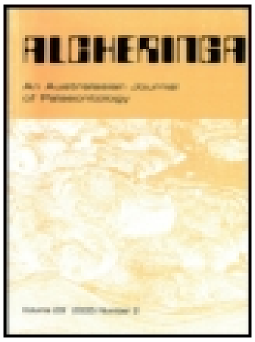

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The northernmost South American fossil record of *Boa constrictor* (Boidae, Boinae) from the Plio–Pleistocene of El Breal de Orocual (Venezuela)

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Boa constrictor is an extant boid widely distributed through the neotropical region, from the north of Central America to central Argentina. The fossil record of the species includes examples from several localities across the Americas that extend beyond the current distribution of the species. Here we report the first Plio–Pleistocene fossils of *Boa* from Monagas state, Venezuela. The material comes from El Breal de Orocual (Maturín municipality), which is an inactive tar seep deposit emplaced within the Mesa Formation. The specimens consist of two isolated anterior trunk vertebrae, an articulated sequence of six mid-trunk vertebrae and two posterior trunk vertebrae. The vertebrae are attributed to *B. constrictor* based on the following features: robust and high vertebrae; thick zygosphene with a notched or concave anterior edge; presence of a paracotylar, subcentral and lateral foramina; marked parasagittal ridges; epizygapophyseal process evident on the dorsal surface of the postzygapophyseal articular facets and high blade-like neural spine. The presence of *B. constrictor* in northern of Venezuela indicates a palaeoenvironment probably like savanna crossed by rivers with riparian forests, and suggests the predominance of a mesothermal climate with a moderate rainfall.

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Key words: *Boa constrictor*, Boinae, late Pliocene–early Pleistocene, Venezuela, El Breal de Orocual.

BOINAE is a well-supported clade among the Macrostomata snakes. It includes *Boa* Linnaeus, 1758, *Corallus* Daudin, 1803, *Epicrates* Wagler, 1830 and *Eunectes* Wagler, 1830, distributed in the neotropics (Kluge 1991, Lee & Scanlon 2002, Burbrink 2005, Noonan & Chippindale 2006, Pyron *et al*. 2014a, Pyron *et al*. 2014b, Caldwell *et al*. 2015). *Boa* is considered monotypic (*Boa constrictor*); however, there are seven subspecies formally recognized by external morphology: *B. constrictor constrictor* Linnaeus, 1758; *B. constrictor orophias* Linnaeus, 1758; *B. constrictor mexicana* Jan, 1863; *B. constrictor occidentalis* Philippl, 1873; *B. constrictor ortonni* Cope, 1877; *B. constrictor amarali* Stull, 1932; and *B. constrictor nebulosa* Lazell, 1964 (Uetz & Hošek 2015). Molecular studies based on sequence divergences also admit another species: *Boa imperator* (Hynková *et al*. 2009, Reynolds *et al*. 2014). Even with such evidence suggesting wide divergence within *Boa*, no subdivisions are currently supported by osteological data.

Boa constrictor has individuals reaching 2–4 m long, distributed from northern Mexico to central Argentina, occupying a diverse range of habitats, such as deserts, tropical woodlands and savannas (Waller & Micucci 1993, Henderson *et al*. 1995, Albino 2011). It has a terrestrial and subarboreal lifestyle, with a generalist diet, inhabiting plains and sub-mountainous regions (less than 1500 m; Waller & Micucci 1993, Henderson *et al*. 1995, Henderson 2004, Albino 2011).

Many *Boa* fossil records come from South American localities (Albino 1993, Albino & Carlini 2008, Camolez & Zaher 2010), with single reports from North America (Auffenberg 1963 after Kluge 1988 and Albino 2011) and Central America (Head *et al*. 2012). The North American fossils comprise isolated precloacal vertebrae from the early Miocene (early Hemingfordian *ca* 18.5 Ma) of the Thomas Farm Fauna in Gilchrist County, Florida (Auffenberg 1963). Originally, these fossils were described as *Neurodromicus stanolseni* and *Neurodromicus barbouri* (Vanzolini 1952), which were revised and grouped into the species *Pseudoepicrates stanolseni* (Auffenberg 1963), but later synonymized with the extant species *Boa constrictor* (Kluge 1988, Albino 2011).

