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NEW INSIGHTS INTO LATE DEVONIAN VERTEBRATES AND ASSOCIATED FAUNA FROM THE CUCHE FORMATION (FLORESTA MASSIF, COLOMBIA)

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ABSTRACT—New vertebrate remains are reported from the Late Devonian (Frasnian) Cuche Formation of northeastern Colombia, including a new taxon of antiarch placoderm (Colombialepis villarroeli, gen. et sp. nov., previously reported as Asterolepis) and a new taxon of arthrodiran placoderm (Colombiaspis rinconensis, gen. et sp. nov.). We also report evidence of a stegotrachelid actinopterygian, a diplacanthid acanthodian (cf. Florestacanthus morenoi), a second antiarch placoderm (Bothriolepis sp.), a putative megalichthyid, and a putative tristichopterid. The absence of typical Euramerican markers, e.g., Asterolepis and Strepsodus, in this assemblage suggests that faunal interchange between Euramerica and Gondwana was less pronounced during the Frasnian–Famennian than previously thought (i.e., the Great Devonian Intercchange hypothesis). Three arthropod taxa, including two families of spinicaudatan branchiopods and the eurypterid Pterygotus cf. bolivianus, are found to be associated with the reported vertebrate fauna. Pterygotus cf. bolivianus represents the first eurypterid described from Colombia and the youngest known pterygotid eurypterid, highlighting that pterygotids, which were competitors for large predatory fishes, did not go extinct during the major vertebrate radiation in the Early and Middle Devonian.

http://zoobank.org/urn:lsid:zoobank.org:pub:08B0A655-7D78-4B09-B4F4-CF548522D205

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP


INTRODUCTION

The Devonian is informally known as the ‘Age of Fishes’ (e.g., Janvier, 1996). Fossil fishes—both microichthyoliths and macrospecimens—are globally relatively abundant in Devonian-aged rocks. In contrast to time-equivalent successions on other continents, however, vertebrate fossils are seemingly scarce and stratigraphically discontinuous in South America (western Gondwana; Janvier and Villarroel, 2000). Only a dozen Devonian vertebrate localities have been reported from South America (see review in Janvier and Maisey, 2010:fig. 1). Notwithstanding its scarcity, the paleobiogeographic and paleobiological importance of this fossil faunal record has been recognized by several authors (Dalziel et al., 1994; Janvier and Villarroel, 1998, 2000; Young et al., 2000; Burrow et al., 2003; Dupret et al., 2005; Janvier and Clément, 2005; Janvier, 2007; Janvier and Maisey, 2010; Olive et al., 2015a). Consequently, any new findings of early vertebrates of South America are of great importance in elucidating early gnathostome relationships and resolving global paleobiogeography during the Devonian (Janvier and Maisey, 2010).

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Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/UJVP.
Two well-defined Devonian vertebrate associations have been reported from South America: (1) a Lochkovian–Eifelian fauna dominated by stem gnathostomes (e.g., Ramirosuarezia Pradel et al., 2009), chondrichthians (e.g., Pucapampella Janvier and Suarez-Rigos, 1986), and acanthodians that were found in several localities in Brazil, Bolivia, and the Falkland Islands (Malvinas); and (2) a younger fauna dominated by placoderms and osteichthians from the Eifelian–Frasnian present in Colombia and Venezuela (Janvier, 2007; Janvier and Maisey, 2010). These two faunal associations present different paleobiogeographic affinities. The former fauna shows clear Gondwanan affinities and high degree of similarity to the Devonian associations of South Africa (Janvier and Suarez-Rigos, 1986; Anderson et al., 1999; Maisey and Anderson, 2001). This association coincides spatially with the well-known ‘Malvinokaffric Realm,’ defined from invertebrate communities, which included the present-day Antarctica, the Falkland Islands, and the southern parts of Africa and South America (Boucot, 1975; Boucot and Racheboeuf, 1993; Boucot et al., 2001). In contrast, the latter fauna (Colombia, Venezuela) suggests a closer affinity with those from the Devonian of Europe and North America. According to Janvier and Maisey (2010), this suggests a Gondwana-Euramerica vertebrate interchange by the Frasnian–Famennian boundary, with an early southward dispersion of reputedly Euramerican endemics (Holotyphichus, Strepodus, and Asterolepis) that had preceded the Famennian northward dispersion of Gondwanan endemics (Groenlandaspis, phyllolepids, rhizodontids, and megalichthyids). Because this interchange mainly involves marginal marine—and freshwater—fishes, it implies a close connection between northern South America and Euramerica in Devonian times. However, as noted by Janvier and Maisey (2010), evidence supporting this paleobiogeographic hypothesis is still scarce and further studies on Middle and Upper Devonian vertebrate faunas from northern South America are necessary to provide more definitive support for this relationship.

One of the richest Devonian vertebrate assemblages from northern South America comes from the Cuche Formation at the Potrero Rincón locality, north central Colombia. First mention of Devonian vertebrate remains from the Cuche Formation of Colombia was made by Mojica and Villarroel (1984), but most of discoveries were made later (1996, 2004, and 2006) by a Franco-Colombian team, in which one of us (P.J.) took part (Janvier and Villarroel, 1998, 2000; Burrow et al., 2003; Janvier and Maisey, 2010). These discoveries have resulted in the Cuche Formation being typified by a rich vertebrate assemblage comprising acanthodians (Nostolepis sp. cf. N. gaujensis, Florestacanthus morenoi), chondrichthians (Antarctilamnidae or Omalodontidae, gen. et sp. indet.), placoderms (Bothriolepis, sp. indet., Asterolepis, sp. indet., and ?Groenlandaspis, sp. indet.), actinopterygians (Stegotrachelidae, gen. et sp. indet.), and sarcopterygians (Holotyphichidae, sp. indet., ?Megalichthyidae, gen. et sp. indet., Rhizodontiformes, gen. et sp. indet.) (Janvier and Villarroel, 1998, 2000; Burrow et al., 2003; Janvier and Maisey, 2010; Monedjar-Fernández and Janvier, 2014). This vertebrate fauna is associated with abundant plant remains (Berry et al., 2000), bivalves, and lingulids, which suggest a low-energy marginal marine to brackish environment (Janvier and Villarroel, 2000).

Here, we report new data on a vertebrate assemblage from Potrero Rincón after a new field expedition in 2017. The vertebrate assemblage from the Cuche Formation is reevaluated, with the description of two new placoderm genera, in addition to new acanthodian, actinopterygian, placoderm, and sarcopterygian material. Also presented are new data on fossil branchiopods and eurypterids, the latter being the first known record from Colombia. These findings have important implications for understanding Late Devonian paleobiogeography and are discussed in this paper.

**Institutional Abbreviations**—SGC-MGJRG, Servicio Geológico Colombiano, Museo Geológico José Royo y Gómez, Bogotá, Colombia; UN-DG, Universidad Nacional de Colombia, Departamento de Geociencias, Bogotá, Colombia; YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.

