Newly discovered fossils provide novel insights on Cenozoic neotropical snakes

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This work is dedicated to my Grandma and my Mom, I owe all to them. I also dedicate this work to my father, friends and of course snakes.

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ABSTRACT

Snakes are a group of squamates with an enormous diversity in the Neotropics. However, the fossil record of this vertebrates is scarce in northern South America. Here I describe some fossil snakes from three different localities in Colombia. First, from the Miocene La Tatacoa Desert, I describe newly discovered precloacal vertebrae of the Alethinophidian snake *Colombophis*, including the first report of parazygantral foramina for this genus. Then, I describe a fossil jawbone of a large constrictor snake, which represents the first ophidian ever described for the Pliocene of Colombia. Finally, with the collaboration of different colleagues, we describe the biota of the Pleistocene locality of Pubenza, which includes turtles, rodents, armadillos and the first report of a fossil viper snake in Colombia.

RESUMEN

Las serpientes son un grupo de reptiles escamados con una enorme diversidad en el Neotrópico. Sin embargo, el registro fósil de estos vertebrados es escaso en el norte de Sur América. Aquí describo algunos fósiles de serpientes de tres diferentes localidades de Colombia. Primero, del Mioceno del Desierto de La Tatacoa, describo varias vértebras precloacales de la serpiente Aletinofidia *Colombophis*, incluyedo el primer reporte de forámenes parazigantrales para este género. Este nuevo material revela una extraña variación en el desarrollo de la espina neural a lo largo de la columna vertebral de este género, y sugiere un modo de vida diferente al fosorial. Luego, describo un fósil correspondiente a una mandíbula de una gran serpiente constrictora, el cual representa la primera descripción de un ofidio para el Plioceno de Colombia. Finalmente, en colaboración con diferentes colegas, describimos la biota de la localidad pleistocénica de Pubenza, donde se incluyen tortugas, roedores, armadillos y el primer reporte fósil de una víbora en Colombia.

INTRODUCTION

Snakes are a group of squamates characterized by having elongated bodies, lack of limbs and highly kinetic skulls (Lee & Palci, 2021 and references therein). They comprise more than 3900 species inhabiting different ecosystems (Guedes et al., 2018; Uetz, 2021), with one third of the extant species occurring in the Neotropics (Azevedo et al., 2019). In Colombia, this diversity is represented by 31 species of “Scolecophidians” (Blind snakes including the families Anomalepididae, Leptotyphlopidae and Typhlopidae); a single species of Tropidophiidae (*Trachyboa boulengeri*), Aniliidae (*Anilius scytale*), and Charinaidae (*Ungaliophis panamensis*); 10 species of Boidae; 30 species of Elapidae (including coral snakes and a sea snake); 20 species of Viperidae, and 239 species of the Colubridae (Uetz, 2021). Such diversity, contrasts with a very scarce fossil record in Colombia; as most of the neotropical fossil snakes known so far are from Brazil (Onary et al., 2017), Argentina (Albino & Brizuela, 2014) and Venezuela (Carrillo-Briceño et al., 2019, 2021; S. Onary et al., 2018, and references therein).

Fossil snakes from Colombia were first studied last century from middle to late Miocene specimens collected in La Tacatoa Desert, Huila Department (Fig. 1). From this region, two species were described; *Colombophis portai* based on a single vertebra, and *Eunectes stirtoni* based on two skull bones and some vertebrae (Hoffstetter & Rage, 1977). From the same region, Hecht & LaDuke (1997) reported fossils of undetermined aniliids, boids, colubroids and “scolecophidians”. Later, *Titanoboa cerrejonensis* was described from the late Paleocene locality of Cerrejón Coal Mine (Fig. 1) (Head et al., 2009), which in addition, represents the largest snake so far known, and it has an evolutionary importance as states a minimum divergence point of ~~at least~~ ~58 Ma between Boidae and Erycidae families (Head, 2015).

Other fossils snakes have been reported from the late Paleocene of Bogotá Formation (Bloch et al., 2008) and the early to middle Miocene of Castilletes Formation (Moreno et al., 2015) (Fig. 1), but without a full description and established systematic paleontology. A similar issue occurs with some Quaternary snakes, which have been assigned to generic level without the support of any description. As it is the case of the Curití locality (Fig. 1), where de Porta

(1965) reported some fossil vertebrae of the extant *Synophis*, while in Pubenza (Fig. 1), Correal-Urrego et al. (2005) reported the presence of *Epicrates* based on a single vertebra.

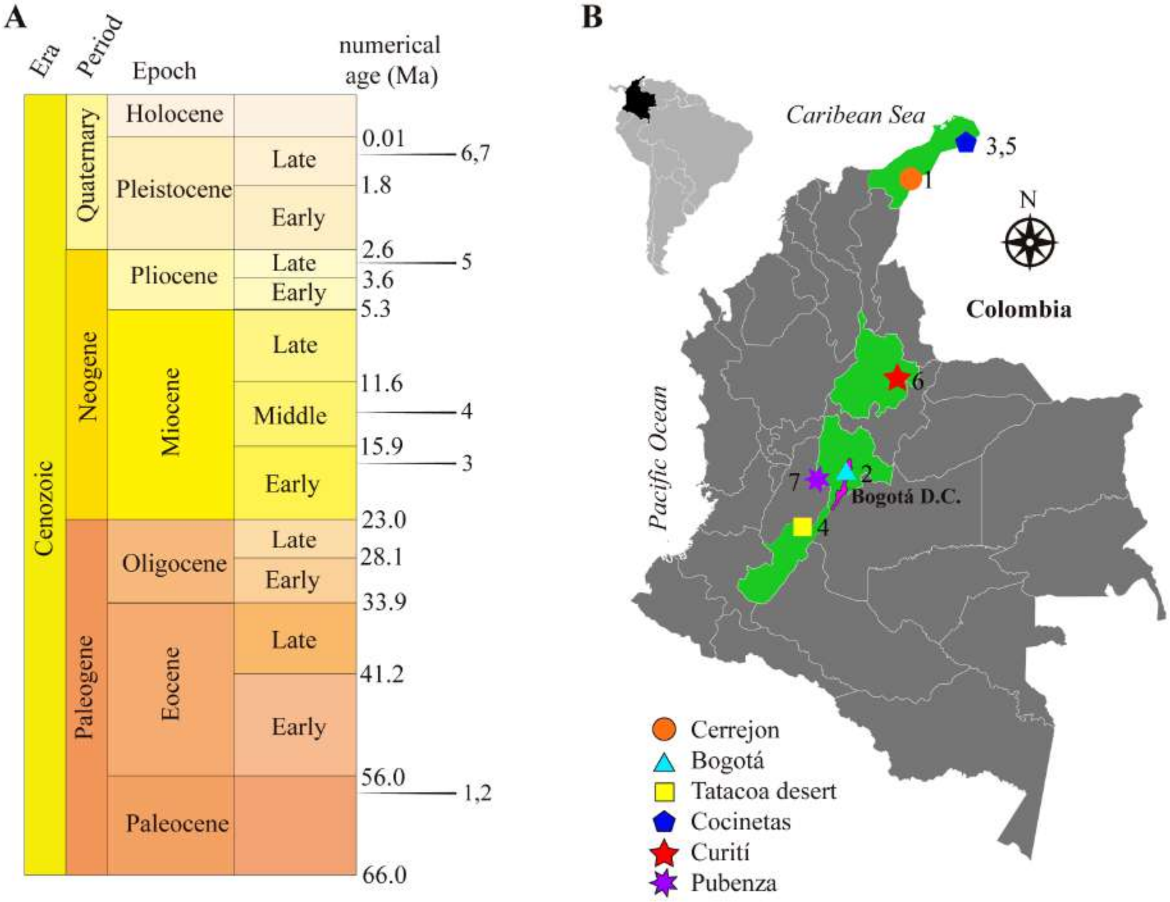

Figure 1. Fossiliferous localities were fossil snakes have been reported in Colombia. (**A**) Position of the localities in the Geologic Time Scale. (**B**) Map of Colombia showing the localities. **1**. Late Paleocene, Cerrejón Fm., Cerrejón Coal Mine, La Guajira Department; **2**. Late Paleocene, Bogotá Fm., Bogotá D.C.; **3**. Early to middle Miocene, Castilletes Fm., La Guajira Department; **4**. Middle Miocene, La Victoria Fm., La Tatacoa Desert, Huila Department; **5**. Late Pliocene, Ware Fm., La Guajira Department; **6**. Quaternary, Curití, Santander Department; and **7**. Late Pleistocene, Pubenza town, Cundinamarca Department.

Recent fieldwork activities in La Tatacoa Desert (Fig. 1), led by the Vigías del Patrimonio Paleontológico La Tatacoa foundation (VPPLT), several Colombian universities including Universidad del Rosario, Universidad de los Andes, EAFIT, and Universidad del Norte, in cooperation with the Smithsonian Tropical Research Institute (STRI) have discovered new and abundant fossil snake specimens. In addition, a fossil snake skull bone collected in the late Pliocene Ware Formation from a previous fieldwork at the Cocinetas basin, Guajira Peninsula (Fig. 1) was available to this study thanks to STRI.

Therefore, the aim of this thesis is the description of new fossil snakes from the aforementioned localities, establishing their systematic paleontology and discussing their potential phylogenetic and paleobiological implications according to their biogeographical context. **Chapter 1.** Includes the description of newly discovered fossils of the Miocene snake *Colombophis,* which affinities with major snake linages remain uncertain. The fossils reveal novel aspects on the caudal anatomy of the snake and suggest a particular ecology and taxonomic affinities of this snake. **Chapter 2.** In this chapter, I describe the compound bone of a large constrictor snake, which represents the first occurrence of this kind of ophidians for the Pliocene of Colombia. Finally, **Chapter 3**. It presents a research published in the Journal of Quaternary Science, where in collaboration with other paleontologists, we describe the Pleistocene biota of Pubenza locality, which includes the description of the first fossil viperid in Colombia.

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CHAPTER 1: Newly discovered fossils provide novel insights on the biology of the South American Miocene snake *Colombophis*.

Manuscript intended for Geodiversitas journal

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ABSTRACT

Colombophis was an alethinophidian snake that inhabited South America during the Miocene. Since its discovery, its position among the snake's phylogenetic tree have been controversial, as its description was based on postcranial elements only. Here, we describe several fossils, potentially representing 50 individuals belonging to this genus, which were discovered in La Tatacoa Desert, Colombia. In addition, we report for the first time the presence of parazygantral foramina in *Colombophis* vertebrae, which are similar to those observed on Madtsoiids. Despite most of the described fossils are fragmentary, they support the placement of this snake among the alethinophidians. In addition, considering the size of most vertebrae and the developmental degree of the neural spine in some specimens, we suggest a potential non-fossorial lifestyle.

KEYWORDS
Snakes, Colombophis, Miocene, South America

INTRODUCTION

During the Miocene, northern South America was the home of a considerable diversity of reptiles, principally turtles (Cadena et al., 2020; Cadena et al., 2019 and references therein) and crocodilians (Aguilera et al., 2006; Langston & Gasparini, 1997; Scheyer et al., 2013; Souza et al., 2021 and references therein). Regarding squamates, perhaps one of the most enigmatic fossils is the alethinophidian snake *Colombophis* Hoffstetter & Rage, (1977), reported for the first time in the famous locality of La Venta, La Tatacoa Desert, Villavieja town, Huila Department, Colombia (Fig. 1). The initial description of this genus and single species *C. portai* was based on around 40 precloacal vertebrae (Hoffstetter & Rage, 1977) (Fig. 2A). Since then, many other specimens have been discovered at the same region (Hecht & LaDuke, 1997), and in other middle to late Miocene localities from Venezuela, Brazil and Peru (Carrillo-Briceño et al., 2021a; Head et al., 2006; Hsiou et al., 2010) (Fig. 1A). Hsiou et al. (2010) proposed the existence of a second species *C. spinosus*, based on the unusual well-developed neural spine, not present on *C. portai*.

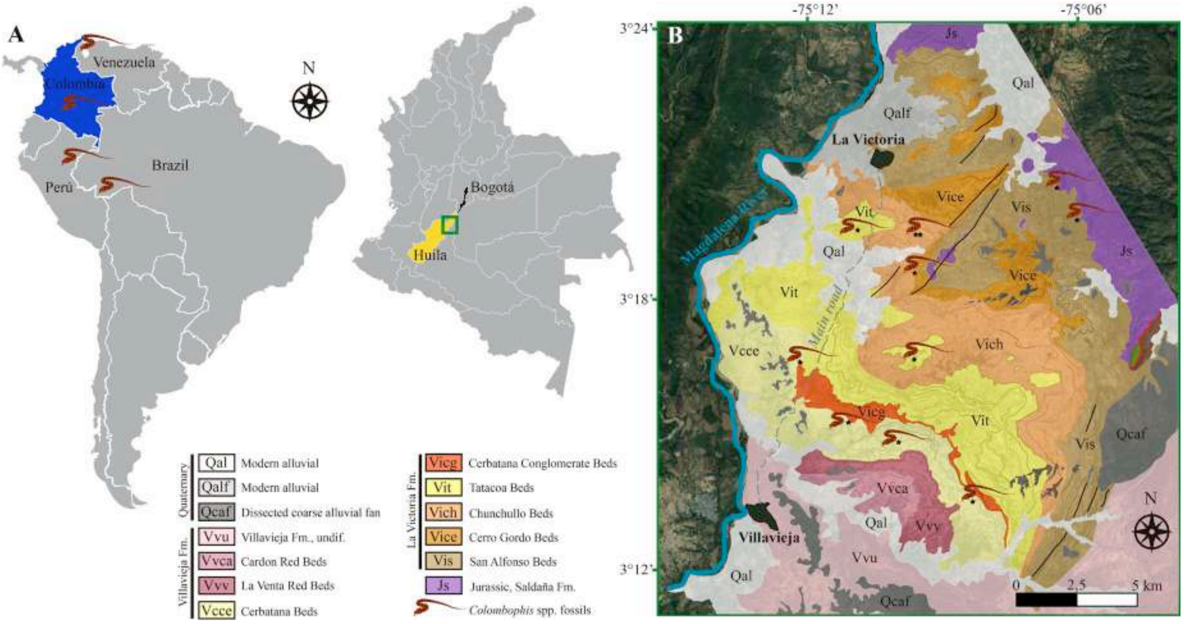

Figure 1. Location map of the different localities where *Colombophis* spp fossils have been collected in: (A) South America; (B) The Tatacoa Desert area. Stratigraphic units and geological map of the Tatacoa Desert were modified from Montes et al., (2021), Figure 4.

Since it was discovered, *Colombophis* has been considered an "anilioid" (Anilioidea) snake, a paraphyletic assemblage grouping extant *Anilius scytale* (red pipe snakes), Cylindrophidae (Asian pipe snakes), Anomochilidae (dwarf pipe snakes), Uropeltidae (shield-tail snakes) and the fossil taxa *Coniophis*, *Australophis*, *Eoanilius* and *Hoffstetterella* (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*, both taxa exhibiting a reduced neural spine, a depressed neural arch, highly inclined prezygapophysis, and the placement of the subcentral foramina (Fig 2A–E). However, molecular studies have demonstrated the paraphyly of "Anilioidea", and grouped Cylindrophiids, Anomochilids and Uropeltids into the superfamily Uropeltoidea, while Aniliidae is now considered as the sister group of Tropidophiidae (dwarft boas) (Burbrink et al., 2020; Figueroa et al., 2016; Pyron et al., 2013; Vidal et al., 2007).

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 primitive snakes (Hsiou et al., 2010) or homoplasies shared by other squamates with a fossorial or cryptozoic lifestyle (Fig. 2) (Head, 2021). Moreover, Head (2021) using six apomorphic characters mapped onto a molecular topology (following Pyron et al., 2013; Reynolds et al., 2014), found that *Colombophis* may have had affinities with extant Aniliidae or Uropeltidae instead.

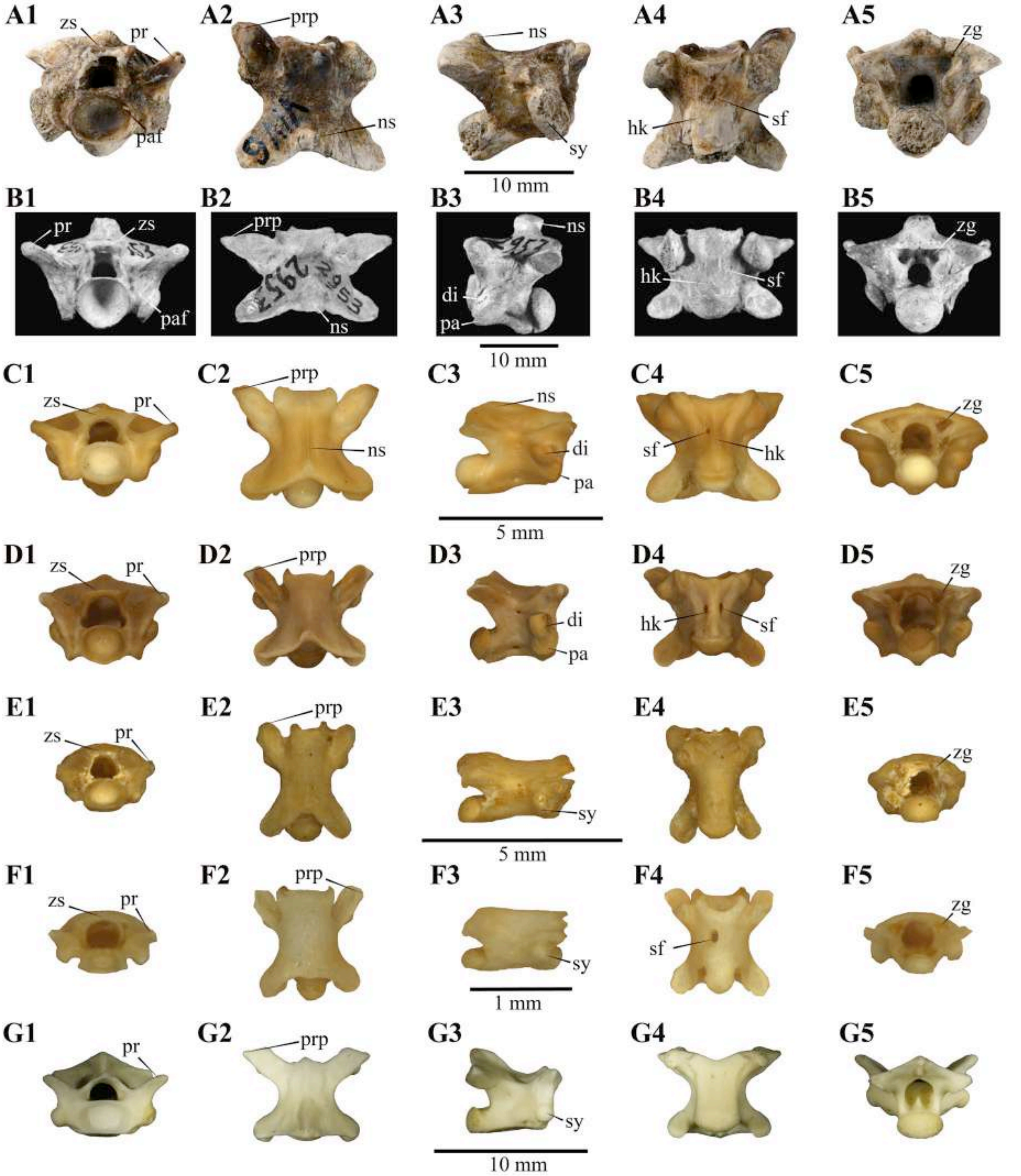

Figure 2. Comparison of *Colombophis portai* mid-trunk vertebrae with extant fossorial squamates. (**A**) *Colombophis portai*, MNHN-VIV-6; (**B**) *Colombophis portai*, UFAC-PV-2953; (**C**) *Anilius scytale*, UF-H-52001; (**D**) *Cylindrophis ruffus* UF-H-52673; (**E**) *Uropeltis*, UF-H-11750; (**F**) *Rena dulcis*, UF-H-11776; (**G**) *Amphisbaena alba*, UR-uncatalogued specimen. Views: (1) anterior, (2) dorsal, (3) lateral, (4) ventral and (5) posterior views.

Recent fieldwork activities led by several Colombian and international universities and 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 50 fossil vertebrae from potentially the same number of individuals that reassemble the vertebral morphology of *Colombophis.* These fossils have been found in 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.

MATERIALS AND METHODS

Abbreviations

INSTITUTIONAL ABBREVIATIONS:
AMU-CURS, Colección Alcaldía de Urumaco, Urumaco, Venezuela; **IGM**, Museo Geológico Nacional José Royo y Gómez, Servicio Geológico Colombiano (former INGEOMINAS), Bogotá, Colombia; **MPNHN**, Muséum National d'Historie Naturelle, Paris, France; **UF-H**, Herpetological collection, Florida Museum of Natural History, University of Florida, Gainesville, USA; **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; **ple**, pleurapophysis; **po**, postzygapophysis; **pr**, prezygapophysis; **pzf**, parazygantral foramen; **sf**, sufcentral foramen; **zg**, zygantrum; **zs**, zygosphene.
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; **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.

Fossils and extant specimens

All fossils studied (see Supplementary Table 1) are housed at the VPPLT collection, and were collected from La Victoria and Villavieja formations, which represent the Serravallian age (middle Miocene), between ~ 12.2 and 13.7 Ma (Montes et al., 2021).

Comparative material used in this study includes the postcranial elements from different specimens of extant Aniliidae, Cylindrophidae, Uropeltidae, Tropidophiidae and "Scolecophidians", which are listed on Supplementary Table 2. Additionally, we used morphological descriptions of *Anilius scytale* and *Cylindrophis ruffus* from Carrillo-Briceño, et al. (2021b) and Ikeda (2007) respectively.

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 parts of the vertebrae which are relevant for vertebrae identification and calculate some vertebral proportions 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 place *Colombophis* into a phylogenetic context, we employed a modified version of the morphological matrix of Scanferla & Smith (2020), which includes 201 osteological characters and 49 terminal taxas including fossil snakes, and representatives of extant "scolecophidians", "anilioids" and macrostomous snakes. 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.

