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Further evidence for the presence of holoptychiid porolepiforms (Sarcopterygii, Dipnomorpha) from the Frasnian of Colombia

Nouvelles preuves de la présence de porolépiformes holoptychiides (Sarcopterygii, Dipnomorpha) dans le Frasnien de Colombie

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ABSTRACT

The Devonian (Frasnian) of Colombia has provided important information on the taxonomical diversity and palaeobiogeographic relationships of the Late Devonian marginal marine vertebrate faunas of South America (northwestern margin of Gondwana). This fauna is mostly composed of Gondwanan endemics, but includes two taxa also known in Euramerica: the antiarchan placoderm *Asterolepis* and the porolepiform sarcopterygian *Holoptychius*. The occurrence of holoptychiid porolepiforms in Colombia was previously suggested based solely on the presence of scales attributed to *Holoptychius*, although with caution. Here, we describe further holoptychiid remains that include a large isolated tooth with dendrodont microstructure, typical of porolepiforms, and additional *Holoptychius* scales. These new findings increase the record of holoptychiid porolepiform occurrences in Gondwana and suggest that dispersion of fish faunas between Euramerica and Gondwana by the beginning of the Late Devonian was possible through South America.

RÉSUMÉ

Le Dévonien (Frasnien) de Colombie a livré des informations importantes sur la diversité taxonomique et les relations paléobiogéographiques des faunes de vertébrés marins d'Amérique du Sud (marge nord-ouest du Gondwana) au Dévonien terminal. Parmi ces faunes, composées majoritairement de taxons gondwaniens, figurent deux taxons trouvés également en Euramérique : le placoderme antiarche *Asterolepis* et le sarcoptérygien porolépiforme *Holoptychius*. L'occurrence de porolépiformes holoptychiides en Colombie reposait exclusivement sur la présence d'écailles attribuées avec prudence à *Holoptychius*. Ici, nous décrivons de nouveaux restes d'holoptychiides qui incluent une grande dent isolée avec une microstructure dendrodonte, typique des porolépiformes, et de nouvelles écailles d'*Holoptychius*. Ces découvertes complètent le registre d'occurrences de porolépiformes

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holoptychiides au Gondwana et suggèrent que la dispersion de faunes ichthyennes entre l'Euramérique et le Gondwana au début du Dévonien terminal était possible au niveau de l'Amérique du Sud.

1. Introduction

Recent discoveries regarding the vertebrate fauna of the Cuche Formation of Colombia and of the Campo Chico Formation of Venezuela (Janvier and Villarroel, 1998, 2000; Young and Moody, 2002; Young et al., 2000) have provided the first information about the diversity of the Late Devonian marginal marine vertebrate faunas from South America, thus of the westernmost Gondwana. Contrary to other South American Devonian fish faunas from deep marine facies (Janvier and Maisey, 2010), the occurrences from Colombia and Venezuela are from siliciclastic, marginal marine to deltaic facies. Thus, their palaeoenvironments can be readily compared to a large number of more or less coeval vertebrate localities from Euramerica, Siberia, China and eastern or northeastern Gondwana. In following, they are important landmarks for reconstructing the palaeobiogeographic relationships of Devonian vertebrates during a time when early tetrapods expanded their distribution, and when Gondwana drifted closer to Euramerica, thereby initiating the assembly of Pangea.

The Venezuelan vertebrate fauna was regarded as essentially composed of Gondwanan taxa known elsewhere from the Middle and Late Devonian of Australia, Antarctica, and South Africa (Young and Moody, 2002; Young et al., 2000). However, in addition to Gondwanan endemics, the approximately coeval Colombian fauna (Janvier and Maisey, 2010; Janvier and Villarroel, 1998, 2000) has yielded two widely distributed Euramerican taxa that have been tentatively referred to the antiarch placoderm *Asterolepis* and the porolepiform sarcopterygian *Holoptychius.* Subsequent field investigations in the Colombian Cuche Formation did not provide additional data that could unambiguously confirm the presence of *Asterolepis*, despite the remarkable resemblance between the isolated plates referred to this genus by Janvier and Villarroel (2000) and those of typical Euramerican *Asterolepis* species. Similarly, the occurrence of porolepiforms in the Cuche Formation has been inferred from the presence of 'holoptychiid-like' scales attributed to *Holoptychius* sp. indet., although with caution (Janvier and Villarroel, 2000). Other occurrences of holoptychiid porolepiforms in the Late Devonian of Gondwana have also been suggested by the recovery of scales (Johanson and Ritchie, 2000; Lelièvre et al., 1993; Young et al., 2010).

Porolepiforms are an exclusively Devonian sarcopterygian taxon known from the Early Lochkovian to the Late Famennian that inhabited near-shore to possibly fresh water environments (Janvier, 1996). They share a number of uniquely derived characters with living and fossil lungfishes and are therefore regarded as the sister group of dipnoans, within the Dipnomorpha (Ahlberg, 1991); however, the inclusion of *Powichthys* in the Porolepiforms (Clément and Janvier, 2004) raises questions about their status as a clade or as a grade of stem-group dipnomorphs (Friedman, 2007a, b; Schultze, 2000). The Porolepiforms comprise two families: the Porolepididae (a possible paraphyletic assemblage of early porolepiforms including *Porolepis* and *Heimenia*) (Ørvig, 1957, 1969; Clément, 2004) and the Holoptychiidae (including notably *Holoptychius*, *Glyptolepis*, *Quebecius* and *Laccognathus*) (Jarvik, 1972; Cloutier and Ahlberg, 1996; Cloutier and Schultze, 1996; Ørvig, 1957).

With the exception of *Powichthys* (Clément et al., 2004; Vorobyeva, 1977), all taxa that are currently classified as porolepiforms share an importantly conspicuous histological character: dendrodont folding of dental dentine (Schultze, 1969). Schultze (1969, 1970) considered three main types of folded tooth structures (namely the dendrodont, polyplocodont and eusthenodont types) and regarded the dendrodont type as unique to taxa that are, on the basis of other skeletal characters, classified as Porolepiforms.

