




First pachycormiform (Actinopterygii, Pachycormiformes) remains from the Late Jurassic of the Antarctic Peninsula and remarks on bone alteration by recent bioeroders

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FIRST PACHYCORMIFORM (ACTINOPTERYGII, PACHYCORMIFORMES) REMAINS FROM THE LATE JURASSIC OF THE ANTARCTIC PENINSULA AND REMARKS ON BONE ALTERATION BY RECENT BIOERODERS

SOLEDAD GOUIRIC-CAVALLI,*¹ , LUCIANO L. RASIA,¹ , GONZALO J. MÁRQUEZ,² VILMA ROSATO,³ ROBERTO A. SCASSO,⁴ and MARCELO REGUERO^{1,5}

¹División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina, CONICET, sgouiric@fcnym.unlp.edu.ar;

lucianorasia@fcnym.unlp.edu.ar;

²Cátedra de Palinología, Facultad de Ciencias Naturales y Museo, La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina, CONICET, cosme@fcnym.unlp.edu.ar;

³Laboratorio de Entrenamiento Multidisciplinario para la Investigación Tecnológica, 52 e/121 y 122, B1900AYB, Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, La Plata, Argentina, CONICET, vilmarosato@yahoo.com.ar;

⁴Instituto de Geociencias Básicas, Aplicadas y Ambientales de Buenos Aires, Departamento de Ciencias Geológicas, FCEN, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA, Buenos Aires, Argentina, CONICET,

rscasso@gl.fcen.uba.ar;

⁵Instituto Antártico Argentino, Campus Miguelete, 25 de Mayo 1151, 3° piso B1650HMK San Martín, Buenos Aires, Argentina, mreguero@dna.gov.ar

ABSTRACT—We describe osteichthyan remains from the Upper Jurassic of the Ameghino (= Nordenskjöld) Formation of the Antarctic Peninsula. The fossils are referred to a suspension-feeding pachycormid based on the shape, morphology, and presence of acus fanunculi (needle teeth) on their gill rakers. Due to the fragmentary condition of the Antarctic material, we refer it to aff. *Asthenocormus*. The remains described here represent the first record of a suspension-feeding pachycormid from the Upper Jurassic of the Antarctic Peninsula and the oldest pachycormid yet recovered from Antarctica. The new fossil fish supports a possible early dispersal route through the Mozambique Corridor (= Trans-Gondwana or South African Seaway). We also describe the weathering produced by modern lichens, which might be misinterpreted as original bone structure.

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

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INTRODUCTION

Pachycormiformes is a stem-teleost marine fish group that was present in the seas during the Jurassic and became extinct at the Cretaceous/Paleogene mass extinction. Pachycormiforms comprise two distinct ecological morphotypes: predatory toothed fishes and suspension-feeding fishes, which are toothless (Lambers, 1992; Liston, 2008). Despite a few exceptionally preserved specimens (e.g., Arratia and Schultze, 2013), most pachycormiform descriptions are based on poorly preserved and mostly fragmentary material (Mainwaring, 1978; Lambers, 1992; Gouiric-Cavalli and Cione, 2015a); thus, much morphological information is still missing.

From the Middle Jurassic to the Late Cretaceous, suspension-feeding vertebrates are represented with certainty by a clade of pachycormid actinopterygians (Wagner, 1863; Liston,

2008; Schumacher et al., 2016). However, an elasmosaurid plesiosaur (O’Keefe et al., 2017) and an elasmobranch family (Shimada et al., 2015) may have used a comparable feeding strategy. Notwithstanding the relatively wide temporal range occupied by these large-bodied pachycormids, they are mainly represented in the fossil record by poorly preserved material (e.g., Lambers, 1992; Liston, 2008; Friedman et al., 2010; Gouiric-Cavalli, 2017). In particular, for suspension-feeding pachycormids, poor preservation could be partly explained by the feeble ossification of their skeleton ossified skeleton (Liston et al., 2013).

Suspension-feeding pachycormids include modestly sized taxa (ranging from 2 to ca. 5 m in standard length, i.e., *Asthenocormus*, *Martillichthys*, *Bonnerichthys*, and *Rhinconichthys*; Liston, 2008; Friedman et al., 2013; Schumacher et al., 2016) and large forms (larger than 8 m, such as *Leedsichthys*; Liston et al., 2013). Suspension feeding involves specialization of the oral cavity, and among actinopterygians these modifications are most clearly visible in the gill arches (Gouiric-Cavalli, 2017).

*Corresponding author.