We performed a maximum parsimony analysis using TNT (Tree Analysis using New Technology) V 1.5 (Goloboff & Catalano, 2016). 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.

SYSTEMATIC PALEONTOLOGY

Order SQUAMATA (Oppel, 1811)
Suborder SERPENTES (Linnaeus, 1758)
Infraorder ALETHINOPHIDIA (Nopcsa, 1923)
Genus *Colombophis* (Hoffstetter & Rage, 1977)
Colombophis portai Hoffstetter & Rage, 1977
(Figures 3–5)

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 precloacal 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 vertebra and a post-cloacal vertebrae (Fig. 4).

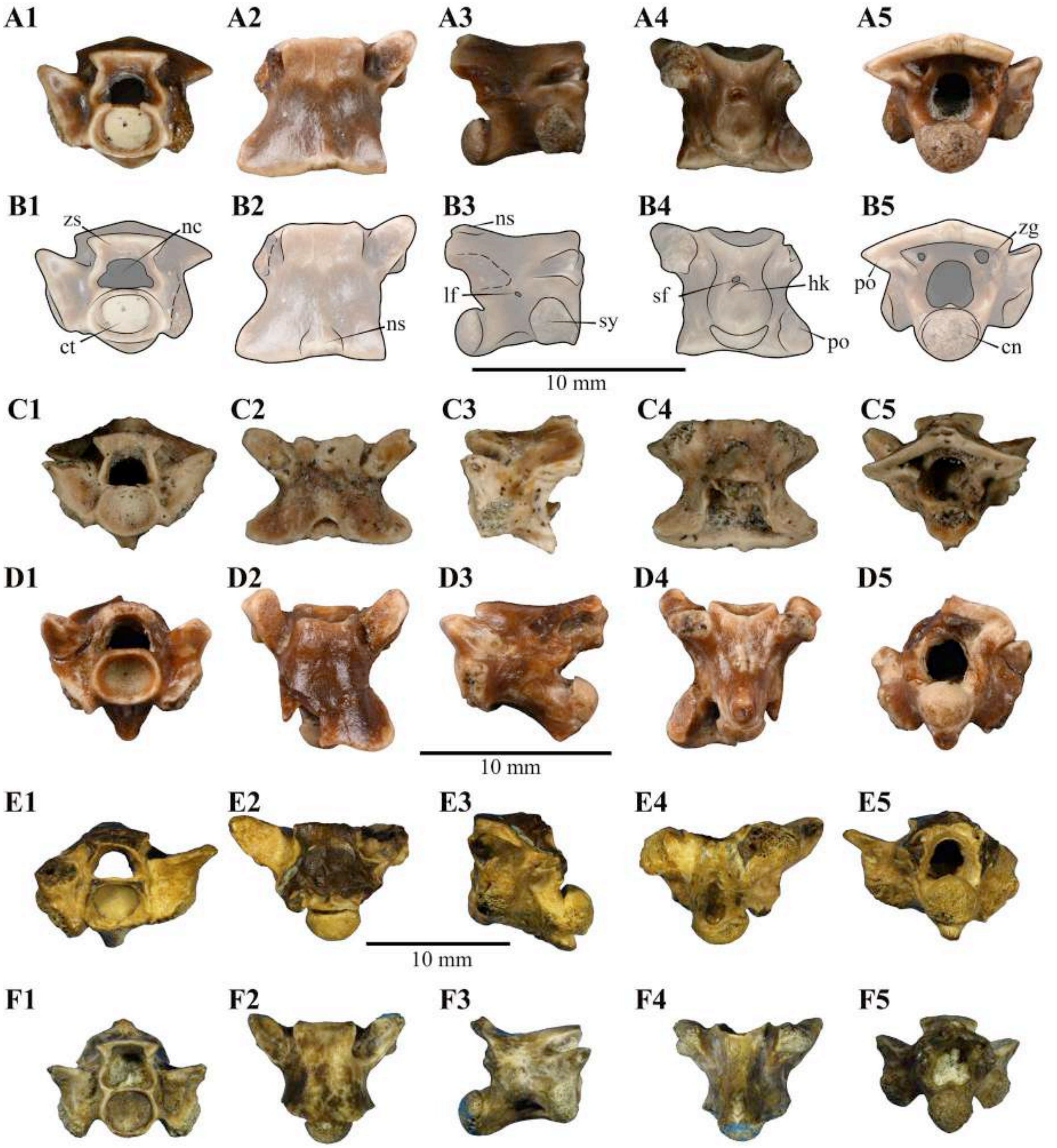

Figure 3. *Colombophis portai* specimens. (**A–B**) VPPLT-1006; (**C**) VPPLT-0067; (**D**) VPPLT-0068; (**E**) VPPLT-1739; (**F**) VPPLT-1735. Views: **(1)** anterior, **(2)** dorsal, **(3)** lateral, **(4)** ventral and **(5)** posterior views.

Remarks — Vertebrae are in overall medium to large (cl~5-11 mm). 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~h). Also, most vertebrae present a reduced neural spine located on the posterior margin of the neural arch, anterolaterally oriented prezygapophyses with a well-developed process and undivided synapophyses.

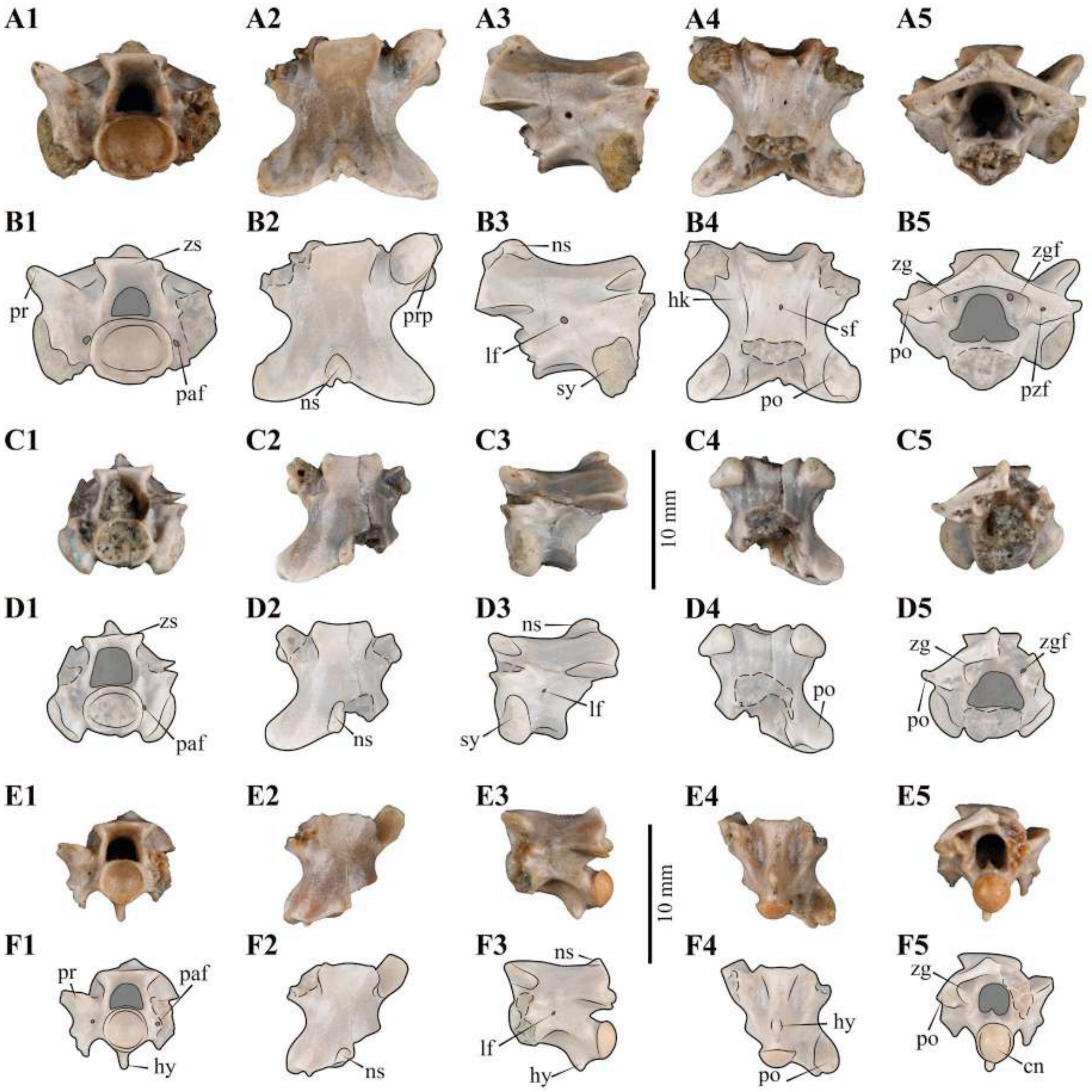

Figure 4. *Colombophis portai* VPPLT-1740 specimen, which consists of seven associated vertebrae. (**A–B**) mid-trunk vertebra; (**C–D**) posterior-trunk vertebra (**E–H**) caudal vertebrae. Views: **(1)** anterior, **(2)** dorsal, **(3)** lateral, **(4)** ventral and **(5)** posterior views.

Colombophis spinosus Hsiou et al., 2010
(Figure 6)

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).

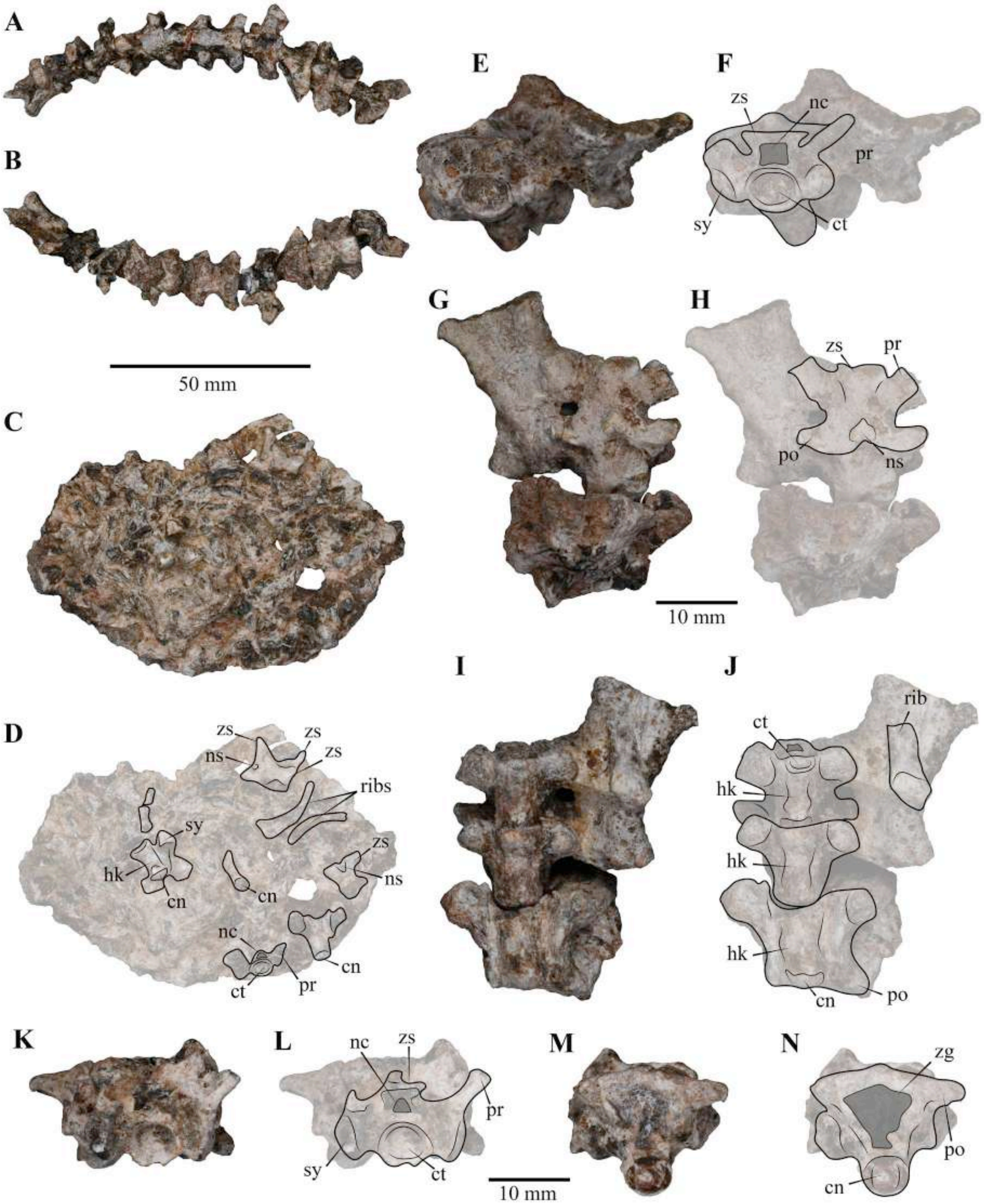

Figure 5. *Colombophis portai* VPPLT-1564 specimen: (**A–B**) nine articulated precloacal vertebrae; (**C–D**) several fragments of precloacal vertebrae and ribs embedded in the rock matrix; three articulated precloacal vertebrae in (**E–F**) dorsal, (**G**) anterior and (**H–I**) ventral views; an isolated vertebra in (**J–K**) anterior and (**L–M**) posterior views.

Remarks — Most vertebrae are similar in size to *C. portai* but are shorter than high (pr-po<h), the centrum length is slightly shorter than the neural arch width (cl<naw) and a wider neural arch (pr-po<naw). In addition, a well-developed neural spine is present, with an

elliptical to triangular shape in dorsal view; prezygapophyses are laterally oriented with well-developed process and synapophyses present a weak division (Hsiou et al., 2010).

Colombophis sp.

Referred material — More than 20 vertebral fragments (see Supplementary Table 1), most 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 ~ 8 mm, po-po ~ 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 other pre-cloacal vertebrae for *Colombophis* spp. Despite broken on most of the specimens, the hypapophyses are postero-ventrally oriented and located behind the subcentral 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 more 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 subcentral 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 possess a deep foramen inside, and in some vertebrae wide parazygantral foramina are present at each side of the zygantrum, inside a shallow fossa (Figs. 4A, B; 6A, B). 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 creates a notched section between the cotyle and the synapophyses (Figs. 3F; 4E, F, D; 6F). Precondylar 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)

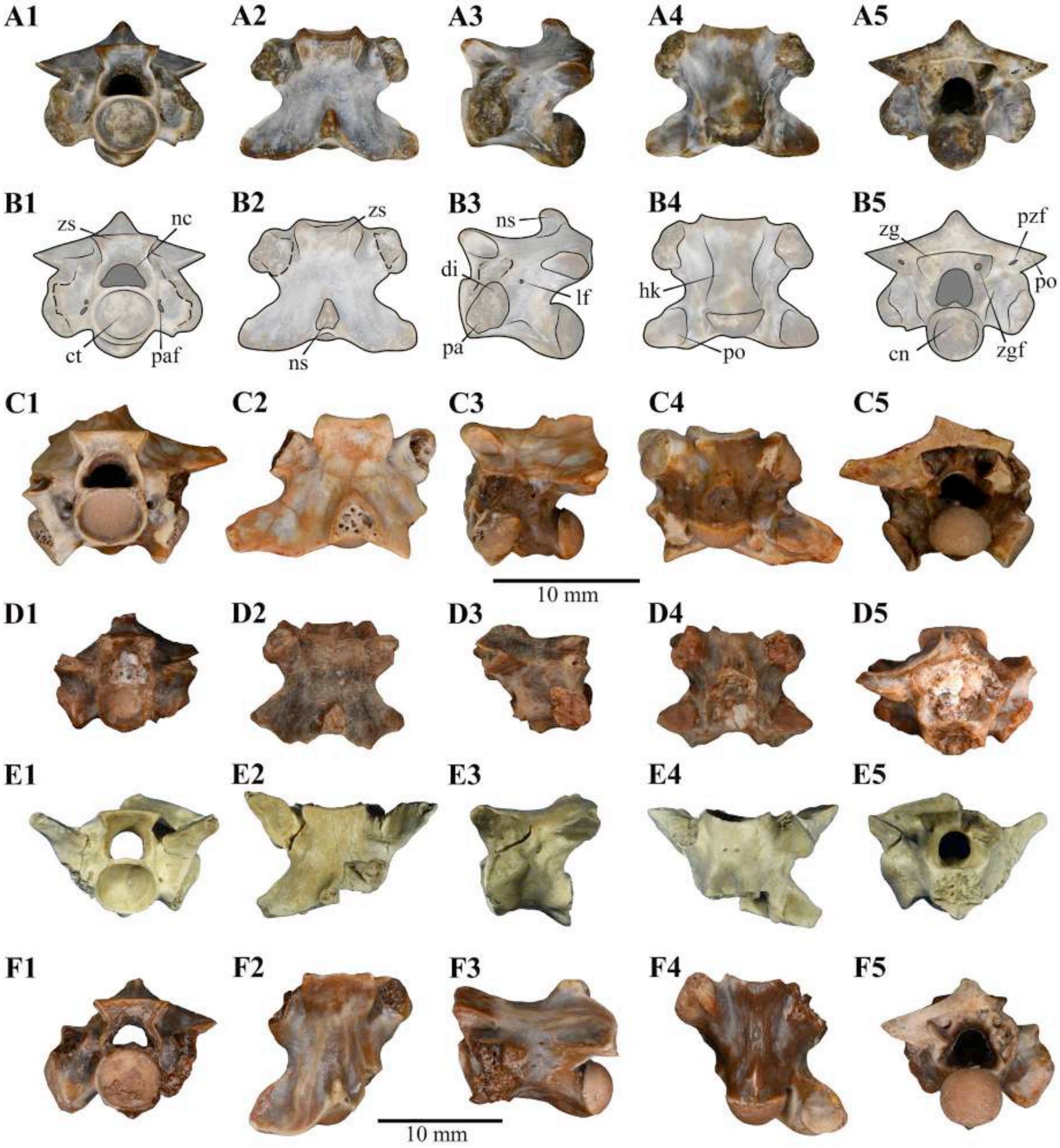

Figure 6. *Colombophis spinosus* from the Tatacoa Desert. (**A–B**) VPPLT-1728; (**C**) VPPLT-0798; (**D**) VPPLT-1093; (**G**) VPPLT-1741; (**F**) VPPLT-1534;Views: **(1)** anterior, **(2)** dorsal, **(3)** lateral, **(4)** ventral and **(5)** posterior views.

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.

Post-cloacal vertebrae — A potential post-cloacal vertebra was found associated to the *C. portai* specimen VPPLT-1740. (Fig.7A) This vertebra are considerably more vaulted than the associated precloacal vertebrae (Fig. 4). Posteroventral blade like structures are present, resembling paired haemapophyses. The subcentral foramina face 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 belongs to adults as they are fully ossified and presents a medium to large size. However, VPPLT-1006 specimen (Figs. 3A, B), may represent a juvenile individual based on its small size and the ovoid shape of the cotyle (Hsiou et al., 2010), it also lacks of developed prezygapophyseal processes, it has a narrow zygosphene and neural canal as it happens in extant and ancient snake neonates (LaDuke, 1991; Xing et al., 2018).

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 parazygantral foramina in both species, which is a feature only reported in Madtsoiidae and few basal snakes from Gondwana (Gómez et al., 2019 and references therein). Also, the neural arch is much longer than wide (pr-po/naw > 1.5) in *C. portai*, than in *C. spinosus* (pr-po/naw < 1,5), which represents another key feature to be considered in the diagnosis of this taxon. Prezygapophyses inclination apparently present a significant variation along the vertebral column, ranging from 18° to 33° (mean = 22,5°), similar to inclinations reported for members of the genera *Anilius*, *Cylindrophis* and *Uropeltis* (Head, 2021) (Fig. 2C–E). Prezygapophyzes from the Anterior-trunk vertebrae usually present an inclination of ~ 18° that increases in middle-trunk vertebral series but reduces in the posterior-trunk.

Regarding the post-cloacal vertebra associated with VPPLT-1740 specimen, 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; Smith, 2013; Szyndlar et al., 2008). Furthermore, the overall morphology of the post-cloacal vertebra resembles those reported in macrostomous snakes (Fig. 7B, C) (Garberoglio et al., 2019).

Additionally, this vertebra presents a well-developed neural spine which contrast with the associated precloacal vertebrae (Fig. 4), that lack of this feature. For the aforementioned reasons and considering the larger size of the post-cloacal vertebra compared to the posterior trunk vertebra of VPPLT-1740, 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.