The morphology and microstructure of porolepiform scales changed distinctly during the Early and Middle Devonian (Ørvig, 1969; Mondéjar-Fernández and Clément, 2012; Schultze, 1977). Specifically, they changed from small, diamond-shaped, cosmine-covered scales in the "porolepidids", to large, rounded scales that lose their cosmine covering and present a vermiculate exposed surface with some patches of enamel and dentine ornamentation in the holoptychiids. The rise of the latter scale morphotype was accompanied by a similar ornamentation in other dermal bones of the head and shoulder girdle that diagnose the Holoptychiidae. Holoptychiids became very abundant in marginal marine environments from the Late Emsian to the Late Famennian of North America and Europe (Cloutier and Schultze, 1996; Schultze, 2000) and were recently confirmed in Australia and Antarctica (Johanson and Ritchie, 2000; Young et al., 1992, 2010).

Here we describe a large and isolated—though poorly preserved—tooth whose typical dendrodont structure provides new and clear evidence for the presence of holoptychiid porolepiforms in the Frasnian fauna of Colombia (northwestern Gondwana). The relevance of the attribution of the isolated scales remains from the Cuche Formation to *Holoptychius* among holoptychiids will also be discussed.

1.1. Institutional abbreviations

MB, Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University, Berlin, Germany; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **UN-DG-PALV**, Universidad Nacional de Colombia, Departamento de Geología, Colección de Paleontología (Vertebrados), Bogotá, Colombia.

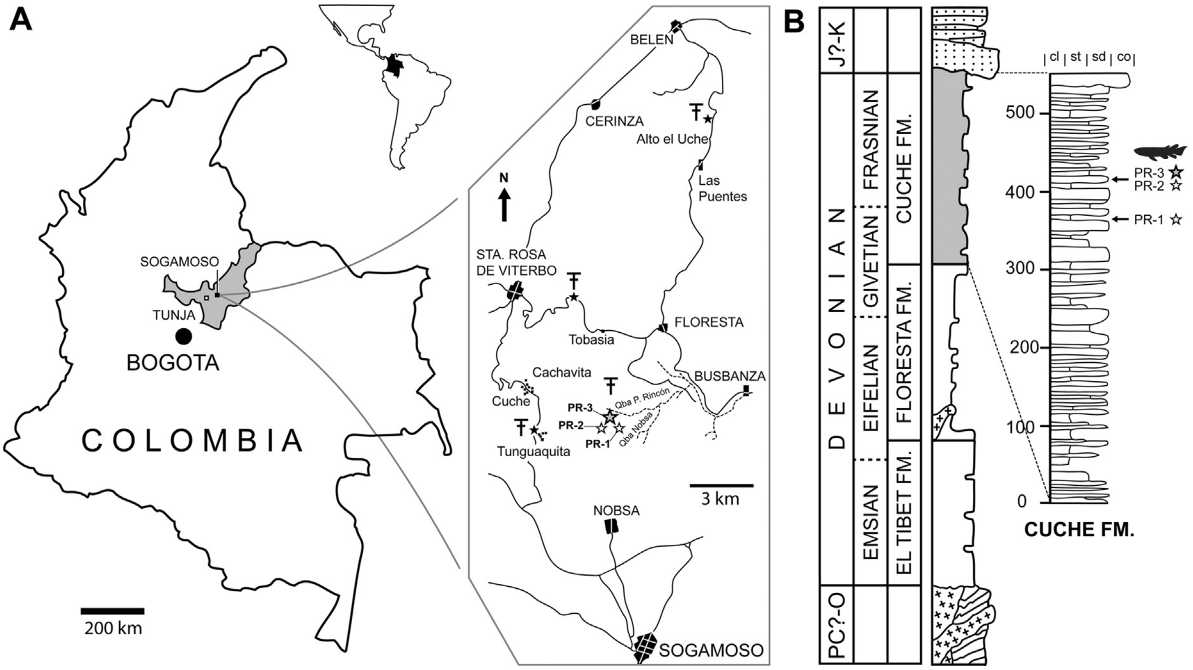

Fig. 1. A. Locality map of the Department of Boyacá (north-central Colombia). **B**. Synthetic log of the Cuche Formation, with special reference to the Potrero Rincón fossil sites (PR 1-3). White stars represent the Potrero Rincón fossil localities. Note that the holoptychiid porolepiform remains come from the PR-3 locality. Smaller black stars represent other fossil fish localities of the Boyacá department (see Janvier and Villarroel, 2000). **Abbreviations: PC?–O**, Precambrian?–Ordovician, **J?–K**, Jurassic?–Cretaceous; **cl**, claystone; **st**, siltstone; **sd**, sandstone; **cg**, conglomerate. Modified and redrawn after Janvier and Villarroel, 2000.

Fig. 1. A. Carte du département de Boyacá (Colombie). **B**. Log synthétique de la formation Cuche, illustrant les sites fossiles de Potrero Rincón (PR 1-3). Les étoiles blanches représentent les localités fossilifères de Potrero Rincón. On notera que les restes de porolépiformes holoptychiides proviennent de la localité PR-3. Les étoiles noires plus petites représentent d'autres localités fossiles du département de Boyacá ayant délivré des poissons (voir Janvier et Villarroel, 2000). **Abréviations** : **PC?–O,** Précambrien ?–Ordovicien, **J?–K,** Jurassique ?–Crétacé; **cl**, argilites; **st**, siltites; **sd**, grès; **cg**, conglomérats. Modifié et redessiné à partir de Janvier et Villarroel, 2000.

1.2. Systematic palaeontology

Osteichthyes (Huxley, 1880).
Sarcopterygii (Romer, 1955).
Dipnomorpha (Ahlberg, 1991).
Porolepiforms (Berg, 1937).
Family Holoptychiidae (Owen, 1860).
Figs. 2 and 3A, B.

Remarks. We do not attempt to assign this tooth material to any existing species or genus of holoptychiid. This decision was made on the basis of the limited number of holoptychiid materials retrieved from the field, the incompleteness of the dental material, and the difficulty of identifying species or genera on the basis of incompletely-preserved, isolated remains.

2. Material and methods

The new specimen described herein consists of an isolated tooth (UN-DG-PALV86) found in the same layer as other isolated and partially preserved scales previously referred to as *Holoptychius* sp. indet. (UN-DG-PALV50-51) by Janvier and Villarroel (2000), with reservations. All the material was collected by P. Janvier (MNHN, Paris) and C. Villarroel (Prof. Emeritus at the Universidad Nacional de Colombia, Bogotá) in 2000 and 2004, and comes from the locality Potrero Rincón 3 of the upper part of the Cuche Formation (Department of Boyacá, Colombia) (Fig. 1). The fossil remains occur in a channel within a thick series of reddish argillaceous sandstones, alongside numerous isolated *Bothriolepis* antiarch plates, and isolated dermal bones and teeth of various other fishes. The specimens are very weathered due to the tropical climate, similar to other vertebrate skeletal remains from the locality. Nevertheless, the internal structure of the basal portion of tooth is partly preserved and two thin transverse sections were performed at two different heights after its inclusion in stratyl resin.

