

FOSSIL SNAKES FROM THE NEOGENE OF VENEZUELA (FALCÓN STATE)

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SYNOPSIS The first fossil snakes from Venezuela are described from three different Formations: *Colombophis* cf. *C. portai* and Boinae indet. from the Middle Miocene Socorro Formation, Boinae indet. from the Late Miocene Urumaco Formation and Viperidae indet. from the Pleistocene gravels at Cucuruchu. Although the Socorro and Urumaco Formations Boinae cannot be unambiguously referred to any particular taxa, the Venezuelan record, combined with the fauna from La Venta in Colombia, demonstrate that Boinae had achieved much of its more Northern distributions by the middle–late Miocene. The occurrence of a viperid in the Pleistocene gravels at Cucuruchu is consistent with a geologically young record of the lineage in South America.

KEY WORDS Urumaco, Miocene, Pleistocene, Caribbean, Viperidae, Boidae

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INTRODUCTION

The South American Cenozoic fossil snake record is paltry relative to other continents (e.g. Rage 1984; Albino 1996a), despite high species richness and endemism among extant snakes (e.g. Cadle 1987; Cadle & Green 1993).

The South American record includes boines and Boidae *sensu lato* from the Palaeogene to Miocene of Argentina (Albino 1987, 1990, 1996a, b), Brazil (Rage 2001), Bolivia (Rage 1991) and Colombia (Hoffstetter & Rage 1977; Hecht & LaDuke 1997), ‘anilids’ from the Palaeocene of Peru, Brazil and Bolivia (Rage 1981, 1991, 1998) and Miocene of

Colombia (Hoffstetter & Rage 1977; Hecht & LaDuke 1997) and taxa referred to Madtsoiidae from the Palaeogene of Argentina, Brazil (Simpson 1933; Albino 1992, 1996a; Rage, 1998) and possibly Bolivia (Rage 1991). The record of derived snakes is limited to colubroids described from the Miocene to Pleistocene of Argentina (Albino 1989, 1996c, Albino & Quintana 1992) and the Miocene of Colombia (Hoffstetter & Rage 1977). Here we provide the first description of Venezuelan fossil snakes (but see Estes & Báez 1985:196 and Aguilera 2004 for listed occurrences) based on isolated vertebrae from the Falcón Basin in North-western Venezuela. The Falcón Basin contains a series of sedimentary deposits from which numerous fossil vertebrates have been recovered (Sánchez-Villagra *et al.* 2003; Aguilera 2004 and references therein). Fossils reported here were found in three different Formations in north-western Venezuela ranging from the Middle Miocene to the Pleistocene.

The oldest Venezuelan fossil snakes were found in the Upper Member of the Socorro Formation, characterised by sandstones and limestones of Middle Miocene age, as established by studies of planktonic foraminifera (Díaz de Gamero 1989) and palynomorphs (Hambalek *et al.* 1994). As described in these works, the Socorro Formation is mostly represented by deltaic and fluvial deposits (Hambalek *et al.* 1994).

The Urumaco Formation preserves one of the richest and most diverse Neogene fossil records in South America (Aguilera 2004; Sánchez-Villagra & Aguilera 2006), including both the World's largest rodent, *Phoberomys* (Sánchez-Villagra *et al.* 2003) and the World's largest turtle, *Stupendemys* (Wood 1976). The snake fossil from Urumaco is from a locality in the upper member (late Miocene) that consists of abundant grey shale towards its superior part, frequently muddy and intercalated with thin sandstone horizons and levels of oxidation. The brown shale is scarcer; it is thinly bedded and contains vertebrate remains. The sand and clays are intercalated with sandstone and ferruginous horizons. The sandstone in the lower part is friable and of fine to medium grain size between shale, sometimes calcareous and with molluscs. The sandstone distribution in this member varies laterally. Close to the top there are important levels with vertebrates in diverse lithologies: brown and grey shales and sandstone with molluscs. The upper layer is thin, with abundant vertical burrows and numerous turtle remains. The palaeoenvironments are interpreted as inner sublittoral and coastal lagoon (Díaz de Gamero 1996).

The Pleistocene gravels from Cucuruchu (Bocquentin-Villanueva 1982) that produced the youngest fossil snake are not as extensive as the Urumaco Formation, but record a large vertebrate fauna including turtles, *Glyptodon* sp. and *Equus* (*Amerhippis*) sp. Additional data are provided in Gruhn & Bryan (1984).

Here, we describe the Venezuelan snakes and discuss both their systematic assignments and the biogeographical implications of their occurrences. Because the record consists of only incomplete vertebrae, we refrain from either erecting new taxa or referring unambiguously to known genera or species. Additional discoveries will be necessary to make lower level taxonomic assignments. Anatomical terminology follows Rage (1984) and Holman (2000) unless otherwise stated.

Institutional abbreviations

AMU-CURS, Colección Alcaldía de Urumaco, Rodolfo Sánchez.

UNEFM-CIAAP, Universidad Nacional Experimental Francisco de Miranda, Coro/Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro, Venezuela.