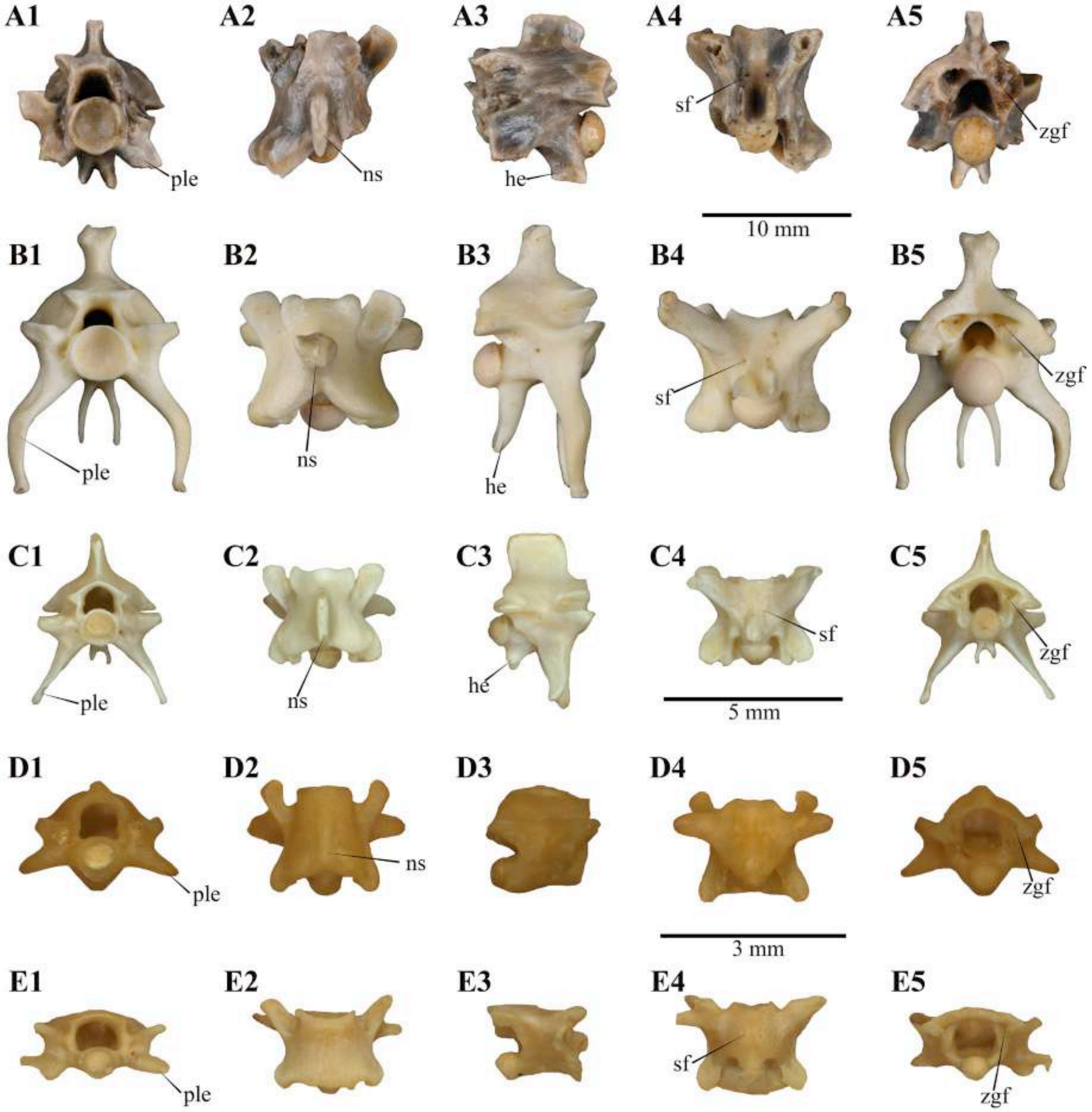

Figure 7. Comparison of *Colombophis portai* caudal vertebrae with extant aletinophidians. (**A**) *Colombophis*, VPPLT-1740; (**B**) *Boa* cf. *constrictor* VPPLT-uncatalogued specimen; (**C**) *Tropidophis melanurus*, UF-H-52001; (**D**) *Anilius scytale*, UF-H-52001; (**E**) *Cylindrophis ruffus* UF-H-52673. Views: **(1)** anterior, **(2)** dorsal, **(3)** lateral, **(4)** ventral and **(5)** posterior views.

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. 8) presents very low Bremer supports (Bremer support value < 1.0) 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. Da Silva et al., 2018; Tonini et al., 2016). *C. portai* and *C. spinosus* are not placed together as part of a monophyletic clade (Fig. 8), but, considering the lower support of the tree, we cannot discard a potential relationship between the two species. Furthermore, *Colombophis* spp are placed among the alethinophidia clade, which agrees with the proposed affinities for these taxa by Hsiou et al. (2010) and Head (2021).

Paleoecology

Colombophis spp. precloacal vertebrae morphology resembles those of fossorial or cryptozoic snakes (Head, 2021; Hoffstetter & Rage, 1977), 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* which may have had a semi fossorial or semi-aquatic lifestyle (Caldwell & Albino, 2001; but see Scanferla et al., 2010).

Still, additional studies are required to test this hypothesis. Evidence suggests that skulls provide confident ecological and phylogenetic hypotheses for fossil snakes (Allemand et al., 2017; Da Silva et al., 2018; Scanferla, 2016). However, the only known skull that potentially could belong to *Colombophis* was not properly described by Hecht & LaDuke (1997) due to lack of preparation. Unfortunately, that specimen was not available for this study as whereabouts of this fossil in either IGM or Duke University collections is unknown (Torres, L. & Borths, M., personal communication). On the other hand, histological analysis will be needed to test an ecological hypothesis for *Colombophis*, as the inner structure of vertebrae (compactness) apparently changes among fossorial, terrestrial or aquatic snakes (Houssaye et al., 2013).

CONCLUSIONS

We described new fossils of *Colombophis* from the Miocene of Colombia, which provide new morphological information about this enigmatic snake. Despite our data do not provide a strong support to solve the phylogenetic placement of this fossil snake, our analysis places *Colombophis* among alethinophidians, as it has been proposed by other authors. Additionally, we reported for the first time the presence of parazygantral foramina for this genus, similar as in fossil Madtsoiids. Considering the overall morphology of the vertebrae and the large size of this snake, we suggest a potential non-fossorial lifestyle. Nevertheless, to unveil the affinities and ecology of this ancient snake, more complete fossil specimens preserving the skull and postcranial elements should be discovered.

Acknowledgments.

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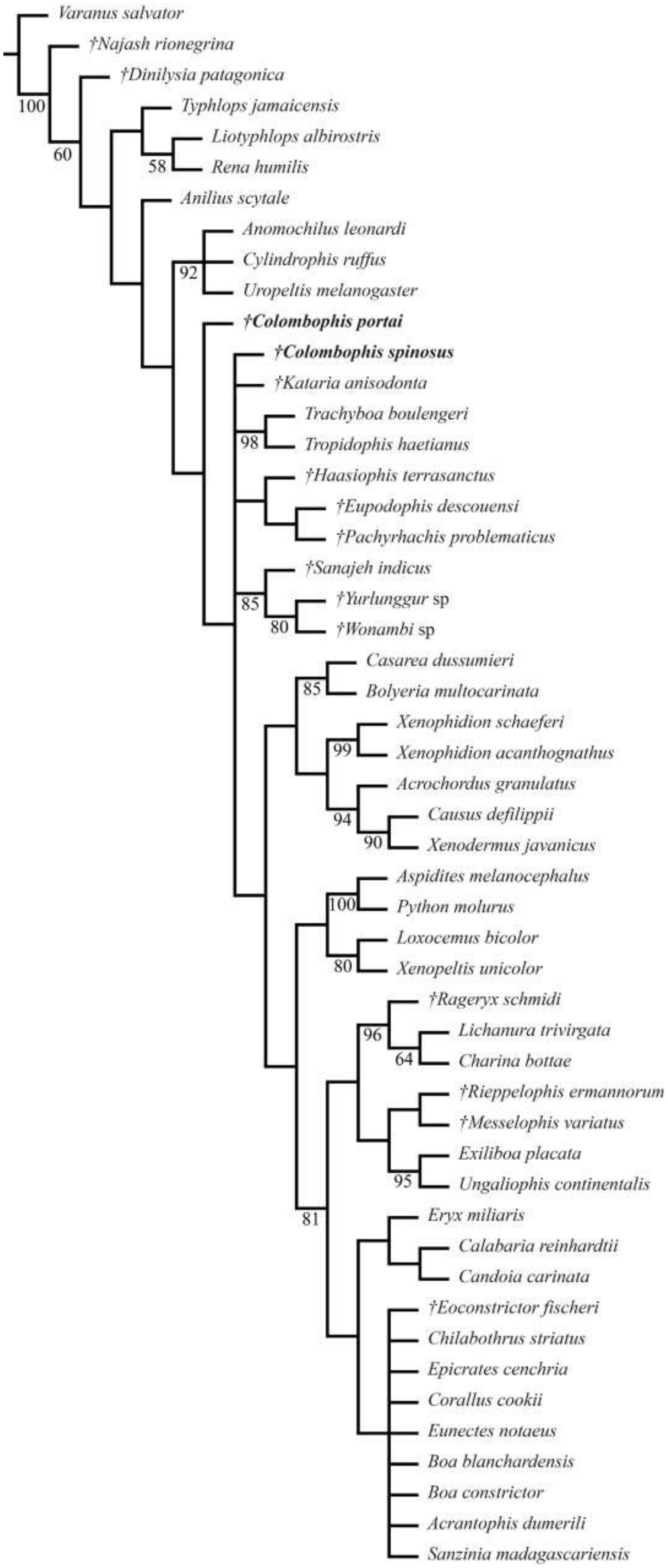

Figure 8. Phylogenetic relationships of *Colombophis.* Strict consensus tree from 79 most parsimonious trees, bootstrap percentages >50% are shown below the branches.

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CHAPTER 2: First record of a large constrictor snake for the late Pliocene of northern Colombia

Manuscript intended for PeerJ journal

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ABSTRACT

Boas and Anacondas are a group of large snakes that inhabit South America today, acting as the top predators in various ecosystems. Despite its size and relevant ecological role, its fossil record especially for the Pliocene is poorly known. The existing gaps in the fossil record difficult the understanding of the evolutionary history of these species and avoid proper reconstructions of past ecosystems. Here we describe a fossil compound bone from a large snake, discovered in the Pliocene Ware Formation, northern of Colombia. Although the specimen lacks many important features (like articular facets, or complete crests) to be attributed to a particular genus, based on its size and robustness, it shares potential affinities with large Boidae taxa like *Boa* or *Eunectes*. Our finding complements the scarce fossil record of Pliocene northern South American snakes, and reveal a potential unique feature among snakes, as it exhibits a deep fossa on its lateral surface whose function and origin have yet to be studied.

INTRODUCTION

Boidae is a family of constrictor snakes (Georgalis & Smith, 2020), which are restricted to western hemisphere (Reynolds & Henderson, 2018). Within them, *Eunectes* (anacondas) and *Boa* (boas) are world recognized for being among the largest snakes living today, both reaching more than 4 m in length (Henderson et al., 1995; Rivas, 2020). The *Eunectes* genus is represented by four species distributed across South America wetlands systems east of the Andes (Thomas & Allain, 2021). Instead, members of the *Boa* genus exhibit a wider geographical distribution including Central and South America regions, except the southern part of the continent (Reynolds & Henderson, 2018) (Fig. 1B). Despite, the ecological importance of both genera in the Neotropics, their evolutionary history and fossil record are still poorly known.

The first fossil record of *Eunectes* comes from the middle Miocene locality of La Venta, Tatacoa Desert, Colombia, where *E. stirtoni* was described based on an associated prootic and basisphenoid bones (Hoffstetter & Rage, 1977). Although some vertebrae were found associated with the skull bones, the affinities of this material with *E. stirtoni* remains dubious as the overall morphology of the vertebrae does not match with the exhibited by extant *Eunectes* (Hecht & LaDuke, 1997). Since then, many fossils of this genus have been reported in Neogene and Quaternary localities from Venezuela, Colombia, Argentina, and Brazil (Fig. 1A, B); including the middle Miocene (Head et al., 2006; Hsiou & Albino, 2010), late Miocene (Carrillo-Briceño et al., 2019; Head et al., 2006; Hsiou & Albino, 2009, 2010) and the Quaternary (Camolez & Zaher, 2010; Carrillo-Briceño et al., 2021; Hsiou et al., 2013). Most of the fossils reported consist of isolated or associated precloacal vertebrae, and only few skull bones have been reported (Camolez & Zaher, 2010; Hoffstetter & Rage, 1977).

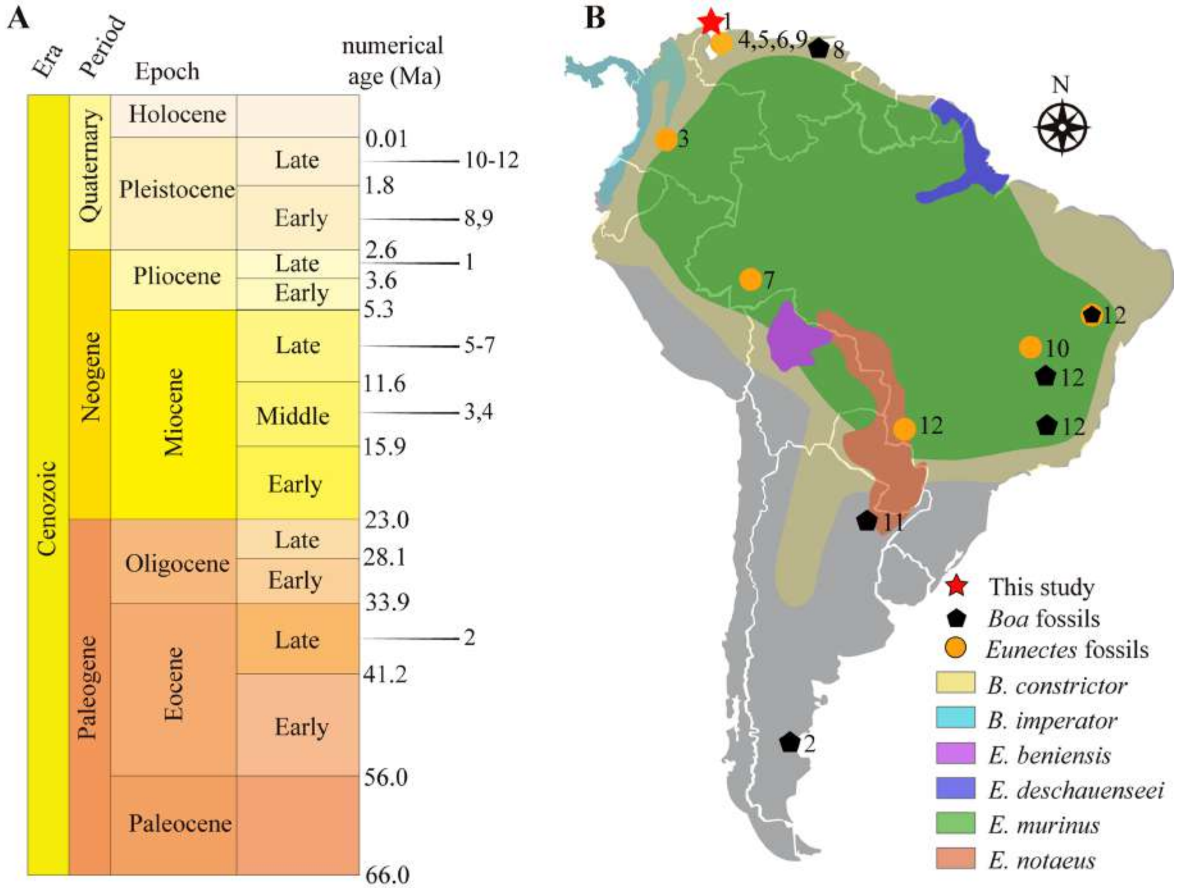

Figure 1. (**A**) Fossil record of *Boa* and *Eunectes* genera in South America. (1) late Pliocene, Colombia, (this study); (2) late Eocene, Argentina (Albino, 1993); (3) middle Miocene, Colombia (Hecht & LaDuke, 1997; Hoffstetter & Rage, 1977); (4) middle Miocene, Venezuela (Head et al., 2006; Hsiou & Albino, 2010); (5) late Miocene, Venezuela (Head et al., 2006; Hsiou & Albino, 2010); (6) late Miocene, Venezuela (Carrillo-Briceño et al., 2019); (7) late Miocene, Brazil (Hsiou & Albino, 2009); (8) Plio-Pleistocene, Venezuela (Onary-Alves et al., 2017); (9) early Pleistocene, Venezuela (Carrillo-Briceño et al., 2021); (10) late Pleistocene, Brazil (Hsiou et al., 2013); (11) Quaternary, Argentina (Albino & Carlini, 2008); and (12) Quaternary, Brazil (Camolez & Zaher, 2010). (**B**) Map showing localities were fossils of *Boa* and *Eunectes* have been found plotted alongside extant distributions of both genera based on IUCN distribution maps.

The oldest record of *Boa* is from the late Eocene of Argentina (Albino, 1993), as the other records come from the Plio-Pleistocene of Venezuela (Onary-Alves et al., 2017); and the Quaternary records of Argentina (Albino & Carlini, 2008) and Brazil (Camolez & Zaher, 2010); again consisting mostly of precaudal vertebrae and only few skull bones reported by Camolez & Zaher (2010).

Considering the aformentioned fossil record, two major temporal gaps exist for *Boa* and *Eunectes* genera, the Oligocene and Pliocene (Albino & Brizuela, 2014; Onary et al., 2017), as it happens for many other South American snake groups. Here we report the first presence of a large Boidae in the northernmost tip of Colombia during for the late Pliocene; based on a partially complete left compound bone collected in the Ware Formation (Moreno et al., 2015); we also discuss the relevance of the anatomical features present in the fossil, and its paleoecological implications for ancient neotropical ecosystems.

MATERIALS & METHODS

Fossil collection and Geological framework.

The fossil specimen was collected in 2014 during a fieldwork in the Cocinetas Basin, La Guajira, Colombia, by a joint Smithsonian Tropical Research Institute (STRI)-Universidad del Norte expedition (Moreno et al., 2015). The fossil specimen was found at Estación de Policía locality (STRI-470064 locality) (11°50’55.5’’N, 71°19’33.56’’W) within a level of conglomerate with purple muddy cement interlayed with sandstones with abundant occurrence of muscovite. This lithology is characteristic of the late Pliocene Ware Formation (dated as 2.78 to 3.40 Ma), which crops out in few areas of the easternmost part of the Guajira Peninsula on top of the middle-Miocene Castilletes Formation, close to the Colombia-Venezuela border (Moreno et al., 2015; fig. 6).

Fossil identification and Nomenclature.

The specimen was photographed and measured using a digital caliper. For taxonomic identification and comparisons, the specimen was compared with skulls of extant snakes from Museo de Historia Natural, Universidad del Rosario, Bogotá, Colombia (**UR**), Bogotá, Colombia; University of California Museum of Paleontology (**UCMP**), Berkeley, California, USA; University of Florida, Florida Museum of Natural History (**UF**), Gainesville, Florida, USA; and Instituto Alexander von Humboldt (**IAvH**), Villa de Leyva, Boyacá, Colombia (see Supplementary Table 1). For the description of the fossil, we used the anatomical terminology defined by Cundall & Irish (2008), Frazzetta (1966), Kluge (1991), McDowell (2008) and references therein.

Data analysis.

Prediction of maximum body length using compound bone length was carried out modeling the relationship between both variables with a linear model, and then calculating the point estimate and prediction interval using the model at the observed fossil compound length. Original data of compound length and total body length were measured on specimens available in collections (Supplementary Table 1). Analyses and plots were generated in R software (R Core Team, 2021) using the base and ggplot2 (Wickham, 2016) graphical systems.

All data and code are available in the supplementary materials as well as in the online repository https://github.com/gaballench/boidae_ware.

RESULTS

Systematic Paleontology

Serpentes Linnaeus, 1758
Alethinophidia Nopcsa, 1923
Constrictores Oppel, 1811 (sensu Georgalis & Smith, 2020)
Boidae Gray, 1825
Genus and Species indet.

Referred material: a left compound bone fragment (STRI-37684) (Fig. 2A–D)

Description: STRI-37684 measures 64,75 mm long and 13,21 mm wide at its anterior end. The articular surfaces and the retroarticular process are not preserved on the specimen. Prearticular and surangular crest are broken on the occlusal border, but they are apparently tall with more than 19,4 mm and 18,8 mm respectively. Despite most of the surangular surface is missing in the specimen, it is possible to distinguish part of the surangular crest, the base of the coronoid eminence and below it, and the anterior surangular foramen (labial foramen sensu McDowell, 2008), where the mandibular nerve (V_3) enters the bone. Anteriorly to this foramen, part of the dentary articular facet is visible. In dorsal view, an eroded remnant of the coronoid articular facet is visible on the anterior end of the fossil. On the mid region, a small channel-like structure (10 mm long) is formed between the base of the surangular and the prearticular crests, where fibers of the adductor musculature may have been attached (Frazzetta, 1966). Posteriorly to this structure, the anterior region of the mandibular fossa is visible, indicating the place of attachment for the *adductor posterior* muscle. On the medial surface, a deep fossa (32.5 mm long) is visible under the prearticular crest, which may have been part of the insertion of the aponeurosis that covers the a*dductor* muscles (Frazzetta, 1966). As both anterior and posterior ends of the bone are missing, it is no possible to establish the dimensions of the bone or make a more detailed description.