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The probable earliest vertebral remains of the genus in South America derive from the early Eocene of Gran Barranca, Argentina (Albino 1993). The material was tentatively attributed to *Boa* sp. (Albino 1993) and later re-evaluated, providing stronger support for the allocation to this genus (Albino & Carlini 2008). In Quaternary strata, vertebrae were reported from the Upper Pleistocene of the Arroyo Toropí Formation, Argentina (Albino & Carlini 2008). Caves and shelters of central and northern of Brazil have yielded several vertebrae and cranial elements, evidencing the broad distribution of *Boa* during the Late Pleistocene (Camolez & Zaher 2010). Although the *Boa* fossil record is becoming more extensive, occurrences are still concentrated in the central (Camolez & Zaher 2010) and southern portions of South America (Albino 1993, Albino & Carlini 2008).

This paper aims to describe vertebral remains of *Boa constrictor* from upper Pliocene–lower Pleistocene deposits of El Breal de Orocual, Venezuela, and discuss their significance for the palaeoenvironmental and palaeobiogeographic record of South America.

Geological setting

The vertebral remains come from El Breal de Orocual, at locality ORS16 of Solórzano *et al*. (2015), situated 20 km from Maturín municipality, Monagas state, northeastern Venezuela (Fig. 1). The locality is an inactive tar seep deposit emplaced within the Mesa Formation (Hackley *et al*. 2006, Rincón *et al*. 2009). The tar pit lacks an absolute date, but the recovered palaeofaunal assemblage of 30 identified taxa, especially the occurrence of *Smilidon gracilis* (Carnivora, Felidae) and cf. *Chapalmatherium* (Rodentia, Hydrochoeridae), suggests at least a late Pliocene–early Pleistocene age for the deposit (Rincón *et al*. 2009, Solórzano *et al*. 2015). Despite the age attributed to this deposit based on its fossil fauna, the Mesa Formation has been dated via thermoluminescence (TL) to range from at least 2 Ma to 0.5 Ma (early to Middle Pleistocene; Carbón *et al*. 1992). Based on the taxa identified in previous studies (Rincón *et al*. 2009, 2011, Holanda & Rincón 2012, Solórzano *et al*. 2015) and geological evidence indicating a possible age of more than 2.0 Ma (see dating issues outlined by Carbón *et al*. 1992), we prefer to follow the conservative approach, retaining a Plio–Pleistocene age (at least *ca* 2.6 Ma.) for deposits at site ORS16, El Breal de Orocual (Solórzano *et al*. 2015).

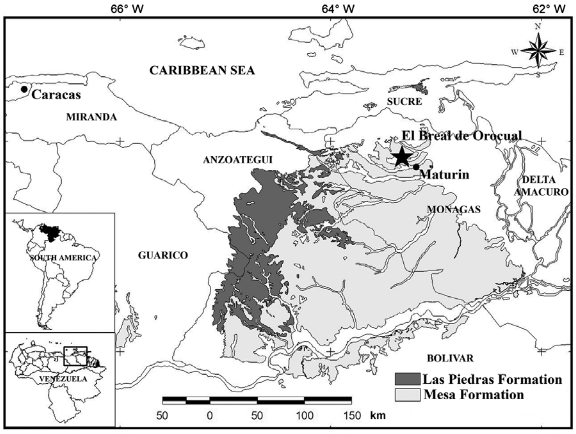

Fig. 1. Geographical map showing the El Breal de Orocual tar seep site, Monagas State, Venezuela, and the schematic geological map of eastern Venezuela, showing the Mesa Formation (lower–Middle Pleistocene) and Las Piedras Formation (upper Pliocene; after Hackley *et al*. 2006).