SYSTEMATIC PALAEOLOGY

OPHIDIA Brongniart, 1800
ALETHINOPHIDIA Nopcsa, 1923
ANILIIDAE Fitzinger, 1826

Colombophis cf. C. portai Hoffstetter & Rage, 1977 (Fig. 1A)

REFERRED MATERIAL. AMU-CURS 154, isolated prelocaal vertebra.

LOCALITY AND AGE. East of Capirote (11° 11' 32.9" N; 70° 11' 22.4" W), road to Quebrada Honda, Municipio Urumaco, Falcón State. Upper Member of Socorro Formation.

DESCRIPTION. The element is deformed but mostly complete, lacking only the left prezygapophysis. In anterior view (Fig. 1A.1), the condyle is distorted but appears to be approximately circular. There are no paracotylar foramina. The neural canal is low, wide and lunate in outline. The zygosphenes are thick, with a broadly convex dorsal margin and small, high-angled articular facets. The prezygapophysis is gracile and elongate. It is strongly angled dorso-laterally and extends beyond the dorsal margin of the zygosphenes. The synapophyses are tall with convex ventromedial margins that form the lateral margins of broad paralympathic channels with a slight squaring of the cotylar ventral margin forming the medial margins. The synapophyses do not extend ventrally to the level of the bottom of the cotyle. The posterior margins of the neural arch are elevated and laterally flared. The neural spine is a low ridge in outline.

In dorsal view (Fig. 1A.2), the zygosphenes are relatively narrow with a shallowly concave anterior margin. The prezygapophysis extends laterally from the body of the element. The articular facet of the prezygapophysis is wide, but its exact shape and orientation are distorted. A small, poorly defined accessory process extends laterally beyond the articular facet. There is only a short interzygapophyseal ridge (Johnson 1955) separating the pre- and postzygapophyses. The lateral margins of both the postzygapophyses and the neural arch are broadly convex. The posterior median is weakly developed. In ventral view (Fig. 1A.3), the centrum is wide and triangular in outline. The synapophyses are narrow and shallow, wide paralympathic channels separate them from the centrum. The haemal keel is broadly and poorly differentiated and capped by a small hypapophysis that is broad with a blunt posterior margin. In lateral view (Fig. 1A.4), the neural spine is restricted to the posterior border of the neural arch and the anterior margin of the spine forms a concave dorsal margin of the element, posterior to the zygosphenes. The postzygapophyseal articular facets are

