# Reappraisal of the south American Miocene snakes of the genus *Colombophis*, with description of a new species

ANNIE S. HSIOU, ADRIANA M. ALBINO, and JORGE FERIGOLO

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A redescription of the extinct snake genus *Colombophis* is presented, on the basis of new specimens from the late Miocene of southwestern Brazilian Amazonia, and those previously reported for the middle Miocene of Colombia and Venezuela. The reappraisal of *Colombophis* allows the recognition of a new species, *C. spinosus* sp. nov. The revised diagnosis of the genus is based on the midtrunk vertebrae, distinct from those of other snakes mainly in the features of the neural arch, position and shape of the neural spine, inclination of the zygapophyses, shape of the centrum, and development of the haemal keel. The affinities of *Colombophis* with "Anilioidea" are still unresolved; it is distinguished from all known extinct and extant "anilioids" due to its great vertebral size and the frequent presence of paracotylar foramina. The posterior paired apophyses of the haemal keel in some vertebrae, and the high neural spine of *C. spinosus* also contrast significantly with the "anilioid" genera, making the allocation of the genus into this probably paraphyletic group not well supported. Here, we recognized *Colombophis* as a basal alethinophidian of uncertain relationships.

Key words: Serpentes, Alethinophidia, *Colombophis*, Miocene, South America.

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## Introduction

*Colombophis* was a medium-size to large genus of snake, hitherto represented exclusively by the type species *Colombophis portai* Hoffstetter and Rage, 1977, based on about 40 midtrunk vertebrae recovered from the middle Miocene Villavieja Formation (Fish Bed) at the Los Mangos locality, near La Venta, Colombia. In spite of its relatively large size, *Colombophis* was considered belong to the "Anilioidea" (Hoffstetter and Rage 1977), a probably paraphyletic group of alethinophidian snakes. Later, Hecht and LaDuke (1997) recognized some additional incomplete vertebrae from the same area, but they did not describe or discuss the morphology of the genus. More recently, Head et al. (2006) referred a single vertebra from the middle Miocene of the Socorro Formation (Venezuela) to *Colombophis* cf. *C. portai*. New specimens from the late Miocene of the Solimões Formation, southwestern Brazilian Amazonia, increase the knowledge of the vertebral morphology of *Colombophis*. Reviewing all the available material assigned to this genus and evaluating the intracolumnar and intrageneric variation, allows us to recognize a new species of *Colombophis* and to evaluate the taxonomic allocation of the genus into the "Anilioidea".

*Institutional abbreviations*.—AMU-CURS, Colección Alcaldía de Urumaco, Rodolfo Sánchez, Urumaco, Venezuela; IB, Instituto Butantan, São Paulo, Brazil; IGM, INGEOMINAS -Instituto Nacional de Investigaciones en Geociências, Minería y Química, Museo Geológico, Bogotá, Colombia; MCN.D., Coleção Didática de Herpetologia, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MPNHN, Muséum National d'Historie Naturelle, Paris, France; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; UFAC-PV, Coleção de Paleovertebrados, Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Rio Branco, Brazil.

*Other abbreviations*.—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; nsh, neural spine height; 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; SALMA, South American Land-Mammal Age.

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# Material and methods

The material comes from the middle Miocene of Colombia (La Victoria and Villavieja formations) and Venezuela (Upper Member of Socorro Formation), and from the late Miocene, southwestern Brazilian Amazonia (Solimões Formation) (Fig. 1).

The La Venta Fauna of Colombia is one of the most conspicuous Cenozoic vertebrate paleofaunas in South America. It originates from Honda Group beds including the La Victoria and the Villavieja formations, in the Magdalena River Valley, between the eastern and central Andes Mountains of southwestern Colombia (Guerrero 1997). The vertebrate fauna from these formations belongs to the Laventan SALMA (South American Land-Mammal Age), middle Miocene (Madden et al. 1997). The holotype of the species *Colombophis portai* Hoffstetter and Rage, 1977, recognized among the remains from La Venta fauna, was not available for this study because the whereabouts of the specimens at MPNHN are currently unknown (Jean-Claude Rage, personal communication 2008). More recently, new specimens of *Colombophis* from the La Victoria and the Villavieja formations were collected during the Duke University-INGEOMINAS expeditions to the upper Magdalena River Valley between 1985 and 1991 (Madden et al. 1997). Part of this material was published by Hecht and LaDuke (1997) and is now stored at IGM. One of us (AA) had the opportunity to reanalyze the squamate material from this collection and found discrepancies regarding the collection numbers of the specimens and the taxonomic assignments published by Hecht and LaDuke (1997). Moreover, different boxes generally contain more than one specimen, including remains corresponding to more than one taxon, under the same collection number. Due to the discrepancies mentioned above and the fact that it was not possible to know exactly which specimens were studied by Hecht and LaDuke (1997), the collection numbers of IGM are distinguished herein by addition of numerals between parentheses. They should not be considered as the same numbers of the published specimens.

The specimen from northwestern Venezuela comes from the Upper Member of the Socorro Formation, which crops out in the Falcón Basin, close to the Urumaco Municipality. It is only one vertebra, referred previously to *Colombophis* cf. *C. portai* by Head et al. (2006) and stored at AMU-CURS. Based on numerous previous studies of foraminifera and palynomorphs, a middle Miocene age was proposed for the Socorro Formation (Sánchez-Villagra and Aguilera 2006).

According to the mammal fauna, the localities in the Solimões Formation in southwestern Brazilian Amazonia are referred to the Huayquerian SALMA, which would correspond to the late Miocene (Cozzuol 2006; Latrubesse et al. 2007) or even to the Montehermosan SALMA (late Miocene/Pliocene) (Latrubesse et al. 1997). In addition, Latrubesse et al. (2007), largely based on palynological data obtained in typical mammal fossil localities, proposed a late Miocene age for the fossils from the Solimões Formation. The snake specimens collected from this formation are stored at UFAC-PV.

Among "Anilioidea", the comparative material used here in the review of *Colombophis* includes postcranial specimens of the extant species *Anilius scytale* (IB 40251, MZUSP 14572, 14573, and 14574). Data from the literature as well as figures of *Cylindrophis ruffus* from Ikeda (2007) were also used. The vertebrae of Uropeltidae and *Anomochilus* are unknown by us due to the difficulties of obtaining comparative material of these taxa, so that data from the literature were used (Lee and Scanlon 2002). The osteological nomenclature and measurements follow Auffenberg (1963), Hoffstetter and Gasc (1969), and Rage (1984, 1998). The inclination of the prezygapophyses was taken considering the horizontal plane at the floor of the neural canal. The systematic arrangement follows Lee and Scanlon (2002). The measurements are expressed in millimeters.

# Systematic paleontology

## Squamata Oppel, 1811

## Serpentes Linnaeus, 1758

## Alethinophidia Nopsca, 1923

## Genus *Colombophis* Hoffstetter and Rage, 1977

*Type species*: *Colombophis portai* Hoffstetter and Rage, 1977, Los Mangos locality, near La Venta, middle Miocene, Colombia.

*Included species*.—*Colombophis portai* Hoffstetter and Rage, 1977 and *Colombophis spinosus* sp. nov.

*Emended diagnosis*.—Fossil snake with midtrunk vertebrae characterized by the following combination of character states: medium to large size; clearly depressed neural arch, not vaulted in posterior view; shallow median notch of the posterior border of the neural arch; long dorsal surface of the neural arch, smooth or even concave, extending from the anterior edge of the zygosphene to the neural spine; neural spine reduced to a tubercle or relatively high and circular in outline, always restricted to the posterior end of the neural arch; zygapophyses prominent and strongly inclined above the horizontal plane, reaching the level of the zygosphene roof; prezygapophyseal process short; variable presence of paracotylar foramina; paradiapophyses weakly divided or even indistinct; centrum not markedly widened anteriorly; haemal keel broad, indistinct, and often only posteriorly developed, with the usual presence of two small and divergent apophyses more or less differentiated; and subcentral foramina placed close to the sagittal plane of the centrum, variably enlarged, reduced or absent.

*Stratigraphic and geographic range*.—Middle to late Miocene, Colombia, Venezuela, and Brazilian Amazonia.

## *Colombophis portai* Hoffstetter and Rage, 1977

Figs. 2–5; Table 1.

1977 *Colombophis portai* Hoffstetter and Rage, 1977: 174–179, fig. 4.
1997 *Colombophis portai*; Hecht and LaDuke 1997: 95–96.