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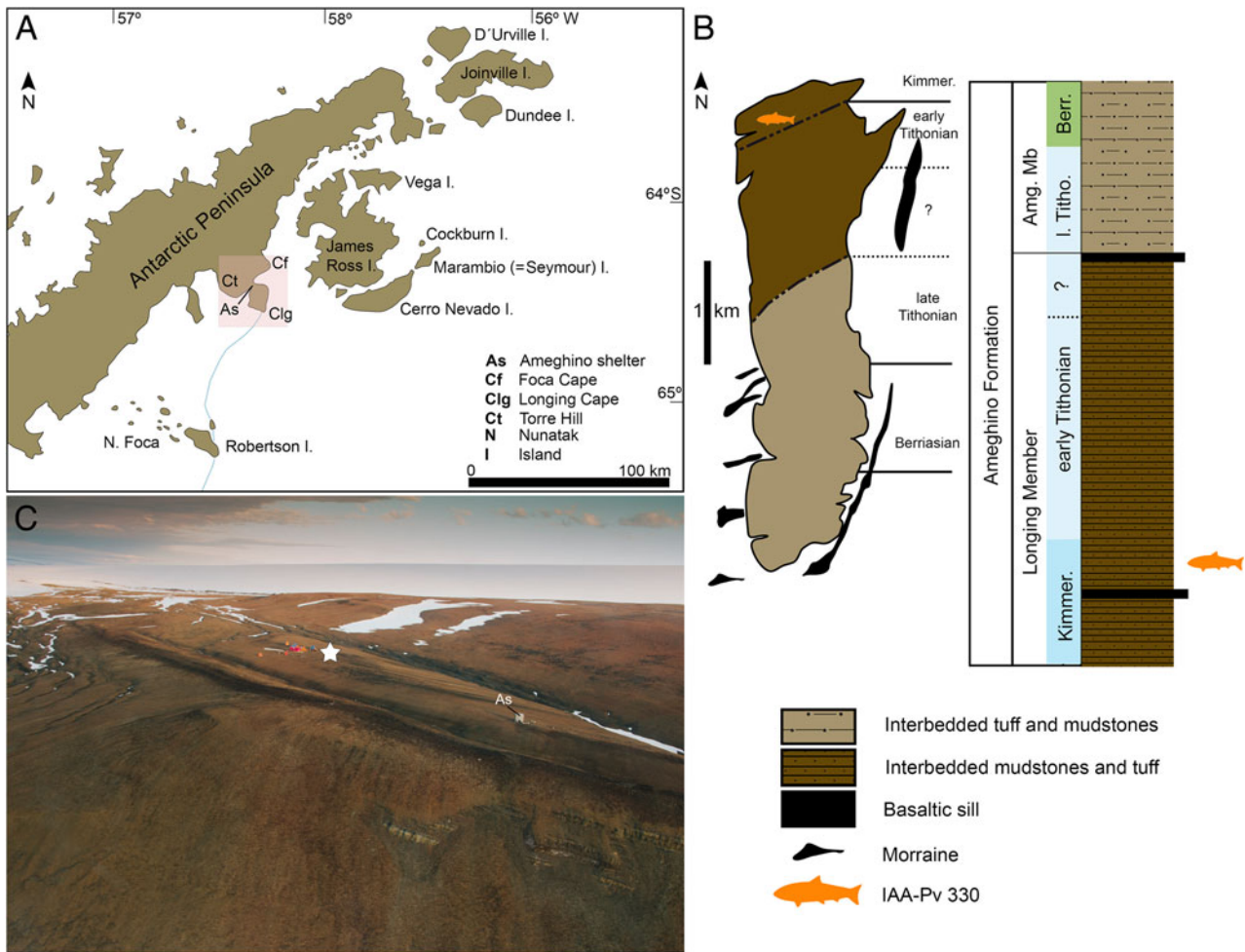


FIGURE 1. **A**, Antarctic Peninsula location map. Modified from del Valle and Nuñez (1988). The square shows the study area. **B**, geological map and lithostratigraphic log of the Ameghino (= Nordenskjöld) Formation. The stratigraphic position of the fish remains is indicated. Modified from Kiessling et al. (1999) and Arratia et al. (2004). **C**, oblique aerial photograph of the study area showing the strata close to the camp site and the position of the studied fossil material (photograph by S. Gouiric-Cavalli). The star indicates the collection site. The prominent black bed is a basaltic sill. **Abbreviation:** As, Ameghino shelter.

Several osteichthyan remains were recovered from Longing Cape near the Ameghino shelter (64°26'S, 58°59'W) during 2016 by an Antarctic summer field expedition carried out by the Instituto Antártico Argentino (Gouiric-Cavalli et al., 2016; Fig. 1). Many of the osteichthyan remains recovered show some degree of structural weathering. We observed that a diverse lichen population proliferated in the area and also that the fish bone had recent lichens attached to its surface. This is not surprising because Antarctica here has a terrestrial vegetation rich in lichens and mosses (Chown et al., 2015), and the lichens form part of the lithobiotic communities living on the surface of rocks or colonizing the inside of lithic substrata (De los Ríos et al., 2005).

The goals of this contribution are (1) to make a taxonomic assignment of the fish remains; (2) to explore and discuss the relevance of a suspension-feeding fish in the Antarctic Peninsula in a paleobiogeographic context; (3) to comment about the ecospace occupied by suspension-feeding vertebrates in the Mesozoic; and (4) to describe the structural weathering observed in the fish bones.

GEOLOGICAL SETTING

The Ameghino (= Nordenskjöld) Formation is a mudstone sedimentary sequence corresponding to the basal infill of the James Ross Basin (Medina and Ramos, 1981, 1983; Farquharson, 1982). It is exposed at a few locations in the northeastern part of the Antarctic Peninsula (Macdonald et al., 1988; del Valle et al., 1992). The Ameghino Formation consists of two members (Whitham and Doyle, 1989): the Longing and Ameghino members (Fig. 1B).