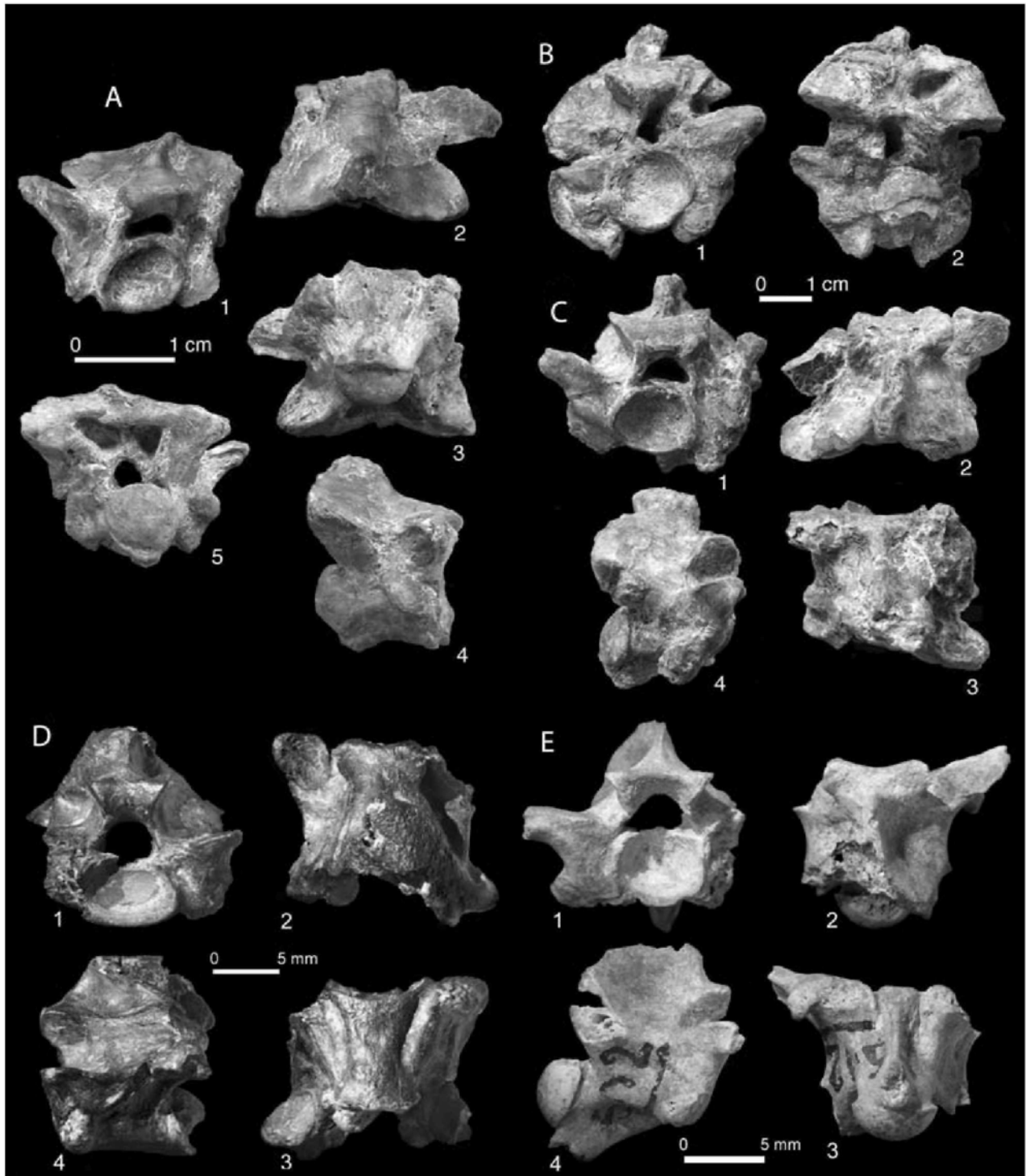


Figure 1 A, *Colombophis* cf. *C. portai* AMU-CURS 154 in (1) anterior, (2) dorsal, (3) ventral, (4) right lateral and (5) posterior views. B, Boinae indet. AMU-CURS 155 in (1) anterior and (2) posterior views. Note strong transverse shear. C, Boinae indet. AMU-CURS 156 in (1) anterior, (2) dorsal, (3) ventral and (4) right lateral views. D, Boinae indet. UNEFM-CIAAP-1477 in (1) anterior, (2) dorsal, (3) ventral and (4) left lateral views. E, Viperidae indet. UNEFM-CIAAP-1478 in (1) anterior, (2) dorsal, (3) ventral and (4) right lateral views. Scale-bars = 1 mm or 5 mm as indicated.

dorsolaterally angled. The haemal keel extends ventrally just anterior to the condyle. In posterior view (Fig. 1A.5), the zygantrum is deep and strongly divided. The posterior margins of both the neural spine and hypapophysis are broad and blunt. The diapophyseal articular facets of the synapophyses

are visible and strongly differentiated from the parapophyseal facets.

DISCUSSION. AMU-CURS 154 is morphologically indistinct from *Colombophis portai* (and *Anilius*, see below) from

the middle Miocene La Venta Formation of Colombia (Hoffstetter & Rage 1977) within the range of intracolumnar variation known for alethinophidian snakes (e.g. LaDuke 1991). Placement of *Colombophis* within Anilidae is problematic, as monophyly of extant taxa previously included in the clade is no longer accepted (e.g. Slowinski and Lawson 2002). Instead, Anilidae is unambiguously represented only by the monotypic *Anilius scytale* among living snakes. A large number of fossil taxa have been referred to Anilidae (e.g. Bailon 1988), but most characters used in these assignments are present in a wide range of fossorial and littoral taxa (e.g. Hoffstetter & Gasc 1969) and are not taxonomically diagnostic.

Colombophis was originally considered to be more similar to *Cylindrophis* than to *Anilius* (Hoffstetter & Rage 1977); however, the characters used in that assessment are subject to considerable variation (e.g. compare with Polly & Head 2004: fig. 2) and it is just as likely that *Colombophis* is closely related to, if not a junior synonym of, extant *Anilius*.

BOIDAE Gray 1825

BOINAE Gray 1825

Gen. et sp. indet. (Figs 1B–D)

REFERRED MATERIAL. AMU-CURS 155, 156, nine associated preloacal vertebrae from the Socorro Formation; UNEFM-CIAAP-1477, isolated preloacal vertebra from the Urumaco Formation.

LOCALITIES AND AGES. Socorro Formation: South East of 'Cerro Los Chivatos' (11° 59' 4" N; 70° 06' 40.7" W), Municipio Urumaco, Falcón State. Upper Member of Socorro Formation. This locality was discovered on 19 June 2004; other fossil specimens found in the same locality include a rostrum and mandible of the crocodile *Thecachamps* sp. (AMU-CURS unnumbered) and a femur of a Megatheriidae indet. (AMU-CURS unnumbered). Urumaco Formation: Corralito locality (11° 14' 57" N; 70° 16' 10" W), north to the town of Urumaco, Falcón State, Venezuela. Upper Member of the Urumaco Formation.

DESCRIPTION. All specimens from the Socorro Formation exhibit plastic deformation and shearing (Figs 1B.1 & 1B.2) and are poorly preserved, with gypsum invasion of the outer periosteum. Specimens are large, with centrum lengths between 14–18 mm. All specimens are robust. In anterior view (Figs 1B.1 & 1C.1) the cotyle is circular. The presence or absence of paracotylar foramina is not discernable. Cotylar ventrolateral processes are absent. The prezygapophyses are slightly angled dorsolaterally and possess small accessory processes. The synapophyses are well developed with distinct dia- and parapophyseal articular facets. The zygosphene is tall with a prominent median process. The neural canal is broad, large and subtriangular. In dorsal view (Fig. 1C.2) the neural spine has a uniform width and extends from the posterior median notch to the posterior margin of the zygosphene anteriorly. The interzygapophyseal ridges have straight lateral margins that are slightly posteromedially angled. Both pre- and postzygapophyses extend at right angles to the body of the element. In ventral view (Fig. 1C.3), a well-defined, tall haemal keel extends from the posterior margin of the cotyle to the anterior margin of the condyle.