Several casts of the scales were produced using elastomer resin stained in grey and brown and whitened with magnesium oxide before being photographed in the MNHN, Paris. The material was compared with other holoptychiid fossil remains (teeth and scales of *Holoptychius nobilis* and *Laccognathus panderi* from the MB, Berlin). The thin sections were examined under natural transmitted and polarized light with a Zeiss Axiovert 35 microscope. The specimens are deposited in the palaeontological collection of the Departamento de Geociencias of the Universidad Nacional de Colombia, Bogotá, Colombia.

3. Geological context

The Floresta Massif is located in the Central-North area of Colombia, in the Boyacá Department (Fig. 1A). It consists of a core of Precambrian metamorphic rocks surrounded by Palaeozoic sediments. The Devonian sediments consist of three formations, from the base to the top: the El Tibet, Floresta, and Cuche Formations (Fig. 1B). The El Tibet Formation (Lochkovian?-Emsian) is composed of cross-bedded kaolinitic sandstone and is virtually barren. The Floresta Formation (Emsian–Givetian/Frasnian) begins with a thick sandstone sequence and progressively passes to marine channel facies that yield rich invertebrate faunas and plants indicating Eifelian to possibly Frasnian ages (Berry et al., 2000). The Cuche Formation (probably all Frasnian) forms the top of the series (Fig. 1B). It consists of reddish sandstone, marls and clay lenses, and is uncomformably overlain by a Jurassic conglomerate. The Cuche Formation at the Potrero Rincón locality yields a rich vertebrate assemblage of acanthodians (*Nostolepis* sp., *Florestacanthus morenoi)* (Burrow et al., 2003; Janvier and Villarroel, 2000), chondrichthyans (*Antarctilamna* sp.?), placoderms (*Bothriolepis* sp., *Asterolepis* sp. and probably *Groenlandaspis* sp.), actinopterygians (Stegotrachelidae gen. et sp. indet.) and sarcopterygians (*Holoptychius* sp. indet., Megalichthyidae gen. et sp. indet. and a rhizodontid erroneously referred to *Strepsodus* sp.) (Burrow et al., 2003; Janvier and Maisey, 2010; Janvier and Villarroel, 1998, 2000; Jeffery, 2003). 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. This assemblage closely compares with that of the Givetian-Frasnian Campo Chico Formation of western Venezuela (Young and Moody, 2002); however, the Cuche Formation lacks lungfishes, phyllolepids, and the asterolepidoid *Venezuelepis*, while the Campo Chico Formation lacks rhizodonts and *Asterolepis*. Nevertheless, in both formations, *Bothriolepis* is very abundant. The Colombian and Venezuelan occurrences are separated by about 500 km but belong to the same large Palaeozoic ensemble of the Central Cordillera that has been referred to as the ‘eastern Andean Terrane’ (see Janvier and Villarroel, 2000; Young and Moody, 2002; Young et al., 2000, for further details).

4. Description

4.1. Tooth

Overall morphology—The tooth (UN-DG-PALV86) measures 2.1 cm in length (from the lowermost point of the exposed portion to the apex) and 0.7 cm in diameter at its base (Fig. 2A). It is slightly curved from the base to the apex. Although the tooth is isolated, it is most plausible that it was curved inwards (lingual curvature), a condition typical for piscine sarcopterygians and early tetrapods (Ahlberg and Clack, 1998; Jarvik, 1972). There is no evidence of a reverse-curvature at the apex, a condition seen in rhizodontids (Jeffery, 2003), onychodontids (Andrews et al., 2006) and in the parasymphysial region of certain porolepiforms (e.g., *Hamodus* in Bystrow, 1939).

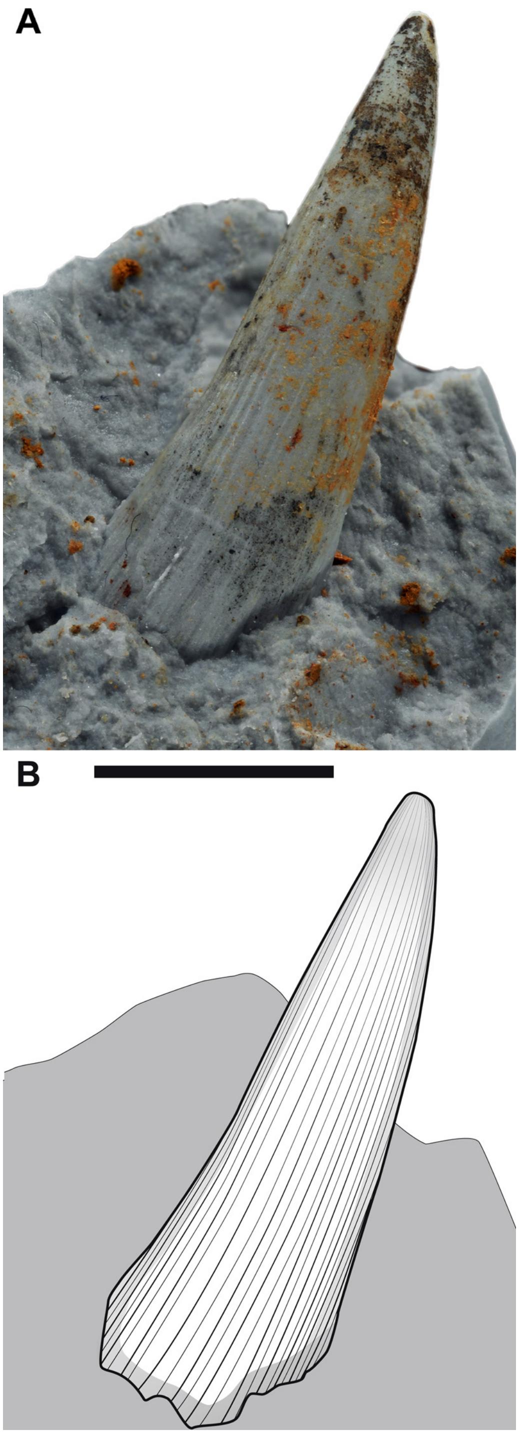

Fig. 2. (Colour online.) Isolated tooth of an undetermined holoptychiid porolepiform from the Frasnian of Colombia (UN-DG-PALV86). **A**. Elastomere cast of the specimen. **B**. Interpretative drawing. Scale bar equals 1 mm.