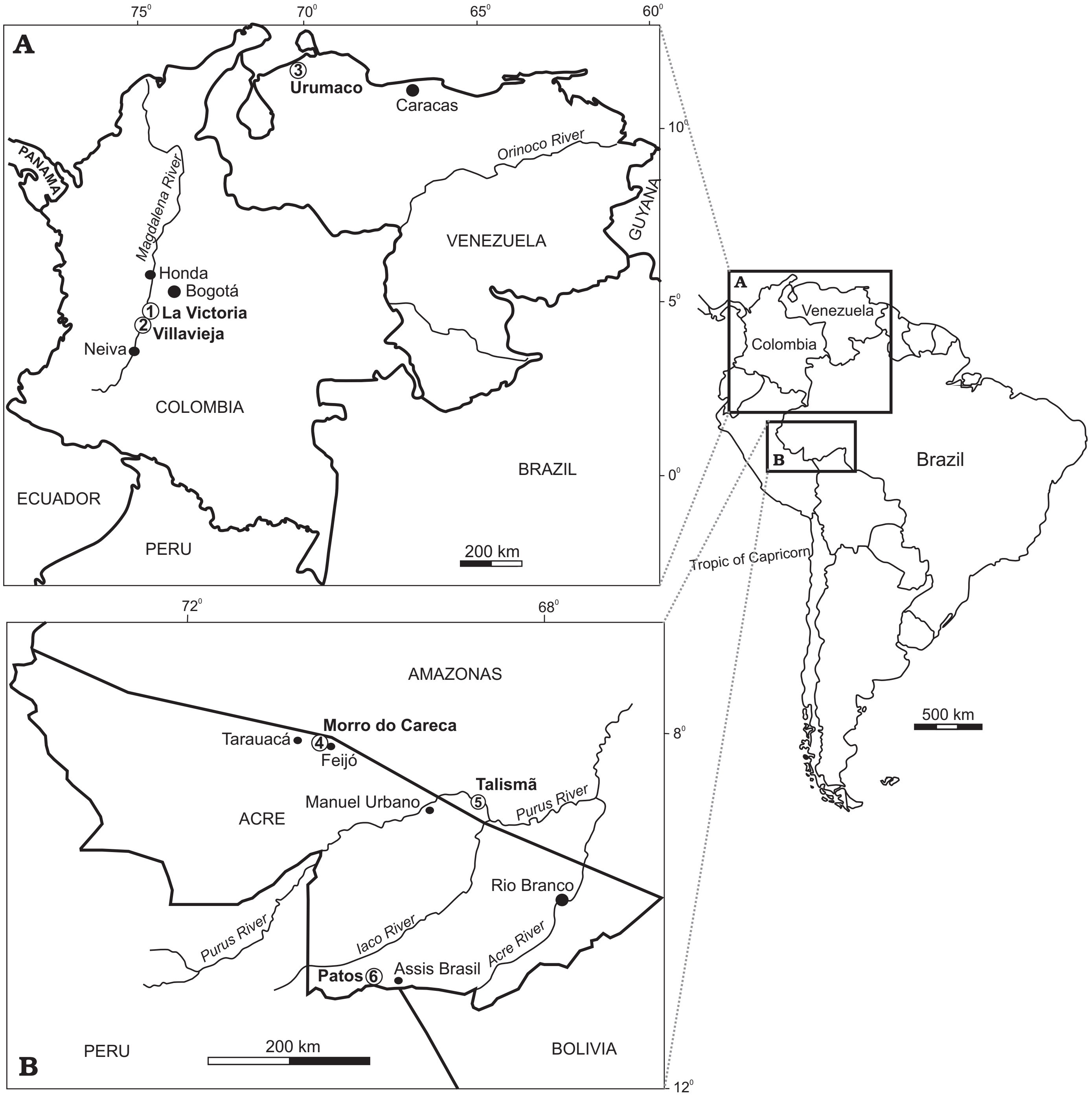

Fig. 1. Location map of the fossiliferous localities of *Colombophis* in northern South America. **A**. La Victoria (1), Villavieja (2), and Urumaco (3). **B**. Morro do Careca (4), Talismã (5), and Patos (6).

*Holotype*: MNHN. VIV 6, one midtrunk vertebra.

*Type locality*: Los Mangos, near La Venta, Departamento de Huila, Colombia; Fish Bed, Villavieja Formation, middle Miocene.

*Emended diagnosis*.—*Colombophis portai* differs from *C. spinosus* sp. nov. by its midtrunk vertebrae longer than broad, with a very low neural spine, resembling a tubercle and circular in outline in dorsal view; thin to moderate zygosphene; anterolaterally orientated prezygapophyses; and undivided paradiapophyses.

*Referred material*.—Four anterior trunk vertebrae, UFAC-PV 5715, IGM 184285 (1 and 3), and 184476 (2); eighteen midtrunk vertebrae, UFAC-PV 3478, 3480, 3484, 4089, 5716B; IGM 183533 (1), 183561 (1 to 2), 183928, 184086, 184131 (1 to 2), 184159 (1–3), 184285 (2), 184476 (1), 184579 (1 to 2), 184788, 184806, and 250914; and two posterior trunk vertebrae, UFAC-PV 2957 and IGM 183533(2).

*Description*.—Most of the vertebrae are fragmented and consist of isolated neural arches, centra, and other very incom-

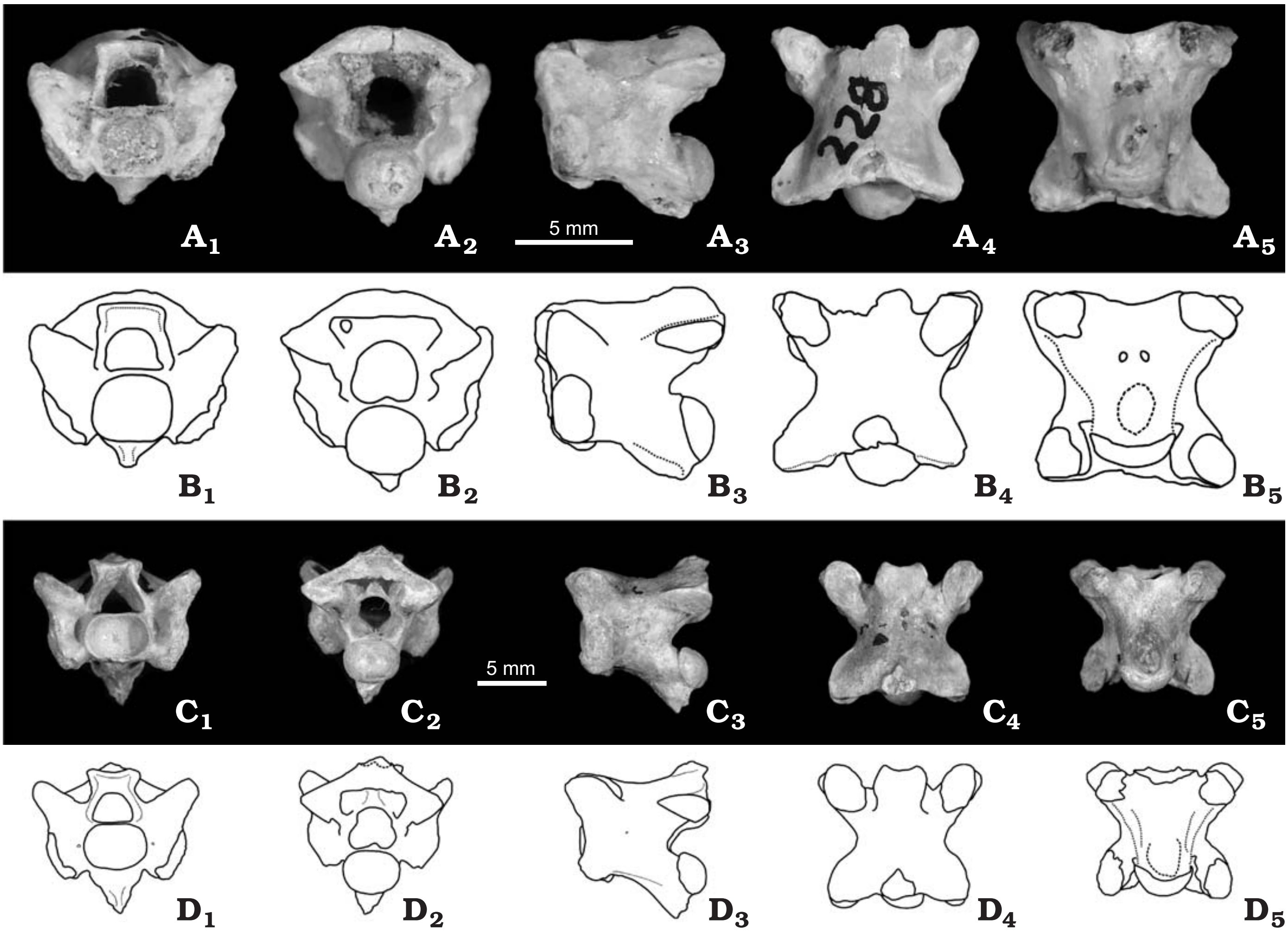

Fig. 2. Alethinophidian snake *Colombophis portai* Hoffstetter and Rage, 1977, anterior trunk vertebrae from the La Victoria and Villavieja formations (middle Miocene, Colombia)–Solimões Formation (late Miocene, Brazil). **A**, **B**. IGM 184285(1). **C**, **D**. UFAC-PV 5715. Photographs (A, C) and schematic drawings (B, D), in anterior ($A_1$–$D_1$), posterior ($A_2$–$D_2$), lateral ($A_3$–$D_3$), dorsal ($A_4$–$D_4$), and ventral ($A_5$–$D_5$) views.

plete remains; nonetheless, they present the general features described by Hoffstetter and Rage (1977) for this species. In general, the vertebrae are medium to large size, in this respect approximating an extant boa of 177 cm (*Boa constrictor,* MCN.D. 333) for the holotype of *Colombophis portai*. Also, the vertebrae are robust and not strongly depressed, although longer and broader than high (pr-po > h, pr-pr > h). The anterior and posterior trunk vertebrae are smaller than the midtrunk vertebrae, but there is also variation in the size of the midtrunk vertebrae among the specimens from Colombia.

