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Newly discovered fossils provide novel insights on the biology of the South American Miocene snake *Colombophis* Hoffstetter & Rage, 1977

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ABSTRACT

Colombophis Hoffstetter & Rage, 1977 was an alethinophidian snake that inhabited South America from Middle to Late Miocene. Since its discovery, its position within the phylogenetic tree of snakes has been controversial, due the fact that it is a taxon based solely on postcranial elements. Here, we describe several fossils, potentially representing 50 individuals belonging to this genus, which were discovered in La Tatacoa desert, Colombia. Furthermore, we report for the first time the presence of parazygantral foramina in *Colombophis* vertebrae, which are similar to those observed on madtsoiids. Although most of the fossils described herein are fragmentary, they support the placement of this snake among the alethinophidians. Additionally, considering the vertebrae size, we suggest a potential non-fossorial lifestyle.

KEY WORDS
Snakes,
Colombophis,
Miocene,
Tatacoa,
South America,
Anilioidea.

MOTS CLÉS
Serpents,
Colombophis,
Miocène,
Tatacoa,
Amérique du Sud,
Anilioidea.

RÉSUMÉ

Des fossiles récemment découverts fournissent de nouvelles informations sur la biologie du serpent miocène sud-américain Colombophis *Hoffstetter & Rage, 1977.*

Colombophis Hoffstetter & Rage, 1977 est un serpent alethinophidien qui a habité l'Amérique du Sud du Miocène moyen au Miocène supérieur. Depuis sa découverte, sa position dans l'arbre phylogénétique des serpents a été controversée, car sa description était basée uniquement sur des éléments postcrâniens. Ici, nous décrivons plusieurs fossiles, représentant potentiellement 50 individus appartenant à ce genre, qui ont été découverts dans le désert de La Tatacoa, en Colombie. De plus, nous rapportons pour la première fois la présence de foramina parazygantraux dans les vertèbres de *Colombophis*, qui sont similaires à ceux observés sur les mastoïdes. Bien que la plupart des fossiles décrits soient fragmentaires, ils soutiennent le placement de ce serpent parmi les alethinophidiens. De plus, compte tenu de la taille des vertèbres, nous suggérons un potentiel mode de vie non fouisseur.

PALABRAS CLAVE
Serpientes,
Colombophis,
Mioceno,
Tatacoa,
América del Sur,
Anilioidea.

RESUMEN

Fósiles recién descubiertos aportan nuevos conocimientos sobre la biología de la serpiente Colombophis *del Mioceno sudamericano.*

Colombophis Hoffstetter & Rage, 1977 fue una serpiente aletinofidia que habitó América del Sur durante el Mioceno medio a superior. Desde su descubrimiento, su posición dentro del árbol filogenético de las serpientes ha sido controversial, debido a que es un taxón definido únicamente por elementos del postcráneo. Aquí describimos varios fósiles que potencialmente representan 50 individuos pertenecientes a este género, los cuales fueron descubiertos en el desierto de La Tatacoa, Colombia. Además, reportamos por primera vez la presencia de forámenes parazigantrales en las vértebras de *Colombophis*, los cuales son similares a aquellos observados en madtsoidos. A pesar de que los fósiles acá descritos son fragmentarios, estos soportan la posición de esta serpiente dentro de los aletinofidios. Adicionalmente, considerando el tamaño de las vértebras, sugerimos un posible estilo de vida diferente al fosorial.

INTRODUCTION

During the Miocene, northern South America was place with a diverse fauna of reptiles, principally turtles (Cadena *et al.* 2020a, b and references therein), crocodilians (Langston & Gasparini 1997; Aguilera *et al.* 2006; Scheyer *et al.* 2013; Souza *et al.* 2021 and references therein), and squamates (Albino & Brizuela 2014; Onary *et al.* 2017; Carrillo-Briceño *et al.* 2019; Carrillo-Briceño *et al.* 2021a and references therein). Regarding squamates, perhaps one of the most enigmatic fossils is the alethinophidian snake *Colombophis* Hoffstetter & Rage, 1977; which was discovered in the Colombian department of Huila, in the locality of La Venta, La Tatacoa Desert, Villavieja town (Fig. 1). The initial description of this genus and single species *C. portai* Hoffstetter & Rage, 1977 was based on around 40 precloacal vertebrae (Hoffstetter & Rage 1977) (Fig. 2A). Since then, many other specimens have been discovered in La Tatacoa Desert (Hecht & LaDuke 1997), and in other Middle to Late Miocene localities from Venezuela, Brazil and Peru (Head *et al.* 2006; Hsiou *et al.* 2010; Carrillo-Briceño *et al.* 2021a) (Fig. 1A). More than a decade ago, Hsiou *et al.* (2010) proposed the existence of a second species *C. spinosus* Hsiou, Albino & Ferigolo, 2010, based on the unusual well-developed neural spine exhibited by some specimens, not present on *C. portai*.

Since it was discovered, *Colombophis* has been considered an "anilioid" (Anilioidea) snake. "Anilioidea" constitutes a paraphyletic group including the extant *Anilius scytale* Linnaeus, 1758 (red pipe snakes), Cylindrophidae (Asian pipe snakes), Anomochilidae (dwarf pipe snakes), Uropeltidae (shield-tail snakes) and the fossil taxa *Coniophis* Marsh, 1892; *Australophis* Gómez, Báez & Rougier, 2008; *Eoanilius* Rage, 1975 and *Hoffstetterella* Rage, 1998 (Hsiou *et al.* 2010 and references therein, but see Head 2021). The attribution of *Colombophis* as potentially member of "Anilioidea" was suggested based on shared vertebral morphology with *Cylindrophis* Wagler, 1828; both taxa exhibiting a reduced neural spine, a depressed neural arch, highly inclined prezygapophysis, and the placement of the subcentral foramina (Fig. 2AE). However, molecular studies have demonstrated the paraphyly of "Anilioidea", grouping cylindrophiids, anomochilids and uropeltids into the superfamily Uropeltoidea, while Aniliidae is now considered as the sister group of Tropidophiidae (dwarft boas) (Vidal *et al.* 2007; Pyron *et al.* 2013; Figueroa *et al.* 2016; Burbrink *et al.* 2020).

The placement of *Colombophis* as member of "Anilioidea" is still controversial as many of the shared characters with other "anilioids" are plesiomorphic, present also in basal snakes (Hsiou *et al.* 2010) or homoplasies shared by other squamates with a fossorial or cryptozoic lifestyle (Head 2021) (Fig. 2). Moreover, Head (2021) using six apomorphic

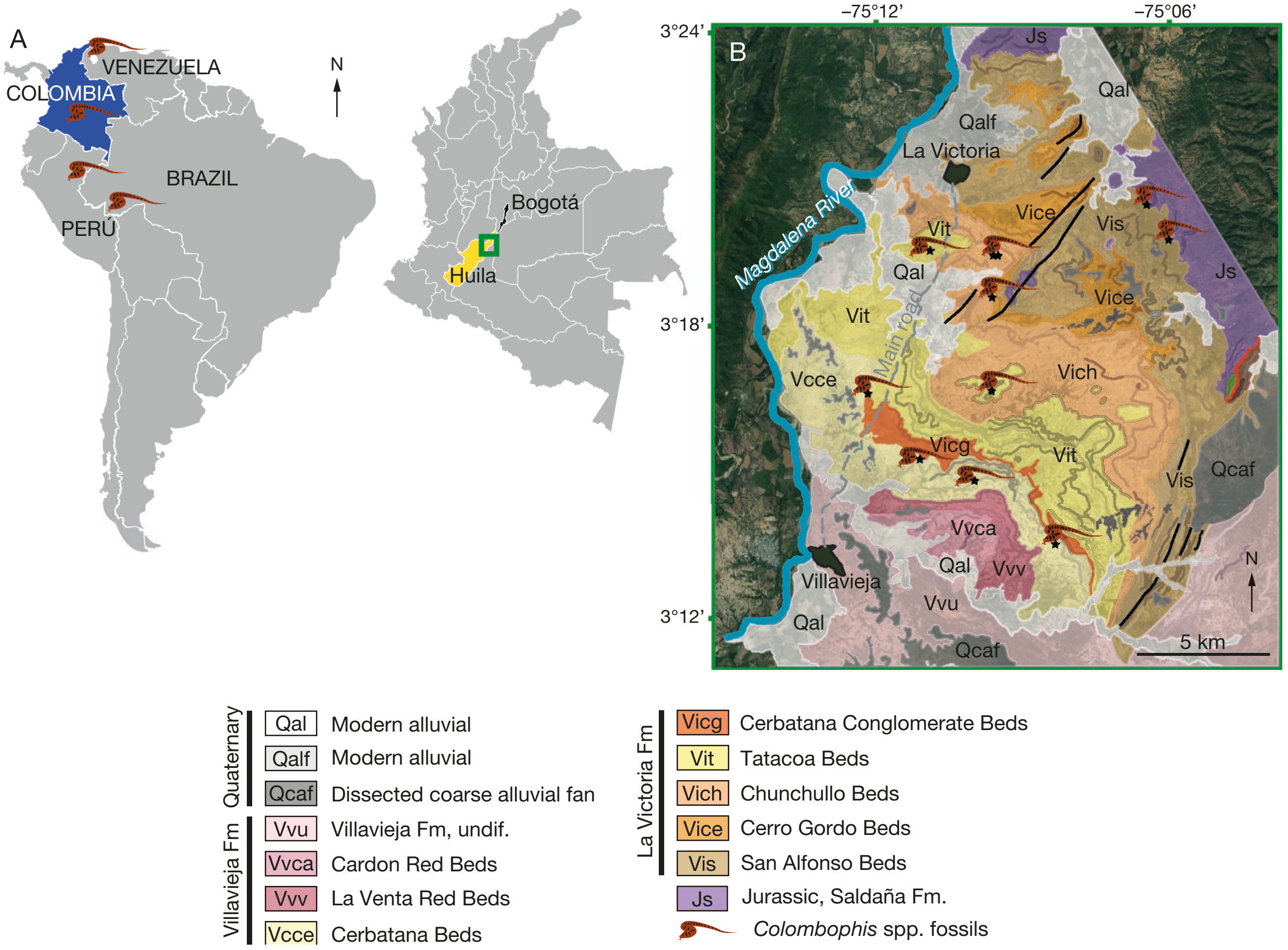

Fig. 1. — Location map of the different localities where *Colombophis* spp. fossils have been collected in: **A**, South America; **B**, The Tatacoa Desert area. Stratigraphic units and geological map of the Tatacoa Desert were modified from Montes *et al.* 2021: fig. 4.

characters mapped onto a molecular topology (following Pyron *et al.* 2013; Reynolds *et al.* 2014), suggested that *Colombophis* may have had affinities with extant Aniliidae or Uropeltidea instead.

Recent fieldwork activities organized by several Colombian universities and international institutions including the Smithsonian Tropical Research Institute, Universidad del Rosario, Universidad de los Andes, and the Grand Valley State University; alongside with a group of local amateur paleontologists called the Vigías del Patrimonio Paleontológico La Tatacoa have discovered more than 60 fossils vertebrae from several different individuals. Most of the new fossils were found disassociated or disarticulated; all of them resembling the vertebral morphology previously described for *Colombophis.* These fossils have been found in 11 different localities along the La Tatacoa Desert (Fig. 1B). Here we describe these fossils, and discuss their implications for understanding the biology, ecology and systematic paleontology of this ancient snake.

MATERIAL AND METHODS

Fossils and extant specimens

All studied fossils studied were collected from different localities across La Victoria and Villavieja formations (see Fig. 1B and Appendix 3). These localities fall within an age range of *c.* 13.8 and 11.8 Ma (Mora-Rojas *et al.* 2023 and references therein), which represents the Serravallian age (Middle Miocene). However, fossils from San Alfonso Beds might be as old as 16 Ma (Mora-Rojas *et al.* 2023). All the specimens are housed in the VPPLT collection.

Comparative material used in this study includes the postcranial elements from different specimens of extant Aniliidae, Cylindrophidae, Uropeltidae, Tropidophiidae and “scolecophidians”, which are listed in Appendix 4. Additionally, we used morphological descriptions of *Anilius scytale* and *Cylindrophis ruffus* Laurenti, 1768; from Carrillo-Briceño *et al.* (2021b) and Ikeda (2007) respectively.

MICROTOMOGRAPHY

The holotype of *Colombophis portai* MNHN-VIV-6 specimen was scanned using a micro-computer tomography on a v|tome|x 240 L from Baker Hughes Digital Solutions at MNHN facilities. The scan was performed using a voltage of 140 kV, a current of 195 mA and a voxel resolution of 27.34 µm. Additionally, five vertebrae of *Colombophis* VPPLT-798, VPPLT-1006, VPPLT-1564 and VPPLT-1740 specimens were scanned using a Multi-Scale X-Ray Micro-CT Bruker SkyScan 2211 in the Microanalysis laboratory at Yachay Tech University, Imbabura, Ecuador. The scans were performed using voltages between 60-100 kV, currents between 200-450 µA and voxel resolutions of 5 to 17 µm. The reconstructions were performed using NRecon v1.7.1. All volumes were analyzed using 3D Slicer v5.0.2 (Fedorov *et al.* 2012).

TERMINOLOGY AND MEASUREMENTS

For osteological terminology, we followed Auffenberg (1967), Hoffstetter & Gasc (1969), and Rage (1984). Precloacal vertebrae were classified in anterior-trunk, mid-trunk and posterior-trunk regions following LaDuke (1991). Even though the use of ratios based on vertebrae measurements has been controversial (Holman 2000). Hsiou *et al.* (2010) found that some proportions may help to distinguish between *Colombophis portai* and *C. spinosus*. Therefore, we measured different regions of the vertebrae, and calculate some vertebral proportions which might be relevant for vertebrae identification following Auffenberg (1967).

Most measurements were taken with a caliper, but inclination angles and small vertebrae were measured using a reference scale in ImageJ 1.52a (Schneider *et al.* 2012). Measurements are expressed in millimeters and inclinations in degrees.

PHYLOGENETIC ANALYSES

In order to test the monophyly of the two species of *Colombophis,* and evaluate their phylogenetic relationships within the Serpentes clade, we modified the morphological matrix of Scanferla & Smith (2020), which includes 201 osteological characters and 48 terminal taxas including fossil snakes, and representatives of extant “scolecophidians”, “anilioids” and macrostomous alethinophidians. The matrix was analized in combination with the molecular data used by Scanferla & Smith (2020), which includes mitochondrial (12S, 16S, Cytb) and nuclear (BDNF, Cmos, NTF3, NGFB and PNN) DNA sequences for the extant taxa (see Appendix 5).