Fig. 2. (Couleur en ligne.) Dent isolée d'un porolépiforme holoptychiide indéterminé du Frasnien de Colombie (UN-DG-PALV86). **A**. Moulage en élastomère du spécimen. **B**. Dessin interprétatif. La barre d'échelle représente 1 mm.

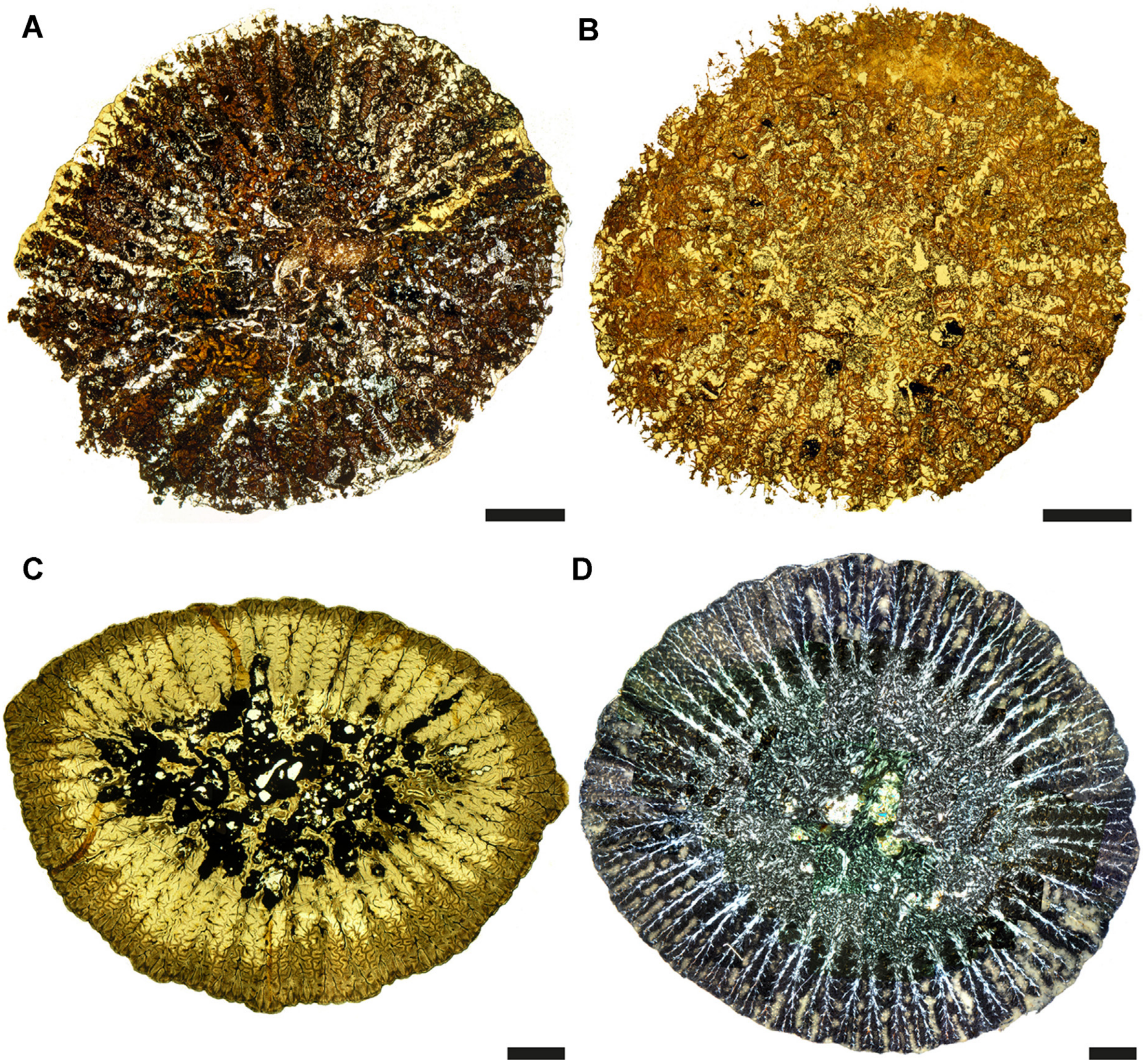

Fig. 3. (Colour online.) Cross-sections of several holoptychiid porolepiform teeth. Note that all cross-sections were made at approximately the same corresponding height at the base of the tooth. **A**. Holoptychiidae indet. from the Frasnian of Colombia (UN-DG-PALV86), lower cross-section. **B**. Holoptychiidae indet. from the Frasnian of Colombia (UN-DG-PALV86), upper cross-section. **C**. *Laccognathus panderi* (MB.f. 1850) from the Givetian–Frasnian of Latvia. **D**. *Holoptychius nobilis* (MB.f. 2129,4) from the Givetian–Frasnian of Latvia (in polarized light). Scale bar equals 1 mm.

Fig. 3. (Couleur en ligne.) Lames minces de dents de plusieurs porolépiformes holoptychiides. On notera que les plans de coupe ont été réalisés à la même hauteur approximative, au niveau de la base de la dent. **A**. Holoptychiidae indet. du Frasnien de Colombie (UN-DG-PALV86), coupe inférieure. **B**. Holoptychiidae indet. du Frasnien de Colombie (UN-DG-PALV86), coupe supérieure. **C**. *Laccognathus panderi* (MB.f. 1850) du Givétien–Frasnien de Lettonie. **D**. *Holoptychius nobilis* (MB.f. 2129,4) du Givétien–Frasnien de Lettonie (en lumière polarisée). La barre d'échelle représente 1 cm.

The base of the tooth is not completely preserved, which is a frequent occurrence for isolated teeth, and so it is not possible to ascertain whether the tooth was also curved at its base. The presence of a swollen base cannot be confirmed either.

The external surface is gently striated by very thin, parallel striae. The striations extend continuously from the base to the apex, and are distributed along the entire surface of the tooth. In the uppermost part of the apex, the striae are more difficult to see but are still present. The striation pattern consists of both deep and more superficial plications, with one superficial thin stria generally located between two deep striae (Fig. 2B). There are about 20 deep striae, and accordingly, about another 20 superficial thin striae.

