

Bromalites from the Ameghino (=Nordenskjöld) Formation Upper Jurassic of Antarctic Peninsula

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Recibido: 20 de octubre 2022 - Aceptado: 11 de abril 2023 - Publicado: 19 de julio 2023

Para citar este artículo: Mauricio A. Bigurrarena Ojeda, Soledad Gouiric-Cavalli, Leandro M. Pérez, & Marcelo A. Reguero (2023). Bromalites from the Ameghino (= Nordenskjöld) Formation Upper Jurassic of Antarctic Peninsula. *Publicación Electrónica de la Asociación Paleontológica Argentina* 23 (2): 45–64.

Link a este artículo: <http://dx.doi.org/10.5710/PEAPA.11.04.2023.446>

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ISSN 2469-0228

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BROMALITES FROM THE AMEGHINO (=NORDENSKJÖLD) FORMATION UPPER JURASSIC OF ANTARCTIC PENINSULA

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Abstract. We present the study of the bromalites retrieved from the Upper Jurassic Ameghino (=Nordenskjöld) Formation at Longing Gap in the Antarctic Peninsula. The material was morphologically and chemically analyzed. We made a qualitative study and a taphonomic analysis of the specimens and tested paleobiological and paleoecological hypotheses. We conclude that the samples analyzed are coprolites and propose a new ichnotaxon, *Antarctoscoprus longinensis* ichnogen. and ichnosp. nov., characterized by being a small and flat coprolite differing from other ichnogenera by its composition, which consists mainly of actinopterygian remains (e.g., scales, vertebrae, skull bones, and teeth). *Antarctoscoprus longinensis* includes three morphotypes (i.e., circular, subcircular, and elongated) derived from an elongated three-dimensional original form by compactation. Based on the internal content, we infer the producers of the coprolites were carnivorous predators, putatively an ichthyophagous taxon. Due to the abundance of actinopterygians—mainly aspidorhynchids and ichthyodectids—and the size of the coprolites we propose macropredator fishes as the putative producers. The mainly undisrupted fish carcasses and coprolites allow us to conduct further studies that might lead to a better understanding of the ancient communities living in the Late Jurassic Sea that surrounded Antarctica.

Key words. Coprolites. Actinopterygian remains. Macropredator vertebrates. West Antarctica. Longing Gap.

Resumen. BROMALITOS DE LA FORMACIÓN AMEGHINO (=NORDENSKJÖLD) JURASICO SUPERIOR DE LA PENÍNSULA ANTÁRTICA. Presentamos el estudio de los bromalitos recuperados de la Formación Ameghino (=Nordenskjöld) del Jurásico Superior en Longing Gap, en la Península Antártica. El material fue analizado morfológica y químicamente. Realizamos un estudio cualitativo y un análisis tafonómico de los especímenes y pusimos a prueba hipótesis paleobiológicas y paleoecológicas. Concluimos que las muestras analizadas son coprolitos y proponemos un nuevo icnotaxón, *Antarctoscoprus longinensis* ichnogen. e ichnosp. nov., caracterizado por ser un coprolito pequeño y plano que se diferencia de otros icnogéneros por su composición, que consiste principalmente en restos de actinopterigios (por ejemplo, escamas, vértebras, huesos del cráneo y dientes). *Antarctoscoprus longinensis* incluye tres morfotipos (es decir, circular, subcircular y alargado) derivados de una forma original tridimensional alargada por compactación. Basándonos en el contenido interno, los productores de los coprolitos eran depredadores carnívoros, putativamente un taxón ictiófago. Debido a la abundancia de actinopterigios—principalmente aspidorrínquidos e ictiodéctidos—y al tamaño de los coprolitos, proponemos a los peces macrófagos como supuestos productores. Los cadáveres de peces y los coprolitos, en su mayoría intactos, nos permiten llevar a cabo nuevos estudios que podrían conducir a una mejor comprensión de las antiguas comunidades que vivían en el Mar Jurásico Tardío que rodeaba la Antártida.

Palabras clave. Coprolitos. Restos de actinopterigios. Vertebrados macropredadores. Antártida Occidental. Longing Gap.

BROMALITES *sensu* Hunt (1992) are any (oral or anal) ejecta and *in situ* intestinal matter (Hunt, 1992, p. 221). Thus, the term bromalite includes coprolites, cololites and regurgitalites (Hunt & Lucas, 2012a; Hunt *et al.*, 2012a–c) and provide direct evidence of the diet and digestive physiology of organisms. Bromalites are relatively common in the fossil record (e.g., Hunt & Lucas, 2014, 2020, 2021) being the co-

prolites the most common and easily identifiable bromalites (Häntzschel, 1975; Hunt *et al.*, 1998; Vallons, 2012; Hunt & Lucas, 2020).

Because bromalites bring direct evidence of the presence of organisms, their analysis and study add meaningful information relative to the paleobiology of extinct animals as indicative of 1) predator/prey interactions (e.g., Hunt &

Lucas, 2021; Hunt *et al.*, 2012a–c; Schweigert & Dietl, 2012; Foster *et al.*, 2022; Dentzien-Dias *et al.*, 2018, 2020), 2) dietary habits (*e.g.*, Hunt & Lucas 2020, 2021; Hunt *et al.*, 2012a–c; Dentzien-Dias *et al.*, 2018, 2020), and 3) trophic levels of an ancient community (*e.g.*, Milán *et al.*, 2015; Luo *et al.*, 2017; Cueillie *et al.*, 2020). Moreover, bromalites study and classification indirectly contribute to biostratigraphic and paleobiogeographical information (*e.g.*, Hunt & Lucas, 2014, 2020, 2021; Hunt *et al.*, 1998, 2012c). The identification of the bromalites producer is difficult and risky (Dentzien-Dias *et al.*, 2020), being this statement especially true for coprolites and regurgitalites.

Mesozoic coprolites are commonly found in deposits of marine and brackish environments from Europe (*e.g.*, Buckland, 1829; Hunt *et al.*, 2007, 2012a, b; Barrios-de Pedro *et al.*, 2018; Hunt & Lucas, 2020, 2021 and references therein). Coprolites are relatively abundant in the Jurassic (Hunt & Lucas, 2021 and references therein). For instance, the chondrichthyan coprolite ichnogenera *Sauropros* and *Liassocpros* were described for the Early Jurassic of England at Lyme Regis (Hunt *et al.*, 2007). Also, the coprolite ichnogenus *Strabelocoprus*—assigned to a chondrichthyan or sarcopterygian fish—was reported from the Early Jurassic of England in Dorset and Somerset (Hunt *et al.*, 2012b). Coprolites attributed to marine reptiles such as *Ichtyosaurolites* ichnosp. were described also from the Early Jurassic of Lyme Regis (Hunt *et al.*, 2012a); other coprolites, termed *Plektecoprus* ichnosp., were recorded from the Early Jurassic of Yorkshire in England (Hunt *et al.*, 2012a). Lastly, the coprolite ichnogenus *Falcatoopros* was described for the Early–Late Jurassic of Peterborough, England (Hunt *et al.*, 2007).

The vast majority of Late Jurassic coprolites were reported from Middle Purbeck and Oxford Clay localities in southern England and from the Solnhofen and Nusplingen *Lagerstätten* in Bavaria, Germany (*e.g.*, Hunt *et al.*, 2012a; Schweigert & Dietl, 2012; Ebert *et al.*, 2015; Hunt & Lucas, 2021). The coprolites from Nusplingen have been interpreted as produced by ammonites, actinopterygians, chondrichthyans and marine thalattosuchian crocodyliforms (Schweigert & Dietl, 2012).

In South America, the vertebrate coprolite record comes from the Paleozoic (Dentzien-Dias *et al.*, 2012, 2017) and Mesozoic of Brazil (Francischini *et al.*, 2018; Souto &

Fernandes, 2015), Miocene of Venezuela (Dentzien-Dias *et al.*, 2018), Pliocene of Chile (Hunt & Lucas, 2018) and Pleistocene of Peru (Hunt & Lucas, 2019).

In Argentina, coprolites interpreted as made by vertebrates were reported from Triassic and Cenozoic continental deposits (*e.g.*, Hofreiter *et al.*, 2003; Chimento & Rey, 2008; Aceñolaza, 2012; Krause & Piña, 2012; Mancuso *et al.*, 2017). Particularly, the published fossil record of coprolites from Antarctica is scant, being restricted to the Permian Buckley Formation (Retallack & Krull, 1997) in the Transantarctic Mountains, and to the Jurassic Ameghino (=Nordenskjöld) Formation in the Antarctic Peninsula (Doyle & Whitham, 1991, fig. 5; Bigurrarena Ojeda *et al.*, 2017; Gouiric-Cavalli *et al.*, 2017, 2019; Fig. 1.1). At Longing Gap (type locality of the Ameghino Formation), an extensive bromalite collection has been retrieved during the Summerfield Argentinian Campaigns (SFAC 2016, 2020, 2022).

The main goals of this contribution are: 1) provide a quantitative morphological characterization of a sample of bromalites retrieved from the Ameghino Formation, 2) make a qualitative description, 3) a taxonomic identification of the bromalites and their internal content, 4) make a taphonomic analysis of the material, and 5) identify the putative producer of the bromalites.

MATERIAL AND METHODS

Material

During three (2016, 2020, and 2022) Summerfield Argentinian Campaigns (SFAC) we retrieved a large amount (*ca.* 600) of bromalite samples at Longing Gap. This study deals with the first retrieved batch in 2016 (IAA-Pv 423), which comprises 170 bromalites and showed to be representative of all the main morphotypes recovered at the Ameghino Formation.

