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A new fossil bristle worm (Annelida: Polychaeta: Aphroditiformia) from the late Cretaceous of tropical America

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Abstract.—A new species of aphroditiform polychaete, *Protopholoe colombiana*, is described from the Coniacian of Colombia, South America, increasing the number of species of this genus known from the fossil record to two. This is the first occurrence of fossil soft-bodied polychaetes in the Tropical Americas, and indicates that aphroditiforms were spread worldwide during the Mesozoic.

Introduction

Polychaetes are among the most abundant marine organisms. They have played important roles in marine ecosystems throughout the Phanerozoic such as sediment reworkers (i.e., bioturbation) and suspension feeders, as revealed by the good fossil record of their traces and the remains of biomineralizing worms such as machaeridians, serpulids, and sabellids (Seilacher, 2007; Vinther et al., 2008; Vinn and Mutvei, 2009). In addition, polychaetes of the order Eunicida have sclerotized jaw parts, or scolecodonts, that are more resilient to decay than soft tissue and other sclerotized parts such as aciculae or chaetae (Briggs and Kear, 1993). The earliest scolecodonts are known from the late Cambrian of North America (Williams et al., 1999). In general, they are common microfossils in Phanerozoic marine sedimentary rocks, at least from the early Middle Ordovician onward (Eriksson and Bergman, 2003). However, little is known about soft-bodied and non-tubiculous polychaetes, principally due to their low potential of preservation (Briggs and Kear, 1993; Fitzhugh et al., 1997), which strongly biases our understanding of the early origins and diversity of many polychaete crown groups through time.

Despite this, several soft-bodied specimens with exceptional preservation are known from Lagerstätte around the world, offering a unique opportunity to study the anatomy of early polychaetes, and to increase our understanding of polychaete evolution, their phylogenetic relationships, and their historical biogeography. These fossil Lagerstätten include the Cambrian Burgess Shale (e.g., Conway Morris, 1979; Eibye-Jacobsen, 2004), the Devonian Hunsrück Slate (e.g. Briggs and Bartels, 2010), and the Carboniferous Mazon Creek fauna (e.g., Fitzhugh et al., 1997), all from the Paleozoic (Briggs and Kear, 1993). The only Mesozoic Lagerstätte containing well-preserved polychaete fossils corresponds to the Cretaceous Haqel fauna (Bracchi and Alessandrello, 2005). The herein reported aphroditiform *Protopholoe colombiana* new species from the Coniacian (mid Late Cretaceous) of Colombia, represents the first fossil soft-bodied polychaete from the Neotropics, and extends the geographic and geologic range of Mesozoic aphroditiforms into the Late Cretaceous of Tropical America.

The aims of the paper are (1) to systematically describe a new exceptionally preserved polychaete fossil from the Cretaceous of Colombia, (2) to discuss its taxonomic affinities, and (3) to discuss the paleobiogeographic distribution of aphroditiforms.

Location and stratigraphy

Protopholoe colombiana n. sp. was found in dark gray terrigenous and fossiliferous mudstones of the Conejo Formation, associated with other benthic macrofossils such as the gastropod *Rostellaria* sp., abundant shrimp caudal fans, indeterminate decapod remains, and the brachyuran crab *Cenomanocarcinus* Van Straelen, 1936 (Luque, unpublished data). The ammonite ?*Paralenticeras spathi* Reyment, 1958, and the bivalve *Magadiceramus* sp., suggest a late Coniacian age (Walaszczyk and Cobban, 2006, 2007; Etayo-Serna, personal communication, 2011). The presence of *Peroniceras* sp.,?*Gauthiericeras margae* (Schlüter, 1867), and ?*G. nouelianum* (D'Orbigny, 1850), approximately 70 meters stratigraphically above the layer containing the palaeoaphroditid, confirms the late Coniacian age for the stratigraphic interval (Kennedy, 1984; Etayo–Serna, pers. comm., 2011). In addition to *P. colombiana* n. sp., the only other known fossil polychaete from the Conejo Formation is a pectinariid-like tubeworm of early Santonian age (Vinn and Luque, 2013).

Methods

The specimen (IGM p880663) was photographed using a Macropod; a technology by Macroscopic Solutions, LLC, which incorporates the Canon 6D, 65 mm 1×–5× lens, 25 II ext. tube, and

MT-24EX twin light flash. The resulting images were processed in Zerene Stacker and enhanced using Photoshop CS5.