The tooth is rounded in cross-section, especially at its base, and becomes slightly flattened towards the apex. However, no carinae (or cutting edges) along the mesial and distal margins are present, contrary to the condition seen in the large teeth of holoptychiids such as *Laccognathus* or *Glyptolepis* (Bystrow, 1939; Jarvik, 1972; pers. obs.). Due to its size, the tooth can be described as a fang, although it is not possible to determine whether it was located in the upper or lower jaw.

Histology—The tooth has been greatly re-crystallized (re-mineralized) during fossilization. Osteo- and orthodentine have been replaced by mineral elements (iron oxide) from the surrounding rock matrix and it is very difficult to identify the boundaries between them (Fig. 3A, B). However, the general branching pattern of the orthodentine matches closely the 'fire-like' branching of the typical dendrodont plicidentine of porolepiforms (Fig. 3C, D). The pulp cavity was probably filled with osteodentine and occupies about one-fourth (Fig. 3A) to one-half (Fig. 3B) of the inner surface of the tooth.

The inward dentine folds are regular and numerous (about 40) and penetrate deeply toward the pulp cavity. Beneath the enamel layer and extending into the folds (i.e., globular zone, see Warren and Turner, 2006), the dentine tubules show a radiating pattern. The outer enamel rim has completely disappeared (Fig. 3A, B). The external plications seen on the external surface of the elastomer cast appear to match those of the missing enamel layer and are directly correlated with the dentine folds, similar to rhizodontids and "osteolepiforms" (Jeffery, 2003). Because of the poor preservation issues and the weathering of the base of the tooth, it is not possible to determine whether the bone of attachment penetrates between the dentine folds or not.

4.2. Scales

Two scales (UN-DG-PALV50, 51; Janvier and Villarroel, 2000) previously figured by Janvier and Villarroel (1998), (fig. 11; 2000, pl.5, figs. 9, 10) and Janvier and Maisey (2010), (fig. 10E, F) are regarded as the best evidence for the occurrence of *Holoptychius* in the Cuche Formation (Fig. 4). They are incompletely preserved due to a fracture (Fig. 4A) or an incomplete exposure (Fig. 4B). They are about 3 cm long, rounded to elongate in shape, and devoid of cosmine. The external ornamentation consists of a series of spoon-shaped tubercles arranged in radiating rows, mostly located on the overlapped surface, and extending posteriorly through the boundary between the overlapped and exposed surfaces. These tubercles extend posteriorly into the exposed surface and anastomose, forming a series of antero-posteriorly elongate ridges that can vary in thickness.

Only the external surface of the scales is preserved and so it is not possible to observe the internal surface or verify whether they possess an inner boss. The absence of internal surface ornamentation (i.e., articular ridges or bosses) in rounded, cosmine-free scales occurs in holoptychiids, derived dipnoans, actinistians, and onychodontids (Mondéjar-Fernández and Clément, 2012; Ørvig, 1957), whereas the presence of a wedge-shaped inner boss is characteristic of the convergently acquired rounded scales of

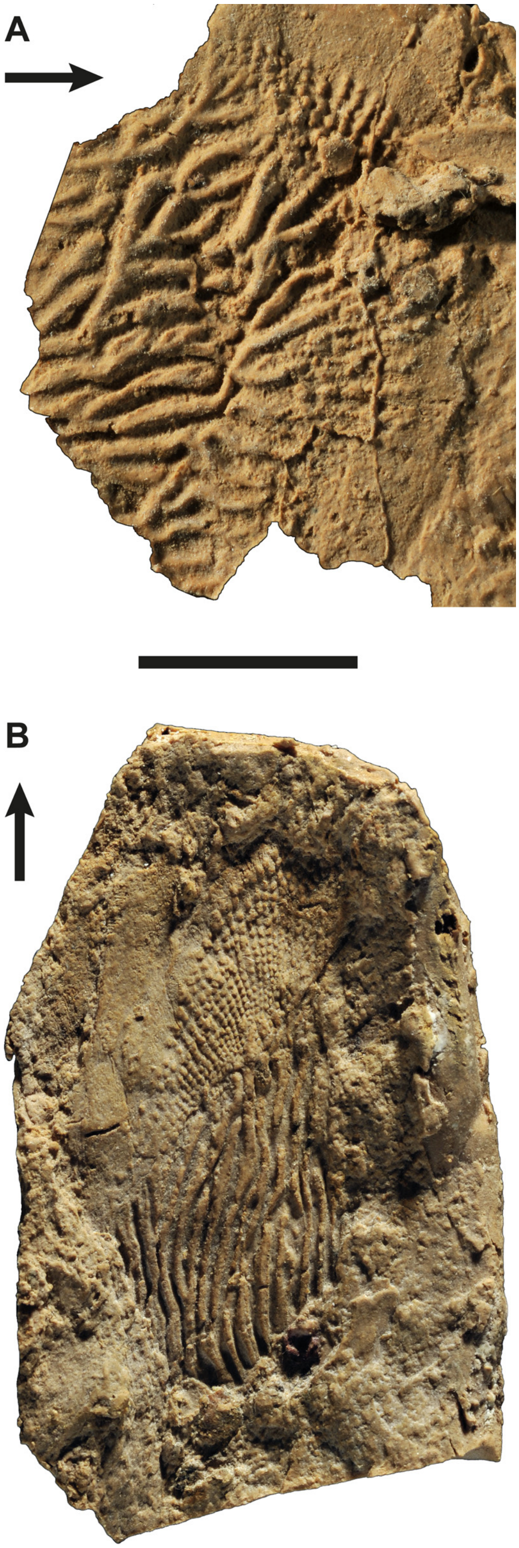

Fig. 4. (Colour online.) Elastomere cast of two isolated *Holoptychius* sp. indet. scales from the Frasnian of Colombia. **A.** Incompletely preserved isolated scale, probably located in the dorsal or flank region of the body (UN-DG-PALV50). **B.** Incompletely preserved isolated scale, slightly antero-posteriorly elongated, located probably near the base of a fin (UN-DG-PALV51). Arrows point anteriorly. Scale bar equals 1 cm.

Fig. 4. (Couleur en ligne.) Moulage en élastomère de deux écailles isolées d'*Holoptychius* sp. indet. du Frasnien de Colombie. **A.** Écaille partiellement conservée se situant probablement au niveau du flanc ou de la région dorsale du corps (UN-DG-PALV50). **B.** Écaille partiellement conservée et légèrement allongée antéropostérieurement, située probablement près de la base d'une nageoire (UN-DG-PALV51). Les flèches indiquent l'avant. La barre d'échelle représente 1 cm.

tetrapodomorphs (such as rhizodontids and tristichopterid ‘osteolepiforms’) (Jarvik, 1980).