The specimens were found in the Longing Member of the Ameghino (=Nordenskjöld) Formation in Longing Gap, Antarctic Peninsula (64° 26' 25.5" S / 58° 58' 44.2" W; Fig. 1). The material is housed in the Repositorio de Colecciones Geológicas y Paleontológicas of the Instituto Antártico Argentino under the number IAA-Pv 423. A letter follows the collection number in those specimens figured in this contribution.

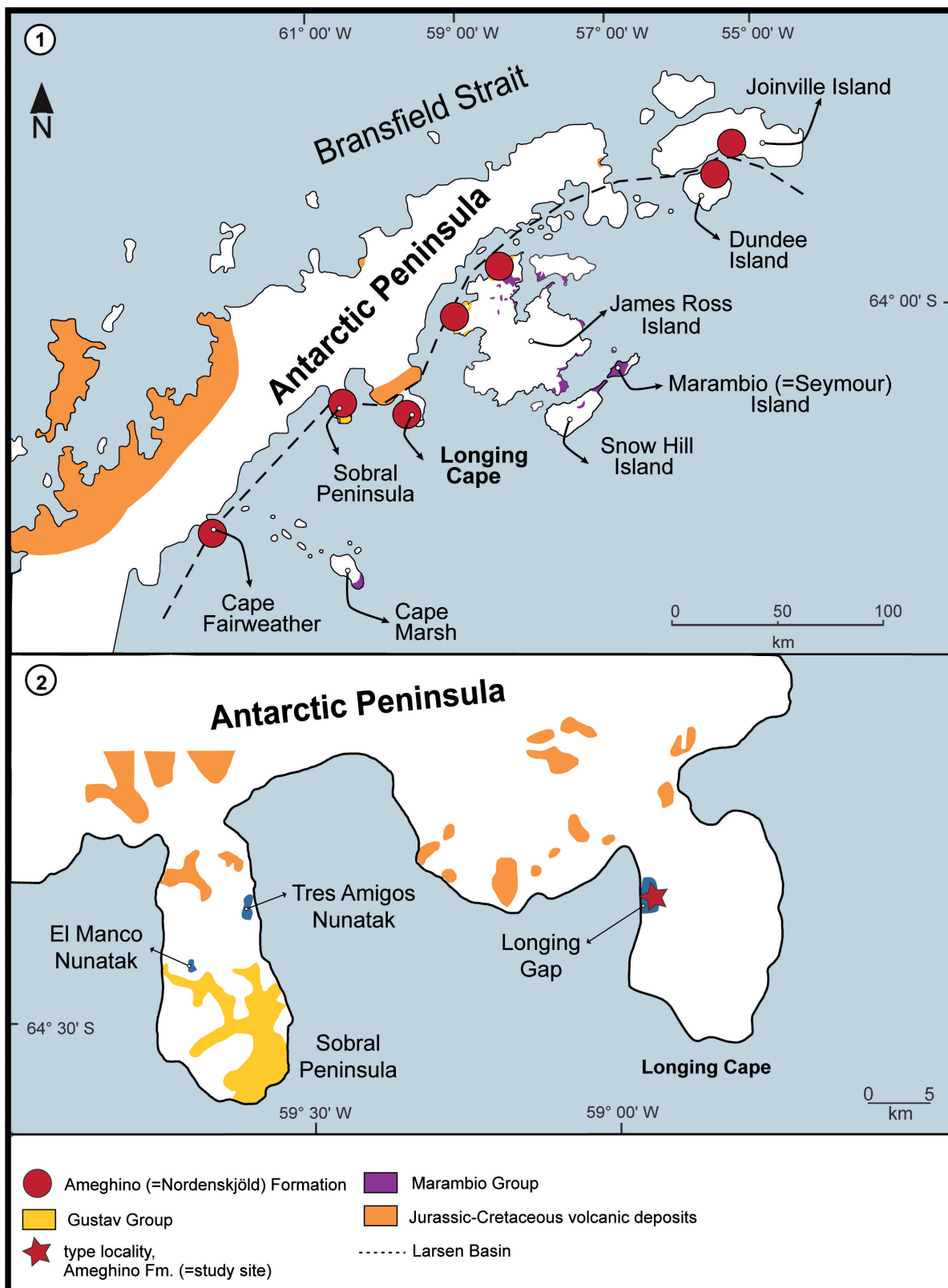


Figure 1. Geographic location map of the Larsen Basin in the Antarctic Peninsula the figure illustrates the Jurassic-Cretaceous outcrops. **1**, Geological scheme of the Larsen Basin showing Jurassic outcrops of the Ameghino Formation in red dots, the Gustav Group in yellow and the Marambio Group in violet; **2**, Geological sketch map of the Sobral Peninsula and the Longing Cape. Red star show the outcrops at the type locality of the Ameghino Formation from where the specimens were retrieved (modified from Elliot, 1988 and Kietzmann & Scasso, 2020).

Methods

The description of the morphology and internal content was based on the 170 specimens. Each sample was analyzed at three scales: macroscopic (measurements were taken using a caliper and definition of contours with the naked eye), mesoscopic (using a stereoscopic microscope), microscopic (under a petrographic microscope and SEM). Specimens with continuous outlines were classified as complete, whereas those with an interrupted outline as incomplete. The morphological classification (Fig. 2) and diagnosis of the new ichnotaxon proposed were based using only complete specimens (62% of samples; $n = 105$; see Supplementary Online Table 1). For the morphological characterization (Fig. 2), we consider the length of the major axis (MA), measured in a straight line that joins the two farthest ends of the coprolite, passing through the center; the length of the minor axis (MI), measured perpendicular to the major axis, passing through the center, and the relationship between both axes.

The bromalites' gross morphology and their internal content were analyzed under the naked eye and with the help of a binocular microscope ZEISS–Stemi 2000–C. Two bromalites were thin-sectioned in order to assess their internal content microstructure. The sections were studied using a petrographic polarizing microscope Nikon® Eclipse E200, with an associated Leica D camera FC290 HD. Photos of the bromalites were taken using a digital camera Canon Powershot G10 attached to the ZEISS–Stemi 2000–C binocular microscope. Digital images were compiled and processed using image software, Adobe Photoshop CC® and Illustrator CC®.

Seven bromalites were analyzed under a Scanning Electron Microscope FEI ESEM Quanta 200 equipped with an electron source from a tungsten filament with 200 V–30 kV accelerating voltage. The samples were analyzed under LV with a precision of 0.1 to 1 Torr, without gold (Au) coating. The EDS SDD Apollo 40 attached to the SEM was used to identify the chemical composition of the bromalites and the host rock. Secondary electron detectors were used to look for a high topographic contrast image of the surface of the bromalite under examination. Backscattered electron detectors of two sectors were employed in order to observe variations in the atomic number of the elements detected

on the bromalite surface. Heterogeneity of the sample is expressed in the image through different gray tonalities depending on the atomic number (Galván Josa *et al.*, 2013).

X-ray diffraction analysis was performed to determine the structure of minerals in the bromalite. The analysis involves sieving the fine material using a mesh of <20 microns, pattern of diffraction was measured using a PANalytical X'Pert PRO diffractometer with a CU lamp ($k = 1.5403 \text{ \AA}$), to 40 m \AA and 40 kV. Diffraction patterns were measured from 4° to 37° , with a scanning speed of $0.04^\circ/\text{s}$. The software Origin was selected for the edition of the results.

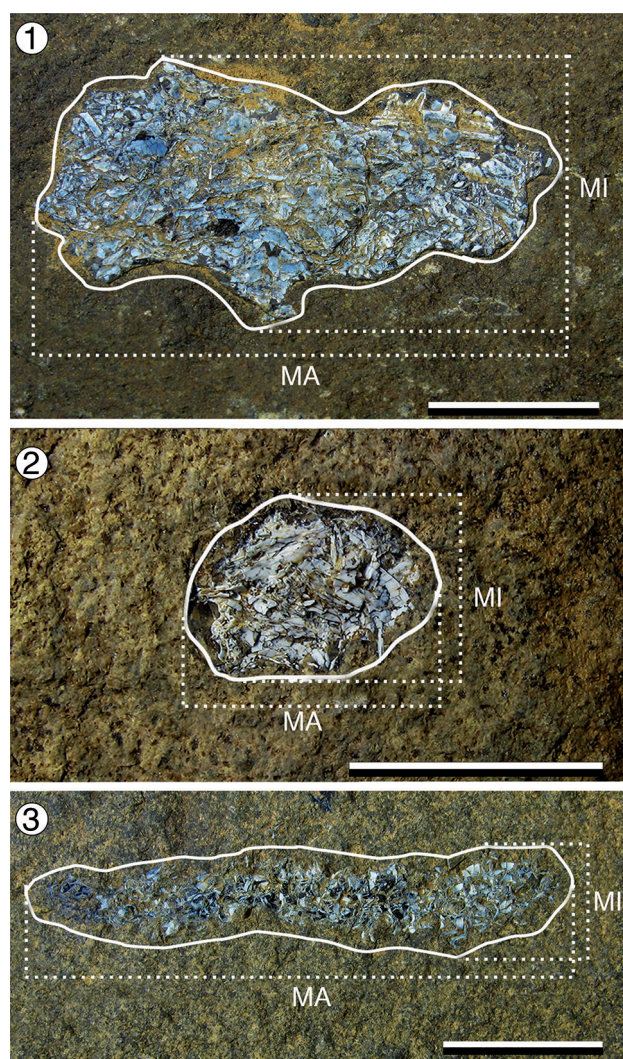


Figure 2. General morphology of coprolites gathered in IAA-Pv 423 (partim). 1, IAA-Pv 423 a subcircular morphotype; 2, IAA-Pv 423 b circular morphotype; 3, IAA-Pv 423 c elongated. Scale bar= 1 cm.