** GEOLOGICAL SETTING**

The Floresta Massif is located in the Eastern Cordillera (Floresta, Boyacá, Colombia; Fig. 1). This anticline is cored by metamorphic and igneous rocks of the respective Precambrian-Cambrian Silgar Formation and Early Ordovician Chuscales Stock (Mantilla-Figueroa et al., 2016; Manosalva-Sánchez et al., 2017). Overlying the core of the anticline is a sedimentary sequence recording Early to early Late Devonian. The Devonian sequence, consisting of the El Tibet Formation (Emsian; based on

![FIGURE 1. Locality map and geological context of Potrero Rincón (PR).](image-url)
a spore assemblage; Grösser and Prössl, 1994), Floresta Formation (late Emsian–Givetian; based on brachiopods and trilobites, Morzadec et al., 2015), and Cuche Formation (late Frasnian?; Janvier and Villarroel, 2000), is a major geological feature of the Massif given its paleontological content. It is unconformably overlain by the Girón Formation, a Jurassic sedimentary sequence (Fig. 1).

During the Frasnian, the siliciclastic platform, which is the Cuche Formation today, was located within a narrow subtropical seaway between Gondwana and Euramerica in the Southern Hemisphere (Scotese, 2002). The Cuche Formation (Fig. 2) lies conformably on the Floresta Formation in a gradational contact (Fig. 2). At its base, the formation is characterized by the occurrence of reddish to pink clays and micaceous mudstones with remains of leaves and roots, interbedded with layers of feldspathic sandstones. A lithological change, reflected by color alteration (from reddish to yellowish) of the clays, mudstones, and fossiliferous levels, then appears in the middle of the sequence (~150–300 m). The last part of the section has the same lithology as the middle part, but sandstone beds are more frequent (Fig. 2). Along the section, the geometry of the finer grain beds is tabular and characterized by heterolithic and wavy planar stratification. By contrast, sandy beds display a trough cross-bedding and heterolithic stratification (Fig. 2). As a result, the depositional environment of this formation has been interpreted as a siliciclastic coastal region where the tidal dominance developed tidal inlets and tidal flats (Janvier and Villarroel, 2000).

We resampled the classical fossiliferous localities of Potrero Rincón (PR-1, PR-2, PR-3) and Tunguaquita (Figs. 1, 2) to intensify the collection effort on Colombian Late Devonian marine faunas. These sites are in the Cuche Formation and were previously sampled and studied by Janvier and Villarroel (1998, 2000). The PR-1, PR-2, and PR-3 levels are located in the first arenaceous beds of the last part of the sequence (Fig. 2). By contrast, the Tunguaquita locality is dominated by red claystone/mudstone beds, which overlie the Potrero Rincón levels stratigraphically (Fig. 2). Both the vertebrates and arthropods described in this paper have been found in the same fossiliferous layers.

MATERIALS AND METHODS

Vertebrate remains are extremely fragile and often disintegrate (partially or totally) during excavation. Accordingly, several specimens have been studied by removing the altered bone and making elastomer casts of their natural impression in the laboratory. Another specimen was prepared virtually to obtain three-dimensional (3D) models of the entire element (SGC-MGJR.R.2018.V.17). The virtually prepared specimen was scanned (computed tomography [CT] scanning) at the Royal Belgian Institute of Natural Sciences, Brussels, using a RX EasyTom instrument (RX Solutions, Chavanod, France; www.rxsolutions.fr) with a copper filter. Images were generated at a voltage of 426 kV and a current of 139 μA, with a set

FIGURE 2. Stratigraphic column of the Cuche Formation with location of the Tunguaquita and Potrero Rincón (PR) localities 1, 2, and 3. Abbreviations: C, conglomerate; Ms, mudstone; Ss, sandstone.
SYSTEMATIC PALEONTOLOGY

Class ACANTHODII Owen, 1846
Family DIPLACANTHIDAE Woodward, 1891
Genus FLORESTACANTHUS Burrow, Janvier, and Villarroel, 2003

Type Species—Florestacanthus morenoi Burrow, Janvier, and Villarroel, 2003.

cf. FLORESTACANTHUS MORENOI
(Fig. 3)

Material—SGC-MGJRG.2018.V.17, complete fin spine (Fig. 3); SGC-MGJRG.2018.V.18, small fragment of fin spine. A three-dimensional image of SGC-MGJRG.2018.V.17 is available in Supplemental Data.

Locality and Horizon—Potrero Rincón 1, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

Description

The complete fin spine (SGC-MGJRG.2018.V.17; Fig. 3) is preserved in a micaceous siltstone block. Although only the most distal part of the spine is exposed, a CT scan of the block allows for an acceptable 3D reconstruction (see Supplemental Data).

The spine body is recurved, laterally compressed, and slightly asymmetrical. It is 99 mm in length and its maximum width (measured perpendicular to maximum length) is 12 mm (near the insertion/exertion boundary), with a ‘U’ section that becomes sub-circular in the distal (closed) part of the spine. The spine appears to be thin-walled, with an enlarged pulp cavity opening proximately in a broad base. The open part of the fin spine base is elongated in shape, and it presents a thin, unornamented section at the base indicating a shallow insertion (less than 10 mm deep, although the spine seems to be partially incomplete proximally).

The dorsal surface of the spine is ornamented with at least 14 fine, evenly spaced ribbings that converge at the tip of the spine. Each ribbing is continuous along the length of the spine. The ribs are smooth and of approximately the same width as the sulcus. The ornamentation of the ventral part is not well preserved, or not well defined after CT scanning. The ventral surface seems smooth (probably an artifact of scanning or segmentation), but some thin parallel ribbing is identifiable at the leading edge.

SGC-MGJRG.2018.V.18 is a small fragment (20 mm length) corresponding to the distal tip of a spine. At least the preserved part is symmetrical and perfectly straight. Although the ornamentation is partially eroded, it is possible to distinguish fine, parallel striations, separated by wider grooves, converging toward the apex.

Remarks

The strong curvature and the asymmetry of the complete spine (SGC-MGJRG.2018.V.17) support its placement as a paired spine, revealing an overall similarity to diplacanthid pectoral spines (e.g., Burrow et al., 2016:figs. 1, 5, 14). Also, pectoral spines in all ‘acanthodian’ groups have only a short insertion base (or lack an insertion base) as shown in SGC-MGJRG.2018.V.17; in the same way, being flattened rather than of similar width and depth is another feature associated with pectoral rather than median spine (e.g., Miles, 1973a; Denison, 1979; Botella et al., 2012).

Diplacanthid remains have been described previously from the Cuche Formation by Burrow et al. (2003). These remains consist of isolated scales, patches of articulated scales, and an unpaired fin spine of Florestacanthus morenoi Burrow, Janvier, and Villarroel, 2003, which came from the same clayey lenses as the spines described here (Potrero Rincón 1 [PR-1] in Janvier and Villarroel, 2000). Like the type spine of Florestacanthus morenoi, our spine appears to be thin-walled and possesses a wide pulp cavity opening proximally. In both spines, the central pulp cavity is large and extends almost to the distal tip. The ornamentation ridges of SGC-MGJRG.2018.V.17 are smooth like those of F. morenoi and without nodes. As in Florestacanthus and other diplacanthiforms, these ridges indicate that thin parallel ribbing underlies the outer ornament layer.

The type of Florestacanthus, a median spine (Burrow et al., 2003), presents a long insertion part, whereas SGC-MGJRG.2018.V.17 possesses a shallow insertion. This is an expected distinction between acanthodian pectoral and median spines (C. Burrow, pers. comm., 2018). Similarly, the ornament layout can be a little different for pectoral versus median spines, as occurs in our case. Finally, our spine (99 mm) is slightly longer than the Florestacanthus type spine (67 mm), which is clearly within the boundaries expected for intraspecific variation.