The keel possesses a posteroventrally angled ventral margin in lateral view, but does not underhang the condyle as seen in vertebrae possessing hypapophyses. The synapophyses are transversely broad. In posterior view (Fig. 1B.2), the dorsal margins of the neural arch are broadly convex and arched. The zygantrum is deep and strongly divided with triangular articular recesses for the zygosphene. The cotyle is circular in outline. In lateral view (Fig. 1C.4), the neural spine is wide, robust and slightly angled posteriorly. The zygosphene articular facets are tall and ovoid in outline. The synapophyses are posteriorly angled. The condyle is underlain by a blunt, deep haemal keel, similar to the condition in *Boa constrictor*.

UNEFM-CIAAP-1477 from the Urumaco Formation is a preloacal vertebra lacking the right prezygapophysis and synapophyses, most of the condyle and the posterior margin of the right neural arch. In anterior view (Fig. 1D.1), the cotyle is ovoid and laterally elongate. A small paracotylar foramen is preserved on the left side of the element between the cotyle and the prezygapophysis. The prezygapophysis is low slung, with small articular facets that do not extend laterally far beyond the synapophysis. Dorsal to the cotyle, the neural canal is tall with triangular margins. The zygosphene is not as wide as the cotyle and possesses a thick, vertically elongate anterior margin. The neural spine is pathologically deformed. The right side of the spine is smooth and continuous with the rest of the element, however the left side consists of a large, irregularly shaped pathology that extends to the postzygapophysis.

In dorsal view (Fig. 1D.2), the interzygapophyseal ridges are posteromedially angled and possess comparatively straight lateral margins. The prezygapophyseal articular facet is short with a transversely straight anterior margin. The anterior margin of the zygosphene is shallowly concave. Behind the zygosphene, the lateral margins of the neural arch extend posterolaterally, giving the arch a triangular shape. The right side of the arch is dominated by the irregular pathology. The surface of the pathology is rugose and includes numerous holes that may represent drainage pits resulting from infection. Where preserved, the posterior margins of the neural arch extend beyond the prezygapophysis, which is approximately triangular in outline.

In ventral view (Fig. 1D.3), the margins of the cotyle are subequal. The articular facets of the synapophysis are small and laterally offset. The centrum is triangular in outline. A wide, flat haemal keel is present and defined by shallow paralympathic fossae. The condyle is incomplete, with only the right lateral margin preserved. The preserved margin is flared laterally beyond the margins of the centrum, giving the contact between the body of the centrum and the condyle a constricted appearance. Posteriorly, the postzygapophyseal articular facets are small, ovoid and posterolaterally angled.

In lateral view (Fig. 1D.4), the neural spine has a broadly concave anterior margin that extends dorsally from the anterodorsal surface of the zygosphene. The dorsal margin of the spine is flat. The neural arch is tall and the zygosphene is elevated well beyond the prezygapophysis in lateral aspect. The synapophyses are small and posterodorsally angled. A shallow pocket is present behind the prezygapophysis, formed by the interzygapophyseal ridge dorsally and a small ridge extending from the synapophysis ventrally. The presence of lateral foramina cannot be determined due to poor preservation.

DISCUSSION. Assignment to Boinae is based on the presence of a tall zygosphenes, triangular neural canal, low-slung prezygapophysis, paracotylar foramina and straight interzygapophyseal ridges. None of these characters are individually diagnostic for Boinae, but their occurrence in concert is unique to derived members of the clade (e.g. Rage 2001). Within Boinae, the character combination is present in the four extant South American genera *Boa*, *Corallus*, *Epicrates* and *Eunectes*. Assignment to these taxa is problematic, however, because no single boine genus or species is diagnosable on the basis of vertebral morphology and the deformation of the Socorro Formation specimens and the pathological distortion of UNEFM-CIAAP-1477 prohibit comparisons on the basis of general similarity. Comparisons with the fossil South American boines *Chubutophis*, *Waincophis* and *Hechtophis* (Albino 1993, 1996b; Rage 2001) are similarly limited, although the dorsoventrally compact morphology of the latter two taxa distinguishes them from the Venezuelan records. All specimens compare favourably with *Eunectes* and *Boa* among extant boines on the basis of large size, but are not outside the maximum size ranges of *Epicrates* or *Corallus*. Differences between the Socorro and Urumaco specimens, especially differences in cotyle shape, haemal keel morphology and neural spine length (Figs 1 B–D), suggest taxonomic differences between the Formations. Broader surveys of intracolumnar and individual variation in vertebral morphology among boine taxa are required in order to corroborate this observation.

Alethinophidia gen et sp. indet.

REFERRED MATERIAL. AMU-CURS 157, isolated preloacal vertebra.