Systematic paleontology

Class Polychaeta Grube, 1850
Order Phyllodocida Dales, 1962
Suborder Aphroditiformia Levinsen, 1882
Family uncertain

Genus *Protopholoe* Alessandrello, Bracchi and Riou, 2004

Type species.—*Protopholoe rhodanitis* Alessandrello, Bracchi and Riou, 2004, by original designation.

Included species.—*Protopholoe rhodanitis* Alessandrello, Bracchi and Riou, 2004; *P. colombiana* n. sp.

Geologic range.—Middle Jurassic to late Cretaceous.

Remarks.—The oldest remains of aphroditiforms (Order Phyllodocida) belong to *Protonimpha* Clarke, 1903 from the Devonian of North America (Alessandrello and Teruzzi, 1986; Conway Morris and Grazhdankin, 2005), while extant aphroditiform families such as Aphroditidae Malmgren, 1867, have their oldest confirmed record in the Triassic (Table 1). *Palaeoaphrodite* Alessandrello and Teruzzi, 1986 is a Mesozoic-restricted aphroditid-like genus known from France, Italy, Madagascar, and Lebanon (Table 1). Palaeoaphroditids share an overall ovate, fusiform outline, the occurrence of chaetae arranged in tufts, and the possession of elytra that suggest affiliation with Aphroditidae (Alessandrello, 1990). Nevertheless, similar characters could be present in Polynoidae Malmgren, 1867 (Fitzhugh, personal communication, 2014), and it is very likely that some of these fossil aphroditiforms have not shared the same most recent common ancestors, and *Palaeoaphrodite* as it currently stands might not be a monophyletic genus. Another aphroditiform-like genus, *Protopholoe*, is known from the Middle Jurassic of France, at a location where *Palaeoaphrodite* is also reported (Table 1). Alessandrello et al. (2004) included *Protopholoe* among aphroditiforms, but with uncertain familial affinities. The authors suggested a plausible affiliation with Sigalionidae Malmgren, 1867 based on overall similarities with the extant genus *Pholoe* Johnston, 1839, which was previously considered as belonging to that family (e.g., Glasby et al., 2000, Alessandrello et al., 2004, Bracchi and Alessandrello, 2005). Although *Pholoe* is currently a genus within Pholoidae, this family has been recovered in phylogenetic analyses as either in a polytomy with sigalionid taxa (e.g., Wiklund et al., 2005), or even nested within Sigalionidae (e.g., Norlinder et al., 2012). Given the scarcity and partial preservation of Mesozoic protopholoids and palaeoaphroditids, their phylogenetic relationships with extant Aphroditidae, Polynoidae, Pholoidae, or Sigalionidae remain to be studied. In particular, the structure of the head region, the jaws, and that of the neurochaetae (compound vs. simple) are very important to distinguish the different families of aphroditiforms, and only fossil material preserving diagnostic traits will shed light onto their phylogenetic affinities. Keeping these limitations in mind, we follow Alessandrello et al. (2004) and maintain *Protopholoe* tentatively within an uncertain aphroditiform family.

Protopholoe colombiana new species
(Figure 1.1–1.2)

Types.—Holotype and sole specimen of *Protopholoe colombiana* n. sp., deposited in the paleontological collections of the Colombian Geological Survey, Bogotá DC, Colombia, under the acronym and catalog number IGM p880663.

Diagnosis.—Aphroditiform-like polychaete of small size, elongate oval in outline, bearing at least ten pairs of chaetae tufts on each margin. Body widest at chaetiger 6. Chaetal tufts about 2.0 mm long and 0.8 mm wide in the middle part of the body, separated by interspaces about as wide as the chaetal tufts. Notochaetae form a radiating bundle, and individual, apparently stout chaetae can be distinguished. The specimen is incomplete posteriorly. No aciculae or elytra are visible on the holotype.

Occurrence.—Dark gray shales from the lower Conejo Formation, Upper Cretaceous (Coniacian, ~88 Ma), outcropping near the town of Toca, Department of Boyacá, Colombia (Latitude 05°37′30″ N, 073°12′36″ W).

