

Encrusting bryozoan attached to terrestrial plant leaves from brackish deposits of the Lefipán Formation (Patagonia, Argentina), close to the K/Pg boundary.

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Abstract.—Cretaceous bryozoans from South America have received limited attention despite their sporadic documentation. The K/Pg boundary has been identified in numerous fossil-rich basins in Patagonia, where bryozoans are frequent components of the faunas. Material recovered from upper Maastrichtian outcrops of the Lefipán Formation in the Cañadón Asfalto Basin (Patagonia, Argentina) includes a unique species of cheilostome bryozoan, *Conopeum foliorum* n. sp., attached to leaf remains of terrestrial plants and associated with scarce euryhaline bivalves. It likely thrived in a warm climate, shallow, well-lit brackish environment influenced by tides, located along the northwest margin of the Paso del Sapo embayment. *Conopeum foliorum* n. sp. is currently among the earliest known bryozoans from brackish water environments, and the second oldest documented instance of a bryozoan encrusting leaves of terrestrial plants, representing the first of such finding in South America. Based on our findings and available sedimentological and paleoecological data from previous studies, we interpreted *Conopeum foliorum* n. sp. as a fast-growing opportunistic taxon displaying euryhaline habits and prone to colonize terrestrial plant leaves deposited in a brackish-water nearshore environment.

Keywords:

Taxonomy

Bryozoa

Maastrichtian

Cañadón Asfalto Basin

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1. Introduction

The Cretaceous/Paleogene (K/Pg) boundary represents one of the most significant extinction events globally, impacting the biota worldwide. In South America, this boundary is well documented in several highly fossiliferous Patagonian basins in which bryozoans are also found. Studies of these basins have revealed significant differences in the impact of the extinction event between the northern and southern hemispheres. For instance, research has shown lower extinction rates across the boundary followed by a rapid recovery in the Danian period for palynomorphs, plant-insect associations, and marine benthic molluscs (Barreda et al., 2012; Aberhan and Kiessling, 2014; Donovan et al., 2016, 2018). Interestingly, bryozoan diversity in Patagonia exhibits little change across the K/Pg boundary, resembling patterns observed in the northern hemisphere (i.e., Europe, United States) (Brezina et al., 2021).

Bryozoans are exclusively aquatic, colonial suspension-feeding benthic animals with a worldwide distribution despite their predominantly sessile mode of life, including some cosmopolitan genera. Upper Cretaceous (Campanian/Maastrichtian) bryozoans are predominantly found in mid-latitudes between 30-60° in both hemispheres, associated with warm-temperate climatic belts (Di Martino and Taylor, 2013); however, they have also been identified in tropical

settings from the Tethys, without significant taxonomic differentiation from those at higher latitudes (Di Martino and Taylor, 2013; Taylor, 1995). Cretaceous bryozoans have primarily been documented in Europe, North America, Central Asia, Madagascar, India, and Australia, while records from South America are limited (among others Taylor, 2019; Brezina et al., 2021; Taylor and Roger, 2021; Sonar et al., 2023; Håkansson et al., 2024; and references therein). In Argentina, Cretaceous bryozoan records are restricted to the Neuquén Basin in northern Patagonia (Canu, 1911; Taylor et al., 2009; Brezina et al., 2021).

Herein we report new records of Cretaceous bryozoans encrusting leaves of terrestrial plants, briefly discussed previously by the present authors (Taboada et al., 2018). We provide a detailed taxonomic analysis of the bryozoans and interpretations of their paleoecological significance. Finally, we propose a new species of bryozoan, being the first to be formally described from the Cañadón Asfalto Basin in central Patagonia.

2. Geological settings

The studied specimens were collected from the Lefipán Formation which overlies conspicuous outcrops of the Paso del Sapo Formation; these units characterize the final infilling of the Cañadón Asfalto Basin, Chubut Province, Patagonia, Argentina (Figure 1A, B). The Lefipán Formation is a siliciclastic unit with continuous intercalated sandstones and mudstones with some coquinas and conglomerates (Medina and Olivero, 1994). The age of the Lefipán Formation is constrained by biostratigraphic proxies to be Maastrichtian/Danian (Barreda et al., 2012). The Lefipán Formation has been interpreted as grading from estuarine or tide-dominated deltaic conditions in the Maastrichtian to a more open marine environment in the Danian, as part

of a shallow embayment (named as Paso del Sapo embayment by Scasso et al., 2012) in the southern branch of the Kawas Sea (Casamiquela, 1978; Goin et al., 2016). This setting corresponds approximately to a paleolatitude of 45 to 48°S in a warm-temperate climatic belt (Olivero and Medina, 1994; Scotese, 2004; Nañez and Malumián, 2008; Cúneo et al., 2021; Scasso et al., 2012).