LOCALITY AND AGE. South East of 'Cerro Los Chivatos' (11° 59' 4" N; 70° 06' 40.7" W), Municipio Urumaco, Falcón State. Upper Member of Socorro Formation.

DESCRIPTION. The specimen is small relative to boine specimens (centrum length 8 mm). In anterior view, the cotyle is circular. A well-developed paracotylar foramen is present on the right side of the element. The neural canal is large and subtriangular. The prezygapophyses are not preserved beyond bases, but the medial margins of the articular facets are preserved, indicating a dorsolateral angle to the processes. The neural spine is broken, but the preserved base is elevated, indicating a tall spine.

In dorsal view, the element is broad. The interzygapophyseal ridges do not preserve enough lateral margin to determine their shape. The neural spine base is short and far posterior to the zygosphenes. The zygosphenes possesses a concave anterior margin. In ventral view, the centrum is broad and triangular. A short, broad haemal keel is present just anterior to the condyle. Subcentral paralympathic fossae and paracotylar accessory processes are not preserved. In lateral view, the neural spine is restricted to the posterior region of the element. The anterior margin forms a concave arc as in *Colombophis* and *Anilius*. Posterior margins of the neural arch are incomplete.

DISCUSSION. The specimen differs from those referred to Boinae in having a shorter neural spine that does not extend to the posterior margin of the zygosphenes anteriorly and in having a broad, poorly defined haemal keel. It shares the

short, restricted neural spine and stout hypapophysis with *Colombophis*, but is much taller and possesses a more circular cotyle and condyle than *Colombophis* or *Anilius*. Because the specimen is so poorly preserved, it cannot be unambiguously referred to either taxon.

CAENOPHIDIA Hoffstetter, 1939

COLUBROIDEA Oppel, 1811

VIPERIDAE Oppel, 1811

Gen. et sp. indet. (Fig. 1E)

REFERRED MATERIAL. UNEFM-CIAAP-1478, isolated preloacal vertebra.

LOCALITY AND AGE. Cucuruchu, 10–15 km East of Coro and 2 km northeast of Tara Tara, Municipio Colina, Falcón State. Late Pleistocene.

DESCRIPTION. The specimen is a preloacal vertebra. It is incomplete, with the left prezygapophysis and synapophysis, postzygapophyses and distal portions of the neural spine and hypapophysis missing. In anterior view (Fig. 1E.1), the cotyle is circular. Anterior openings of paralympathic channels are visible as notches in the ventral margin of the cotyle. The neural canal is subtriangular, low and as wide as the cotyle. The zygosphenes is wide with a broadly convex dorsal margin. The prezygapophysis is well developed, with approximately horizontal articular facets. The broken base of a large accessory process is present just below the articular facet. The right diapophysis is the only preserved portion of the synapophyses on the specimen. It is large, ventrolaterally angled and differentiated from the body of the centrum.

In dorsal view (Fig. 1E.2), the anterior margin of the zygosphenes is strongly concave. The neural spine originates on the dorsal surface of the zygosphenes. The spine is elongate and thin with a uniform thickness in cross section. The interzygapophyseal ridge is smoothly concave with the apex of curvature at the anteroposterior midpoint of the neural arch. The prezygapophysis is anterolaterally angled with an elongate, ovoid articular facet. A small portion of the prezygapophyseal accessory process projects beyond the articular facet.

In ventral view (Fig. 1E.3), the centrum is elongate. A prominent haemal is present at the midline of the centrum and is defined laterally by two deep paralympathic channels. The keel is capped by a large hypapophysis that is ovoid in cross section. The preserved base of the parapophysis indicates that it was wide and probably elongate, as in all viperids. The diapophysis is approximately hemispherical in outline, with a posterior margin that includes a wide lip extending posterolaterally beyond the synapophysis. Posteriorly, the condyle is circular and comparatively large.

In lateral view (Fig. 1E.4), the element is anteriorly angled. The preserved margins of the neural spine indicate that it was well-developed and probably tall. The posterior margins of the neural arch are tall and elevated beyond the zygosphenes. The hypapophysis is large and posteroventrally angled, with the anterior margin extending ventrally in a wide, concave arc from the ventral margin of the cotyle. The posterior margin of the hypapophysis originates at the ventral

margin of the condyle and descends at a slightly steeper angle than the anterior margin. Although the hypapophysis is broken, the angles of the anterior and posterior margins and the distance between them indicate that the process was elongate.

REMARKS. Assignment of UNEFM-CIAAP-1478 to Viperidae is based on the presence of a well-developed, posteroventrally angled hypapophysis and the combined occurrence of a comparatively large cotyle and condyle, well-developed parapophyses (inferred) and a low, wide neural canal. Within Viperidae, it is not possible to unambiguously assign the specimen to generic or specific levels or either Viperinae *sensu lato* or Crotalinae, because crotaline vertebral morphology is poorly known and no discrete axial skeletal character differentiates the clades (e.g. Szyndlar & Rage 1999). In addition, there is considerable intracolumnar variation in viperid vertebral shape (Thireau 1967), which restricts lower-level taxonomic assignments based on isolated vertebrae. All New World viperids are crotaline, but we refrain from invoking geography in making taxonomic assignments, because it prohibits subsequent biogeographical reconstructions (Bell *et al.* 2004).