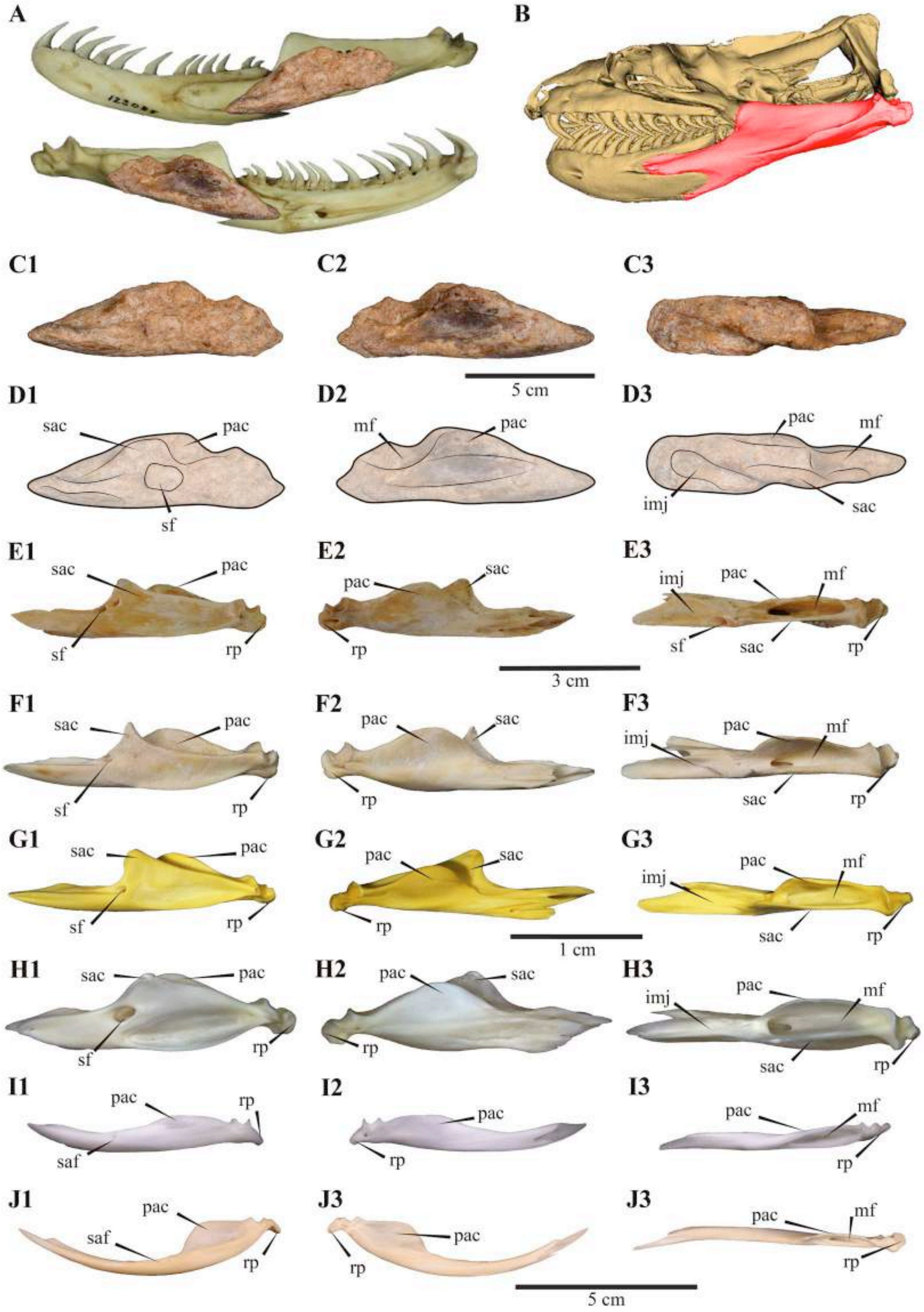

Figure 2. Fossil specimen STRI-37684 and comparisons with some extant boids. (**A**) Position of the fossil in a left compound bone from *E. murinus* IAvH-R-8225 in lateral (top) and medial (bottom) views. (**B**) Compound bone in a 3D model skull from *Eunectes murinus,* UF-HERP-84822 morphosource (**C**) STRI-37684 left compound fossil bone. (**D**) Sketch of the fossil showing key anatomical features. Compound bones from (**E**) *E. murinus*, IAvH-R-8234; (**F**) *Boa* aff. *constrictor*, VPPLT-uncatalogued specimen; (**G**) *Epicrates maurus*, UR; (**H**) *Corallus caninus*, UF-HERP-99407 (**I**) *Pseudoboa neuwiedii*, UR; (**J**) *Bothrops* aff *asper*, UR-uncatalogued specimen. In (1) lateral, (2) medial, (3) Dorsal, and (4) ventral views. Abbreviations: **imj**,

intramandibular joint facet; **mf**, mandibular fossa; **pac**, preaerticular crest; **rp**, retroarticular process; **sac**, surangular crest; **saf**, supraangular foramen **sf**, surangular foramen.

Comparisons: Despite of its poor preservation, STRI-37684 is similar to the compound bones of *Eunectes* and *Boa* genera (Fig. 2E, F) sharing its large size and robustness. The base of the surangular crest is apparently wide, as in the specimens of *Eunectes*, *Corallus* and *Epicrates*. Ventral surface of the fossil is relatively wide and flat, as in *Eunectes* and *Boa*, while in *Corallus* it shows a ventro-lingual projected ridge. We discarded potential relationships with viperids and colubrids (Fig. 2I, J), as those taxa lack of surangular crest, as well as a coronoid eminence (Cundall & Irish, 2008; Lee & Scanlon, 2002). Even though, some features of the specimen suggest affinities to *Eunectes* (anacondas), we refrain to assign it to generic level, as the fossil does not preserve most of the surangular and posterior region of the compound bone, where apomorphies for this genus are usually recognized (Kluge, 1991; Lee & Scanlon, 2002).

Size estimation: Based on measurements from the comparative material (Supplementary Table 2), we found a linear correlation between the compound length and total body length of extant snakes. This allowed us to estimate that STRI-37684 specimen belonged to an individual of a total body length of ~3.0 m (prediction interval of 95% 1.91–4.09 m) (Figure 3). However, it is important to point out that that actual body length of the individual should be longer, as the fossil specimen is broken on the anterior and posterior ends.

DISCUSSION

The fossil specimen described herein corresponds to the first Colombian boid described for the late Pliocene, which based on its size may have affinities either to *Boa* or *Eunectes* genera. Despite of the poor preservation of STRI-37684 specimen and the absence of undisputable apomorphies, issues that has been also discussed in general for the extant and some fossil snakes (Head, 2015); this discovery contributes to fill the existing Pliocene gap in the fossil record of South American snakes. Our results also suggest that bones from the jaw, such as the compound could be used to estimate the total body length in fossil snakes.

This finding also gains relevance considering that for fossil snakes, skull elements are scarce (Holman, 2000; Lee & Scanlon, 2002 and references therein), as well as the rarity of boid fossils compared with other snake lineages (for example Erycidae and Madtsoiidae); as according to the Paleobiology Database (Peters & McClennen, 2016) only 84 of 301 records of fossil snakes belong this family on the Americas.

The occurrence of large boidae in the northernmost tip of South America during the Pliocene was previously reported by Carrillo-Briceño et al. (2021), where *Eunectes* fossils were found in San Gregorio Formation (Venezuela). This locality presents a strong stratigraphic correlation with Ware Formation (this study) (Moreno et al., 2015). Both localities also reveal a transitional paleoenvironment (coastal to fluvio-deltaic) were a variety of vertebrates like fishes, turtles, birds and mammals lived (see Carrillo-Briceño et al., 2019; Carrillo-Briceño et al., 2021 and references therein). In Neotropical ecosystems, large snakes share the position as top predators with crocodilians and felines (Amorós & Manrique, 2008), that sometimes result in agonistic interactions (Cavalcanti et al., 2016). Considering that the aforementioned fauna shares similarities with extant preys of extant *Boa* and *Eunectes* (Henderson et al., 1995; Rivas, 2020; Thomas & Allain, 2021), a large boid (STRI-37684) can be considered as one of the top predators of northern South America during the late Pliocene.

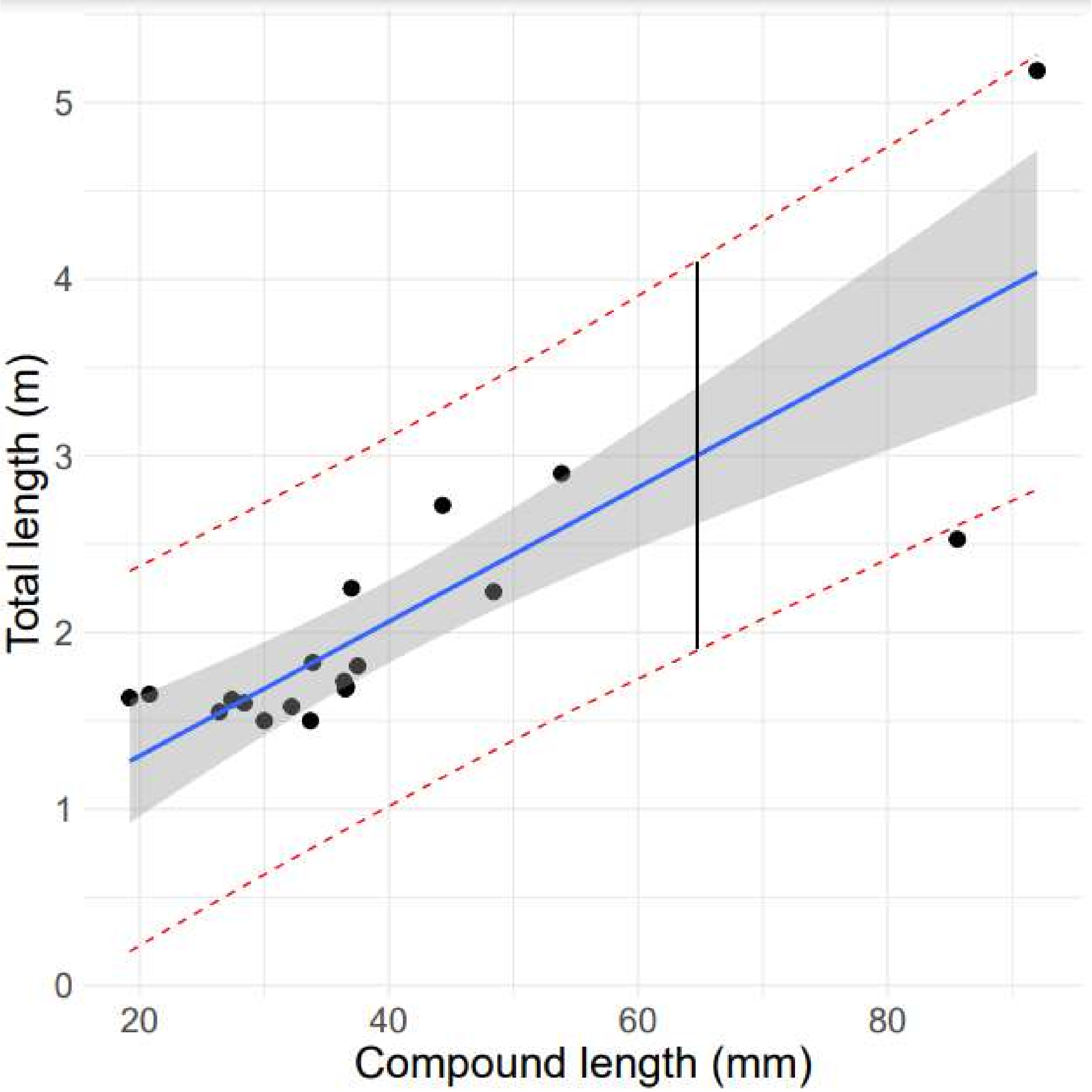

Figure 3. Linear model for estimation of the total length (in m) of STRI-37684. as a function of compound length (in mm) using an array of different boid species. Gray area represents the confidence region for the linear model, while the dashed lines represent the prediction interval. The vertical black line at 64.75 mm in x is the prediction interval for the fossil specimen, which should have been between 1.9 and 4.1 m total length.

Perhaps the most distinctive feature of STRI-37684 specimen is a very deep fossa on the medial surface of the prearticular, which could have functioned as a muscular attachment surface. However, no evidence of similar structures were found in the comparative material (Fig. 2E–I) or in literature (Frazzetta, 1966). At this time is difficult to identify the origin of this structure considering the preservation of the fossil. To unveil the true nature of this structure, future studies will be needed, including a μCT scan, which will allow us to verify taphonomic or paleopatological effects (Rothschild & Tanke, 1992).

CONCLUSIONS

The compound fossil bone from a large boid described herein represents the first late Pliocene record of a snake for Colombia, which also helps to fill the existing Pliocene gap for snakes of South America. Even though constrictor snakes have been reported previously in the transitional environment that lasted in northern South America by the end of the Neogene, this fossil is unique among snakes as it exhibits a very distinct fossa for which its anatomical function is still unknown. Although, the possible relationship between the size of the compound bone and the total body length of the snakes has not been fully studied yet, it is a topic that deserved furthermore studies, because it could help to differentiate some genera, particularly *Eunectes* from *Boa*, and also to serve as a proxy for size estimation in fossil snakes. Based on our observations and analyses, it is reliable that STRI-37684 could have reached far more than 3 m long, functioning as a top predator in this paleoecosystem.

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CHAPTER 3: Late Pleistocene biota from Pubenza, Colombia; turtles, mammals, birds, invertebrates and plant remains

Late Pleistocene small fauna that shared habitat with some of the first humans of Colombia

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ABSTRACT:

Pubenza is a remarkable archaeological site, having one of the oldest evidence of humans in northern South America. Previous paleontological research in this site has mainly focused on the megafauna. Here we describe and establish the systematic paleontology for the small fauna that inhabited this ancient lacustrine ecosystem, including the first report of birds, tortoises, and vipers for the Late Pleistocene in Colombia. Furthermore, exceptionally preserved fossilized wasp nests are morphological and elementally characterized, which correspond to the first report of an ichnofossil of this kind in northern South America. In addition, new material of kinosternid turtles, armadillos, and rodents is also described herein. Our results reveal that the Bogotá River Basin, where Pubenza is located, was a rich ecosystem during the Late Pleistocene, in which the early humans of Colombia could interact and coexist with a biota similar to the extant.

KEYWORDS: Pubenza; Caviomorpha; Crotophaginae; Viperidae; Paleoichnoentomology; Testudines.

Introduction

Colombia, due to its geographical position connecting the Panama isthmus to continental South America, provides key evidence of the early colonization of humans to Americas Southern Hemisphere (Aceituno *et al*., 2013). In fact, the oldest known evidence of human manufactured tools in northern South America comes from the archaeological and paleontological locality of Pubenza, Cundinamarca (Correal-Urrego, 1993; Correal-Urrego *et al*., 2005; Muttillo *et al*., 2017). However, it is still poorly known the identity of many of the faunal components that first colonizers encounter once they entered the continent. Intensive archaeological research in the Sabana de Bogotá and its surroundings discovered the presence of megafauna such *Glyptodon clavipes*, *Propaopus sulcatus (P. magnus)*, and the gomphotheriidae *Notiomastodon platensis* (*Haplomastodon waringi),* together with some lithic artifacts (Correal-Urrego, 1981, 1993; Correal-Urrego *et al*., 2005; Muttillo *et al*., 2017, 2019). However, in the specific locality of Pubenza, other faunistic components of this ancient lacustrine environment (Salgado-López and Varón-Barbosa, 2019) like small mammals, reptiles and invertebrates have only been briefly mentioned (Correal-Urrego *et al*., 2005), lacking of proper description and illustration; except for the first Late Pleistocene mud turtle *Kinosternon* sp. in northern South America (Cadena *et al*., 2007).

Here we examine and describe several fossils housed at the paleontological collections of the Museo Geológico Nacional José Royo y Gómez (MGNJRG) from the Servicio Geológico Colombiano (SGC), as well as some new discoveries from recent fieldwork activities that we have conducted in the region. The fossils represent the first Late Pleistocene records for several groups of vertebrates in Colombia, including tortoises, viper snakes, various cingulates, and the first record of a hymenopteran nest. We discuss also the relevance of these fossils in terms of their age, geographical occurrence, and implications for reconstructing the ecosystem that the first colonizers found when they arrived to northern South America.

Geological Settings

The fossils described herein come from a site located near to the small village of Pubenza (4°24'39''N, 74°44'44''W, 340 m altitude), ~18 km southwest of the town of Tocaima, Cundinamarca Department, Colombia (Figure 1a). The study area corresponds to the northwest flank of the Bogotá River Basin, a region with abundant outcrops of the early Miocene Barzalosa Formation, some spots of the Cretaceous Seca Formation, and an isolated alluvial deposit from the Pleistocene (Figure 1b). This deposit is characterized by calcareous sandy clays interbedded with thin laminae of gypsum and volcanic ash formed in a marsh (Correal-Urrego *et al*., 2005). The stratigraphy profile includes 13 recognizable layers (Figure 1c, d); some of them previously dated by Van der Hamen and Correal-Urrego (2001). Fossils were found between layers 10 to 13 of the profile, which are characterized by abundant fragments of calcified wood inside a gray clay with some clasts of gypsum and charcoal dated as 16400 ± 420 AP (Van der Hammen and Correal-Urrego, 2001). Most of the fossils from this locality correspond to small, disarticulated bone fragments usually covered by thick calcium carbonate matrix, except for the massive bones of *Notiomastodon platensis,* which apparently was the largest animal of this environment.

Materials and Methods

Fossils collection and identification

Most of the fossils described herein were collected in 2007 by Dr. M. Páramo-Fonseca and geologists from the SGC (formerly known as Ingeominas). Since then, the fossils have been housed at the paleontological collections of MGNJRG. All the fossil material was manipulated using sterile gloves and facemasks, following the protocols of the museum to avoid any contamination. Additionally, we describe here new fossils that we recently discovered during fieldwork activities that took place in 2019. The fossils were collected using sterile gloves, wrapped in aluminum foil, and placed in plastic bags for storage in the paleontological collection of the Universidad del Rosario (UR-CP).

Taxonomic identification of fossils was performed by comparing them to specimens housed at the collections from Instituto de Ciencias Naturales (ICN), Bogotá, Colombia; Chelonian Research Institute (CRI), Oviedo, Florida, USA; University of California Museum of Paleontology, Berkeley (UCMP), California, USA; Field Museum of Natural History (FMNH), Chicago, USA; and from previous research works. Squamates identification was based on works from Estes (1983), Rage (1984), and Lee and Scanlon (2002).

Radiocarbon dating

In order to validate the age of the deposit and fossils, a sample of charcoal collected during the 2019 fieldwork at the base of Corte 8 fossil site was obtained directly from the rock matrix using nitrile gloves and packaged separately in sterilized aluminum foil, then it was sent to Beta Analytic Testing Laboratory (BETA), Miami, USA. Radiocarbon dating was conducted using the Accelerator Mass Spectrometry technique, which after burning the sample at 800°C under a 100% oxygen atmosphere use the CO_2 obtained by the combustion and reduces into graphite (https://www.radiocarbon.com/beta-lab.htm). The Conventional Radiocarbon age was corrected for total isotopic fractionation effects (natural and laboratory induced). The reported d13C was measured separately in an IRMS (isotope ratio mass spectrometer). All work on this sample was performed by BETA in its Miami lab under strict chain of custody and quality control under ISO/IEC 17025:2005.

Scanning Electron Microscopy and elemental analysis (SEM/EDS)

We explore the microstructural morphology and elemental composition of the fossil hymenopteran nests using Scanning Electron Microscopy coupled with Energy Dispersive X-Ray Spectroscopy (SEM/EDS). Two small fragments of the combs of UR-CP-0035 specimen were mounted in sterile carbon stubs and storage in sterile boxes before the SEM/EDS analysis, which was performed at the Microscopy Core Facility of

Universidad de los Andes, Bogotá, Colombia. Samples were analyzed without adding any coating. Imaging and elemental mapping composition were obtained at 20 kV using a TESCAN-Lyra3 SEM.

Nomenclature

Positional terms—For vertebrates postcraneal descriptions, anterior, posterior, lateral, medial, proximal, distal, dorsal and ventral; for dentition, anterior, posterior, labial, lingual and occlusal.

Dental nomenclature—Dental descriptions use in general the terminology from Dong and Chen (2015) and partially Wheatley and Ruez. (2006).

Postcranial nomenclature—Vertebrates postcranial descriptions follow the *Nomina Anatomica Veterinaria* (Schaller and Constantinescu, 2007) and medical anatomy (Gray, 2016).

Birds nomenclature—We follow the osteological terminology according to Baumel and Witmer (1993) for descriptions and comparisons of bird humerus fossil anatomy.

Squamates nomenclature—We follow the osteological terminology according to Williston and Gregory (1925), for the descriptions and comparisons of the squamates vertebrae.

Cingulates osteoderms nomenclature—We follow the nomenclature used by Ciancio *et al.*, 2013 and Krmpotic *et al.*, 2015 for the description of osteoderms morphology.

Systematic Paleontology

Vertebrates

Testudines Batsch, 1788
Cryptodira Cope, 1868
Testudinidae Batsch, 1788
Chelonoidis Fitzinger, 1835
Chelonoidis sp.
(Figure 2)

Referred material—MGNJRG-C26-EF-9-10, a left epiplastron; MGNJRG-C24-ZonaB, a right costal 4? fragment; MGNJRG-C27-CD-5-6, a hypoplastron? fragment; MGNJRG-C23-GH-1-2, a right xiphiplastron.

Remarks—Other isolated bones morphologically similar to the epiplastron or peripheral plates were also found in the Pubenza MGNJRG collection. Despite they clearly belong to *Chelonoidis*, the fossils were extremely eroded at most of the bone surface, in consequence we only list them in Supplementary Table S1. Also it is important to notice that all the bones describe herein were found isolated and could correspond to a single or several individuals.

Descriptions and comparisons—MGNJRG-C26-EF-9-10 (Figure 2a–d) is an almost complete left epiplastron, missing its posterolateral portion, and cracked at its most dorsomedial and ventromedial regions. The bone is 60 mm wide and 42 mm long, with a thickness range between 12.5 to 27 mm. Despite of the slightly eroded bone surface, the sulcus between the gular and the humeral scutes is well defined in both, dorsal and ventral views; and it runs from the anterolateral margin of the epiplastron towards the midline of the plastron suggesting that the gular scute covered the most anterior corner of the entoplastron. As usual in *Chelonoidis*, the anterior rim of the epiplastron is thickened to form a distinct dorsovisceral lip (Joyce and Bell, 2004; Vlachos, 2018).

MGNJRG-C24-ZonaB (Figure 2e, f) corresponds to a costal bone fragment possibly right costal 4, measuring 38 mm wide, 36 mm long, and 4.7 mm thick. A close-up view under the stereomicroscope reveals a slightly rugose texture of the bone surface with a microvermiculated pattern close to the sulcus (Figure 2g). The attribution of this costal as right costal 4 is based on the proportions between the pleurals sulci and its similarities with the same bone in specimens of the extant *Chelonoidis* spp.

MGNJRG-C27-CD-5-6 (Figure 2h, i) represents a small fragment of the plastron, potentially from the right hypoplastron or hypoplastron due to the extreme flatness of the bone. The fragment is 28 mm wide and 23 mm long with a visible sulcus that crosses the bone longitudinally on the ventral surface of the bone. The sulcus exhibits the typical testudinid sulcus shape, similar to a canal with high lateral walls, and bone surface exhibiting a fine and highly dense vermiculation without long dichotomized lines (Figure 2j) (Cadena and Jaramillo, 2015).

MGNJRG-C23-GH-1-2 (Figure 2k–n) represents a nearly complete right xiphiplastron fragment. Part of its anterolateral and medial edges are missing. In dorsal view there is a depression that indicates the limit where the anal scute covered the bone versus the visceral surface. The sulcus between the femoral and the anal scutes is well defined on ventral surface of the bone, indicating that the anal scute was restricted to the most posterior region of the xiphiplastron with a very short medial margin, similar to the extant *Chelonoidis* spp. The anatomical position of the referred material is shown in an outline of the carapace (Figure 2o) and plastron (Figure 2p) of the extant *Chelonoidis carbonarius*.