Abbreviations. **BS**, Backscattered electrons. **Ch**, ceratohyal. **CIG**, Centro de Investigaciones Geológicas (CONICET-UNLP). **CONICET**, Consejo Nacional de Investigaciones Científicas y Técnicas. **d.ps**, damaged periosteal surface. **d.tt**, damaged trabecular tissue. **EDS**, Energy Dispersive X-ray spectroscopy. **f.v**, fractures developed in vertebral centra. **IAA**, Repositorio Antártico de Colecciones Paleontológicas y Geológicas, Instituto Antártico Argentino (Pv is for vertebrate paleontology collection). **LIMF**, Servicio de Microscopía Electrónica de Barrido y Microanálisis, Departamento de Mecánica, Facultad de Ingeniería (UNLP). **LV**, Low Vacuum mode. **MA**, major axis. **MA/MI**, ratio between major axis to minor axis. **m.f**, mosaic fractures. **MI**, minor axis. **MLP**, Museo de La Plata (UNLP). **SEM**, Scanning Electron Microscope. **TL**, total sample. **UNLP**, Universidad Nacional de La Plata. \bar{X} , average. **2D**, two dimensions. **3D**, three dimensions.

GEOLOGICAL SETTING

The Ameghino (=Nordenskiöld) Formation (Medina & Ramos, 1981; Farquharson, 1982) outcrops are scattered along the eastern margin of the Antarctic Peninsula between the James Ross Island in the North and the Cape Fairweather in the South. The outcrops mostly occur in isolation, being surrounded by extensive ice fields (Fig. 1.1) or in complex tectonic contact with other rocks (Kiessling *et al.*, 1999). The Ameghino Formation consists of beds of mudstone and tuff, gathered in two members: Longing and Ameghino (Whitham & Doyle, 1989). The Ameghino Formation deposited in a marine, pelagic to hemipelagic environment close to an active volcanic arc, under anoxic (Longing Member) to dysoxic (Ameghino Member) conditions (Doyle & Whitham, 1991; Whitham, 1993; Scasso, 2001; Kietzmann *et al.*, 2009).

The Ameghino Formation is considered Kimmeridgian to Berriasian in age (Doyle & Whitham, 1991; Kiessling *et al.*, 1999). The Longing Member is interpreted to be Kimmeridgian–lower Tithonian in age, and the Ameghino Member is considered upper Tithonian–Berriasian in age (Kietzmann & Scasso, 2020). Although both the Longing and Ameghino members contain ash layers, those in the Ameghino Member are thicker and more numerous (Doyle & Whitham, 1991). Bioturbation (mainly *Chondrites* ichnosp., but also, *Planolites* ichnosp. and *Zoophycos* ichnosp.) is

common in the middle and uppermost part of the Ameghino Member (Doyle & Whitham, 1991). Coprolites have been reported only from the Longing Member (Doyle & Whitham 1991, p. 402, fig. 5).

Macroinvertebrates such as ammonoids, nautiloids, and bivalves (*e.g.*, Medina & Ramos, 1981, 1983; Farquarson, 1982; Doyle & Whitham, 1991) characterize the invertebrate fossil record of the Ameghino Formation at the Longing Gap type locality (Fig. 1.2). Microfossils (radiolarians and calcispheres) were also retrieved (Kiessling & Scasso, 1996; Kiessling *et al.*, 1999; Kietzmann & Scasso, 2020). The vertebrate fossil record consists mainly of actinopterygian fishes (Arratia *et al.*, 2004; Gouiric-Cavalli *et al.*, 2017, 2019). Recently, there have been reports of a few and scattered marine reptiles (O’Gorman *et al.*, 2018; Campos *et al.*, 2021).

RESULTS

Macroscopic analysis

Examined specimens are preserved two-dimensionally. However, they are derived from a 3D structure, crushed and partially deformed by sediment weight (diagenesis) (see below). Macroscopic analysis of the sample revealed a marked variation in morphology and size characterized by MI ranging from 5–25 mm and MA ranging from 7–40 mm.

Based on the external features (mainly the outline) and using the ratio MA/MI, we identified three main morphotypes (Fig. 2.1–2.3). Morphotype S shown in Figure 2.1 corresponding to a subcircular morphotype ($n=33$), has an \bar{X} MA= 23.32 mm, \bar{X} MI= 14.16, MA/MI= 1.65. Morphotype C shown in Figure 2.2 corresponding to a circular morphotype ($n=61$) has an \bar{X} MA= 21.21 mm, \bar{X} MI= 16.80 mm, MA/MI= 1.26. Morphotype E illustrated in Figure 2.3 corresponding to an elongated morphotype ($n=11$) has an \bar{X} MA= 25.53 mm, \bar{X} MI= 10.52, MA/MI= 2.43. Supplementary Online Table 1 summarizes the preservational features recognized in the different morphotypes.

The bromalites have a fine internal biogenic matrix associated with large elements corresponding to the consumed prey (Fig. 3). The large elements (bones, scales and teeth) appear to be incompletely digested and show taphonomic features (*e.g.*, fractures, microdiaclasses, dissolution marks; Fig. 3). The bromalites do not exhibit scrolling and are non-spiral cylindrical (*i.e.*, without any internal structure,

compared to Rakshit *et al.*, 2018). A general feature observed in the analyzed sample is the coloration of the in-

ternal content, which can appear as white, black, blue or a combination of these colors (Fig. 3).

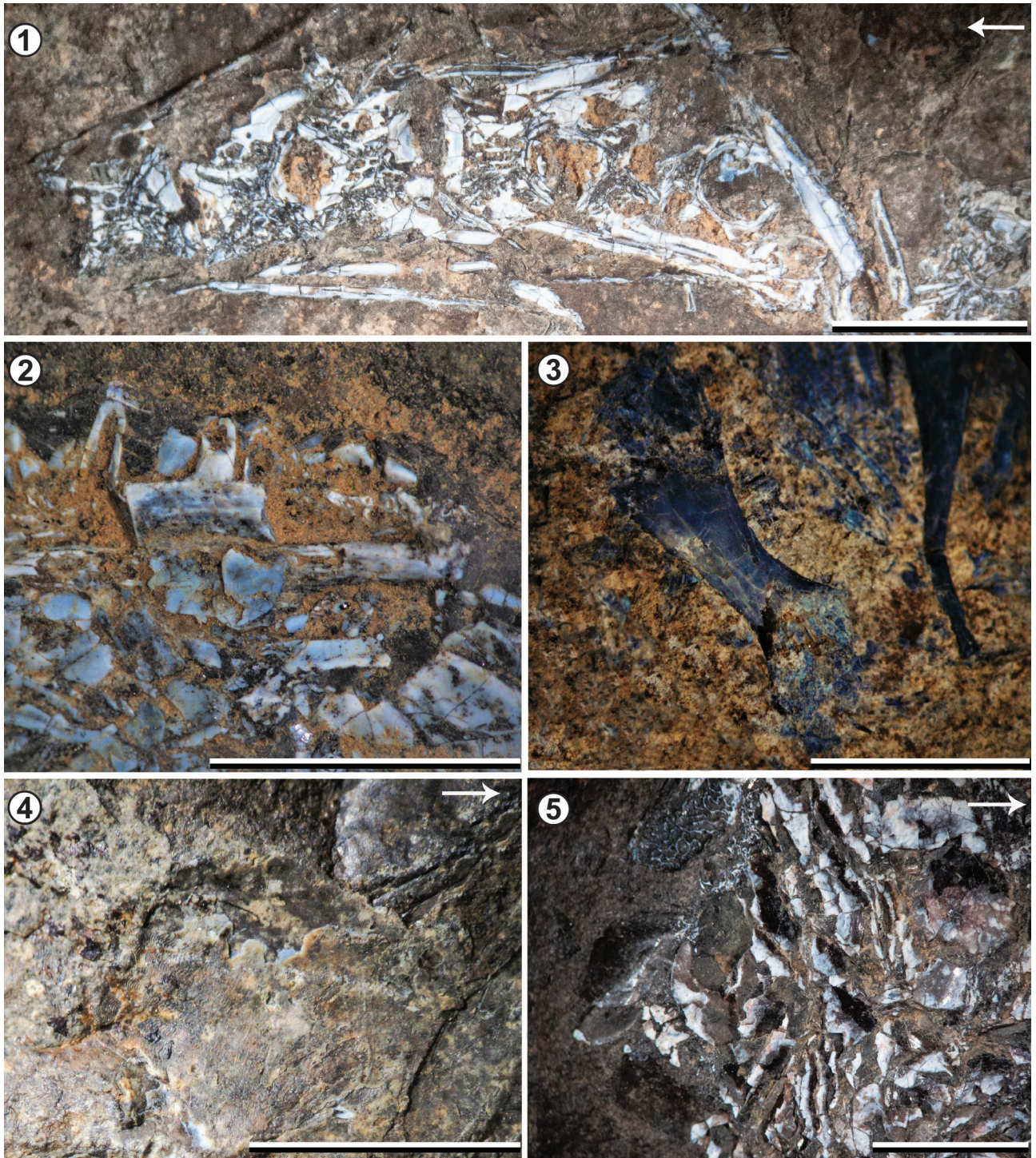


Figure 3. IAA-Pv 423 (partim) coprolite internal content. 1, IAA-Pv 423 d, an Ichthyodectiformes vertebral column showing corrosion and cracking; 2, IAA-Pv 423 a, an Aspiorhynchiformes dentosplenial and scales; the dentosplenial shows fractured teeth and corrosion meanwhile scales shows fractures; 3, IAA-Pv 423 e, teleostean ceratohyal showing blue coloration due to exposure; 4, IAA-Pv 423 d, an elasmoid Ichthyodectiformes scale; 5, IAA-Pv 423 f, imbricated Aspiorhynchiformes scales with enameloid. Arrows points antieriad. Scale bars 1= 10 mm; 2-5= 5 mm.

