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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 Interchange 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](http://www.tandfonline.com/UJVP)

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### 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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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), chondrichthyans (e.g., *Pucapampella* Janvier and Suarez-Riglos, 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 osteichthyans 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-Riglos, 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 (*Holoptychius*, *Strepsodus*, and *Asterolepis*) that had preceded the Famennian northward dispersion of Gondwanan endemics (*Groenlandaspis*, phyllolepid, 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*), chondrichthyans (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 (Holoptychiidae, sp. indet., *?Megalichthyidae*, 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). 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 Silgara 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

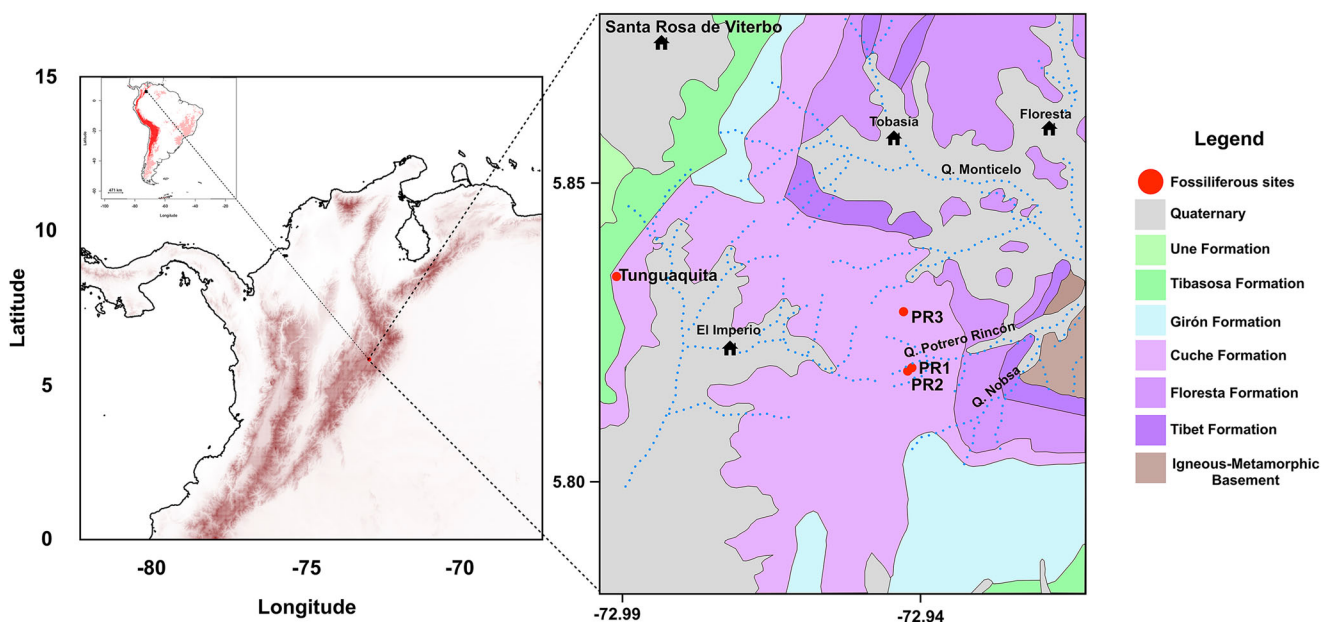


FIGURE 1. Locality map and geological context of Potrero Rincón (PR).

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 claystones 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 claystones, 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-MGJRG.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.rx-solutions.fr](http://www.rx-solutions.fr)) with a copper filter. Images were generated at a voltage of 426 kV and a current of 139  $\mu$ A, with a set

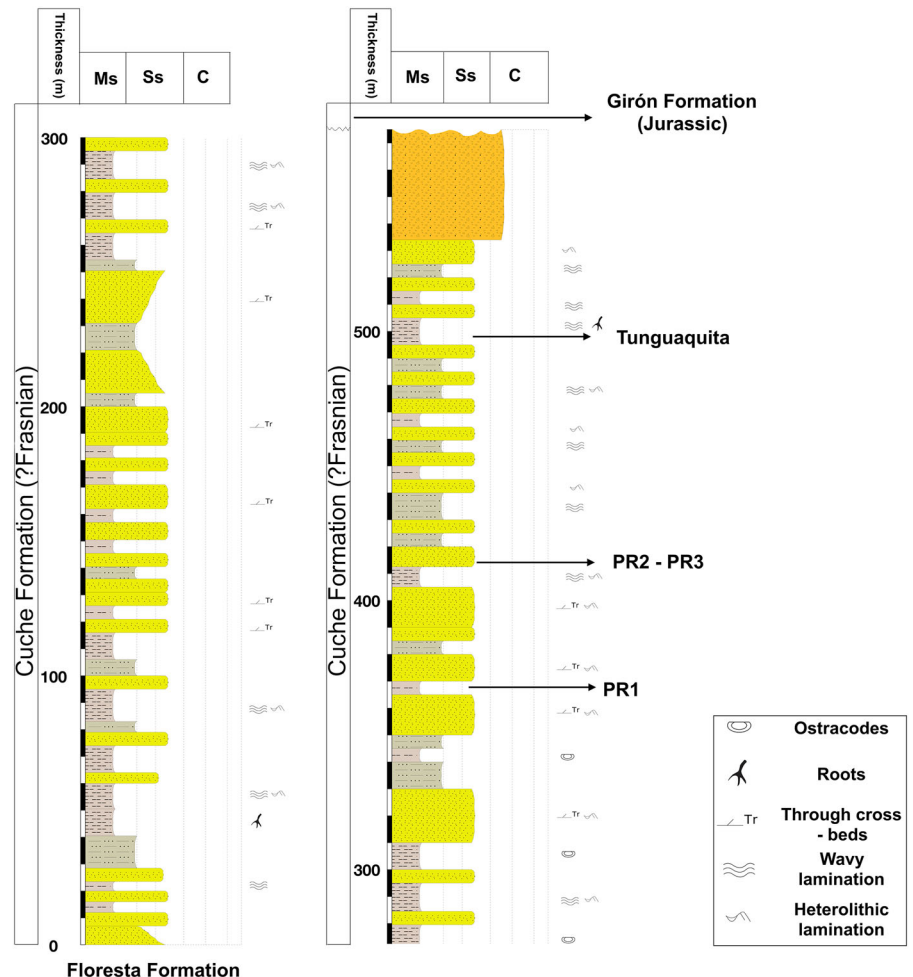


FIGURE 2. Stratigraphic column of the Cuche Formation with location of the Tunguaquita and Potrero Rincón (PR) localities 1, 2, and 3. **Abbreviations:** C, conglomerate; Ms, mudstone; Ss, sandstone.



frame rate of 12.5 and average 3 frames per image. This generated 2,880 images and a voxel size of 76.14  $\mu\text{m}$ . This specimen has been virtually reconstructed with MIMICS 20.0 (Materialise's Interactive Medical Image Control System) software (Materialise Inc.; proprietary software at the Muséum national d'Histoire naturelle [MNHN], Paris) at the Atelier 3D, Centre de Recherche en Paléontologie (CR2P), MNHN, Paris.

Specimens collected in 2017 are deposited in the Museo Geológico José Royo y Gómez, Servicio Geológico Colombiano. However, some additional studied specimens were collected before the field trip of 2017 and are deposited in the paleontological collection of the Departamento de Geociencias, Universidad Nacional de Colombia, Bogotá, Colombia.