Material and methods

The specimens were collected in consolidated blocks of sediments impregnated with asphalt and stored at the Instituto Venezoelano de Investigaciones Científicas (IVIC), Caracas, Caracas State, Venezuela. Skeletons of extant boines were used for comparison (see Appendix). Data on fossil boines were taken from Albino & Carlini (2008), Hsiou & Albino (2009), Albino (2011), Head *et al*. (2012) and Teixeira (2013). The osteological nomenclature and descriptive terminologies follow mainly Auffenberg (1963), Hoffstetter & Gasc (1969), Rage (1984, 2001), Lee & Scanlon (2002), Hsiou & Albino (2009), Hsiou *et al*. (2010) and Hsiou *et al*. (2013). Quantitative data for vertebral proportions follow LaDuke (1991a, b). The systematic scheme follows Noonan & Chippindale (2006).

Institutional abbreviations. IVIC, Instituto Venezoelano de Investigaciones Científicas, Caracas, Caracas state, Venezuela; OR, El Breal de Orocual; MCND, Coleção Didática de Herpetologia, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCN-PV DR, Seção de Paleontologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Coleção de Paleontologia de Vertebrados, Coleção Didática de Répteis, Porto Alegre, Brazil; UFMT, Coleção da Universidade Federal do Mato Grosso, Mato Grosso, Brazil.

Other abbreviations cl, centrum length; cn, condyle; coh, condyle height; cow, condyle width; ct, cotyle; cth, cotyle height; ctw, cotyle width; ctw > cth, cotyle width greater than cotyle height; h, total height of vertebra; hy, hypapophysis; naw, neural arch width at interzygapophyzeal ridge; nch, neural canal height; ncw, neural canal width; nc, neural canal; ns, neural spine; po–po, distance between postzygapophyses; ppz, prezygapophyseal process; pr, parasagittal ridges (=laminar crests *sensu* Albino 2011); pr–pr, distance between prezygapophyses; pr–po, distance between prezygapophyses and postzygapophyses of the same side; pr > po, prezygapophyses width greater than postzygapophyses width; prl, prezygapophyses length; prw, prezygapophyses width; ptz, postzygapophysis; pz, prezygapophysis; sc, spinal crest; sb, spinal blade; zg, zygantrum; zh, zygosphene height; zw, zygosphene width; zs, zygosphene; zw > ctw, zygosphene width greater than cotyle width.

Systematic palaeontology

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
MACROSTOMATA Müller, 1831
BOIDAE Gray, 1825
BOINAE Gray, 1825

Boa Linnaeus, 1758

Boa constrictor Linnaeus, 1758 (Fig. 2A–E)

Referred specimens. Two almost complete anterior trunk vertebrae (IVIC OR-2623 and IVIC OR-2620), an articulated sequence of six mid-trunk vertebrae (IVIC OR-6445) and two almost complete posterior trunk vertebrae (IVIC OR-3674 and IVIC OR-6107).

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

Description. The specimens are well preserved. In anterior view, all vertebrae are robust, large and short, with the neural arch wider than the vertebral centrum length (cl < naw). The zygosphene is very robust and wider than the cotyle (zw > ctw). The mid-ventral region is slightly concave and seems to have more marked concavity in the anterior than posterior vertebrae. The prezygapophyses are slightly inclined above the horizontal plane on the mid- and posterior trunk vertebrae, whereas in the anterior ones, the same structures are oriented nearly horizontally. A small prezygapophyseal process is present and somewhat prominent beyond the articular facet of the prezygaphophysis facet. The neural canal is wide and has a triangular morphology. Three crests are present in the interior of the neural canal: two located on the lateral walls and one on the floor, which, combined, produce a trilobed aspect to the neural canal. On the anterior and posterior vertebrae, the neural canal is wider than high (ncw > nch), whereas, on the mid-trunk vertebrae the height exceeds the width (ncw < nch). The cotyle is oval and weakly flattened dorsoventrally (ctw > cth). On each side of the cotyle are moderately deep paracotylar fossae, with paracotylar foramina (one on each side), which are visible only on mid-trunk vertebrae. The paradiapophyses are eroded on the posterior vertebra, but well preserved on mid- and anterior trunk vertebrae. In general view, the paradiapophyses are robust, expanded laterally and lateroventrally oriented. Diapophyses are strongly convex, whereas the parapophyses are slightly concave.