The neural arch is longer than broad (pr-po > pr-pr) and its roof is depressed, especially in the posterior vertebrae (Fig. 4), whereas there is a slightly vaulted neural arch in the anterior trunk vertebrae (Fig. 2). The posterodorsal notch of the neural arch is well defined but not very deep; each half of the roof being notably flattened. In lateral view, the neural arch rises posteriorly from about the origin of the anterior border of neural spine, which is restricted to the posterodorsal end of the neural arch, so far from the zygosphene. The roof of the neural arch between the anterior edge of the zygosphene and the anterior edge of neural spine is slightly concave. The neural spine is very low but relatively robust, similar to an almost imperceptible tubercle, circular in outline. The zygosphene is thin to moderate, but broader than the cotyle (zw > ctw). The anterodorsal edge of the zygosphene is variable between specimens, probably due to intraspecific variation. It can be rectilinear, notched or even slightly convex in dorsal view. The zygantra are small and deep, with a small foramen inside each zygantrum. The roof of the zygantra is almost rectilinear and continuous. The neural canal is large, high, and triangular in outline. The medial borders of the prezygapophyses lie at a high position, at the level of the middle of the neural canal. They are anterolaterally directed and strongly inclined dorsally from the horizontal plane. The prezygapophyseal facet is oval and large (prl > prw). The prezygapophyseal process is short, although, in dorsal view, it can be seen exceeding laterally the tip of the prezygapophyseal facet due to the strong inclination of the prezygapophyses. The postzygapophyses are also well inclined dorsally and posterolaterally orientated. The

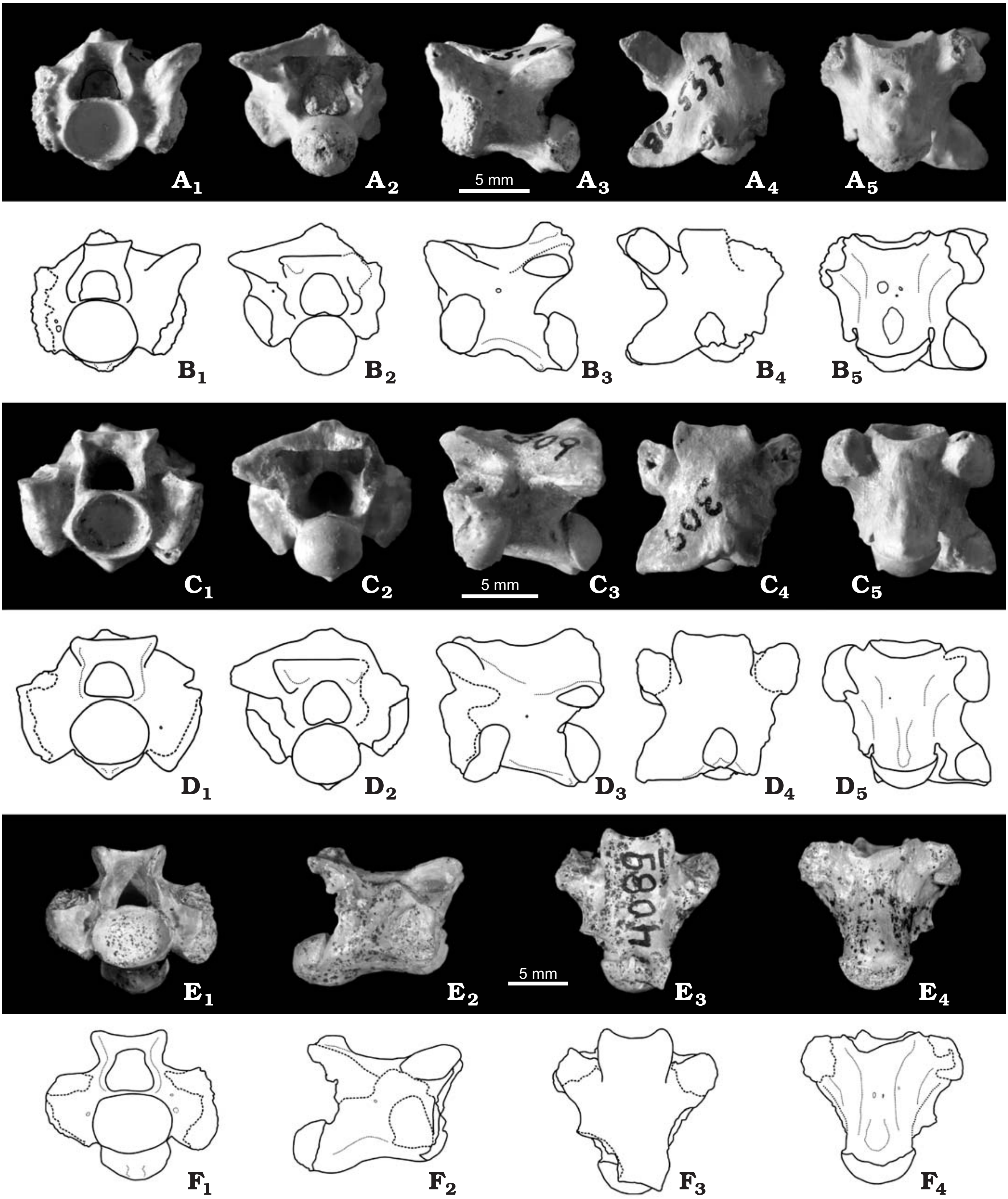

Fig. 3. Alethinophidian snake *Colombophis portai* Hoffstetter and Rage, 1977, midtrunk vertebrae from the La Victoria and Villavieja formations (middle Miocene, Colombia)–Solimões Formation (late Miocene, Brazil). **A**, **B**. IGM 183561. **C**, **D**. IGM 183928. **E**, **F**. UFAC-PV 4089. Photographs (A, C, E) and schematic drawings (B, D, F), in anterior ($A_1$–$F_1$), posterior ($A_2$–$D_2$), lateral ($A_3$–$D_3$, $E_2$, $F_2$), dorsal ($A_4$–$D_4$, $E_2$, $F_2$), and ventral ($A_5$–$D_5$, $E_4$, $F_4$) views.

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Table 1. Vertebral measurements of anterior, mid-, and posterior trunk vertebrae of the species of *Colombophis*. Non-available data are marked with a dash. Abbreviations: 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; nsh, neural spine height; 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.

| Specimens | cl | coh | cow | cth | ctw | h | naw | nch | ncw | nsh | po-po | pr-pr | pr-po | prl | prw | zh | zw |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Colombophis portai* | | | | | | | | | | | | | | | | | |
| IGM 183533 (1) | 7.6 | – | – | 2.6 | 3 | – | – | 2.5 | – | – | – | – | – | – | – | – | – |
| IGM 183561 (1) | 9.1 | – | 3.9 | 3.8 | 5 | – | – | – | – | – | – | 14.8 | – | 5 | 3.5 | – | – |
| IGM 183561 (2) | 7.9 | 4.2 | 4.7 | 3.8 | 4.4 | 10.6 | 7.7 | 4.1 | 3.4 | 1.4 | 10 | – | – | 4.3 | 2.8 | – | – |
| IGM 183928 | 8.7 | 3.4 | 4.4 | 4 | 4.4 | 9.6 | 7.7 | 3.5 | 3.2 | 0.9 | – | – | – | – | – | 1 | 5.3 |
| IGM 184086 | 8.1 | 3.3 | 5 | 3.6 | 4.9 | – | – | – | – | – | – | – | – | – | – | – | – |
| IGM 184131 (1) | 9.6 | 4.8 | 5.5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| IGM 184131 (2) | 7.4 | 3.4 | 4 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| IGM 184159 | 7.6 | 3.2 | 3.6 | 3.3 | 3.5 | – | 6.8 | – | – | – | – | – | – | – | – | – | – |
| IGM 184285 (1) | 6.6 | 2.6 | 3.4 | 2.8 | 3 | 6.3 | 5.6 | 2.6 | 2.3 | – | 8.4 | 8.7 | 7.9 | 2.8 | 2.1 | 1 | – |
| IGM 184285 (2) | 6.5 | 2.7 | 3.5 | 2.5 | 3.3 | 8.1 | 5.7 | – | – | 1 | 8.9 | – | – | – | – | 0.8 | – |
| IGM 184285 (3) | 8.3 | 3.4 | 4 | 3.3 | 4 | – | – | – | – | – | – | – | – | 3.5 | 2.7 | – | – |
| IGM 184476 (1) | 6.3 | 2.3 | 3.3 | 2.4 | 3 | – | – | – | – | – | – | – | – | – | – | – | – |
| IGM 184476 (2) | 8.3 | 4 | 5.1 | 5 | 4 | – | – | – | – | – | – | – | – | – | – | – | – |
| IGM 184579 (1) | 8.9 | 4.2 | 5.1 | 4.3 | 5.2 | – | – | – | – | – | – | – | – | – | – | – | – |
| IGM 184788 | 8.6 | 3.5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| UFAC-PV 2957 | 9.3 | 3.4 | 4.1 | 3.2 | 4 | 9.8 | 6.2 | 2.7 | 2.7 | – | 10.3 | – | 10.8 | 3.9 | 2.5 | 1.3 | 5.2 |
| UFAC-PV 3478 | 7.3 | 3.4 | 4.1 | – | – | – | – | 2.3 | 2.7 | – | – | 10.4 | – | 3.4 | 2.8 | 1 | 3.8 |
| UFAC-PV 3480 | 8.8 | 4 | 4.7 | 3.5 | 4.5 | 9.3 | 8.8 | – | – | – | – | – | 10.9 | 4 | 3.8 | – | – |
| UFAC-PV 3484 | 6.4 | 3.1 | 3.2 | – | 3.4 | 8.2 | 5.9 | 2 | 2.7 | – | – | 10.3 | 7.5 | 3 | 2.5 | 1 | 3.8 |
| UFAC-PV 4089 | 12 | 4.7 | 6.5 | 4.3 | 6.1 | 12.8 | – | 3.2 | 4.5 | – | – | – | – | – | – | 1.3 | 6.5 |
| UFAC-PV 5715 | 9.1 | 3.3 | 4.6 | 3 | 4.6 | 10.8 | 7.3 | 2.7 | 4 | – | 11.4 | 12.7 | 11.4 | 4.5 | 3.3 | 1.7 | 4.3 |
| UFAC-PV 5716B | 10.8 | 4.6 | 5.6 | | | | | | | | | | | 3.8 | 3.3 | | |
| *Colombophis spinosus* sp. nov. | | | | | | | | | | | | | | | | | |
| AMU-CURS 154 | 10.7 | 6 | 6.7 | 5.9 | 6.1 | 16 | 13.9 | 3.1 | 4.2 | – | – | – | 11.5 | – | – | 2.7 | 7.2 |
| IGM 184176 (1) | 8.2 | 3.8 | 5 | 3.9 | 5 | – | – | – | – | – | – | – | – | – | – | – | – |
| UFAC-PV 1609 | 7.4 | 4.6 | 5.3 | 4.3 | 5.3 | 14 | – | 2.5 | 4 | 3.2 | – | – | – | – | – | 2.5 | 6.3 |
| UFAC-PV 2952 | 9 | 6.4 | 6 | 5.7 | 6.9 | 16.6 | – | 2.7 | 4.7 | 4.4 | – | – | – | 6.2 | 6.2 | 2.8 | 7 |
| UFAC-PV 2953 | 10.9 | 6.3 | 6.6 | 6.2 | 6.5 | 16.3 | 12 | 4.5 | 3 | 3 | 19 | 19.5 | 11.7 | 6.7 | 4.3 | 2 | 6.7 |
| UFAC-PV 2955 | 8.6 | 5.3 | 6.4 | – | 6.1 | – | – | – | 4.5 | – | – | – | – | – | – | 2.8 | 7.3 |
| UFAC-PV 2956 | 7.5 | 5 | 5.8 | 4.5 | 5.1 | 14.4 | – | 2.9 | 4.1 | 2.3 | 18.6 | – | 10.2 | 5.4 | 3.9 | 2.3 | 6.6 |
| UFAC-PV 3485 | 8.4 | 5 | 6.1 | 4.2 | 5.7 | – | – | 2.5 | 4.3 | – | – | 10.5 | – | – | – | 2.1 | 5.7 |
| IGM 184176 (1) | 8.2 | 3.8 | 5 | 3.9 | 5 | – | – | – | – | – | – | – | – | – | – | – | – |
| UFAC-PV 1609 | 7.4 | 4.6 | 5.3 | 4.3 | 5.3 | 14 | – | 2.5 | 4 | 3.2 | – | – | – | – | – | 2.5 | 6.3 |
| UFAC-PV 2952 | 9 | 6.4 | 6 | 5.7 | 6.9 | 16.6 | – | 2.7 | 4.7 | 4.4 | – | – | – | 6.2 | 6.2 | 2.8 | 7 |
| UFAC-PV 2953 | 10.9 | 6.3 | 6.6 | 6.2 | 6.5 | 16.3 | 12 | 4.5 | 3 | 3 | 19 | 19.5 | 11.7 | 6.7 | 4.3 | 2 | 6.7 |
| UFAC-PV 2955 | 8.6 | 5.3 | 6.4 | – | 6.1 | – | – | – | 4.5 | – | – | – | – | – | – | 2.8 | 7.3 |
| UFAC-PV 2956 | 7.5 | 5 | 5.8 | 4.5 | 5.1 | 14.4 | – | 2.9 | 4.1 | 2.3 | 18.6 | – | 10.2 | 5.4 | 3.9 | 2.3 | 6.6 |
| UFAC-PV 3485 | 8.4 | 5 | 6.1 | 4.2 | 5.7 | – | – | 2.5 | 4.3 | – | – | 10.5 | – | – | – | 2.1 | 5.7 |
| UFAC-PV 4027 | 9.6 | 5.3 | 6.3 | 5 | 6.4 | 16.5 | – | 3 | 4.4 | 4.1 | 18 | – | 10.8 | 3.4 | 4.1 | 1.9 | 6 |
| UFAC-PV 5424 | 7.7 | 4.5 | 5.2 | – | – | 14.3 | 10 | – | – | 3 | – | – | – | – | – | 2.4 | 5.5 |
| UFAC–PV 5716C | – | – | – | – | – | – | – | – | – | – | – | – | – | | 3.6 | 2 | 5.3 |
| UFAC-PV 5716E | 8.5 | 5.5 | 6.3 | 5 | 6.2 | 16.6 | – | 3 | 4.4 | 5.2 | – | 16.9 | 10.1 | – | 4.3 | 2.9 | 6.1 |