#### 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.

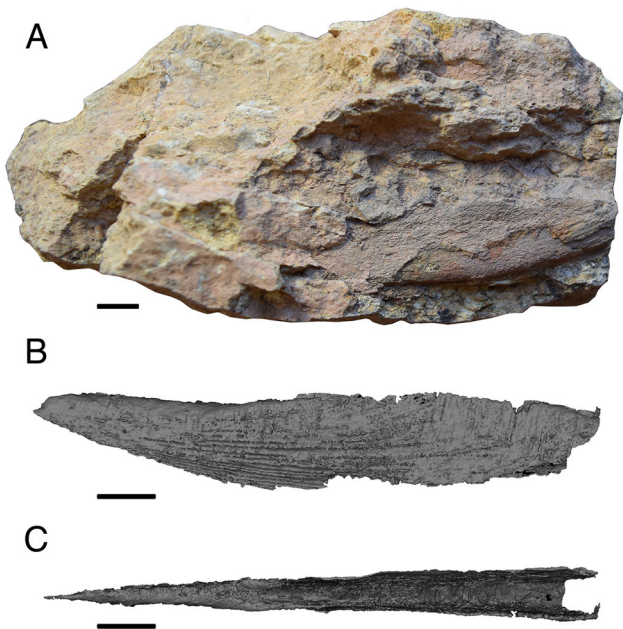


FIGURE 3. cf. *Florestacanthus morenoi*, SGC-MGJRG.2018.V.17, block displaying the paired fin spine from Potrero Rincón 1, Colombia, Cuche Formation, Upper Devonian. A, photograph of paired fin spine. B, 3D model of paired fin spine in dorsal view. C, 3D model of paired fin spine in internal view. Scale bars equal 1 cm.

#### 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 proximally 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

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 Villarroel (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. 4E–H).

**Localities and Horizon**—Potrero Rincón 2 and 3 and Tunguaquita, 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 (Upeniec 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

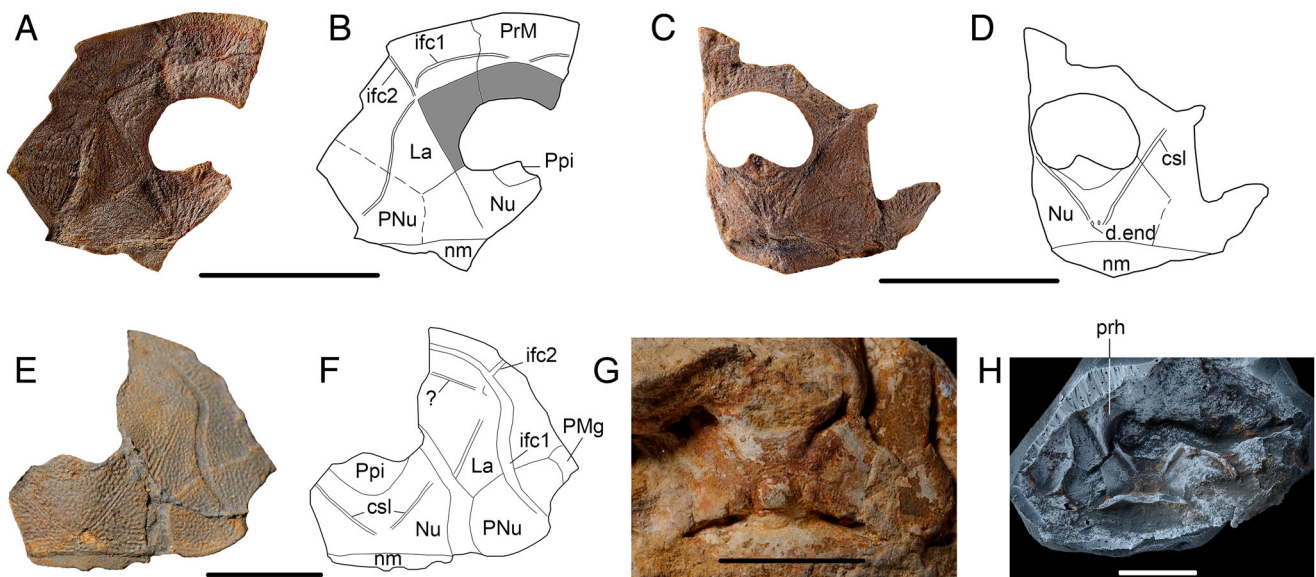


FIGURE 4. *Bothriolepis* sp., Potrero Rincón 2, Colombia, Cuche Formation, Upper Devonian. **A**, SGC-MGJRG.2018.V.21a, juvenile partial skull roof, external view, counterpart; **B**, interpretive drawing of same. **C**, SGC-MGJRG.2018.V.21b, juvenile partial skull roof, external view; **D**, interpretive 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, elastomer cast, 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, obtect nuchal area; Nu, nuchal plate; PMg, postmarginal plate; PNu, paranuchal plate; Ppi, postpineal 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 obteched 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. Janvier and Villarroel (1998).  
*Asterolepis*? sp. indet., in Janvier and Villarroel (2000).  
*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. Janvier and Villarroel (1998).  
*Asterolepis*?, sp. indet., in Janvier and Villarroel (2000).  
*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 postpineal 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), Cvl1.

**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 Postpineal Plates**—UN-DG-PALV32 (Fig. 5A) displays the posterior median part of a skull roof with part of the nuchal and postpineal plates. The two plates are distinguishable by the different orientations of the ornamentation. Only the posterior portion of the postpineal 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*; Karatajute-Talimaa, 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 endolymphatic 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