Table 1. List of species of *Protopholoe* and *Palaeoaphrodite* known to date, their ages, geographic provenance, lithostratigraphic units, and size range

Taxon	Age	Unit/Locality	Lithology	Size (mm)
Protopholoe rhodanitis Alessandrello, Bracchi and Riou, 2004 (type)	Mid Jurassic (Early Callovian)	La Voulte-sur-Rhône, Ardèche, France	Pyritized	L = 13; W = 4
Protopholoe colombiana n. sp.	Late Cretaceous (Late Coniacian)	Conejo Fm., Boyacá, Colombia	Dark grey shale	L = 9.5; W = 3.2 (excluding chaetae), W = 5.5 (including chaetae)
Palaeoaphrodite adeliae Alessandrello, Bracchi and Riou, 2004	Mid Jurassic (Early Callovian)	La Voulte-sur-Rhône, Ardèche, France	Pyritized	L = 51; W = 17 (excluding chaetae)
Palaeoaphrodite anaboranoensis Alessandrello, 1990	Early Triassic (Early Scythian)	Eotrias, Anaborano, Madagascar	Ferruginous nodule in shales	L = 28; W = 19
Palaeoaphrodite briggsiana Alessandrello, Bracchi and Riou, 2004	Mid Jurassic (Early Callovian)	La Voulte-sur-Rhône, Ardèche, France	Pyrite–bearing silty shales	L = 67; W = 18
Palaeoaphrodite gallica Alessandrello, Bracchi and Riou, 2004	Mid Jurassic (Early Callovian)	La Voulte-sur-Rhône, Ardèche, France	Pyrite–bearing silty shales	L = 18 to 34; W = 5 (excluding chaetae)
Palaeoaphrodite libanotica Bracchi and Alessandrello, 2005	Late Cretaceous (Cenomanian)	Haquel, Lebanon	Sub-lithographical limestone	L = from 15 to 20; W = from 2 to 5
Palaeoaphrodite raetica Alessandrello and Teruzzi, 1986 (type)	Late Triassic, (Rhaetic)	Argilliti di Riva di Solto Fm., Bergamo, Italy	Black shale	L = 40; W = 30

L = length; W = width.

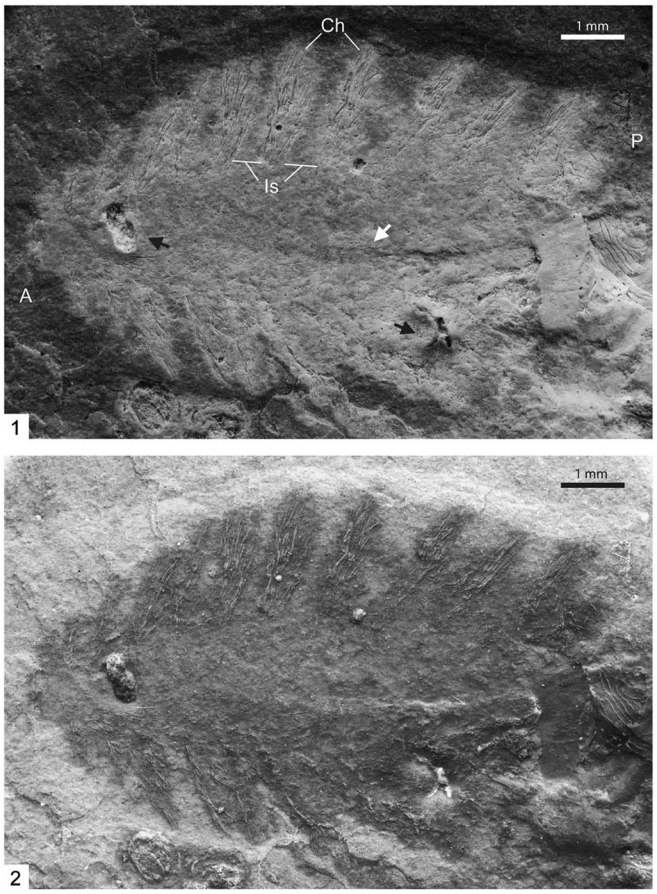

Figure 1. *Protopholoe colombiana* n. sp. holotype IGM p880663, Upper Cretaceous (Coniacian), lower Conejo Formation, Boyacá, Colombia. (**1**) Specimen in dorsal view showing the anterior (A) and posterior (P) margins, the chaetal tufts (Ch), the intersegmental spaces (Is), the neural cord (white arrow), and the two perforations produced by fossil remains (black arrows); (**2**) negative image for topographic contrast.

