent with the hypothesis of a South American colonization of “coral-snakes” during
754 the Plio/Pleistocene (Fig. 8C) and represents an interesting addition to our current
755 understanding of the biogeography of the group.

756

757 **CONCLUSIONS**

758 The Venezuelan fossil snake record is becoming increasingly better understood, and this
759 report contributes to our knowledge of Cenozoic squamate fossils from South America as
760 a whole. The tar pit material described herein demonstrates the presence of several
761 snake groups, including Boidae, Viperidae, “colubrids”, and the putative oldest South
762 American record of Elapidae. The presence of *Corallus*, *Epicrates*, and viperids, together
763 with the previously described *Boa constrictor*, further supports the mosaic nature of the
764 palaeoenvironment of El Breal de Orocuá, being composed of forested areas together
765 with savannah and dry open areas. The presence of Colubroidea (*sensu* Zaher et al.
766 2009), especially the occurrence of putative fossils of *Crotalus* and cf. *Micurus*, is
767 consistent with the hypothesis of a second episode of dispersion and colonization of the

768 group into South America, following the total uplift of the Panama Isthmus. This material
769 therefore contributes genuine insight into specific palaeobiogeographic and
770 palaeoenvironmental patterns, representing an important preliminary step. However, only
771 identification to lower taxonomical levels can furnish more precise inferences regarding
772 the dispersion patterns of these snake groups into South America. In this sense, the
773 exhaustive anatomical analysis of postcranial material in addition to the application of new
774 methodologies, such as three-dimensional morphometrics, constitutes a crucial future
775 direction for research into this part of the palaeontological record.

776

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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
<i>Boa constrictor</i> imperator	Boidae	AMNH R 155261, AMNH R 155257, AMNH R 77590, AMNH R 74737, AMNH R 57472
<i>Boa constrictor</i>	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
<i>Corallus caninus</i>	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
<i>Crotallus durissus</i>	Viperidae	AMNH 56455, AMNH 744442
<i>Crotallus durissus</i> terrificus	Viperidae	AMNH 77027
<i>Clelia clelia</i>	Colubroidea	AMNH 57797
<i>Bothrops atrox</i>	Viperidae	AMNH 29885
<i>Bothrops bilineatus</i>	Viperidae	AMNH R 140856
<i>Corallus</i> cf. <i>C. caninus</i>	Boidae	AMNH R 57804
<i>Corallus annulatus</i>	Boidae	AMNH R 114496
<i>Corallus batesi</i>	Boidae	UFMT-R 05362
<i>Drymarchon corais</i> couperi	Colubroidea	AMNH R 155299
<i>Eunectes murinus</i>	Boidae	AMNH 57474, MCN.D 306, MCN.D 316, MCN.D 319, MCN.D 342
<i>Epicrates crassus</i>	Boidae	MCN-PV DR 0003
<i>Epicrates striatus</i>	Boidae	AMNH R 140542
<i>Epicrates striatus</i> striatus	Boidae	AMNH R 155262
<i>Epicrates striatus</i> strigilatus	Boidae	AMNH 155259, AMNH R 70263, AMNH R 155259
<i>Epicrates striatus</i> fosteri	Boidae	AMNH R 77633, AMNH R 77057
<i>Corallus cropanii</i>	Boidae	AMNH R 92997
<i>Corallus hortulanus</i> cookii	Boidae	AMNH R 141098, AMNH R 74832, AMNH R 7812,