We performed a maximum parsimony analysis in TNT (Tree Analysis using New Technology) V 1.5 (Goloboff & Catalano 2016), using *Varanus salvator* Laurenti, 1768 as outgroup. All characters were used in a traditional search under equal weights, using 1000 replicates obtained by random addition sequence and search for new tree topologies with the tree bisection and reconnection algorithm (TBR), saving 20 trees per replicate. For the resulting strict consensus tree we calculated the Bremer support values, as well as the consitency (CI) and retention (RI) indices. We used the script STATS.RUN to obtain CI and RI indices.

PALEOECOLOGY

To infer the potential ecology of *Colombophis*, we performed a bone compactness analysis using the micro-tomographed specimens (see Appendix 1). We followed the approach proposed by Houssaye *et al.* (2013), calculating the global compactness as the total area of the transverse section (not including the neural canal), minus the area occupied by cavities, multiplied by 100 and divided by total area of the section (not including the neural canal). We used the global compactness in transverse section (Cts) only, as it has proven to be more reliable regarding ecological habits (Houssaye *et al.* 2019). To compare our results, we combined the Ecology and Cts values of different snakes (Appendix 6) from Houssaye *et al.* (2013: table 1) and Houssaye *et al.* (2019: table 2).

ABBREVIATIONS

Institutional abbreviations

IGM	Museo Geológico Nacional José Royo y Gómez, Servicio Geológico Colombiano (former INGEOMINAS), Bogotá;
MNHN	Muséum national d’Histoire naturelle, Paris;
UF-H	Herpetological collection, Florida Museum of Natural History, University of Florida, Gainesville;
UR	Museo de Historia Natural, Universidad del Rosario, Bogotá, Colombia;
VPPLT	Colección Museo de Historia Natural la Tatacoa, Villavieja, Colombia.

Anatomical abbreviations

cn	condyle;
ct	cotyle;
di	diapophysis;
he	hemapophysis;
hk	haemal keel;
hy	hypapophysis;
lf	lateral foramen;
nc	neural canal;
ns	neural spine;
pa	parapophysis;
paf	paracotylar foramen;
po	postzygapophysis;
pr	prezygapophysis;
pzf	parazygantral foramen;
sf	subcentral foramen;
zg	zygantrum;
zs	zygosphene.

Anatomical measurements

cl	centrum length;
coh	condyle height;
cow	condyle width;
cth	cotyle height;
ctw	cotyle width;
h	total height of vertebra;
naw	neural arch width at interzygapophyseal ridge;
nch	neural canal height;
ncw	neural canal width;

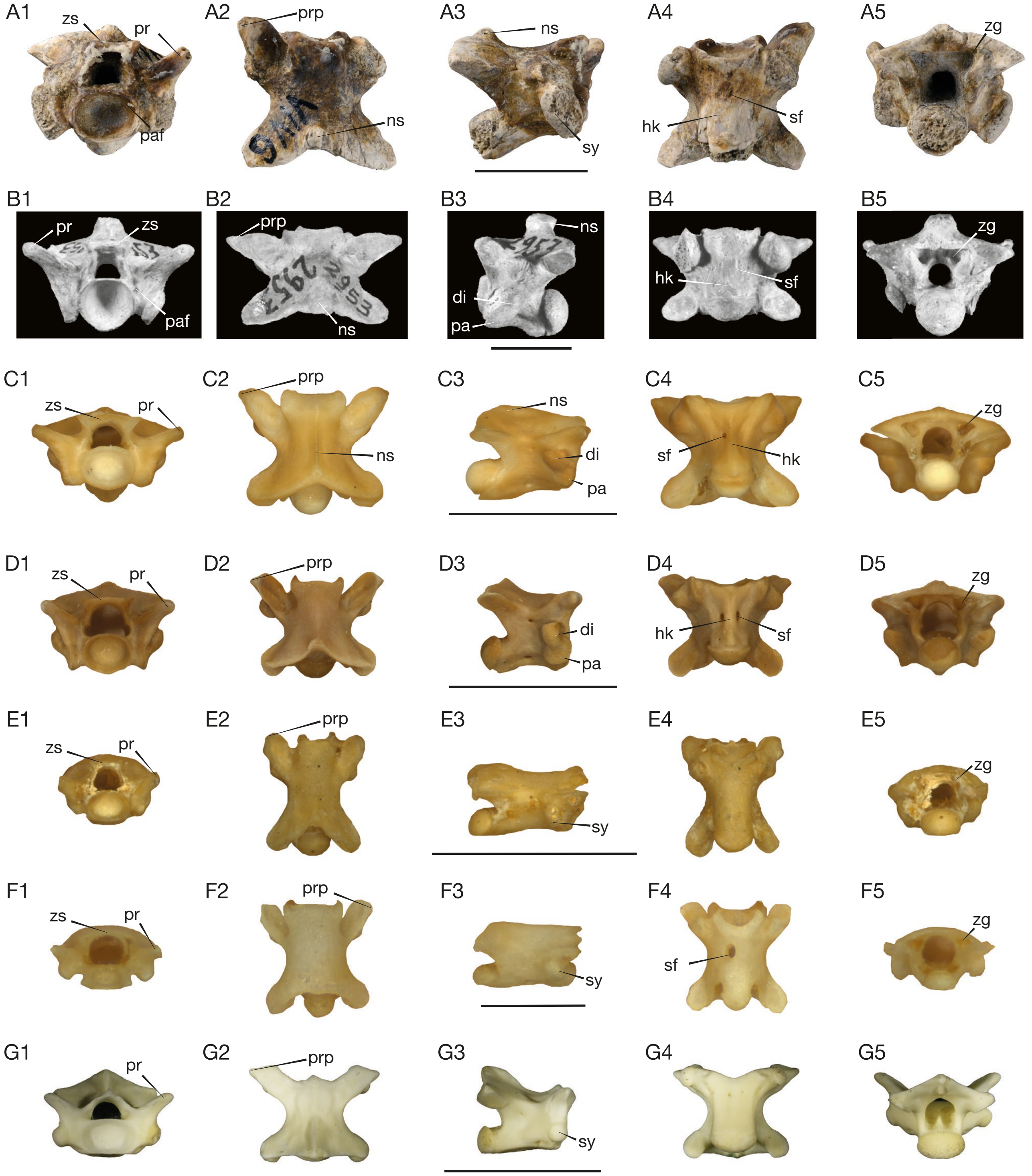

FIG. 2. — Comparison of *Colombophis* Hoffstetter & Rage, 1977 mid-trunk vertebrae with extant fossorial squamates: **A**, *Colombophis portai* Hoffstetter & Rage, 1977, MNHN-VIV-6; **B**, *Colombophis spinosus* Hsiou, Albino & Ferigolo, 2010, UFAC-PV-2953, modified from Hsiou *et al.* (2010); **C**, *Anilius scytale* Linnaeus, 1758, UF-H-52001; **D**, *Cylindrophis ruffus* Laurenti, 1768 UF-H-52673; **E**, *Uropeltis* Cuvier, 1829, UF-H-11750; **F**, *Rena dulcis* Baird & Girard, 1853, UF-H-11776; **G**, *Amphisbaena alba* Linnaeus, 1758, UR-uncatalogued specimen. Views: **1**, anterior; **2**, dorsal; **3**, lateral; **4**, ventral; **5**, posterior views. Scale bars: A, B, G, 10 mm; C, D, E, 5 mm; F, 1 mm.

po-po	width across postzygapophyses;
pr-pr	width across prezygapophyses;
pr-po	distance between pre and postzygapophyses of the same side;
prl	prezygapophysis length;
prw	prezygapophysis width;
zh	zygosphene height;
zw	zygosphene width;
<pr	orientation of prezygapophyses measured on the anterior face from the horizontal plane.

SYSTEMATIC PALEONTOLOGY

Order SQUAMATA Oppel, 1811
Suborder SERPENTES Linnaeus, 1758
Infraorder ALETHINOPHIDIA Nopcsa, 1923
Genus *Colombophis* Hoffstetter & Rage, 1977

Colombophis portai Hoffstetter & Rage, 1977
(Figs 3-5)

Colombophis portai Hoffstetter & Rage, 1977: 174.

REVISED DIAGNOSIS. — Fossil snake with pre-cloacal vertebrae medium to large in size (cl = *c.* 5-11 mm); the neural arch is depressed, with a shallow median notch in the posterior border; neural spine is reduced to a small tubercle with a circular or triangular outline from dorsal view, and is restricted to the posterior end of the neural arch; prezygapophyses are anterolaterally oriented and highly inclined above the horizontal plane, reaching the level of the zygosphene roof; prezygapophyzeal process is short; presence of paracotylar and parazygantral foramina is variable; synapophyses are undivided; haemal keel is broad with a single or divergent apophysis in the posterior end; subcentral foramina are usually placed close to the sagittal plane, usually small but can be enlarged or absent; the centrum length is longer than the neural arch width (cl > naw); the neural arch is longer than width (pr-po > naw) and the length is proportional to its high (pr-po = *c.* h).

REFERRED MATERIAL . — VPPLT-0067, an anterior-trunk vertebra (Fig. 3C); VPPLT-0068 (Fig. 3D), an anterior-trunk vertebra; VPPLT-0070, a posterior-trunk vertebra; VPPLT-0430, a mid-trunk vertebra; VPPLT-0799, a mid-trunk vertebra; VPPLT-0845, a fragmentary mid-trunk vertebra; VPPLT-0869, a posterior-trunk vertebra; VPPLT-0871, a fragmentary mid-trunk vertebra; VPPLT-1006, a mid-trunk vertebra (Fig. 3A, B); VPPLT-1160, a fragmentary posterior-trunk vertebra; VPPLT-1166, a posterior-trunk vertebra; VPPLT-1253, a posterior-trunk vertebra; VPPLT-1551, two associated mid-trunk vertebrae; VPPLT-1564, nine pre-cloacal articulated vertebrae together with seven associated and badly preserved fragments of rock matrix with ribs and vertebral fragments embedded (Fig. 5); VPPLT-1731, a fragmentary mid-trunk vertebra; VPPLT-1734, a mid-trunk vertebra; VPPLT-1735, four mid-trunk vertebrae fragments associated with a posterior-trunk vertebra (Fig. 3F); VPPLT-1738, a mid-trunk vertebra; VPPLT-1739, an anterior-trunk vertebra (Fig. 3E); VPPLT-1740, five mid-trunk vertebrae fragments associated with a posterior-trunk vertebrae and a post-cloacal vertebrae (Fig. 4).

Colombophis spinosus Hsiou, Albino & Ferigolo, 2010
(Fig. 6)

Colombophis spinosus Hsiou, Albino & Ferigolo, 2010: 371.

REVISED DIAGNOSIS. — Fossil snake with similar characteristics of *C. portai* but differs as most vertebrae are significantly shorter than high (pr-po < h), and shorter than wide (pr-po < pr-pr). The neural arch is wider than long (pr-po < naw). In addition, a well-developed neural spine is present, also restricted to the posterior margin of the neural arch, with an elliptical to triangular shape in dorsal view. The prezygapophyses are laterally oriented with well-developed process and the synapophyses present a weak division.

REFERRED MATERIAL. — VPPLT-0798, a mid-trunk vertebra (Fig. 6C); VPPLT-0864, a fragmentary mid-trunk vertebra; VPPLT-1093, eight associated mid-trunk vertebral fragments (Fig. 6D); VPPLT 1194, five associated mid-trunk vertebral fragments; VPPLT 1534 five unassociated vertebral fragments (Fig. 6F); VPPLT 1728, a mid-trunk vertebra (Fig. 6A, B); VPPLT-1741, four associated, anterior-trunk vertebrae (Fig. 6E).

Colombophis sp.

REFERRED MATERIAL. — More than 20 vertebral fragments (see Appendix 3), most of them correspond to partially complete or fragmentary precloacal vertebrae.

REMARKS

Listed specimens were assigned to *Colombophis* as they exhibit the following features: medium to large size (cl = *c.* 8 mm, po-po = *c.* 11 mm); slightly depressed neural arch with a shallow median notch on the posterior border; the neural spine is reduced and restricted to the posterior end of the neural arch; moderately inclined prezygapophyses which usually reach the zygosphene roof level; short prezygapophyseal process; paracotilar foramina present in most vertebrae; weakly divided synapophyses; broad haemal keel with small to absent subcentral foramina close to the sagittal plane and bear one or two small apophyses with a tubercular shape placed on the ventral margin on anteriorly to the condyle. Lateral foramina located near the base of the neural canal anteriorly to the neural arch constriction.

DESCRIPTIONS

Anterior-trunk vertebrae

These vertebrae are shorter (cl < h) than the pre-cloacal vertebrae for *Colombophis* spp. (*C. portai*, *C. spinosus*, and *C.* sp.). Despite being broken on most of the specimens, the hypapophyses are postero-ventrally oriented and located behind the sub-central foramina also, hypapophyses have a circular (Fig. 3D) or a flattened shovel-like shape (Figs 3E; 6E) in posterior view.

Mid-trunk vertebrae

These vertebrae are the largest and most distinctive of *Colombophis* spp. Prezygapophyses are anterolaterally oriented, and usually reach the zygosphene roof level. Ventrally, the haemal keel is broad, usually with a pair of small sub-central foramina placed anterior to the coronal plane (Figs 3A, B; 4A, B; 5I, J; 6A-C). The posterior end of the haemal keel usually presents a tubercular or bifid structure. Neural arch is broad and slightly depressed, visible from posterior region view. The zygantra possesses a deep foramen inside. Neural spines are restricted to the posterior region of the neural arch, being poorly developed (tubercle like) in *C. portai* (Figs 3A, B; 4A-D; 5G, H), but well developed in *C. spinosus* where the anterior edge of this structure rarely reach the coronal plane of the vertebra (Fig. 6A-D).