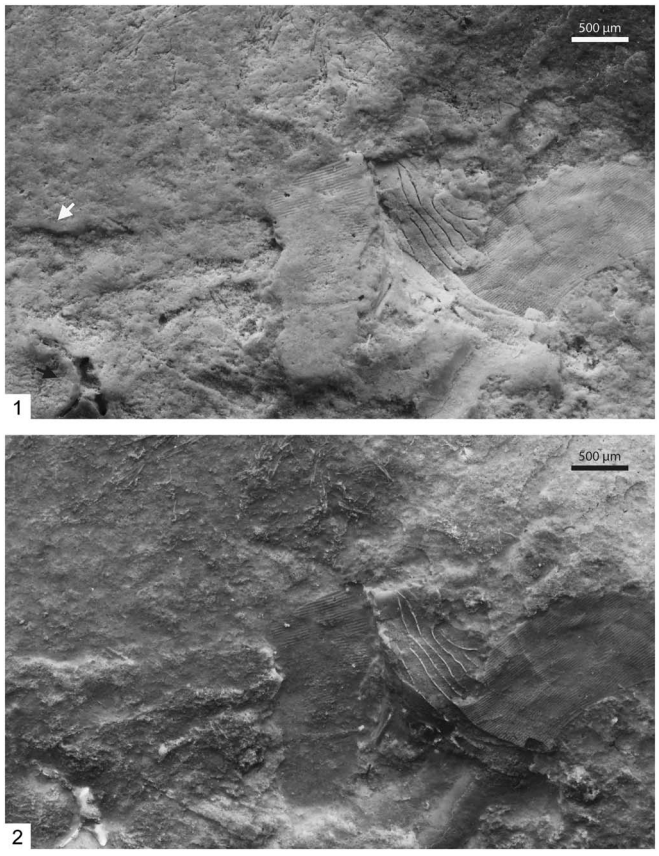

Figure 2. Close-up of indeterminate fossil remains overlapping the posterior margin of *Protopholoe colombiana* n. sp. holotype IGM p880663, Upper Cretaceous (Coniacian), Lower Conejo Formation, Boyacá, Colombia. (**1**) Specimen showing the posterior portion of the neural cord (white arrow), and the most posterior perforation produced by a fossil remain (black arrow), plus three different fossil cuticular? remains; (**2**) negative image for topographic contrast.

Description.—Polychaete elongate, oval in outline, completely compressed dorsoventrally, ~9.5 mm long measured from anterior margin to the posteriormost preserved portion. Body widest at chaetiger 6, ~5.5 mm including chaetae (~3.2 mm, excluding chaetae). An elongated structure of darker coloration runs nearly axially, which could represent neural cord or digestive tract visible due to dorsoventral compression. An elongated structure also protrudes at the level of the second chaetigerous segment, which could correspond to jaw parts, or a puncture artifact of the preservation by another fossil remain. Posterior margin poorly exposed. Small indeterminate cuticular? fragments, probably from other taxa, are found scattered along the posterior portion of specimen (Fig. 2). Chaetae grouped in tufts, with at least ten pairs on each margin. On some of the anterior parapodia, the neurochaetae and notochaetae are visible, although their detailed structure (i.e., compound vs. simple) remains unclear (Fig. 1). Notochaetae form a radiating bundle, and individual, apparently stout chaetae can be distinguished. Due the small size of the specimen and despite its exceptional preservation, it is not possible to determine if notochaetae are simple or compound. The neurochaetae are probably much thinner (individual chaetae are undistinguishable). Chaetal tufts are at most ~2.0 mm long and 0.8 mm wide in the middle part of the body. There are interspaces between chaetal tufts that are at most as wide as chaetal tufts. No aciculae are visible on the specimen. The segments and parapodia cannot be clearly delineated, and their location can only be inferred based on the positions of chaetal fascicles. The specimen is white to beige, contrasting with the dark gray mudstone matrix that it is embedded in.

Etymology.—The specific epithet derives from the country where the specimen was collected.

Remarks.—Many of the characters necessary to affiliate this specimen with extant aphroditiform families with certainty are not apparent (e.g., elytra, jaws, compound neurochaetae, structure of the head region). However, based on observed characters like the overall arrangement of chaetal tufts and the ovate body outline, the Colombian specimen resembles *Palaeoaphrodite* and *Protopholoe* species. All palaeoaphroditids described to date comprise approximately 20 segments, the shorter ones being incomplete specimens. Roughly three general shapes can be distinguished: (1) a distinctively oval shape (*Palaeoaphrodite adeliae* Alessandrello, Bracchi, and Riou, 2004, *P. briggsiana* Alessandrello, Bracchi, and Riou, 2004, *P. libanotica* Bracchi and