DISCUSSION

The occurrence of *Colombophis* cf. *C. portai* in the Socorro Formation provides a Northeastern range extension for the taxon and indicates at least a general ecological similarity between the La Venta depositional systems in Colombia and the Socorro Formation in Venezuela. Extant *Anilius* and *Cylindrophis* are cryptic, littoral specialists that favour covered forest floors (Greene 1997; Starace 1998), a habitat preference that can be inferred for *Colombophis* in the absence of evidence to the contrary and suggests the presence of canopied forests proximal to Socorro depositional environments.

The Socorro and Urumaco Formations boines contribute to a fossil record of the lineage that is reported to extend into the Palaeocene (e.g. Rage 2001), as well as reports of Boidae *sensu lato* in the Cretaceous (Albino 1996a). Biogeographical distributions of extant Boinae are considered to be the result of vicariance driven by Gondwanan fragmentation during the Early Cretaceous (e.g. Underwood & Stimson 1990; Kluge 1991). However, no fossils referable to Boinae are known prior to the Palaeocene, requiring a 45–50 million year unrecovered history for this hypothesis to be corroborated (see also Austin 2000). Much of the Palaeogene boine record is from southern South America (Albino 1996a, b), whereas most extant taxa have a more northerly distribution. Although the Socorro and Urumaco Formations' boine specimens cannot be unambiguously referred to any extant taxa, the Venezuelan record, combined with the fauna from La Venta, demonstrate that, to at least higher orders, Boinae had achieved much of its more northern distributions by the middle–late Miocene.

The occurrence of a viperid in the Pleistocene gravels at Cucuruchu is consistent with a geologically young record of the lineage in South America. Globally, the oldest fossil viperids are represented by isolated vertebrae from the early Miocene of Weisenau (MN 1), Germany (Szyndlar & Böhme 1993; Szyndlar & Rage 1999) and the Harrison Formation

(Arikareen), Nebraska (Holman 1981). Hypotheses of viperid biogeographical origins are complex and include either an African or Asian late Palaeogene origin with Tethyan sea-level changes mediating dispersal patterns (e.g. Marx & Rabb 1965; Lenk *et al.* 2001). Within Viperidae, the oldest definitive crotaline record consists of multiple isolated maxillae from the early late Miocene (MN 9) of Gristev, Ukraine (Ivanov 1999). Crotalines are considered to have dispersed from Asia (Ivanov 1999) into North America and then South America (Cadle 1987).

The timing of dispersal into South America is poorly constrained. The only other fossil records of South American viperids is from the latest Pleistocene of Bolivia (Hoffstetter 1968, although see Albino, 1989 'Colubroidea indet.' for a possible Pliocene occurrence). Conversely, the fossil record of colubrids extends into the middle Miocene of Argentina (Albino 1996c) and Colombia (Hoffstetter & Rage 1977). The fossil record of South American snakes is poor, but the absence of viperids from older faunas that include other derived snakes is inconsistent with hypotheses of pre-Pliocene faunal exchange of viperids between South and Central/North America (Vanzolini & Heyer 1985; Cadle & Greene 1993). This combined with further examination of the Venezuelan Neogene may indicate independent dispersals of snakes into South America during the Neogene, as opposed to a larger, single biogeographical event.

ACKNOWLEDGEMENTS

For access to specimens, we thank Marcia López (CIAAP) and Rodolfo Sánchez (AMU-CURS). We also thank Rodolfo Sánchez (Alcaldía de Urumaco, Sección de Paleontología) for permission to work in Urumaco and the Instituto de Patrimonio Cultural in Caracas for permission to conduct palaeontological fieldwork. We thank Aurelio Pulgar and Cathy Villalba for help and camaraderie in the field, as well as Jasmin Winkler, who found the Socorro snakes. Dennis Parmley and Jean-Claude Rage provided helpful reviews of the manuscript. Fieldwork was financially supported by the Committee for Research and Exploration of the National Geographic Society (Grant 7600-04 to MRSV). Research on the snake specimens was funded by a National Science Foundation Bioinformatics Postdoctoral Fellowship (NSF 98-162, award number 0204082) to J.J.H.

REFERENCES

- Aguilera, O. A. 2004. *Tesoros paleontológicos de Venezuela: Urumaco, Patrimonio Natural de la Humanidad*. Editorial Arte: Caracas, 148 pp.
- Albino, A. M. 1987. Un nuevo Boidae (Reptilia: Serpentes) del Eoceno temprano de la Provincia del Chubut, Argentina. *Ameghiniana* **24**: 61–66.
- 1989. Primer registro de Colubroidea (Reptilia: Serpentes) de Argentina (edad Montehermosense S.L., Plioceno). *Ameghiniana* **25**: 281–287.
- 1990. Las serpientes de São José de Itaboraí (Edad Itaboraiense, Paleoceno medio), Brasil. *Ameghiniana* **27**: 337–342.
- 1992. Primer registro de un Boidae (Reptilia: Serpentes) en el Plioceno de la Provincia de Buenos Aires, Argentina. *Pesquisas* **19**: 106–109.
- 1993. Snakes from the Paleocene and Eocene of Patagonia (Argentina): Paleocology and coevolution with mammals. *Historical Biology* **7**: 51–69.