interzygapophyseal constriction, between pre- and postzygapophyses, is deep and anteroposteriorly short. The centrum is longer than the width of the neural arch (cl/naw > 1). It is smooth, not markedly widened anteriorly and rather narrow. The subcentral ridges are not developed or only weakly defined. The anterior trunk vertebrae bear a prominent hypapophysis on the posterior surface of the centrum, broken in all specimens (Fig. 2). In the midtrunk vertebrae, there is a weakly developed haemal keel, which is anteriorly broad, smooth or convex, and usually narrower and prominent in the most posterior portion of the centrum (Fig. 3). The posterior trunk vertebrae have a well developed haemal keel that is

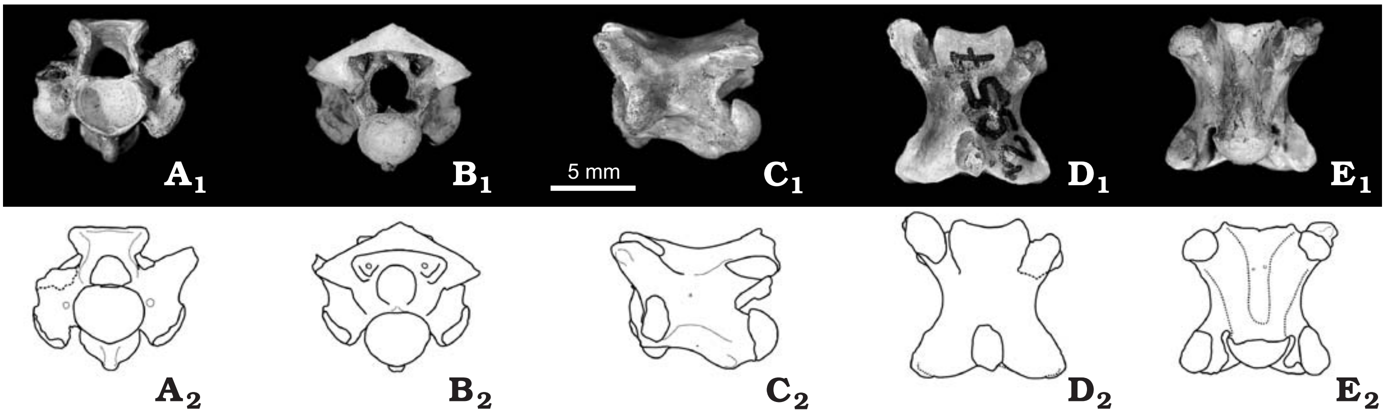

Fig. 4. Alethinophidian snake *Colombophis portai* Hoffstetter and Rage, 1977, posterior trunk vertebra from the Solimões Formation (late Miocene, Brazil), UFAC-PV 2957. Photographs ($A_1$–$E_1$) and schematic drawings ($A_2$–$E_2$), in anterior (**A**), posterior (**B**), lateral (**C**), dorsal (**D**), and ventral (**E**) views.

defined by the subcentral grooves (Fig. 4). The subcentral grooves are shallow in the anterior, mid-, and posterior trunk vertebrae, from the ventral margin of the cotyle to the middle of the centrum. They delimit the haemal keel anterolaterally, and they narrow toward the precondylar constriction. The subcentral foramina are variably enlarged, reduced, or absent, and when present, located anterior to the prominent part of the haemal keel, and close to the sagittal plane of the centrum. They are usually located on the broad and flat anterior portion of the haemal keel (Fig. 5). Most specimens have a haemal keel with a rounded distal end, slightly projecting below the ventral surface of the centrum. In some specimens (mainly observed in the midtrunk vertebrae), the haemal keel has a bilobed distal end, where there are two small and divergent apophyses more or less differentiated (Fig. 5). The subcentral ridges and grooves are also morphologically distinct among specimens. The vertebrae that show bilobed haemal keel usually have relatively deep subcentral grooves. Despite the poor preservation of the vertebrae, we infer that these different morphologies are probably linked to regionalization of the column. The cotyle and condyle are almost circular, slightly broader than high. The cotyle is not or scarcely visible in ventral view because it is not inclined and its rim is continuous and prominent. The main axis of the condyle is not notably inclined above the horizontal plane. Only two specimens (UFAC-PV 3484 and 3478) could represent juveniles, due to the small size, and because the cotyle and condyle are very dorsoventrally depressed. The presence of paracotylar foramina is irregular, indicating probably an intraspecific variation. Some specimens have only one foramen or a pair of foramina on each side of the cotyle (UFAC-PV 4089, Fig. 3C), but others do not show any foramina. In most specimens, the paradiapophyses are not preserved; when present they are relatively small, usually surpassing the ventral margin of the cotyle, and separated from it by well defined notches that become deeper in the posterior trunk vertebrae. The paradiapophyses are undivided. In the anterior and posterior trunk vertebrae, the paradiapophyses are almost vertical in lateral view, and in the midtrunk vertebrae they are posteroventrally inclined. In the posterior trunk vertebrae, the paradiapophyses are more prominent lateroventrally, although they maintain far from the level of the prezygapophyseal tip (Fig. 4).

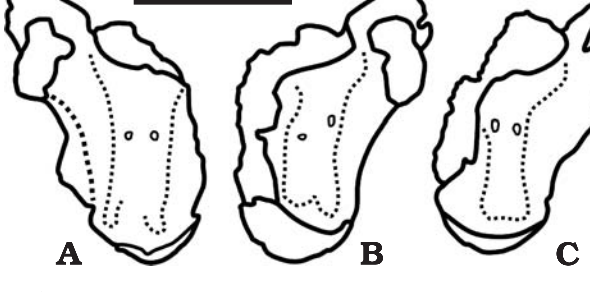

Fig. 5. *Colombophis portai* Hoffstetter and Rage, 1977, schematic drawings of variations in the haemal keel from three incomplete midtrunk vertebrae (IGM 184159) from the La Victoria and Villavieja formations (Fish and Monkey beds) in ventral view. **A**. IGM 184159-1. **B**. IGM 184159-2. **C**. IGM 184159-3.