Mesoscopic analysis

The internal contents of the bromalites consist of isolated and fragmentary actinopterygian cranial bones, teeth, vertebrae, fin rays and scales. These remains show signs of structural modification (e.g., cracking, abrasion, corrosion; Fig. 3). IAA-Pv 432 a, has a fragment of dentosplenic with teeth (Figs. 2.1, 3.2).

Among the bone fragments preserved as internal contents, the vertebral column (Fig. 3.1), the dentosplenic (Fig. 3.2), and the ceratohyal (Fig. 3.3) are characteristic of teleosteans. These bones show different types of fractures (see below) with different orientations (parallel and/or perpendicular) relative to the bone tissue fibers (see Discussion). The scales present as internal contents are of two types, rounded and rhombic. The elasmoid rounded scales are interpreted as belonging to Ichthyodectiformes (Fig. 3.4). These scales are usually well-preserved and show *radii*. The rhombic (=ganoid) scales are imbricated and are interpreted here as belonging to Aspidorhynchiformes (Fig. 3.5). These scales preserve the enameloid and show minor surface modifications (e.g., cracking, dissolution). We interpret these modifications as a result of digestion (Fig. 3.5).

Microscopic analysis

Petrography. The thin sections of IAA-Pv 432 g, h (Fig. 4) show different coloration between the interior of the bromalite and the host rock; a homogeneous light brown coloration can be observed inside the bromalite, which easily distinguishes it from the dark brown host rock composed of a fine matrix (Scasso & Kiessling, 2001; Fig. 4.1). The contact between the internal matrix of the bromalite and the host rock is defined by a dark line, which is the product of the differential oxidation of the elements that composes both matrices (Fig. 4.1, light blue arrowhead). We recognize two types of internal matrices in the studied bromalites; both matrices have different densities, and are heterogeneously distributed. One matrix is composed of bioclast fragments of bone together with fine to very fine amorphous organic material (Fig. 4.1–4.2). This matrix is loosely arranged producing internal conspicuous poral spaces, sometimes larger than 50 μm . These spaces are observed to be filled with amorphous silica (opal) (Fig. 4.1). The second type of internal matrix consists mainly of fine to very fine amorphous

organic matter with too small pore spaces filled with amorphous silica (Fig. 4.1–4.4). This last type of matrix is abundant within the bromalites. It still preserves folds or micro-folds that were formed when the matrix was still behaving in a plastic way, probably during the digestive process (Fig. 4.3–4.4). We report that the brownish microspheres found in the outer contours of bone fragments and internal bone lumens (Fig. 4.5) are the result of the bacterial activity (see below). In some cases, the original anatomical position of the bone fragments (e.g., vertebrae) is preserved despite the grinding of the material due to digestion (Fig. 4.2).

The fractures observed in the bones are of two types: 1) mechanical by digestion (being parallel to the bone fibers; Fig. 4.1–4.2 dark blue arrowhead), and 2) diagenetic (grouped in several small fractures perpendicular to the major axis of the bone fibers; Fig. 4.1–4.2 green arrowheads), with several fractures and “microdiaclasses” forming a mosaic pattern mainly in those elements with planar surfaces.

The host rock microfossils are mainly radiolarians and a few sponge spicules (Fig. 4.6). The preservation of the radiolarians (mainly conical and septate) is characterized by the recrystallization as well as dissolution of their shells. The size of radiolarians varies from 0.05 mm to 0.2 mm (Fig. 4.6).

SEM. Some large and nearly flat bones, such as the ceratohyal, remained complete. On the ceratohyal shown in Figure 5.1, the observed damage of the periosteal surface is interpreted as the product of a long period in the intestinal cavity. This interpretation is supported by the presence of a pelitic fine-groundmass surrounding the ceratohyal and other flat bones. The distal portion of the ceratohyal shows extensive damage of the trabecular tissue (Fig. 5.2). Recrystallization is also characterized by authigenic geodetic euhedral crystals (Fig. 5.2 arrowhead). Several mosaic-like fractures are present in the bone surface. They are interpreted here as the product of fossil-diagenetic processes of lithostatic pressure (Fig. 5.3). This pattern of fractures is accompanied by a superficial lamination or desquamation of the bone, defined by an irregular polygonal pattern that becomes visible on the flattened surfaces of the bones. Figure 5.4 illustrates two vertebral centra in which fractures are observed.

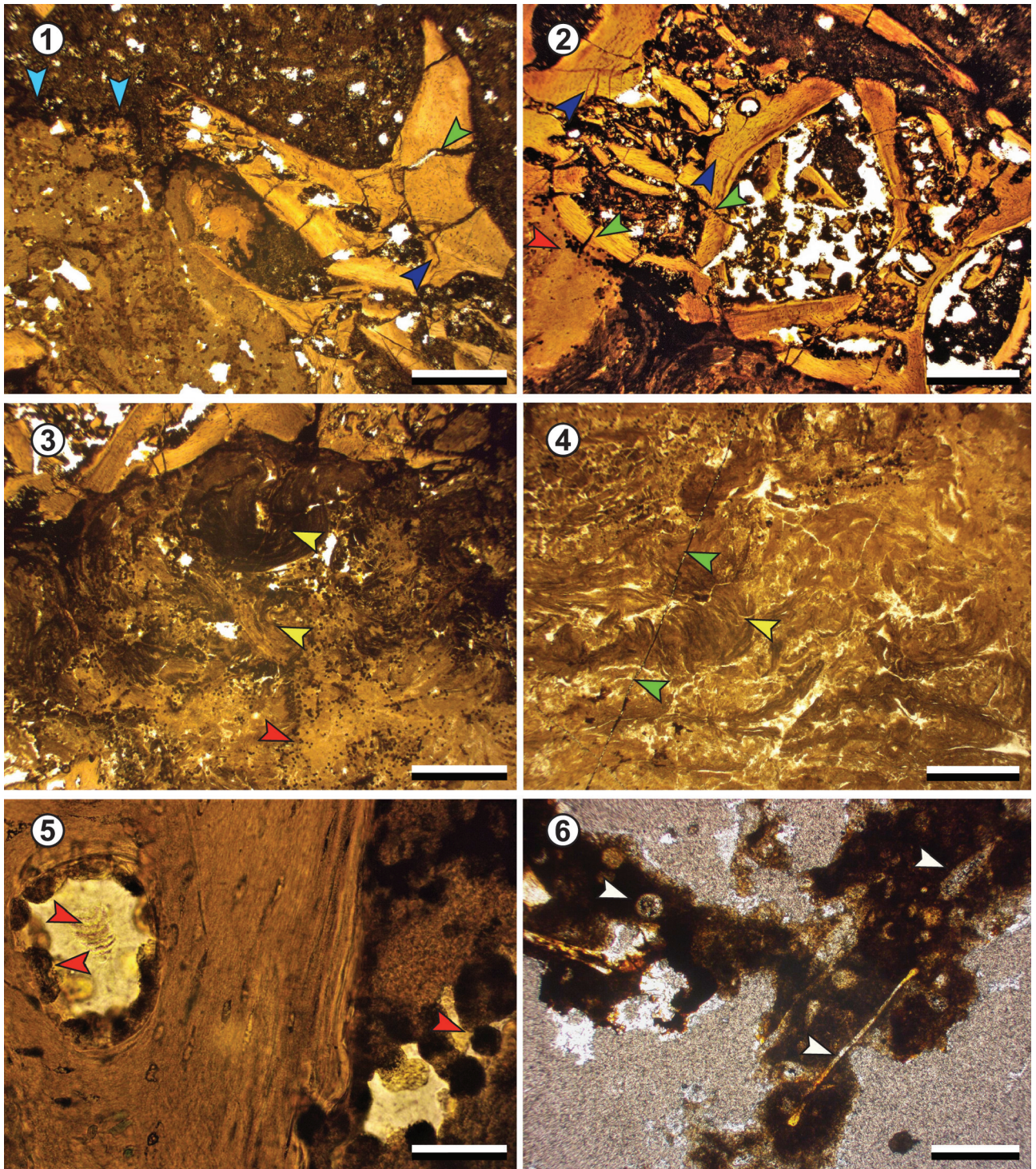


Figure 4. IAA-Pv 423 (partim) coprolite thin sections. 1–5, IAA-Pv 423 g; 6, IAA-Pv 423 h; 1, IAA-Pv 423 g, coprolite internal content showing the outline (light blue arrowhead) and a bone fragment with diagenetic fractures (green arrowhead); 2, IAA-Pv 423 g vertebral centra showing diagenetic cracking (green arrowhead), biostratinomic cracking (dark blue arrowhead), microspheres (red arrowhead); 3, IAA-Pv 423 g coprolite fine internal matrix showing microfolds (yellow arrowhead) and microspheres (red arrowhead); 4, IAA-Pv 423 g coprolite fine internal matrix showing diagenetic fracture (green arrowhead) and microfolds (yellow arrowhead); 5, IAA-Pv 423 g coprolite internal content showing a bone with microspheres (red arrowhead); 6, IAA-Pv 423 h host rock showing a spicula and radiolarians. Scale bars 1–4, 6= 500 μ m; 5= 50 μ m.