In posterior view, the neural arch is vaulted on all vertebrae. In the mid-trunk vertebrae, the left lateral edge of the neural arch is broken, whereas on the anterior and posterior vertebrae, the neural arch is still preserved. A thick neural spine rises from the mid-portion of the neural arch and is preserved only in the anterior and mid-trunk vertebrae. Each lateral face of the neural spine bears a distinct ascending spinal crest (*sensu* Albino, 2011), which is derived from the continuation of the posterior edge of the neural arch. The spinal crest is well marked and prominent in the mid-trunk vertebrae, slightly visible in the anterior vertebrae, and not preserved in the posterior vertebrae. Above the postzygapophyseal articular facets, a short epizygapophyseal process is evident, being more prominent in the mid-trunk vertebrae. The zygantrum is deep and robust, with paired zygantral foramina on each side of the vertebra. These small foramina can only be seen in mid-trunk vertebrae. The postzygapophyses are slightly inclined above the horizontal plane on anterior and mid-trunk vertebrae, whereas they are oriented nearly horizontally on the anterior examples. The condyle is broken on the anterior trunk vertebrae; however, on the mid- and posterior trunk vertebrae, it is oval and dorsoventrally flattened (cow > coh).

In lateral view, the neural spine is high, well developed and oriented slightly posteriorly. Mid- and posterior trunk vertebrae are more inclined posteriorly than the anterior trunk vertebrae. The neural spine is short anteroposteriorly and rises from the zygosphene roof, extending to the posterior edge of the neural arch, characterizing a blade-like neural spine (*sensu* Hsiou *et al*. 2010). The zygosphene shows elliptical articular facets oriented laterally. On the vertebral centrum, there are paired lateral foramina on each side of the vertebrae. The centrum shows a well-defined precondylar constriction, with a prominent haemal keel on the mid- and posterior trunk vertebrae that extends anteroposteriorly beyond the precondylar constriction. The haemal keel outline has a slightly convex morphology on the mid-trunk vertebrae, but more prominent and convex on the posterior trunk vertebrae.

In ventral view, the centrum is shorter than the neural arch (cl < naw), with the anterior region wider than the posterior region, resembling a triangle. The anterior trunk vertebrae preserve only the base of the hypapophyses, rising from the mid-portion of the centrum. On the anterior and mid-trunk vertebrae, poorly defined depressions are present on each side of the haemal keel, with a foramen on each side. On the posterior trunk vertebrae, the depression becomes a subcentral groove (=paramedian lymphatic fossae *sensu* LaDuke, 1991b), which is deep and well defined. The postzygapophyseal articular facets are triangular and broad on mid- and posterior trunk vertebrae, whereas they are nearly oval on the anterior trunk vertebrae.

In dorsal view, the neural arch is wider than long (pr–pr > pr–po). The prezygapophyses are oriented slightly anterolaterally in the anterior trunk vertebrae, whereas they are nearly transverse in the mid- and