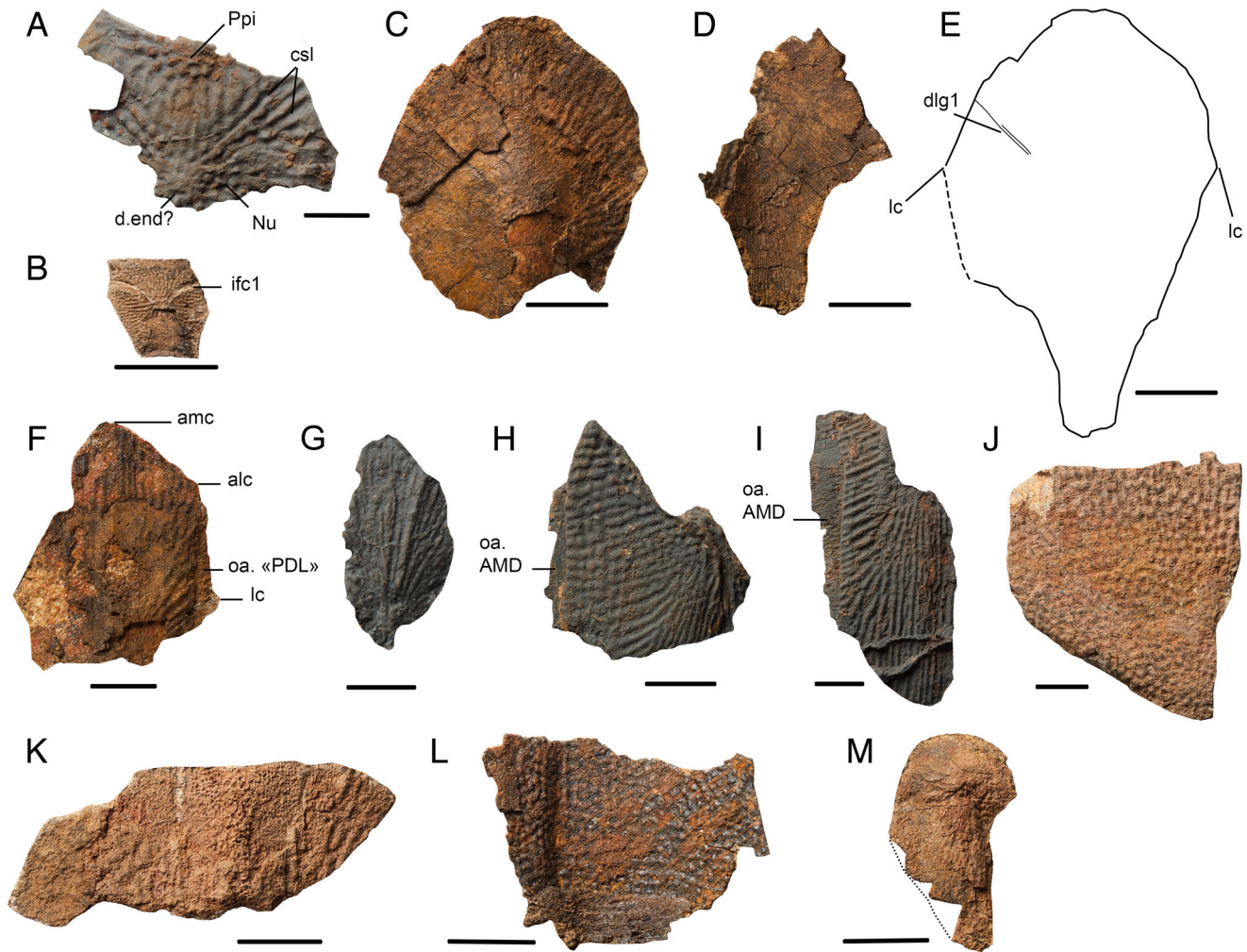


FIGURE 5. *Colombialepis villarroeli*, gen. et sp. nov., Potrero Rincón 1, Colombia, Cuiche Formation, Upper Devonian. **A**, UN-DG-PALV32, posterior median part of a skull roof, elastomer cast, external view. **B**, SGC-MGJRG.2018.V.22, premedian plate, external view. **C**, SGC-MGJRG.2018.V.19, anterior portion of an anterior median dorsal plate, external and internal views. **D**, SGC-MGJRG.2018.V.19, posterior portion of an anterior median dorsal plate, internal view. **E**, reconstruction of an anterior median dorsal plate based on SGC-MGJRG.2018.V.19. **F**, SGC-MGJRG.2018.V.29, posterior median dorsal plate, external and internal views. **G**, UN-DG-PALV33, anterior dorsolateral plate, elastomer cast, external view. **H**, UN-DG-PALV52, anterior dorsolateral plate, elastomer cast, external view. **I**, UN-DG-PALV53, anterior dorsolateral plate, elastomer cast, external view. **J**, SGC-MGJRG.2018.V.30, posterior ventrolateral plate, external view. **K**, SGC-MGJRG.2018.V.32, unidentified lateral plate, external view. **L**, SGC-MGJRG.2018.V.31, unidentified lateral plate, external view. **M**, SGC-MGJRG.2018.V.33, ventral central plate 1, external view. Dashed line indicates unpreserved margin. Dotted line indicates margin preserved on the counterpart. **Abbreviations:** alc, anterolateral corner; amc, anterior median corner; csl, central sensory line groove; dlgl1, anterior oblique dorsal sensory line groove; ifc1, principal branch of the infraorbital canal; lc, lateral corner; Nu, nuchal plate; oa. AMD, anterior median dorsal plate overlap area; oa. 'PDL', posterior dorsolateral plate or mixilateral plate overlap area; Ppi, postpineal plate. Scale bars equal 1 cm.

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-PAL-V34 was attributed by Janvier and Villarroel (2000:fig. 10c) to both an anterior median dorsal plate (in the text) and a mixilateral plate (in the figure caption). In our opinion, it is too fragmentary to be anatomically assigned. Specimen UN-DG-PALV053 was attributed by Janvier and Maisey (2010:fig. 10) 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 antiarch 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 *Venezuelepis* from the Upper Devonian of Venezuela (Young and Moody, 2002). The remarkably long posterior division of this AMD is most closely approached by *Pterichthyodes* (e.g., Denison, 1978), but it is much narrower in *Colombialepis*. The ontogenetic processes are well documented for the genus *Asterolepis* (Upeniec 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 PHLYCTAENIOIDEI Miles, 1973b  
Infraorder PHLYCTAENII Miles, 1973b  
Family GROENLANDASPIDIDAE Obruchev, 1964  
Genus *COLOMBIASPIS*, gen. nov.

Arthrodira in Janvier and Villarroel (1998).  
Arthrodira, gen. et sp. indet., in Janvier and Villarroel (2000).  
? *Groenlandaspis*, sp. indet., in Janvier and Maisey (2010).

**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)

Arthrodira in Janvier and Villarroel (1998).  
Arthrodira, gen. et sp. indet., in Janvier and Villarroel (2000).  
? *Groenlandaspis*, sp. indet., in Janvier and Maisey (2010).

**Holotype**—UN-DG-PALV38, a posterior dorsolateral plate (Potrero Rincón 1; Fig. 6G–H).

**Localities and Horizon**—Potrero Rincón 1 and 3, Boyaca Department, Colombia, Cuche Formation, Upper Devonian.

**Other Material**—Potrero Rincón 3: UN-DG-PALV35, nuchal plate (Fig. 6A, B). Potrero Rincón 1: SGC-MGJRG.2018.V.34, ? postpineal plate (Fig. 6C); SGC-MGJRG.2018.V.35 (Fig. 6F) and UN-DG-PALV085 (Fig. 6D–E), median dorsal plates; UN-DG-PALV37, posterior lateral plate (Fig. 6I); SGC-MGJRG.2018.V.23 (Fig. 6K) and UN-DG-PALV36 (Fig. 6J), spinal plates.

**Diagnosis**—A groenlandaspidid arthrodira, in which the nuchal plate has an elongated anterior process and elongated infranuchal pits separated by a sharp internal ridge. The skull roof shows putatively two pineal plates. The median dorsal plate displays fine striations radiating from the apex to the ventral margin and a furrow parallel to the anterior margin. The posterior dorsolateral plate shows a connection between the overlapped areas for the anterolateral and anterior dorsolateral plates. The ventral embayment is strongly pronounced. The spinal plate displays anterior, posteriorly oriented ridges.

**Etymology**—From the name of the Potrero Rincón locality.

### Description of the Skull Roof

**Nuchal Plate**—The nuchal plate was figured and described by Janvier and Villarroel (2000) and attributed to an Arthrodira, gen. et sp. indet. It is preserved in both external and internal views (Fig. 6A, B). The anterior portion of the plate is relatively narrow. The external surface is strongly arched posteriorly. The ornamentation consists of coarse tubercles. The internal surface shows long, parallel overlap areas for the paranuchal plates. Posteriorly, the ventral surface bears paired, elongated infranuchal pits separated by a sharp ridge, whereas the anterior part is slightly convex.

**Postpineal Plate**—A putative postpineal plate (Fig. 6C), triangular in shape and with a thick anterior margin, is included in our material. Its ornamentation is made of scattered tubercles.

### Description of the Thoracic Armor

**Median Dorsal Plate**—A median dorsal plate (Fig. 6D–E) was figured by Janvier and Maisey (2010:fig. 10c) but not described in detail. Only a part of the anterior portion of the plate is preserved in three dimensions. Thus, it is impossible to say whether the plate was high-crested or low and whether the tip of the plate was pointed or blunt. The anterior edge of the plate is sharp. Its ventral margin is not preserved either, and the embayments for the dorsolateral plates are not observable. The ornamentation is made of fine striations radiating from the apex to the ventral margin. It is, however, noticeable that this ornamentation is so light that the plates look smooth. A strongly marked furrow is present anteriorly, parallel to the anterior edge.

A triangular element (Fig. 6F), possibly a median dorsal plate, was also found in Potrero Rincón 1. The ventral part is not preserved, nor is the apex. It is thus impossible to know the exact shape of the plate and to know whether its dorsal tip is pointed or blunt. The asymptotic lines of the anterior and posterior edges form an angle of about 70°. There are thin striations perpendicular to the anterior margin. As for the first median dorsal plate, a furrow is present anteriorly and parallel to the anterior margin. However, it is less marked here.