Backscattered. Interpretation of the analysis allows the distinction of two modal distributions of elements in the internal content of the bromalite. In Figure 5.4, the bone fragments with a light (whitish) color of equal intensity correspond to the bone with the highest density in the atomic packing. Conversely, the dark spots indicate a lower density, allowing the identification of the areas where the finer-grained internal matrix of bromalite is better represented. The darker black spots (minor packing) correspond to the primary porosity (original packing) and all types of fractures (Fig. 5.4).

EDS. The spectra obtained show a variation in the composition of the major elements inside and outside the coprolite (Fig. 6). Starting with the composition of the bone fragments (Fig. 6.1), inside of the structure, a clear predominance of calcium (Ca), phosphorus (P) and oxygen (O) can be observed (Fig. 6.2), these being parts of the hydroxyapatite molecule of the bone tissue. Other elements such as silicon (Si), iron (Fe), magnesium (Mg), sodium (Na), aluminum (Al) and carbon (C) are also found. The matrix of the rock containing the bromalite (Fig. 6.3), shows the marked presence of elements Si and O, accompanied by Al with a lower presence,

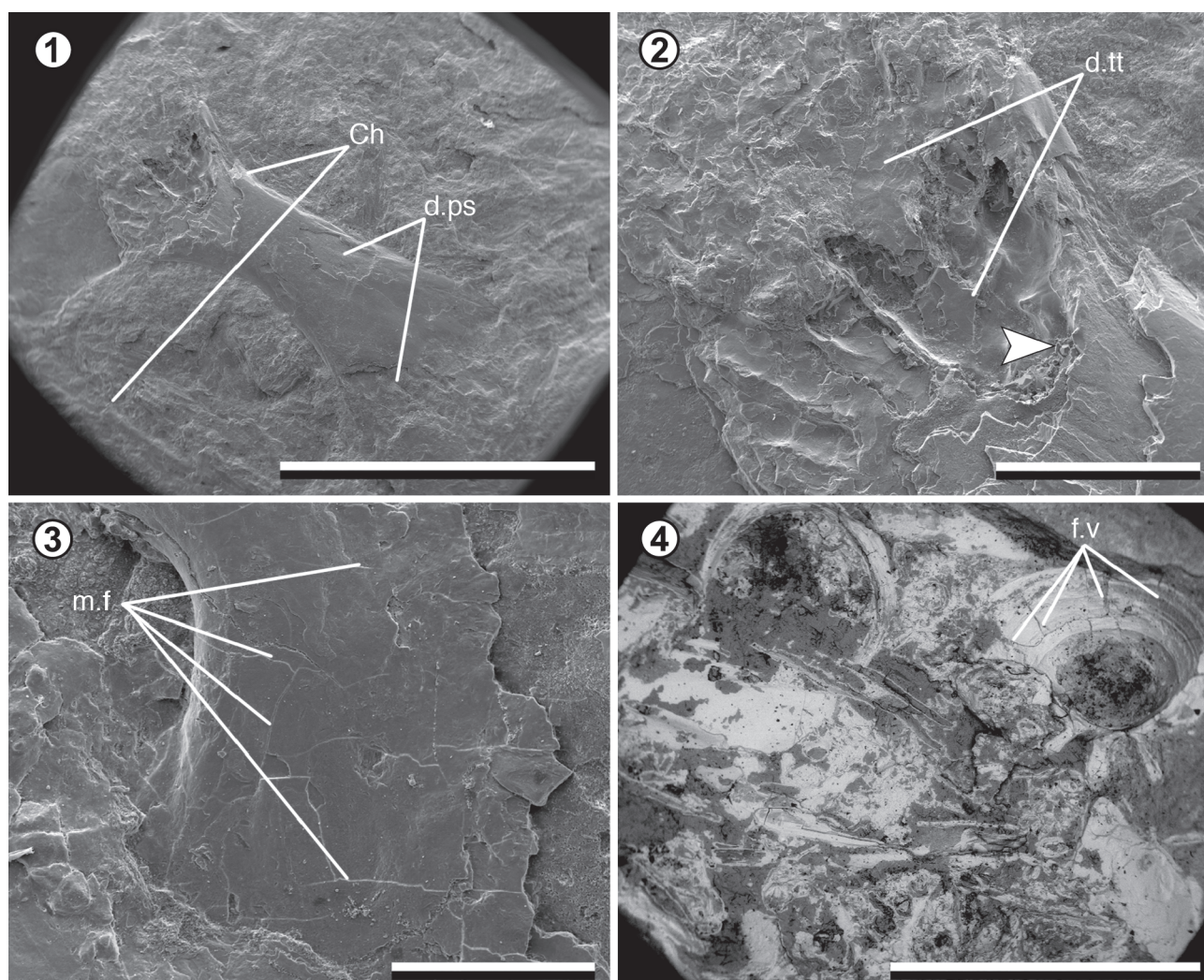


Figure 5. IAA-Pv 423 (partim) coprolite SEM analysis. 1, IAA-Pv 423 e illustrates a teleostean ceratohyal (Ch) to show damage of the periosteal surface (d.ps); 2, IAA-Pv 423 e detail of distal portion of the ceratohyal illustrated in 1 to show the damaged trabecular tissue (d.tt), the arrowhead indicates an euhedral crystal; 3, IAA-Pv 423 e detail of the ceratohyal shaft to show the mosaic fractures (m.f.); 4, IAA-Pv 423 i backscattered image showing two vertebral centra and associated spines, f.v indicates fractures in the vertebral centra. Scale bars 1, 4= 5 mm; 2= 2mm; 3= 500 μ m.

to the detriment of Ca and P (Fig. 6.4), different from what is observed in the bone fragments. Regarding the external matrix, the sediment shows a clear dominance of Si, accompanied by O and to a lesser extent Al, which dominate over the rest of the minority elements such as Mg, fluorine (F), Na, C and potassium (K), all of them present in the sample.

X-ray analysis. The results from the 'Whole Rock' analyses indicate that the samples are dominated by quartz (Q) with good crystallinity over the rest of the minerals composing the matrix. The presence of plagioclase (Pl) and K-feldspar (Fk) in smaller proportions defines the detrital origin of the material composing the sedimentary matrix (Fig. 7.1). This analysis with a 'Clays' technique shows a slight presence

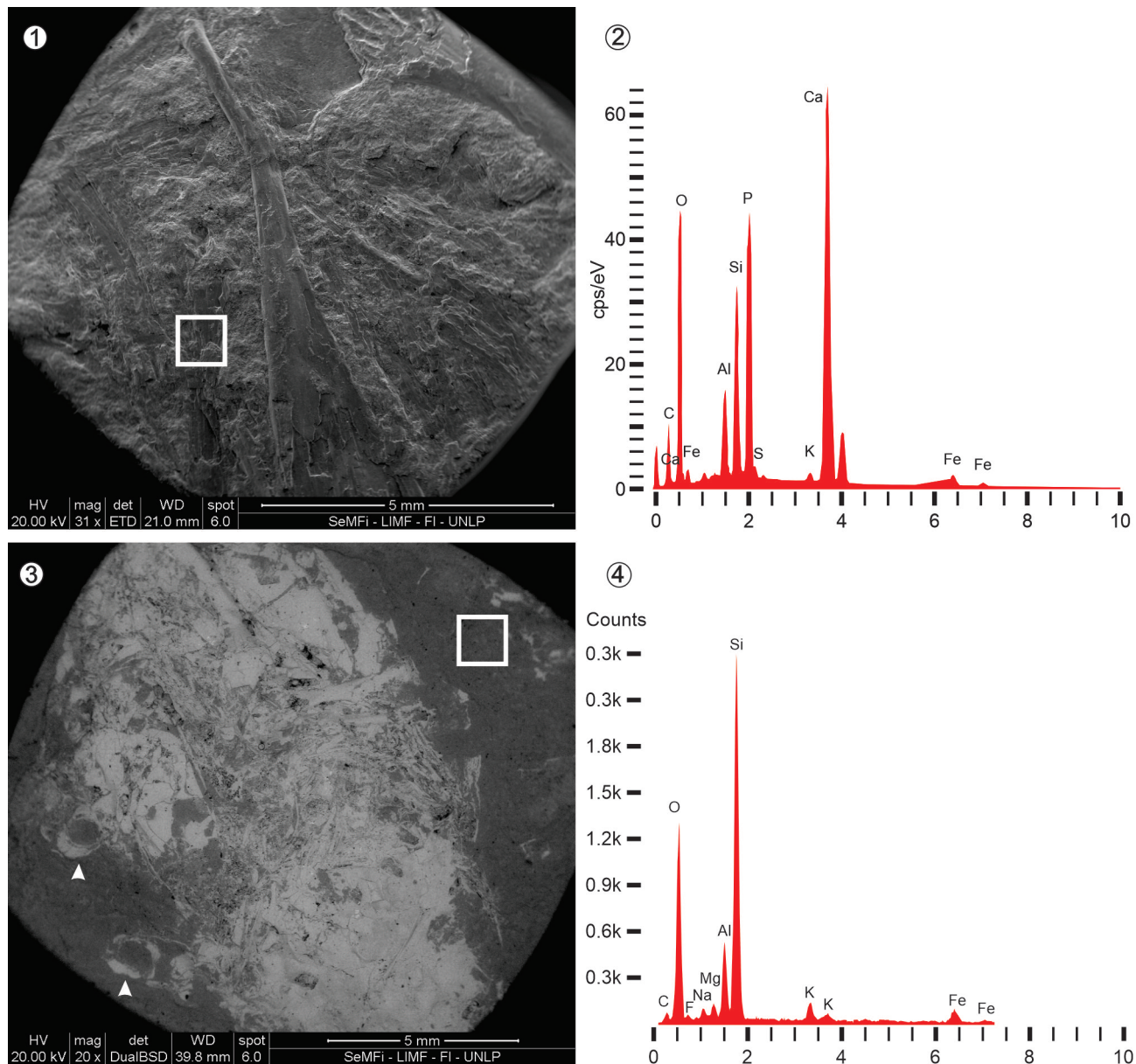


Figure 6. IAA-Pv 423 (partim) Coprolite SEM analysis. **1,** IAA-Pv 423 e observed by LV, the image shows the lepidotrichium of an actinopterygian with a superficial laminate or desquamation, with diagenetic fractures in the fragment bones; **2,** content of chemical elements in the internal biogenic matrix with bone fragments; **3,** IAA-Pv 423 j BS image of the internal content of the bromalite. The arrows indicate two vertebral centra; **4,** Elements in the external matrix. The squares indicate the area of the EDS analysis. Abbreviations: Al, aluminum; C, carbon; Ca, calcium; Fe, iron; K, potassium; Mg, magnesium; Na, sodium; O, oxygen; P, phosphorus; Si, silicon.