The sedimentary environment of the Ameghino Formation is inferred to be marine, pelagic to hemipelagic, close to an active volcanic arc, and under anoxic (Longing Member) to dysoxic (Ameghino Member) conditions (Doyle and Whitham, 1991; Whitham, 1993; Scasso, 2001; Kietzmann et al., 2009).

The paleontology of the Ameghino Formation is mainly characterized by invertebrates such as ammonoids, nautiloids, bivalves, and radiolarians (e.g., Medina and Ramos, 1983; Whitham and Doyle, 1989; Kiessling and Scasso, 1996; Kiessling et al., 1999). Among vertebrates, there is a predominance of osteichthyan remains (Arratia et al., 2004; Gouiric-

Cavalli et al., 2016), but a few marine reptiles were also recently reported (Gouiric-Cavalli et al., 2016, 2018; O’Gorman et al., 2018). A few fossilized leaves and some fossil wood have also been recovered (e.g., Gouiric-Cavalli et al., 2016).

The Ameghino Formation is considered to be Kimmeridgian to Berriasian in age (Doyle and Whitham, 1991; Kiessling et al., 1999), with the Longing Member being Kimmeridgian–lowermost early Tithonian in age and the Ameghino Member being late Tithonian–Berriasian in age. Ameghino Formation outcrops are scattered along the Antarctic Peninsula. They mostly occur in isolation and are surrounded by ice, or in a complex tectonic contact with other rocks (Kiessling et al., 1999). Some reworked blocks of the Ameghino Formation are present on James Ross Island. These blocks are embedded in the Lower Cretaceous rocks of the Whisky Bay Formation (Macdonald et al., 1988; Richter and Thomson, 1989).

Institutional Abbreviation—**IAA-Pv**, Repositorio Antártico de Colecciones Paleontológicas y Geológicas of the Instituto Antártico Argentino (IAA), San Martín, Argentina.

MATERIALS AND METHODS

The studied specimens were collected at the Longing Gap locality, in the Longing Member of the Ameghino (= Nordenskjöld) Formation (Fig. 1). Fish remains were recovered from one fossiliferous level of late Kimmeridgian age located behind the camp site and gently dipping to the south (Fig. 1C). An exploration grid of 2 × 3 m was studied in the field. Each bone fragment was carefully cleaned with a soft brush and observed with a magnifying glass. In spite of the material being severely crushed and affected by weathering, we have established that all the remains belong to a single specimen. The specimen was studied with a stereoscopic microscope, using different magnifications, at the laboratory of the Vertebrate Paleontology Division of the La Plata Museum. Many fragments were restored and glued with cyanoacrylate.

The bioerosion was analyzed with an FEI Quanta 200 scanning electron microscope (SEM). A chemical microanalysis using the electron probe energy-dispersive X-ray spectroscopy silicon drift detector (EDX SDD) Apollo 40 was carried out to compare the composition of the materials found on the remains with that of the unaltered bone and matrix surfaces. Digital images were compiled and processed using the image software programs Adobe Photoshop and Adobe Illustrator. Measurements were taken with vernier calipers on the specimens and with the free software Fiji, using high-resolution photographs. The descriptive bone terminology follows Lambers (1992) and Liston (2006, 2013). Open nomenclature follows Bengtson (1988).

Lichens were identified using the systematic classification of Øvstedal and Lewis Smith (2001). Apothecia were mounted in glycerin gelatin. The asci and ascospores were measured (25 spores for each sample) using a Nikon Eclipse E200 optic microscope (1000×) and a Nikon Coolpix S10 camera. The usual histochemical reactions were performed: K (KOH 10%) to detect anthraquinones (typical in Teloschistaceae such as *Caloplaca* spp. and allied genera), C (NaClO₂) that gives a pink reaction with depsides such as lecanoric or gyrophoric acid of *Cryptothecia* and *Xanthoparmelia*, and I (KI₃) that indicates the amyloid reactions of the asci and hamathecium with blue staining.

SYSTEMATIC PALEONTOLOGY

ACTINOPTERYGII Cope, 1887

NEOPTERYGII Regan, 1923

PACHYCORMIFORMES Berg, 1937

PACHYCORMIDAE Woodward, 1895

aff. *ASTHENOCORMUS* Woodward, 1895

(Figs. 2, 3)

Material—IAA-Pv 330 consists of several fragments of a single individual preserved in slabs 3–20 mm thick.

Geographic and Stratigraphic Occurrence—Tierra de San Martín (= Graham Land), Antarctic Peninsula, Longing Member of the Ameghino (= Nordenskjöld) Formation (late Kimmeridgian), 64°26′25.5″S, 58°58′44.2″W (Fig. 1).

Remarks—Most of the bones in IAA-Pv 330 could not be identified with any degree of certainty, but nevertheless we identified a fragmentary hyomandibula, ceratohyal, epibranchial, and gill rakers. The morphology of the gill rakers (fanunculi) allowed us to identify the specimen as belonging to a suspension-feeding fish of the order Pachycormiformes (Figs. 2, 3). Suspension-feeding pachycormids are large fishes whose size varies between 2.5 and ca. 16 m in total length (Liston, 2008). They are usually represented by fragmentary material. Their low preservation potential might be associated with the poorly ossified nature of their skeleton (Liston, 2013; Gouiric-Cavalli, 2017).