*Stratigraphic and geographic range*.—The material at UFAC-PV was recovered from Talismã (Purus River, Amazonas State) and Patos (Acre River, Acre State) localities, Solimões Formation, late Miocene, Brazil; and the material of the IGM belongs to the La Venta Fauna, La Victoria and Villavieja formations (Fish and Monkey Beds), Honda Group, middle Miocene, Colombia.

### *Colombophis spinosus* sp. nov.

Figs. 6–8, Tables 1, 2.

2006 *Colombophis* cf. *C. portai*; Head et al. 2006: 234–236, fig. 1A.

*Etymology*: From the Latin *spinosus*, meaning spined, a reference to the high neural spine.

*Holotype*: UFAC-PV 2953, one almost complete midtrunk vertebra.

*Type locality*: Talismã locality, Purus River, Amazonas State, Brazil.

*Type horizon*: Late Miocene, Solimões Formation.

*Diagnosis*.—*Colombophis spinosus* differs from *C. portai* in having shorter than broad vertebrae; robust and high neural spine, with a vertical main axis, and cylindrical in dorsal view; moderately thick zygosphene; prezygapophyses well laterally oriented; and weakly divided paradiapophyses.

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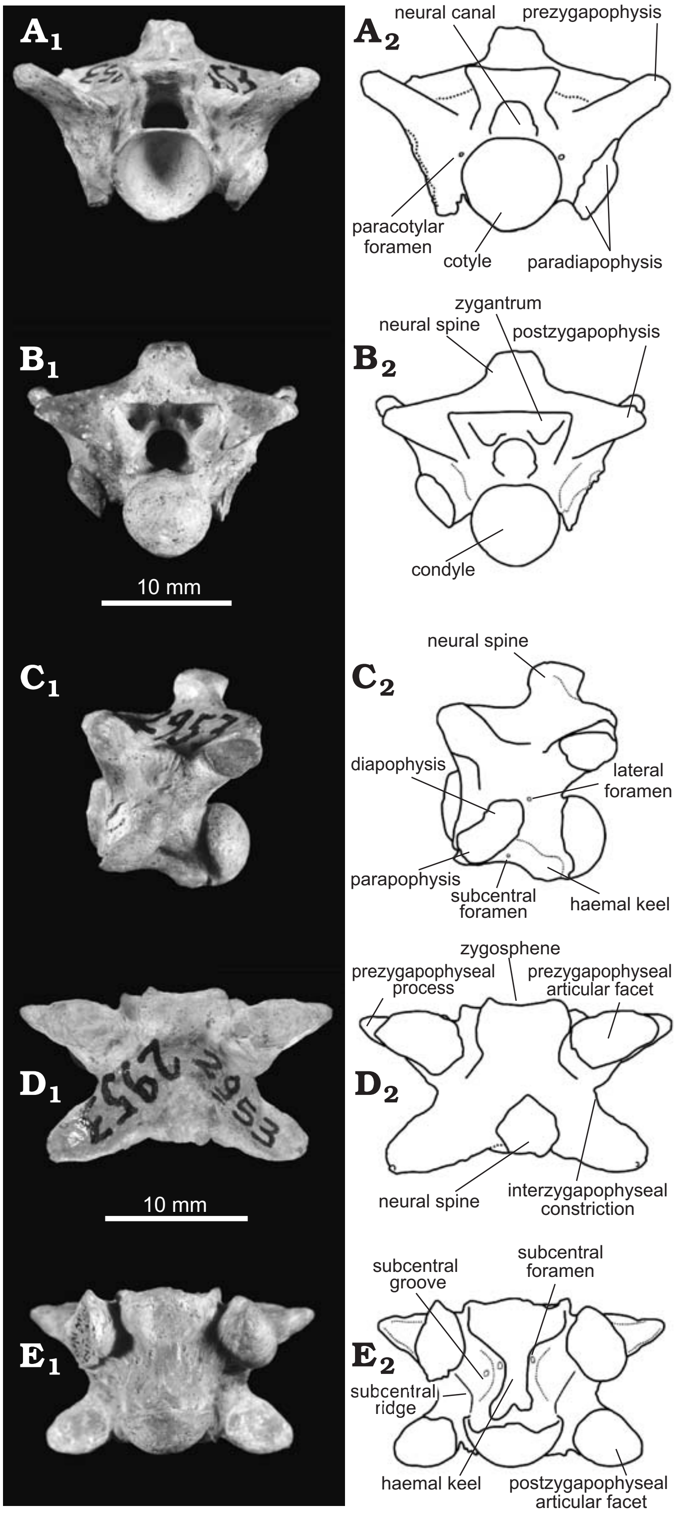

Fig. 6. Alethinophidian snake *Colombophis spinosus* sp. nov., holotype, UFAC-PV 2359, midtrunk vertebra from the Solimões Formation (middle Miocene, Brazil). Photographs ($A_1$–$E_1$) and schematic drawings ($A_2$–$E_2$), in anterior (**A**), posterior (**B**), lateral (**C**), dorsal (**D**), and ventral (**E**) views.

*Referred material*.—Two incomplete anterior trunk vertebrae, UFAC-PV 1609 and 2952; eight incomplete midtrunk vertebrae, AMU-CURS 154, IGM 184176(1), UFAC-PV 2955, 2956, 4027, 5424, 5716C, and 5716E; and one incomplete posterior trunk vertebra, UFAC-PV 3485.

*Description*.—Although some vertebrae are somewhat fragmented, data association, comparisons and description were possible, mainly based on the holotype. There are variations in vertebral morphology, but in general, the vertebrae are large, robust and high; higher than long (h > pr-po) and broader than high (pr-pr > h), with a centrum that is shorter than the width of the neural arch (cl/naw<1), and a neural arch much shorter than broad (pr-po < pr-pr).

In anterior view, the neural arch is broad due to the long prezygapophyses. The zygosphene is rather thick and shows a straight dorsal margin, having small zygosphenal articular facets that are inclined dorsally. In two anterior trunk vertebrae (UFAC-PV 1609 and 2952), the dorsal margin of the zygosphene is slightly elevated in the middle. The width of the zygosphene varies considerably relative to the transverse diameter of the cotyle, being nearly equal as in the holotype (zw~ctw), wider, or even narrower than the cotyle. The prezygapophyses are slender, long and strongly inclined dorsolaterally, around 25° from the horizontal plane, reaching the level of the dorsal margin of the zygosphene (Figs. 6

Table 2. Comparative measurements of *Colombophis* and of the fossil and living Anilioidea species. Non-available data are marked with a dash. Abbreviations: cl, centrum length; h, total height of vertebra; pr-pr, width across prezygapophyses.

| Specimens | h | pr-pr | cl |
|---|---|---|---|
| *Colombophis spinosus* | | | |
| UFAC-PV 1609 | 14 | – | 7.4 |
| UFAC-PV 2952 | 16.6 | – | 9 |
| UFAC-PV 2953 (holotype) | 16.3 | – | 10.9 |
| UFAC-PV 2956 | 14.4 | 10.2 | 7.5 |
| UFAC-PV 4027 | 16.5 | 10.8 | 9.6 |
| UFAC-PV 5424 | 14.3 | – | 7.7 |
| UFAC-PV 5716E | 16.6 | – | 8.5 |
| *Colombophis portai* | | | |
| IGM 183561 | 10.6 | – | 7.9 |
| IGM 184285 | 6.3 | – | 6.6 |
| UFAC-PV 2957 | 9.8 | 10.8 | 9.3 |
| UFAC-PV 3480 | 9.3 | 10.9 | 8.8 |
| UFAC-PV 4089 | 12.8 | – | 12 |
| UFAC-PV 5715 | 10.8 | 11.4 | 9.1 |
| *Australophis anilioides* | 6 | 7.28 | 5.58 |
| *Coniophis* cf. *C. precedens* | 2.2 | 3 | 2.4 |
| *Eoanilius europae* | 2 | 2.3 | 1.8 |
| *Hoffstetterella brasiliensis* | 3.5 | 4.2 | 3.2 |
| *Michauxophis occitanus* | 4 | 4.4 | 3.4 |
| *Cylindrophis ruffus* | 3.8 | 4.8 | 3.2 |
| *Anilius scytale* | | | |
| IB 40251 | 5.7 | 6.4 | 5.1 |
| MZUSP 14572 | 4.9 | 4.3 | 4 |
| MZUSP 14573 | 5.2 | 4.8 | 3.6 |
| MZUSP 14574 | 3.2 | 4.1 | 3.2 |