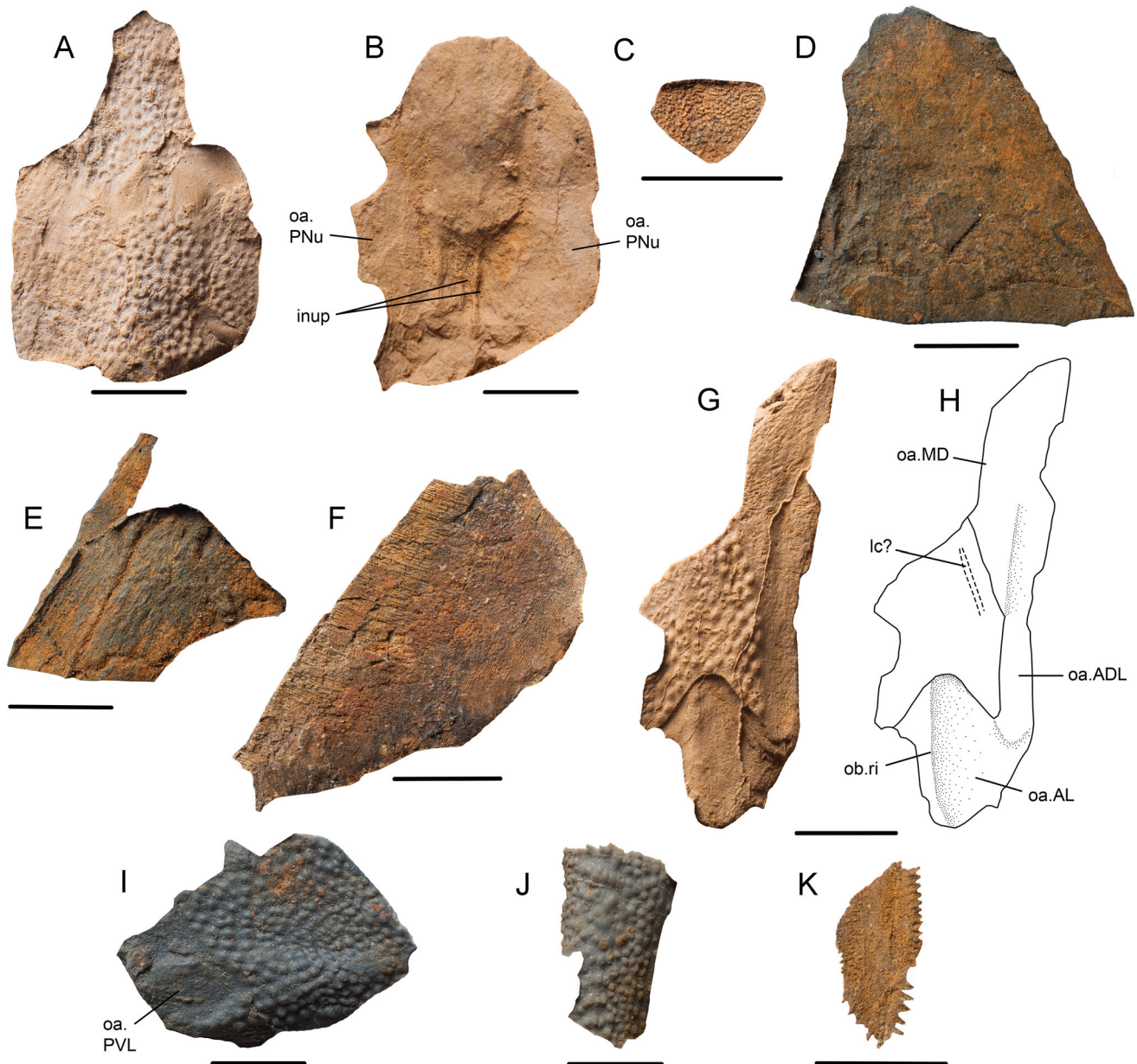


FIGURE 6. *Colombiaspis rinconensis*, gen. et sp. nov., Potrero Rincón 1 and 3, Colombia, Cuche Formation, Upper Devonian. **A**, external and **B**, internal views of UN-DG-PALV35, nuchal plate, elastomer cast. **C**, SGC-MGJRG.2018.V.34, postpineal plate, external view. **D**, right and **E**, left sides of UN-DG-PALV085, median dorsal plate, elastomer cast, external view. **F**, SGC-MGJRG.2018.V.35, median dorsal plate, left side, external view. **G**, photograph and **H**, interpretive drawing of UN-DG-PALV38, posterior dorsolateral plate, elastomer cast, external view. **I**, UN-DG-PALV37, posterior lateral plate, elastomer cast, external view. **J**, UN-DG-PALV36, spinal plate, elastomer cast, external view. **K**, SGC-MGJRG.2018.V.23, spinal plate, external view. **Abbreviations:** **inup**, infranuchal pit; **lc?**, main lateral sensory groove?; **oa.AL**, anterolateral plate overlap area; **oa.PNu**, paranuchal plate overlap area; **oa.PVL**, posterior ventrolateral plate overlap area; **ob.ri**, oblique ridge. Scale bars equal 1 cm.

**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 Villarreal (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 riniensis* (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 spinelets, which are very likely situated on the medial margin, as in other groenlandaspids, e.g., *Groenlandaspis potyi* (Olive et al., 2015a). The spinelets on the lateral margin are smaller.

## Remarks

*Colombiaspis*, gen. nov., differs from all other groenlandaspids 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 groenlandaspids, 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 ACTINOPTERYGII Klein, 1885  
Family STEGOTRACHELIDAE Gardiner, 1963  
STEGOTRACHELIDAE, gen. et sp. indet.  
(Fig. 7)

‘Stegotrachelid actinopterygian’ in Janvier and Villarroel (1998).  
Stegotrachelidae, gen. et sp. indet., in Janvier and Villarroel (2000).

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 recurves 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 anterior 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 dorso-ventrally, 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 mesoracoid process, but this might be a preservation artifact. As in *Mimipiscis* and *Moythomasia* (Gardiner, 1984), the mesoracoid 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 glenoid 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.