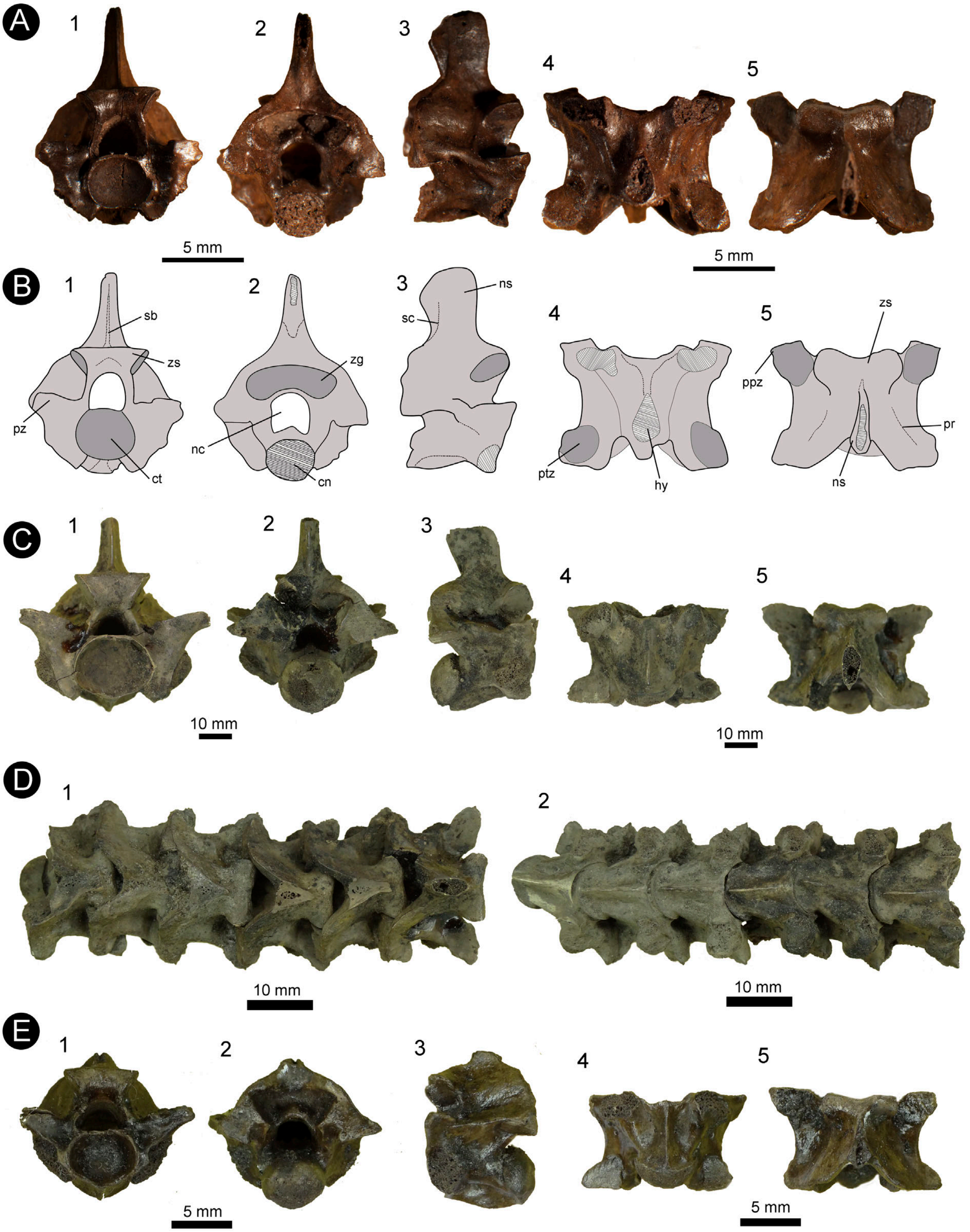

Fig. 2. Vertebral remains attributed to *Boa constrictor*: **A**, Anterior precloacal vertebra, IVIC OR-2623; **B**, Schematic outline of IVIC OR-2623; **C**, Mid-trunk vertebra, isolated mid-trunk vertebra IVIC OR-6445; **D**, Articulated sequence of mid-trunk vertebrae IVIC OR-6445; **E**, Posterior precloacal vertebrae IVIC OR-6107 in (1) anterior, (2) posterior, (3) lateral, (4) ventral and (5) dorsal views.