- 1996a. The South American fossil Squamata (Reptilia: Lepidosauria). Pp. 185–202 in G. Arratia (ed.) *Contributions of southern South America to Vertebrate Paleontology. Münchner Geowissenschaften Abhandlungen A* 30.
- 1996b. Snakes from the Miocene of Patagonia (Argentina). Part I: The Booidea. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 199: 417–434.
- 1996c. Snakes from the Miocene of Patagonia (Argentina). Part II: The Colubroidea. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 200: 353–360.
- & Quintana, C. A. 1992. Los Colubridae (Reptilia: Serpentes) del Chapadmalalense y Uquiense (Plioceno tardío-Pleistoceno temprano?) de la Provincia de Buenos Aires, Argentina. *Ameghiniana* 29: 125–133.
- Austin, C. C. 2000. Molecular phylogeny and historical biogeography of Pacific Island Boas (*Candoia*). *Copeia* 2000: 341–352.
- Bailon, S. 1988. Un Aniliidé (Reptilia, Serpentes) dans le Pliocène supérieur européen. *Comptes Rendus de l'Académie de Sciences, Série 2* 360: 1255–1258.
- Bell, C. J., Head, J. J. & Mead, J. I. 2004. Synopsis of the herpetofauna from Porcupine Cave. Pp. 117–126 in A. D. Barnosky (ed.), *Biodiversity Response to Climate Change in the Middle Pleistocene. The Porcupine Cave Fauna from Colorado*. University of California Press: Berkeley, CA.
- Bocquentin-Villanueva, J. 1982. Notas sobre la fauna del Pleistoceno superior de Taima–Taima depositada en el Museo del hombre de Coro, Estado Falcón, Venezuela. *Acta Científica Venezolana* 33: 479–487.
- Brongniart, A. 1800. Essai d'une classification naturelle des reptiles. 1ère partie. Etablissement des Orders. *Bulletin des Sciences, par la Société Philomatique, Paris* 11: 81–82.
- Cadle, J. E. 1987. Geographic distribution: problems in phylogeny and zoogeography. Pp. 77–105 in R. A. Seigel, J. T. Collins & S. S. Novak (eds) *Snakes: Ecology and Evolutionary Biology*. McGraw-Hill Publishing: New York.
- & Greene, H. W. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. Pp. 281–293 in R. E. Ricklefs & D. Schluter (eds) *Species diversity in ecological communities. Historical and geographical perspectives*. University of Chicago Press: Chicago and London.
- Díaz de Gamero, M. L. 1989. El Mioceno Temprano y Medio de Falcón Septentrional. *GEOS* 29: 25–35.
- 1996. The changing course of the Orinoco River during the Neogene: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123: 385–402.
- Estes, R. & Baez, A. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: evidence for interchange? Pp. 139–197 in F. G. Stehli & S. D. Webb (eds) *The Great American Biotic Interchange*. Plenum Press: New York and London.
- Fitzinger, 1826. *Neue Klassifikation der Reptilien nach ihren Natürlichen Verwandtschaften-Tafel und einem Verzeichnisse der Reptilien-Sammlung des kaiserlich-Königlichen*. Zoologischen Museum zu Wien. J. G. Hübner, Wien, 66 pp.
- Gray, J. E. 1825. A synopsis of the genera of Reptilia and Amphibia. *Annals of Philosophy* 10: 193–217.
- Greene, H. W. 1997. *Snakes, the evolution of mystery in nature*. University of California Press: Berkeley, CA.
- Gruhn, R. & Bryan, A. L. 1984. The record of Pleistocene megafaunal extinction at Taima-Taima, Northern Venezuela. Pp. 128–138 in P. S. Martin & R. G. Klein (eds) *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press: Tucson, AZ.
- Hambalek, N., Rull, V., de Digiaco, E. de. & Díaz de Gamero, M. L. 1994. Evolución paleoecológica y paleoambiental de la secuencia del Neógeno en el Surco de Urumaco, Estado Falcón. Estudio palinológico y litológico. *Boletín de la Sociedad Venezolana de Geología* 19: 7–19.
- Hecht, M. K. & LaDuke, T. C. 1997. Limbless tetrapods. Pp. 95–99 in R. F. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn (eds) *Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia*. Smithsonian Institution Press: Washington, DC.
- Hoffstetter, R. 1939. Contribution a l'étude des Elapidae actuels et fossiles et de l'ostéologie des ophidiens. *Archives du Muséum d'Histoire Naturelle de Lyon* 15: 1–78.
- 1968. Nuapua, un gisement de vertebres Pleistocenes dans le Chaco Bolivien. *Bulletin du Muséum National d'Histoire Naturelle, Série 2* 40: 823–836.
- & Gasc, J.-P. 1969. Vertebrae and ribs of modern reptiles. Pp. 201–310 in C. Gans (ed.) *Biology of the Reptilia, Volume 1: Morphology*. Academic Press: London.
- & Rage, J.-C. 1977. Le gisement de Vertebres Miocenes de La Venta (Colombie) et sa faune de Serpentes. *Annales de Paléontologie (Vertebres)* 63: 161–190.
- Holman, J. A. 1981. A herpetofauna from an eastern extension of the Harrison Formation (Early Miocene: Arikareean), Cherry County, Nebraska. *Journal of Vertebrate Paleontology* 1: 49–56.
- 2000. *Fossil snakes of North America. Origin, evolution, distribution, paleoecology*. Indiana University Press: Indianapolis, IN.
- Ivanov, M. 1999. The first European pit viper from the Miocene of Ukraine. *Acta Palaeontologica Polonica* 44: 327–334.
- Johnson, R. G. 1955. The adaptive and phylogenetic significance of vertebral form in snakes. *Evolution* 9: 367–388.
- Kluge, A. G. 1991. Boine snake phylogeny and research cycles. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 178: 1–58.
- LaDuke, T. C. 1991. The fossil snakes of Pit 91, Rancho La Brea, California. *Natural History Museum of Los Angeles County Contributions in Science* 424: 1–28.
- Lenk, P., Kalyabina, S., Wink, M. & Jorger, U. 2001. Evolutionary relationships among the true vipers (Reptilia: Viperidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 19: 94–104.
- Marx, H. & Rabb, G. B. 1965. Relationships and zoogeography of the viperine snakes (Family Viperinae). *Fieldiana Zoology* 44: 161–225.
- Nopsca, F. 1923. *Eidosaurus* und *Pachyophis*, Zwei neue Neocom-Reptilien. *Palaeontographica* 55: 97–154.
- Oppel, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien als Prodom einer Naturgeschichte derselben*. Joseph Lindauer Verlag: München.
- Polly, P. D. & Head, J. J. 2004. Maximum-likelihood identification of fossils: taxonomic identification of Quaternary marmots (Rodentia, Mammalia) and identification of vertebral position in the pipe snake *Cylindrophis* (Serpentes, Reptilia). Pp. 197–222 in A. M. T. Elewa (ed.) *Morphometrics – applications in biology and paleontology*. Springer-Verlag: Berlin, Heidelberg, New York, 263 pp.
- Rage, J.-C. 1981. Les contiens péri-atlantiques au Crétacé supérieur: migrations des faunes continentales et problèmes paléogéographiques. *Cretaceous Research* 2: 65–84.
- 1984. *Encyclopedia of Paleoherpétology, part 11, Serpentes*. Gustav Fischer Verlag: Stuttgart.
- 1991. Squamate reptiles from the early Paleocene of the Tiupampa area (Santa Lucía Formation), Bolivia. Pp. 503–508 in R. Suárez-Soruco (ed.) *Fósiles y facies de Bolivia. Vol. 1. Vertebrados*. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos: Santa Cruz.
- 1998. Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part I, Madtsoiidae, Aniliidae. *Palaeovertebrata, Montpellier* 27: 109–144.
- 2001. Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part II, Boidae. *Palaeovertebrata, Montpellier* 30: 111–150.
- Sánchez-Villagra, M. R. & Aguilera, O. A. 2006. Neogene vertebrates from Urumaco, Falcón State, Venezuela: diversity and significance. *Journal of Systematic Palaeontology* 4: 213–220.
- , — & Horovitz, I. 2003. The anatomy of the World's largest extinct rodent. *Science* 301: 1708–1710.