Based on these similarities (and the fact that the new spine was found in the same levels as Florestacanthus), we assigned the new spine to Florestacanthus morenoi (pectoral fin spine). However, because it appears isolated, neither in association with scales

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**FIGURE 3.** cf. Florestacanthus morenoi, SGC-MGJRG.2018.V.17, block displaying the paired fin spine from Potrero Rincón 1, Colombia, Cuche Formation, Upper Devonian. A, photograph of paired fin spine. B, 3D model of paired fin spine in dorsal view. C, 3D model of paired fin spine in internal view. Scale bars equal 1 cm.
nor with unpaired spines of *F. morenoi*, we prefer to retain it as cf. *Florestacanthus morenoi*, pending the discovery of more articulated material.

Specimen SGC-MGJRG.2018.V.18 is compatible with unpaired fin spines of *Florestacanthus morenoi* described by Burrow et al. (2003). However, because only the most distal part of the spine is preserved, it seems more cautious to also maintain it as cf. *F. morenoi*.

Class PLACODERMI McCoy, 1848
Order EUANTIARCHA Janvier and Pan, 1982
Suborder BOTHRIOLEPIDOIDEI Miles, 1968
Family BOTHRIOLEPIDIDAE Cope, 1886
Genus BOTHRIOLEPIS Eichwald, 1840

Type Species — *Bothriolepis ornata* Eichwald, 1840, subsequently designated by Woodward (1891). Priksha River, Russia, Lnyanka Beds, upper Famennian, Upper Devonian.

*Bothriolepis* sp.

(Fig. 4)

**Material** — All the material published by Janvier and Villa-rollo (2000) under the name *Bothriolepis*, sp. indet. Potrero Rincón 2: SGC-MGJRG.2018.V.21, an almost complete juvenile skull roof (Fig. 4A–D); SGC-MGJRG.2018.V.20, an almost complete adult skull roof (Fig. 4D–H).

**Locality and Horizon** — Potrero Rincón 2 and 3 and Tungua-quita, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

**Description of the Juvenile Skull Roof**

SGC-MGJRG.2018.V.21 (Fig. 4A–D) is strongly compacted, and the details observed on the part and counterpart are partly overprinted. The preorbital recess, usually observable in internal view, is here observable on the counterpart of the external view because of the compression. Moreover, this compression of the preorbital recess hides the central sensory line. The preorbital recess is of the pentagonal type. The orbital fenestra is larger, and the postpineal plate longer, than in adult skull roofs, a typical condition for juvenile *Bothriolepis* specimens (Werdelin and Long, 1986). This is also known in other juvenile euantiarch genera, such as in *Asterolepis*, which shows a proportionally broad skull roof with a large orbital fenestra and proportionally long pectoral fins (Upenieze and Upenieks, 1992). There is no internal median constriction in the anterior margin of the orbital fenestra. The posterior margin of the orbital fenestra is convex, due to the triangular shape of the postpineal plate, like in most other *Bothriolepis* species. The premedian plate is narrower than the orbital fenestra. The nuchal plate is wide, extends beyond the lateral limits of the orbital fenestra, and carries the central sensory line groove and the endolymphatic ducts. The borders of the paranuchal plate are difficult to distinguish, and the presence of a post marginal plate is difficult to ascertain.

**Description of the Adult Skull Roof**

The adult skull (Fig. 4E–H) is slightly different from the attempted reconstruction proposed by Janvier and Villarroel (2000: fig. 9a), which was based on isolated plates from the same locality. The size of the skull agrees with that of the largest isolated plates found in the locality. The postpineal plate is firmly fused to the nuchal plate and the orbital fenestra is small, these are typical adult traits (Fig. 4E–F; Werdelin and Long, 1986). The notch of the nuchal plate for the postpineal plate is deep, and the posterior edge of the postpineal plate is situated at the same level as the median angle formed between the paranuchal and lateral plates. The infraorbital sensory line grooves are unusually broad and well defined. An unidentified sensory line groove is located posterior to the

**FIGURE 4. Bothriolepis sp., Potrero Rincón 2, Colombia, Cuche Formation, Upper Devonian.**

**A**. SGC-MGJRG.2018.V.21a, juvenile partial skull roof, external view, counterpart; **B**. interpretive drawing of same. **C**. SGC-MGJRG.2018.V.21b, juvenile partial skull roof, external view; **D**. interpretive drawing of same. **E**. SGC-MGJRG.2018.V.20a, adult partial skull roof, elastomer cast, external view; **F**. interpretive drawing of same. **G**. SGC-MGJRG.2018.V.20b, adult partial skull roof, internal view. **H**. SGC-MGJRG.2018.V.20b, adult partial skull roof, elastomer cast, internal view. Dashed lines indicate unpreserved margins. **Abbreviations:** csl, central sensory line groove; d.end, endolymphatic duct; ifc1, principal branch of the infraorbital canal; ifc2, lateral branch of the infraorbital canal; La, lateral plate; nm, obtused nuchal area; Nu, nuchal plate; Pmg, postmarginal plate; PNu, paranuchal plate; Ppi, postpinnate plate; prh, preorbital recess; PrM, premedian plate. Scale bars equal 1 cm.
most anterior extension of the infraorbital sensory groove. The latter might represent an effect of the ornamentation pattern. The nuchal plate shows an obstructed area with a median posterior process. The natural mold of the skull internal surface is visible, and the preorbital recess was almost certainly either trilobate or pentagonal in shape (Fig. 4G–H). This is similar to the condition in one of the lateral plates figured by Janvier and Villarroel (2000:fig. 7b).

Remarks

The remains of Bothriolepis published by Janvier and Villarroel (2000) are incomplete, disarticulated, and consist mainly of postcranial plates. The two skulls described here were found in the same locality (Potrero Rincón 2) as the material described by Janvier and Villarroel (2000). Both skulls are useful for completing the descriptions made by Janvier and Villarroel (2000).

Bothriolepis perija, from the Late Devonian of Sierra de Perija, Venezuela (Young and Moody, 2002), is known from several isolated plates and one articulated specimen, which is unfortunately exposed in ventral view and shows almost nothing of the skull roof. Several diagnostic characters of this species are shared with the adult skull roofs that have been previously described from Colombia, i.e., the reticulate ornamentation (somewhat denser in B. perija) and the exceptionally broad infraorbital sensory line groove. However, a few other characters of B. perija do not match the Colombian material, such as the relatively deep mixilateral plate with a sharp dorsolateral ridge in the thoracic armor (Young and Moody, 2002). Moreover, Janvier and Villarroel (2000) suggested that two different Bothriolepis species could be present in the outcrop of Potrero Rincón 2, on the basis of two different shapes of the preorbital recess (elliptical and pentagonal, respectively; the material described herein belongs to the latter type) and shapes of the lateral marginal plate 2. A large number of species included in the genus Bothriolepis are defined on the basis of isolated and often undiagnostic plates. Those remains display a high rate of individual and ontogenetic variability. In spite of Long’s (1983) and Young’s (1988) works aiming to classify the diversity of Bothriolepis, difficulties still remain in identifying Bothriolepis species that display no conspicuous, and unique, characters. For all these reasons, and instead of further complicating the systematics of Bothriolepis, we decided to leave the Colombian material in open nomenclature.

Suborder ASTEROLEPIDOIDEI Miles, 1968
Genus COLOMBIALEPIS, gen. nov.