One of the best exposures of the Lefipán Formation corresponds to the San Ramón Section (Figures 1C, 2), located 20 km W of Paso del Sapo village and 3 km south of the Chubut River. This stratigraphic section is approximately 400 m thick, 270 m of which are of Maastrichtian age (Scasso et al., 2012). The studied bryozoans were collected from a single fossil-bearing bed indicated as PLE –after *Perfil Lefipán* East– on the figured section (= LefE as detailed in Donovan, et al., 2016, 2018; Wilf et al., 2017; Escapa et al., 2018; Stiles et al., 2020) (Figure 1C). The stratigraphic position of the PLE lies within the terminal Maastrichtian, presumably a few stratigraphic meters above the monotypic *Corbicula* assemblage and 21.5 m below the lower Paleocene (lower Danian) *Turritella* marker bed as described in Scasso et al., (2012) (Figure 1C).

Five facies associations and eight biofacies were recognized from the Lefipán Formation by Scasso et al. (2012). PLE belongs to lithofacies H2 (weakly bioturbated heterolithics), and consists of horizontally laminated mud-sand couplets with coaly plant remains in the muddy part. Sedimentary environments for H2 correspond to tidal flats near vegetated coasts (marsh) along the margins of tide-dominated delta channels with substantial salinity reduction at the K/Pg boundary, changing to oxygenated subtidal transitional environments with rapid sedimentation and frequent changes in salinity in the Danian (Scasso et al., 2012). In this sense, sand deposition occurred during periods of current activity and mud deposition during tidal slack-water periods

(Scasso et al., 2012). Further, H2 is often found around the K/Pg boundary within upper levels of Facies Association III (tidal channel, tidal gully and tidal flat deposits) at the San Ramón Section (Scasso et al., 2012). The following biofacies have been associated, but not necessarily restricted to the lithofacies H2: *Struthioptera-Panopea* association in the Maastrichtian, *Corbicula* faunal assemblage at the K/Pg boundary, and *Corbicula-Venericardia* followed by *Meretrix-Ledina* associations in the early Danian (Scasso et al., 2012). The former authors did not record bryozoans associated with the lithofacies, biofacies mentioned above or with any other fossil-bearing bed from the Lefipán Formation.

3. Material and methods

3.1. Material preservation and preparation

Bryozoans appear as adjacent and nearly neighbouring colonies encrusting plant leaves. They are regularly preserved in two ways: attached to plant leaves with exposed frontal surfaces or as natural moulds produced by sediment infilling. In the first case, morphological characteristics are poorly preserved. In the second, a silicon rubber cast was prepared for one sample following Kelly and McLachlan (1980). Similar preservation was described in Dick et al. (2009). Samples were cleared of sediment with a hand brush, and some were coated with sublimated magnesium oxide for the first optical microscopy exploration (Jeffords and Miller, 1960).

3.2. Morphological data collection

Linear measurements were obtained on digital images using Image J software (Schneider et al., 2012; <https://imagej.net>). Coated specimens were photographed optically with digital cameras at the Museo Paleontológico Egidio Feruglio (MEF). Some details were also photographed from uncoated specimens with a Jeol JSM-6460LV scanning electron microscope (SEM) in low vacuum and backscattered electron signal conditions (at ALUAR S.A., Puerto Madryn, Chubut). Because of the low relief of the colonies they are challenging to photograph. All morphological measurements are in millimetres, and they are presented as arithmetic mean (Mean), sample standard deviation (SD), coefficient of variation (CV), minimum and maximum values (MIN and MAX respectively), and number of measurements made (N). Measurement abbreviations: autozoid length as seen on colony surface (ZL); autozoid width as seen on colony surface (ZW).

3.3. Repository and institutional abbreviation

Studied specimens are stored under the prefix MPEF-PI at the MEF's paleo invertebrate collection in Trelew, Chubut, Argentina.