5. Discussion

5.1. Tooth histology

The diversity of the tooth structure in vertebrates, and especially in sarcopterygians, has been well studied and documented since the pioneering works of Bystrow (1938, 1939). Bystrow’s observations on the teeth of ‘crossopterygians’ were summarized and emphasized by Schultze (1969, 1970). Schultze (1969) used the term plicidentine, first coined by Owen (1841), which was then formalised by Tomes (1878), as “a tissue with true dentinal tubules, which is derived from the calcification of a pulp, the odontoblast-carrying surface of which has been rendered complicated by foldings of its surface” (Tomes in Warren and Turner, 2006: 125). The structure and arrangement of the plicidentine has proven to be a key character for the study of tooth histological diversity in osteichthyans (Janvier, 1996).

The presence of plicidentine around the pulp cavity at the base of a tooth was considered a diagnostic feature of rhipidistians; i.e. sarcopterygians crownward to onychodontids and actinistians such as dipnomorphs and tetrapodomorphs (Vorobyeva, 1977). However, folded dentine has also been described in the stem-sarcopterygian *Psarolepis* from the Early Devonian of China (Yu, 1998; Zhu et al., 1999). Therefore, the presence of dentine folding can no longer be considered a synapomorphy of rhipidistians (Cloutier and Ahlberg, 1996) but rather the plesiomorphic state for sarcopterygians.

Onychodontids and actinistians have simple, non-plicated teeth, which could be considered a secondary and probably convergent loss, whereas dipnomorphs and tetrapodomorphs show different dentine-folding morphotypes. Based on the degree and regularity of the dentine folding, Schultze (1969, 1970) identified three principal different plicidentine morphologies:

- Polyplocodont: the pulp cavity is free from osteodentine; the orthodentine is folded simply and irregularly with branches of first or second degree; and the bone of attachment extends between the folds (the labyrinthodont folding of early tetrapods is a variant of the polyplocodont one in which the branches of the folds are apparently lost and the bone of attachment does not penetrate into the folds);
- Eusthenodont: the pulp cavity is filled with osteodentine; the orthodentine folding is often more complicated; and the bone of attachment extends between the folds as well;
- Dendrodont: the pulp cavity is filled with osteodentine, the orthodentine shows complicated and regular folding (‘fire-like’ branching); and the bone of attachment is restricted to the base of the tooth and does not extend between the folds.

The different types of dentine folding have been usually regarded as organisational grades without a strong phylogenetic signal (Jeffery, 2003; Warren and Turner, 2006). Polyplocodont plicidentine is primitively present in piscine sarcopterygians and early tetrapods; and is thus phylogenetically uninformative. However, the labyrinthodont folding (present in several Carboniferous tetrapods) and the eusthenodont folding (characteristic of certain derived tristichopterids such as *Eusthenodon* and *Platycephalichthys*) can be considered as autapomorphic traits in these taxa. By contrast, dendrodont folding seems to be restricted to the Porolepiforms, and constitutes a well-established synapomorphy of the clade (Panchen and Smithson, 1987; Schultze, 1969). Vorobyeva (1977) cautioned that the dendrodont teeth could also have evolved in parallel among sarcopterygians from a primitive polyplocodont folding, by analogy with the eusthenodont condition. However, dendrodont plicidentine has not been found in any other sarcopterygian group so far. This suggests that the dendrodont plicidentine may be a reliable character of the Porolepiforms.

5.2. Holoptychiid affinities of the specimens

Tooth—The absence of a curved apex clearly distinguishes our isolated tooth from the ‘rhizodontid-like’ teeth already described in the Cuche Formation (Janvier and Villarroel, 2000), which are tentatively attributed to *Strepsodus* (but see Jeffery, 2003 for an alternative interpretation). Further, the rhizodontid teeth with folded enamel have striation patterns that differ from our specimen. *Rhizodus*, for example, has deep plications that are restricted to the base of the crown (Jeffery, 2003, fig. 6). However, other rhizodontids, such as *Strepsodus*, have striations that extend across the entire surface of the crown, but which do not follow the contour of the tooth (Jeffery, 2003, fig. 11c–d). In our specimen, the striae run parallel to each other, merge at the apex, and follow the contour of the tooth. This pattern is identical to that of porolepiforms, such as *Glyptolepis*, *Hamodus* and *Holoptychius* (Bystrow, 1939).

In porolepiforms, the size and recurvature of the teeth is variable, not only between parasymphysial teeth and coronoid fangs, but also among coronoid fangs, depending on their location in the jaw (Ahlberg, 1991, 1992a; Jarvik, 1972). In the lower jaw, the parasymphysial fangs are slightly recurved at their apex but do not exceed in height the coronoid fangs, except in the case of *Duffichthys* (Ahlberg, 1992a).

In our specimen, the absence of recurvature at the apex, the uniform striation pattern, and the absence of well-developed carinate margins are consistent with the dental characters in holoptychiid porolepiforms such as *Holoptychius*, *Glyptolepis* and *Hamodus* (Bystrow, 1939). However, unlike *Hamodus*, UN-DG-PALV86 lacks a hooked apex and sigmoid aspect. The absence of carinate margins is common in several sarcopterygian groups (e.g., porolepiforms and “osteolepiforms”) and it is considered to be another example of tooth variability related to their position along the jaws, especially in the lower jaw (Ahlberg, 1992a; Jarvik, 1972).

When histology is considered, Schultze (1969, 1970) noticed that in the “porolepidid” *Porolepis* the osteodentine of the pulp cavity and the orthodentine are separated by a clear boundary. In holoptychiids, both ortho- and osteodentine grow closely connected, and no trace of a well-delimited boundary between these tissues is visible. Such a boundary is not visible in any of our histological sections (Fig. 2), thus supporting its assignation to the Holoptychiidae. However, we should note that this boundary between ortho- and osteodentine is also absent in the "porolepidid" *Heimenia* from the Early-Middle Devonian of Spitsbergen (pers. obs.), thus adding a new feature suggesting the intermediate condition of *Heimenia* between *Porolepis* and holoptychiids (Mondéjar-Fernández and Clément, 2012).