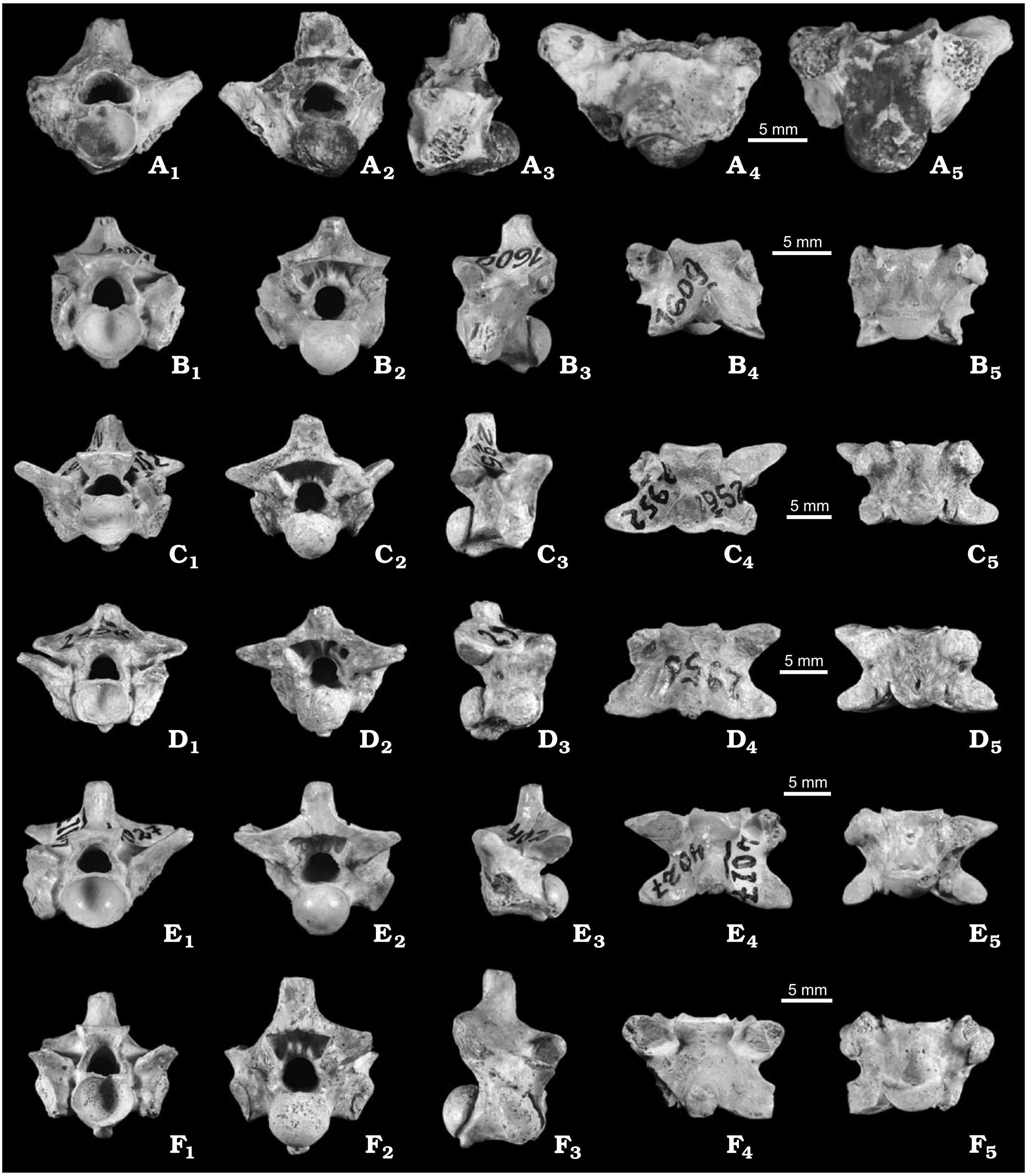

Fig. 7. Alethinophidian snake *Colombophis spinosus* sp. nov., photographs of anterior and midtrunk vertebrae from the La Victoria and Villavieja formations (middle Miocene, Colombia)–Solimões Formation (late Miocene, Brazil), IGM 184176-1 (**A**), UFAC-PV 1609 (**B**), UFAC-PV 2952 (**C**), UFAC-PV 2956 (**D**), UFAC-PV 4027 (**E**), and UFAC-PV 5716E (**F**), in anterior ($A_1$–$F_1$), posterior ($A_2$–$F_2$), lateral ($A_3$–$F_3$), dorsal ($A_4$–$F_4$), and ventral ($A_5$–$F_5$) views.

and 7). The prezygapophyseal process is small and robust. The neural canal is small and high, trapezoidal in the holotype but triangular in most specimens. The cotyle is nearly circular (ctw~cth). One pair of paracotylar foramina is observed in all specimens (one foramen on each side of the cotyle), except in AMU-CURS 154, which does not have any

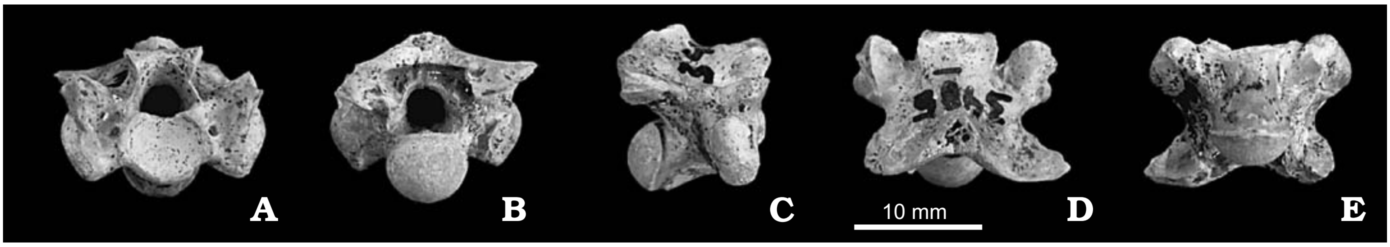

Fig. 8. Alethinophidian snake *Colombophis spinosus* sp. nov., UFAC-PV 3485, photograph of posterior trunk vertebra, from the Solimões Formation (late Miocene, Brazil), in anterior (**A**), posterior (**B**), lateral (**C**), dorsal (**D**), and ventral (**E**) views.

foramen, considered consistent with intraspecific variation as in *C. portai*. The paradiapophyses, fragmented on the left side in the holotype, are relatively small, not surpassing the ventral margin of the cotyle. In the posterior trunk vertebra (UFAC-PV 3485), the paradiapophyses extend further laterally, almost reaching the median level of the prezygapophyses, the parapophyseal facet almost exceeding the ventral limit of the cotyle, probably due to the greater lateral expansion and the anteroventral orientation of the parapophyseal facet (Fig. 8).

In posterior view, the two halves of the neural arch are considerably flattened. The neural spine is robust and cylindrical, remarkably high and columnar. The posterodorsal notch of the neural arch is relatively well marked. The neural arch is more depressed in the posterior trunk vertebra (UFAC-PV 3485). The postzygapophyses are elongated and strongly inclined dorsolaterally. The zygantra are large and deep, with a small foramen inside. The articular surfaces are well developed, and the roof of each zygantrum constitutes a continuous and straight dorsal margin in the holotype. The condyle is nearly circular. Ventral to the condyle, the haemal keel can be seen sometimes as a posterior prominence (mid- and posterior trunk vertebrae), or as a well developed hypapophysis in the anterior trunk vertebrae.

In lateral view, the neural spine is robust and well developed, being considerably higher in some specimens (UFAC-PV 1609, 2952, 2956, 4027, and 5716E), and has an epiphyseal articular facet in the distal end. It is very short anteroposteriorly and its anterior margin is slightly concave, distant from the zygosphene. It is restricted to the posterior extremity of the neural arch, and is vertical in orientation. On the posterolateral margin of the neural spine, a crest follows up on each side, as the continuation of the posterior margin of the neural arch. The side walls of the neural arch are short. The paradiapophyses are robust and are located ventrally far from the prezygapophyseal articular surfaces. The dia- and parapophysial surfaces are weakly separated; the diapophysis is slightly convex and the parapophysis is rather concave. The cotyle is strongly prominent in some specimens, where the anterolateral edge surpasses the level of the anterior edge of the zygosphene. Small lateral foramina are visible on the lateral walls of the neural arch, more or less positioned at the diapophysial level (holotype) or just above it (other specimens). The length of the centrum is smaller than the width of the neural arch (cl/naw < 1), and clearly inclined posteroventrally in the holotype and other specimens, where it distally bears a relatively prominent haemal keel that is limited laterally by relatively well marked and deep subcentral grooves.

In dorsal view, the neural arch is much shorter than broad (pr-po < pr-pr). The posterodorsal notch of the neural arch is well-marked but not deep, and the broad and robust base of the neural spine grows up in its midline. The surface between the anterior edge of zygosphene and the neural spine is horizontally oriented and smooth, where the distance between the two structures is relatively large, due to fact that the neural spine is situated well posteriorly. The articular facets of the prezygapophyses are comparatively slender, longer than broad (prl > prw), and the main axis is strongly laterally orientated. A small and sharp-edged prezygapophyseal process projects beyond the articular facet of the prezygapophysis. In the posterior trunk vertebra, the prezygapophyses are anterolaterally directed. The postzygapophyses are strongly oriented laterally. The interzygapophyseal constriction is well-marked and very short, between the pre- and postzygapophysis on each side. The anterior margin of the zygosphene is straight or concave.

In ventral view, the centrum is triangular, its ventral face being broadly rounded anteriorly, very short (cl < naw), and wide. In the holotype, UFAC-PV 3485, 4027, and 5716E (midtrunk vertebrae), the subcentral grooves are deep from the ventrolateral margin of cotyle until mid-length of the centrum, limiting anterolaterally the haemal keel, which narrows posteriorly. In the UFAC-PV 1609, 2952, and 2956 (anterior vertebrae), the subcentral grooves are limited and more evident in the middle portion of the centrum, and there is a hypapophysis in the most posterior portion. The haemal keel is conspicuous, although not very prominent in the midtrunk vertebrae. Usually, it has two divergent margins in its posterior rim that produce a bilobed aspect, attaining the precondylar constriction. Near mid-length of the centrum, on each side of the haemal keel, there are small subcentral foramina, anterolaterally situated and very close together. The subcentral ridges are relatively well marked, extending approximately from the level between the dia-and parapophyses to the condyle. In the holotype and in UFAC-PV 2952, 3485, 4027, and 5716E, the paradiapophyses are separated from the ventrolateral edge of the cotyle by a small and shallow notch. In other specimens, this constriction is discreet and subtle, probably in part due to the high degree of fragmentation in this region. Much of the condylar surface is exposed in ventral view, where the precondylar constriction is moderately marked.