4. Systematic paleontology

Phylum **Bryozoa** Ehrenberg, 1831

Class **Gymnolaemata** Allman, 1856

Order **Cheilostomata** Busk, 1852

Suborder **Membraniporina** Ortmann, 1890

Superfamily **Membraniporoidea** Busk, 1852

Family **Electridae** Stach, 1937

Genus ***Conopeum*** Gray, 1848

Type species. Millepora reticulum Linnaeus, 1767, Recent, North Atlantic Ocean.

Occurrence. Worldwide. Upper Cretaceous to Recent.

Remarks. Based on features observed, our specimens are assigned to *Conopeum*. Key diagnostic features of *Conopeum* include the presence of a single, non-twinning ancestrula; development of normally unilaminar, multiseriate encrusting colonies; elongate autozooids with extensive opesia; gymnocyst absent or poorly developed relative to the cryptocyst; and absence of ovicells and avicularia (after Hayward and Ryland, 1998; Dick et al., 2014; Gordon et al., 2020; Taylor and Rogers, 2021). Our specimens align closely with the defining traits of *Conopeum*.

Conopeum differs from the two Maastrichtian *Conopeum*-like genera *Eokotosokum* Taylor and Cuffey, 1992 and *Bullaconopeum* Taylor, 1995 in the absence of two large distolateral spine bases and four prominent gymnocystal tubercles, respectively (see Taylor and McKinney, 2006). The Albian/Maastrichtian genus *Iyarispora* Martha, Taylor and Rader, 2019 differs from *Conopeum* mainly in having some zooids with calcified closure plates containing pores (Martha et al., 2019; Taylor and Rogers, 2021). The Cenomanian/Maastrichtian genus *Heteroconopeum* Voigt, 1983 differs from *Conopeum* in having erect colonies comprising narrow, transversally cylindrical branches with distinct endozone and exozone (Voigt, 1983; Taylor and Rogers, 2021).

Therefore, based on these comparative morphological characteristics, *Conopeum* remains the most suitable genus for the taxonomic assignment of our specimens.

Conopeum foliorum new species

Figures 3–5; Table 1

LSID identifier. urn:lsid:zoobank.org:act:6D236CA5-2EBE-4630-A800-C24B6F0FFB2A

Derivation of name. In reference to its occurrence attached to leaves of diverse terrestrial plants, *foliorum* (Latin) of the leaves.

Material. Holotype: MPEF-PI 7101-1; paratypes: MPEF-PI 7101-2; MPEF-PI 7101-3; MPEF-PI 7102-1; MPEF-PI 7102-2; MPEF-PI 7102-3; MPEF-PI 7106 (a-b). Additional material: MPEF-PI 7103 (a-b); MPEF-PI 7104 (a-b); MPEF-PI 7105 (a-b); MPEF-PI 7107 (a-b). From the PLE heterolithic fossil-bearing bed located 20 km west of Paso del Sapo village and 3 km south of the Chubut River, 21.5 m stratigraphically below the K/Pg boundary at the San Ramón section, Lefipán Formation (Cañadón Asfalto Basin).

Diagnosis. Colony unilaminar, spot- to sheet-like. Ancestrula budding a distal and two distolateral zooids. Autozooids medium-sized, elongate rectangular with extensive opesia, arranged in a brickwall-like alternation pattern between adjacent rows; gymnocyst absent; cryptocyst narrow forming a thin mural rim, with rarely preserved rounded granules; spine bases and closure plates not observed, presumably absent. Kenozooids not observed.

Description. Colony encrusting, unilaminar and multiserial, with radial growth pattern (Figures 3A-B; 4A-B; 5A). Early astogeny is commonly preserved. The ancestrula is single, oval in outline; a distal and two distolateral zooids budding directly from the ancestrula, the other three to four periancestrular zooids budding from postancestrular zooids (Figures 3C,E; 4B-C,F; 5B-C). Zooids are monomorphic and of medium average size. In the zone of early astogeny autozooids are oval to polygonal in shape, arranged in irregular quincunx. In the zone of astogenetic repetition, they are larger and longitudinally rectangular, more regular and linearly arranged, in a brickwall-like alternation pattern between adjacent rows (Figures 3D; 4D-E; 5D). In the zone of astogenetic repetition, row bifurcations preceded by a wide zooid and followed by two narrow zooids, one of which is longer than the other (Figures 3D; 4D-E; 5D); occurring approximately after two to six consecutive zooids. Extensive opesia occupy almost the entire frontal surface of autozooids. Gymnocyst presumed absent. Cryptocyst narrow, forming a thin mural rim; normally smooth and worn, with rounded granules rarely preserved (Figure 5D). Spines bases were not observed and presumed absent. A thin fissure marks zooidal boundaries. Closure plates not observed. Septula not observed. Kenozooids not observed, presumed absent.