Asterolepis sp. indet., in Janvier and Maisey (2010).

Type Species—Colombialepis villarroeli, gen. et sp. nov. Potrero Rincón 1 and Tunguaquita, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

Diagnosis—As for type and only species.

Etymology—From ‘Colombia,’ where the material was found, and ‘lepis’ (Greek) for scale.

COLOMBIALEPIS VILLARROELI, gen. et sp. nov. (Fig. 5)

Asterolepis sp. indet., in Janvier and Maisey (2010).

Holotype—SGC-MGJRG.2018.V.19, an anterior median dorsal plate (Potrero Rincón 1; Fig. 5C–E).

Localities and Horizon—Potrero Rincón 1 and Tunguaquita, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

Other Material—Tunguaquita: UN-DG-PALV34, fragment of a large plate. Potrero Rincón 1: UN-DG-PALV32, nuchal and postpinel plates (Fig. 5A); SGC-MGJRG.2018.V.22, premedian plate (Fig. 5B); SGC-MGJRG.2018.V.29, posterior median dorsal plate (Fig. 5F); UN-DG-PALV33 (Fig. 5G), UN-DG-PALV52 (Fig. 5H), and UN-DG-PALV53 (Fig. 5I), anterior dorsolateral plates; SGC-MGJRG.2018.V.30, posterior ventrolateral plate (Fig. 5J); SGC-MGJRG.2018.V.31 (Fig. 5L) and SGC-MGJRG.2018.V.32 (Fig. 5K), unidentified lateral plates; SGC-MGJRG.2018.V.33 (Fig. 5M), Cv1.

Diagnosis—An asterolepid antiarch, in which the premedian plate is as long as broad. The nuchal plate displays probably two divergent central sensory line grooves. The anterior median dorsal plate displays a narrow, elongated posterior part, lateral corners placed in the anterior half of the plate, and short anterior and posterior margins. The posterior median dorsal overlaps the posterior dorsolateral plate (or mixilateral plate). The ornamentation is made of vermiculate parallel ridges.

Etymology—A tribute to Dr. Carlos Villarroel, a Colombian geologist, who has greatly improved our knowledge on the Devonian of Colombia.

Description of the Skull Roof

Nuchal and Postpinel Plates—UN-DG-PALV32 (Fig. 5A) displays the posterior median part of a skull roof with part of the nuchal and postpinel plates. The two plates are distinguishable by the different orientations of the ornamentation. Only the posterior portion of the postpinel plate is preserved. Thus, the margin with the orbital fenestra cannot be observed. The posterior portion of the nuchal plate is not preserved either. As mentioned by Janvier and Villarroel (2000), it seems that there are two divergent central sensory line grooves, which would rather suggest a bothriolepid pattern. However, in some antiarch species (e.g., Asterolepis radiata; Karatayute-Tulima, 1963), the lineation of the ornamentation in this region of the skull roof may also be developed in the same way. A depression in the center of the nuchal plate might correspond to the position of the endolympatic duct opening.

Premedian Plate—SGC-MGJRG.2018.V.22 (Fig. 5B) is a small plate that is as broad as long. Its posterior margin is shorter than the anterior one. The principal section of the infraorbital sensory line is located anteriorly. The size of the plate, in comparison with the rest of the material, is suggestive of juvenile status for SGC-MGJRG.2018.V.22. However, the position of the sensory line and the shape of the plate indicate that this specimen belongs to an adult (Werdelin and Long, 1986). There is not enough information to make a firm determination.

Description of the Thoracic Armor

Anterior Median Dorsal Plate—This plate (AMD) displays a rounded anterior portion and a narrow posterior expansion (SGC-MGJRG.2018.V.19; Fig. 5C–E). The lateral corners are distinct and placed in the anterior half of the plate. The anterior and posterior margins are short. The anterior part of the lateral margin is concave, whereas its posterior part is rather convex. The plate is slightly arched anteriorly and more strongly arched posteriorly. It seems that there is an anterior oblique dorsal sensory line groove on the left side. The latter runs from the middle of the anterior lateral margin toward the center of the plate. The overlap area for the anterior dorsolateral plate
cannot be observed. The overlap areas for the posterior median dorsal plate and the posterior dorsolateral plate are not distinguishable, because the posterior part of the only preserved AMD is in visceral view; the latter is smooth and concave. The ornament is composed of smooth, vermiculate parallel ridges.

**Posterior Median Dorsal Plate**—The external surface (Fig. 5F) shows a smooth dorsal median ridge and vermiculate parallel ridges. The anterior median, anterolateral, and lateral corners are well marked. The posterolateral corners, as well as the posterior margin, are not preserved in our material. The overlap area for the anterior median dorsal plate cannot be observed, because the only posterior median dorsal plate is preserved in external view. A small part of the area overlapping the posterior dorsolateral plate (or mixilateral plate) is observable. A slight median ventral ridge is observable in internal view.

**Anterior Dorsolateral Plate**—None of the specimens (Fig. 5G–I) displays the lateral lamina except for UN-DG-PALV52, which shows a small part of it. The processus obstans is reduced and the articular fossa unpreserved. The dorsolateral ridge is sharp, but the angle formed between the lateral and dorsal laminae is impossible to estimate due to the strong compression. The anteromedian process is well pronounced. The area overlapped by the anterior median dorsal plate is long and narrow.

**Posterior Ventrolateral Plate**—Only the pointed posterior part of the ventral lamina is preserved in our material (Fig. 5J). The ornamentation is made of vermiculate parallel ridges too, but the orientation of these ridges varies on the plate. They are parallel to the ventrolateral ridge along this ridge and vary medially.
Unidentified Lateral Plates—Two fragmentary plates (SGC-MGJRG.2018.V.32 and SGC-MGJRG.2018.V.31; Fig. 5K–L) show a ridge and parts of two laminae. These fragments probably belong either to an anterior dorsolateral plate or to a posterior dorsolateral plate or to an anterior ventrolateral plate, and less probably to a posterior ventrolateral plate because of the convex margin. The lateral ridge in SGC-MGJRG.2018.V.31 is more acute than in SGC-MGJRG.2018.V.32.

Description of the Pectoral Fin Armor

Ventral Central Plate 1—The plate (Fig. 5M) is short, with a well-developed external dorsal articular area and a prominent ventromedial margin. The lateral corner is located at the mid-length of the plate. Vermiculate parallel ridges are distributed proximodistally.

Remarks

Specimen UN-DG-PALV053 was attributed by Janvier and Maisey (2010) to a mixilateral plate. On the basis of the obtuse posterior angle, it is more likely to be an anterior dorsolateral plate.

The assignment of this taxon to the Asterolepidoidei is based on the association of elements of the trunk and pectoral fin, which display characteristic asterolepid features such as the vermiculate ornamentation that tends to develop into parallel ridges. Janvier and Villarroel (2000) described large and fragmentary antarch plates that they already attributed to the family Asterolepididae and cautiously to the genus Asterolepis. New field investigations in Colombia provided supplementary material and notably the anterior median dorsal (AMD) plate, which is highly distinctive and sufficient to separate Colombialepis, gen. nov., from all previously known asterolepids, including Venezuelaepis from the Upper Devonian of Venezuela (Young and Moody, 2002). The remarkably long posterior division of this AMD is most closely approached by Asterolepis (Upeniece and Upenieks, 1992), and the AMD of Colombialepis differs from all known ontogenetic stages. This observation strengthens the attribution of the Colombian material to a new genus.