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

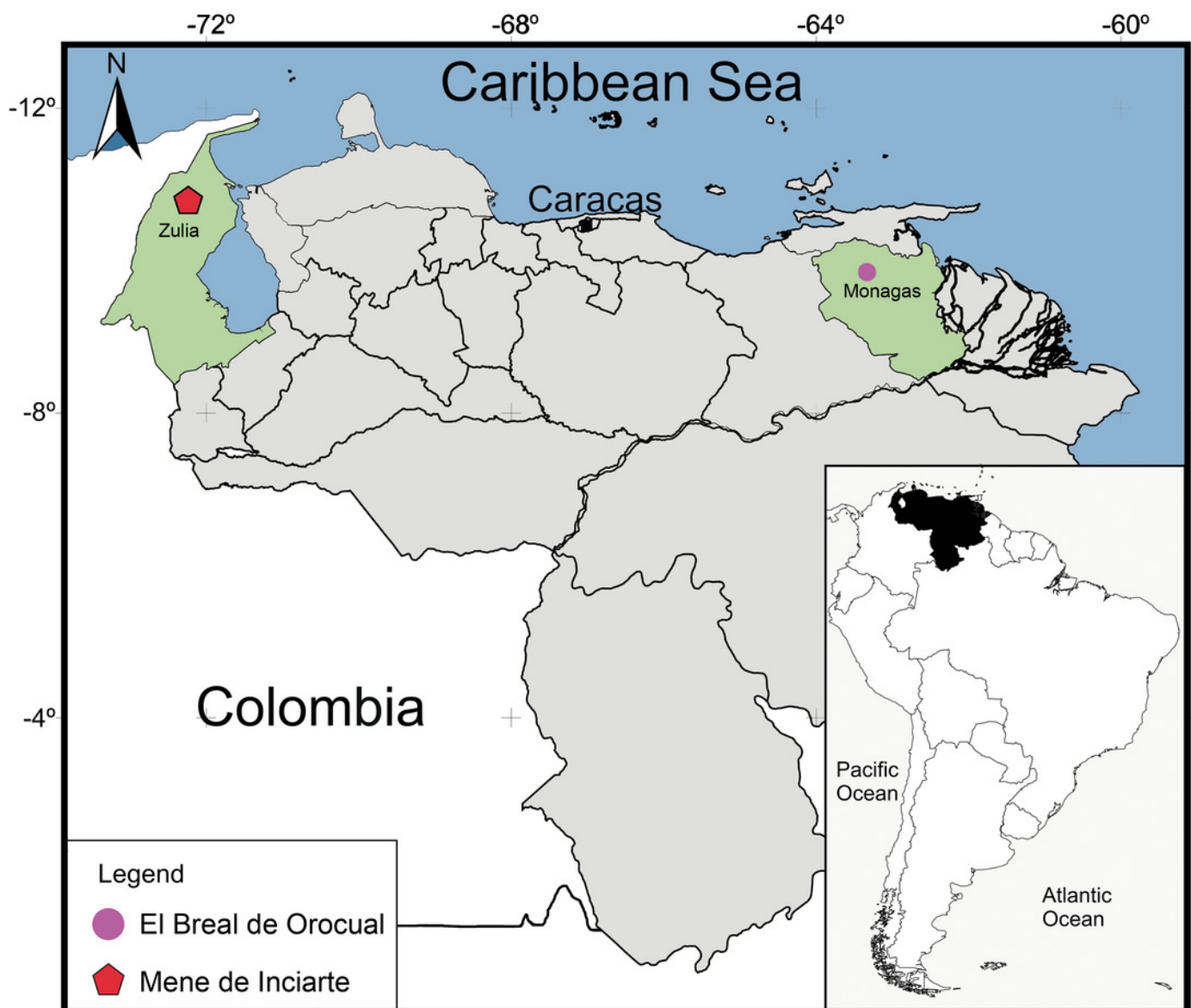


Figure 2

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, postzygapophysis; pz, prezygapophysis; sf, subcentral foramen; zgf, zygantral foramen; zh, zygosphene height; zw, zygosphene width. (Photography source: Silvio Onary)