Scales—As described above, the external exposed surface of our scale material bears a series of tubercles and stout ridges. Among porolepiforms, the presence of such ridges has been identified in holoptychiids such as *Holoptychius*, *Quebecius* and *Glyptolepis* (Cloutier and Schultze, 1996; Ørvig, 1957; Schultze and Arsenault, 1987). The ridges in *Glyptolepis* and *Quebecius* are made of dentine and are narrower and more numerous than in *Holoptychius*. This primitive condition is present in several other sarcopterygian groups (e.g., actinistians, holodipterid dipnoans, and to a lesser extent onychodontids). *Laccognathus* shows a unique ornamentation composed of rounded dentine tubercles or small ridges capped with enamel (Downs et al., 2011; Ørvig, 1957), probably derived from narrow dentine-made ridges as seen in *Glyptolepis*.

The condition of *Holoptychius* is also derived relative to the condition seen in *Glyptolepis*; the ridges are solely made of bone and look thicker than in any other holoptychiid. However, their morphology and ornamentation varies throughout ontogeny, even at different points along the body (Ørvig, 1957). For example, the scales of the ventral region can exhibit stout bony tubercles that are arranged in rows, whereas dorsal and flank scales display antero-posteriorly oriented bony ridges (Cloutier and Schultze, 1996). Moreover, the numerous nominal species of *Holoptychius* have been mostly diagnosed on the basis of disarticulated material and isolated scales (Cloutier and Schultze, 1996; Downs et al., 2013). The assignation of isolated scales to different species of *Holoptychius* can thus be considered suspect and poorly informative when such assignations rely exclusively on external descriptions of scale remains (Downs et al., 2013; Miller and Brazeau, 2007).

Nonetheless, among holoptychiids, the combination of coarse bony ridges in the exposed surface associated with a fan of spoon-shaped tubercles in the overlapped surface diagnoses *Holoptychius*. The occurrence of these scale characters in our isolated scale material supports the previous attribution of these scales to *Holoptychius* sp. indet. (Janvier and Villarroel, 2000).

5.3. Paleobiogeographic implications

Reconstructing the biogeographic history of Devonian fish is made difficult by the patchy distribution of data (Ahlberg, 1992b). Much data from Africa, the Middle East, and South America remain largely unknown, but these regions will most certainly reveal new taxa and unexpected biogeographic patterns in the coming years. Nonetheless, the discovery and description of new fossil sites from Venezuela, Colombia, Brazil, Bolivia, and the Falkland Islands have greatly improved our knowledge of vertebrate diversity in the Devonian of South America (Janvier and Maisey, 2010).

Placoderm- and osteichthyan-dominated assemblages from the Devonian 'intertropical belt' characterize the Eifelian–Frasnian vertebrate assemblages from Venezuela and Colombia (Janvier, 2007; Janvier and Maisey, 2010). The Floresta Formation and the overlying Cuche Formation (Late Frasnian) of Colombia are thought to represent a shallow, low energy, marine influenced depositional environment (Janvier and Villarroel, 1998, 2000). This is consistent with the classical environments associated with Euramerican holoptychiid porolepiforms (Cloutier and Schultze, 1996).

Porolepiforms are still considered a rare component of Gondwanan faunas, despite their reported presence in Iran (Lelièvre et al., 1993; Schultze, 1973), Australia (Johanson and Ritchie, 2000; Johanson et al., 2013; Young et al., 2010), and Antarctica (Young et al., 1992). Porolepiforms, especially holoptychiids, have been well studied and more commonly found in Euramerican localities, from North America to Russia (Fig. 5). This lead to the assumption that holoptychiids might be considered Euramerican endemics in the Middle Devonian with a worldwide distribution of certain genera, such as *Holoptychius*, by the Late Devonian. However, this misinterpretation is likely explained by the poor sampling and preservation of Gondwanan material.

Holoptychiids occur in Euramerica by the late Lower Devonian (Emsian) (*Nasogaluakus* in Schultze, 2000), with *Holoptychius* first undisputed occurrences by the Frasnian (P. Ahlberg pers. comm.). *Holoptychius* presents a more ubiquitous mode of life and a greater potential of dispersion than any other sarcopterygian taxon (Cloutier and Schultze, 1996). This potential for a great dispersal ability appears to have favored its expansion between Euramerica and Gondwana, probably through both eastern and western routes (Middle East and South America, respectively), and likely as soon as the Frasnian. Similarly, "porolepidids" like *Porolepis* are known from both marine and freshwater deposits from Euramerica, and recently from eastern Gondwana (Johanson et al., 2013). By contrast, holoptychiids appear to have been somehow restricted to freshwater and possibly estuarine or lagoon environments (Ahlberg, 1992b). However, both families are widely distributed throughout the Devonian, which suggests a great adaptability and dispersal potential of porolepiforms as a whole.

Holoptychius has been reported from the Frasnian of Iran (northern margin of Gondwana) (Lelièvre et al., 1993) and is well represented in numerous sites from Euramerica (e.g., Cloutier and Schultze, 1996). The presence of *Holoptychius* in the Frasnian of Colombia thus represents one of the earliest occurrences of the genus, both in Euramerica and Gondwana. South America may have functioned as a bridge between northern Gondwana and southern Euramerica (Fig. 5), which allowed fish faunas to disperse more easily from one continent to the other. This suggests that the earliest range of *Holoptychius* extends from the southern margin of Euramerica to the northern margin of Gondwana. The rich Middle Devonian holoptychiid record of Euramerica