Order ARTHRODIRA Woodward, 1891
Suborder PHLYCTAENOIDEI Miles, 1973b
Infraorder PHLYCTAENII Miles, 1973b
Family GROENLANDASPIDIDAE Obruchev, 1964
Genus COLOMBIASPIS, gen. nov.


Type Species—Colombiaspis rinconensis, gen. et sp. nov., Potrero Rincón 1 and 3, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

Diagnosis—As for type and only species.

Etymology—From ‘Colombia,’ where the material was found, and ‘aspis’ (Greek) for shield.

COLOMBIASPIS RINCONENSIS, gen. et sp. nov. (Fig. 6)
Posterior Dorsolateral Plate — This plate (Fig. 6G, H) was interpreted as either a putative posterior ventrolateral plate or a posterior dorsolateral plate by Janvier and Villarroel (2000:pl. 4, fig. 5). The anteroposterior orientation of the plate was decided based on the oblique ridge on the ventral overlap area, whose dorsal extremity points toward the posterior part of the plate, as in, e.g., Groenlandaspis rinconensis (Long et al., 1997b:fig. 8). The posterior part of the plate is not preserved, and its dorsal part is poorly preserved. The main lateral sensory line groove is not clearly observable. The area overlapped by the anterior dorsolateral plate is much extended and regular in width along its height. Dorsally, it is difficult to distinguish this area from the area overlapped by the median dorsal plate. The overlapped areas for the anterolateral and anterior dorsolateral plates are continuous. The anterior ventral embayment is strongly pronounced. It is impossible to decide whether there was another posterior embayment or the one observed is the only one (implying a shortened posterior portion of this area). The ornamentation consists of coarse tubercles in the ventral part and minute tubercles in the dorsal portion of the plate.

Posterior Lateral Plate — A fragment of a putative posterior lateral plate (Fig. 6I) is present in the material. Only the
posteroventral part of the plate is preserved. A large overlap area for the posterior ventrolateral plate is visible. The ridge crossing the plate from the posteroventral corner to the center of the plate can be partly observed. The ornamentation consists of coarse tubercles.

**Spinal Plate**—Two fragments of spinal plates are present. One represents the free distal part of the plate (Fig. 6 K), and the other one is a segment of its medial part (Fig. 6 J). The medial fragment is ornamented with strong tubercles, which become smaller posteriorly and tend to form ridges. The posterior portion of the spinal plate displays at least two longitudinal ridges. It shows coarse spines, which are very likely situated on the medial margin, as in other groenlandaspidids, e.g., *Groenlandaspis potyi* (Olive et al., 2015a). The spines on the lateral margin are smaller.

**Remarks**

*Colombiaspis*, gen. nov., differs from all other groenlandaspidids by the shape of its posterior dorsolateral (PDL) plate. The latter displays a ventral overlap area, which corresponds either (1) to the anterior embayment usually observed in groenlandaspidids, but here strongly pronounced (the posterior embayment not being preserved here), or (2) to the fusion of both embayments (anterior and posterior). In both cases, this is unusual for the entire group, and it strengthens the attribution of this material to a new genus.

Moreover, *Colombiaspis rinconensis*, gen. et sp. nov., probably possessed two pineal plates. This is a condition only observed in *Turrisaspis* (Daeschler et al., 2003; Olive et al., 2015b) and in some undescribed Australian forms (pers. comm. of A. Ritchie in Daeschler et al., 2003). The ornamentation, shape of the nuchal, median dorsal, and PDL plates do not resemble those of *Turrisaspis*.

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGI Kleinn, 1885
Family STEGOTRACHELIDAE Gardiner, 1963
STEGOTRACHELIDAE, gen. et sp. indet. (Fig. 7)


Actinopterygii, gen. et sp. indet., in Janvier and Maisey (2010).

**Material**—Potrero Rincón 1 (material described by Janvier and Villarroel, 2000): UN-DG-PALV40a, right half of a skull roof plate; UN-DG-PALV40b, impression of a gular plate; UN-DG-PALV41, imperfect right maxilla; UN-DG-PALV42, fragmentary right dentary; UN-DG-PALV40d, scale; UN-DG-PALV43, fulcrum. New material: SGC-MGJRG.2018.V.24, left lower jaw (Fig. 7A, B); SGC-MGJRG.2018.V.25, left cleithrum and associated endoskeleton (Fig. 7C, D).

**Locality and Horizon**—Potrero Rincón 1, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

**Description**

**Lower Jaw**—Most of the lower jaw (Fig. 7A, B) is preserved as an imprint of the original material, which was probably lost during excavation, and only the teeth and their bases were preserved as such. The poor preservation of the material makes interpretation difficult, but it seems to be an impression of the internal surface of the lower jaw that has retained the overprinted ornamentation of the external surface, probably because of the extreme thinness of the bones. The lower jaw comprises a dentary bone and an angular bone posterior to it. There is no evidence for supra-angular or articular bones.

The dentary is convex, slender, and tapers anteriorly. Its anterior extremity recures dorsally slightly. An open mandibular canal for the external mandibular branch of the facial nerve is present on the lateral surface of the dentary. The canal runs obliquely from the ventral edge of the posterior portion to the dorsal surface of the anterior portion of the lower jaw. The lateral surface of the dentary is ornamented with thin ridges. Above the mandibular canal, these ridges are parallel and horizontal. The ridges are more oblique in the most dorsal part of the dentary. Ventral to the mandibular canal, they are anterodorsally directed.

The dorsal surface of the dentary is overhung by a thin, black layer of bone. Above this layer is a series of stout, square-shaped bumps, which probably represent the infilling of the tooth alveolae, because two pointed, anteriorly directed teeth are emerging from two of the bumps after mechanical preparation.

The angular bone forms the posterior portion of the lower jaw, and it is mostly not ornamented. There is no evidence of a pit for the ceratohyal ligament on its posterior margin.

**Shoulder Girdle**—The dermal shoulder girdle consists of a stout and deep left cleithrum exposed in lateral view (Fig. 7C, D). It displays the characteristic shape of Devonian actinopterygian cleithra, i.e., large, high with a marked concave anterior margin, and strongly convex posterior margin (e.g., *Mimipiscis*, *Moythomasia*; Gardiner, 1984). Unfortunately, the clavicle, the supracleithrum, and the posttemporal bones are missing. Part of the endoskeletal skeleton seems preserved.

The lateral surface of the cleithrum is convex, and it possesses a slender, vertical blade, which ends dorsally with a sharp tip. The posterior concave margin forms a shelf from the apex of the blade to approximately one-third of the bone, probably for the connection to the supracleithrum. The connection area for the supracleithrum thus appears narrow but elongated dorsoventrally, which is different from the condition in *Mimipiscis*, *Moythomasia*, and *Howqualepis* (Gardiner, 1984; Long, 1988). The anteroventral part of the cleithrum is rounded and smooth, and it probably represents the overlapped area for the clavicle.

The posterior, convex margin possesses a deep, rounded ventral embayment that would have accommodated the pectoral fin. A crest is passing from the dorsal margin of this posterior embayment to the dorsal margin of the overlap area for the clavicle, so that the cleithrum is dipping deeply ventrally from either side of that crest. This crest might mark the subdivision of the ventral fin musculature, as does the rostrocaudally directed ridge on the ventral surface of the coracoid region of *Moythomasia* (Gardiner, 1984).