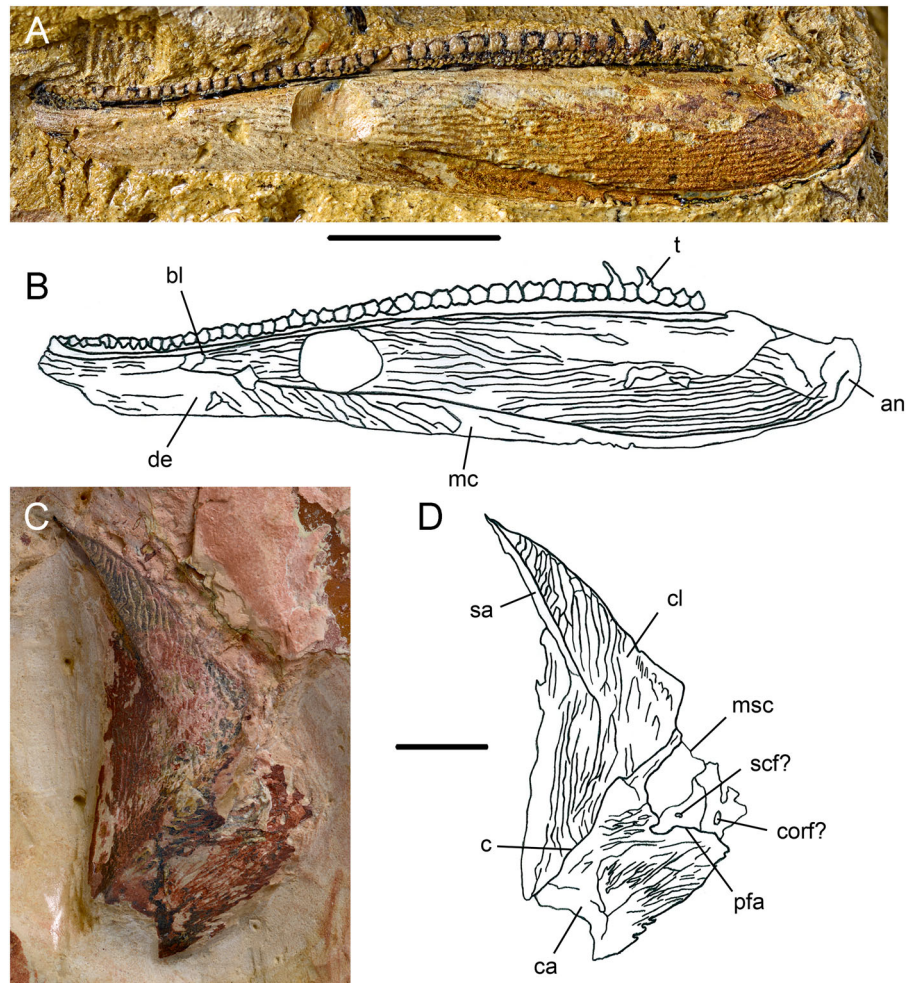


FIGURE 7. Stegotrachelidae, gen. et sp. indet., Potrero Rincón 1, Colombia, Cuche Formation, Upper Devonian. **A**, photograph and **B**, interpretative drawing of SGC-MGJRG.2018.V.24, left lower jaw, internal view with impressions of the external ornamentation. **C**, lateral view and **D**, interpretative drawing of SGC-MGJRG.2018.V.25, left cleithrum and associated endoskeletal remains. **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.

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 supra-angular (Patterson, 1982). However, because the original bones are mostly missing, and the lower jaw is preserved as an impression, the absence of supra-angular 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.

Subclass SARCOPTERYGII Romer, 1955  
Order OSTEOLEPIFORMES Berg, 1937  
Family OSTEOLEPIDIDAE Cope, 1889  
?MEGALICHTHYIDAE, gen. et sp. indet.  
(Fig. 8A)

**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



FIGURE 8. Sarcopterygian remains, Potrero Rincón 1, Colombia, Cuche Formation, Upper Devonian. **A**, SGC-MGJRG.2018.V.26, ?Megalichthyidae left opercular, internal view. **B**, SGC-MGJRG.2018.V.28, ?Tristichopteridae scale, external view. **C**, SGC-MGJRG.2018.V.27, ?Tristichopteridae scale, external view. Scale bars equal 1 cm.

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 EOESTHERIOIDEA 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).

**Localities and Horizons**—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, tightly spaced and covering the entire surface of the valve; no ornamentation nor internal anatomy is preserved.



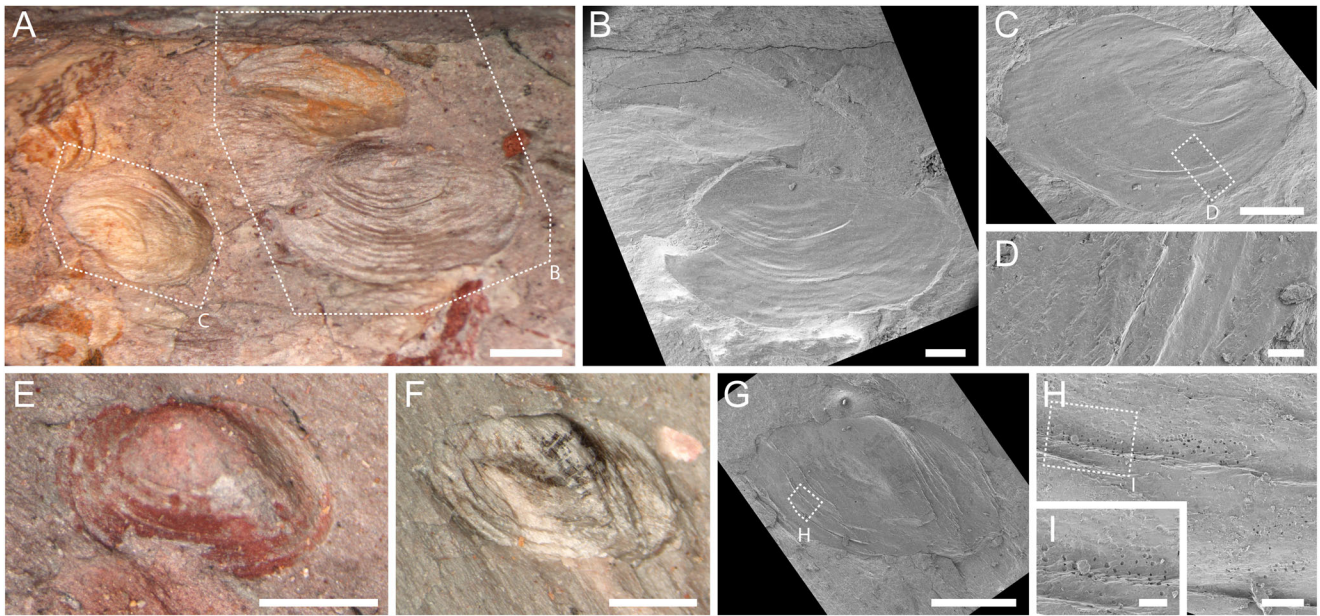


FIGURE 9. Spinicaudatan branchiopod crustaceans from Tunguaquita, Colombia, Cuche Formation, Upper Devonian. **A**, three valves in lateral view; left, SGC-MGJRG.2018.I.2; bottom right, SGC-MGJRG.2018.I.1. **B**, SEM image of SGC-MGJRG.2018.I.1, left valve in lateral view, head oriented to the left. **C**, SEM image of SGC-MGJRG.2018.I.2, right valve in lateral view, head oriented to the right; **D**, close up SEM view on some growth lines of same. **E**, SGC-MGJRG.2018.I.3, left valve in lateral view, head oriented to the left. **F**, photograph and **G**, SEM image of SGC-MGJRG.2018.I.4, left valve in lateral view, head oriented to the left. **H–I**, close up SEM views of some growth lines in SGC-MGJRG.2018.I.4. SEM with “secondary electrons” mode, low vacuum, 3 kV (**H–I**), 4 kV (**C**, **D**, **G**), and 6 kV (**B**). Scale bars equal 1 mm (**A**, **E–G**), 500  $\mu$ m (**B**, **C**), 50  $\mu$ m (**D**, **H**), and 20  $\mu$ m (**I**).

## 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  $1.46 \pm 0.06$ ; 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  $\mu$ m 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 PTERYGOTIDAE 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.





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 equilateral 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, equilateral 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 denticulation to the material described here, the proximal denticles being broad and equilateral, 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.

## DISCUSSION

### Diversity of the Vertebrate Fauna

Owing to new excavations and a reevaluation of the material previously collected, new interpretations 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 stegotrachelid 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 megalichthyid 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*), chondrichthyans (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 (Stegotrachelidae, gen. et sp. indet.), and sarcopterygians (Holoptychiidae, sp. indet., *?Megalichthyidae*, 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*, *Holoptychius*, and *Bothriolepis* with a non-trilobate preorbital recess). According to these authors, this faunal similarity could indicate a close geographic link between Euramerica and northwestern Gondwana. Indeed, it is considered that antiarchs (*Asterolepis* and *Bothriolepis*) were probably poor swimmers (Janvier and Clément, 2005; Dupret et al., 2011), and because this faunistic interchange involves marginal marine fishes such as *Strepsodus* (rhizodontid sarcopterygians are generally bound to marginal environments; Janvier and Clément, 2005), it implies a close contact between northern South America and Euramerica by Late Devonian times (Janvier and Villarroel, 2000). Interestingly, this is also supported by marine invertebrate faunas (Boucot and Racheboeuf, 1993), which displayed a strong cosmopolitanism during the Late Devonian (contrary to a high provincialism, corresponding to the Malvinokaffric Realm, during the Early Devonian).