Posterior-trunk vertebrae

These vertebrae are easily recognized by the presence of subcentral paramedian lymphatic fossae, which create a notched

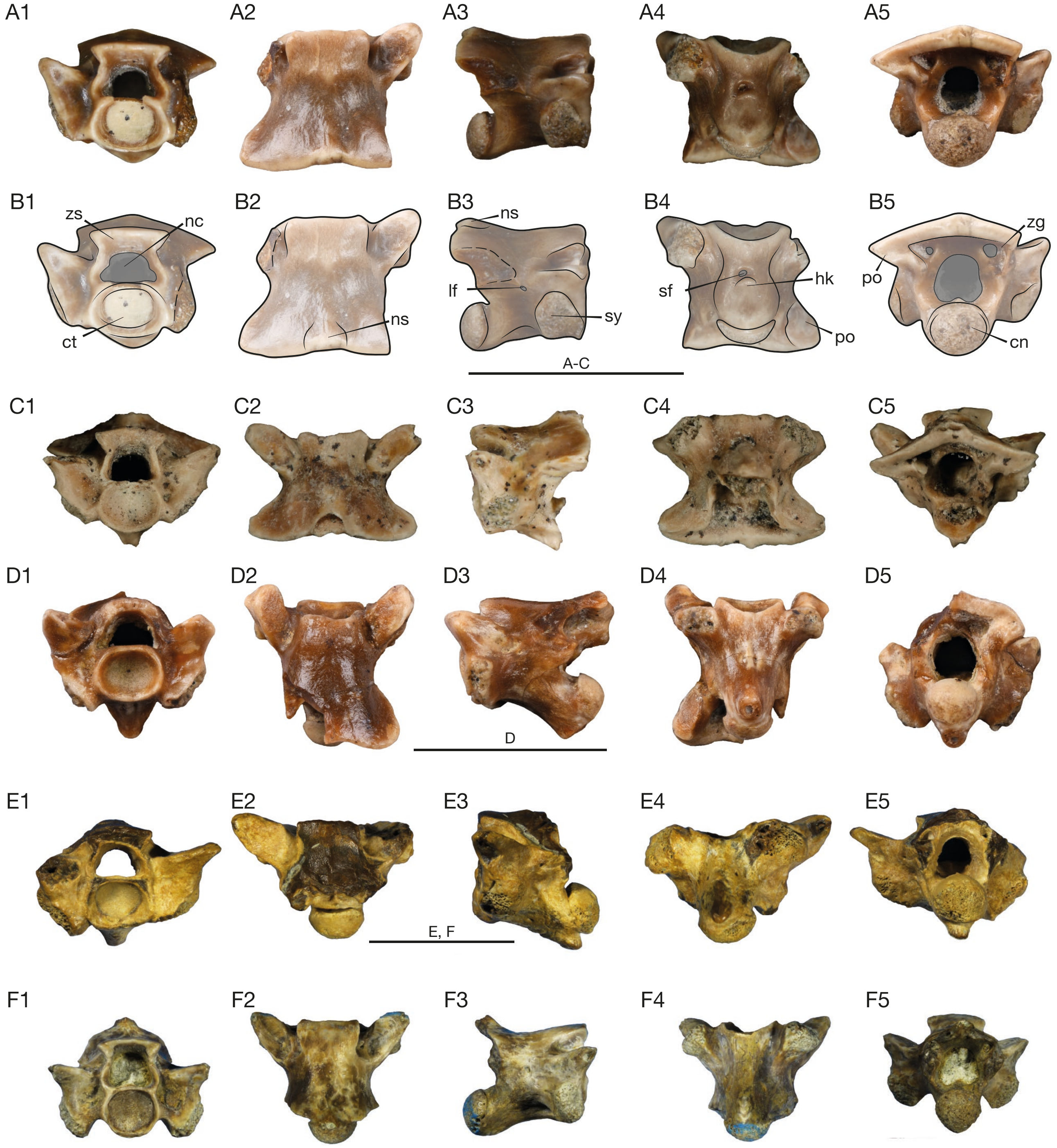

FIG. 3. — *Colombophis portai* Hoffstetter & Rage, 1977 specimens! **A**, **B**, VPPLT-1006; **C**, VPPLT-0067; **D**, VPPLT-0068; **E**, VPPLT-1739; **F**, VPPLT-1735. Views: **1**, anterior; **2**, dorsal; **3**, lateral; **4**, ventral, **5**, posterior views. Scale bars: 10 mm.

section between the cotyle and the synapophyses (Figs 3F; 4E, F; 6F). Pre-condylar constriction of the centrum is strong compared to anterior or mid-trunk vertebrae, which also makes the haemal keel less broad. Prezigapophyses are less inclined and do not reach the zygosphene level. In some specimens of *C. portai*, the posterior end of the haemal keel extends ventrally creating a structure similar to a hypapophysis (Fig. 4E,F)

Ribs

Ribs are only present in VPPLT-1564 specimen, unfortunately they are badly preserved. However, they seem to be fully ossified and slender, apparently longer than the vertebral centrum (Fig. 5C, D). The articular facet is smooth without a clear division on the articular facets, which corresponds to undivided synapophyses.

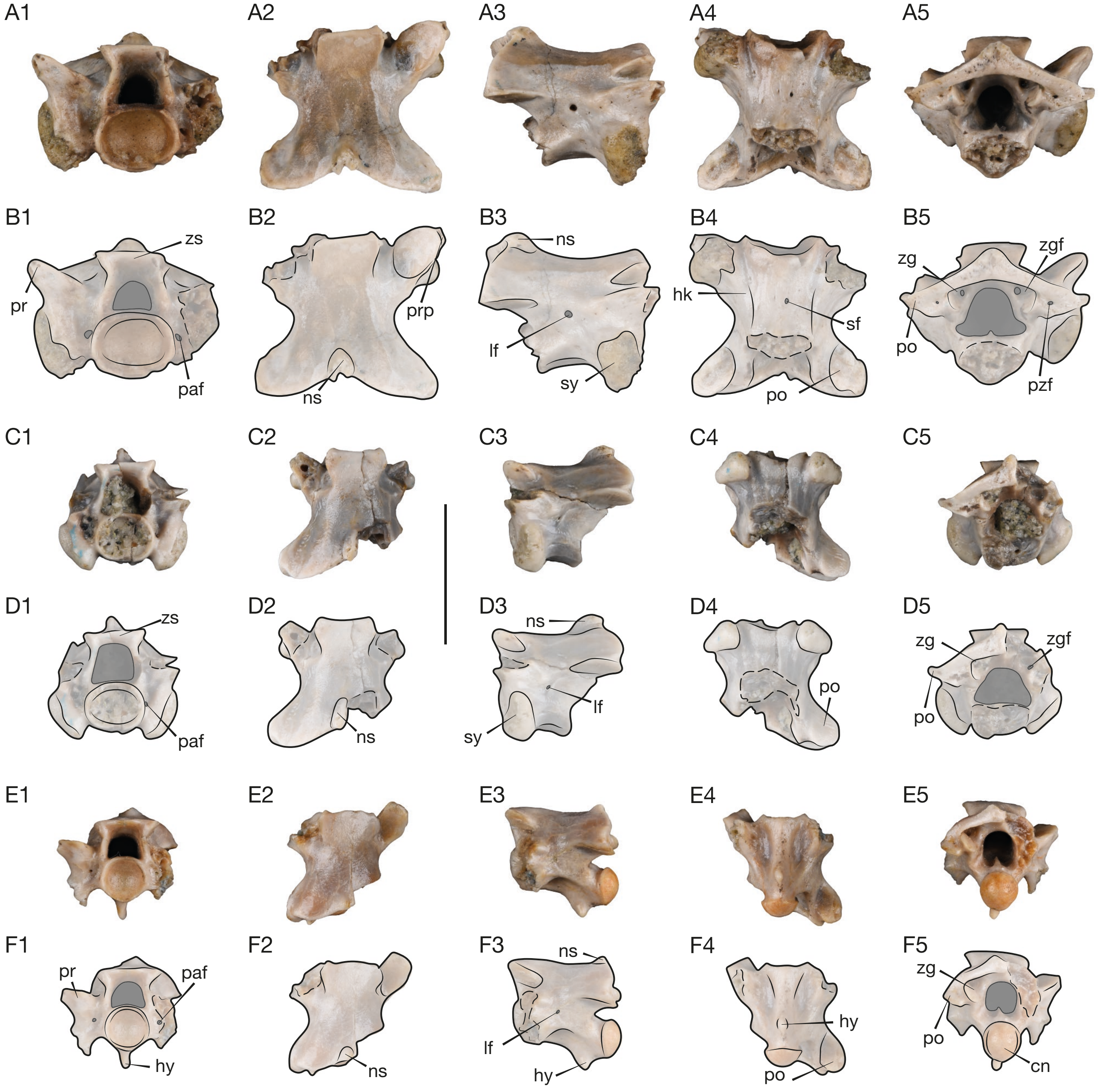

FIG. 4. — *Colombophis portai* Hoffstetter & Rage, 1977 VPPLT-1740 specimen, which consists of seven associated vertebrae: **A**, **B**, mid-trunk vertebra; **C**, **D**, mid-trunk vertebra; **E**, **F**, posterior-trunk vertebra. Views: **1**, anterior; **2**, dorsal; **3**, lateral; **4**, ventral; **5**, posterior views. Scale bar: 10 mm.

Post-cloacal vertebrae

A potential post-cloacal vertebra was found associated in the *C. portai* specimen VPPLT-1740. (Fig. 7A) This vertebra is considerably more vaulted than the associated precloacal vertebrae (Fig. 4). Posteroventral blade like structures are present, resembling paired haemapophyses. The subcentral foramina faces antero-ventrally near to the base of haemapophyses. Prezygapophyses are short and more laterally oriented, with little or no inclination. The neural spine is a relatively high lamina, considerably different from the neural spine shape of *Colombophis* spp.

Ontogenetic variation

Most of the specimens belong to adults as they are fully ossified and present a medium to large size. However, VPPLT-1006 specimen (Fig. 3A, B), may represent a juvenile or sub adult individual based on its small size and the ovoid shape of the cotyle (Hsiou *et al.* 2010), it also lacks a developed prezygapophyseal processes, it has a narrow zygosphene and a relatively large neural canal as it happens in extant and ancient snake neonates (LaDuke 1991; Xing *et al.* 2018).

Parazygantral foramina

Parazygantral foramina are present in both species of *Colombophis*, but only in two specimens (VPPLT-1728 and VPPLT-1740), as well as in the holotype MNHN-VIV-6 (Figs 4A, B; 6A, B; 7). These structures appear as a single foramen with or without small pits aside, which are interconnected internally with the foramen, (Fig. 8). Pits may appear also in specimens

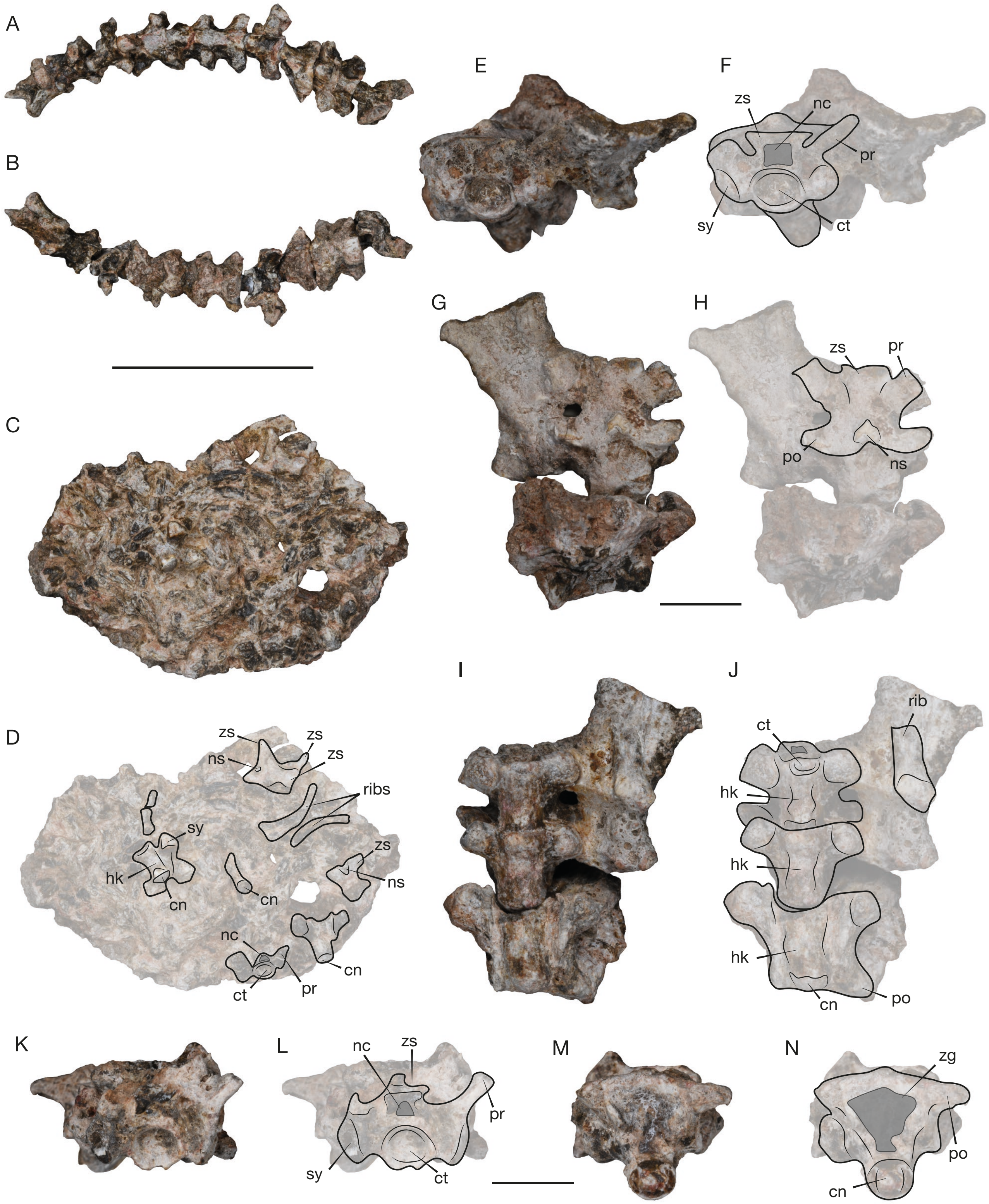

Fig. 5. — *Colombophis portai* Hoffstetter & Rage, 1977 VPPLT-1564 specimen: **A**, **B**, nine articulated precloacal vertebrae; **C**, **D**, several fragments of precloacal vertebrae and ribs embedded in the rock matrix; **E**-**I**, three articulated precloacal vertebrae in dorsal (**E**, **F**), anterior (**G**) and ventral (**H**, **I**) views; **J**-**M**, isolated vertebra in anterior (**J**, **K**) and posterior (**L**, **M**) views. Scale bars: A, B, 50 mm; C-N, 10 mm.

with no clearly defined foramen (Figs 6C; 8E, F). The internal structure of the vertebrae reveals that the dorso-posterior region of the vertebra (postzygapophyses and neural arch) is highly vascularized, where the parazygantral foramina and its associated pits are interconnected with the zygantral and lateral foramina. This feature is particularly visible in VPPLT-1728 specimen, where the internal structure is infilled with a denser material that creates a perfect endocast of the vertebra (Fig. 8G, H).