- Simpson, G. G.** 1933. A new fossil snake from the *Notostylops* beds of Patagonia. *Bulletin of the American Museum of Natural History* **67**: 1–22.
- Slowinski, J. B. & Lawson, R.** 2002. Snake phylogeny: evidence from nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* **24**: 194–202.
- Starace, F.** 1998. *Guide des serpents et amphibènes de Guyane*. IBIS Rouge: Guadeloupe, Guyane, 449 pp.
- Szyndlar, Z. & Böhme, W.** 1993. Die fossilen Schlangen Deutschlands: Geschichte der Faunen und ihrer Erforschung. *Mertensiella* **3**: 318–431.
- & **Rage, J.-C.** 1999. Oldest fossil vipers (Serpentes: Viperidae) from the Old World. *Kaupia, Darmstädter Beiträge zur Naturgeschichte* **8**: 9–20.
- Thireau, M.** 1967. Contribution a l'étude de la morphologie caudale et de l'anatomie vertébrale et costale des genres *Atheris*, *Actractaspis*, et *Causus* (Viperidés de l'Ouest africain). *Bulletin du Muséum National Histoire Naturelle, Paris, Series 2* **39**: 454–470.
- Underwood, G. & Stimson, A. F.** 1990. A classification of pythons (Serpentes, Pythoninae). *Journal of Zoology, London* **221**: 565–603.
- Vanzolini, P. E. & Heyer, W. R.** 1985. The American herpetofauna and the interchange. Pp. 475–487 in F. G. Stehli & S. D. Webb (eds) *The Great American Biotic Interchange*. Plenum Press: New York and London.
- Wood, R. C.** 1976. *Stupendemys geographicus*, the World's largest turtle. *Breviora* **436**: 1–31.