Kinosternidae Agassiz, 1857
Kinosternon Spix, 1824
Kinosternon sp.
(Figure 3)

Referred material—MGNJRG-C17-QR-3-4, a left peripheral 8; MGNJRG-C26-EF-9-10, a left costal 5; MGNJRG-C27-CD-1-2, neural 2?; MGNJRG-C25-EF-3-4, neural 4?; MGNJRG-C27-GH-1-2, a left humerus; MGNJRG-C26-ST-1-2, a pygal bone;

MGNJRG-C20-YZ-5-6, a right hypoplastron; and MGNJRG-C26-WX-1-2, a left hypoplastron.

Remarks—Many isolated bones, including costals and peripherals were found in the SGC-Pubenza collection, and although their size and sculptural pattern indicate that they belong to kinosternids, we exclude them from an extensive description here due to their too fragmentary preservation. However, they are listed in Supplementary Table S1. Also, it is important to notice that all the bones describe herein were found isolated and could correspond to a single or several individuals.

Descriptions and comparisons—MGNJRG-C17-QR-3-4 (Figure 3a, b) is a left peripheral 8. In dorsal view is evident a microvermiculation pattern typical of kinosternids and the sulci between pleurals 3 and 4, and marginals 8 and 9 are clearly visible. The lateral margin of the bone is slightly thicker than the rest of the peripheral plate.

MGNJRG-C26-EF-9-10 (Figure 3c, d) corresponds to a left costal 4, missing most of its lateral portion. The assignation of this plate as a left costal 4 is based on the proportions between pleural scutes, which resemble the ones observed by the same plate in extant *Kinosternon* spp. The preserved sulci patterns on the dorsal surface of the bone indicate a contact between vertebral 3, and pleurals 2 and 3.

MGNJRG-C27-CD-1-2 (Figure 3e, f) and MGNJRG-C25-EF-3-4 (Figure 3g, h) represent complete isolated neural bones, potentially neural 2 and 4 respectively, based on comparisons with similar bones of the extant *Kinosternon leucostomun*; neurals that usually lack the sulcus between vertebral scutes.

MGNJRG-C27-GH-1-2 (Figure 3i, j) represents a left humerus, which is 13.4 mm long. The proximal region exhibits well-defined medial and lateral processes and a slightly rounded articular condyle. The shaft region is narrow and exhibiting a circular outline. The proximal end is flatter and laterally having the well-defined ectepicondylar foramen.

MGNJRG-C26-ST-1-2 (Figure 3k, l) is a complete pygal bone. In dorsal view the sulcus between vertebral 5 and marginal 11 is visible. The bone exhibits a nearly pentagonal inverted shape, being wider than long and it has a slightly convex shape in lateral view.

MGNJRG-C20-YZ-5-6 (Figure 3m, n) and MGNJRG-C26-WX-1-2 (Figure 3o, p) represent a right and left hypoplastra respectively. Both bones are flat and exhibit the sulci between abdominal and femoral scutes, as well as of these with some inframarginal scutes in ventral view. As in other *Kinosternon* spp., the posterior sutural edge of both bones is hinged indicating plastral lobe kinesis (Joyce and Bourque, 2016). The anatomical position of the referred material is shown in an outline of the carapace (Figure 3q) and plastron (Figure 3r) of the extant *Kinosternon leucostomun*.

Mammalia Linnaeus, 1758
Xenarthra Cope, 1889
Cingulata Illiger, 1811

Dasypodidae Gray, 1821
Dasypodinae Gray, 1821
Dasypodini Gray, 1821
Propraopus Ameghino, 1881
Propraopus sulcatus (Lund, 1842)
(Figure 4a–p)

Referred material—Isolated osteoderms unassociated. MGNJRG-C19-ST-3-4, buckler osteoderm; MGNJRG-C17-V-1-2, buckler osteoderms; MGNJRG-C22-AB-5, buckler osteoderm; MGNJRG-C24-YZ-7-8, movable osteoderm (broken, the anterior portion of the osteoderm is lost); MGNJRG-C23-GH-1-2, osteoderm of the caudal sheath; MGNJRG-C17-CD-3-4, osteoderm of the caudal sheath; MGNJRG-C24-ST-3-4 osteoderm of the caudal sheath.

Remarks—Many other isolated osteoderms were found in the SGC-Pubenza collection, and although their size and shape indicate that they potentially belong to *Propraopus*. However, we avoid an extensive description, as most of their surface is completely eroded. However, they are listed in Supplementary Table S1.

Descriptions and comparisons— The osteoderms of armadillos are distributed in several different parts of the animal: the cephalic shield, on the top of the head; the carapace, consisting of the anterior (or scapular) buckler, movable bands, and posterior (or pelvic) buckler; the caudal sheath; and several non-articulated osteoderms in different portions of the body (within the integument above the rostrum, in the ventral surface of the trunk and the limbs legs) (Krmpotic *et al.*, 2009, Ciancio 2006). The osteoderms described here are identified as a buckler, movable and caudal osteoderms. The exposed surface of the fixed osteoderms is smooth to finely wrinkle. Most are hexagonal, and the central figure is circular to subcircular and displaced posteriorly up to be close to the margin of the osteoderm. Radial sulci separate three (Figure 4a, b) to five peripheral figures (Figure 4c–f), three of those are located in the anterolateral zone are larger and better defined. In the sulcus that separates the central figure of the peripheral ones are two (Figure 4g, h) to five (Figure 4c, d) glandular foramina, which are relatively large. These foramina are restricted to the cranial half of the osteoderm (only one osteoderm (Figure 4c, d), has one on the posterolateral margin), and are never located in the intersection between the principal and the radial sulci. The measurements of osteoderms range from 12 to 16 mm in width and from 14 to 18 mm in length.

The unique movable osteoderm (Figure 4i, j) lacks the anterior portion (the portion that is overlapped for the posterior portion of the osteoderm of the preceding movable row). The main or posterior portion of the osteoderm has two curving, diverging sulci that diverge toward the posterior border, reaching this border. These are anteriorly disconnected and delineated a lageniform-shaped figure with a wide and long neck. Those sulci are filled with sediment; however, it is possible to distinguish four or five foramina in one of them.

These characteristics of osteoderms morphology are diagnostics for *Propraopus* (Castro *et al.*, 2013; Castro, 2015). The only valid species recognized of the genera are *P.*

sulcatus (synonymous with *P. grandis*) and this species is known for the Pleistocene-Early Holocene of Argentina, Brazil, Venezuela, Uruguay, and Bolivia (Castro *et al.*, 2013; Soibelzon *et al.*, 2015).

The caudal sheath of dasypodins is arranged in rings, conformed by two rows of osteoderms each. The osteoderms proximal row, have a short anterior portion (not exposed, covered for the osteoderm of the distal row of the anterior ring), and a posterior portion (exposed) with an ornamented surface (Holmes and Simpson, 1931; Carlini *et al.*, 1997; Castro, 2015). The osteoderm from the contiguous distal row of a ring lacks the anterior portion; the anterior border has an inverted v-shape and not have ornamentation. The caudal osteoderms described here (Figure 4k–p) pertain to a second raw of caudal sheath rings. In their exposed surface they have three to five foramina arranged as an arch in the anterior and lateral margins and lack sulcus and figures. The caudal osteoderms are similar to those described by Rodriguez-Bualó *et al.* (2017) for *P. sulcatus*, but in this specimen, the osteoderms of the second raw lack foramina.

Dasypus Linnaeus, 1758
Dasypus sp.
(Figure 4q, t)

Referred material—unassociated osteoderms. MGNJRG-C23-EF-1-2, buckler osteoderm; MGNJRG-C24-QR-3-4, osteoderm of the caudal sheath.

Descriptions and comparisons— The buckler osteoderm is hexagonal, with a smooth external surface that has deep punctuations (Figure 4q, r). The ornamentation shows a large circular central figure occupying almost its entire surface and two small peripheral figures developed on its anterior edge. In the sulcus between the central figure and the peripheral figures, there are three small foramina, which are on the right side of this sulcus. The caudal osteoderm (Figure 4s, t) has the morphology of those of a second raw of caudal sheath rings of dasypodins (see explanation above), it lacks figures and has six foramina distributed on the anterior and left margins of osteoderms. According to these characteristics, the specimen is assigned to *Dasypus*, but a more specific entity is not possible, because the osteoderm probably corresponds to a marginal zone of the caparace, where the morphology of the osteoderm deviates from its typical pattern and is simplified. Furthermore, the caudal osteoderm does not present diagnostic characteristics to differentiate between species. The measurements of the osteoderm fit the measurement range of *Dasypus novemcinctus*.

Artiodactyla Owen, 1848
Cervidae Goldfuss, 1820
Cervidae, gen. et sp. indet.
(Figure 5a–d)

Referred material— MGNJRG-C26-QR-1-2, an isolated molar.

Descriptions and comparisons—MGNJRG-C26-QR-1-2 corresponds to an isolated left M2. It is a nearly square (12.46 mm long and 14 mm wide) brachydont molar with four roots and a "half-moon" occlusal pattern, a feature commonly present in cervids. This molar has a strongly worn crown and eroded roots (Figure 5a, b). In labial view, the posterior lobe of the crown (as indicated by the labial border of the enamel limiting the crown from the root) is slightly lower than the anterior one. The labial surface of the crown is soft, lacking vertical ribs ascending from the base of the crown to the tip of both the paracone and metacone; there are only wide blunt longitudinal prominences instead (mainly visible at the upper most portion). In occlusal view (Figure 5c, d), the molar is composed by four main cusps, the paracone, metacone, protocone and metaconule; and two small cuspules, the parastyle, mesostyle, metastyle and a protostyle (Wheatley and Ruez-Jr, 2006). There is a lingual rupture affecting the base of the crown at the level of the metaconule and the upper portion of the posterolingual root, so the presence of a hypocone and entocingulum is not clear. However, on the anterolingual portion of the metaconule base, there is a small broken portion of a structure that could correspond to the anterior end of an ectocingulum or a fragment of the entostyle. The outline of the worn main cusps, and their crests form open V-shaped crescents. The stylar cusps are strongly worn. The parastyle and mesostyle are apparently well developed, while the metastyle is apparently strongly reduced. The cuspule interpreted as a protostyle (Wheatley and Ruez-Jr, 2006) is located between the paracone and protocone, in a posterior position, close to the posterolingual margin of the paracone. It is circular (slightly ellipsoidal: slightly anteroposteriorly compressed) in cross section.

Rodentia Bowdich, 1821
Caviomorpha Wood, 1955
Caviomorpha, fam. et gen. indet.
Sp. 1
(Figure 5e–h)

Referred material—MGNJRG-C19-ST-3-4, distal portion of left radius.

Descriptions and comparisons—MGNJRG-C19-ST-3-4 corresponds to a distal portion of left radius, including the complete distal epiphysis and a distal fragment of diaphysis. This element is deformed and eroded, so it is difficult to identify the structures. The diaphysis is slightly triangular in cross-section, becoming more trapezoidal at the border with the distal epiphysis. In the anterior view (Figure 5e, f), an irregular, roughly triangular facet is still observable (despite the preservation), for the articulation with the ulna. In medial and anteromedial views, there is a small crest on the diaphysis descending until the distal epiphysis, reaching the ulnar articular facet. In posterolateral view, there is a rugous surface, probably for the attachment of the *abductor pollicis longus* and *extensor pollicis brevis* (Gray, 2016); and a distal depression on the posterolateral face of the styloid process, probably corresponding to the surface for the attachment of the *extensor carpi radialis longus, extensor carpi radialis brevis,* and *extensor pollicis longus*. However, all these structures are very worn and posterior revisions could change these interpretations.

The distal epiphysis is irregular in shape. Its most conspicuous feature is the styloid process, developed on the medial side of the epiphysis. This process is roughly oval-shaped and distally projected. The distal surface of the epiphysis is roughly trapezoidal (rectangle trapezoid) in shape, roughly concave and smooth, bearing two main oval articular facets (Figure 5g, h). This facet, for articulation with the scaphoid bone, extends from the distal surface of the epiphysis to the lateral surface of the styloid process.

Sp. 2
(Figure 5i–p)

Referred material—MGNJRG-C27-GH-1-2, metapodial (right Mtt III?)

Descriptions and comparisons—MGNJRG-C27-GH-1-2 corresponds to a metapodial (right Mtt III?). The proximal epiphysis is laterodorsally protruding, defining a small roof. The proximal articular facet is roughly triangular in shape. The plantar tubercle is strong and continues on the diaphysis as a short blunt crest. The medial surface is almost straight and bears a thin articular facet for articulation with metatarsal II. The lateral margin of the proximal epiphysis is deeply concave; it bears a circular articular facet, extended on a great portion of the lateral margin of this epiphysis. This facet articulates with metatarsal IV, which is overlapped by metatarsal III. The shaft is oval in cross section in the most proximal portion (with the main axis dorso-plantar), rounded at the middle, and oval again distally (with the main axis horizontal). The distal trochlea is symmetrical, with a strong median keel on the plantar face. In dorsal view, the tarsal head is moderate in size and cylindrical in shape (with the main axis horizontal). There is a shallow concavity over the head, distoproximally short and lateromedially elongated, with the main axis parallel to the trochlea; and small processes on the lateral and medial sides. Below these processes and on the lateral and medial sides, there are deep roughly circular concavities.

Sp. 3
(Figure 5q–w)

Referred material—MGNJRG-C31-UV-1-2, proximal fragment of left tibia.

Descriptions and comparisons—MGNJRG-C31-UV-1-2 corresponds to a proximal fragment of left tibia, including the complete epiphysis and a proximal portion of the diaphysis. The proximal epiphysial line is still marked at the anterior face of the tibia, on the tibial tuberosity (see below), while it is diffuse, almost completely ossified, in the other faces This indicates the specimen could be a subadult or young adult. In proximal view, the proximal epiphysis is roughly triangular in cross-section, with a posterior face and an anterior angle. There is a shallow wide concavity at the posterior face of the triangle and another deeper and narrower at the anteromedial one. The lateral condyle is roughly ellipsoidal, posterolaterally elongated. Dorsally, the lateral condyle bears a smooth, slightly concave surface for articulation with the lateral condyle of the femur. The medial condyle is roughly circular, posteromedially protrudent, with a lateral curved entrance formed by the medial tubercle of the intercondylar eminence. The intercondylar eminence is composed of two elongated tubercles (medial and lateral), both of them posterolaterally oriented. The medial tubercle is slightly shorter anteroposteriorly, but more developed than the lateral one (more evident in posterior view). Anteriorly, the condyles continue in a soft, shallow, and wide concave surface, the anterior intercondiloid fossa, which anteriorly ends in a broad roughly triangular, perforated by large vascular foramina. This surface extends anteriorly on a large rounded elevation, the tibial tuberosity (for the attachment of the *ligamentum patellae*; Gray (2016). Posteriorly, the condyles are separated from each other by a shallow depression, the intercondyloid fossa.

In posterior view, the medial condyle is convex, subspherical, and markedly more protrudent than the lateral one. On the distal portion of this condyle, there is an irregular shallow transverse groove, for the insertion of the tendon *semimembranosus* (Gray, 2016). Below the lateral condyle, there is roughly oval facet below the lateral condyle for articulation with the fibula. Additionally, below the intercondylar eminence, there is a concavity probably for the *popliteus* (Gray, 2016). Additionally, dorsomedially to the fibular facet, at the posterolateral end of the intercondyloid fossa, there is a small concavity, probably corresponding to the popliteal notch. In anterior view, from the level of the tibial tuberosity, descends a strong, blunt crest, the cnemial or tibial crest, which becomes weaker distally.

The diaphysis (shaft) is straight the preserved portion, triangular in cross-section in the proximal portion. In the shaft and below the level of the condyles, the cnemial crest normally delimits two fossae. However, the lateral fossa in this specimen so shallow, that it is almost absent, very poorly defined. On the other hand, the medial fossa is deep and well defined. It would correspond to the area of origin of the muscle tibialis (Osgood, 1921). In the most proximal portion of the medial fossa, between the condyle and the shaft, there is a more pronounced cavity that probably bonds mainly to the area of attachment of the muscles *gracilis*, *sartorius*, and *semitendinosus* (Elftman, 1929). In posterior view, the shaft bears a marked vertical ridge, which apparently starts proximally below the epiphysial line, and descends distally.

Rodentia Bowdich, 1821
Rodentia, fam. et gen. indet.
(Figure 5x–y)

Referred material—MGNJRG-C31-AB-3-4, an isolate incisor.

Descriptions and comparisons—MGNJRG-C31-AB-3-4 corresponds to a small incisor fragment, broken on both ends. It is elongated, curved and presents a longitudinal groove along the lateral face (Figure 5x, y).

Remarks—Despite of a single incisor is not enough taxonomically informative, based on the size, it probably belongs to a small Sigmodontinae caviomorph, as the presence of these rodents was reported previously for this locality (Correal-Urrego *et al*., 2005).

Aves Linnaeus, 1758
Cuculiformes Wagler, 1830
Cuculidae Vigors, 1825
Crotophaginae Swainson, 1837
Crotophaginae, gen. et sp. indet.
(Figure 6).

Referred material—MGNJRG-C27-GH-1-2, a proximal and distal end portion of right humerus.

Descriptions and comparisons—MGNJRG-C27-GH-1-2 (Figure 6a, b). It represents a distal portion of a right humerus, with epiphysis in palmar or cranial surface. It is attributed to the Cuculidae family (Hughes, 2000), based on that exhibits a rounded condylus ventralis localized in the central axis of the humerus, not flattened or oblong as in other bird families. In this family the distal end is greatly expanded ventrally, yielding an elongated "finger-like" processus flexorius, and epicondylus ventralis; those anatomic elements are partially broken in the specimen, which avoids any further taxonomic identification. Also, the fossa musculo brachialis is oval and clearly defined. Specifically, in the specimen, the tuberculum supracondylare dorsale is more marked and dorsally protruding than in other cuculid genera such as *Coccyzus*, *Morococcyx* or *Geococcyx,* and old World genera *Clamator*, *Centropus* and *Eudynamys* (Steadman, 2008; Shute *et al*., 2016). The observed condition for the proportion and shape of tuberculum supracondylare dorsale respect to the condylus dorsalis curvature forms a broad and deep sulcus between them. Alike, the shape of the condylus dorsalis and the epicondylus dorsalis in relation to the process supracondylaris dorsalis forms a straight angle with the tuberculum supracondylare dorsale at the top. Thus, the traits describe above for the specimen have similar proportions to those observed in *Crotophaga,Guira* and *Tapera*, but significantly different in other genera of the Crotophaginae subfamily such as, *Morococcyx* or *Geococcyx* (Steadman, 2008). According to the distal portion in anconal or caudal view (Figure 6c, d) is clear the presence of the sulcus scapulotricipitatis, but it is no so deep respect to the distal view (Figure 6e, f).

In caudal surface (Figure 6g, h), the humerus proximal epiphysis presents a globusus caput humeri rotated slightly towards the cranioventral region, also evidenced in the proximal view (Figure 6k, l). The specimen presents an outstanding wide incisura capitis orientated more proximodistally than dorsoventrally. The tuberculum ventrale is large and prominent, it is oriented quite proximally, the specimen has a fracture in front face of this process, near to the fossa pneumotricipitatis which is small, well defined and with visible internal structure (Figure 6g). Specifically, in *Crotophaga* this bone trait is shallow and the foramen usually single (Shufeldt, 1901) while is wider in other cuculid genera such as *Centropus* (Shute *et al*., 2016). In cranial surface (Figure 6i, j) the intumescentia humeri is less inflated and the impression coracobrachialis is shallow and oriented proximodistally. The crista deltopectoralis is not preserved. The distal end portion have 18.4 mm length and 6,9 mm distal width (Figure 6a, b), its proximal portion have 13.2 mm length and 9,1 mm proximal width. Based on its size and preserved morphology, we estimate a total length of around 40 mm for this humerus, with a central axis having a slight sigmoidal curve. MGNJRG-C27-GH-1-2 is identified as a member of the Neotropical Crotophaginae subfamily by its stout overall proportions and by the shape and marked proportion of delimited fossa musculi brachialis; a very distinct feature in most of other Cuculidae members as *Coccyzus* or *Clamator*, both members of Cuculinae subfamily. Comparing it with published measures for other cuculids (Steadman, 2008), the distal width (considering the broken tip) suggests a size closer to those reported for *Crotophaga ani* and *Dromococcyx pavoninus*, members of Crotophaginae subfamily with recent distribution in Colombia (Hilty and Brown, 2001).

Squamata Oppel, 1811
Serpentes Linnaeus, 1758
Colubroides (*sensu* Zaher, 2009)
Viperidade Laurenti, 1768
Crotalinae Oppel, 1811
Crotalinae, gen. et sp. indet.
(Figure 7a–h)

Referred material—MGNJRG-C20-WX-5-6, a precloacal viperid vertebra.

Descriptions and comparisons—MGNJRG-C20-WX-5-6 corresponds to a trunk vertebra missing the whole neural spine, both synapophyses and postzygapophyses, as well as parts of the zygosphene, right prezygapophyses, and the condyle. In anterior view (Figure 7a, b), the vertebra presents a thin broken zygosphene, which reveals a triangular depressed neural canal. The right prezygapophysis is completely broken, but the left is slender and presents and inclination of ~25° in relation to the horizontal plane, and is anterolaterally projected. A pair of well-developed paracotylar foramina are visible in deep paracotylar fossae. The cotyle is large and nearly circular (ctw~cth). The parapophyseal processes are absent, but their presence is inferred from the broken surfaces visible under the ventral rim of the cotyle Despite the posterior portion of the vertebra is highly damaged, is possible to appreciate both zygantral foramina (Figure 7c, d). The base of the condyle reflects a circular shape, which is connected ventrally to the hypapophysis. In left lateral view (Figure 7e, f), a foramen is visible on the lateral margin of the neural canal, positioned aside the diapophysis. On the ventral surface of the centrum a prominent hypapophysis ventroposteriorly inclined, but with the posterior edge broken. On the left anterior margin, the broken surfaces reveal a well-developed paradiapophyses. In dorsal view, the prezygapophyseal articular surface is broad, with an obovate shape (Figure 7e, f). The specimen is regarded to viperidae, as it possesses the following combination of features: Vertebral centrum not elongate; big rounded cotyle and condyle; relatively depressed neural canal, a prominent ventroposteriorly angled hypapophysis and an obovate prezygapophysial articular surface anterolateral oriented (Auffenberg, 1967; Rage, 1984; Hsiou and Albino, 2010). The specimen is assigned to Crotalinae, considering that all of the New World extant viperids belong to this subfamily (Head *et al.*, 2006).