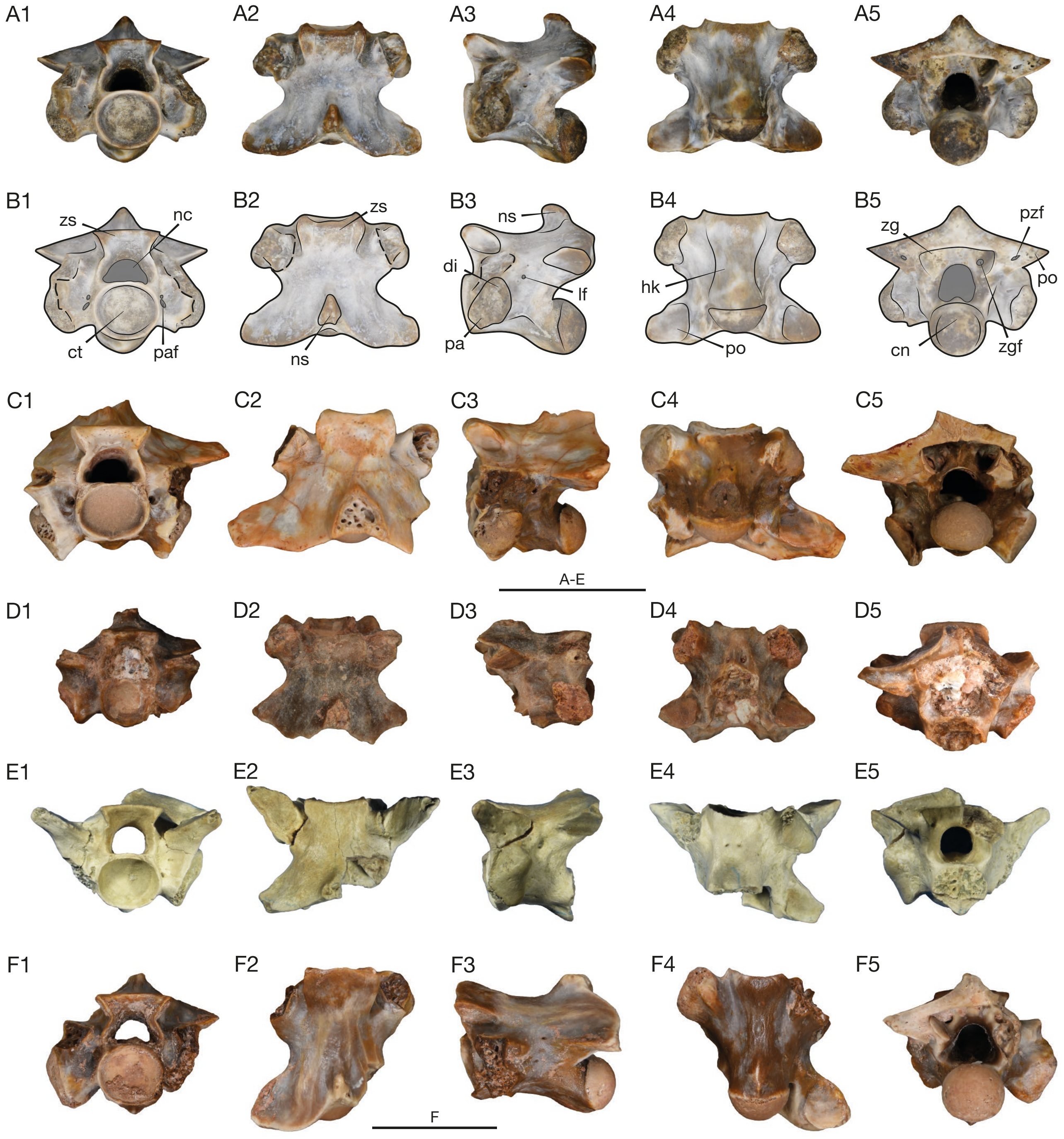

FIG. 6. — *Colombophis spinosus* Hsiou, Albino & Ferigolo, 2010 from the Tatacoa Desert: **A**, **B**, VPPLT-1728; **C**, VPPLT-0798; **D**, VPPLT-1093; **E**, VPPLT-1741; **F**, VPPLT-1534. Views: **1**, anterior; **2**, dorsal; **3**, lateral; **4**, ventral, **5**, posterior views. Scale bars: 10 mm.

DISCUSSION

VERTEBRAE MORPHOLOGY

The new *Colombophis* specimens from the Miocene La Victoria and Villavieja formations of Colombia described herein, provide new information regarding the anatomical features of the two valid taxa of the genus, *C. portai* and *C. spinosus*. The new findings include the occurrence of large parazygantral foramina in both species (Fig. 8), which is a feature considered as a synapomorphy of Madtsoiidae but present also in some basal snakes from Gondwana and some boids and colubrids (Gómez *et al.* 2019; Machado-Filho 2020; Singh *et al.* 2021, and references therein). However, the true nature of the parazygantral foramina in *Colombophis* remains debatable, considering that only have been discovered in few mid-trunk vertebrae, and apparently provided the same function of the small pits present in the parazygantral region of other specimens (Fig. 8E, F) in terms of vascularization of the vertebra.

Considering that the finding of new specimens contributes to a better understanding of the intra-columnar variation

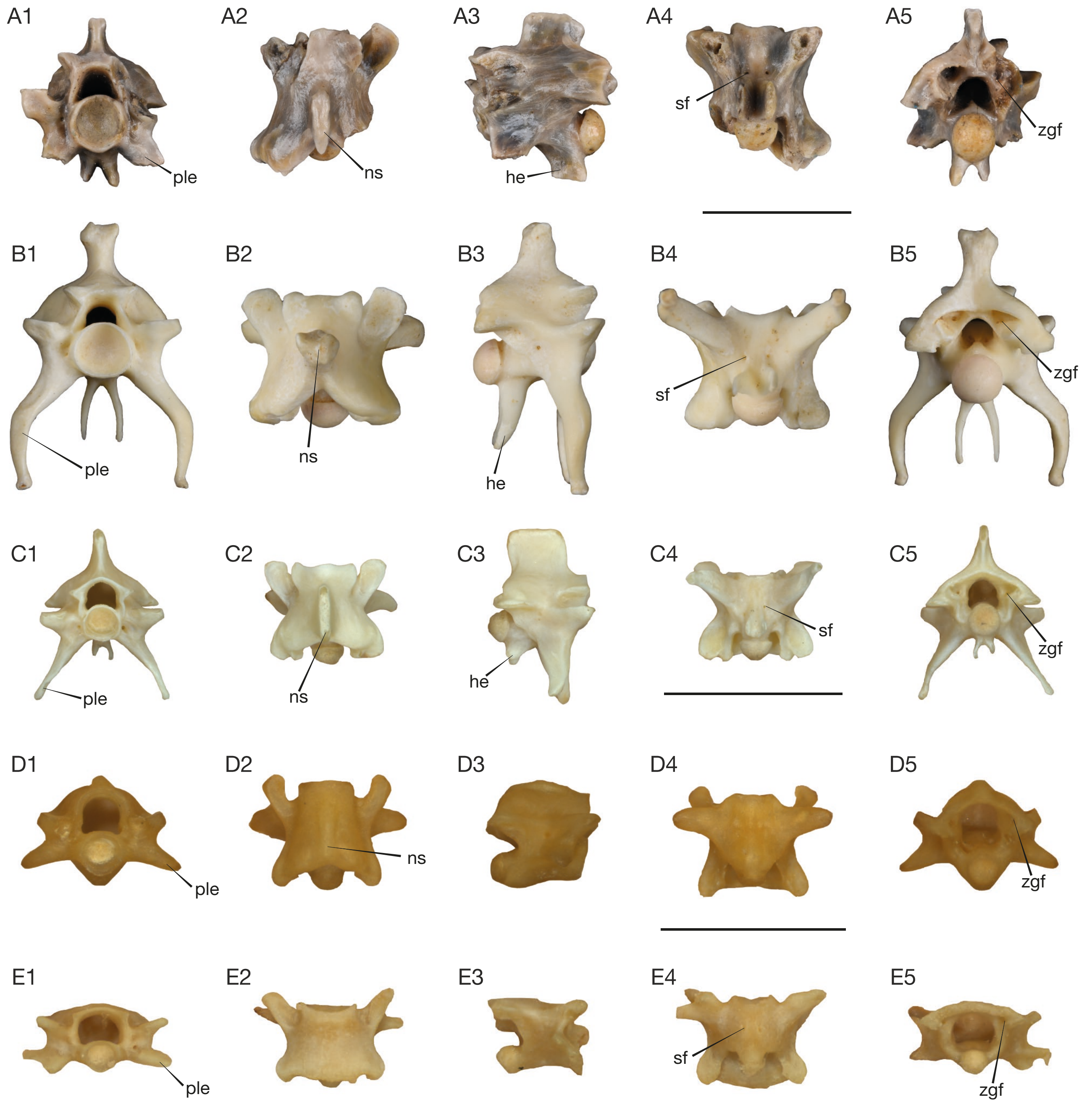

FIG. 7. — Comparison of VPPLT-1740 post cloacal vertebrae with extant aletinophidians: **A**, VPPLT-1740 specimen; **B**, *Boa* cf. *constrictor* Linnaeus, 1758, VPPLT-uncatalogued specimen; **C**, *Tropidophis melanurus* (Schlegel, 1837), UF-H-52001; **D**, *Anilius scytale* Linnaeus, 1758, UF-H-52001; **E**, *Cylindrophis ruffus* Laurenti, 1768, UF-H-52673. Views: **1**, anterior; **2**, dorsal; **3**, lateral; **4**, ventral, **5**, posterior views. Scale bars: A, B, 10 mm; C, 5 mm; D, E, 3 mm.

Colombophis spp. vertebrae, we tested the utility of the proportions used by Hsiou *et al.* (2010) to differentiate *C portai* from *C. spinosus* (see Fig. 9; Appendix 5). Our results suggest that the depression of the neural arch is similar for both species of *Colombophis*, as well as the proportion between the centrum length and the neural arch width or the proportions between the widths of the zygosphene and the cotyle (Fig. 9C-E). But we confirmed that in overall, vertebrae of *C portai* are more elongated (pr-po>h, pr-po> pr-pr), which is also reflected in a neural arch, which is much longer than wide (pr-po/naw > 1.5) in *C. portai*, than in *C. spinosus* (pr-po/naw < 1.5) (Fig. 9A, B, F), which represents another key feature to be considered in the diagnosis of this taxon.

With respect to the prezygapophyses inclination, it apparently presents a significant variation along the vertebral column, ranging from 18 to 33° (mean = 22.5°). These values are similar to inclinations reported for members of the genera *Anilius* Oken, 1816; *Cylindrophis* and *Uropeltis* Cuvier, 1829 (Head 2021) (Fig. 2C-E). Prezygapophyzes from the anterior-trunk vertebrae usually present an inclination of *c.* 18° that increases in middle-trunk vertebral series but reduces in the posterior-trunk.

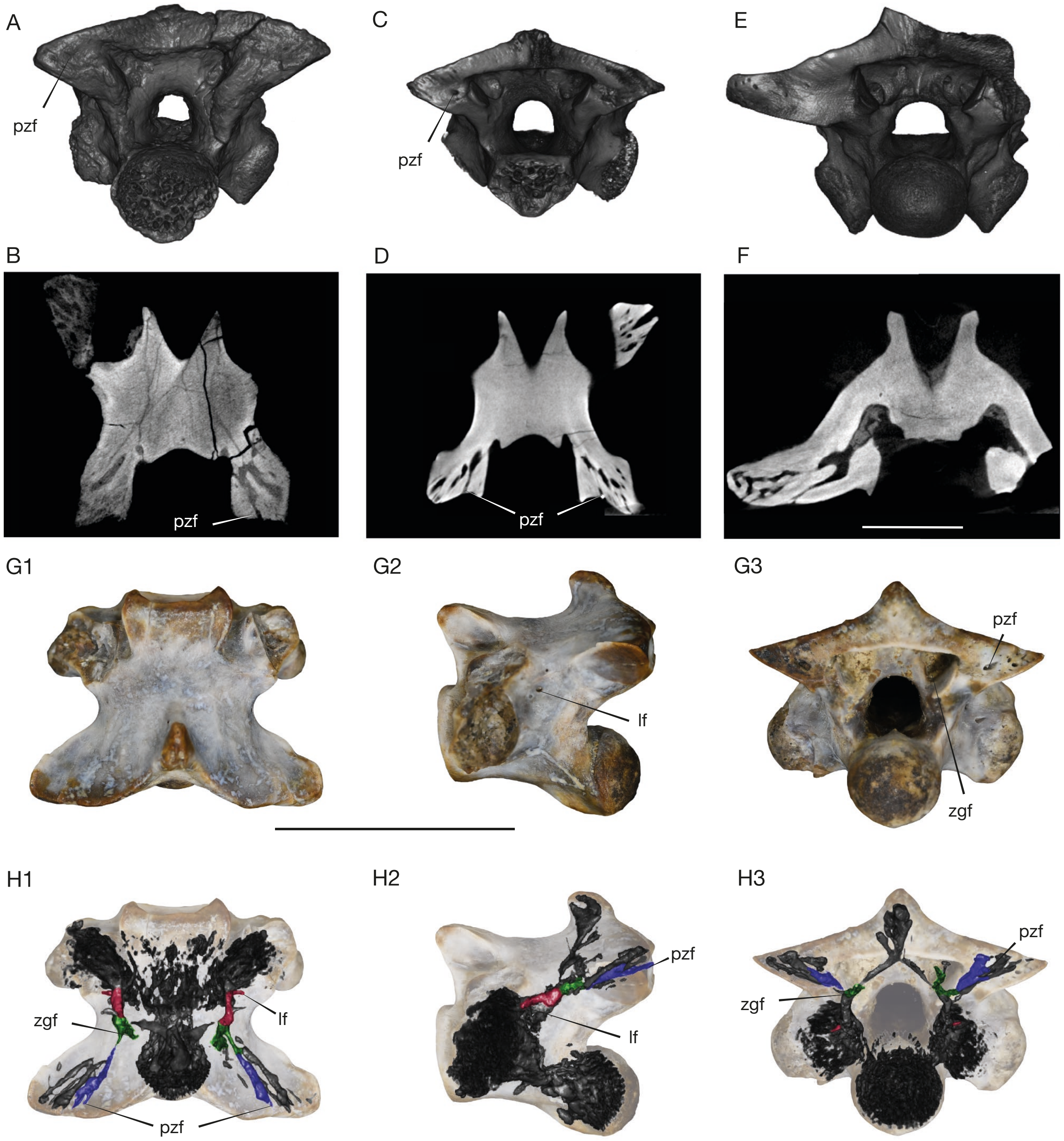

Fig. 8. — Parazygantral foramina in *Colombophis* spp. vertebrae: **A**, **B**, *C. portai* Hoffstetter & Rage, 1977, MNHN VIV-6 (see also Appendix 7); **C**, **D**, *C. portai*, VPPLT-1740; **E**, **F**, *C. spinosus* Hsiou, Albino & Ferigolo, 2010, VPPLT-798; **G**, *C. spinosus*, VPPLT-1728; **H**, endocast of VPPLT-1728 showing the internal vascularization of the vertebra. Colors: **blue**, parazygantral foramina; **green**, zygantral foramina; **red**, lateral foramina. Views: **1**, dorsal; **2**, lateral; **3**, posterior. Scale bars: A-F, 5 mm; G, H, 10 mm.