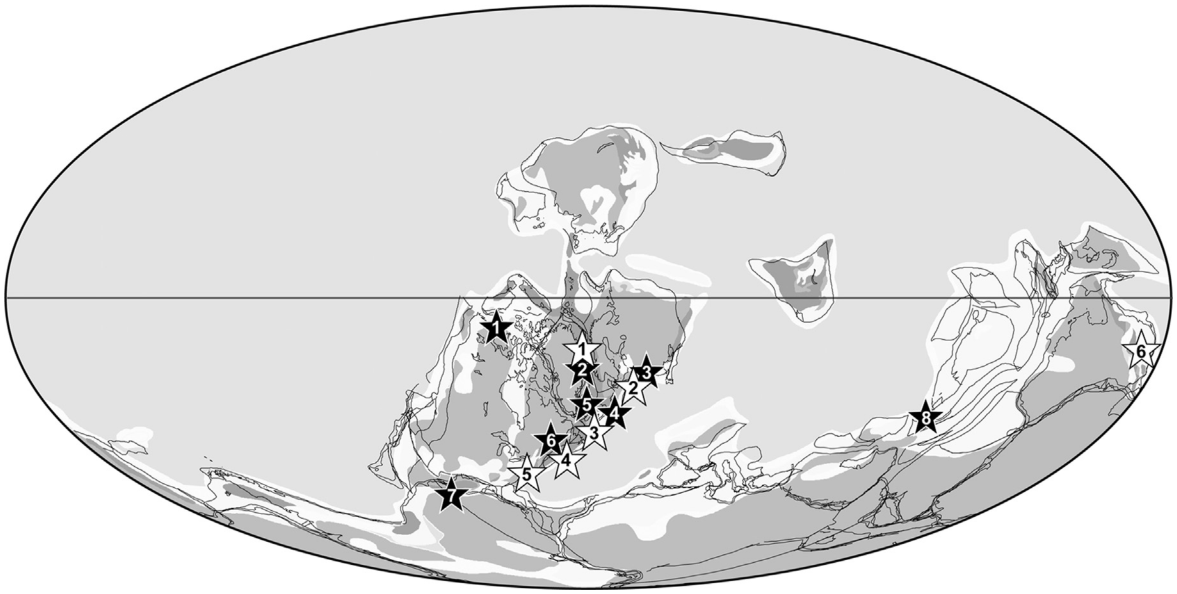

Fig. 5. Palaeogeographical map for the Late Devonian illustrating the reported occurrence of holoptychiid porolepiforms in Euramerica and Gondwana. Emsian–Frasnian localities (black stars): 1. Arctic Canada (*Nasogaluakus*, *Laccognathus*) (Downs et al., 2011; Schultze, 2000); 2. East Greenland (*Holoptychius*, *Glyptolepis*) (Jarvik, 1972); 3. Russia and Latvia (*Holoptychius*, *Glyptolepis*, *Laccognathus*, *Hamodus*, *Paraglyptolepis*) (Obrutschew, 1933; Vorobyeva, 1987); 4. Germany (*Glyptolepis*) (Gross, 1936); 5. Scotland (*Duffichthys*, *Holoptychius*, *Glyptolepis*) (Ahlberg, 1992a, b); 6. Québec (*Holoptychius*, *Quebecius*) (Cloutier and Schultze, 1996); 7. Colombia (*Holoptychius*) (Janvier and Villarroel, 2000; this study); 8. Iran (*Holoptychius*) (Lelièvre et al., 1993; Schultze, 1973). Famennian localities (white stars): 1. East Greenland (*Holoptychius*) (Jarvik, 1972); 2. Latvia (*Ventalepis*) (Schultze, 1980); 3. Belgium (*Holoptychius*) (Clément et al., 2004); 4. Eastern Canada (*Holoptychius*) (Miller and Brazeau, 2007); 5. Pennsylvania (*Holoptychius*, *Glyptolepis*); 6. Australia (*Holoptychius*) (Johanson and Ritchie, 2000; Young et al., 2010). Redrawn and modified from Golonka (2000) and Blakey (2012).

Fig. 5. Carte paléogéographique du Dévonien terminal illustrant l'occurrence de porolépiformes holoptychiides en Euramérique et au Gondwana. Localités du Emsien–Frasnien (étoiles noires) : 1. Arctique Canadien (*Nasogaluakus*, *Laccognathus*) (Downs et al., 2011 ; Schultze, 2000) ; 2. Groenland (*Holoptychius*, *Glyptolepis*) (Jarvik, 1972) ; 3. Russie et Lettonie (*Holoptychius*, *Glyptolepis*, *Laccognathus*, *Hamodus*, *Paraglyptolepis*) (Obrutschew 1933 ; Vorobyeva, 1987) ; 4. Allemagne (*Glyptolepis*) (Gross, 1936) ; 5. Écosse (*Duffichthys*, *Holoptychius*, *Glyptolepis*) (Ahlberg, 1992) ; 6. Québec (*Holoptychius*, *Quebecius*) (Cloutier and Schultze, 1996) ; 7. Colombie (*Holoptychius*) (Janvier et Villarroel, 2000 ; cette étude) ; 8. Iran (*Holoptychius*) (Lelièvre et al., 1993 ; Schultze, 1973). Localités du Famennien (étoiles blanches) : 1. Groenland (*Holoptychius*) (Jarvik, 1972) ; 2. Lettonie (*Ventalepis*) (Schultze, 1980) ; 3. Belgique (*Holoptychius*) (Clément et al., 2004) ; 4. Canada de l'Est (*Holoptychius*) (Miller et Brazeau, 2007) ; 5. Pennsylvanie (*Holoptychius*, *Glyptolepis*); 6. Australie (*Holoptychius*) (Johanson et Ritchie, 2000 ; Young et al., 2010). Redessiné et modifié à partir de Golonka, 2000 et Blakey, 2012.

might point to a Euramerican origin of *Holoptychius*, but this remains to be tested.

Finally, the co-occurrence of *Holoptychius* and *Asterolepis* in the Cuche Formation of Colombia suggests the dispersion of fish faunas between Euramerica and Gondwana through South America by the beginning of the Late Devonian.

6. Conclusion

This new discovery confirms the presence of holoptychiids in the Colombian Cuche Formation, represented by *Holoptychius* sp. scales and an undetermined holoptychiid tooth, which may belong to *Holoptychius*.

The co-occurrence of *Holoptychius* and other Euramerican taxa (e.g., the antiarch *Asterolepis*) in the Late Devonian of Colombia suggests that prior to the Famennian dispersion of Gondwanan endemics (such as phyllolepid and groenlandaspid placoderms, and rhizodontid and megalichthyid sarcopterygians) in Euramerica, there might have been a limited incursion of Euramerican faunas into Gondwana by the end of the Frasnian (Janvier, 2007; Janvier and Maisey, 2010; Janvier and Villarroel, 1998, 2000).

As Janvier and Maisey (2010) pointed out, this Frasnian-Famennian interchange could have involved exclusively fishes that were bound to marginal marine or fresh waters environments. Further, this would confirm that south-western Euramerica and north-western Gondwana continental landmasses were in close geographic proximity during the Late Devonian (e.g., McKerrow et al., 2000).

Holoptychiid remains (e.g., *Holoptychius*) are found in the vast majority of Devonian tetrapod localities of the world (Blieck et al., 2010; Clément et al., 2004; Lebedev and Zakharenko, 2010). The presence of *Holoptychius* in the Frasnian of Colombia opens the possibility for the Cuche Formation to yield additional remains of Late Devonian sarcopterygian fishes and possibly even early tetrapods.

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