Serpentes Linnaeus, 1758
Serpentes, fam. et gen. indet.

(Figure 7i–n)

Referred material—MGNJRG-C23-AB-1-2-3-4, an isolated vertebra.

Descriptions and comparisons—MGNJRG-C23-AB-1-2-3-4 corresponds to a single procelic vertebra with all the posterior face broken and eroded. In anterior view (Figure 7i, j), a big rounded cotyle is visible, wider than the neural canal. The specimen presents also an elliptic paracotylar foramen on the right margin of the cotyle. The prezygapophyses are anterolaterally oriented and present a ~20° inclination from the horizontal plane. Despite much of the zygosphene is broken, on its lateral margin, it is relatively thin, and it has a subtriangular neural canal. On the lateral surfaces, is possible to appreciate the subcentral and lateral foramina (Figure 7i, j). The last one is located on the lateral margin of the neural canal, and placed aside from the broken surfaces of the paradiapophyses. The hemal keel is completely missing. In dorsal view, is possible to distinguish the base of the neural spine and a fragment of the right prezygapophysis articular surface (Figure 7m, n). The vertebra lacks the whole postzygapophyseal structures, as well as the cotyle, which makes it very difficult to add any further description, and taxonomic identification. Even though, the specimen shares certain characteristics with colubroids, like a big rounded cotyle, the presence of the paracotylar foramen, a thin zygosphene, and a well-developed paradiapophyses (inferred) (Auffenberg, 1967; Albino, 1989); we avoid to assign the specimen to this clade, as most of the posterior and ventral features are missing.

Squamata Oppel, 1811
Squamata, fam. et gen. indet.
(Figure 7o–t)

Referred material—MGNJRG-C20-WX-5-6, an isolated vertebral centrum

Descriptions and comparisons—MGNJRG-C20-WX-5-6 is a medium-sized (Length: 6.37 mm; width: 5 mm), short procelic vertebral centrum. The cotyle is dorsoventrally flattened and is broken on its anterior rim (Figure 7o, p). The condyle is rounded (Figure 7q, r) and partially broken ventrally. Ventrally, the specimen lack of any visible foramina, but presents a reduced hemal keel (Figure 7s, t). The dorsal surface is completely eroded, which avoids any undisputable further taxonomic identification beyond squamates. However, based on the shape of the cotyle, which is dorsoventrally flattened, the conical shape of the centrum, and the presence of a sagittal ventral ridge; it is possible that the specimen belongs to a family of lizards (Hoffstetter and Gasc, 1969; Brizuela *et al*., 2015; Camolez, 2006).

Invertebrates

Arthropoda von Siebold, 1848
Myriapoda Latreille, 1802
Myriapoda indet.
(Figures 7u–w)

Referred material—MGNJRG-C17-CD-3-4, a nearly complete exoskeleton.

Descriptions and comparisons—MGNJRG-C17-CD-3-4 (Figure 7u, v) represents a partial exoskeleton of a myriapod, preserved in a calcium carbonate matrix. The specimen consists of 19 articulated body segments with a total length of 21 mm and 1.7 mm diameter in cross-section. As the specimen is slightly coiled, is possible to determine a segment length of 0.5 mm expandable to 1.3 mm length when coiled. Some places in the dorsum and laterals presents holes, which reveal a hollow interior which does not allow us to determine if the specimen corresponds to a death animal or is just the remaining cuticle of the exuviae, as the specimen presents a hyaline texture with distinguishable laminar layers (Figure 7w).

Hymenoptera Linnaeus, 1758
Vespidae Latreille, 1802
cf. *Protopolybia* Ducke, 1905
(Figures 8–9)

Referred material—MGNJRG-C27-CD-5-6, an almost complete nest; MGNJRG-C30-AB-7-8, an inferior part of nest; MGNJRG-C30-EF-5-6, a nest fragment; UR-CP-0035 a complete nest.

Descriptions and comparisons—MGNJRG-C27-CD-5-6 (Figure 8a–f) is a partial conical in shape nest, with rounded corners. It measures as preserved 13.53 mm long and 11.37 mm wide. It has approximately 6 sessile cell combs and an entrance located in the second comb (from top to bottom) (1.13 mm long and 1.22 mm wide). A more detailed view of an entrance to one of the nests is shown in Figure 8c, measuring 1.79 mm long and 2.32 mm wide. The architecture of the sessile cell combs is characterized by micro pentagonal structures joined together, some of them being slightly irregular in elongation (Figure 8f). MGNJRG-C30-AB-7-8 (Figure 8g, h) is partial conical nest measuring 10.57 mm long and 9.27 mm wide. In the second comb from bottom to top located on the left side of the front view of the nest is an entrance (1.06 mm long and 1.25 mm wide) (Figure 8h). MGNJRG-C30-EF-5-6 (Figure 8i, j) corresponds to a partial nest with a semi-conical shape, irregular edges and measures 9.01 mm long and 10.19 mm wide. It has six combs as preserved, with an entrance located at the middle portion of its dorsal surface (Figure 8j).

UR-CP-0035 (Figure 9a) is a conical nest measuring 19.75 mm long and 14.97 mm wide. In its external morphology, can be evidenced approximately 8 sessile cell combs, placed one after the other with heterogeneous width between them. It has an entrance located in the upper right part (1.42 mm long and 1.20 mm wide), exactly at the intersection between the fourth and fifth combs (from top to bottom). SEM/EDS analysis of two small fragments of the combs (Figure 9b, c) shows details of some of the apertures filled with rock matrix (Figure 9d), and preservation of some tracheid-like plant fiber-like structures (Figure 9e). The microstructural architecture of the combs show that they are formed by pentagonal to irregular polygonal units (Figure 9f–h). The elemental composition (Figure

9i–n) of these units shows predominance of calcium with less abundant content of carbon, silicon, and sulfur. A test using hydrochloric acid (HCl) 10% show high effervescent bubbling indicating that the composition was mostly calcium carbonate (CaCO3).

Based on the aforementioned, it can be assumed that these fossil nests were created by wasps, potentially belonging to the genus *Protopolybia*. This conjecture arises mainly for two reasons, the first based on their morphology of wasps of the genus *Protopolybia* and the second for the arrangement, shape, and process of nest creation. *Protopolybia* is a genus of Neotropical social wasps from the Epiponini tribe and the Vespide family. This family is characterized by mainly using plant material to make their nests and the tribe is characterized by building nests in swarms (Somavilla *et al*., 2012), tracheid-like plant fiber-like were found in these fossil nest supporting our interpretation that they were created by paper wasps. *Protopolybia* species build their nests under or between the leaves. When located under the leaves, they have a very fragile and generally whitish shell. When they nest between the leaves, they hold their nests in one of them and with oral secretion, they stick a leaf close to the other side of the brood cells, in this way the leaf of the plant itself works as the envelope (Somavilla *et al*., 2012).

Plants

Plantae *sensu* Copeland, 1956
Magnoliophyta Cronquist, 1968
Magnoliophyta indet.
(Figures 7x)

Referred material—MGNJRG-C21-YZ-9-1 a single isolated seed; MGNJRG-C23-AB-1-2-3-4 single isolated seed; MGNJRG-C24-UV-1-2 single isolated seed; MGNJRG-C24-WX-7-8 single isolated seed; MGNJRG-C24-YZ-1-2 and MGNJRG-C27-GH-1-2, four isolated seeds.

Descriptions and comparisons—All the specimens share the same morphology as they are similar to achenes which are 8 mm long and 3 mm wide in equatorial diameter, (Figure 7x). The seeds in general present a smooth surface, but some exhibit a rounded side indentation on upper half, which can be interpreted as the funiculum, however, no additional characteristic structures are recognizable. A few of the seeds present signs of herbivory like MGNJRG-C23-AB-1-2-3-4 which presents a hole in the surface revealing a hollow interior or MGNJRG-C27-GH-1-2 which has broken surface, similar to a bite mark. Previous work (Correal-Urrego *et al*., 2005) described the presence of at least four families (Fabaceae, Juncaginaceae, Spindaceae and Verbenaceae). However, our specimens do not match with any of the descriptions reported. The overall morphology of the seeds suggests they represent monocots, without any further classification at this point.

Discussion

Validating the radiocarbon age

The charcoal sample analyzed from Corte 8 fossil site indicates an age of 16889–16412 cal BP (95.4% confidence), which indicates that the deposit and fossils describe herein are from the Late Pleistocene.

Relevance of the fossil turtles

The occurrence of *Chelonoidis* sp. in the Late Pleistocene site of Pubenza represents one of the youngest fossil records of this genus in northern South America. Although the material is too fragmentary to be assigned to the species level, we hypothesize that could correspond to *C. carbonarius* based on that it shares with this extant taxon a gular scute that reaches the entoplastron, in contrast to the condition of *C. denticulatus* where the gulars are smaller and restricted to the epiplastra (see Supplementary Figure S1). Currently, *C. carbonarius* is the only taxon of this genus occurring west of the Eastern Cordillera of Colombia (Turtle Taxonomy Working Group, 2017), supporting that the fossils from Pubenza could correspond to this taxon more than to *C. denticulatus* that currently is restricted east of this geographical faunistic barrier. The new fossil material of *Kinosternon* sp. expands the number of known material for this taxon at this locality, however, it is still challenging to establish an undisputable species affinity due to the lack of cranial material and complete shells.

The mammals of Pubenza

Our reports show that wide diversity of small mammals coexisted with the first humans in Colombia, together with the megafauna like *Notiomastodon*, *Glyptodon* and *Eremotherium,* which inhabited the Bogota River Basin during the Late Pleistocene (Correal-Urrego *et al*., 2005; Correal-Urrego, 1993). Armadillos genera like *Propaopus* and *Dasypus* were reported in previous works (Correal-Urrego *et al*., 2005; Van der Hammen and Correal-Urrego, 2001) but without a proper description of the material. In addition to a formal and detailed description of the fossils, our findings also provide an update to some of the taxonomical assignments provided by Correal-Urrego *et al*. (2005), as the armadillo species *P. magnus* is now synonymous of *P. sulcatus*. Cervids were also common in Pubenza as indicated by MGNJRG-C26-QR-1-2 specimen, which complements previous reports made by Correal-Urrego *et al*. (2005), who mentioned bones, teeth, and antlers fragments attributed to *Odocoileus*; an extant deer that inhabits in many Colombian ecosystems. Our findings reveal a variety of rodents that have not be considered in the past, as the only record for this group consisted of a single incisor (Van der Hammen and Correal-Urrego, 2001). Here we identify at least four different individuals mainly referable to caviomorphs, which range in size from small to medium size and probably correspond to different species.

The fossil birds

The crotophagins and cuculids of Pubenza constitute the first fossil occurrence of these lineages of birds in Colombia, expanding the avian fossil record of the country;

previously limited to five species from the middle Miocene of La Venta fauna (Huila, Colombia) (Rasmussen, 1997) and two taxonomically indeterminate reports from Castilletes (ca. 16.7–14.2 Ma) and Ware (ca. 3.5–2.8 Ma) formations in the Guajira Peninsula (Moreno *et al*., 2015).

Late Pleistocene birds in tropical South America are known from the Mene de Inciarte in northwestern Venezuela (Steadman *et al*., 2015); La Carolina, in southwestern Ecuador (Campbell, 1976); and Talara, in northwestern Peru (Campbell, 1979). From these localities, the only one with the occurrence of cuculid birds is Mene de Inciarte, represented by the species *Coccyzus americanus* (Seymour, 2015). Additional records of cuculids in South America include the genera *Piaya* from Brazil, and the Holocene record of *Coccyzys* from Bolivia (Hoffstetter, 1968). For the Crotophaginae subfamliy, the only known fossil records for South America are *Crotophaga* and *Tapera* from the Late Pleistocene of Brazil (Vuilleumier, 1984).

Extant representatives of the Crotophaginae subfamily are represented by nine species in Colombia (del Hoyo and Collar, 2014). Considering proportions and size in diverse anatomical elements, we hypothesize that the cuculid fossils from Pubenza could correspond to either *Crotophaga* or *Dromococcyx* genera, both representing species with a slim body and long tail, differing in their coloring patterns (del Hoyo and Collar, 2014). *Crotophaga* species are communal breeders associated to lowland environments and especially semi-open landscapes associated to dry scrub and forestal areas, these birds have a generalist character benefited from deforestation and fragmentation of tropical dry forests, which has currently allowed them to reach a wide distribution in the neotropics (del Hoyo and Collar, 2014; Hilty and Brown, 2001). Meanwhile, *Dromococcyx* presents a parasitic reproductive strategy, typical of cuculidae. Actually, these species-inhabit in a wide spectrum of biome conditions ranging from lowland tropical rainforest to tropical deciduous woodland, associated with forest limits and understory scrub (Hilty and Brown, 2001). The generalist ecological traits and niche requirements of these genera are in concordance with the scenario of forest fragmentation and the subsequent development of open dry environments associated with the cooling trends due to glaciation processes during the Late Pleistocene (Correal-Urrego *et al*., 2005). Thus, our reports from Colombia and the Brazil findings indicate a wider geographical distribution of Crotophaginae species during Late Pleistocene. According with published evidence, possibly the ecological generalist condition allowed the subsequent expansion of species towards North America and Caribbean islands since Late Pleistocene and Holocene as evidence in fossil sites from México (Steadman *et al*., 2003) and the Antilles (Bernstein, 1965).

Relevance of Pubenza squamates

Our findings reveal that lizards and snakes inhabited the Bogota River Basin during the Late Pleistocene, supporting previous reports of the boid *Epicrates* (Correal-Urrego *et al*., 2005). At the same time, the occurrence of fossil squamates indicates that the ecosystem of Pubenza was healthy and diverse, as has been suggested for similar extant environments (Fulton, 2018). The fossil snakes from Pubenza resemble extant species occurring in this region for example *Bothrops asper* and different colubrids, supporting the hypothesis of "evolutionary stasis" proposed for snakes during the Pleistocene (Holman, 2000), as many of extant genera had been recognized from the Neogene-Quaternary fossil record (Scanferla *et al*., 2009, Albino and Brizuela, 2014, Scanferla and Agnolín, 2015, Onary *et al*., 2018, Aranciaga-Rolando *et al*., in press).

A relevant aspect of the fossil snakes from Pubenza is the first record of viperids in Colombia. Viperids arrived in South America possibly during the Miocene (Albino and Montalvo, 2006), exhibiting a geographically board Pleistocene fossil record, with reports from Argentina, Brazil, Bolivia, and Venezuela (Albino and Brizuela, 2014; Onary *et al*., 2018; Onary *et al*., 2017, Aranciaga-Rolando *et al*., in press).

The fossil snakes from Pubenza increase the Colombian snakes fossil record which is now represented by the giant boid *Titanoboa cerrejonensis* (Head *et al*., 2009) from the late Paleocene of Cerrejón (La Guajira, Colombia) and other boids, aniliids and scolecophidians from the Miocene localities of Castilletes (La Guajira, Colombia) (Moreno *et al*., 2015) and La Venta (Huila, Colombia) (Hecht and LaDuke, 1997). Caenophidians snakes are even scarcer, as only a few specimens identified as 'Colubroidea' have been reported from La Venta (Hecht and LaDuke, 1997) and an isolated vertebra attributed to *Synophis* aff *S. bicolor* from a potential Pleistocene in age deposit in Santander (De Porta, 1965).

Paleoichnoentomology and new fossil invertebrates

The wasp nests potentially created by members of the *Protopolybia* genus reported here from the Pubenza locality represent the first record of this type of trace structures in the fossil record of hymenopterans in northern South America, where previously full body insects were only known occurring as (sub)fossils in copal from Santander, Colombia (Hinojosa-Diaz and Engel, 2007; Penney *et al*., 2013; Poinar *et al*., 2017). The elemental characterization using SEM/EDS of the nests from Pubenza presented here show an advanced process of replacement to calcium carbonate, enough to call these structures fossils and not just simple (sub)fossils, however, some of their original constituents including tracheid-like plant fibers are still preserved (Figure 9e).

Another relevant fossil invertebrate added in here to the Pubenza fauna is the occurrence of a myriapod exoskeleton, which is also partially preserved in calcium carbonate as it reacts to HCl 10%, however, the presence fibrous laminated structures makes plausible that some original chitinous material is still preserved in its internal walls and septa (Figure 7w). MGNJRG-C17-CD-3-4 specimen constitutes the first fossil record for this group in South America with an age precisely known (Late Pleistocene), considering that the age of the Colombian copal is still highly controversial potentially ranging between 60 years (postbomb) to 2.5 Ma (Holocene–Pleistocene–Pliocene) (Poinar *et al*., 2017), and the record of myriapods in this copal is only known informally in some websites (www.fossilmuseum.net). Our results increase the knowledge of the invertebrate fauna of Pubenza, where gastropods and decapods have been previously reported by Correal-

Urrego *et al*. (2005) and are also present in the MGNJRG collection (see Supplementary Table 1).

Fauna and human interactions

Besides providing descriptions and illustrations for the small vertebrates of the Pubenza locality, which for many years remained undescribed and only mentioned in previous works (Correal-Urrego *et al*., 2005); we added the first occurrences of birds, hymenopteran nests, and myriapods for this fossiliferous site. Together, the fossils of Pubenza indicate a rich ecosystem with different groups of vertebrates, invertebrates, and plants (Supplementary Table S1), that offered a variety of dietary opportunities for earlier humans inhabiting this region. Interactions of humans with this ecosystem, particularly with the paleofauna was initially suggested by Correal-Urrego *et al*. (2005), based on the occurrence of bone fragments, probably belonging to mastodons, which exhibit parallel incisions, however, this possible interaction and association between scare lithics and megafauna have been considered dubious due to the lack of a clear correlation between their stratigraphic occurrence and age (Politis, 2009; Muttillo *et al*., 2017). On this respect, we examined a bone fragment that presents three parallel incisions on its external surface (MGNJRG-C27-AB-5-6) (Figure 10a–c), in cross-section these incisions exhibit an almost symmetrical U-shaped valley shape (Figure 10c), differing from typical acute V-shape caused by cut marks (Braun *et al*., 2016). However, it is possible that the smoother shape and margins of the incisions in MGNJRG-C27-AB-5-6 were the product of taphonomical modifications, particularly abrasion and erosion before burial. Another evidence of potential bone modifications in this bone comes from its ventral surface, which exhibits some striations (Figure 10d–f). Some relicts of tool making process are also common in the examined material from Pubenza (Figure 10g). With this, we provide new evidence that could support the initial hypothesis suggested by Correal-Urrego *et al*. (2005) that some of the earlier humans of Colombia interact with the paleofauna at the evidence is found at the Pubenza site.

Conclusions

The ancient lacustrine enviroment of Pubenza reveals a diverse biota, which coexisted with the early humans in Colombia. This lacustrine ecosystem apparently was an encounter point for many vertebrates and invertebrates in their seek for water or food. *Dasypus, Propaopus* and caviomorph rodents were apparently the most common mammals in the locality, but not in the same proportion of the turtles, as *Chelonoidis* and *Kinosternon* represent the most abundant fossil remains found in this locality. The report of birds (Crotophaginae) and snakes (Crotallinae) shows the great potential that this locality has for future findings of these lineages of vertebrates. Similarly, the description of land invertebrates increases the knowledge of the invertebrate paleontology of the Pleistocene of Colombia, since only snails and crabs had been reported for Pubenza. The fossil material described herein reaffirms that Pubenza is a prolific and remarkable locality for future paleontological and archeological studies that could help to improve our knowledge on the origin of the actual fauna of the Bogotá River Basin and Colombia, as well as their changes in the last 16800 years.

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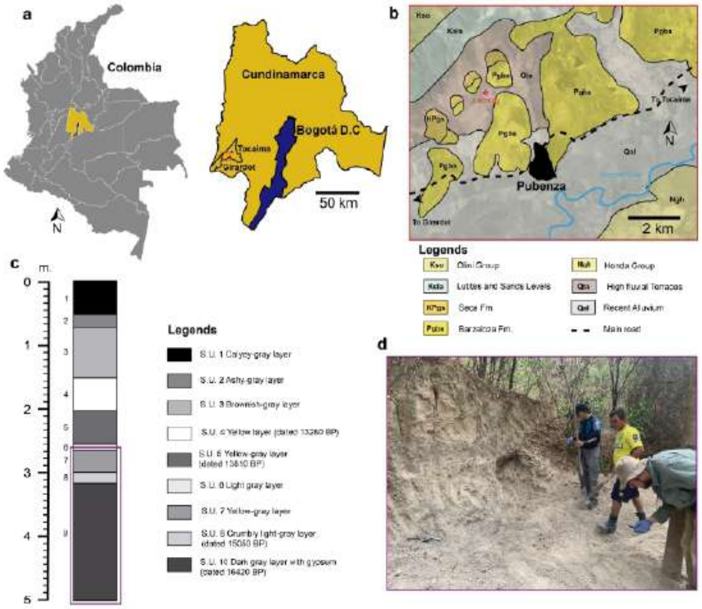


Figure 1. Maps and geology of the Pubenza locality. (a) Location map of Colombia and Cundinamarca Department, showing the Pubenza region in red square; (b) Geological map of the Pubenza region (red square shown in a); (c–d) General stratigraphic column of the Pleistocene deposits, modified from Correal-Urrego et al. (2005), photograph of the outcrop indicated by a purple rectangle in c. Abbreviations: S.U, stratigraphic unit.