However, it seems that the affinities of the Cuche Formation with the Euramerican vertebrate fauna are not as strong as thought. Indeed, Jeffery (2002) excluded the Colombian material 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 ?Antarctilamnidae in Colombia (even if it seems that antarctilamnids were a rather widespread group because some antarctilamnid 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 acanthodian assemblage from the Cuche Formation is not useful for biogeographic issues because of their nektonic 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 phyllolepid, groenlandaspids, rhizodontids, and possibly megalichthyids 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 (Tetlie, 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 (Romer, 1933; Lamsdell and Braddy, 2010; Klug et al., 2011; Friedman and Sallan, 2012) or abiotic environmental pressures (Briggs et al., 1988; Tetlie 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 (?Frasnian) Cuche Formation from northeastern Colombia. The new material includes a new taxon of antiarch 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 stegotrachelid actinopterygian, a diplacanthid acanthodian (cf. *Florestacanthus morenoi*), a second antiarch placoderm (*Bothriolepis* sp.), a putative megalichthyid, and a putative tristichopterid. To date, the vertebrate fauna from the Cuche Formation includes acanthodians (*Nostolepis* sp. cf. *N. gaujensis*, *Florestacanthus morenoi*), chondrichthyans (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 (Stegotrachelidae, gen. et sp. indet.), and sarcopterygians (Holoptychiidae, sp. indet., ?Megalichthyidae, 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*, phyllolepid, 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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## LITERATURE CITED

- Agassiz, J. L. R. 1844. Monographie des poisons fossiles du Vieux Grès Rouge, ou Système Dévonien (Old Red Sandstone) des Iles Britanniques et de Russie. Jent and Gassman, Neuchâtel, 171 pp.
- Anderson, M. E., J. E. Almond, F. J. Evans, and J. A. Long. 1999. Devonian (Emsian-Eifelian) fish from the Lower Bokkeveld Group (Ceres Subgroup), South Africa. *Journal of African Earth Sciences* 29:179–193.
- Astrop, T. I., and T. A. Hegna. 2015. Phylogenetic relationships between living and fossil spinicaudatan taxa (Branchiopoda Spinicaudata): reconsidering the evidence. *Journal of Crustacean Biology* 35:339–354.
- Bellec, L., and N. Rabet. 2016. Dating of the Limnadiidae family suggests an American origin of Eulimnadia. *Hydrobiologia* 773:149–161.
- Berg, L. S. 1937. A classification of fish-like vertebrates. *Bulletin de l'Académie des Sciences de l'URSS, Classe des Sciences mathématiques et naturelles (série biologique)* 4:1277–1280.
- Berry, C. M., E. Morel, J. Mojica, and C. Villarroel. 2000. Devonian plants from Colombia, with discussion of their geological and palaeogeographical context. *Geological Magazine* 137:257–268.
- Borgen, U. J., and H. A. Nakrem. 2016. Morphology, phylogeny and taxonomy of osteolepiform fishes. *Fossils and Strata* 61:1–514.
- Botella, H., C. Martínez-Pérez, and R. Soler-Gijón. 2012. *Machaeracanthus goujeti* n. sp. (Acanthodii) from the Lower Devonian of Spain and northwest France, with special reference to spine histology. *Geodiversitas*, 34:761–783.
- Boucot, A. J. 1975. Evolution and Extinction Rate Controls. *Developments in Palaeontology and Stratigraphy* 1. Elsevier, Amsterdam, The Netherlands, 427 pp.
- Boucot, A. J., and P. R. Racheboeuf. 1993. Biogeographic summary of the Malvinokaffric Realm Silurian and Devonian fossils; pp. 71–75 in R. Suárez-Soruco (ed.), *Fósiles y Facies de Bolivia. 2, Invertebrados y Paleobotánica. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos*, Santa Cruz, Bolivia.
- Boucot, A. J., A. J. Rowell, P. R. Racheboeuf, E. Pereira, J. G. De Melo, and L. P. De Siqueira. 2001. Position of the Malvinokaffric Realm's northern boundary (Early Devonian) based on newly discovered brachiopods from the Parecis Basin (Brazil). *Journal of the Czech Geological Society* 46:109–120.
- Briggs, D. E. G., R. A. Fortey, and E. N. K. Clarkson. 1988. Extinction and the fossil record of arthropods; pp. 171–209 in G. P. Larwood (ed.), *Extinction and Survival in the Fossil Record*. Clarendon Press, Oxford, U.K.
- Brünnich, M. T. 1772. *Zoologiae fundamenta praelectionibus academicis accommodata: Grunde i Dyrelaeren*. Friderici Christiani Pelt, Copenhagen.
- Burmeister, H. 1843. Die Organisation der Trilobiten, aus ihren leben den Verwandtenentwickelt; nebst systematische Uebersicht aller zeither beschriebenen Arten. G. Reimer, Berlin, 148 pp.
- Burrow, C. J., P. Janvier, and C. Villarroel. 2003. Late Devonian acanthodians from Colombia. *Journal of South American Earth Sciences* 16:155–161.
- Burrow, C. J., J. den Blaauwen, M. Newman, and R. Davidson. 2016. The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. *Palaeontologia Electronica* 19(1):10A. <https://palaeo-electronica.org/content/2016/1398-scottish-diplacanthid-fishes>
- Clarke, J. M., and R. Ruedemann. 1912. The Eurypterida of New York. *New York State Museum Memoirs* 14:1–439.
- Cope, E. D. 1886. An interesting connecting genus of Chordata. *The American Naturalist* 20:1026–1031.
- Cope, E. D. 1889. Synopsis of the families of Vertebrata. *The American Naturalist* 23:849–877.
- Daeschler, E. B., A. C. Frumes, and C. F. Mullison. 2003. Groenlandaspidid placoderm fishes from the Late Devonian of North America. *Records of the Australian Museum* 55:45–60.
- Dalziel, I. W., L. H. Dalla Salda, and L. M. Gahagan. 1994. Paleozoic Laurentia-Gondwana interaction and the origin of the Appalachian-Andean mountain system. *Geological Society of America Bulletin* 106:243–252.
- Defretin-Lefranc, S. 1965. Étude et révision de phyllopoïdes conchostracés en provenance d'U.R.S.S. *Annales de la Société Géologique du Nord* 85:15–48.
- Denison, R. H. 1978. Placodermi; pp. 1–128 in H.-P. Schultze (ed.), *Handbook of Paleichthyology*, Volume 2. Gustav Fischer, Stuttgart, Germany.
- Denison, R. H. 1979. Acanthodii; pp. 1–62 in H.-P. Schultze (ed.), *Handbook of Paleichthyology*, Volume 5. Gustav Fischer, Stuttgart, Germany.
- Donoghue, P. C. J., and M. A. Purnell. 1999. Growth, function, and the conodont fossil record. *Geology* 27:251–254.
- Dupret, V., G. Clément, and P. Janvier. 2005. The Frasnian–Famennian interchange between Gondwanan and Euramerican vertebrate faunas. Which way? Middle East or South America?; pp. 8–9 in V. Hairapetyan and M. Ginter (eds.), *Devonian Vertebrates of the Continental Margins*. Yerevan, Armenia, May 22–27, 2005. *Ichthyolith Special Publication*.
- Dupret, V., P. Carls, C. Martínez-Pérez and H. Botella. 2011. First Perigondwanan record of actinolepids (Vertebrata: Placodermi: Arthrodira) from the Lochkovian (Early Devonian) of Spain and its palaeobiogeographic significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310:273–282.
- Eichwald, E. I. von. 1840. Die Tier- und Pflanzenreste des alten Sandsteins und Berkalks im Novogrodschen Gouvernement. *Bulletin de l'Académie Impériale des Sciences de Saint-Petersbourg* 7:78–91.
- Friedman, M. and L. C. Sallan. 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology* 55:707–742.
- Gardiner, B. G. 1963. Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bulletin of the British Museum (Natural History)*, *Geology* 8:255–325.
- Gardiner, B. G. 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum (Natural History)*, *Geology* 37:173–428.
- Ginter, M., J.-C. Liao, and J. I. Valenzuela-Ríos. 2008. New data on chondrichthyan microremains from the Givetian of the Renanué section in the Aragonian Pyrenees (Spain). *Acta Geologica Polonica* 58:165–172.
- Grösser, J. R., and K. F. Prossl. 1994. Palynologische Untersuchungen der Devonbasis in Floresta Massiv, Ostkordillere, Kolumbien. *S. A. Giessener Geologische Schriften* 51:105–121.
- Heymons, R. 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica* 13:1–244.
- Huxley, T. H. 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 43:649–662.
- Janvier, P. 1996. Early Vertebrates. *Monographs on Geology and Geophysics*. Clarendon Press, Oxford, U.K., 393 pp.
- Janvier, P. 2007. The Devonian vertebrates of South America: Malvinokaffric fishes and Gondwana-Euramerica faunal interchange. *Cuadernos del Museo Geominero* 8:223–227.
- Janvier, P., and G. Clément. 2005. A new groenlandaspidid arthrodire (Vertebrata: Placodermi) from the Famennian of Belgium. *Geologica Belgica* 8:51–67.
- Janvier, P., and J. G. Maisey. 2010. The Devonian vertebrates of South America and their biogeographical relationships; pp. 431–459 in X.-B. Yu, D. Elliott, and J. G. Maisey (eds.), *Morphology, Phylogeny and Biogeography of Fossil Fishes*. Pfeil, Munich, Germany.
- Janvier, P., and J. Pan. 1982. *Hyracanthaspis bliecki* n. g. n. sp., a new primitive euantiarch (Antiarcha, Placodermi) from the Middle Devonian of northeastern Iran, with a discussion on the antiarch phylogeny. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 164:634–392.
- Janvier, P., and M. Suarez-Riglos. 1986. The Silurian and Devonian vertebrates of Bolivia. *Bulletin de l'Institut Français d'Etudes Andines* 15:73–114.
- Janvier, P., and C. Villarroel. 1998. Los peces devónicos del Macizo de Floresta (Boyacá, Colombia). *Consideraciones taxonómicas, bioestratigráficas, biogeográficas y ambientales*. *Geología Colombiana* 23:3–18.
- Janvier, P., and C. Villarroel. 2000. Devonian vertebrates from Colombia. *Palaeontology* 43:729–763.
- Jarvik, E. 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *Kungliga Svenska Vetenskaps-akademiens Handlingar* 25:1–301.