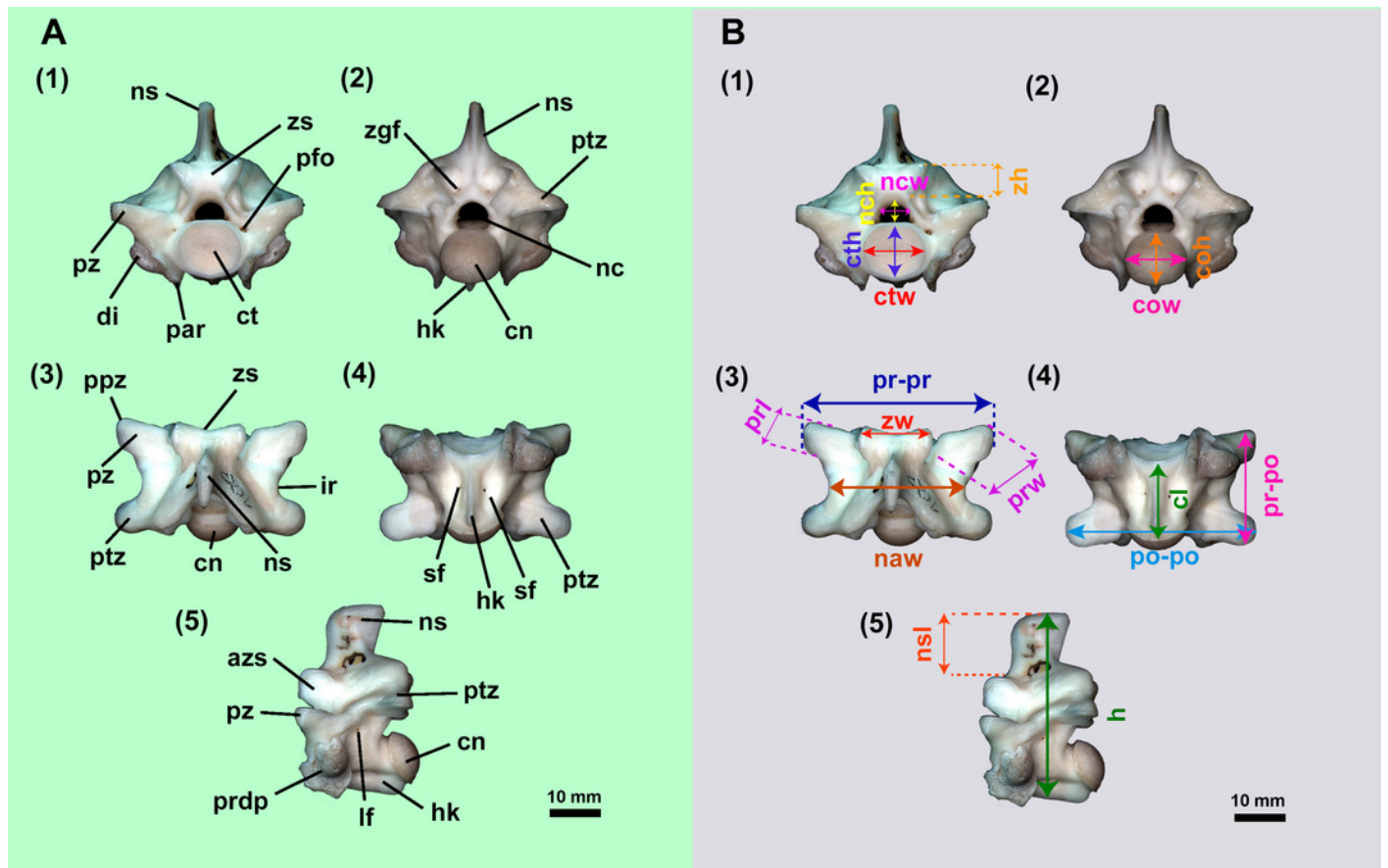


Figure 3

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)