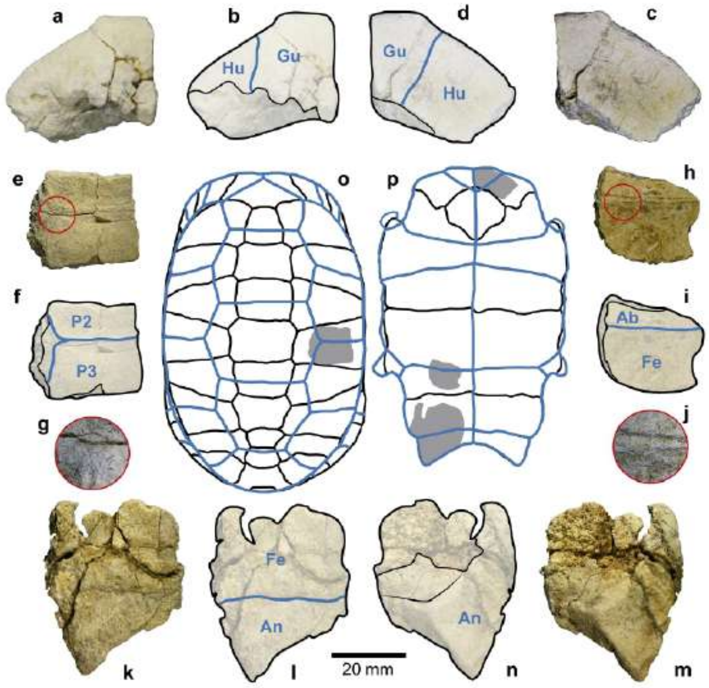


Figure 2. Fossils of Chelonoidis sp. from Pubenza. MGNJRG-C26-EF-9-10(100-120) left epiplastron in dorsovisceral (a–b), and ventral views (c–d); MGNJRG-C24-ZonaAmpliacionB costal 4 fragment in dorsal view (e-f); close-up of the costal bone sculpture (g), red circle in e; MGNJRG-C27-CD-5-6(100-125) right hypoplastron fragment in ventral view (h–i); close-up of the bone surface of the hypoplastron (j), red circle in h; MGNJRG-C23-GH-1-2(75-100) right xiphiplastron in ventral (k–l), and dorsovisceral views (m–n); Outline of the carapace of the extant C. carbonarius (o) in dorsal view, indicating the anatomic correspondence with the fossil elements of Chelonoidis sp. from Pubenza shadowed in gray; Outline of the carapace of the extant C. carbonarius (p) in ventral view, indicating the anatomic correspondence with the fossil elements of Chelonoidis sp. from Pubenza shadowed in gray. Abbreviations: Ab, abdominal scute; An, anal scute; Fe, femoral scute; Gu, gular scute; Hu, humeral scute, P, pleural scute.

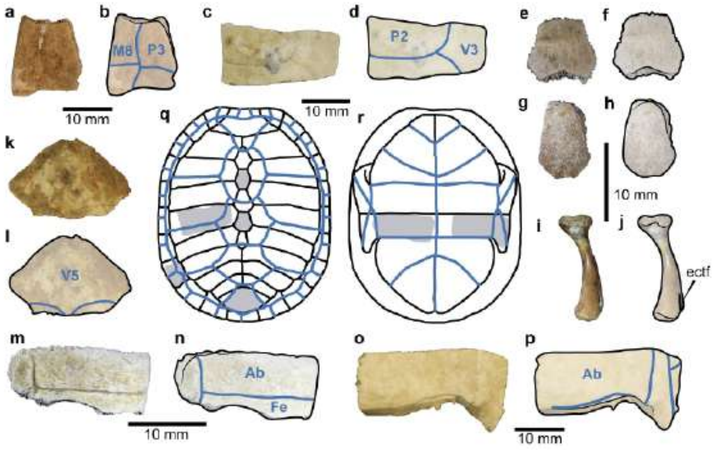


Figure 3. Fossils of Kinosternon sp. from Pubenza. MGNJRG-C17-QR-3-4(20-40), peripheral 8 in dorsal view (a–b); MGNJRG-C26-EF-9-10(100-120)51, costal 4 in dorsal view (c–d); MGNJRG-C27-CD-1-2 (75-100), neural 2 in dorsal view (e–f); MGNJRG-C25-EF-3-4(100-125), neural 4 in dorsal view (g–h); MGNJRG-C27-GH-1-2(75-100) left humerus in dorsal view (i–j); MGNJRG-C26-ST-1-2(100-120) pygal bone in dorsal view (k–l); MGNJRG-C20-YZ-5-6(40-60) right hypoplastron fragment in ventral view (m–n); MGNJRG-C26-WX-1-2(100-120) left hypoplastron fragment in ventral view (o–p); Outline of the carapace of the extant K. leucostomun carapace in dorsal view (q), modified from Cadena et al. (2007, fig. 2), indicating the anatomic correspondence with the fossil elements of Kinosternon sp. from Pubenza shadowed in gray; Outline of the plastron of the extant K. leucostomun plastron in dorsal view (r), modified from Cadena et al. (2007, fig. 2), indicating the anatomic correspondence with the fossil elements of Kinosternon sp. from Pubenza shadowed in gray. Abbreviations: Ab, abdominal scute; ectf, ectepicondylar foramen; Fe, femoral scute; M, marginal scute; P, pleural scute; V, vertebral scute.

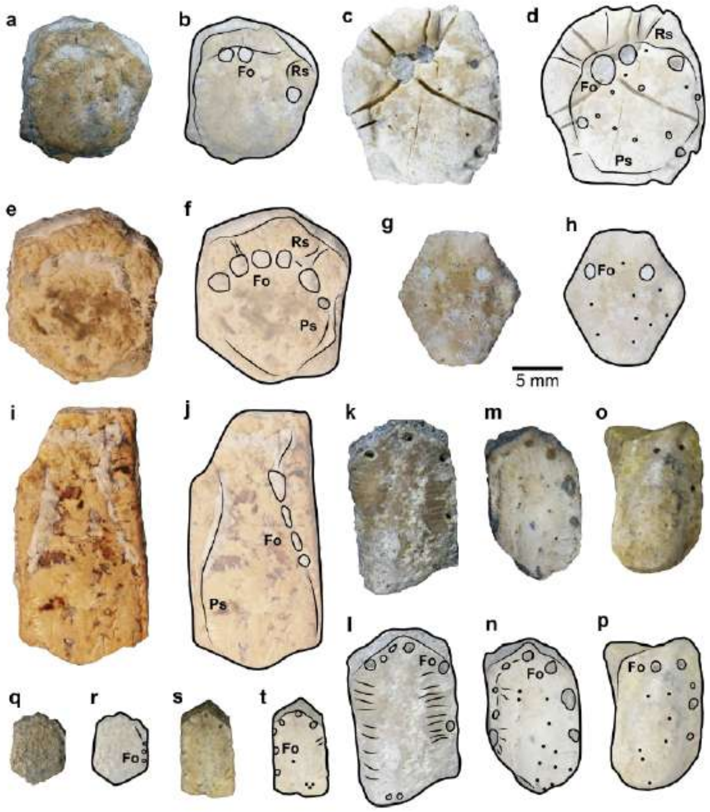


Figure 4. Fossils of Dasypodinae from Pubenza. Propaopus sullcatus: Buckler osteoderms, MGNJRG-C17-V-1-2(20-40) (a–b), MGNJRG-C19-ST-3-4(40-60) (c–d), MGNJRG-C17-V-1-2(20-40) (e–f), MGNJRG-C22-AB-5(80) (g-h); movable osteoderm, MGNJRG-C24-YZ-7-8(80-100) (i–j); caudal osteoderms, MGNJRG-C23-GH-1-2(75-100) (k–l), MGNJRG-C17-CD-3-4(20-40)26 (m–n), MGNJRG-C24-ST-3-4(80-100) (o–p). Dasypus sp: Buckler osteoderm, MGNJRG-C23-EF-1-2(75-100) (q–r); caudal osteoderm, MGNJRG-C24-QR-3-4(80-100) (s–t). Abbreviations: F, foramina; Ps, principal sulcus; Rs, radial sulcus.

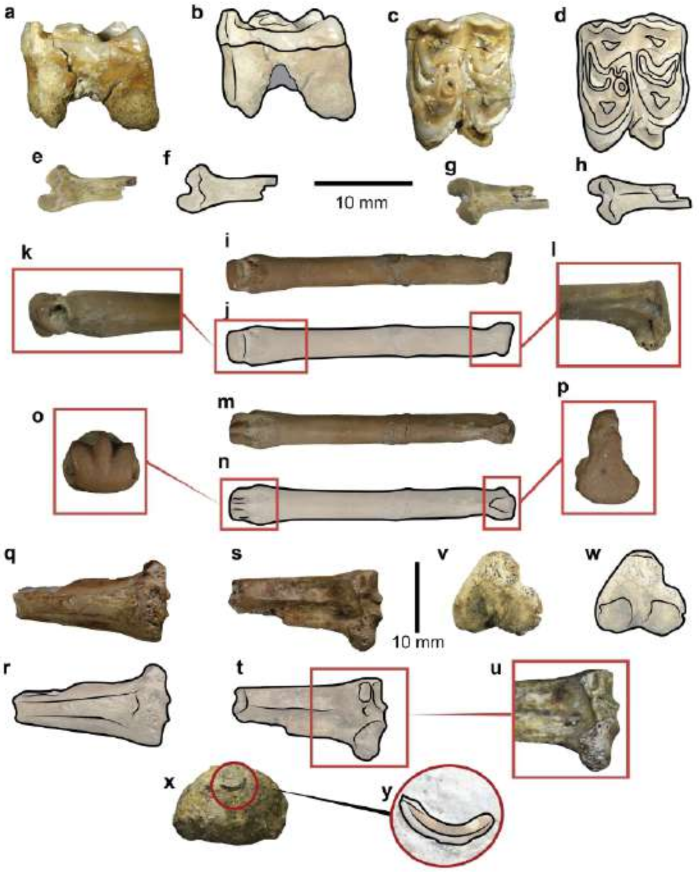


Figure 5. Other mammals from Pubenza locality. MGNJRG-C26-QR-1-2(100-120), artiodactyl molar in anterior (a–b) and occlusal (c–d) views; MGNJRG-C19-ST-3-4(40-60), distal fragment of caviomorph radius in anterior (e–f) and posterodistal (g–h) views; MGNJRG-C27-GH-1-2(75-100) caviomorph metapodial in dorsal view (i–j), distal portion in medial view (k); proximal portion in medial view (l), plantar view (m–n), distal trochlea in distal view (o), and proximal epiphysis in proximal view (p); MGNJRG-C31-UV-1-2(120-140) proximal fragment of caviomorph tibia in anterior (q–r) and posterior (s–t) views, proximal epiphysis in posterior view (u), and proximal view (v–w); MGNJRG-C31-AB-3-4(140-160), rodent incisor in mesial view (x–y).

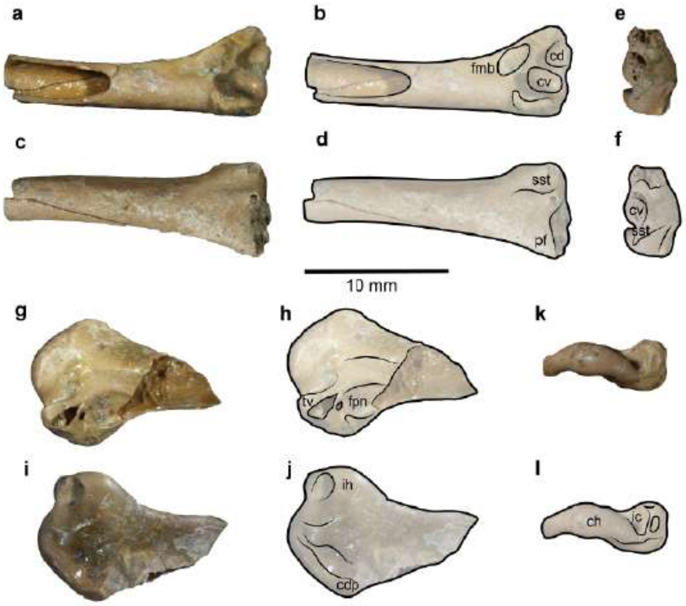


Figure 6. MGNJRG-C27-GH-1-2(75-100) humerus of Crotophaginae from Pubenza. Distal epiphysis in cranial (a–b), caudal (c–d) and distal (e–f) views; proximal epiphysis in cranial (i–j), caudal (g–h) and proximal (k–l) views. Abbreviations: cd, condilus dorsalis; cdp, crista deltopectoralis; ch, caput humeri; cv, condilus ventralis; fmb, fossa m. brachialis; fpn, fossa pneumotricipitalis; ic, incisura capitis; ih, intumescentia humeri; pf, processus flexorius; sst, sulcus scapulotricipitalis; tv, tuberculum ventrale.

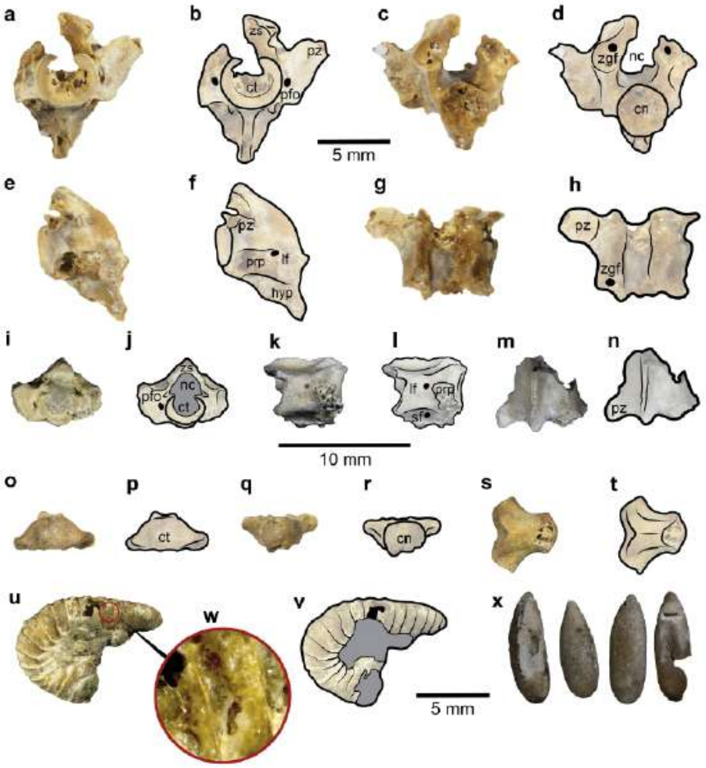


Figure 7. Miscellaneous fossils from Pubenza locality. MGNJRG-C20-WX-5-6(40-60), viperid vertebra in anterior view (a–b), posterior view (c–d), lateral view (e–f), and dorsal view (g–h); MGNJRG-C23-AB-1-2-3-4(80-100), undetermined snake vertebra in anterior view (i–j), lateral view (k–l), and dorsal view (m–n); MGNJRG-C20-WX-5-6(40-60), squamate vertebral centrum in anterior view (o–p), posterior view (q–r), and ventral view (s–t); MGNJRG-C17-CD-3-4(20-40)26, Myriapod fossil (u–v), with a detail of a body segment (w); MGNJRG-C27-GH-1-2(75-100), seeds from Pubenza (x). Abbreviations: cn, condyle; ct, cotyle; hyp, hypapophysis; lf, lateral foramen; nc, neural canal; pfo, paracotylar foramen; prp, paradiapophysis; pz, prezygapophysis sf, subcentral foramen zgf, zygantral foramen; zs, zygosphene.

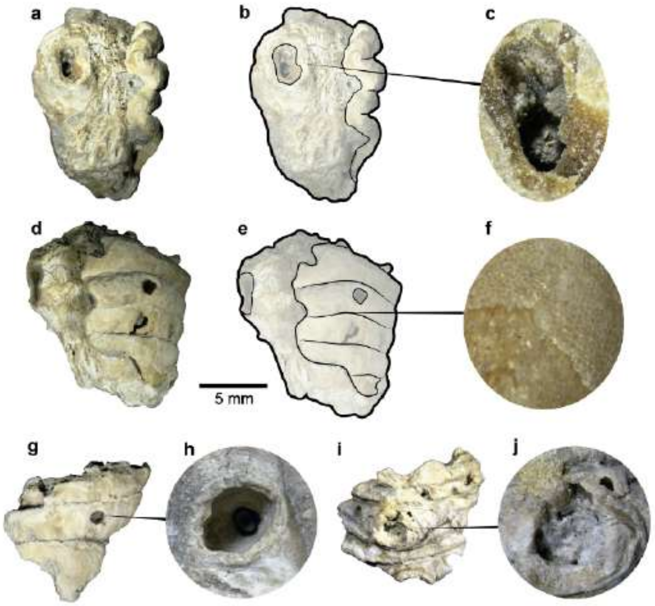


Figure 8. Fossil nest of Protopolybia (paper wasps) from Pubenza. MGNJRG-C27-CD-5-6(100-125) a nest in lateral view (a–b) and in frontal view (d–e), with details from the entrance (c), and the architecture (f). MGNJRG-C30-AB-7-8(100-125) a nest fragment (g) with detail from the entrance (h); MGNJRG-C30-EF-5-6(100-125) a nest fragment (i), with details of the entrance (j).

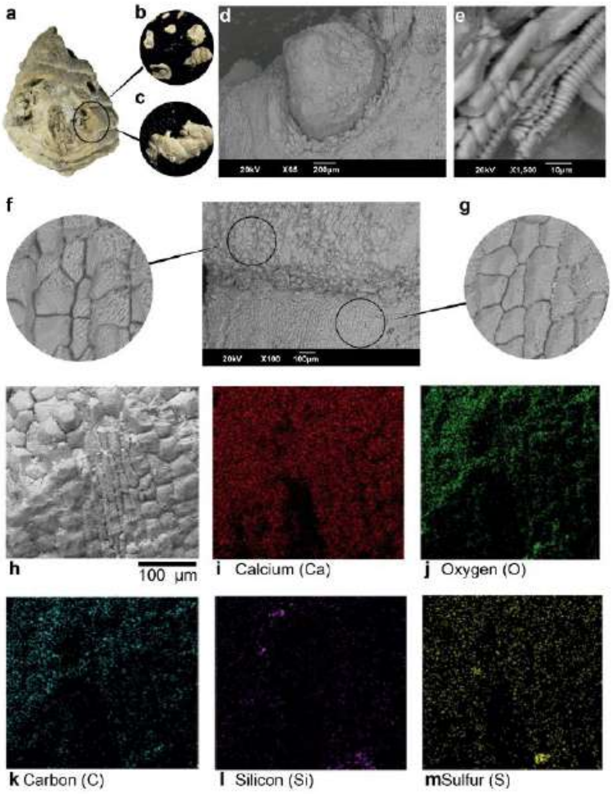


Figure 9. SEM/-EDS micrographs and elemental composition analyses of a fossil wasps nest from Pubenza. UR-CP-0035 specimen (a–c); Clogged fossil nest entrance (d); Vegetable fibers similar to tracheids (e); Pentagonal architecture of sessile cells (f); Elongated pentagonal sessile cells (g). Elemental analysis where the specimen is observed (f), and elements are referred as Calcium (i); Oxygen (j); Carbon (k); Silicon (l) and Sulfur (m).

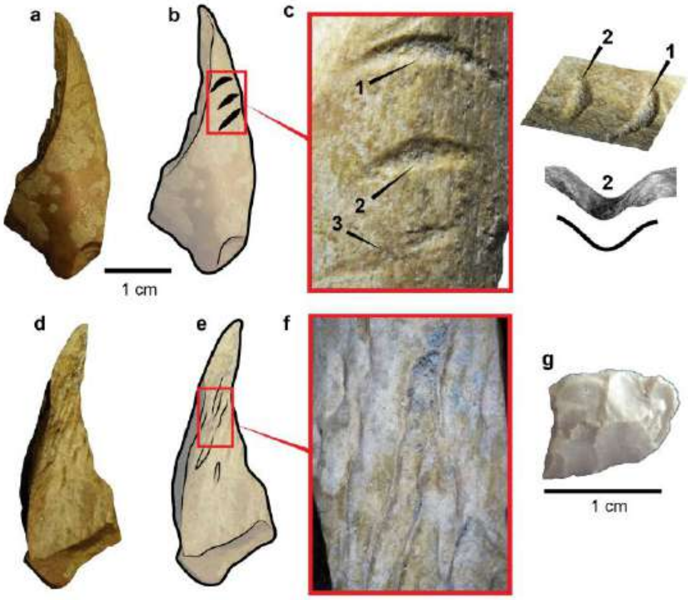


Figure 10. Bone fragments with marks from Pubenza MGNJRG-C27-AB-5-6(100-125), external view of the bone fragment with predatory marks (a–b); detail of predatory marks (c); internal view of the bone fragment (d–e); with a detailed view of the bone topography (f). MGNJRG-C17-ST-3-4(20-40), archaeological piece, probably a residual flake (g).

CONCLUSIONS

In the previous three chapters I described fossil snakes from three different snake groups that inhabited Colombia during the Neogene and Quaternary. Also, I discussed the major implications of these fossils regarding its paleobiological aspects in terms of their anatomy and their lifestyle. For the Miocene *Colombophis* I described novel anatomical features and suggest a lifestyle different from fossorial or cryptozoic. Also, I confirm the affinities of this fossil snake with the alethinophidians.

The Ware Formation fossil described in chapter 2 is the first report of a squamate for the Pliocene of Colombia. Furthermore, it gains relevance as our knowledge about Pliocene faunas is scarce. Finally, the description of the Pleistocene biota of Pubenza (chapter 3), not only represents the first fossil reports of many animals such birds, wasps and snakes (vipers), but also helps to understand the ancient ecosystems which first humans may have encountered in northern South America, and open the possibility of further collaborations between paleontologists and archaeologists.

This work also reveals one of the major challenges that face the paleontology of snakes, which is the lack of complete skeletons and the absence of diagnostic characters in the vertebrae for most of the lineages. Such problems have been addressed by many other paleontologists and perhaps the only way to solve it will be the discovery of more complete specimens. Therefore, further fieldwork activities will be needed to reveal major aspects on the biology, ecology and taxonomy of most of the specimens described.

Finally, the major constraint for the development of this thesis was lack of reference material. In Colombia almost none of the consulted Natural History Museums, (most of them associated to universities) have squamates skeletons in their collections. This was the reason why I had to travel overseas to train myself and learn about the anatomical variations and adaptations of snake skeletons. Therefore, I encourage Colombian Natural History Museums and Universities Biological Collections to increase the sampling of extant snakes, to have a robust skeletons database for comparisons and statistical/modeling studies.