The ornamentation consists of dorsoventrally directed, thin ridges on the vertical blade and anterior margin, except in the contact areas for the supracleithrum and the clavicle. The ventral part of the cleithrum is ornamented with thin rostrocaudally directed ridges.

The endoskeletal shoulder girdle has a complex shape. There is no evidence of a mesocoracoid process, but this might be a preservation artifact. As in *Mimipiscis* and *Moythomasia* (Gardiner, 1984), the mesocoracoid arch is dorsally directed toward the posterior margin of the cleithrum. Possible large coracoid and scapular foramina are present near the ventral edge of the pectoral fin embayment of the cleithrum. There is no clear evidence of a glemoid fossa.

**Remarks**

The ornamentation and overall morphology of the new collected elements are very similar to those of other Devonian actinopterygians, such as the Stegotrachelidae. However, it is not possible to erect a new taxon, nor to assign it to any already known taxon because of the absence of articulated material showing diagnostic features.
The lower jaw is very similar to that of other Devonian stegotrachelids, such as *Mimipiscis* (Gardiner, 1984), in the ornamentation and the presence of only two dermal bones, the dentary and the angular. The presence of only these two bones is also seen in *Polypterus* and *Cheirolepis* (Gardiner, 1984), whereas in many ‘palaeonisciformes’ (e.g., *Moythomasia*; Gardiner, 1984) and primitive neopterygians there is a third dermal bone, the suprangular (Patterson, 1982). However, because the original bones are mostly missing, and the lower jaw is preserved as an impression, the absence of suprangular might be a preservation artifact.

Contrary to *Mimipiscis* and *Moythomasia* (Gardiner, 1984), the mandibular canal is completely open and there is no evidence of a pit for the ceratohyal ligament on the posterior margin of the mandible. A dentary with a recurved anterior tip is also present in other Devonian actinopterygians, such as *Doorosenia* and *Howqualepis* (Long et al., 2008).

The ornamentation is slightly different from that of the other dentary found in the same locality (Janvier and Villarroel, 2000) in having less-chevron-shaped ridges.

**Material**—Potrero Rincón 1: SGC-MGJRG.2018.V.26, opercular (Fig. 8A). Potrero Rincón 2: UN-DG-PALV44, opercular (Janvier and Villarroel, 2000:fig. 15a).

**Localities and Horizon**—Potrero Rincón 1 and 2, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

**Description**

**Opercular**—The discovery of an opercular bone was noted by Janvier and Maisey (2010), who neither described nor figured it. Specimen SGC-MGJRG.2018.V.26 is interpreted here as the left opercular of a large megalichthyid tetrapodomorph because of its originally extensive cosmine covering. As it often occurs in cosmine-covered dermal bones when freed from the matrix, the cosmine broke down into minute prisms when the block was split. However, it clearly showed no evidence for Westoll lines, a condition that may rule out lungfish affinities. The same bed also yielded large, cosmine-covered, rhombic scales which would also agree with megalichthyid affinities. Another opercular (UN-DG-PALV44), previously referred to an Osteolepididae, gen. et sp. indet., was described from Potrero Rincón 2 (Janvier and Villarroel, 2000:fig. 15a). Specimen UN-DG-PALV44 shows no evidence for Westoll lines either and could belong to the same taxon as SGC-MGJRG.2018.V.26. The latter specimen shows a pointed anterodorsal process that filled the gap

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**Abbreviations:**
- an: angular
- bl: black layer of original bone
- c: crest
- ca: clavicle articulation
- cl: cleithrum
- corf?: coracoid foramen
- de: dentary
- mc: mandibular canal
- msc: mesocoracoid arch
- pfa: pectoral fin articulation
- sa: supracleithrum articulation
- scf?: scapular foramen
- t: tooth

Scale bars equal 5 mm.
between the extratemporal and the squamosal, and a dorsomedial depressed area that probably accommodated the lateral part of the lateral extrascapular. The natural cast of its internal surface shows no evidence of muscle scars for the attachment of the dilatator opercula muscle seen in *Gogonasus* (Long et al., 1997a). Its overall shape agrees with the operculars described in various megalichthyids, notably in *Askerichthys* by Borgen and Nakrem (2016) and in *Medoevia* by Lebedev (1995). Studies on large populations of *’Osteolepis’* from the Devonian of Scotland (e.g., Säve-Söderbergh, 1933, 1941; Jarvik, 1948) have shown that the proportions of the opercular are quite variable and can hardly be used for specific and even generic assignment. Therefore, we do not assign this material to an existing taxon or erect a new taxon for it because the material is not adequate for an accurate assignment.

**Family TRISTICHOPTERIDAE Cope, 1889**

?

**TRISTICHOPTERIDAE, gen. et sp. indet.** (Fig. 8B–C)

**Material**—SGC-MGJRG.2018.V.27 (Fig. 8C) and SGC-MGJRG.2018.V.28 (Fig. 8B), scales.

**Locality and Horizon**—Potrero Rincón 1, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

**Description**

Specimen SGC-MGJRG.2018.V.28 (Fig. 8B) is pear-shaped and preserved in external view. The posterior margin is slightly indented, with vermiculate ridges in the posterior part of the scale. Concentric ridges, parallel to the margin, are present in the anterior part, with a dense network of radial circuli. SGC-MGJRG.2018.V.27 (Fig. 8C) is only a scale fragment. It displays, in the central area of the scale, a sensory groove and pores.

**Remarks**

The presence of ?tristichopterid scales was noted by Janvier and Maisey (2010:435), who remarked that “scales that are clearly not derived from a rhizodontiform, and resemble scales of, e.g., *Eusthenopteron.*” The material was not figured. The visceral boss that allows assignment to Tristichopteridae is not observable in our material. Thus, a ?tristichopterid assignment has been preferred for our material.

**ARTHROPOD SYSTEMATIC PALEONTOLOGY**

Subphylum CRUSTACEA Brünnich, 1772

Class BRANCHIOPODA Latreille, 1817

Suborder SPINICAUDATA Linder, 1945

A few ‘conchostracan’ (branchiopod) crustaceans have been recovered, all from the Tunguaquita locality, Cuche Formation. The material is poorly preserved but can be ascribed confidently to Spinicaudata Linder, 1945, based upon the presence of growth lines on the carapace (the other bivalved branchiopods Laevicaudata and most Cladoceromorpha have a smooth carapace because the oldest laminae are not retained during molting; Roessler, 1995). Moreover, two distinct morphologies can be recognized: one with numerous, tight growth lines covering the whole carapace, the other with only a few growth lines, well spaced and only covering part of the carapace (Fig. 9).

**Superfamily EOSESTHERIOIDEA Zhang and Chen in Zhang et al., 1976**

**Family EUESTHERIIDAE Defretin-Lefranc, 1965**

**EUESTHERIIDAE, gen. et sp. indet.** (Fig. 9A, B)

**Material**—SGC-MGJRG.2018.I.1, incomplete carapace with growth lines (largest specimen in Fig. 9A).

**Locality and Horizon**—Tunguaquita, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

**Description**

Subovate carapace, broken (approximate length = 3.56 mm; height = 1.87 mm; mean length/height ratio = 1.90); presence of numerous (at least 13) growth lines covering the entire surface of the valve; no ornamentation nor internal anatomy is preserved.
Remarks

We assign this material to Euestheriidae based upon its anterior, small larval carapace followed by regular, tightly spaced growth lines (see Astrop and Hegna, 2015). Due to the scarcity of the material and poor preservation, this fossil is left in open nomenclature.