Regarding the post-cloacal vertebra associated with VPPLT-1740 specimen (Fig. 7A), it presents two distinctive heameapophyses which differ from the morphology of post-cloacal vertebrae of extant “anilioids” (Fig. 7D, E) and “scolecophidians”, for which these structures are poorly developed or absent (Hoffstetter & Gasc 1969; Szyndlar *et al.* 2008; Smith 2013). Furthermore, the overall morphology of the post-cloacal vertebra resembles those reported in macrostomous snakes (Garberoglio *et al.* 2019) (Fig. 7B, C). Additionally, this vertebra is larger than the posterior trunk vertebra (Fig. 4E, F) and presents a well-developed neural spine which contrast with the associated precloacal vertebrae (Fig. 4), that lacks this feature. For those reasons we exclude a potential taxonomic affinity with *Colombophis* spp. The association of the post-cloacal vertebra with *Colombophis* material could be the result of a collection bias or a taphonomic artifact.

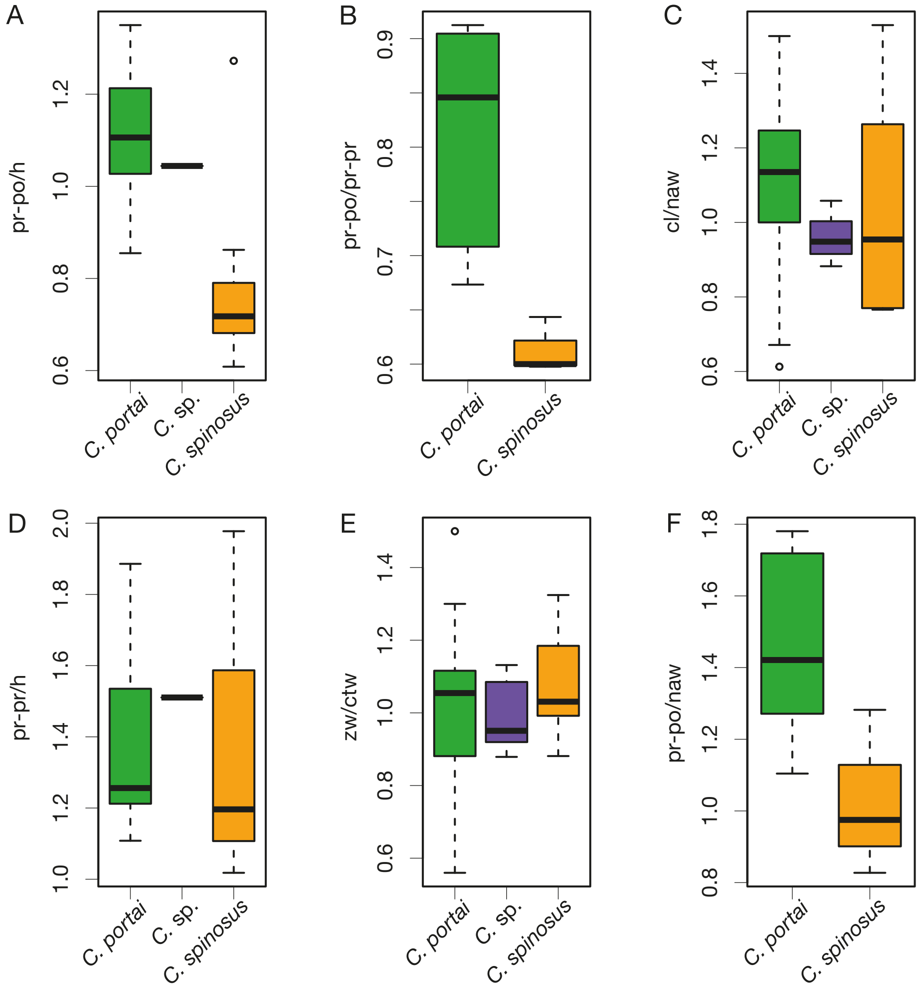

Fig. 9. — Comparison of vertebrae ratios for *Colombophis* spp.: **A**, pr-po/h, vertebra length to high ratio; **B**, pr-po/pr-pr vertebra length to width ratio; **C**, cl/naw, centrum length to neural arch width ratio; **D**, pr-pr/h vertebra width to high ratio; **E**, zw/ctw, zygosphene width to cotyle width ratio; **F**, pr-po/naw, vertebrae length to neural arch width ratio.

Phylogenetic considerations

Phylogenetic analysis using Maximum Parsimony produced 80 equally most parsimonious trees with very low supports (Consistency index CI = 0.459, Retention index RI = 0.405, Tree length = 9525). The strict consensus tree (Fig. 10) presents very low Bremer supports (Bremer support value < 1) however, we recovered different groups like Uropeltoidea, Booidea, Phythonidae, Tropidophidae and Bolyeridae with high bootstrap support (> 80), as has been demonstrated by molecular only phylogenies (e.g. Tonini *et al.* 2016; Da Silva *et al.* 2018). *C. portai* and *C. spinosus* are placed among the Alethinophidia clade, which agrees with the proposed affinities for these taxa by Hsiou *et al.* (2010) and Head (2021). But they are not placed together as part of a monophyletic clade (Fig. 10). However, considering the lower support of the tree, and that we are relying only with some vertebral characters (*c.* 12% of total morphological characters) we cannot discard the monophyly between the two species.

Paleoecology

Colombophis spp. pre-cloacal vertebrae morphology resembles those of fossorial or cryptozoic snakes (Hoffstetter & Rage 1977; Head 2021), based on the reduced neural spine, and the depressed neural arch. However, the relatively large size of the snake and development of a neural spine in *C. spinosus* makes a fossorial or cryptozoic lifestyle dubious (Scanferla 2016). Hsiou *et al.* (2010) suggested a potential semi-aquatic lifestyle (specially for *C. spinosus*) based on the paleoenvironment of northern South America during the Miocene, which was dominated by large waterbodies and channels, a wetland system called Pebas (Hoorn *et al.* 2010) and the vertebral similarities shared with the Cretaceous *Dinilysia patagonica* Smith-Woodward, 1901; which may have had a semi fossorial or semi-aquatic lifestyle (Caldwell & Albino 2001, but see Scanferla *et al.* 2010).

From the bone compactness analysis, we obtained a mean compactness in transverse section of Cts = 87.3 % (n = 6) which is similar to values reported by Houssaye *et al.* (2013) and Houssaye *et al.* (2019) for fossorial and aquatic snakes. However, such results don't have enough statistical support, as our analysis only show significant differences between Arboreal-Ground dwellers and

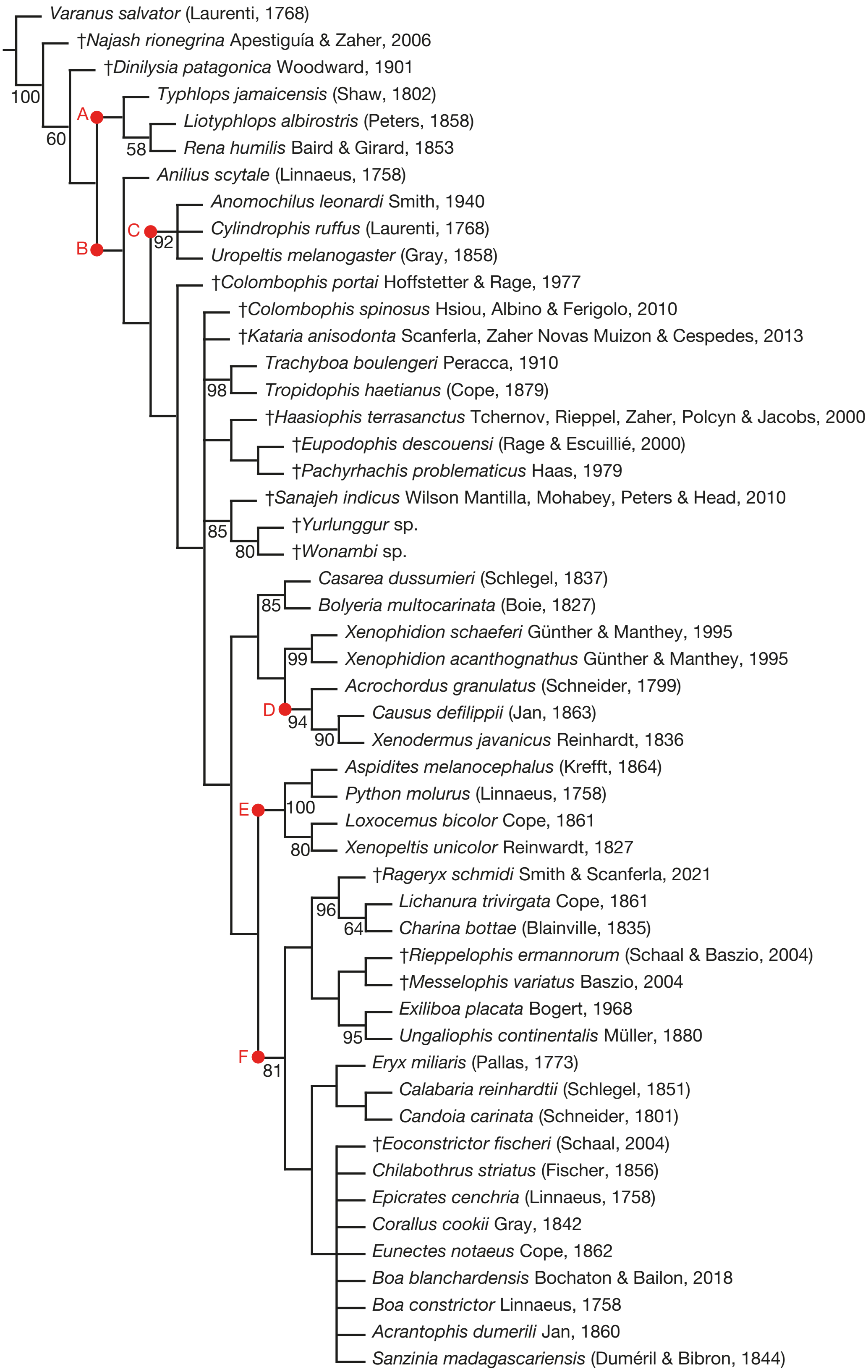

FIG. 10. — Phylogenetic relationships of *Colombophis* Hoffstetter & Rage, 1977. Strict consensus tree from 79 most parsimonious trees, bootstrap percentages > 50% are shown below the branches. Major clades: **A**, Scolecophidia; **B**, Alethinophidia; **C**, Uropeltoidea; **D**, Caenophidia; **E**, Pythonoidea; **F**, Booidea.

Aquatic snakes (see Appendix 2). More complete fossils are required to unveil *Colombophis* spp. ecological habits, as evidence suggests that skulls provide confident information to support ecological and phylogenetic hypotheses for fossil snakes (Scanferla 2016; Allemand *et al.* 2017; Da Silva *et al.* 2018).