Remarks. *Conopeum foliorum* n. sp. resembles the Holocene to Recent type species *Conopeum reticulum* (Linnaeus, 1767) (after López-Gappa and Pereyra, 2020), by having longitudinally rectangular zooids, by the lack of closure plates, and by having a comparable autozooidal length (range 0.290 – 0.509, mean 0.392 mm vs range 0.410 – 0.530 mm) and autozooidal width (range 0.129 – 0.271, mean 0.201 vs range 0.210 – 0.320 mm). However, the type species differs by having a vestigial gymnocyst, cryptocyst strongly developed proximally, and often two triangular kenozooids present at the proximolateral corners of each autozooid.

Conopeum foliorum n. sp. resembles the extant *Conopeum seurati* (Canu, 1928), as re-described by Gordon et al. (2020), in having elongated autozooids, often twice as long as wide, and a narrow cryptocyst ornamented with rounded granules. However, *C. seurati* differs from *C. foliorum* n. sp. by having larger autozooids (range 0.432 – 0.722 mm, mean 0.574 mm vs mean 0.392 mm), longitudinally sub-rectangular to elongated-oval in shape, cryptocyst surrounded by a narrow furrow, a slight proximal gymnocyst, up to two distolateral spine bases, and adventitious kenozooids.

Conopeum flumineum Taylor and Roger, 2021 from the Upper Cretaceous (upper Campanian) of the northwestern United States, is closely related to *C. seurati*, and also is similar to *C. foliorum* n. sp. in having a similar zooid length (range 0.291 – 0.629, mean 0.444 mm vs mean 0.392), autozooids longitudinally rectangular in outline shape, and in the lack of closure plates; however, it differs from the new species by its wider autozooids (range 0.291 – 0.629, mean 0.295 mm vs mean 0.201 mm), with narrow peripheral gymnocyst, cryptocyst surrounded by a narrow furrow, and the occasionally developed intramural buds. Furthermore, *C. foliorum* n. sp. shows autozooids normally arranged in well-defined longitudinal rows, in a brickwall-like alternation pattern between adjacent rows, unlike *C. flumineum*.

Conopeum foliorum n. sp. resembles *Conopeum okaiana* (Canu, 1911), from the lower Danian of northern Patagonia, in having no gymnocyst and no pustulose, shelf-like cryptocyst. However, the Danian species differs from *C. foliorum* n. sp. mainly by its longer (mean 0.476 mm vs mean 0.392 mm) and wider (mean 0.395 mm vs mean 0.201 mm) rounded hexagonal autozooids with oval or inverted pear-shaped opesia and imperforate closure plates in some autozooids.

?*Conopeum* sp., from the Upper Cretaceous (upper Campanian) of New Mexico, United States (Kues, 1983) differs from *C. foliorum* n. sp. by its small distal spine bases and longer autozooids (~0.55 mm vs mean 0.392 mm). In addition, *Conopeum* sp. from the Upper Cretaceous (upper Campanian) of southern Utah, United States (Roberts et al., 2008) differs from *C. foliorum* n. sp. by its substantially longer autozooids (~0.70 mm vs mean 0.392 mm). *Conopeum foliorum* n. sp. also differs from bryozoan specimens identified as ‘membraniporimorph’ cheilostomes encrusting an angiosperm tree-leaf from the Upper Cretaceous (Coniacian) in Lower Silesia, Poland (Halamski and Taylor, 2022) by its substantially longer autozooids (~0.4 mm vs ~0.3 mm).

Conopeum foliorum n. sp. from the Lefipán Formation differs from other Upper Cretaceous/Danian *Conopeum* species by normally having longitudinally rectangular-shaped autozooids (including the extensive opesia of the same shape), and presumably lacking gymnocyst, pustulose shelf-like cryptocyst, closure plates, and polymorphs. The authors know of no other comparable species. Although the available material may lack the reliability needed for discerning some additional fine diagnostic features, *Conopeum foliorum* n. sp. is not conspecific with any of the known Upper Cretaceous/Danian or younger species referred to *Conopeum*, supporting the introduction of a new species for this taxon.