APPENDIX

CHAPTER 1 SUPPLEMENTARY DATA

Supplementary Table 1.

Id	zh	zw	nch	ncw	cth	ctw	coh	cow	pr-pr	prl	prw	naw	po-po	cl	pr-po	nsl	h	<pz
***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
VPPLT-0577	0,8	2,8			-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0801	-	-	-	-	4	7	2,9	3	-	-	-	6,9	-	7,3	-	-	-	-
VPPLT-0802	0,7	3,2	0	0	2,4	2,9	2,1	2,6	-	-	-	-	-	4,1	-	-	-	-
VPPLT-0817	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0818	2	4,3	2,8	3,6	4	3,8	-	-	-	2,8	-	6,7	-	-	-	-	-	-
VPPLT-0840	1,3	5,6	2,5	4	5,4	6,1	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0841	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0842	1,1	4,5	2,3	3,7	4,3	4,7	-	-	-	-	-	7,1	-	-	-	-	-	-
VPPLT-0843	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0865	-	-	-	-	-	-	-	-	-	-	-	-	-	8,1	-	-	-	-
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
VPPLT-0873	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0874	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0875	1,3	5,7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-0880	-	-	-	-	-	-	-	-	-	-	-	-	-	6,6	-	-	-	-
VPPLT-0892	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-1201	2,1	5,8	2,9	4,2	6,1	6,6	5,1	5,6	-	-	-	11,9	-	10,5	-	-	-	-
VPPLT-1218	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-1241	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VPPLT-1736	-	-	-	-	-	-	3,21	4	-	-	-	-	-	4,72	-	-	-	-
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
VPPLT-1732			2,89	3,72	4,98	6,07	4,63	4,94	-	3,19	-	-	-	7,16	-	-	9,2	
Colombophis portai																		
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
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
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

VPPLT-0070	2,2	-	2,1	2,5	3,2	3,4	-	-	-	3	1,9	4,6	-	-	8,1	-	6,4	23
VPPLT-0430	-	4,5	3,5	2,8	3,9	4,3	-	-	-	4	2,6	-	-	-	-	-	-	29
VPPLT-0845	0,6	2,7			2,6	3,1	2	1,6	-	-	-	4,4	-	5,3	-	-	-	-
VPPLT-0869	-	3,9	2,5	3,2	2,8	3,5												-
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
VPPLT-1160																		-
VPPLT-1166																		-
VPPLT-1253	-	-	0	0	2,7	3,2	2	2,2	-	-	-	-	-	5,9	-	-	-	-
VPPLT-1551	2,6	4,9	3,1	3,6	4,1	4,5	-	-	-	-	-	6,5	11,4	4,8	-	-	9,3	-
VPPLT-1551	-	3	2,2	2,3	3,1	2,7	-	-	-	-	-	4,8	8,2	-	-	-	6,4	-
VPPLT-1564					4,4	4,9	-	-	15	-	-	8,5	16,8	8,5	10,1			33,5
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
VPPLT-1735	-	-	-	3,17	3,95	4,29	-	-	-	2,52	3,93	-	-	6,65	-	-	3,78	18
VPPLT-1735	-	-	-	-	5,12	-	4,37	-	-	-	-	-	-	9,43	-	-	4,54	-
VPPLT-1735	1,51	3,31	2,87	3,52	-	3,96	3,5	3,89	-	2,86	4	-	-	7,16	-	-	10,6	18
VPPLT-1735	-	-	-	-	5,08	5,69	-	-	-	2,79	4,03	-	-	8,26	-	-	9,32	13
VPPLT-799	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
VPPLT1734	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
VPPLT-1731	1,64	4,43	3	3,3	4	5,28	4	4,63	-	-	-	-	-	7,74	-	-	7,96	-
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
VPPLT-1740	1	3,61	-	-	3,73	3,52	3,16	2,74	-	2,33	3	6,19	-	8,15		2,81	11	-
VPPLT-1740	1,14	4,5	-	-	3,28	3,48	2,79	2,61	-	2,1	3,1	5,34	-	6,9		-	8,23	28,5
VPPLT-1740	1,71	4,2	-	-	3,49	3,92	-	-	-	-	-	5,96	-	4	-	-	6,81	-
VPPLT-1740	1,88	3,84	2,47	3,46	5,37	6,86	4,86	5,7	-	-	-	-	-	9,19	-	-	10,63	-
VPPLT-1740	1,93	4,64	2,51	3,47	-	-	-	-	-	-	-	7,44	-	-	-	-	6,8	-
VPPLT-1740	-	-	-	-	-	-	5,15	6,39	-	-	-	-	-	9,63	-	-	4,23	-
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	-	-	-	-
Colombophis spinosus																		
VPPLT-0798	2	6,1	2,8	5,7	4,2	5,6	3,8	5,1	-	-	-	11,1	-	8,5	-	-	11,7	-
VPPLT-0864	-	-	-	-	-	-	-	-	-	-	-	8,5	-	8,5	-	-	-	-
VPPLT-1093	-	4,9	2,7	3,1	3,9	3,7	-	-	-	-	-	7,7	11,5	-	-	-	-	19,5
VPPLT-1194																		-
VPPLT-1534	1,1	5,5	3,8	4	4,6	4,8	4,1	4,3	-	-	-	6,8	-	10,4	-	-	11	31

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	-
VPPLT-1741	1,74	4,8	2,33	3,51	5,01	5,4	-	-	-	-	-	-	-	6,34	-	-	9,06	-
VPPLT-1741	-	-	-	-	2,97	3,61	2,56	3,02	-	-	-	-	-	5,98	-	-	3,7	-
VPPLT-1741	-	-	-	-	3,52	3,62	3	3,57	-	2,71	4	5,83	-	7,78	-	-	6,11	17
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

Supplementary Table 1. List of specimens of *Colombophis* spp used in the study with their respective vertebral measurements.

Supplementary Table 2.

Collection	**Specimen**	**Family**	**Genus**	**Species**
UR	XXX	Amphisbaenidae	*Amphisbaena*	*A. alba*
UF-H	11769	Aniliidae	*Anilius*	*A. scytale*
UF-H	11786	Aniliidae	*Anilius*	*A. scytale*
UF-H	62496	Aniliidae	*Anilius*	*A. scytale*
UF-H	11748	Cylindrophiidae	*Cylindrophis*	*C. lineatus*
UF-H	51669	Cylindrophiidae	*Cylindrophis*	*C. ruffus*
UF-H	52673	Cylindrophiidae	*Cylindrophis*	*C. ruffus*
UF-H	52698	Leptotyphlopidae	*Leptotyphlops*	*L. conjunctus*
UF-H	11776	Leptotyphlopidae	*Rena*	*R. dulcis*
UF-H	11725	Tropidophiidae	*Trachyboa*	
UF-H	11765	Tropidophiidae	*Tropidophis*	*T. melanurus*
UF-H	52001	Tropidophiidae	*Tropidophis*	*T. melanurus*
UF-H	56844	Tropidophiidae	*Tropidophis*	*T. haetianus*
UF-H	99429	Tropidophiidae	*Tropidophis*	*T. canus*
UF-H	11750	Uropeltidae	*Uropeltis*	
VPPLT	XXX	Boidae	*Boa*	*B. cf constrictor*

Supplementary Table 2. List of comparative material used in the study.

CHAPTER 2 SUPPLEMENTARY DATA

Supplementary Table 1.

Collection	**Specimen**	**Family**	**Genus**	**Species**
IAvH-R	8224	Colubridae	*Clelia*	*C. clelia*
IAvH-R	8234	Boidae	*Eunectes*	*E.murinus*
IAvH-R	8225	Boidae	*Eunectes*	*E.murinus*
IAvH-R	8223	Colubridae	*Spilotes*	*S. pullatus*
UF-HERP	11786	Aniliidae	*Anilius*	*A. scytale*

UF-HERP	62496	Aniliidae	*Anilius*	*A. scytale*
UF-HERP	11985	Boidae	*Boa*	*B. constrictor*
UF-HERP	50668	Boidae	*Boa*	*B. constrictor*
UF-HERP	153493	Boidae	*Boa*	*B. constrictor*
UF-HERP	169132	Boidae	*Boa*	*B. constrictor*
UF-HERP	14301	Boidae	*Chilabothrus*	*C. anguifer*
UF-HERP	56282	Boidae	*Chilabothrus*	*C. striatus*
UF-HERP	63866	Boidae	*Chilabothrus*	*C. striatus*
UF-HERP	47337	Boidae	*Corallus*	*C. caninus*
UF-HERP	56081	Boidae	*Corallus*	*C. caninus*
UF-HERP	56402	Boidae	*Corallus*	*C. hortulanus*
UF-HERP	57146	Boidae	*Corallus*	*C. hortulanus*
UF-HERP	62359	Boidae	*Corallus*	*C. hortulanus*
UF-HERP	57427	Boidae	*Corallus*	*C. caninus*
UF-HERP	60830	Boidae	*Corallus*	*C. caninus*
UF-HERP	69251	Boidae	*Corallus*	*C. caninus*
UF-HERP	69272	Boidae	*Corallus*	*C. caninus*
UF-HERP	99407	Boidae	*Corallus*	*C. caninus*
UF-HERP	54847	Boidae	*Epicrates*	
UF-HERP	55563	Boidae	*Epicrates*	*E. cenchria*
UF-HERP	60832	Boidae	*Epicrates*	*E. cenchria*
UF-HERP	2210	Boidae	*Eunectes*	*E.murinus*
UF-HERP	20637	Boidae	*Eunectes*	*E.murinus*
UF-HERP	21216	Boidae	*Eunectes*	*E.murinus*
UF-HERP	57041	Boidae	*Eunectes*	*E.murinus*
UF-HERP	11765	Tropidophiidae	*Tropidophis*	*T. melanurus*
UF-HERP	56844	Tropidophiidae	*Tropidophis*	*T. haetianus*
UF-HERP	99429	Tropidophiidae	*Tropidophis*	*T. canus*
UF-HERP	41279	Charinaidae	*Lichanura*	*L. trivirgata*
VPPLT	XXX	Boidae	*Boa*	
UR	XXX	Boidae	*Epicrates*	*E. maurus*
UR	XXX	Colubridae	*Pseudoboa*	*P. neuwiedii*
UR		Viperidae	*Bothops*	*B. asper*

Supplementary Table 1. List of extant snakes specimens used for comparisons.

Supplementary Table 2.

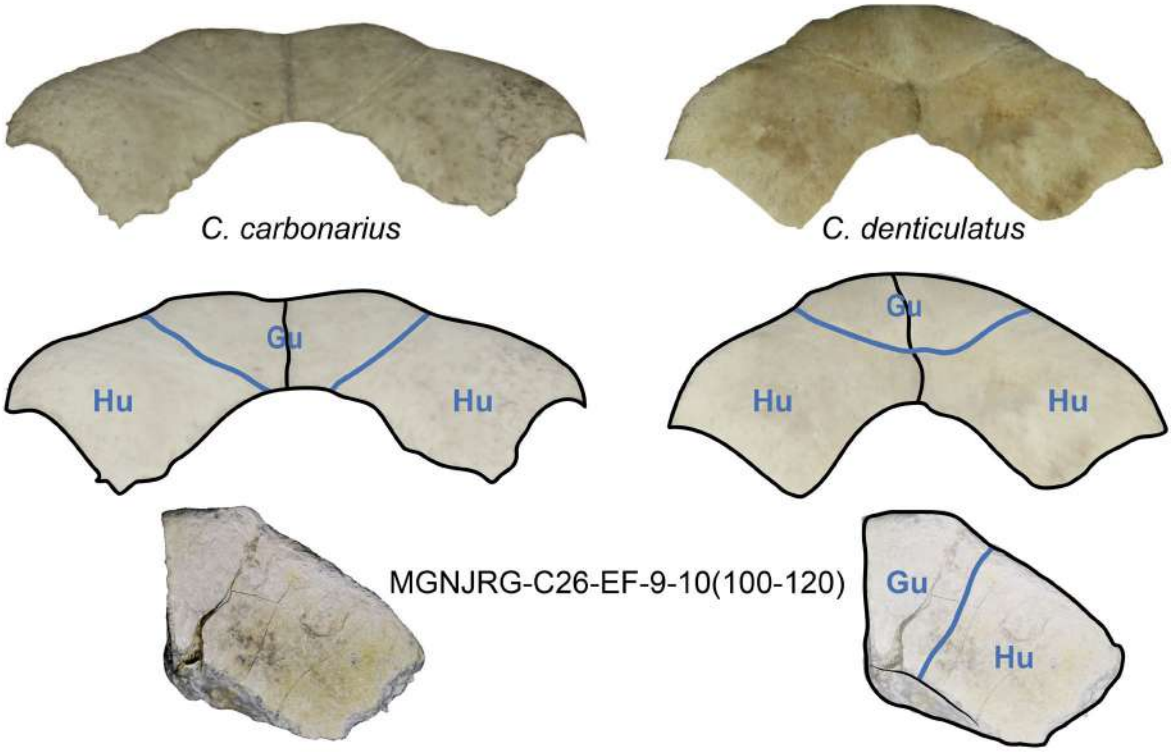
Compound bone measurements									
Collection	**Specimen**	**Genus**	**Species**	**CP total length**	**Prearticular crest height**	**Surangular crest height**	**SVL**	**TOT**	**Comments**
IAvH-R	8236	*Eunectes*	*E.murinus*	53,85	11,59	11,92		2900	TOT measured from the skeleton
UF-HERP	63866	*Chilabothrus*	*C. striatus*	37	9,2	9,2	1950	2250	

UF-HERP	56282	*Chilabothrus*	*C. striatus*	27,4	4,9	6,8	1450	1620	
UF-HERP	14301	*Chilabothrus*	*C. anguifer*	33,9	6	8,3		1830	
UF-HERP	2210	*Eunectes*	*E.murinus*	92	20,3	21		5181	Female, estimated TOT 17 ft
UF-HERP	57041	*Eunectes*	*E.murinus*	44,3	8,2	10,1	2280	2720	Male
UF-HERP	21216	*Eunectes*	*E.murinus*	85,6	16	19		2527	TOT 8ft 3,5 inches
UF-HERP	55563	*Epicrates*	*E. cenchria*	26,4	7	7,2	13,8	1550	Female
UF-HERP	56081	*Corallus*		36,4	8,6	11,2	1470	1723	
UF-HERP	57427	*Corallus*		32,2	9,4	10,1	1330	1580	Female
UF-HERP	69251	*Corallus*		36,6		8,6	1432	1690	Male
UF-HERP	69272	*Corallus*		33,7	10,05	10,09	1240	1500	
UF-HERP	47337	*Corallus*		30	8,3	9,5	1250	1500	
UF-HERP	60830	*Corallus*		36,5	9,4	11,6	1420	1680	
UF-HERP	57146	*Corallus*		19,2	4,5	6	1239	1630	Male
UF-HERP	56402	*Corallus*		20,8		6,7	1300	1650	Male
UF-HERP	60832	*Epicrates*		28,4	6,7	6,4	1400	1600	Male
UF-HERP	50668	*Boa*	*B. constrictor*	29,3	6,8	7,6	1370		Male
UF-HERP	169132	*Boa*	*B. constrictor*	48,4	10	9,9	1940	2230	SVL is not clear on the specimen label
UF-HERP	153493	*Boa*	*B. constrictor*	37,5	9	8,9		1810	

Supplementary Table 1. Measurements of compound bones of extant boidae and its respective the body size. Measurements expressed in millimeters.

CHAPTER 3 SUPPLEMENTARY DATA

Supplementary Figure 1.



Supplementary Figure 1. Comparison of extant *Chelonodidis carbonarius* and *Chelonoidis denticulatus* epiplastra with fossil *Chelonoidis* MGNJRG-C26-EF-9-10(100-120)..

Supplementary Table 1.

Fossil ID	Class	Order	Clade	Family	Subfamily	Genus	Observation
C26-QR-1-2 (100-120)	Mammalia	Artiodactyla		Cervidae			Isolated molar
C17-CD-3-4 (20-40)26	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Propaopus*	Buckler osteoderm and osteoderm of the caudal sheath
C17-UV-5-6 (20-40)	Mammalia	Cingulata		Dasypodidae	Dasypodinae		Osteoderm-undet
C17-V-1-2 (20-40)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Propaopus*	Buckler osteoderms
C19-ST-3-4 (40-60)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Propaopus*	Buckler osteoderm
C22-AB-5 (80)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Propaopus*	Buckler osteoderm
C23-EF-1-2 (75-100)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Dasypus*	Buckler osteoderm
C23-GH-1-2 (75-100)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Propaopus*	Osteoderm of the caudal sheath
C24-QR-3-4 (80-100)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Dasypus*	Osteoderm of the caudal sheath
C24-ST-3-4 (80-100)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Propaopus*	Osteoderm of the caudal sheath
C24-YZ-7-8 (80-100)	Mammalia	Cingulata		Dasypodidae	Dasypodinae	*Propaopus*	Movable osteoderm

C26-CD-9-10 (100-120)45	Mammalia	Cingulata		Dasypodidae	Dasypodinae		Osteoderm-undet
C28-Zona Ampliacion B	Mammalia	Cingulata		Dasypodidae	Dasypodinae		Osteoderm-undet
C22-UV-1-2 (60-80)95	Mammalia	?Pilosa					Limb bone-undet
C19-ST-3-4 (40-60)	Mammalia	Rodentia	Caviomorpha				Distal portion of left radius
C27-1 (20-40)	Mammalia	Rodentia	Caviomorpha				Limb bone-undet
C31-UV-1-2 (120-140)	Mammalia	Rodentia	Caviomorpha				Proximal portion of left tibia
C27-GH-1-2 (75-100)	Mammalia	Rodentia	Caviomorpha				Metapodial (Right Mtt III)
C29-GH-9-10 (100-120)59	Mammalia	Rodentia					Broken incisor
C31-AB-3-4 (140-160)	Mammalia	Rodentia	Myomorpha	Cricetidae	Sigmodontinae		Incisor
C27-GH-1-2 (75-100)	Aves	Cuculiformes		Cuculidae	Crotophaginae		Distal and proximal parts of the humerus and two undetermined bone fragments
C20-WX-5-6 (40-60)	Reptilia	Squamata	Lacertilia				Vertebral centrum
C23-AB-1-2-3-4 (80-100)	Reptilia	Squamata	Colubroidea				Isolated vertebra
C20-WX-5-6 (40-60)	Reptilia	Squamata	Colubroidea	Viperidae	Crotalinae		Isolated precloacal vertebra
C19-ST-1-2 (40-60)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Left epiplastron
C20-WX-5-6 (40-60)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Undetermined bone
C23-GH-1-2 (75-100)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Right xiphiplastron
C26-EF-9-10 (100-120)51	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Left epiplastron
C26-UVWX-1-2 (100-120)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Undetermined carpace plate
C27-AB-1-2-3-4 (120-140)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Undetermined plastron plate
C27-CD-5-6 (100-125)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Right hypoplastron fragment
C28-Zona Ampliacion B	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Two costal plates fragments
C30-AB-11-12 (100-125)39	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Undetermined plastron plate
C30-CD-11-12 (100-125)28	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Undetermined bone
C30-GH-7-8 (100-125)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Undetermined plastron plate
C31-AB-1-2 (120-140)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Peripheral plate
C31-CD-9-10 (140-150)90	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Epiplastron
C31-WX-7-8 (140-150)	Reptilia	Testudines	Cryptodira	Testudinidae		*Chelonoidis*	Undetermined bone
C17-CD-3-4 (20-40)26	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Two peripheral plates and a humerus fragment
C17-QR-3-4 (20-40)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral plate
C19-QR-5-6 (40-60)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Two udetermined carpace plates
C19-ST-1-2 (40-60)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Two peripheral plates
C19-ST-3-4 (40-60)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral plate

C20-YZ-5-6 (40-60)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	A costal and a peripheral plates
C21-5-(CD-5-6 aprox)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral plate
C21-ST-1-2 (60-80)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	A peripheral and a presumable nuchal plate
C21-UV-1-2 (60-80)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Two peripheral plates
C22-OP-3-4 (60-80)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Undetermined bone
C23-AB-1-2 (75-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Costal plate
C23-GH-1-2 (75-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Three peripheral plates
C23-GH-3-4 (75-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Undetermined bone
C24-ST-3-4 (80-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral plate
C24-UV-1-2 (80-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral plate
C25-EF-3-4 (100-125)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Second neural plate
C26-CD-9-10 (100-120)45	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Undeterminded carpace plate
C26-EF-9-10 (100-120)51	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Fourth costal plate
C26-ST-1-2 (100-120)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Pygal plate
C26-UVWX-1-2 (100-120)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Undetermined plate
C26-WX-1-2 (100-120)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Left hypoplastron
C26-YZ-1-2 (100-120)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Limb bone-undet
C27-1 (20-40)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Costal plate
C27-AB-1-2-3-4 (120-140)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	A costal and a peripheral plates
C27-AB-7-8 (100-125)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral plate and an undertermined bone
C27-AB-9-10 (100-125)58	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral and costal plates and a limb bone fragment
C27-CD-1-2 (75-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Five costal plates and the second neural plate
C27-CD-5-6 (100-125)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Five costal plates and two peripheral plates
C27-EF-7-8 (100-125	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Limb bone-undet
C27-GH-1-2 (75-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Humerus
C27-UV-3-4 (40-60)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Four costal plates
C27-UV-3-4 (120-140)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Peripheral plate
C27-YZ-7-8 (80-100)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Two peripheral plates and an undetermined platron fragment
C28-Zona Ampliacion B	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Three undetermined carpace plates
C30-AB-7-8 (100-125)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Proximal epiphysis of the femur
C30-CD-11-12 (100-125)42	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Two peripheral plates
C30-GH-5 (100-125)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Two peripheral plates

C31-AB-1-2 (120-140)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Undetermined plate
C31-UV-1-2 (120-140)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Undetermined plate
C31-WX-7-8 (140-150)	Reptilia	Testudines	Cryptodira	Kinosternidae	Kinosterninae	*Kinosternon*	Costal plate

Supplementary Table 1. List of fossils from Pubenza used in the study.