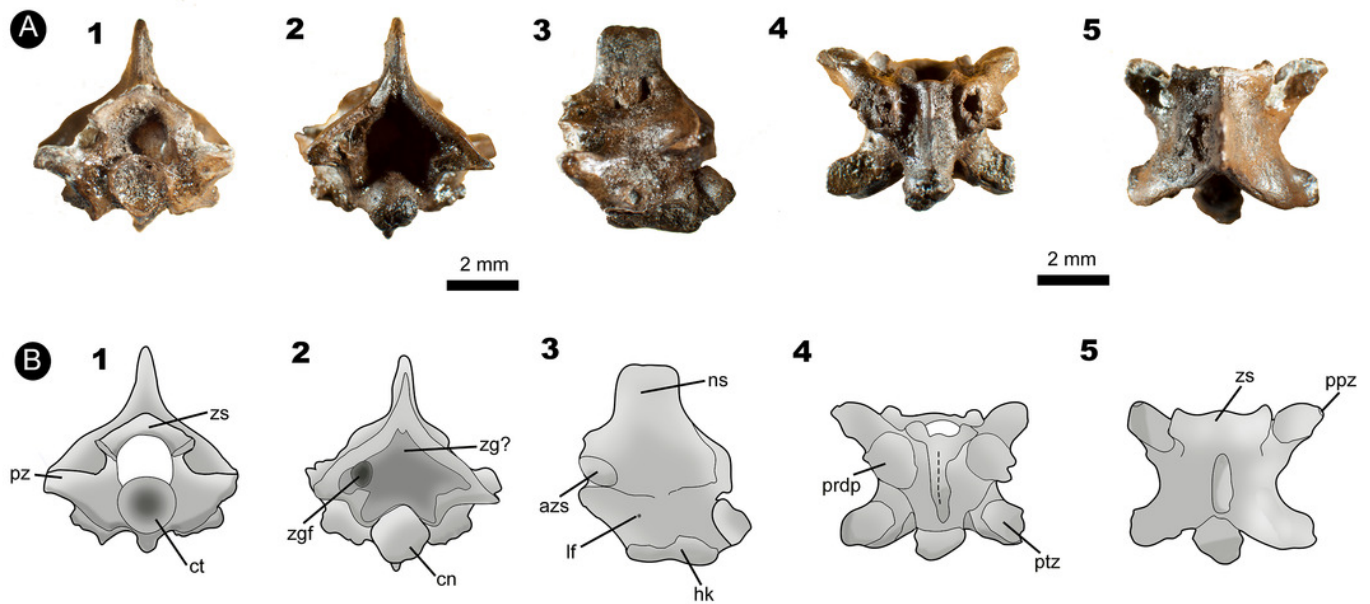


Figure 4

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)

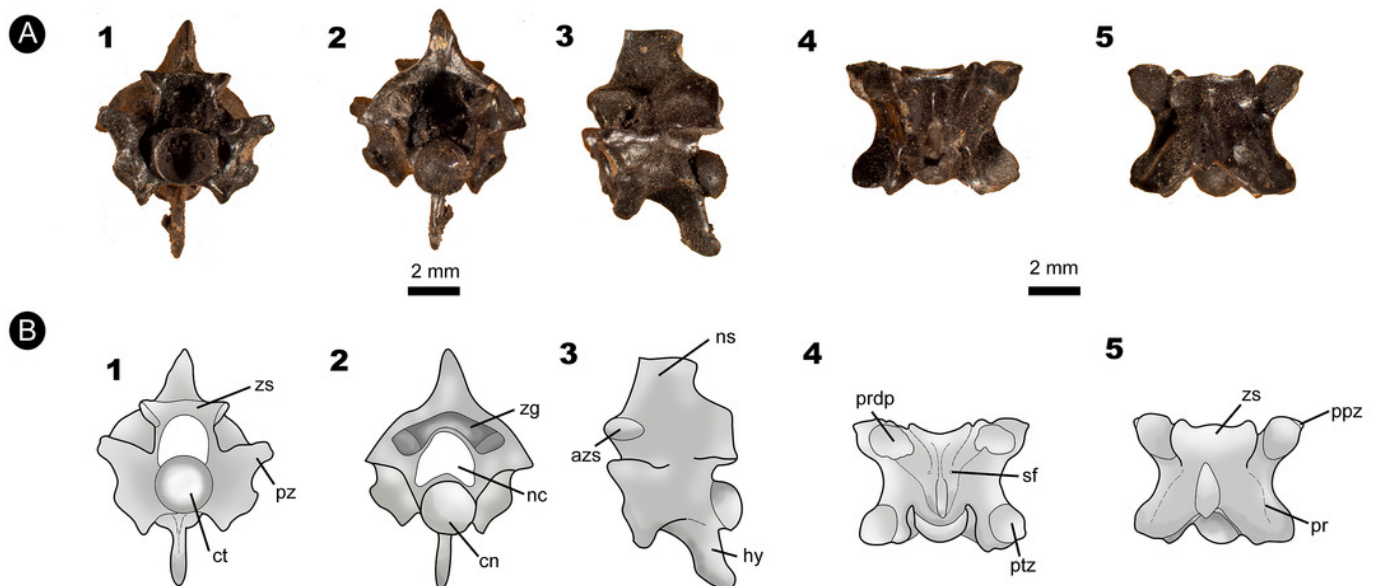


Figure 5

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)