We compared the Antarctic gill raker with homologous structures in other suspension-feeding pachycormids, i.e., *Asthenocormus*, *Leedsichthys*, *Martillichthys*, and *Rhinconichthys* (in *Bonnerichthys*, the gill rakers are unknown) and conclude that the Antarctic gill rakers (IAA-Pv 330) resemble those of *Asthenocormus* because they have a short bone that bears four to eight well-developed teeth in its distal part (Lambers, 1992:fig. 2b; Liston, 2013; Figs. 2A, B, 3). In contrast, *Rhinconichthys*, *Leedsichthys*, and *Martillichthys* gill rakers (fanunculi) are composed of a stalk with fimbriations directed toward the oral cavity (see Liston, 2013; Schumacher et al., 2016; Gouiric-Cavalli, 2017).

The branchial acus fanunculi (needle teeth) of IAA-Pv 330 are located on a short bone (Figs. 2, 3). The external surface of the teeth is smooth (Fig. 2D). Internally, they do not have a single central pulp cavity but instead possess a pulp cavity divided by dentine trabeculae and completed by infilling denteons formed around each vascular canal (see Ørvig, 1951; Fig. 2B, C). We interpret that the acus fanunculi of the gill rakers might form a capture network when they are in contact with the acus fanunculi of the opposing gill rakers, as is shown in Figure 3A. We note that more information and better-preserved specimens are needed to support this hypothesis because the juxtaposition of these two elements—which are not associated with the stalk—could be simply by chance. The taxonomic assignment of IAA-Pv 330 indicates a potentially new taxon, but as yet we only have little and poorly preserved material to make this assertion.

Paleobiogeographic Implications—Suspension-feeding pachycormids have a bipolar or antitropical distribution, being restricted to high latitudes (Gouiric-Cavalli and Rasia, 2016; Fig. 4), approximately between 30–60° paleolatitude in both hemispheres. This distribution pattern is also clear for some Mesozoic bivalves (Crame, 1986, 1993) and for living large-bodied suspension-feeding vertebrates such as some sharks (e.g., Hubbs, 1952) and baleen whales (e.g., Davies, 1963; Rice, 1967). The opening of the Hispanic Corridor (Fig. 4) played a key role, because it produced a substantial change in the patterns of water circulation, with the establishment of a circum-equatorial current and reduced seasonality in the water circulation within the Tethys Sea (Damborenea, 2017). The