Superfamily VERTEXIOIDEA Kobayashi, 1954, sensu Zhang et al., 1976
Family PALEAOLIMNADIIDAE Tasch, 1956, sensu Zhang et al., 1976

PALEAOLIMNADIIDAE, gen. et sp. indet. (Fig. 9A, C–I)

Material—SGC-MGJRG.2018.I.2 (leftmost specimen in Fig. 9A; Fig. 9A, C, D), SGC-MGJRG.2018.I.3 (Fig. 9E), and SGC-MGJRG.2018.I.4 (Fig. 9F–I), carapaces with growth lines.

Locality and Horizon—Tunguaquita, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

Description

Limnadiiform carapace (length = 2.05 and 2.27 mm; height = 1.46 and 1.49 mm, respectively, for SGC-MGJRG.2018.I.2 and SGC-MGJRG.2018.I.3, which are the only two specimens that could confidently be measured because SGC-MGJRG.2018.I.4 appears highly deformed); mean length/height ratio 1.46 ± 0.06; umbo pronounced; few growth lines (each specimen seems to have 4), irregularly spaced and only covering the margin of the valve; large smooth larval carapace; straight hinge line about half the total length of the carapace; 2–4 µm pits along some growth lines of SGC-MGJRG.2018.I.4 (Fig. 9H–I) may represent some ornamentation; no internal anatomy is preserved.

Remarks

Although this material differs from SGC-MGJRG.2018.I.1 by its smaller size and length/height ratio, the most striking difference lies in its growth line pattern, which only covers the marginal part of the carapace. This points to a development characteristic of the extant family Limnadiidae (Rogers et al., 2012), also observed in many fossils clustered with limnadiids in Vertexioidea Kobayashi, 1954, sensu Zhang et al., 1976 (see Astrop and Hegna, 2015). Because limnadiids are very likely younger than 200 Ma (Bellec and Rabet, 2016), we assign this material to the family Paleolimnadiidae, which are characterized by a limnadiiform or cycladiform carapace with few growth lines, smooth ornamentation, and a large smooth larval carapace (see Astrop and Hegna, 2015). Due to the scarcity of material and poor preservation, these fossils are left in open nomenclature.

Subphylum CHELICERATA Heymons, 1901
Order EURYPTERIDA Burmeister, 1843
Suborder EURYPTERINA Burmeister, 1843
Superfamily PTERYGOTOIDEA Clarke and Ruedemann, 1912
Family PTERYGOTOIDAE Waterston, 1964
Genus PTERYGOTUS Agassiz, 1844

Type Species—Pterygotus anglicus Agassiz, 1844.

PTERYGOTUS cf. BOLIVIANUS Kjellesvig-Waering, 1964 (Fig. 10)

Material—SGC-MGJRG.2018.I.5, ramus of chelicera (Fig. 10).

Locality and Horizon—Tunguaquita, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.
Kjellesvig-Waering, 1961, which is known from the Pterygotus chelicera but actually the coxal gnathobase of Shale of Ohio, U.S.A., does not represent the free ramus of a

2. FIGURE 10. Pterygotid eurypterid specimen from Tunguaquita, Colombia, Cuche Formation, Upper Devonian. SGC-MGJRG.2018.I.5, fragmentary ramus of chelicera. Scale bar equals 1 cm.

Description

Specimen SGC-MGJRG.2018.I.5 is a ramus of a chelicera preserving 19 denticles. The total preserved length is 7 mm, and the preserved width is 2 mm. The denticles are of uniform equilaterial shape and decrease regularly in size along the ramus from 0.6 mm long, 0.3 mm tall to 0.1 mm long, 0.1 mm tall, although it is unclear whether the denticles decrease in size distally or proximally to the cheliceral articulation. The larger denticles begin to merge at their base; their margins demarcated by shallow grooves.

Remarks

Although fragmentary, the available material most likely represents portions of an enlarged pterygotid chelicera. The specimen cannot be readily assigned to any other group; the lack of a socket between the denticles and the ramus precludes a gnathostome affinity. The denticles do resemble those of some conodont elements (e.g., Purnell and von Bitter, 1992; Donoghue and Purnell, 1999); however, the specimen is an order of magnitude larger than the largest known conodont elements (Liu et al., 2017), so a conodont affinity is considered unlikely.

Pterygotid cheliceral denticulation patterns can be variable within genera, and it has been cautioned against as a defining character for higher taxonomy (Lamsdell and Legg, 2010). The denticulation of SGC-MGJRG.2018.I.5 is, however, highly unusual in consisting of uniform, equilaterial denticles. Similar denticulation has only been reported from two pterygotid species, Erettopterus serratus Kjellesvig-Waering, 1961, and Pterygotus bolivianus Kjellesvig-Waering, 1964, and are also present in the less-pronounced chelicerae of the genus Slimonia Page, 1856. A species of Slimonia has been previously described from South America, in the Silurian of Bolivia (Kjellesvig-Waering, 1973). However, the new specimen is incompatible with the known morphology of Slimonia because the chelicera of Slimonia are not enlarged to the same degree as in pterygotids (J.C.L., pers. observ. of YPM IP 33437).

Of the two pterygotid species, the single specimen assigned to Erettopterus serratus from the Lower Devonian Holland Quarry Shale of Ohio, U.S.A., does not represent the free ramus of a chelicera but actually the coxal gnathobase of Pterygotus carmani Kjellesvig-Waering, 1961, which is known from the same formation (J.C.L., pers. observ.). The other species, Pterygotus bolivianus, from the Middle Devonian of Bolivia, is known from a single cheliceral ramus that exhibits a similar dention to the material described here, the proximal denticles being broad and equilaterial, lacking a clear directional angle, merging at the base with a shallow groove between them. Given the paucity of material, SGC-MGJRG.2018.I.5 is therefore assigned to Pterygotus cf. bolivianus Kjellesvig-Waering, 1964, herein.

Diversity of the Vertebrate Fauna

Owing to new excavations and a reevaluation of the paleoichthyology of the Cuche Formation are possible. Accordingly, a new species of antiarch (Colombialepis villarroeli, gen. et sp. nov.), previously reported as Asterolepis or Asterolepis? by Janvier and Villarroel (1998, 2000) and Janvier and Maisey (2010), and a new arthrodiran placoderm (Colombiaspis rinconensis, gen. et sp. nov.), previously referred to Arthrodira indet. or ?Groenlandaspis (Janvier and Villarroel, 1998, 2000; Janvier and Maisey, 2010), have been erected, both taxa being endemic to Colombia. In addition, the study of the new material has confirmed the presence of a diplacanthid acanthodian (cf. Florestacanthus morenoi), the antiarch placoderm Bothriolepis sp., and a stegotrich elid actinopterygian, which were already reported at Potrero Rincón by Janvier and Villarroel (1998, 2000). Finally, despite the poor preservation of the osteichthyan remains, we confirmed the presence of a putative megalichthysid and a putative tristichopterid. These new data complete the faunal list previously reported by Janvier and Maisey (2010) and suggest that the Colombian fish assemblage is more endemic (the two new placoderm taxa, together with the presence of Florestacanthus) than previously thought. Therefore, to date, the vertebrate fauna from the Cuche Formation includes acanthodians (Nostolepis sp. cf. N. gaujensis, Florestacanthus morenoi), chondrichthians (Antarctilamnidae or Omalodontidae, gen. et sp. indet.), placoderms (Bothriolepis, sp. indet., Colombialepis villarroeli, gen. et sp. nov., and Colombiaspis rinconensis, gen. et sp. nov.), actinopterygians (Seytrachaelidae, gen. et sp. indet.), and sarcopterygians (Holotoptichidae, sp. indet., ?Megalichthiidae, gen. et sp. indet., ?Tristichopteridae, gen. et sp. indet., and Rhizodontiformes, gen. et sp. indet.) (Janvier and Villarroel, 1998, 2000; Burrow et al., 2003; Janvier and Maisey, 2010; Mondéjar-Fernández and Janvier, 2014).