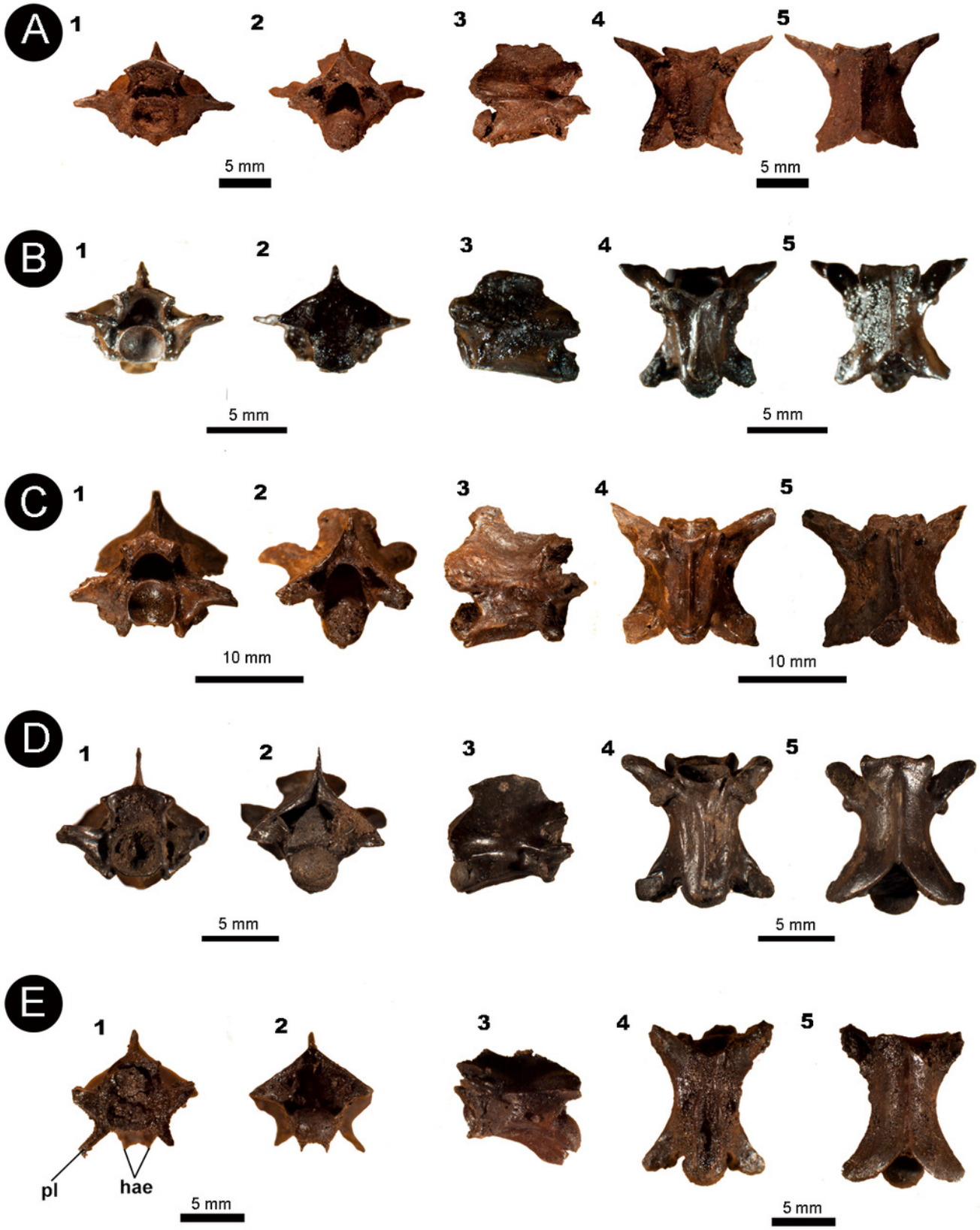


Figure 6

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)