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REFERENCES

Aguilera O. A., Riff D. & Bocquentin-Villanueva J. 2006. — A new giant *Purussaurus* (crocodyliformes, alligatoridae) from the upper Miocene Urumaco formation, Venezuela. *Journal of Systematic Palaeontology* 4 (3): 221-232. https://doi.org/10.1017/S147720190600188X

Albino A. M. & Brizuela S. 2014. — An overview of the South American fossil squamates. *The Anatomical Record* 297 (3): 349-368. https://doi.org/10.1002/ar.22858

Allemand R., Boistel R., Daghfous G., Blanchet Z., Cornette R., Bardet N., Vincent P. & Houssaye A. 2017. — Comparative morphology of snake (Squamata) endocasts: evidence of phylogenetic and ecological signals. *Journal of Anatomy* 231 (6): 849-868. https://doi.org/10.1111/joa.12692

Auffenberg W. 1967. — The fossil snakes of Florida. *Tulane Studies in Zoology* 10: 132-215. https://doi.org/10.5962/bhl.part.4641

Burbrink F. T., Grazziotin F. G., Pyron R. A., Cundall D., Donnellan S., Irish F., Keogh J. S., Kraus F., Murphy R. W., Noonan B., Raxworthy C. J., Ruane S., Lemmon A. R., Lemmon E. M. & Zaher H. 2020. — Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology* 69 (3): 502-520. https://doi.org/10.1093/sysbio/syz062

Cadena E. A., Vanegas A., Jaramillo C., Cottle J. M. & Johnson T. A. 2020a. — A new Miocene turtle from Colombia sheds light on the evolutionary history of the extant genus *Mesoclemmys* Gray, 1873. *Journal of Vertebrate Paleontology* 39 (5): 1-11. https://doi.org/10.1080/02724634.2019.1716777

Cadena E. A., Scheyer T. M., Carrillo-Briceño J. D., Sánchez R., Aguilera-Socorro O. A., Vanegas A., Pardo M., Hansen D. M. & Sánchez-Villagra M. R. 2020b. — The anatomy, paleobiology, and evolutionary relationships of the largest extinct side-necked turtle. *Science Advances* 6 (7): 1-14. https://doi.org/10.1126/sciadv.aay4593

Caldwell M. W. & Albino A. M. 2001. — Palaeoenvironment and palaeoecology of three cretaceous snakes: Pachyophis, Pachyrhachis, and Dinilysia. *Acta Palaeontologica Polonica* 46 (2): 203-218. https://doi.org/10.7939/R3rz8C

Carrillo-Briceño J. D., Reyes-Cespedes A. E., Salas-Gismondi R. & Sánchez R. 2019. — A new vertebrate continental assemblage from the Tortonian of Venezuela. *Swiss Journal of Palaeontology* 138 (2): 237-248. https://doi.org/10.1007/s13358-018-0180-y

Carrillo-Briceño J. D., Aguilera O. A., Benites-Palomino A., Hsiou A. S., Birindelli J. L. O., Adnet S., Cadena E.-A. & Scheyer T. M. 2021a. — A historical vertebrate collection from the Middle Miocene of the Peruvian Amazon. *Swiss Journal of Palaeontology* 140 (1): https://doi.org/10.1186/s13358-021-00239-7

Carrillo-Briceño J. D., Sánchez R., Scheyer T. M., Carrillo J. D., Delfino M., Georgalis G. L., Kerber L., Ruiz-Ramoni D., Birindelli J. L. O., Cadena E. A., Rincón A. F., Chavez-Hoffmeister M., Carlini A. A., Carvalho M. R., Trejos-Tamayo R., Vallejo F., Jaramillo C., Jones D. S. & Sánchez-Villagra M. R. 2021b. — A Pliocene–Pleistocene continental biota from Venezuela. *Swiss Journal of Palaeontology* 140 (1): https://doi.org/10.1186/s13358-020-00216-6

Cuvier G. 1829. — *Le Règne animal distribué d'après son organisation, pour servir de base à l'Histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Deterville, Paris. https://doi.org/10.5962/bhl.title.39612

Da Silva F. O., Fabre A. C., Savriama Y., Ollonen J., Mahlow K., Herrel A., Müller J. & Di-Poï N. 2018. — The ecological origins of snakes as revealed by skull evolution. *Nature Communications* 9 (1): 1-11. https://doi.org/10.1038/s41467-017-02788-3

Fedorov A., Beichel R., Kalpathy-Cramer J., Finet J., Fillion-Robin J.-C., Pujol S., Bauer C., Jennings D., Fennessy F., Sonka M. & Others 2012. — 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging* 30 (9): 1323-1341. https://doi.org/10.1016/j.mri.2012.05.001

Figueroa A., Mckelvy A. D., Grismer L. L., Bell C. D. & Lailvaux S. P. 2016. — A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PloS One* 11 (9): 1-31. https://doi.org/10.1371/journal.pone.0161070

Garberoglio F. F., Gómez R. O., Simões T. R., Caldwell M. W. & Apesteguía S. 2019. — The evolution of the axial skeleton intercentrum system in snakes revealed by new data from the Cretaceous snakes Dinilysia and Najash. *Scientific Reports* 9 (1276): 1-10. https://doi.org/10.1038/s41598-018-36979-9

Goloboff P. A. & Catalano S. A. 2016. — TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32 (3): 221-238. https://doi.org/10.1111/cla.12160

Gómez R. O., Báez A. M. & Rougier G. W. 2008. — An anilioid snake from the Upper Cretaceous of northern Patagonia. *Cretaceous Research* 29 (3): 481-488. https://doi.org/10.1016/j.cretres.2008.01.002

Gómez R. O., Garberoglio F. F. & Rougier G. W. 2019. — A new Late Cretaceous snake from Patagonia: Phylogeny and trends in body size evolution of madtsoiid snakes, *in* Folie A., Buffetaut E. , Bardet N., Houssaye A., Gheerbrant E. & Laurin M. (eds), Palaeobiology and palaeobiogeography of amphibians and reptiles: An homage to Jean-Claude Rage. *Comptes Rendus Palevol* 18 (7): 771-781. https://doi.org/10.1016/j.crpv.2019.09.003

Head J. J. 2021. — A South American snake lineage from the Eocene Greenhouse of North America and a reappraisal of the fossil record of "anilioid" snakes. *Geobios* 66-67: 55-65. https://doi.org/10.1016/j.geobios.2020.09.005

Head J. J., Sánchez-Villagra M. R., Aguilera O. A., Sánchez-Villagra M. R. & Aguilera O. A. 2006. — Fossil snakes from the Neogene of Venezuela (Falcón state). *Journal of Systematic Palaeontology* 4 (3): 233-240. https://doi.org/10.1017/S1477201906001866

Hecht M. K. & Laduke T. C. 1997. — Limbless tetrapods, Vertebrate Paleontology in the Neotropics, *in* Kay R. F., Madden R. H., Cifelli R. L. & Flynn J. J. (eds), *The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, London: 95-99.

Hoffstetter R. & Gasc J.-P. P. 1969. — Vertebrae and ribs of modern reptiles. *Biology of the Reptilia* 1 (5): 201-310.

Hoffstetter R. & Rage J. C. 1977. — Le gisement de vertébrés miocènes de la Venta (Colombie) et sa faune de serpents. *Annales de Paléontologie (Vertébrés)* 63 (2): 161-190.

Holman J. A. 2000. — *Fossil Snakes of North America: Origin, Evolution, Distribution, Paleoecology*. Indiana University Press, 357 p.

Hoorn C., Wesselingh F. P., Ter Steege H., Bermudez M. A., Mora A., Sevink J., Sanmartín I., Sanchez-Meseguer A., Anderson C. L., Figueiredo J. P. & Others 2010. — Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330 (6006): 927-931. https://www.science.org/doi/10.1126/science.1194585

Houssaye A., Boistel R., Böhme W. & Herrel A. 2013. — Jack-of-all-trades master of all? Snake vertebrae have a generalist inner organization. *Naturwissenschaften* 100 (11): 997-1006. https://doi.org/10.1007/s00114-013-1102-x

Houssaye A., Herrel A., Boistel R. & Rage J. C. 2019. — Adaptation of the vertebral inner structure to an aquatic life in snakes: Pachyophiid peculiarities in comparison to extant and extinct forms, *in* Folie A., Buffetaut E. , Bardet N., Houssaye A., Gheerbrant E. & Laurin M. (eds), Palaeobiology and palaeobiogeography of amphibians and reptiles: An homage to Jean-Claude Rage. *Comptes Rendus Palevol* 18 (7): 783-799. https://doi.org/10.1016/j.crpv.2019.05.004

Hsiou A. S., Albino A. M. & Ferigolo J. 2010. — Reappraisal of the south American Miocene snakes of the genus *Colombophis*, with description of a new species. *Acta Palaeontologica Polonica* 55 (3): 365-379. https://doi.org/10.4202/app.2009.1111

Ikeda T. 2007. — A comparative morphological study of the vertebrae of snakes occurring in Japan and adjacent regions. *Current Herpetology* 26 (1): 13-34. https://doi.org/10.3105/1345-5834(2007)26[13:Acmsot]2.0.Co;2

Laduke T. C. 1991. — The fossil snakes of pit 91, Rancho La Brea, California. *Contributions in Science* 424: 1-28. https://doi.org/10.5962/p.226807

Langston W. & Gasparini Z. 1997. — Crocodilians, *Gryposuchus*, and the south American gavials, *in* Kay R. F., Madden R. H., Cifelli R. L. & Flynn J. J. (eds), *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, London: 113-154.

Laurenti J. N. 1768. —*Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium Austriacorum*. Trattner, 217 p. https://doi.org/10.5962/bhl.title.5108

Linnaeus C. V. 1758. — *Systema naturae per regna tria naturae :secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentii Salvii, Stockholm, 881 p. https://doi.org/10.5962/bhl.title.559

Machado-Filho P. R. 2020. —*Descrição e comparação do esqueleto axial da Damília Boidae (Serpentes, Alethinophidia) [Doutorado*. Universidade Estadual Paulista, 170 p. http://hdl.handle.net/11449/192014

Marsh O. C. 1892. — Notice of new reptiles from the Laramie Formation. *American Journal of Science* 3 (257): 449-453. https://doi.org/10.2475/ajs.s3-43.257.449

Montes C., Silva C. A., Bayona G. A., Villamil R., Stiles E., Rodriguez-Corcho A. F., Beltran-Triviño A., Lamus F., Muñoz-Granados M. D., Pérez-Angel L. C., Hoyos N., Gomez S., Galeano J. J., Romero E., Baquero M., Cardenas-Rozo A. L. & Von Quadt A. 2021. — A Middle to Late Miocene Trans-Andean Portal: Geologic Record in the Tatacoa Desert. *Frontiers in Earth Science* 8: https://doi.org/10.3389/feart.2020.587022

Mora-Rojas L., Cárdenas A., Jaramillo C., Silvestro D., Bayona G., Zapata S., Moreno F., Silva C., Moreno-Bernal J., Jaramillo J. S., Valencia V. & Ibañez M. 2023. — Stratigraphy of a middle Miocene neotropical Lagerstätte (La Venta Site, Colombia), *in* Carrillo J. D. (ed.), Neotropical palaeontology: the Miocene La Venta biome. *Geodiversitas* 45 (6): 197-221. https://doi.org/10.5252/geodiversitas2023v45a6. http://geodiversitas.com/45/6

Nopcsa F. 1923. — *Eidolosaurus* und *Pachyophis*. Zwei neue Neocom-Reptilien. *Palaeontographica* 65: 97-154.

Oken L. 1816. — *Lehrbuch der Naturgeschichte*. Dritter Theil. *Zoologie*. Zweite Abtheilung. Fleischthiere, 1272 p. https://doi.org/10.5962/bhl.title.166403

Onary S. Y., Fachini T. S. & Hsiou A. S. 2017. — The snake fossil record from Brazil. *Journal of Herpetology* 51 (3): 365-374. https://doi.org/10.1670/16-031

Oppel M. 1811. — *Die ordnungen, familien und gattungen der reptilien als prodrom einer naturgeschichte derselben*. J. Lindauer, München. https://doi.org/10.5962/bhl.title.4911

Pyron R. A., Burbrink F. T. & Wiens J. J. 2013. — A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13 (1): https://doi.org/10.1186/1471-2148-13-93

Rage J. 1975. — Les serpents des Phosphorites du Quercy. *Palaeovertebrata* 6 (3-4): 274-303. https://palaeovertebrata.com/Articles/view/175

Rage J. C. 1984. — Serpentes, in Verlag G. F. (ed.), *Handbuch der Palaoherpetologie*. Stuttgart: 129-129.

Rage J.-C. 1998. — Fossil snakes from the Palaeocene of São José de Itaborai, Brazil. Part I. Madtsoiidae, Aniliidae. *Palaeovertebrata* 27 (3): 109-144. https://palaeovertebrata.com/Articles/view/228

Reynolds R. G., Niemiller M. L. & Revell L. J. 2014. — Toward a Tree-of-Life for the boas and pythons: Multilocus species-level phylogeny with unprecedented taxon sampling. *Molecular Phylogenetics and Evolution* 71: 201-213. https://doi.org/10.1016/j.ympev.2013.11.011

Scanferla A. 2016. — Postnatal ontogeny and the evolution of macrostomy in snakes. Royal Society Open Science 3 (11): https://doi.org/10.1098/rsos.160612

Scanferla A. & Smith K. T. 2020. — Exquisitely preserved fossil snakes of Messel: insight into the evolution, biogeography, habitat preferences and sensory ecology of early boas. Diversity 12 (3): 100. https://doi.org/10.3390/d12030100

Scanferla C. A. I., Fernández M. & Novas F. E. 2010. —*El origen y evolución temprana de las serpientes: análisis anatómico y filogenético de los ofidios Cretácicos y Paleógenos de la Patagonia y Bolivia*. Phd thesis, Facultad de Ciencias Naturales y Museo. https://doi.org/10.35537/10915/4305

Scheyer T. M., Aguilera O. A., Delfino M., Fortier D. C., Carlini A. A., Sánchez R., Carrillo-Briceño J. D., Quiroz L. & Sánchez-Villagra M. R. 2013. — Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nature Communications* 4 (1): 1-9. https://doi.org/10.1038/ncomms2940

Schneider C. A., Rasband W. S. & Eliceiri K. W. 2012. — Nih Image to ImageJ: 25 years of image analysis. *Nature Methods* 9 (7): 671-675. https://doi.org/10.1038/nmeth.2089

Singh N. P., Singh N. A., Sharma K. M., Patnaik R., Singh Y. P. & Chaudhary D. 2021. — A colubrid snake from the late Miocene of Kutch, Gujarat, India. *Journal of the Palaeontological Society of India* 66 (2): 381-387.

Smith-Woodward A. 1901. — On some extinct reptiles from Patagonia, of the genera *Miolania*, *Dinilysia*, and *Genyodectes*. *Proceedings of the Zoological Society of London* 70 (2): 169-184. https://doi.org/10.1111/j.1469-7998.1901.tb08537.x

Smith K. T. 2013. — New constraints on the evolution of the snake clades Ungaliophiinae, Loxocemidae and Colubridae (Serpentes), with comments on the fossil history of erycine boids in North America. *Zoologischer Anzeiger* 252 (2): 157-182. https://doi.org/10.1016/j.jcz.2012.05.006

Souza L. G., Bandeira K. L. N., Pêgas R. V., Brum A. S., Machado R., Guilherme E., Loboda T. S. & Souza-Filho J. P. 2021. — The history, importance and anatomy of the specimen that validated the giant *Purussaurus brasiliensis* Barbosa-Rodrigues 1892 (Crocodylia: Caimaninae). *Anais da Academia Brasileira de Ciências* 93: e20200369. https://doi.org/10.1590/0001-3765202120200369

Szyndlar Z., Smith R. & Rage J. C. 2008. — A new dwarf boa (Serpentes, Booidea, 'Tropidophiidae') from the Early Oligocene of Belgium: A case of the isolation of Western European snake faunas. Zoological *Journal of the Linnean Society* 152 (2): 393-406. https://doi.org/10.1111/j.1096-3642.2007.00357.x

Tonini J. F. R., Beard K. H., Ferreira R. B., Jetz W. & Pyron R. A. 2016. — Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation* 204: 23-31. https://doi.org/10.1016/j.biocon.2016.03.039

Vidal N., Delmas A.-S. & Hedges S. B. 2007. — The higher-level relationships of alethinophidian snakes inferred from seven nuclear and mitochondrial genes, *in* Henderson R. W. & Powell R. (eds), *Biology of the Boas and Pythons*. Eagle Publishing, LC, Eagle Mountain: 27-33.