5. Paleoecology and paleoenvironment

Previous studies have regarded the Paso del Sapo Embayment as an environmental setting with warm-temperate to warmer conditions and some degree of seasonality. Palynological

analyses indicate warm-temperate to subtropical conditions during the deposition of the Lefipán Formation (Baldoni and Askin, 1993; Nañez and Malumián, 2008). Additionally, the presence of vegetation adapted to warm and humid conditions, including shore-line mangroves, further suggests a tropical environment (Barreda et al., 2012). Leaf margin analysis (LMA) and leaf area analysis (LAA) have estimated an inferred continental mean annual air temperature (MAT) of approximately 18.5 °C, along with a mean annual precipitation of about 1000 mm (Cúneo et al., 2021). Evidence of seasonality in the lower Lefipán Formation (Maastrichtian) at the Cañadón del Loro locality has been inferred from foliar dimorphism of *Araucaria lefipanensis* (Anduchow-Colombo et al., 2018). Moreover, quantitative estimations indicate a mean annual sea surface temperature (SST) of around 27 °C for the upper Maastrichtian of the Lefipán Formation at the San Ramon section, approximately 15 m below the *Turritella* marker bed (Vellekoop et al., 2017).

Conopeum foliorum n. sp. is inferred to be from a shallow, likely brackish, environment within the Lefipán Formation at the San Ramón section. It came from the muddy component of a horizontally laminated heterolithic bed, associated with coaly plant remains and a few specimens of euryhaline molluscs (*i.e.*, *Corbicula*, *Ledina*, ?*Nucula*). This sedimentary environment corresponds to tidal flats (lithofacies H2 of Scasso et al., 2012), supported by the presence of typical euryhaline bivalves, flat-spiral agglutinated foraminiferans and a high abundance of peridinioid dinocyst suggesting brackish conditions close to the K/Pg boundary (Nañez and Malumián, 2008; Vellekoop et al., 2017).

The membraniporiform growth habit of *Conopeum foliorum* n. sp. represents one of the most opportunistic among bryozoan morphotypes, allowing rapid-growth and early reproduction and colonization of surfaces under suitable conditions (Taylor, 2020; Taylor and Rogers, 2021; and

references therein). This growth pattern is common in shallow shelf environments, ranging from intertidal to upper tidal settings with moderate to high energy levels, where it encrusts hard to flexible substrates (Bone and Wass, 1990; Nelson et al., 1988; Smith, 1995).

Many extant membraniporiform bryozoans, including some comparable *Conopeum* species, thrive in brackish settings (i.e., lagoons, deltas, estuaries) (Occhipinti Ambrogi, 1985; Poluzzi and Sabelli, 1985; O'Dea and Okamura, 1999; Taylor, 2020, and references therein). For example, *Conopeum reticulum* prefers nearshore environments and has been found in estuarine and euhaline harbours (López-Gappa and Pereyra, 2020), while *Conopeum seurati* exhibits tolerance to mesohaline to euhaline conditions (14 ‰ to 33 ‰) and even oligohaline (< 5 ‰) waters (Occhipinti Ambrogi, 1985; O'Dea and Okamura, 1999), categorized recently as euryhaline (Taylor and Rogers, 2021). These and other brackish water bryozoans typically form low-diversity communities dominated by non-mineralized ctenostomes and/or cheilostomes with weakly calcified skeletons (Taylor, 1987, 2005). In addition, some occurrences of brackish water cheilostome bryozoans have also been identified in the upper Campanian of the Western Interior Seaway (WIS) in the United States (Kues, 1983; Roberts et al., 2008; Taylor and Rogers, 2021).

Upper Cretaceous encrusting cheilostomes demonstrated a versatile ability to colonize various substrates, including organic and inorganic settlements (Taylor, 2020, and references therein). They are commonly found cemented to biogenic hard substrates such as mollusc shells (Aguirre-Urreta and Olivero, 1992; Taylor and McKinney, 2006; Taylor, 2020; Brezina et al., 2021). In rare cases, bryozoans encrusting dinosaur bones were reported from Upper Cretaceous rocks of the WIS (Kues, 1983; Taylor and Rogers, 2021). Epiphytic bryozoans have been documented in the Upper Cretaceous (Maastrichtian) of the Netherlands, associated with fossil sea-grass (Voigt, 1981). Recently, bryozoans encrusting an angiosperm tree-leaf were found in

Upper Cretaceous (Coniacian) rocks of Poland (Halamski and Taylor, 2022). *Conopeum foliorum* n. sp. utilized remains of both angiosperm and gymnosperm leaves from diverse terrestrial plants as a substrate (*e.g.*, cf. *Agathis* and several dicot morphotypes).