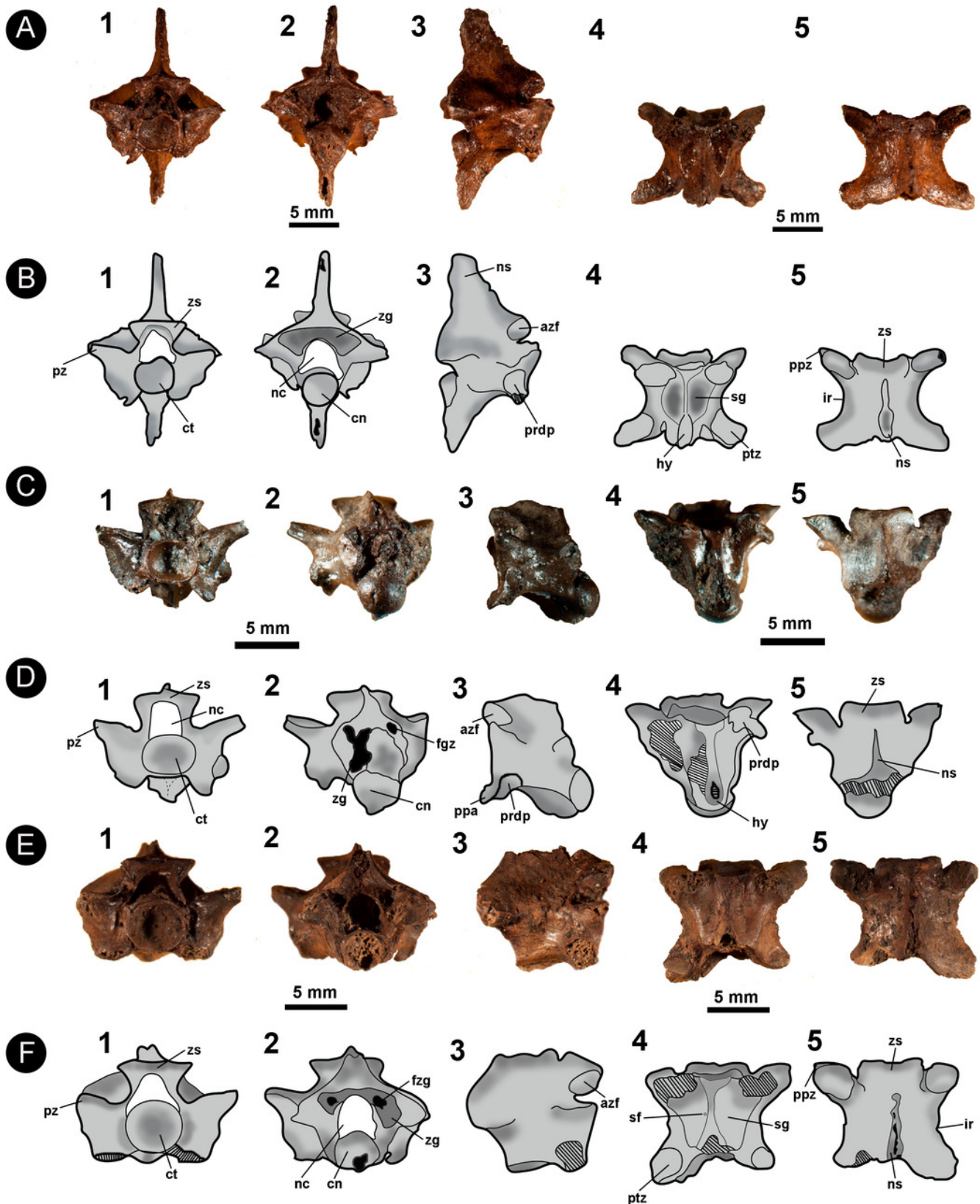


Figure 7

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)