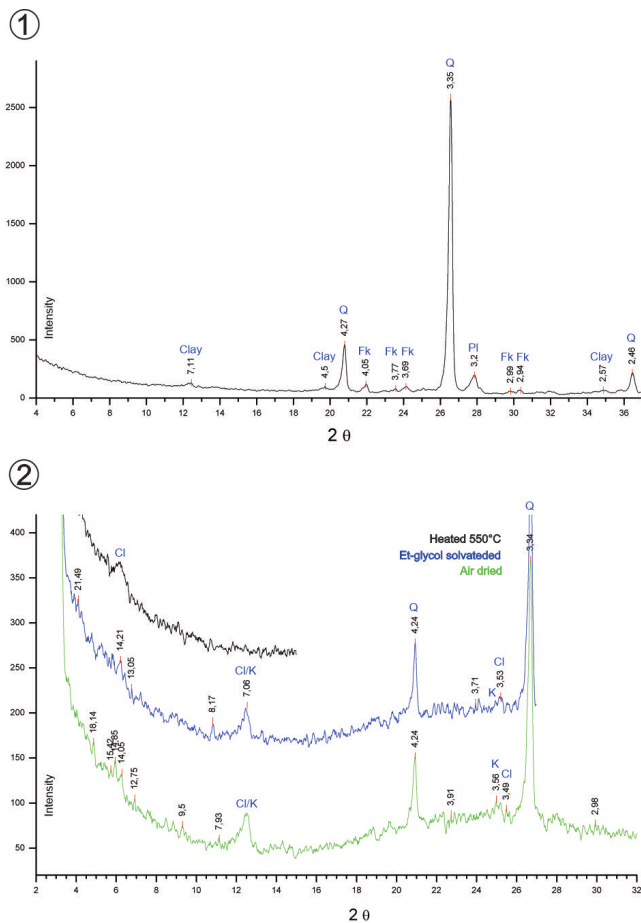


Figure 7. IAA-Pv 423 (partim) X-ray diffractograms. 1, 'Whole rock'; 2, 'Clay' in the fraction. Intensity = counts per second. Abbreviations: Cl, chlorite; Fk, K-feldspar; K, kaolinite; Pl, plagioclase; Q, quartz.

of minerals from the clays, and in this sense, the determination of a considerable amount of chlorite (Cl) could be identified as forming the sedimentary matrix (Fig. 7.2), this formed as the product of alteration of minerals such as feldspars (Scasso & Kiesling, 2001). In addition, there is little kaolinite, represented by less than 5%, and other silicate minerals, mostly containing elements such as Mg, Fe and Al.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Antarctoscopus* ichnogen. nov.

Type ichnospecies. *Antarctoscopus longinensis*, Longing Gap locality in the Antarctic Peninsula.

Etymology. *Antarctos* referring to Latin *Antarctica* and *kopros* (κοπριά, Greek) referring to dung.

Diagnosis. Roughly rounded to elongate small coprolite (62–7 mm) with a well-defined outline, typically preserved in 2D, with an internal content composed of actinopterygian remains and a groundmass or mucus.

Remarks. The coprolites reported here were previously mentioned by Doyle & Whitham (1991, p. 402, fig. 5) and described as typical and probably fish-derived coprolites of the Ameghino Formation. The bromalites in this ichnogenus encompass three morphotypes (circular, subcircular and elongate) that are interpreted as derived from a 3D shape that acquired different morphotypes through diagenesis. The morphotypes proposed here (*i.e.*, C, S, and L) resemble some of the morphotypes proposed by Hunt & Lucas (2012b, *i.e.*, H and I). A few specimens recovered from the Ameghino Formation (*i.e.*, those without a clear, continuous and well-defined outline) resemble the K morphotype of (Hunt & Lucas, 2012b).

Geographic and stratigraphic occurrence. Longing Gap in the North of the Antarctic Peninsula (Doyle & Whitham, 1991; fig. 5).

Antarctoscopus longinensis ichnosp. nov.

Figures 2–5

Etymology. *longinensis* refers to Longing Gap type locality in the Antarctic Peninsula.

Diagnosis. As for the ichnogenus *Antarctoscopus*.

Holotype. IAA-Pv 423 (partim), coprolite (Fig. 2)

Type locality. Longing Gap, Antarctic Peninsula.

Type horizon. Longing Member of the Ameghino (=Nordenskjöld) Formation (Kimmeridgian–early–?late Tithonian).

Referred specimens. IAA-Pv-423 (partim), coprolites (Figs. 3–6).

Description. *Antarctoscopus longinensis* ichnosp. nov., is characterized by the small size, ranging from 62 mm to 7 mm in the major axis (MA) and 45 mm to 5 mm in the minor axis (MI); it occurs in three morphotypes (see above); its internal content consists mainly of fish bones. The internal content is usually grouped and well-delimited from the host rock by a clear or well-defined margin (Figs. 2–3). To date, the specimens retrieved in the field are mainly preserved in 2D, concordant with a stratigraphic plane.

The internal actinopterygian remains content is dis-

tributed in a dense arrangement of bone and scale fragments that are in close contact or overlapping. The bony remains correspond to scales, vertebrae, fin rays and cranial elements (e.g., ceratohyal, dentary with teeth), in addition to other indeterminate bony fragments. Vertebral centra show a high degree of dissolution and cracks. The neural and haemal arches are—in some cases—articulated to the vertebral centrum, but the spines are incompletely preserved, cracked and even broken (Figs. 3.1, 5.4). The osteocytes of the vertebral centra, however, retain their shape. The bone mineralization of the preserved fish remains seems to be consistent with an adult or subadult actinopterygian fish. The bones do not show widely distributed cartilaginous zones (Fig. 4). Bone fragments show varying degrees of disarticulation and grinding. Brownish microspheres are observed in close association with them and also in the fine amorphous organic matter (see Discussion). Bone fragments are surrounded by an organic compound interpreted as mucus in life. Also, as part of the internal content of the bromalite is a large amount of fine material that show micro-folding and is light brown (Fig. 4).

Primary porosity can be recognized in the spatial arrangement of the content and can be interpreted as initial free space. Pore sizes can exceed 50 μm and are usually filled with amorphous silicate compounds (Fig. 4).

Geographic and stratigraphic occurrence. As for ichnogenus.

DISCUSSION

Bromalites include coprolites, cololites and regurgitalites (Hunt, 1992; Hunt & Lucas, 2012a), as well as consumulites (Hunt & Lucas, 2021), being the direct evidence of the organism's diet. Distinguishing coprolites from regurgitalites is not always easy, but several attempts have been made (e.g., Hunt & Lucas, 2012a, 2021; Silva *et al.*, 2017; Hoffmann, 2019; Foster *et al.*, 2022). Regurgitation (intentional or accidental) of ingested bone fragments or other hard elements is a widely documented behavior in recent fishes (e.g., Stewart, 1998; Vignon & Dierking, 2011; Zhao *et al.*, 2020). Regurgitation has been hypothesized for fossil fishes (Hoffmann *et al.*, 2019, table 2; Foster *et al.*, 2022), fossil aquatic reptiles (mesosaurids, crocodiles and probably ichthyosaurs; Silva *et al.*, 2017), and fossil semiaquatic mammals and reptiles (Foster *et al.*, 2022).

There are several features that can be used to distinguish regurgitalites from coprolites (Hoffmann *et al.*, 2019; Foster *et al.*, 2022 and references therein). These features can be summarized as follows:

1. Geometry and matrix. Regurgitalites range from three-dimensional cylindrical to amorphous. Because regurgitalites lack (or have very little) matrix, the general shape is flat with a diffuse appearance characterized by an irregular outline. Coprolites have a well-developed matrix, which in some cases allows them to maintain a three-dimensional structure, such as an elongated or spiral shape.

2. Internal content. Regurgitalites are characterized by a dominance of indigestible hard content representing one or more specimens and/or species; dominance of different types of hard parts (e.g., bones, spines, belemnite rostra) or specific hard parts (e.g., only scales); the presence of otherwise dissolved food particles (e.g., thin aragonitic or calcitic structures); fractured or partially fractured hard parts due to chewing and biting; presence of surface pits, rounded edges due to the activity of stomach acids; polishing and staining of bones; identifiable mineralized food particles (e.g., bones, belemnite rostra, echinoid spines); large hard parts are comparatively larger and more often articulated in regurgitalites than in coprolites. In regurgitalites, the elements are often aligned about their long axes and closely packed. Regurgitalites lack (or have a low proportion) of groundmass which, if present, may be preserved as carbon, iron sulfides, oxides, or phosphates. Coprolites show a dominance of faecal groundmass.