Wagler J. 1828. — *Descriptiones et icones amphibiorum*. Sumtibus JG Cotttae [sic]. https://doi.org/10.5962/bhl.title.101419

Xing L., Caldwell M. W., Chen R., Nydam R. L., Palci A., Simões T. R., Mckellar R. C., Lee M. S. Y., Liu Y., Shi H., Wang K. & Bai M. 2018. — A mid-Cretaceous embryonic-to-neonate snake in amber from Myanmar. *Science Advances* 4 (7): https://doi.org/10.1126/sciadv.aat5042

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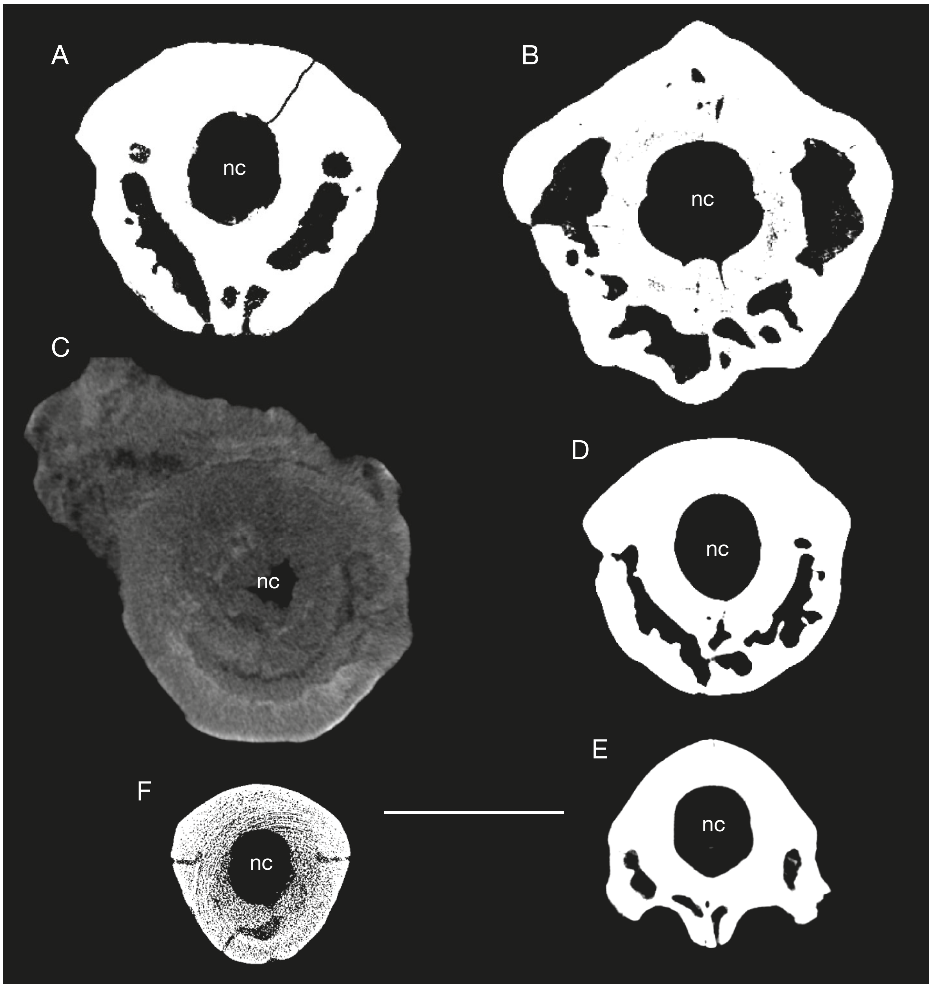
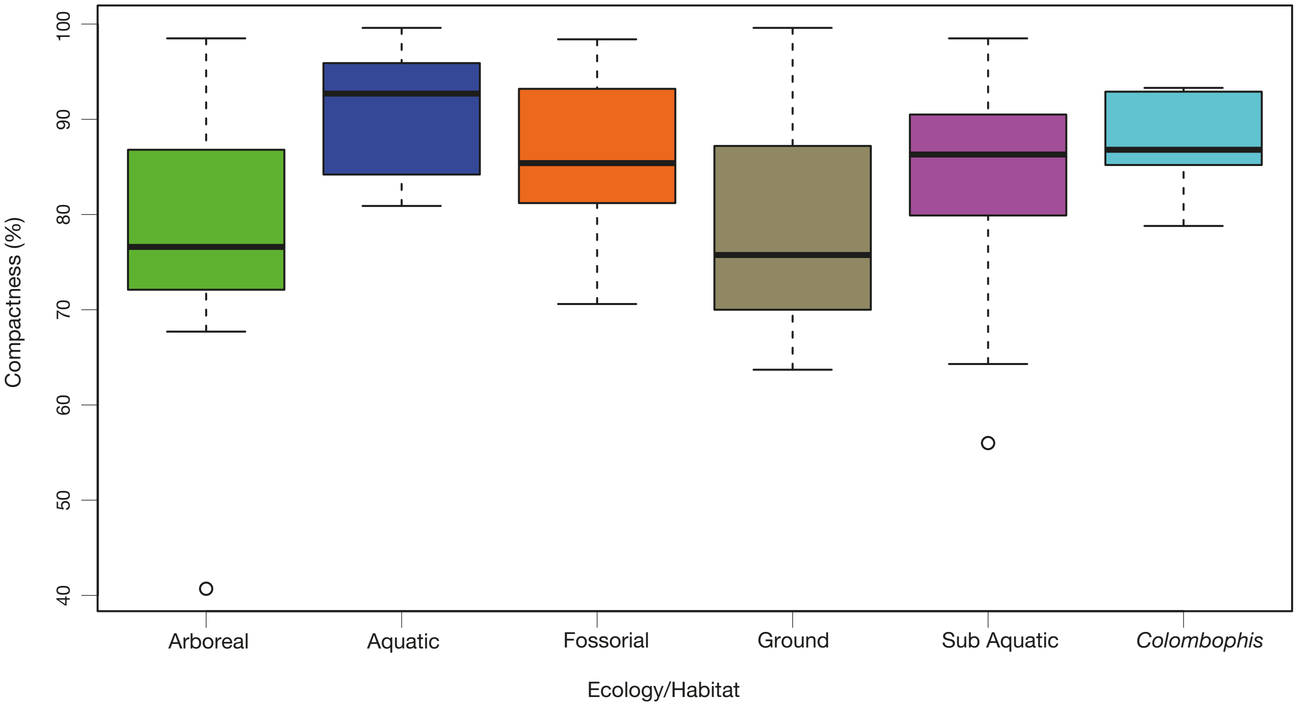
APPENDICES

APPENDIX 1. — Transverse sections of *Colombophis* spp. vertebrae: **A**, *C. portai* Hoffstetter & Rage, 1977, MNHN VIV-6 (see also Appendix 7); **B**, *C. spinosus* Hsiou, Albino & Ferigolo, 2010, VPPLT-798; **C**, *C. portai*, VPPLT-1564; **D**, **E**, *C. portai*, VPPLT-1740; **F**, *C. portai*, VPPLT-1006. Scale bar: 5 mm.



APPENDIX 2. — Comparison of bone compactness in transverse section (**Cts**) between different ecomorphs (Aquatic, Subaquatic, Arboreal, Ground dweller and Fossorial) and with *Colombophis* Hoffstetter & Rage, 1977 values.



Appendix 3. — List of *Colombophis* spp. specimens from La Victoria and Villavieja formations.

Id	zh	zw	nch	ncw	cth	ctw	coh	cow	pr–pr	prl	prw	naw	po–po	cl	pr–po	nsl	h	<pz	Position	Locality	lat.	long.	
Colombophis sp.																							
VPPLT-0064	1.3	3.2	2.1	2.3	2.6	3	2.4	2.6	–	1.8	3.5	–	–	4.6	–	–	–	17.5		–	–	–	
VPPLT-0071	2	–	2.9	–	–	–	4.5	4.6	–	3.5	6.1	–	–	8	11.8	–	11.3	15		Kilometro 121	3.325	–75.182	🌐
VPPLT-0577	0.8	2.8			–	–	–	–	–	–	–	–	–	–	–	–	–	–		Tatacoita	3.328	–75.100	🌐
VPPLT-0801	–	–	–	–	4	7	2.9	3	–	–	–	6.9	–	7.3	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0802	0.7	3.2	0	0	2.4	2.9	2.1	2.6	–	–	–	–	–	4.1	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0817	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0818	2	4.3	2.8	3.6	4	3.8	–	–	–	2.8	–	6.7	–	–	–	–	–	–	Mid	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0840	1.3	5.6	2.5	4	5.4	6.1	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0841	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0842	1.1	4.5	2.3	3.7	4.3	4.7	–	–	–	–	–	7.1	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0843	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0865	–	–	–	–	–	–	–	–	–	–	–	–	–	8.1	–	–	–	–	Ant	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0866	1.6	3.5	2.4	2.5	3	3.8	3.2	3.3	–	2.5	4	5.8	–	5.5	–	–	–	28		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0873	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0874	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0875	1.3	5.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0880	–	–	–	–	–	–	–	–	–	–	–	–	–	6.6	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0892	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-1201	2.1	5.8	2.9	4.2	6.1	6.6	5.1	5.6	–	–	–	11.9	–	10.5	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-1218	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-1241	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-1736	–	–	–	–	–	–	3.21	4	–	–	–	–	–	4.72	–	–	–	–		LA2 – Fishbeds	–	–	–
VPPLT-1739	1.68	4.21	2.21	3.11	3.76	4.46	3.26	3.84	12.25	2.82	4.5	–	–	6.97	–	–	8.11	16		LA2 – Fishbeds	–	–	–
VPPLT-1732			2.89	3.72	4.98	6.07	4.63	4.94	–	3.19	–	–	–	7.16	–	–	9.2			Behind Observatory – Fishbeds	–	–	–
Colombophis portai Hoffstetter & Rage, 1977																							
VPPLT-1738	1.18	4	1.73	2.94	4.35	5.41	3.46	4.15	13.39	3.09	3.67	–	–	8.4	–	–	7.1	23-24	Mid	La Manguita – Polonia redbeds	–	–	–
VPPLT-0067	1.5	3.00	2.1	2.2	2.7	2.00	–	–	7.7	1.6	2.9	4.8	7.6	–	5.3	–	6.2	18.5	Ant-Mid	Kilometro 121	3.325	–75.182	🌐
VPPLT-0068	–	–	1.6	3	2.3	3	2.3	2.3	8.2	2.5	1.7	4.3	–	6.1	7.39	–	7.4	28	Ant-Mid	Kilometro 121	3.325	–75.182	🌐
VPPLT-0070	2.2	–	2.1	2.5	3.2	3.4	–	–	–	3	1.9	4.6	–	–	8.1	–	6.4	23	Post	–	–	–	–
VPPLT-0430	–	4.5	3.5	2.8	3.9	4.3	–	–	–	4	2.6	–	–	–	–	–	–	29	?	Tatacoita	3.328	–75.100	🌐
VPPLT-0845	0.6	2.7			2.6	3.1	2	1.6	–	–	–	4.4	–	5.3	–	–	–	–	?	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-0869	–	3.9	2.5	3.2	2.8	3.5												–	Post	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-1006	1.3	3.4	2	3	2.7	3.2	2.4	2	–	1.5	2.9	4.7	–	4.1	–	–	6	22	Mid	Kilometro 121	3.325	–75.182	🌐
VPPLT-1160																		–	Mid-Post	Kilometro 121	3.325	–75.182	🌐
VPPLT-1166																		–	Post	Kilometro 121	3.325	–75.182	🌐
VPPLT-1253	–	–	0	0	2.7	3.2	2	2.2	–	–	–	–	–	5.9	–	–	–	–	Mid-Post	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐
VPPLT-1551	2.6	4.9	3.1	3.6	4.1	4.5	–	–	–	–	–	6.5	11.4	4.8	–	–	9.3	–	Mid	Kilometro 121	3.325	–75.182	🌐
	–	3	2.2	2.3	3.1	2.7	–	–	–	–	–	4.8	8.2	–	–	–	6.4	–	Mid				
VPPLT-1564					4.4	4.9	–	–	15	–	–	8.5	16.8	8.5	10.1			33.5	Mid	Valle de los Miocochilius–Salinas	3.309	–75.160	🌐
VPPLT-1735	1.35	4.12	2.3	2.82	3.48	3.57	3.08	2.84	10.5	1.95	3.16	5.76	–	7.38	–	–	6.84	20	Post	LA12	–	–	–
	–	–	–	3.17	3.95	4.29	–	–	–	2.52	3.93	–	–	6.65	–	–	3.78	18	?				
	–	–	–	–	5.12	–	4.37	–	–	–	–	–	–	9.43	–	–	4.54	–	?				
	1.51	3.31	2.87	3.52	–	3.96	3.5	3.89	–	2.86	4	–	–	7.16	–	–	10.6	18	?				
	–	–	–	–	5.08	5.69	–	–	–	2.79	4.03	–	–	8.26	–	–	9.32	13	?				
VPPLT-0799	2.29	6.24	2.75	3.77	6.82	6.27	5.02	5.99	–	3.28	4.05	–	–	11.37	–	–	9.5	14	Mid	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌐

Appendix 3. — Continuation.