posterior vertebrae. The prezygapophyseal articular facets are longer than wide (prl > prw) and subtriangular. The anterior edge of the zygosphene bears a V-shaped notch in the anterior trunk vertebrae, whereas the mid- and posterior examples hold a concave anterior margin. The neural arch roof bears a distinct margin that extends from the lateral surface of the zygosphene towards the posterior region of the neural arch, forming the parasagittal ridges (*sensu* Hsiou *et al*. 2014; =laminar crests *sensu* Albino 2011). The parasagittal ridges are strongly marked in the mid-trunk and posterior vertebrae but weakly developed in the anterior ones. The interzygapophyseal ridge extends between the prezygapophysis and postzygapophysis, and it is short, curved and little constricted. The neural spine has a lacriform outline in cross-section and the anterior portion is less thick than the posterior portion, forming a distinct spinal blade crest (*sensu* Albino 2011). The posterodorsal notch is deep and located in the posterior edge of the neural arch.

Measurements (in millimetres). IVIC OR-2623 cl: 5.4; cth: 3.1; ctw: 3.8; naw: 8.1; nch: 2.2; ncw: 3.1; nsl: 4.9; nsh: 5.2; po–po: 10.1; pr–pr: 10.2; pr–po: 8.0; prl: 2.9; prw: 2.8; zh: 2.1; zw: 5.9. IVIC OR-6445: cl: 11.5; coh: 7.0; cow: 8.0; cth: 7.0; ctw: 9.0; h: 25.2; naw: 13.5; nch: 8.0; ncw: 2.0; nsl: 5.9; nsh: 7.8; po–po: 22.7; pr–pr: 23.5; pr–po: 11.2, prl: 6.6; prw: 4.5; zh: 4.9; zw: 9.6. IVIC OR-6107: cl: 7.0; coh: 4.3; cow: 5.2; cth: 4.3; ctw: 4.9; naw: 10.3; nch: 2.5; ncw: 2.9; po–po: 13.1; pr–pr: 13.9; pr–po: 8.2; prl: 4.0; prw: 3.1; zh: 2.8; zw: 6.1.

Comparisons with other neotropical boids. The new material shares the following combination of vertebral characters with the neotropical boids: robust, short, wide and high vertebrae; neural arch not strongly depressed; short prezygapophyseal process; well-developed neural spine; presence of a posterodorsal notch; vertebral centrum shorter than the width of the neural arch (cl/naw < 1); thick zygosphene; inclination of the prezygapophyseal articular facets <15°; strongly marked precondylar constriction; presence of a hypapophysis on anterior vertebrae and prominent haemal keel on mid-trunk examples; vaulted neural arch and presence of lateral, subcentral and paracotylar foramina (Rage 1984, 2001, Lee & Scanlon 2002, Szyndlar & Rage 2003, Albino & Carlini 2008, Hsiou & Albino 2009).

The fossil specimens are assigned to the extant species *Boa constrictor* based on a specific combination of vertebral features: high and massively built vertebrae; vaulted neural arch; thick, notched or concave zygosphene edge in dorsal view; presence of paracotylar, subcentral and lateral foramina; marked parasagittal ridges above the neural arch; presence of a epizygapophyseal process on the postzygapophyseal articular facets, and a blade-like neural spine morphology (Albino & Carlini 2008, Hsiou & Albino 2009, Hsiou *et al*. 2010, Albino 2011).

It is noteworthy that, although there is another species recognized (*B. imperator*; Hynková *et al*. 2009, Reynolds *et al*. 2014) and seven subspecies of *B. constrictor* (Uetz & Hošek 2015), there are no osteological differences between the fossils and the comparative material examined. The presence of the few characters listed above, can not be used as taxonomic criteria to assign the material below generic level. Among the neotropical boids, the fossils are similar to mid-sized vertebrae of *Eunectes* and *Boa*, differing from the smaller and more gracile vertebral build of *Corallus* and *Epicrates* (Hsiou & Albino 2009, Camolez & Zaher 2010).