The bromalites of the Ameghino Formation studied here are interpreted as coprolites, adding some distinctive features to allow their identification: 1) abundant convolitional fine-groundmass (abundant mucus), 2) a fine-grained (pelitic) dense-packed organic matrix with microfoldings (faecal groundmass), 3) a high degree of fragmentation and/or disarticulation of the fish bones and scales, interpreted as resulting from digestion, 4) a well-defined outline in most cases, and 5) a high phosphate content compared to the host rock. The organic matrix may represent the digestion of the most labile materials (soft, cartilaginous tissues, and slightly calcified bony elements) that were not reabsorbed. The micro-folds are interpreted as the result of the material movement of material through the intestine.

We agree with previous studies interpreting the bromalites of the Ameghino Formation as coprolites of fishes (Doyle & Whitham, 1991, p. 402). We do not concord that the disseminated scales commonly present in the Longing Member are derived from coprolites (Doyle & Whitham, 1991, p. 402), but are the product of a natural process of detachment during fish decay.

Compared to other periods, Jurassic coprolites are not commonly cited in the literature and remain largely unstudied (Hunt & Lucas, 2014, 2020, 2021). Exceptions are the marine coprolites of the Early Jurassic of England (*e.g.*, Martill, 1985; Hunt *et al.*, 2007, 2012a; Hunt & Lucas, 2014, 2021). A few coprolites have been reported from Europe in Holzmaden, Germany (Hauff, 1921), and putative marine reptile's coprolites come from the Early Jurassic of Italy (Grassino & Donovan, 2000; Hunt & Lucas, 2021).

Gondwanan marine coprolite records are scarce, characterized by the Upper Jurassic–Lower Cretaceous microcoprolites of the Neuquén Basin, which have been interpreted as produced by crustaceans (*e.g.*, Kietzmann *et al.*, 2010; Kietzmann & Palma, 2011; Kietzmann & Olivo, 2020). Microcoprolites from the Miocene of India have been interpreted as produced by a fish (Kapur *et al.*, 2019).

Actinopterygian coprolites have been reported from the non-marine Late Jurassic of Australia (Beattie & Avery, 2012). The content of these coprolites consists of crushed fish bones, gastropods and unidentifiable remains (Beattie & Avery, 2012, p. 455, fig. 9). Marine actinopterygian coprolites have been recorded from several Late Jurassic German localities, notably the Nusplingen (Schweigert & Dietl, 2012), Solnhofen (Barthel *et al.*, 1990; Kemp & Trueman, 2001; Röper, 2005) and Ettling (Ebert *et al.*, 2015) Lithographic Limestones. The coprolites recovered from Nusplingen are phosphatic, and their content consists mainly of undigested fish bones with minor proportions of crustaceans and coleoid hooks (Schweigert & Dietl, 2012). These coprolites have been interpreted as having been produced primarily by bony fishes and sharks (Schweigert & Dietl, 2012). In the Solnhofen Lithographic Limestones, the coprolites are also phosphatic and are used to interpret paleoenvironmental conditions (Kemp & Trueman, 2002). The Solnhofen coprolites have been found concentrated on bedding planes together with the bodily remains (Kemp & Trueman, 2002).

These coprolites contain fish fragments and echinoderms being interpreted as produced by actinopterygians (Barthel *et al.*, 1990; Kemp & Trueman, 2002 and references therein). At Ettling, many of the recovered coprolites are phosphatic, with pycnodonts, and teleosts as contents, or calcitic with echinoids and ophiuroids as main content (Ebert *et al.*, 2015).

Ettling and Longing Gap share some similarities, for instance, the vertebrate fossils from both localities are dominated by actinopterygians and the coprolites retrieved are mainly composed of fish remains. Notably, Eichstätt, Solnhofen and Longing Gap also share some similarities, for instance, these localities are characterized by the abundance of isolated heads and caudal fins of relatively small actinopterygians. The abundance of isolated heads and tails at Eichstätt and Solnhofen has been interpreted as coleoid feeding behavior (Ebert *et al.*, 2015).

Other coprolite records with actinopterygian remains interpreted as produced by an ichthyophagous organism, come from the Upper Barremian of the La Huérguina Formation in Las Hoyas, Spain (Barrios-de Pedro & Buscalioni, 2018; Barrios-de Pedro *et al.*, 2018, 2020; Barrios-de Pedro, 2019). The Middle Eocene Messel deposits in Germany (Richter & Baszio, 2001; Richter & Wedmann, 2005) contain coprolites with internal content of bones, teeth and scales of small fishes. These coprolites have been interpreted as being produced by an ichthyophagous predator.

Some of the coprolite morphotypes proposed here for the Ameghino Formation (*i.e.*, C, S, and L) resemble some of the morphotypes proposed by Hunt & Lucas (2012b, *i.e.*, H and I). A few specimens retrieved from the Ameghino Formation (*i.e.*, those without a clear, continuous and well-defined outline) resemble the K morphotype of Hunt & Lucas (2012b). The circular and elongate morphotypes proposed here are similar to the oval and cylindrical coprolites recovered from the Eocene of USA (Dentzien-Dias *et al.*, 2020) and interpreted as produced by actinopterygians.

Taphonomy

The internal content of some coprolites reveals paleoecological traits of the predator, as well as characteristics of the type of digestion and the effects of passing prey through the digestive tract. The disposition of the pieces has few articulated elements (vertebrae) and imbricated planar

elements (scales; Fig. 3.5). These features are interpreted as related to a weak digestive process that was unable to disarticulate the scales and vertebrae. Fractures produced by digestion are common (Fig. 4.1 and 4.2). These fractures are easily distinguished from those produced by diagenesis (Fig. 4.1), where the space between the fragments of bone tissue usually contains a mineral filler—argillomineral (Fig. 4.2). Noteworthy, some bones have zones in which chemical digestion is easily distinguished (Fig. 5.1 and 5.2).

The compact fine-grained matrix and the convoluted micro-folds are produced during digestion (Fig. 4.1 and 4.3–4.4), thus supporting the idea that grinding is the most obvious feature among the coprolites analyzed.

Coprolite packing varies depending on the ocean, seafloor currents and burial rates (Dentzien-Dias *et al.*, 2020). The outlines of the coprolites studied here are well-defined or diffuse due to the dispersion of the bony elements (Figs. 2, 3.1). We hypothesize that the 2D arrangement, adopted by the pieces, is derived from an original coprolite with an ovoid or subcylindrical morphology in 3D, probably was generated by the plasticity of these structures and compaction at the time of deposition on the substrate. The taphonomic history of the coprolites studied here follows the rapid burial path proposed by Dentzien-Dias *et al.*, (2020, fig. 10). After burial, there is a generalized loss of porosity and fluids in the sediment. In this fossil diagenetic process, the coprolites have been compacted by the sedimentary overload and are preserved mainly in 2D, with the original contour. This results in a laminar structure parallel to the layers of the substrate.

In thin section, groups of brownish microspheres were observed and interpreted as bacteria (Fig. 4.5). The presence of bacteria in extant feces is common, as these organisms inhabit the intestine cavities of living vertebrates promoting the decomposition of organic material prior to evacuation (Thulborn, 1991; Hollocher & Hollocher, 2012; Mancuso *et al.*, 2017; Dentzien-Dias *et al.*, 2017, 2018, 2020). Similarly, the presence of bacteria in the feces studied here could be related to the calcium-phosphate precipitation in the cell structures that may facilitate the preservation of bacterial structures (Li *et al.*, 2015; Qvarnström *et al.*, 2016).

The general chemical composition of the bromalites shows a predominance of Ca, P and O in the bone tissue

fragments of the internal content. The chemical analyses reveal a predominantly phosphatic composition. Phosphorus is sourced by the calcium phosphate present in bones, as well as by components of animal soft tissues and/or subsequent microbial activity (*e.g.*, Bradley, 1946; Dietrich, 1951; Mancuso *et al.*, 2017; Häntzschel *et al.*, 1968).

Abundant phosphatic elements have traditionally been interpreted as produced by carnivorous taxa (*e.g.*, Bradley, 1946; Häntzschel *et al.*, 1968; Chin *et al.*, 2003; Hollocher *et al.*, 2010; Mancuso *et al.*, 2017). The abundance of bone fragments and scales in the coprolites studied, coupled with a phosphatic groundmass with convoluted micro-folds, provide compelling evidence that the producers of these coprolites were carnivorous (*i.e.*, predatory and/or scavenging) animals. The preservation of the original structure of the mucus in the internal matrix, suggests a rapid burial in a protective medium (Dentzien-Dias *et al.*, 2020).

The mineralogical composition of the host rock, where quartz predominates, with a low presence of feldspars and a high amount of chlorite (caused by alteration of minerals such as feldspars; Scasso & Kiesling, 2001), combined with the fossil record of marine fishes, macro and micro-invertebrates, suggests a marine depositional environment with a marked diagenetic signal in the mineralogical composition of the host rock (Scasso *et al.*, 1991).

Finally, the external color observed among the bony elements is interpreted here as a result of the taphonomic process (biostratinomy and fossil diagenesis) of the bone fragments of prey, probably related to the passage of the bones through the digestive system of the predator.