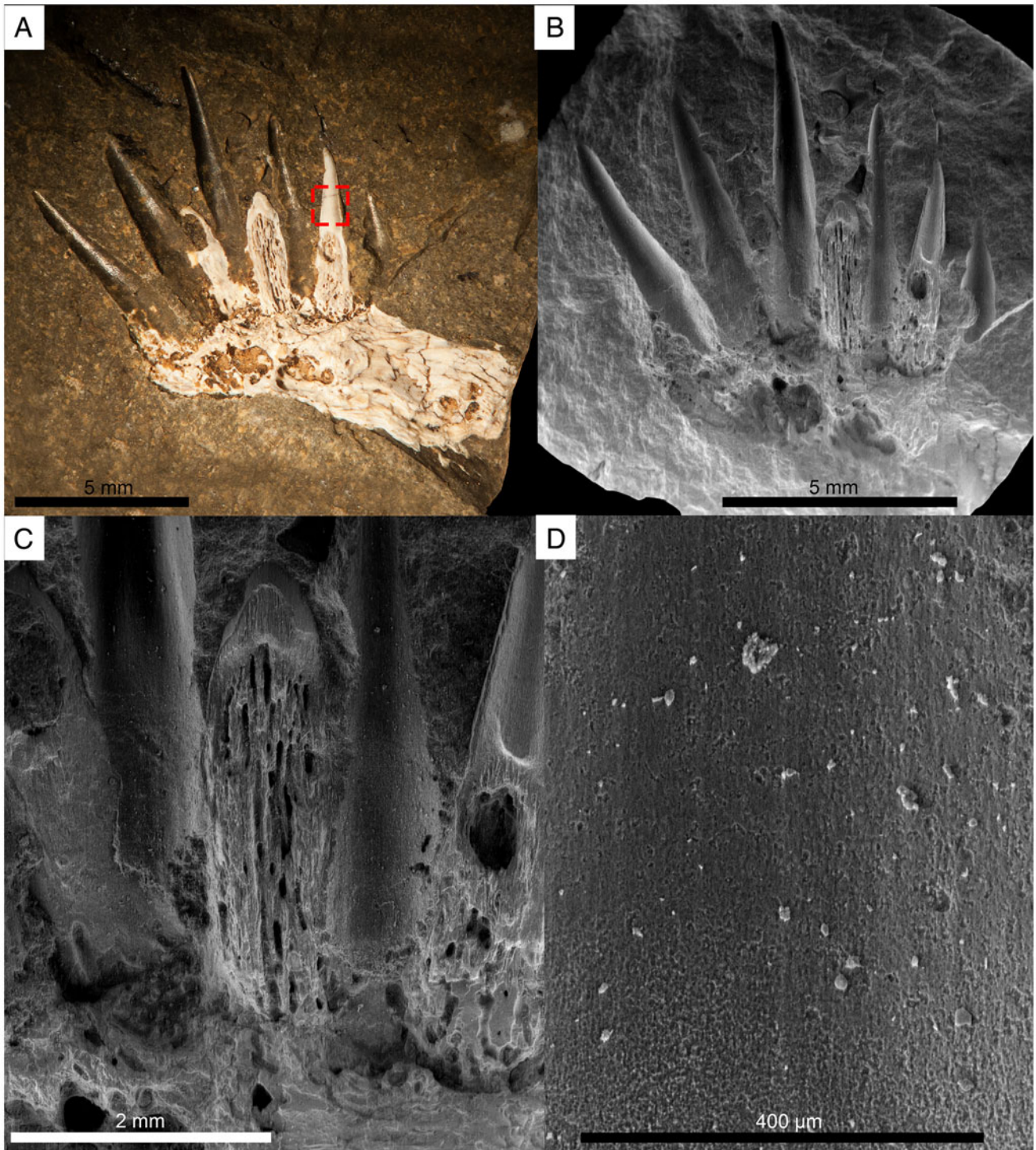


FIGURE 2. IAA-Pv 330 (pars), aff. *Asthenocormus* gill raker with acus fanunculi (needle teeth)-like structures. **A**, acii located over a short bone. **B**, close-up of acii. **C**, detail of acii, showing the pulp cavity divided by dentine trabeculae. **D**, detail of **A** (red square) showing the smooth tooth surface.

opening of the Mozambique Corridor (= Trans-Gondwana or South African Seaway), which connects the Tethys with the Panthalassic (= PaleoPacific) Ocean and separates Africa from India-Antarctica (Fig. 4), also caused significant climatic and paleoceanographic changes, allowing the flow of polar marine waters to the north (Damborenea, 2017).

It has been proposed that during the Tithonian–Berriasian, the Mozambique Corridor functioned as a route for faunal interchange (Leanza, 1995; Fernández, 1997; Shultz et al., 2003; Damborenea, 2017; Prasad et al., 2017; O’Gorman et al., 2018; Gouiric-Cavalli et al., 2018) as the counterpart of the Hispanic Corridor (e.g., Damborenea, 2000, 2017;

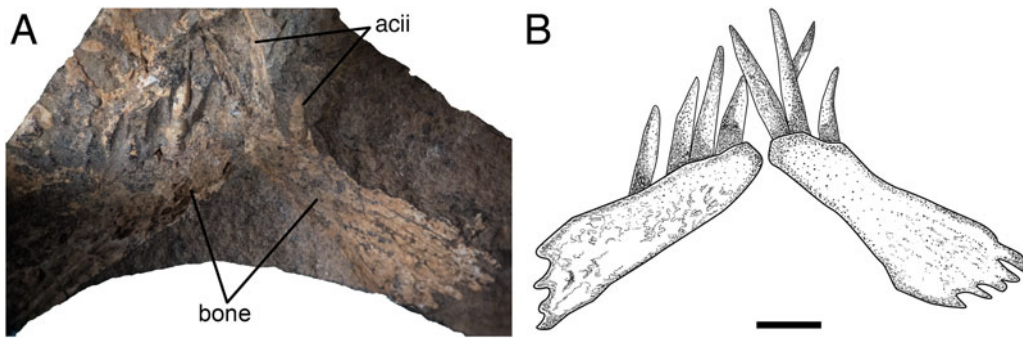


FIGURE 3. Pachycormid gill raker morphology. **A**, aff. *Asthenocormus* opposing gill rakers with opposing acii touching; **B**, interpretative drawing of **A**. Scale bar = 4 mm.