The neural arch in *Eunectes* and *Corallus* is less vaulted compared with *Boa* and *Epicrates* (Hsiou & Albino 2009, Teixeira 2013). The paracotylar foramina are irregular and smaller in *Eunectes*, but large and clearly defined in specimens of *Boa*, *Corallus* and *Epicrates* (Hsiou & Albino 2009, Teixeira 2013); however, these two last genera have irregularly distributed foramina through the axial skeleton, whereas *Boa* retains the paracotylar foramina on all vertebrae.

In dorsal view, the zygosphene of *Epicrates* has a medial lobe, whereas *Corallus* has a crenate zygosphene (*sensu* Auffenberg 1963), and *Eunectes* has a prominent median tubercle, which is a projection of the dorsal edge of the neural canal roof (Hsiou & Albino 2009). The thickness of the zygosphene of *Corallus* and *Epicrates* in anterior view is lesser than in *Boa* and *Eunectes* (Hsiou & Albino 2009, Teixeira 2013). Nevertheless, the zygosphene of *Eunectes* is thicker and more robust among the other three genera (Hsiou & Albino 2009). The neural spine of *Boa* is higher than in *Eunectes* and the anterior margin is thin, whereas the posterior one is thicker, characterizing the blade-like neural spine (Hsiou & Albino 2009, Hsiou *et al*. 2010, Albino 2011).

The centrum of *Boa* has a different relative size, being shorter than in *Eunectes* (e.g., cl/naw of *Boa* < cl/naw of *Eunectes* Hsiou & Albino, 2009). The prezygapophyses of *Epicrates*, *Eunectes* and *Boa* have a similar orientation above the horizontal plane, whereas in *Corallus* they have a nearly horizontal orientation (Teixeira 2013). Although there are similarities, proportionally the prezygapophyses of *Boa* are long compared with those of *Eunectes*, *Epicrates* and *Corallus* (Albino & Carlini 2008).

Discussion

The first Venezuelan snake fossils were reported by Head *et al*. (2006) followed by the reviews of Hsiou *et al*. (2010) and Hsiou & Albino (2010). Most of the material comes from the Socorro (middle Miocene) and Urumaco (upper Miocene) formations (Hambalek *et al*. 1994, Head *et al*. 2006, Sánchez-Villagra & Aguilera 2006). The snake fauna of the Socorro Formation was represented originally by *Colombophis* sp. cf. *C. portai* and an indeterminate Boinae (Head *et al*. 2006), which subsequently, were attributed to *Colombophis spinosus* (Hsiou *et al*. 2010) and *Eunectes* (Hsiou & Albino 2010), respectively. From the Urumaco Formation, an isolated precloacal vertebra was described as an indeterminate Boinae (Head *et al*. 2006), and later reassigned to cf. *Eunectes* (Hsiou & Albino 2010). Additionally, a single record of an indeterminate Viperidae was recorded from the Late Pleistocene of the Cucuruchu gravels (Bocquentin-Villanueva 1982, Head *et al.* 2006).

These records clearly highlight the importance of South America for the evolution of boines, aiding evaluation of biogeographical patterns of taxa through the geological record (Burbrink 2005, Noonan & Chippindale 2006).

Among the boines, *Boa* has the broadest ecological, climatic, altitudinal and latitudinal range, extending from 30°N to 36°S (Fig. 3; Henderson *et al.* 1995). This ecological tolerance supports the previous palaeoenvironmental interpretation for northern Venezuela as an expansive lowland hosting savannas crossed by rivers flanked by patches of gallery forest (Rincón *et al.* 2009, 2011, Holanda & Rincón 2012).

The recovered mammalian fauna also indicates an open and seasonally dry savanna, together with scattered forests and humid-climate vegetation components (Rincón *et al.* 2009, Solórzano *et al.* 2015). It is noteworthy that taxa, such as rodents, capybaras and tapirs in the assemblage, were potential prey for a local population of *B. constrictor*. The palaeoenvironmental interpretation is similar to the modern northern Venezuelan Llanos biome (Rincón *et al.* 2011), which is characterized by an extensive area of savanna with a small proportion of forest associated with perennial streams, and abundant rivers (Monasterio 1970) supporting diverse animals, especially reptiles (Rivas *et al.* 2012).