Ecology of the coprolite producer

Trophic studies are fundamental to understanding the biology and ecology of organisms and to hypothesize about their role in the ecosystem. In addition, the feces produced by extant fishes were considered a viable food source for macroscopic animals.

For fossil organisms, inferences about trophic interactions are based on direct evidence, mostly on tooth morphology and coprolites. According to Kapoor *et al.* (1976), contrarily to the rest of vertebrates, fishes consume a wide variety of foods and have many different modes of feeding. Fortunately, the exquisite fossil preservation in some

Lagerstätte provides a good glimpse of the paleoecology (e.g., Viohl, 1990; Maisey, 1994; Kogan & Licth, 2013; Ebert *et al.*, 2015; Gouiric-Cavalli & Arratia, 2022). Empirical behavioral information on fossil predator-prey relationships is mainly based on few isolated cases of individual prey (Maisey, 1994), these events have little potential for deeper insights into past trophic organizations or community structures (Maisey, 1994).

Gut content and *in situ* bromalites are the only unambiguous documents of an animal's diet. However, it is important to highlight that in recent fishes, "the contents of most guts cannot be unambiguously separated into prey categories for quantification because of the presence of unidentifiable and inseparable partially digested material. Even where separation is possible, the composition of a gut at one point in time is affected by many unquantifiable factors unrelated to the actual composition of the diet" (Baker *et al.*, 2013, p. 170).

The gut (foregut, midgut and hindgut) of fishes shows variation that is reflected in phylogeny, ontogeny, diet and environment (Wilson & Castro, 2010). Gut morphological data are key to understanding fish nutrition, development and physiological adaptations to a changing environment (Wilson & Castro, 2010). For example, there are many fishes that have a secondary lack of stomach (*i.e.*, chimaeras, dipnoans and several teleosteans; Chao, 1973; Le *et al.*, 2019; Facey *et al.*, 2022), others have a specialized stomach (*i.e.*, as grinding structure in Acipenseridae and Mugillids or as a respiratory structure in Loricariidae), some teleosteans have a short intestine and lack the pyloric caeca. The intestines of chondrichthyans and some actinopterygians (e.g., coelacanth, lungfishes, cladistians, chondrostreans, and holosteans) have a spiral valve, agnathans have a typhlosole and some teleosteans have intestinal caeca.

Despite the above, current knowledge of the evolutionary history of the vertebrate gastrointestinal tract is hampered by the low preservation potential of soft tissues in fossils (Neumayer, 1919; Diedrich, 2012; Argyriou *et al.*, 2016). In general, the intestine of basal teleostean fishes is mainly straight, but derived teleosteans have a folded intestine.

The vertebrates reported from the Ameghino Formation consist mainly of actinopterygian fishes (teleosteans and

holosteans) and a few marine reptiles (plesiosaurs and ichthyosaurs, e.g., Arratia *et al.*, 2004; Gouiric-Cavalli *et al.*, 2017, 2022). No chondrichthyans have been reported so far. The gut of the actinopterygians reported remains unknown. However, it is well-known that at least some pachycormiforms and caturids have a spiral valve in the hindgut (Neumayer, 1919; Argyriou *et al.*, 2016; Cooper *et al.*, 2022), and many extant non-teleostean actinopterygians also have a spiral valve (*i.e.*, polypterids, amiids, lepisosteids, acipenserids, saurichthyids). Thus, we investigate whether those fishes could produce the coprolites reported here.

To date, the only direct evidence of predation in the Ameghino Formation at Longing Gap has been provided by an Aspidorhynchiformes, a stem-teleost that has remains of an indeterminate teleostean fish in its jaws (SGC pers. obs., 2016). Remains of the teleostean, *Orthogonikleithrus hoelli* were found in the pharynx and stomach of the aspidorhynchids retrieved from the Upper Jurassic at Ettling in Germany (Ebert *et al.*, 2015). Other actinopterygians retrieved from the Ameghino Formation are pachycormiforms, this group gather suspension-feeding taxa as well as carnivorous predators, which are ichthyophagous and invertivorous taxa (Gouiric-Cavalli & Arratia, 2022). Among the non-teleostean fishes, the Ameghino Formation yielded amiids and dapediids (SGC pers. obs.).

From the analysis of the material (coprolites, vertebrates and invertebrates) recorded at Longing Gap, we conclude that the producer of the coprolites was most likely a carnivorous predator with a rather specialized diet based mainly on bony fishes. The infrequent and rare records of marine reptiles at the unit, as well as the size and shape of the coprolites found, allow us to discard them as the producers of the coprolites.

Macroinvertebrates (ammonites, belemnites and gastropods) are extremely abundant at Longing Gap, therefore, we cannot discard that the coprolite producer might have been a fish or an invertebrate. However, the coprolites were not found in association with either macroinvertebrates or actinopterygians. Furthermore, according to the size of the coprolites and the well-preserved bone fragments of the prey, we believe that predators were adult medium-sized fishes (*ca.* 50 cm to 1 m in total length) instead of marine reptiles or macroinvertebrates.

The qualitative analysis of the coprolite content (mainly vertebrae and scales) reveals that the major prey corresponds to teleostomorphs (aspidorhynchids) and teleosts *sensu stricto* (ichthyodectiforms). Aspidorhynchiformes and Ichthyodectiformes are the most commonly bony-fishes retrieved at Longing Gap (Arratia *et al.*, 2004; Gouiric-Cavalli *et al.*, 2017).

The presence of sponge spicules in a sample seems to be circumstantial; however, they are common in host rock (Fig. 4.6). Regarding the fragility of bony elements of juveniles to digestion and/or taphonomic processes, we do not discard a juvenile prey for the carnivore coprolite producer.

The absence of macro and micro invertebrates as coprolite content suggests that they were not a significant food source for the coprolite producer. Because the coprolites studied have abundant bone fragments and do not show scrolling, we propose that the producer was an organism without a spiral valve in the intestine. Extant carnivorous actinopterygians have the shortest intestines (*e.g.*, Kapoor *et al.*, 1976) and some are stomachless. This supports our idea of a carnivorous actinopterygian predator as the putative producer of the coprolites. The significant abundance of coprolites recovered from the Ameghino Formation, suggests a direct relationship with the depositional environment, and fossil preservation potential, but also with digestive processes and defecation ratio.

The information provided opens a new debate based not only on the ichnotaxonomy of bromalites and the putative producer paleobiology but also on the environment and taphonomic processes. However, this is not the aim of this contribution and further research and studies are needed to clarify it.

CONCLUSIONS

The bromalite samples recorded in the Longing Member of the Ameghino Formation, correspond to coprolites. The morphology and content of the coprolites allow the definition of a new ichnotaxon, *Antarctoscoprus longinensis* which includes three main morphologies: Morphotype C (circular), Morphotype S (subcircular) and Morphotype E (elongate). The analysis of the internal contents of the coprolite, allows us to state that the gross mass of the coprolite is composed of skeletal fragments of bony fishes associated with digested

fine material and mucus. The flattened condition of the coprolites indicates that they were malleable prior to final burial and were deformed by the overlying sediment during burial. The Longing Member coprolites lack evidence of burrows or other fossil traces, indicating a rapid burial and early mineralization. The coprolite producers may have been carnivorous organisms that fed almost exclusively on actinopterygians. The size of the coprolites excludes marine reptiles. No folded or scrolled coprolites were recorded, ruling out sharks and non-teleostean actinopterygians (*i.e.*, pachycormiforms and amiids) as putative producers. However, carnivorous teleosteans such as ichthyodectiforms could have produced these coprolites.

ACKNOWLEDGMENTS

This contribution was mainly funded by the Dirección Nacional del Antártico and the Instituto Antártico Argentino, project: PICTO 2010-0093 and PICT 2017-0607 to M.R. Partial funding was provided by the Consejo Nacional de Investigaciones Científicas y Técnicas, Agencia Nacional de Promoción Científica y Tecnológica, and the Universidad Nacional de La Plata through PICT 2015-0253 and PICT 2019-02419 to S.G. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank L. Acosta Burllaile, Y. Herrera, J. J. Moly, J. P. O'Gorman (Universidad Nacional de La Plata), B. Carigliano (Museo Argentino Ciencias Naturales "Bernardino Rivadavia"), A. Iglesias (Instituto de Investigaciones en Biodiversidad y Medioambiente) and S. Santillana (Dirección Nacional del Antártico–Instituto Antártico Argentino) for their valuable assistance in the field; F. Medina and R. Scasso (Universidad Nacional de Buenos Aires) for providing valuable information of the study locality and valuable literature. The CIG and LIMF, for supporting the preparation and processing of the samples and the images. The logistic support of the Fuerza Aérea Argentina for their support in the Antarctic field. We thank to C. Amenábar and A. Cuparo Rentsch (Dirección Nacional del Antártico–Instituto Antártico Argentino) who are responsible for loaning and providing access to fossil specimens housed at the Repositorio Antártico de Colecciones Paleontológicas y Geológicas of the Instituto Antártico Argentino; P. Fontana, and R. del Valle (Dirección Nacional del Antártico–Instituto Antártico Argentino) are thanked for providing valuable literature. We thank to the reviewers (R. Scasso and S. Lucas) and the editors (L. Salgado and B. Carigliano) for their valuable comments and suggestions that improve the manuscript.

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LSID urn:lsid:zoobank.org:pub:0ADE2DBA-9FE9-4C53-A8EF-218F3BE55C0F

doi: 10.5710/PEAPA.11.04.2023.446

Recibido: 20 de octubre 2022

Aceptado: 11 de abril 2023

Publicado: 19 de julio 2023



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