Id	zh	zw	nch	ncw	cth	ctw	coh	cow	pr–pr	prl	prw	naw	po–po	cl	pr–po	nsl	h	<pz	Position	Locality	lat.	long.	
Colombophis portai (continuation)																							
VPPLT-1734	1.82	4.74	2.87	4.03	4.46	5.32	–	–	13.26	3.06	3.35	8.16	10.7	5	10.53	–	7.8	25-32	Mid	Los Hoyos	–	–	–
VPPLT-1731	1.64	4.43	3	3.3	4	5.28	4	4.63	–	–	–	–	–	7.74	–	–	7.96	–	?	Pachingo Fishbeds	–	–	–
VPPLT-1740	1.58	4.71	2.35	3.31	4.49	5.5	–	–	–	2.97	3.83	6.93	12.15	5.73	11.06	–	9.6	30	Mid	Quebrada La Venta – Fishbeds	–	–	–
	1	3.61	–	–	3.73	3.52	3.16	2.74	–	2.33	3	6.19	–	8.15		2.81	11	–		Quebrada La Venta – Fishbeds	–	–	–
	1.14	4.5	–	–	3.28	3.48	2.79	2.61	–	2.1	3.1	5.34	–	6.9		–	8.23	28.5	Post	Quebrada La Venta – Fishbeds	–	–	–
	1.71	4.2	–	–	3.49	3.92	–	–	–	–	–	5.96	–	4	–	–	6.81	–		Quebrada La Venta – Fishbeds	–	–	–
	1.88	3.84	2.47	3.46	5.37	6.86	4.86	5.7	–	–	–	–	–	9.19	–	–	10.63	–		Quebrada La Venta – Fishbeds	–	–	–
	1.93	4.64	2.51	3.47	–	–	–	–	–	–	–	7.44	–	–	–	–	6.8	–		Quebrada La Venta – Fishbeds	–	–	–
	–	–	–	–	–	–	5.15	6.39	–	–	–	–	–	9.63	–	–	4.23	–	?	Quebrada La Venta – Fishbeds	–	–	–
VPPLT-0063	1.5	3	2.1	2.8	1.7	3	2.7	2	8	1.5	3.1	4.1	–	5.1	7.3	–	6.6	–	–	–	–	–	–
VPPLT-0871	–	–	–	–	2.8	3.6	–	–	–	–	–	5	–	5.9	–	–	–	–	?	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌎
Colombophis spinosus Hsiou, Albino & Ferigolo, 2010																							
VPPLT-0798	2	6.1	2.8	5.7	4.2	5.6	3.8	5.1	–	–	–	11.1	–	8.5	–	–	11.7	–	Mid	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌎
VPPLT-0864	–	–	–	–	–	–	–	–	–	–	–	8.5	–	8.5	–	–	–	–	Mid-Post	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌎
VPPLT-1093	–	4.9	2.7	3.1	3.9	3.7	–	–	–	–	–	7.7	11.5	–	–	–	–	19.5	Mid	Tatacoita	3.328	–75.100	🌎
VPPLT-1194																		–	Mid	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌎
VPPLT-1534	1.1	5.5	3.8	4	4.6	4.8	4.1	4.3	–	–	–	6.8	–	10.4	–	–	11	31	Post	Morrongo – Distrito Tres Pasos	3.340	–75.107	🌎
VPPLT-1728	1.1	5.2	3.4	4.5	4.6	5.1	4	4.3	–	–	–	7.8	14.9	9.3	10	–	11.6	–	Mid	Cholupo – Libano	–	–	–
VPPLT-1741	1.74	4.8	2.33	3.51	5.01	5.4	–	–	–	–	–	–	–	6.34	–	–	9.06	–	?	Quebrada La Venta – Above ferruginous beds	–	–	–
VPPLT-1741	–	–	–	–	2.97	3.61	2.56	3.02	–	–	–	–	–	5.98	–	–	3.7	–	Mid-Post				
VPPLT-1741	–	–	–	–	3.52	3.62	3	3.57	–	2.71	4	5.83	–	7.78	–	–	6.11	17	Mid-Post				
VPPLT-1741	1.1	4.15	2.53	3	3.98	4.71	–	–	13.21	2.73	4.46	–	–	4.92	8.5	–	6.68	27	Mid				

Appendix 4. — Reference material from extant snakes skeletons.

Collection	Specimen	Family	Genus	Species
UR-CH	–	Amphisbaenidae	*Amphisbaena*	*Amphisbaena alba* Linnaeus, 1758
UF-H	11769	Aniliidae	*Anilius*	*Anilius scytale* (Linnaeus, 1758)
UF-H	11786	Aniliidae	*Anilius*	*A. scytale*
UF-H	62496	Aniliidae	*Anilius*	*A. scytale*
UF-H	11748	Cylindrophiidae	*Cylindrophis*	*Cylindrophis lineatus* Dennys, 1880
UF-H	51669	Cylindrophiidae	*Cylindrophis*	*C. ruffus* (Laurenti, 1768)
UF-H	52673	Cylindrophiidae	*Cylindrophis*	*C. ruffus*
UF-H	52698	Leptotyphlopidae	*Leptotyphlops*	*Leptotyphlops conjunctus* (Jan, 1861)
UF-H	11776	Leptotyphlopidae	*Rena*	*Rena dulcis* Baird & Girard, 1853
UF-H	11725	Tropidophiidae	*Trachyboa*	–
UF-H	11765	Tropidophiidae	*Tropidophis*	*Tropidophis melanurus* (Schlegel, 1837)
UF-H	52001	Tropidophiidae	*Tropidophis*	*T. melanurus*
UF-H	56844	Tropidophiidae	*Tropidophis*	*T. haetianus* (Cope, 1879)
UF-H	99429	Tropidophiidae	*Tropidophis*	*T. canus*
UF-H	11750	Uropeltidae	*Uropeltis*	–
VPPLT	–	Boidae	*Boa*	*Boa* cf. *constrictor* Linnaeus, 1758

Appendix 5. — Supplementary material (ZIP file) containing: 1) combined NEX matrix (NEX file); 2) combined measurements (TXT file); and 3) statistics (R file). https://doi.org/10.5852/geodiversitas2023v45a13_s5

Appendix 6. — Ecology and compactness values of extant snakes from Houssaye *et al*. (2013) and Houssaye *et al.* (2019). *, available in the MNHN thin section collection of Paleontology.

Family	**Taxon**	**Ecology**	**Collection reference**	**Cts**
Leptotyphlopidae	*Leptotyphlops bicolor* (Jan, 1860)	F	MNHN-RA-1993.3431a	93.2
Anomalepididae	*Typhlophis squamosus* (Schlegel, 1839)	F	MNHN-RA-1997.2042a	98.4
Typhlopidae	*Typhlops punctatus* Scortecci, 1928	F	ZFMK 56090b	81.2
Aniliidae	*Anilius scytale* (Linnaeus, 1758)	F	MNHN-RA-1996.2701b	78.2
	Anilius scytale	F	MNHN-RA-1997.2106a	95.8
Cylindrophiidae	*Cylindrophis ruffus* (Laurenti, 1768)	F	MNHN-RA-1998.201	96.1
	Cylindrophis maculatus (Linnaeus, 1758)	F	ZFMK 16 549b	89.4
Tropidophiidae	*Trachyboa boulengeri* Peracca, 1910	F	AH S0001b	83.1
Xenopeltidae	*Xenopeltis unicolor* Reinwardt, 1827	F	MNHN-RA-1990.5174	85.4
Pythonidae	*Bothrochilus boa* (Schlegel, 1837)	G	ZFMK 5203b	86.9
	Python reticulatus (Schneider, 1801)	G	MNHN-ZA-AC-2002-18	70.0
	Python reticulatus	G	MNHN SQ-Vert 12*	84.9
	Python reticulatus	G	MNHN SQ-Vert 13*	70.5
	Python curtus Schlegel, 1872	G	ZFMK 81 777b	99.6
	Morelia carinata (Smith, 1981)	Ar	AH S0002b	72.1
	Morelia viridis (Schlegel, 1872)	Ar	MNHN SQ-Vert 10*	79
Boidae	*Eryx jaculus* (Linnaeus, 1758)	F	MNHN-ZA-AC-2005-58	78.8
	Calabaria reinhardti Calabaria reinhardtii (Schlegel, 1851)	F	ZFMK 89190b	81.9
	Acrantophis madagascariensis (Duméril & Bibron, 1844)	G	ZFMK 86 469b	88.7
	Sanzinia madagascariensis (Duméril & Bibron, 1844)	Ar	ZFMK 70 428b	67.7
	Boa constrictor Linnaeus, 1758	G	ZFMK 54844b	79.2
	Corallus hortulanus (Linnaeus, 1758)	Ar	AH S0003b	40.7
	Epicrates cenchria (Linnaeus, 1758)	Ar	ZFMK 86470b	96.2
	Eunectes murinus (Linnaeus, 1758)	SA	MNHN-ZA-AC-1893-197	73.8
	Eunectes murinus	SA	MNHN SQ-Vert 9*	78.4
Acrochordidae	*Acrochordus javanicus* Hornstedt, 1787	SA	MNHN SQ-Vert 14*	77.5
	Acrochordus javanicus	SA	AH S0004b	56
	Acrochordus granulatus (Schneider, 1799)	EA	ZRC 2.2334	97.5
Pareatidae	*Pareas carinatus* (Wagler, 1830)	Ar	MNHN-RA-2000.4272	76.6
Viperidae	*Bitis arietans* Merrem, 1820	G	MNHN-ZA-AC-1885-246	77.4
	Bothrops lanceolatus Bonnaterre, 1790	G	MNHN-ZA-AC-1887-934	66.6
	Agkistrodon contortrix (Linnaeus, 1766)	G	AH S0005b	63.7
	Agkistrodon piscivorus (Lacépède, 1789)	SA	MNHN-RA-1990.3854	64.3
Colubrinae	*Chrysopelea ornata* (Shaw, 1802)	Ar	MCZ R 177291a	98.5
	Leptophis mexicanus Duméril, Bibron & Duméril, 1854	Ar	AH S0007b	86.8
	Salvadora grahamiae Baird & Girard, 1853	G	AH S0008b	70
	Orthriophis taeniurus (Cope, 1861)	G	ZFMK 5215b	72.8
	Elaphe quatuorlineata Lacepede, 1789	G	ZFMK 5218b	76.6
	Pantherophis guttatus (Linnaeus, 1766)	G	MNHN SQ-Vert 15*	64.3
	Rhinocheilus lecontei Baird & Girard, 1853	F	AH S0009b	86.4
Natricinae	*Xenochrophis piscator* Schneider, 1799	SA	ZFMK 74 287b	80.8
	Afronatrix anoscopus (Cope, 1861)	SA	ZFMK 65488b	81.1
	Natriciteres fuliginoides (Günther, 1858)	SA	AH S0010b	89.1
	Amphiesma stolatum (Linnaeus, 1758)	SA	ZFMK 18169b	95.5
	Thamnophis sauritus (Linnaeus, 1766)	G	AH S0011b	88.2
	Natrix natrix (Linnaeus, 1758)	SA	ZFMK 64057b	93
	Natrix tessellata (Laurenti, 1768)	SA	ZFMK 24680b	84.1
Homalopsidae	*Enhydris plumbea* (Boie, YEAR)	SA	ZFMK 44891	79.9
	Erpeton tentaculatum Lacépède, 1800	SA	AH S0012a	83.5
	Enhydris bocourti (Jan, 1965)	SA	MNHN-RA-1999.8361	87.7
	Enhydris sp.	SA	ZRC 2.5507b	98.5
	Myrrophis chinensis (Gray, 1842)	SA	ZRC 2.4805	86.3
	Phytolopsis punctata Gray, 1849	SA	ZRC 2.3554	87.2
	Cerberus rynchops (Schneider, 1799)	SA	MNHN-RA-1998.8583	96
	Homalopsis buccata (Linnaeus, 1758)	SA	ZRC 2.6411	98.5
	Bitia hydroides Gray, 1842	EA	ZRC 2.4374	98.9
	Cantoria violacea Girard, 1858	SA	ZRC 2.3672	90.5
	Fordonia leucobalia (Schlegel, 1837)	SA	MNHN-RA-1912.26	87.6

Appendix 6. — Continuation.

Family	Taxon	Ecology	Collection reference	Cts
Atractaspididae	*Atractaspis microlepidota* Günther, 1866	F	MNHN-RA-1999.8559	70.6
Elapidae	*Micrurus lemniscatus* (Linnaeus, 1758)	G	MNHN-RA-1997.2353a	88
	Naja nivea (Linnaeus, 1758)	G	AH S0013b	74.9
	Ophiophagus hannah (Cantor, 1836)	G	MNHN SQ-Vert 17*	64.4
	Ophiophagus hannah	G	MNHN-ZA-AC-2002-42b	72.1
	Dendroaspis jamesoni (Traill, 1843)	Ar	MNHN SQ-Vert 16*	72.4
	Bungarus fasciatus (Schneider, 1801)	G	ZFMK 61719b	87.5
	Hydrophis sp.	EA	MNHN SQ-Vert 18*	84
	Hydrophis sp.	EA	MNHN-ZA-AC-1887-897	84.2
	Pelamis platura (Linnaeus, 1766)	EA	AH S0014b	82.9
	Laticauda laticaudata (Linnaeus, 1758)	EA	ZFMK 36425	80.9
	Hydrophis major (Shaw, 1802)	EA	MNHN-RA-1990.4557	94.2
	Hydrophis peronii (Duméril, 1853)	EA	ZRC 2.2018	95.9
	Hydrophis ornatus (Gray, 1842)	EA	MNHN-RA-1994.6997	87.4
	Hydrophis jerdonii (Gray, 1849)	EA	ZRC 2.2105	96.1
	Hydrophis gracilis (Shaw, 1802)	EA	ZRC 2.2155	99.6
	Aipysurus duboisii Bavay, 1869	EA	MNHN-RA-1990.4519	93.5
	Aipysurus eydouxii (Gray, 1849)	EA	MNHN-RA-0.7704	91
	Aipysurus laevis Lacépède, 1804	EA	MNHN-RA-1990.4506	83.2
	Hydrophis curtus (Shaw, 1802)	EA	ZRC uncat	92.3
	Hydrophis elegans (Gray, 1842)	EA	MNHN-RA-0.1879	94
	Hydrophis stokesii (Gray, 1846)	EA	ZRC 2.2032	87.3
	Hydrophis schistosus Daudin, 1803	EA	ZRC 2.2043	93.1
Aniliidae	*Colombophis* sp.	U	MNHN-VIV-6	85.3
	Colombophis sp.	U	VPPLT 1006	92.9
	Colombophis sp.	U	VPPLT 1564	88.3
	Colombophis sp.	U	VPPLT-0798	78.8
	Colombophis sp.	U	VPPLT-1740A	85.2
	Colombophis sp.	U	VPPLT-1740B	93.3

Appendix 7. — Supplementary material (ZIP file) with the 3D model of the specimen MNHN-VIV-6 (*c.* 80 MB). The associated CT scan data is available on request from the curator. https://doi.org/10.5852/geodiversitas2023v45a13_s7