*Remarks*.—After comparison of *Colombophis* vertebrae, it became clear that some differences cannot be attributed to intraspecific or intracolumnar variation, and hence warrant the erection of a new species. These differences are mainly the proportions of the vertebrae, the height of the neural spine, the morphology of the paradiapophyses, and the robustness of the zygosphene. The neural arch and centrum of the midtrunk vertebrae of *C. spinosus* are shorter than in *C. portai.* This is a result of the zygapophyses being laterally oriented in *C. spinosus*, producing a short neural arch, and values of the centrum length much lower than the width of the neural arch in the middle (cl/naw < 1). In contrast, the zygapophyses are more anterolaterally directed in *C. portai* and the centrum length is subequal to or greater than the width of the neural arch in the middle (cl/naw ≥ 1). In addition, the paracotylar notches and subcentral grooves seem to be relatively more marked in *C. spinosus* than in *C. portai*. The neural spine is high, clearly distinctive, very robust, with the main axis vertical in *C. spinosus*, but it is very low and reduced to a small tubercle in *C. portai*. The dia- and parapophyseal articular surfaces are weakly distinguishable in *C. spinosus*, but they are undistinguishable in *C. portai*. Furthermore, the zygosphene of *C. portai* is thin to moderate, whereas it is usually thicker in *C. spinosus*. Based on these characters, it is possible to support the recognition of two species of *Colombophis*.

Recently, Head et al. (2006: fig. 1A) assigned one precloacal vertebra from the middle Miocene of Venezuela to *Colombophis* cf. *C. portai* (AMU-CURS 154). According to the authors, the specimen is morphologically indistinguishable from the specimens of *C. portai* from the middle Miocene of the La Venta Fauna. Nevertheless, the description of this specimen and the direct observation of its features are consistent with the vertebral morphology of *C. spinosus*. According to the description of Head et al. (2006), this specimen shows no paracotylar foramina (congruent with the intracolumnar variation of *Colombophis*) and has paradiapophyses strongly divided. The latter is a character that contrasts with the diagnosis of the genus, but according to our observations, AMU-CURS 154 displays paradiapophyses weakly divided into two articular facets, where the diapophysis is slightly convex and the parapophysis is rather concave, which support its reference to *C. spinosus.* In addition, this vertebra is evidently short (neural arch and centrum), the zygapophyses are laterally oriented and define a very short interzygapophyseal constriction, the neural spine looks higher than in *C. portai*, and the zygosphene is thick, all characters observed in *C. spinosus.*

*Stratigraphic and geographic range*.—Eight trunk vertebrae (UFAC-PV 1609, 2952, 2955, 2956, 3485 4027, 5716C, and 5716E) recovered from the Talismã locality, Purus River; one vertebra (UFAC-PV 5424) collected at the Morro do Careca locality. All of them come from the Solimões Formation, late Miocene, Amazonas State, Brazil. The vertebra IGM 184176 (1) belongs to the La Venta Fauna, La Victoria Formation (Duke University Locality 084), Honda Group, middle Miocene, Colombia. The material at the AMU-CURS is from the Upper Member of the Socorro Formation, middle Miocene of Venezuela.

# Discussion

Traditionally recognized as "Anilioidea", this group of basal alethinophidians is comprised of taxa that retain certain lizard-like features and are as well specialized to fossorial habits (Greene, 1997). "Anilioidea" is considered by some authors to be a paraphyletic group (Rieppel 1988; Rage 1998; Lee and Scanlon 2002; Vidal and Hedges 2002, 2004; Wilcox et al. 2002; Gower et al. 2005). Recent molecular evidence is now quite strong in favor of splitting *Anilius* (as close relative of tropidophiids s.s.) and Uropeltidae s.l. (*Cylindrophis*, *Anomochilus*, uropeltines), as closer relatives of booids, pythons and advanced snakes (Wiens et al. 2008). Traditionally, the "anilioids" include the South American genus *Anilius* (red pipe snake or false coral snake), the Asian *Anomochilus* (dwarf pipe snakes) and *Cylindrophis* (Asian pipe snake), and the Uropeltidae family (shield-tailed snakes) (Greene 1997). The three former genera are generally included in the Aniliidae, although there is no consensus about its monophyly (Rage 1998; Lee and Scanlon 2002). Six fossil genera have been described for the group, and nearly all are tentatively referred to the family Aniliidae (*Australophis* Gómez, Báez, and Rougier, 2008; *Colombophis* Hoffstetter and Rage, 1977; *Coniophis* Marsh, 1892; *Eoanilius* Rage, 1974; *Hoffstetterella* Rage, 1998; and *Michauxophis* Bailon, 1988). Although placement among the "Anilioidea" is well supported for most genera, the set of snakes allocated to *Coniophis* shows a large range of variation and represents probably a paraphyletic or polyphyletic grouping of pre-macrostomatan snakes (Rage 1998).

The genus *Colombophis* was reported from the middle Miocene of Colombia and Venezuela, in northern South America (Hoffstetter and Rage 1977; Hecht and LaDuke 1997; Head et al. 2006). Hence, the new material described in this paper extends the record of the genus to the late Miocene of southwestern Brazilian Amazonia.

All previous descriptive works on *Colombophis* agree in including this genus in the "Anilioidea" (Hoffstetter and Rage 1977; Hecht and LaDuke 1997; Head et al. 2006), although comparisons with other snakes have not been reported. The new vertebral remains of *Colombophis* from the middle Miocene of Colombia and Venezuela, and the late Miocene of southwestern Brazilian Amazonia, provide some basis for revision of the genus and consideration of its affinities.

The diagnosis of the genus *Colombophis* was originally based on around 40 midtrunk vertebrae from the middle Miocene of the Villavieja Formation, Colombia (Hoffstetter and Rage 1977). According to the authors, the vertebral morphology of *Colombophis* is similar to that of the extant "anilioid"

*Cylindrophis*, differing in their size and their undivided paradiapophyses (Hoffstetter and Rage 1977). Later, Hecht and LaDuke (1997), based on new material from the same formation, added a new character to the diagnosis of *Colombophis*: the unusual placement of the subcentral foramina, which occurs close to the sagittal plane and just posterior to the level of the paradiapophyses; however, this condition is also observed in most "Anilioidea" (our personal observation). Hecht and LaDuke (1997) made a mistake during the English translation of the French diagnosis of the genus as provided by Hoffstetter and Rage (1977), because according to the last authors, the articular facets of the zygapophyses are noticeably inclined above the horizontal, whereas Hecht and LaDuke (1997) considered that they are slightly inclined.

Some features of *Colombophis* are shared with *Dinilysia patagonica* Woodward, 1901, a Late Cretaceous basal snake from Patagonian Argentina. Both are of medium to large size and have vertebrae with the following characteristics: depressed neural arch, long and strongly inclined zygapophyses, short prezygapophyseal process, and a variable presence of paracotylar foramina. However, *Dinilysia* shows a straight (not notched) posterior border of the neural arch (Rage and Albino 1989; Scanferla and Canale 2007). Despite variable neural spine height in *Colombophis* (see below), *C. spinosus* displays a well developed neural spine as in *Dinilysia.* In the latter taxon, however, the neural spine is blade-like and posteriorly inclined, with an elongated base, rising close to the dorsal edge of the zygosphene; thus, it is different from the neural spine of both *C. spinosus* and *C. portai*, which is restricted to the posterior end of the neural arch. *Dinilysia* also differs from *Colombophis* in having: a better developed haemal keel in midtrunk vertebrae, the anterior edge of the zygosphene strongly notched, and an anteriorly widened vertebral centrum. According to Apesteguía and Zaher (2006), *Najash rionegrina*, the earliest limbed snake from Patagonian Argentina, shows the neural arch flattened without posterodorsal notch, but the vertebrae of this genus are characterized by the presence of parazygantral foramina on each side of the zygantrum and the absence of prezygapophyseal process, as in the extinct Madtsoiidae, differing considerably from *Colombophis*.

Some authors indicate a probable relationship between *Colombophis* and the extant uropeltids (McDowell 1987; Szyndlar 1994); nevertheless, the large size of *Colombophis* and the presence of neural spine and haemal keel, especially in *C. spinosus*, contrast markedly with uropeltid vertebrae, which are small and strongly modified for fossorial habits, losing the neural spine and haemal keel. These and other characters, such as the long prezygapophyseal process, and condyles and cotyles markedly oval, differentiate the primitive Scolecophidia from *Colombophis* , although the frequent presence of large subcentral foramina is reminiscent of this group (Hoffstetter and Rage 1977).

In spite of numerous records in most continents, the fossils assigned to the "Anilioidea" usually consist of isolated vertebrae, and the characters that support the identifications are thought to be mostly primitive. The vertebrae of the extant "Anilioidea" *Anilius* and *Cylindrophis* share the following characters also present in *Colombophis*: a clearly depressed neural arch; prominent and strongly inclined zygapophyses; short prezygapophyseal process; a shallow median notch in the posterior border of the neural arch; and a centrum not markedly widened anteriorly. In the comparison of *Colombophis* with extinct and extant "anilioids", the inclination of the prezygapophyses at more than 20° is a character-state shared with *Australophis*, *Hoffstetterella*, *Anilius*, and *Cylindrophis* (Rage 1998; Gómez et al. 2008; our personal observation). The exceptions are *Eoanilius* and *Michauxophis*, which display almost horizontal prezygapophyses (Rage 1974; Bailon 1988; Szyndlar 1994); and *Coniophis*, in which the condition is variable (Hecht 1959; Rage 1984, 1998; Albino 1990). According to Lee and Scanlon (2002), an inclination between 15° and 30° is interpreted as an intermediate condition in modern snakes. Our observations support this statement.