The faunal evidence as a whole indicates that the Plio–Pleistocene environment of El Breal de Orocual consisted of a mosaic of habitats (Rincón *et al.* 2011), and the presence of *Boa* suggests the predominance of a moist (1500–3000 mm annual rainfall regime) mesothermal vegetation, based in the biology of extant boines (Henderson *et al.* 1995, Henderson 2004).

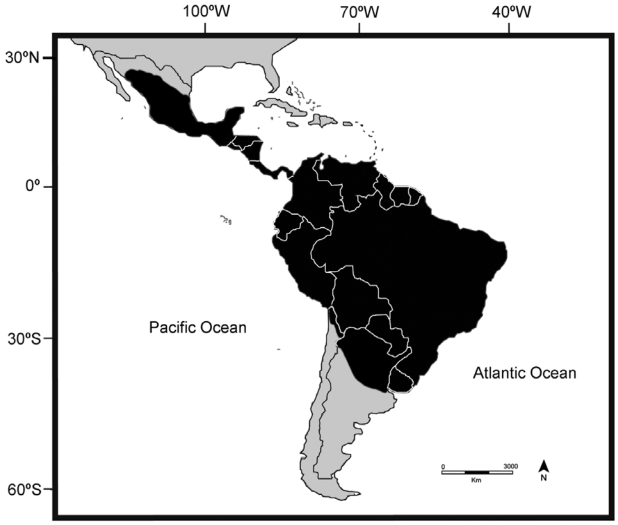

Fig. 3. Geographical map of Central and South America showing the current distribution of *Boa constrictor*. Distributional range is based on Waller & Micucci (1993) and records of the reptile database (Uetz & Hošek 2015).

Currently, populations of *B. contrictor* are widespread through most of Venezuela, although not occurring in coastal regions (Rivas *et al.* 2012). Although absent from coastal habitats, they have a great aquatic dispersal capability, being found even on the archipelagos of northern Venezuela (Rivas *et al.* 2012). Episodes of overwater dispersal are commonly inferred to have promoted boid diversification and evolution (e.g., Hedges 1996, Burbrink 2005, Noonan & Chippindale 2006). Thus, knowledge from the fossil record is extremely important for understanding colonization events and episodes of interchange in the herpetofauna before the closure of the Panama isthmus (Albino 2011, Head *et al.* 2012).

The occurrence of *Boa* fossils in northern South America near the Lesser Antilles Archipelago, together with the hypothesis of an ancient colonization of the entire West Indies during the Miocene (Albino 2011), could help explain the presence of the extant populations on Saint Lucia and Dominica (Henderson 2004). However, only further phylogeographic studies can resolve these issues (e.g., Martin *et al.* 2015 for the case of *Iguana delicatissima*).

Additionally, the El Breal de Orocual deposit represents the oldest known tar pit assemblage from South America (Solórzano *et al.* 2015) and has great potential to reveal records of additional squamate taxa and fill other gaps in knowledge of the Plio–Pleistocene history of neotropical vertebrates (Rincón *et al.* 2009).

Conclusions

The *Boa* from El Breal de Orocual represents the northernmost fossil record of the genus in South America and the first formal report of *B. constrictor* in the Venezuelan fossil record. Based on the ecological and geographical range of extant populations, the material supports the interpretation of a mosaic of savanna palaeoenvironments crossed by rivers and patches of gallery forest within annual precipitation regime of 1500–3000 mm during the late Pliocene–early Pleistocene.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix. Comparative material examined in this study

Boa constrictor: MCN.D 333, 335, 343, 344, 347, 351
Corallus hortulanus: MCN-PV DR 0001 UFMT 02389, 02398
Corallus batesii: UFMT-R 05362
Epicrates cenchria: MCN-PV DR 0002
Epicrates crassus: MCN-PV DR 0003
Eunectes murinus: MCN.D 306, 316, 319, 342