Paleobiogeographic Considerations

Janvier and Villarroel (2000) highlighted the similarity of the fish assemblage from the Cuche Formation with the Euramerican vertebrate fauna of the same age (presence of Asterolepis, Strepsodus, Holoptichius, and Bothriolepis with a non-trilobate preoral ratchet). According to these authors, this faunal similarity could indicate a close geographic link between Euramerica and northwestern Gondwana. Indeed, it is considered that antiarchs of Strepsodus from this genus and the present study contradicts the presence of Asterolepis in south Colombia. Young et al. (2000) described a Late Devonian fish fauna from western Venezuela and concluded that it was dominantly of Gondwanan affinity. Further investigations on the phylogenetic relationships of the two new placoderm genera from the Cuche Formation are needed, but if they display Gondwanan affinities, together with...
the presence of ?Antarc tilamnidae in Colombia (even if it seems that antarc tilamnids were a rather widespread group because some antarc tilamn spines or teeth are now known from the Devonian of North America and Spain; Ginter et al., 2008; Potvin-Leduc et al., 2015), then it could argue for a Gondwanan affinity of the Cuche Formation material. These results would be consistent with Venezuelan faunal endemism, considering that the two localities are circumscribed to a thin siliciclastic shelf located in the northwestern part of Gondwana (Scotese, 2002).

Holoptychius is usually regarded as a Middle and Upper Devonian Euramerican marker. Its presence in the late Famennian of Australia (Young, 1993), as well as its presence in Colombia, could suggest that it was a widespread genus during Middle–Late Devonian times or, as suggested by Janvier and Maisey (2010), an Euramerican migrant into Gondwana at the Frasnian–Famennian boundary. The antac thodian assemblage from the Cuche Formation is not useful for biogeographical issues because of their nektic lifestyle, which enhanced its wide dispersal pattern (Burrow et al., 2003).

In sum, the Euramerican vertebrate faunal affinity previously attributed to the Colombian Cuche Formation vertebrate fauna (Janvier and Villarroel, 2000; Janvier and Maisey, 2010) is less supported, given that our findings are in favor of a more endemic Colombian community. The Frasnian–Famennian faunal interchange (Young, 1990, 1993, 2003; Janvier and Clément, 2005; Janvier and Maisey, 2010), with the immigration of phyllolepids, groenlandaspidids, rhizodontids, and possibly meg alichthyids from Gondwana into Euramerica during the Famennian and with the dispersion of Euramerican taxa (Holoptychius and Asterolepis) toward Gondwana before or during the Frasnian, may still be a likely hypothesis but is less supported in the southward direction, i.e., absence of Asterolepis in the Frasnian of Colombia (southward dispersion less supported or even absent if Holoptychius is considered as a widespread genus during the Middle–Late Devonian). Therefore, more evidence supporting any of these paleobiogeographic proposals is necessary to provide more definitive information.

Paleobiogeographic Considerations on Eurypterids, and Vertebrate–Eurypterid Competition

The material described here represents the first eurypterid described from Colombia and is only the fourth from South America (Tettke, 2007). Eurypterids are traditionally considered rare in Gondwanan territories, although recent discoveries indicate that the Gondwanan eurypterid record is undersampled rather than nonexistent (Lamsdell et al., 2013). Furthermore, Pterygotus cf. bolivianus represents the youngest known pterygotid eurypterid. Pterygotids were previously considered to have gone extinct during the Middle Devonian (Lamsdell and Braddy, 2010; Lamsdell and Selden, 2017). There has been much discussion on the causes of the decline in eurypterid diversity across the Devonian, focusing on two competing hypotheses: ecological competition with vertebrates (Romero, 1999; Lamsdell and Braddy, 2010; Klug et al., 2011; Friedman and Sallan, 2012) or abiotic environmental pressures (Briggs et al., 1988; Tettke and Briggs, 2009; Lamsdell and Selden, 2017). The new specimen alone does not provide support for either hypothesis, but it does reveal that pterygotids (the clade considered to most directly compete with large predatory fish; Lamsdell and Braddy, 2010) did not go extinct during the major vertebrate radiation in the Early and Middle Devonian.

CONCLUSION

The new excavations and the reevaluation of the material previously collected have provided a new interpretation of the fish content of the Late Devonian (?Frasian) Cuche Formation from northeastern Colombia. The new material includes a new taxon of antarctilamn placoderm (Colombialepis villarroeli, gen. et sp. nov., previously reported as Asterolepis) and a new arthrodiran placoderm (Colombiaspis rinconensis, gen. et sp. nov.). This study also provides new evidence for a stegotrichelid actinopterygian, a diplacanthid acanthodian (cf. Florestacanthus morenoi), a second antarctilamn placoderm (Bothriolepis sp.), a putative megelichthyid, and a putative tristichopterygian. To date, the vertebrate fauna from the Cuche Formation includes acanthodians (Nostolepis sp. cf. N. gaujensis, Florestacanthus morenoi), chondrichthians (Antarctilamnidae or Omalodontidae, gen. et sp. indet.), placoderm (Bothriolepis, sp. indet., Colombialepis villarroeli, gen. et sp. nov., and Colombiaspis rinconensis, gen. et sp. nov.), actinopterygians (Stegotrachelidae, gen. et sp. indet.), and sarcopterygians (Holoptichiiidae, sp. indet., ?Megelichthyidae, gen. et sp. indet., ?Tristichopteridae, gen. et sp. indet., and Rhizodontiformes, gen. et sp. indet.).

The Gondwana–Euramerica Devonian vertebrate interchange hypothesis, occurring at the Frasnian–Famennian boundary, purports that an early southward dispersion of reputedly Euramerican endemics (Holoptychius, Strepsodus, and Asterolepis) preceded the Famennian northward dispersion of Gondwanan endemics (Groenlandaspis, phyllolepids, rhizodontids, and megalichthyids). The updated vertebrate assemblage, presented in this study, highlights the absence of typical Euramerican markers Asterolepis and Strepsodus in Colombia. This suggests that the Colombian fish assemblage at this time was more endemic (the two new placoderm taxa, together with the presence of Florestacanthus) than previously thought, weakening the Frasnian–Famennian faunal interchange hypothesis, in the southward direction.

Associated with the vertebrate fauna, three arthropod taxa, including two families of spinicaudatan branchiopods and the eurypterid Pterygotus cf. bolivianus, have been reported. The latter represents the first eurypterid described from Colombia and the youngest known pterygotid eurypterid, highlighting that pterygotids, which represented competitors for large predatory fishes, did not go extinct during the major vertebrate radiation in the Early and Middle Devonian.

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