A posterior margin of the neural arch not well-notched in dorsal view is observed in all genera of "Anilioidea" (Rage 1998; Gómez et al. 2008), although *Coniophis* has an almost rectilinear posterior edge (Albino 1990) and *Eoanilius*, *Hoffstetterela*, and *Colombophis* have a relatively deeper median notch (Hoffstetter and Rage 1977; Rage 1998; our personal observation). The absence of a strong notch of the neural arch is considered a plesiomorphic condition in snakes (Lee and Scanlon 2002).

*Colombophis* shares with "anilioids", especially with *Anilius*, *Cylindrophis*, *Australophis*, and *Hoffstetterella*, the presence of a small and robust prezygapophyseal process (Rage 1998; Gómez et al. 2008; our personal observation), which is considered an intermediate condition (Lee and Scanlon 2002) that, among other characters, distinguishes "anilioids" from more derived snakes, such as Acrochordidae and most Colubroidea, which have longer processes (Rage 1984; Holman 2000; Lee and Scanlon 2002; Ikeda 2007).

As said above, the depressed neural arch of *Colombophis* and "anilioids" is frequently present in other primitive snakes such as *Dinilysia*, *Najash*, Scolecophidia, and Uropeltidae. The centrum not markedly widened anteriorly is found in the two last groups (Rage 1984; Rage and Albino 1989). Thus, the combination of character states that *Colombophis* shares with "anilioids" are mostly present in primitive snakes.

Other characters of *Colombophis* are less broadly distributed. Concerning the neural spine, *Colombophis* differs from *Australophis*, *Hoffstetterella*, some species of *Eoanilius*, and *Anilius*, because these taxa have a thin, blade-like neural spine with an elongated base that rises close to or in the midline of the neural arch, being anteroposteriorly inclined. *Colombophis spinosus* shares with *Hoffstetterella* a neural spine relatively better developed than in the other mentioned genera, but it is higher in *C. spinosus* than *Hoffstetterella*. Other "anilioid" genera (the extant *Cylindrophis* and the extinct *Coniophis*, *Eoanilius*, and *Michauxophis*) have a low and posteriorly restricted neural spine as in *C. portai.* Among snakes, the presence of a low neural spine is considered a derived condition by Lee and Scanlon (2002). This feature is common in extinct and extant "anilioids", and implies that, if *C. spinosus* is considered an "anilioid", it would be an exception within this group. In conjunction with the position and shape of the neural spine, *Colombophis* shows a large smooth or slightly concave area between the dorsal margin of zygosphene and the neural spine. This character is also present in *Cylindrophis*, *Coniophis*, *Michauxophis*, and some *Eoanilius* specimens.

The dia- and parapophysial surfaces of the paradiapophyses are slightly distinguishable in *C. spinosus,* whereas *C. portai* has indistinguishable paradiapophyses (Hoffstetter and Rage 1977; Hecht and LaDuke 1997). Rage (1998) comments that the dia- and parapophysis are slightly different from one another in *Hoffstetterella*, *Cylindrophis*, and *Michauxophis*, whereas they are not distinguishable in *Colombophis portai*, *Anilius*, and some species of *Coniophis*, and variably distinguishable in *Eoanilius*, *Coniophis platycarinatus*, and *C. precedens*. The presence of slightly divided paradiapophyses is also observed in some specimens of *Anilius* (our personal observation) and *Australophis* (Gómez et al. 2008). According to some authors, distinguishable dia- and parapophysis is a derived condition found in all alethinophidian snakes (Rieppel et al. 2002; Apesteguía and Zaher 2006), although it should be considered present in many but not all alethinophidians all (e.g., all macrostomatans and various "anilioids", Jean-Claude Rage, personal communication 2009). Thus, the presence of undivided paradiapophyses in *C. portai* is primitive.

Although the haemal keel is variable along the column, it is more developed and prominent in the posterior portion of the vertebral centrum, which is in part different from some "anilioids". In *Hoffstetterella*, the haemal keel is a low blade poorly delimited laterally by subcentral grooves (Rage 1998). In *Coniophis*, it is broad and flat, somewhat delimited laterally by subcentral grooves (see Albino 1990; Rage 1998), but has a very convex surface (also in *Eoanilius*, which displays a large convex ventral surface). *Colombophis* differs from *Anilius* in which the projecting part of the haemal keel extends further anteriorly. It differs from *Cylindrophis* because in this genus the centrum is extremely convex, although somewhat rounded anteriorly like in *Colombophis*. Although showing a flattened haemal keel, *Australophis* somewhat resembles the condition observed in *Colombophis,* in which the keel is slightly prominent in the median portion of the vertebra, being delimited by the subcentral grooves (Gómez et al. 2008). In the most posterior portion of the haemal keel of *Australophis* there are two rounded depressions, one on each side of the distal margin of the haemal keel (Gómez et al. 2008). This character contrasts with the presence of the laterally paired projections that *Colombophis* shows in the same place, reminiscent of the posterior apophyses of some madtsoiid snakes (Rage 1998; Scanlon 1997, 2005) and not reported in other "anilioid" genus. Scanlon (1997, 2005) interpreted these projections as an autapomorphic condition of madtsoiids, which could be correlated with intracolumnar variation; however, its presence in *Colombophis* is probably an independent acquisition.

In addition, some characters of *Colombophis* are not present in any extant or extinct "Anilioidea". The most conspicuous of these characters are the large size and the presence of paracotylar foramina in many vertebrae. The vertebrae of *Colombophis* are larger than those of all other fossil and extant "anilioids" (Table 2); the considerable disparity in vertebral size between specimens is consistent with intracolumnar variation. The presence of paracotylar foramina is irregular in *Colombophis*. Some specimens have one or more foramina on each side of the cotyle (Hoffstetter and Rage 1977; our personal observation), whereas others do not show any foramina (our personal observation). *Anilius* and *Cylindrophis*, as well as the extinct "anilioid" taxa, do not exhibit paracotylar foramina (Rage 1974, 1984; Bailon 1988; Albino 1990; Gómez et al. 2008). According to Lee and Scanlon (2002), the presence of paracotylar foramina on most or all vertebrae, as seems to be the case in *Colombophis*, is a plesiomorphic condition.

Based on the detailed comparisons made above, the affinities of *Colombophis* with "Anilioidea" still cannot be resolved, because many characters are plesiomorphies, shared with other primitive snakes. Also, *Colombophis* is distinguished from all known extinct and extant "anilioids" due to its great vertebral size and the frequent presence of paracotylar foramina. The posterior paired apophyses of the haemal keel in some vertebrae, and the high neural spine of *C. spinosus*, also contrast significantly with all extinct and extant "anilioid" genera. The allocation of the genus into this probably paraphyletic group is not well supported at present.

The combination of characters found in *Colombophis* is not present in any other extant or fossil snake, supporting its identity as a distinct genus; however, the fact that many of these features are observed in primitive snakes suggests that *Colombophis* belongs among the broad array of basal alethinophidian snakes.

# Conclusions

In this paper we report the first record of *Colombophis* from the Solimões Formation, late Miocene of Southwestern Brazilian Amazonia. This record extends the distribution of the genus to the southeast during the Miocene, and implies its survival until the late Miocene. Reassessment of the genus permits the recognition of the new species *Colombophis spinosus*. The allocation of the genus into the probably paraphyletic "Anilioidea" cannot be resolved for the moment and it should be considered a probable basal alethinophidian of uncertain affinities.

The presence of *Colombophis* in the middle Miocene of Colombia and Venezuela, and the late Miocene of Brazil (Hoffstetter and Rage 1977; Hecht and LaDuke 1997; Head et al. 2006; this paper) suggests the possibility of general ecological similarity among these Miocene faunas. This resemblance is also supported by the presence of the boid snake *Eunectes* and the teiid lizard *Paradracaena* in La Venta

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fauna and Brazilian Amazonia (Hsiou and Albino 2009; Hsiou et al. 2009). Some authors report similarities among these faunas based on mammalian fossils, but finding more affinities of the southwestern Brazilian Amazonia with Urumaco than with La Venta (Cozzuol 2006).

The Solimões Formation, southwestern Brazilian Amazonia, includes a freshwater vertebrate fauna (rodents, crocodiles, turtles, and freshwater fishes) and, together with palynological data, indicates open areas and forest galleries along rivers, swamps, and shallow lakes. It would have been subject to variation in the water level in a seasonal dry-humid tropical climate (Latrubesse et al. 2007). For the Urumaco Fauna, in the Socorro Formation, there is a scenario that includes deltaic and fluvial deposits (Hambalek et al. 1994) with crocodiles, freshwater turtles, and catfishes which inhabited swamps, associated with other kinds of catfishes, sharks, and sirenians frequent in estuarine environments and in large freshwater rivers (Aguilera 2004; Sánchez-Villagra 2006). The La Venta Fauna is a continental deposit, with diverse and abundant freshwater fishes, turtles, and crocodilians indicative of aquatic habitats that developed in a tropical rainforest, mixed with forest/grassland mosaics and open grasslands (Kay and Madden 1997). The presence of similar fossil snakes in southwestern Brazilian Amazonia, Urumaco, and La Venta is consistent with these restorations.

The vertebral morphology of *Colombophis*, especially that of *C. spinosus*, is in part compatible with the lifestyle proposed for *Dinilysia patagonica* due to the combination of medium-large size, depressed neural arch, and high neural spine. According to Albino and Caldwell (2003), the vertebral morphology of *Dinilysia* indicates a semi-burrowing or semi-aquatic lifestyle. Considering the proposed paleoenvironment for the Solimões Formation, the habits of *Colombophis* are well compatible with a semi-aquatic lifestyle.

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