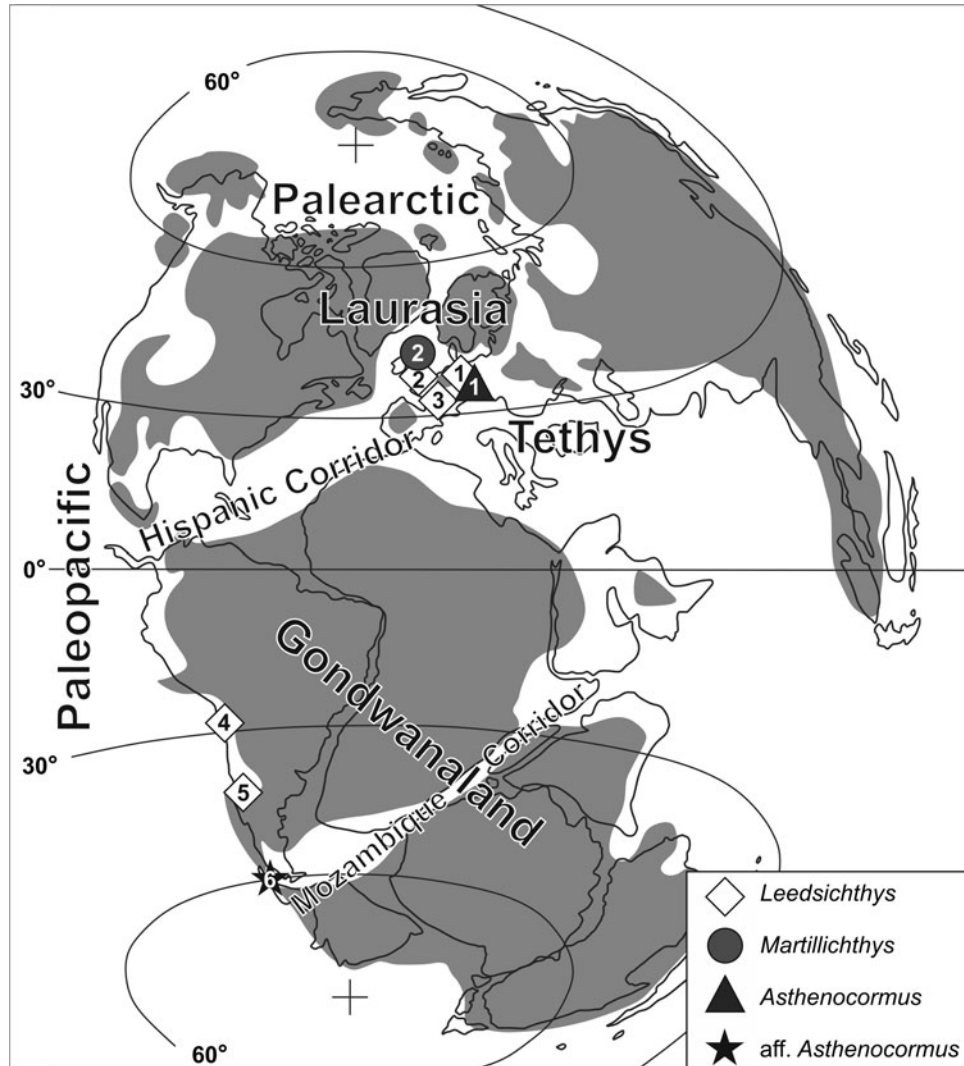


FIGURE 4. Paleobiogeographic map showing the distribution of Jurassic suspension-feeding pachycormids. Map modified from Damborenea (2017). Key: 1, Germany; 2, England; 3, France; 4, Chile; 5, Argentina; 6, Antarctica.

Gasparini et al., 2007; Gasparini, 2009; Damborenea et al., 2013; Gouiric-Cavalli, 2013, 2017; Gouiric-Cavalli and Cione, 2015a, 2015b; Gouiric-Cavalli and Rasia, 2016; Fig. 4).

Regarding the paleobiogeographic distribution of suspension-feeding pachycormids, their fossil record in the Southern Hemisphere remains patchy, being represented by fragmentary

material such as gill rakers referred to *Leedsichthys* found in the Oxfordian of Chile (e.g., Liston, 2010), an isolated *Leedsichthys* gill raker from the Tithonian of Argentina (Gouiric-Cavalli, 2017), and fragments of fin rays in the Maastrichtian of Seymour (= Marambio) Island (Cione et al., 2018). However, suspension-feeding pachycormids are well represented in the Northern