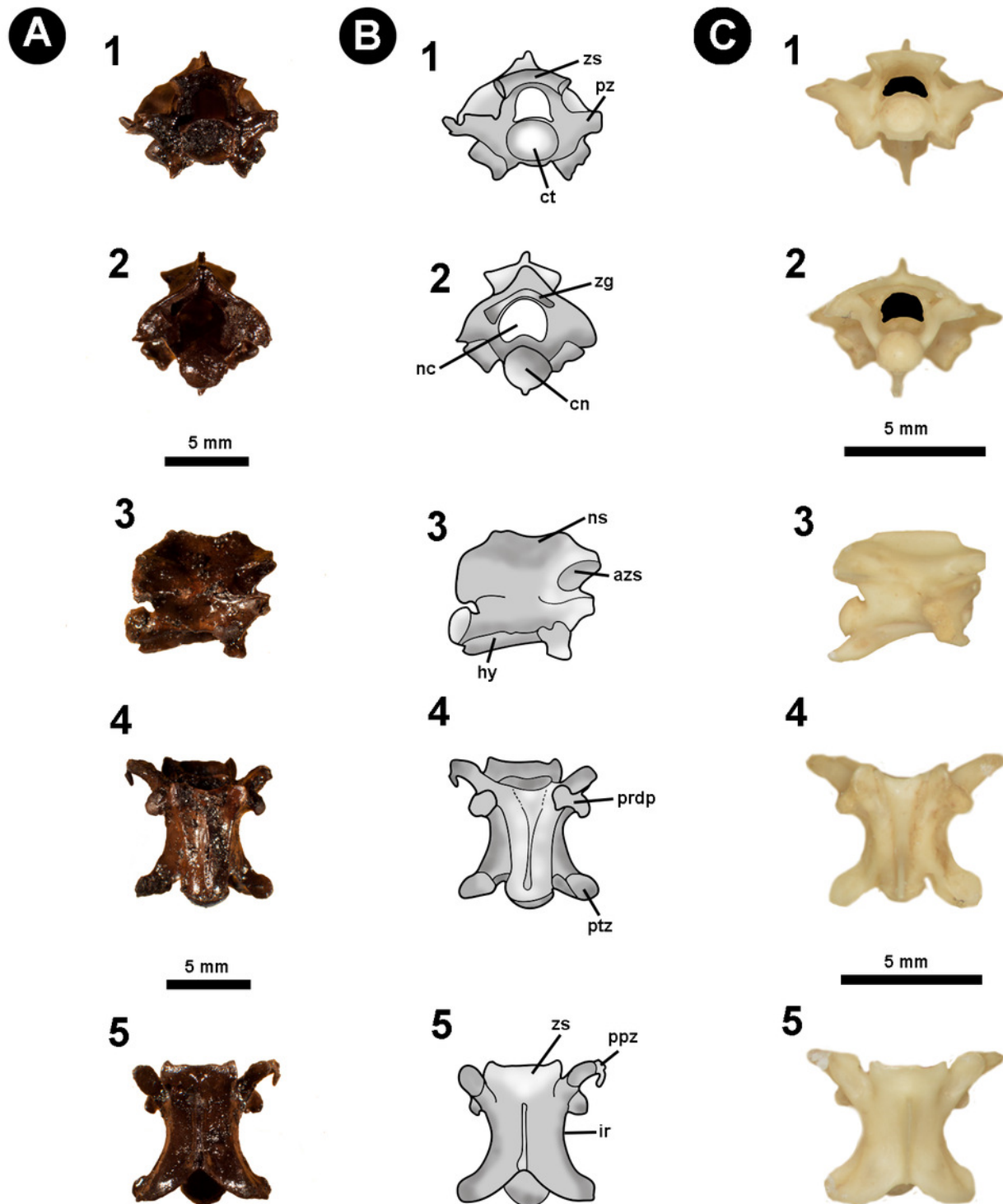


Figure 8

The historical biogeography of Colubroidea (sensu Zaher et al. 2009) throughout the American continent during the Eocene to Pleistocene, based on the fossil record. (A) representative maps of Eocene; (B) Miocene; and (C) Pleistocene of America.

(1) The oldest American "Colubridae" recorded from the late Eocene of Georgia, North America (Parmley & Holman, 2003); (2) "Colubridae" record from the early Miocene of Argentina, South America (Colhuehuapiense South America Land Mammal Age, SALMA) (Albino, 1996b); (3) 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); (4) First entrance of Colubroidea from North America to South America by dispersion via Central American island complex during the Miocene (Hoffstetter, 1967; Cadle & Greene, 1993; Albino, 1996b); (5) Second event of dispersion of Colubroidea from North America to South America during the Plio/Pleistocene (Head, Sánchez-Villagra & Aguilera, 2006); (6) Viperidae remains from Cucuruchu gravels, late Pleistocene of Venezuela (Head, Sánchez-Villagra & Aguilera, 2006); and (7) 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). 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 designed by Silvio Onary)