- Jeffery, J. E. 2002. Mandibles of rhizodontids: anatomy, function and evolution within the tetrapod stem-group. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 93:255–276.
- Karatajute-Talimaa, V. N. 1963. The genus *Asterolepis* from the Devonian of the Russian Platform. In Grigelis A. & Karatajute-Talimaa, V. (eds), *The data of geology of the Lithuania: 65–223*, Geologic and Geographic Institute of the Academy of Sciences of the Lithuanian SSR, Vilnius, (Russian with English summary).
- Kjellesvig-Waering, E. N. 1961. Eurypterids of the Devonian Holland Quarry Shale of Ohio. *Geology* 14:79–98.
- Kjellesvig-Waering, E. N. 1964. A synopsis of the family Pterygotidae Clarke and Ruedemann, 1912 (Eurypterida). *Journal of Paleontology* 38:331–361.
- Kjellesvig-Waering, E. N. 1973. A new Silurian *Slimonia* (Eurypterida) from Bolivia. *Journal of Paleontology* 47:549–550.
- Klein, E. F. 1885. Beiträge zur Bildung des Schädels der Knochenfische, 2. Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg 42:205–300.
- Klug, C., B. Kröger, W. Kiessling, G. L. Mullins, T. Servais, J. Frýda, D. Korn, and S. Turner. 2011. The Devonian nekton revolution. *Lethaia* 43:465–477.
- Kobayashi, T. 1954. Fossil estherians and allied fossils. *Journal of the Faculty of Science, University of Tokyo, Section 2, Geology, Mineralogy, Geography, Geophysics* 9:1–192.
- Lamsdell, J. C., and S. J. Braddy. 2010. Cope's Rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biology Letters* 6:265–269.
- Lamsdell, J. C., and D. A. Legg. 2010. An isolated pterygotid ramus (Chelicerata: Eurypterida) from the Devonian Beartooth Butte Formation, Wyoming. *Journal of Paleontology* 84:1206–1208.
- Lamsdell, J. C., and P. A. Selden. 2017. From success to persistence: identifying an evolutionary regime shift in the diverse Paleozoic aquatic arthropod group Eurypterida, driven by the Devonian biotic crisis. *Evolution* 75:95–110.
- Lamsdell, J. C., I. Hoşgör, and P. A. Selden. 2013. A new Ordovician eurypterid (Arthropoda: Chelicerata) from Southeast Turkey: evidence for a cryptic Ordovician record of Eurypterida. *Gondwana Research* 23:354–366.
- Latreille, P. A. 1817. Les Crustacés, les Arachnides, les Insectes; pp. 1–688 in G. Cuvier (ed.), *Le Règne Animal Distribué d'après son Organisation, pour Servir de Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée*, Volume 3. Déterville, Paris.
- Lebedev, O. A. 1995. Morphology of a new osteolepidid fish from Russia. *Bulletin du Muséum national d'Histoire naturelle, Paris, 4ème série* 17:287–341.
- Linder, F. 1945. Affinities within the Branchiopoda with notes on some dubious fossils. *Arkiv för Zoologi* 37:1–28.
- Liu, H. P., S. M. Bergström, B. J. Witzje, D. E. G. Briggs, R. M. McKay, and A. Ferretti. 2017. Exceptionally preserved conodont apparatuses with giant elements from the Middle Ordovician Winneshiek Konservat-Lagerstätte, Iowa, USA. *Journal of Paleontology* 91:493–511.
- Long, J. A. 1983. New bothriolepid fish from the Late Devonian of Victoria, Australia. *Palaeontology* 26:295–320.
- Long, J. A. 1988. New palaeoniscoid fishes from the Late Devonian and Early Carboniferous of Victoria. *Memoirs of the Association of Australian Palaeontologists* 7:1–64.
- Long, J. A., R. E. Barwick, and K. S. W. Campbell. 1997a. Osteology and functional morphology of the osteolepiform fish *Gogoniasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum* 53 (Supplement):1–89.
- Long, J. A., B. Choo, and G. C. Young. 2008. A new basal actinopterygian fish from the Middle Devonian Aztec Siltstone of Antarctica. *Antarctic Science* 20:393–412.
- Long, J. A., M. E. Anderson, R. Gess, and N. Hiller. 1997b. New placoderm fishes from the Late Devonian of South Africa. *Journal of Vertebrate Paleontology* 17:253–268.
- Maisey, J. G., and M. E. Anderson. 2001. A primitive chondrichthyan braincase from the Early Devonian of South Africa. *Journal of Vertebrate Paleontology* 21:702–713.
- Manosalva-Sánchez, S. R., W. E. Naranjo-Merchán, C. A. Ríos-Reyes, R. Amorcho, and O. Castellanos. 2017. Estudio petrográfico de las rocas metamórficas del Macizo de Floresta, Cordillera Oriental, Andes Colombianos. *Boletín de Geología* 39:83–103.
- Mantilla-Figueroa, L. C., C. A. García-Ramírez, and V. A. Valencia. 2016. Nuevas evidencias que soportan la escisión de la Formación Silgará y propuesta de un nuevo marco estratégico para el basamento metamórfico del Macizo de Santander (Cordillera Oriental de Colombia). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 40:323–336.
- McCoy, F. 1848. On some new fossil fish of the Carboniferous period. *Annals and Magazine of Natural History* 2:1–10.
- Miles, R. S. 1968. The Old Red Sandstone antiarchs of Scotland: family Bothriolepididae. *Palaeontographical Society Monography* 122:1–130.
- Miles, R. S. 1973a. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. *Bulletin of the British Museum of Natural History (Geology)* 24:111–213.
- Miles, R. S. 1973b. An actinolepid arthrodire from the Lower Devonian Peel Sound Formation, Prince of Wales Island. *Palaeontographica* 143:109–118.
- Mojica, J., and C. Villarroel. 1984. Contribución al conocimiento de las unidades Paleozoicas del área de Floresta (Cordillera Oriental Colombiana; Departamento de Boyacá) y en especial al de la Formación Cuiche. *Geología Colombiana* 13:55–79.
- Mondéjar-Fernández, J., and P. Janvier. 2014. Further evidence for the presence of holoptychiid porolepiforms (Sarcopterygii, Dipnomorpha) from the Frasnian of Colombia. *Comptes Rendus Palevol* 13:587–597.
- Morzadec, P., M. Mergl, C. Villarroel, P. Janvier, and P. R. Racheboeuf. 2015. Trilobites and inarticulate brachiopods from the Devonian Floresta Formation of Colombia: a review. *Bulletin of Geosciences* 90:331–358.
- Obruchev, D. V. 1964. [Agnathes. Pisces]; pp. 1–522 in J. A. Orlov (ed.), [Fundamentals of Paleontology, Volume 11]. Nauka, Moscow. [Russian]
- Olive, S., C. Prestianni, and V. Dupret. 2015a. A new species of *Groenlandaspis* Heintz, 1932 (Placodermi, Arthrodira), from the Famennian (Late Devonian) of Belgium. *Journal of Vertebrate Paleontology*. doi: 10.1080/02724634.2014.935389.
- Olive, S., G. Clément, E. B. Daeschler, and V. Dupret. 2015b. Characterization of the placoderm (Gnathostomata) assemblage from the tetrapod-bearing locality of Strud (Belgium, Upper Famennian). *Palaeontology* 58:981–1002.
- Owen, R. 1846. Lecture on the Comparative Anatomy and Physiology of the Vertebrate Animals, Delivered at the Royal College of Surgeons of England in 1844 and 1846, Volume I, Fishes. Longman, Brown, Green, and Longmans, London, 308 pp.
- Page, D. 1856. *Advanced Text-book of Geology, Descriptive and Industrial*. William Blackwood and Sons, London, 325 pp.
- Patterson, C. 1982. Morphology and interrelationships of primitive actinopterygian fishes. *American Zoologist* 22:241–259.
- Potvin-Leduc, D., R. Cloutier, N. Landing, L. Vanaller Hernick, and F. Mannolini. 2015. Givetian (Middle Devonian) sharks from Cairo, New York (USA): evidence of early cosmopolitanism. *Acta Palaeontologica Polonica* 60:183–200.
- Pradel, A., J. G. Maisey, P. Tafforeau, and P. Janvier. 2009. An enigmatic gnathostome vertebrate skull from the Middle Devonian of Bolivia. *Acta Zoologica* 90:123–133.
- Purnell, M. A., and P. H. von Bitter. 1992. Blade-shaped conodont elements functioned as cutting teeth. *Nature* 359:629–631.
- Roessler, E. W. 1995. Review of Colombian conchostraca (Crustacea)—morphotaxonomic aspects. *Hydrobiologia* 298:253–262.
- Rogers, D. C., N. Rabet, and S. C. Weeks. 2012. Revision of the extant genera of Limnadiidae (Branchiopoda: Spinicaudata). *Journal of Crustacean Biology* 32:827–842.
- Romer, A. S. 1933. Eurypterid influence on vertebrate history. *Science* 78:114–117.
- Romer, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes, or Sarcopterygii? *Nature* 176:126.
- Säve-Söderbergh, G. 1933. The dermal bones of the head and the lateral line system in *Osteolepis macrolepidotus* Ag. with remarks on the terminology of the lateral line system and on the dermal bones of certain other crossopterygians. *Nova Acta Regiae Societatis Scientiarum Upsaliensis, series* 4:1–129.
- Säve-Söderbergh, G. 1941. Notes on the dermal bones of the head in *Osteolepis macrolepidotus* Ag. and the interpretation of the lateral