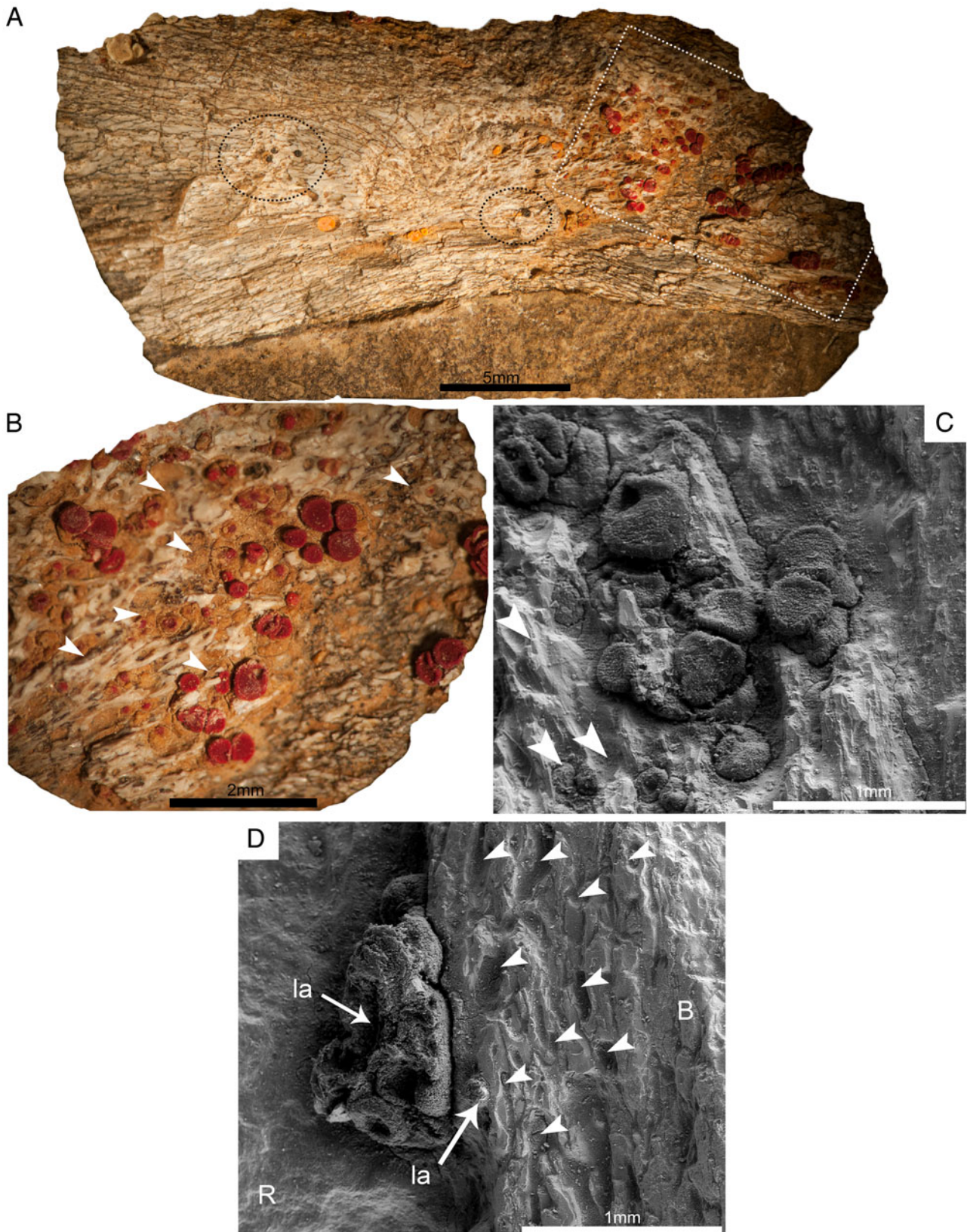


FIGURE 5. Partial ceratohyal with lichens. **A**, lichens that produce bioerosion over the bone. Black dotted ellipse refers to *Sarcogyne privigna* apothecia. White rectangle refers to *Caloplaca iomma* apothecia. **B**, detail of **A**, the lichen *Sarcogyne privigna* invades the bone surface; arrowheads point to bioerosion. **C**, SEM photograph of a fish gill raker with apothecia. **D**, SEM photograph of lichen apothecia in the contact between rock and bone; arrows indicate boring. **Abbreviations:** **B**, fish bone; **ia**, apothecia; **R**, rock matrix.

Hemisphere (e.g., Lambers, 1992; Liston, 2008; Friedman et al., 2010, 2013; Schumacher et al., 2016).

The discovery of a Kimmeridgian suspension-feeding pachycormid in the eastern Antarctic Peninsula provides support for the early migration/dispersal of these fish along the Mozambique Corridor (Fig. 4). However, the direction of migration/dispersal through both pathways (Mozambique and Hispanic corridors) is still not known with certainty, because the Jurassic units in part of Europe and especially in the Southern Hemisphere, have been poorly explored (Liston, 2010; Gouiric-Cavalli, 2013, 2017; Gouiric-Cavalli and Cione, 2015a, 2015b). This finding supports the hypothesis that the bipolar distribution was a large-scale phenomenon during the Jurassic, and that it was related to changes in ocean circulation and the establishment of a circumequatorial current (Damborenea, 2017).

Remarks on Ecospace (= Mode of Life)—The concept of ecospace “refers to possible combinations of important ecological parameters without reference to limiting conditions, resources or competition among species” (Bambach et al., 2007:4). This concept implies that an organism adapts to exploit an available ecospace. The suspension-feeding ecospace is occupied by large nektonic coastal and oceanic vertebrates (Cione and Reguero, 1998) that today include baleen whales, some sharks (whale, megamouth, and basking sharks), mobulid rays, and, putatively, some seals (crabeater, leopard, and Antarctic fur seals; see Sanderson and Wassersug, 1993; Croll et al., 2018).

In the Jurassic, a similar ecospace was exclusively occupied by a clade of actinopterygian fishes: the suspension-feeding Pachycormiformes (represented by *Leedsichthys*, *Asthenocormus*, *Martillichthys*, and the aff. *Asthenocormus* reported here). Similarly, during the Paleozoic, large placoderms such as *Titanichthys* may have occupied a suspension-feeding ecospace (Boyle and Ryan, 2017). In the Cretaceous, the suspension-feeding ecospace was occupied by the pachycormids: *Rhinconichthys*, *Bonnerichthys*, and an indeterminate suspension feeder (Friedman et al., 2010, 2013; Cione et al., 2018), plus other large putative suspension-feeding vertebrates (sharks and plesiosaurs; Cavin, 2010; Shimada et al., 2015; O’Keefe et al., 2017; Supplementary Data, Fig. S1).

Pachycormiforms were certainly the most successful vertebrate group exploiting the suspension-feeding ecospace in the Mesozoic. The Mesozoic large suspension-feeding vertebrates became extinct at the K–Pg boundary (Fig. S1). Strikingly, we note that all large suspension-feeding taxa (both extinct and extant) and not only mysticetes and osteichthyans, as was suggested by Friedman (2012), are closely related to large pelagic predators. Suspension-feeding pachycormids were considered mesoplanktonic fishes that probably fed on small fishes (Liston, 2006, 2008) as well as juvenile ammonites and belemnites (Tajika et al., 2018).

Remarks on Modern Bioerosion—Bioerosion implies “the destruction and removal of consolidated mineral or lithic substrate by direct action of organisms” (Neumann, 1966:92). The process involves the weakening and breakdown of structures due to the chemical and mechanical activities of biotic agents (Glynn and Manzello, 2015). Biodeterioration (= biodegradation) is any change—deterioration or degradation—of any material due to biological causes (Hueck, 1965).