Alessandrello, 2005, and *P. raetica* Alessandrello and Teruzzi, 1986); (2) a more elongated and flexible shape (*P. gallica* Alessandrello, Bracchi, and Riou, 2004); and (3) a slender, apparently stiffer shape with marked intersegmental spaces (*Protopholoe rhodanitis*). *Palaeoaphrodite anaboranoensis* Alessandrello, 1990, is missing its anterior part (only 14 segments long), but its body shape seems to fall into the elongated and flexible shape type. Based on these traits, the Colombian specimen most closely resembles *Protopholoe rhodanitis* in the slender and stiffer shape with intersegmental spaces (Fig. 1); thus, we have assigned tentatively the new species to this genus. In addition, *Protopholoe colombiana* n. sp. and *P. rhodanitis* have similar proportions and are widest at the sixth chaetiger. Although incomplete posteriorly, the overall shape of the holotype of *P. colombiana*, and the reference provided by *P. rhodanitis* suggest the species should comprise about twice the number of segments that are visible. *Protopholoe rhodanitis* lacks the longitudinal groove found in *P. colombiana*, but this could be due to the difference of preservation. In addition, *P. rhodanitis* is a three-dimensional fossil and *P. colombiana* is dorsoventrally compressed, rendering the comparison of the shape of the segments difficult. The outline of the anterior part of *P. colombiana*, however, is more triangular than that of *P. rhodanitis*, which is bullet-shaped. Although elytra cannot be clearly distinguished, these soft structures could have been degraded as in *P. rhodanitis*.

Protopholoe colombiana n. sp. differs from all species of *Palaeoaphrodite* in the marked intersegmental spaces, but in general, the new species shares an elongate oval body and relatively long chaetal tufts with *Palaeoaphrodite raetica* and *P. anaboranoensis*, although differs on its broader body. It also shares long chaetal tufts with *P. adeliae*, *P. briggsiana*, and *P. gallica*, but differs in body proportions. *Palaeoaphrodite libanotica* differs from *P. colombiana* in the longer chaetae with respect to the body maximum width, particularly those positioned anteriorly and posteriorly, being noticeably shorter in *P. colombiana*.

Discussion

The holotype of *Protopholoe colombiana* n. sp. was discovered in black shales that were deposited under relatively low oxygen conditions, which could have favored the preservation of soft tissue, restricted bacterial decay, and prevented scavenging. The specimen exhibits an elongated, transversal structure protruding anteriorly at the level of the second chaetigerous segment (Fig. 1, upper left black arrow). The nature of this structure is uncertain and could correspond to poorly preserved jaw elements, or even represent an artifact association of a structure similar to those found in the same sample near the specimen (Fig. 2.1, bottom left black arrow). Such structures, likely organic remains, could have punctured the specimen after burial and compaction.

Decay experiments on the extant nereidid *Alitta virens* (M. Sars, 1835) by Briggs and Kear (1993) showed that specimens went through different morphological stages of decay in a matter of days: from freshly killed to only the jaws and chaetae remaining, passing through intermediate stages of degradation. The overall preservation of *Protopholoe colombiana* n. sp., characterized by its flattened body with conspicuous body contour, the lack of associated cuticle, elytra, or aciculae, but with chaetae still attached to the parapodia, and the brownish axial structure that could represent the digestive tract or the neural cord indicate that the specimen must have undergone a rapid, early diagenetic mineralization. This type of preservation is reminiscent of the morphological stage of decay 3 of Briggs and Kear (1993), suggesting that the worm must have been preserved in matter of days. Regarding the brownish axial structure, the lack of lateral segmental paired caecae might indicate that it does not correspond to the digestive tract, but rather the neural cord. As for most polychaetes, the neural cord of extant aphroditiforms is flanked by two thick bundles of longitudinal muscles that create a groove in which the neural cord is visible. After compression and preservation in a fossil, it is possible that the groove remains visible dorsally.

Conclusions

Among fossil aphroditiform-like polychaetes, the overall morphology and arrangement of chaetal tufts seen in *Protopholoe colombiana* n. sp. are reminiscent of those seen among species of *Palaeoaphrodite* and *Protopholoe*. *Protopholoe colombiana*, from the Coniacian (late Cretaceous) of Colombia, appears to be closer to *Protopholoe rhodanitis* from the mid-Jurassic of France, because both share the presence of well-developed intersegmental spaces unlike *Palaeoaphrodite* species. Although the familiar affiliations of *Palaeoaphrodite* and *Protopholoe* are unclear due preservational biases, the new species represents the first record of soft-bodied fossil polychaetes in the Neotropics, and the second *Protopholoe* species known to date, indicating that aphroditiform-like polychaetes may have been more widely distributed during the Mesozoic than previously thought.

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