- line system in certain primitive vertebrates. *Zoologiska Bidrag från Uppsala* 20:523–541.
- Scotese, C. R. 2002. Paleomap Web site. Available at [www.scotese.com](http://www.scotese.com). Accessed July 21, 2018.
- Tasch, P. 1956. Three general principles for a system of classification of fossil conchostracans. *Journal of Paleontology* 30:1248–1257.
- Tetlie, O. E. 2007. Distribution and dispersal history of Eurypterida. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252:557–574.
- Tetlie, O. E., and D. E. G. Briggs. 2009. The origin of pterygotid eurypterids (Chelicerata: Eurypterida). *Palaeontology* 52:1141–1148.
- Upeniec, I., and J. Upenieks. 1992. Upper Devonian antiarch (*Asterolepis*) individuals from the lode quarry, Latvia; pp. 167–174 in E. Mark-Kurik (ed.), *Fossil Fishes as Living Animals*. Akademia 1, Tallinn, Estonia.
- Waterston, C. D. 1964. Observations on pterygotid eurypterids. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 66:9–33.
- Werdelin, L., and J. A. Long. 1986. Allometry in the placoderm *Bothriolepis canadensis* and its significance to antiarch evolution. *Lethaia* 19:161–169.
- Woodward, A. S. 1891. Catalogue of the fossil fishes in the British Museum of Natural History. Part II. Containing the Elasmobranchii (Acanthodii), Holocephali, Ichthyodolites, Ostracodermi, Dipnoi, and Teleostomi (Crossopterygii), and chondrosteian Actinopterygii. British Museum of Natural History, London, 567 pp.
- Young, G. C. 1988. Antiarchs (placoderm fishes) from the Devonian Aztec sandstone, southern Victoria Land, Antarctica. *Palaeontographica Abteilung A* 202:1–125.
- Young, G. C. 1990. Devonian vertebrate distribution patterns, and cladistic analysis of palaeogeographic hypotheses. Geological Society, London, *Memoirs* 12:243–255.
- Young, G. C. 1993. Vertebrate faunal provinces in the Middle Palaeozoic; pp. 293–323 in J. A. Long (ed.), *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. Belhaven Press, London.
- Young, G. C. 2003. North Gondwana mid-Palaeozoic connections with Euramerica and Asia: Devonian vertebrate evidence. *Courier Forschungsinstitut Senckenberg* 242:169–185.
- Young, G. C., and J. M. Moody. 2002. A middle-Late Devonian fish fauna from the Sierra de Perijá. *Fossil Record* 5:155–206.
- Young, G. C., J. M. Moody, and J. Casas. 2000. New discoveries of Devonian vertebrates from South America, and implications for Gondwana-Euramerica contact. *Comptes Rendus de l'Académie des Sciences, Paris* 331:755–761.
- Zhang, W.-T., P.-J. Chen, and Y.-B. Shen. 1976. *Fossil Conchostraca of China*. Science Press, Beijing, China, 325 pp.

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