Bioerosion might be misinterpreted as original bone structures (e.g., ornamentation) and is widely distributed across the actinopterygian bones and feces from the Late Jurassic Ameghino (= Nordenskjöld) Formation. The bones of aff. *Asthenocormus* IAA-Pv 330 show discrete ellipsoidal to oval borings and microborings (Fig. 5). The holes show a variable degree of corrosion and weathering (Fig. 5). Boring measurements are given in Table S1; note that the length is always greater than the width (Fig. 5B–D). Both borings and

microborings are isolated or grouped to form a dense network (similar to an egg box) on the surface of the bone (Fig. 5). Also, some extremely elongated marks are associated with some fish bones (Fig. 5D), those marks having the major axis parallel or subparallel to the major axis of the bone.

Recent lichen activity on Cenozoic Antarctic material was previously reported by Acosta Hospitaleche et al. (2011). Crustose-type lichens *Caloplaca iomma* Olech and Söchting and *Sarcogyne privigna* (Ach.) A. Massal were identified on bone surfaces. Consequently, the bioerosion on IAA-Pv 330 is assumed to be the product of recent lichen activity (Fig. 5). Note that the agent that produces the extremely elongated marks on fish bones remains unknown, but lichens cannot be dismissed from consideration. *Caloplaca iomma* is an endemic Antarctic lichen species inhabiting the South Orkney and South Shetland islands, as well as the Antarctic Peninsula (Øvstedal and Lewis Smith, 2001; Fig. S2B, D, E). *Caloplaca iomma* is characterized by having a sessile apothecium whose morphology varies with age, being a flat disc in younger specimens and somewhat convex in adults. The apothecia pigmentation also varies from reddish orange to reddish brown (Fig. 5A). *Sarcogyne privigna* is a cosmopolitan lichen species (Øvstedal and Lewis Smith, 2001; Fig. S2A, C) characterized by a sessile apothecium of black to dark red color, not pruinose (Fig. 5A).

The biogenic process on bones of aff. *Asthenocormus* IAA-Pv 330 is classified as endolithic activity produced by lichens on subaerial surfaces (Mikuláš, 2001). The lichen activity results in an increase in porosity and weakening of the bone, producing alteration through corrosion of the material. The biodeterioration in bones of aff. *Asthenocormus* IAA-Pv 330 includes a variable degree of corrosion and dissolution of the fossil, not only at the contact between the thalli and the fossil bone but also beyond the margins of the thalli where the carbonic acid may penetrate (Fig. 5B). The rounded holes of weathering origin correspond in shape to the lichens (Fig. 5).

EDX Spectra—The EDX spectrum of the lichen surface shows major peaks of silica, oxygen, and calcium, and minor peaks of aluminum, carbon, phosphorus, potassium, and iron were also observed (Fig. S3). The lichen spectrum shows that lichens may take advantage of the high calcium and phosphorous concentrations of the bones. The EDX spectrum from the bottom of the marks over the actinopterygian bone (Fig. S3) shows peaks of calcium, phosphorus, and oxygen with minor peaks of carbon, silicon, aluminum, and iron; this spectrum is consistent with calcium phosphate. The EDX spectrum of the matrix revealed high concentration of oxygen, iron, and silicon and minor peaks of aluminum, magnesium, sodium, and potassium (Fig. S3), which is the composition of a typical silicate rock.

The occurrence of carbon and the high proportion of calcium might indicate the presence of calcium oxalate attributable to the lichen action. The high levels of calcium and phosphorus (Fig. S3) are typical for a fossilized bone. Potassium might be responsible for the orange and yellow coloration of lichens, which produce pulvinic acids.

CONCLUSIONS

Based on the results provided, we conclude the following: (1) we report the first record of a suspension-feeding pachycormid from the late Kimmeridgian of the Antarctic Peninsula, which is the southernmost record in the world and the oldest suspension-feeding fish in Antarctica; (2) the Antarctic record of suspension-feeding pachycormids provides support for an early migration/dispersal through the Mozambique Corridor (= Trans-Gondwana or South African Seaway); (3) the direction of the migration/dispersal of suspension-feeding pachycormids through the Hispanic/

Mozambique corridors remains unknown until more field work and study of the recovered material in the Northern, and especially the Southern Hemisphere, are conducted; (4) suspension-feeding pachycormiforms have a wider distribution than previously recognized, being present in the late Kimmeridgian of the Antarctic Peninsula; (5) in the Mesozoic, pachycormiforms were the most successful vertebrates exploiting the large suspension-feeding ecospace; (6) when in opposition, acus fanunculi (needle teeth) on the gill rakers might form an effective network for capturing invertebrates and small fish; (7) the new Antarctic record supports the hypothesis of an early bipolar or antitropical distribution for the clade of suspension-feeding pachycormids; (8) the bioerosion on the surface of the bones has been demonstrated to be produced by recent epilithic lichen activity; (9) recent lichens present in the Jurassic fish remains played the role of a biological weathering agent producing biochemical erosion of the bone; and (10) the lichens that produced the marks over the bone surface correspond to at least two different extant lichen species, *Caloplaca iomma* and *Sarcogyne privigna*.

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ORCID

Soledad Gouiric-Cavalli  <http://orcid.org/0000-0003-2026-5973>

Luciano L. Rasia  <https://orcid.org/0000-0002-0300-4918>

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