Bryozoans attach to the substrate/host for life, necessitating favourable environmental conditions for larval settlement and colony growth, including substrate availability, low sedimentation rates, and sufficient food supply. Given these requirements, the muddy substrate found at the PLE fossil horizon likely posed challenges to larval settlement for many suspension feeders, including encrusting bryozoans. Conversely, high sedimentation rates could potentially impair the filter apparatus, while limited food supply might restrict colony growth. In this regard, we presumed the required environmental conditions were sufficiently favourable for the settlement and growth of *Conopeum foliorum* n. sp. Based on sedimentological and paleoecological data, this setting is interpreted as tidal flats close to vegetated coasts (marsh) along the margins of tide-dominated delta channels, under significant stress caused by salinity fluctuations (Scasso et al., 2012). Therefore, *Conopeum foliorum* n. sp. is considered an ancient opportunistic fast-growing taxon displaying euryhaline habits and preferably colonizing flexible substrates composed of terrestrial plant leaves deposited in a brackish-water nearshore environment.

6. Concluding remarks

We present a new finding regarding a Cretaceous cheilostome bryozoan that encrusts terrestrial plant leaves, along with a comprehensive taxonomic analysis. We describe and illustrate

Conopeum foliorum n. sp. discovered in the upper Maastrichtian strata of the Lefipán Formation using contemporary taxonomic methodologies and microscopy techniques. This newly identified taxon in Patagonia likely thrived in a shallow, well-lit, brackish environment influenced by tides, situated within a warm climate at the northwest margin of the Paso del Sapo embayment. Our discoveries also establish *Conopeum foliorum* n. sp. among the earliest known bryozoans from brackish water environments and the second oldest documented instance of bryozoan encrusting terrestrial plant leaves, representing the first such finding in South America.

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Figure captions

Figure 1. Location map and stratigraphic section of the K/Pg boundary at San Ramón section, Lefipán Formation. A. Localization of the study area. B. Upper Cretaceous/Paleogene outcrops of Paso del Sapo/Lefipán Formations, including the study area. C. The partial stratigraphic section of the study area corresponds to the upper Maastrichtian/Danian beds of the Lefipán Formation in the San Ramón section. Studied bryozoans were collected from a single fossil-bearing bed indicated as PLE on the figured section (42°40'12"S, 69°49'60" W). The lower Paleocene (lower Danian) is indicated by the *Turritella* bed (Scasso et al., 2012).

Figure 2. The northern face of a high cliff shows outcrops of the Lefipán Formation at the San Ramón section, south of the Chubut River.

Figure 3. Digital camera photographs and scanning electron micrographs of selected specimens of *Conopeum foliorum* n. sp. encrusting a leaf remain of cf. *Agathis* sp. described in Escapa et al., (2018). A. General view of leaf specimen MPEF-PB 8171 overgrowth by numerous bryozoan colonies; (1) MEF-PI 7101-1 (Holotype), (2) MEF-PI 7101-2 (Paratype), (3) MEF-PI 7101-3 (Paratype), scale bar = 10 mm. B. SEM detail of the specimens MPEF-PI 7101-1 (Holotype) and MPEF-PI 7101-2 (Paratype) in (A); showing encrusting, multiserial colonies with radial growth pattern, scale bar = 1 mm. C. SEM detail of early astogeny of specimen MPEF-PI 7101-1 (Holotype) in (B); showing ancestrula (*) and periancestrular zooids, scale bar = 0.5 mm. D.

SEM detail of specimen MPEF-PI 7101-1 (Holotype) in (C); showing elongate rectangular autozooids arranged in a brick-wall pattern and two bifurcated rows, scale bar = 0.1 mm. E. SEM detail of early astogeny of specimen MPEF-PI 7101-2 (Paratype) in (B); showing ancestrula (*) and periancestrular zooids, scale bar = 0.01 mm.

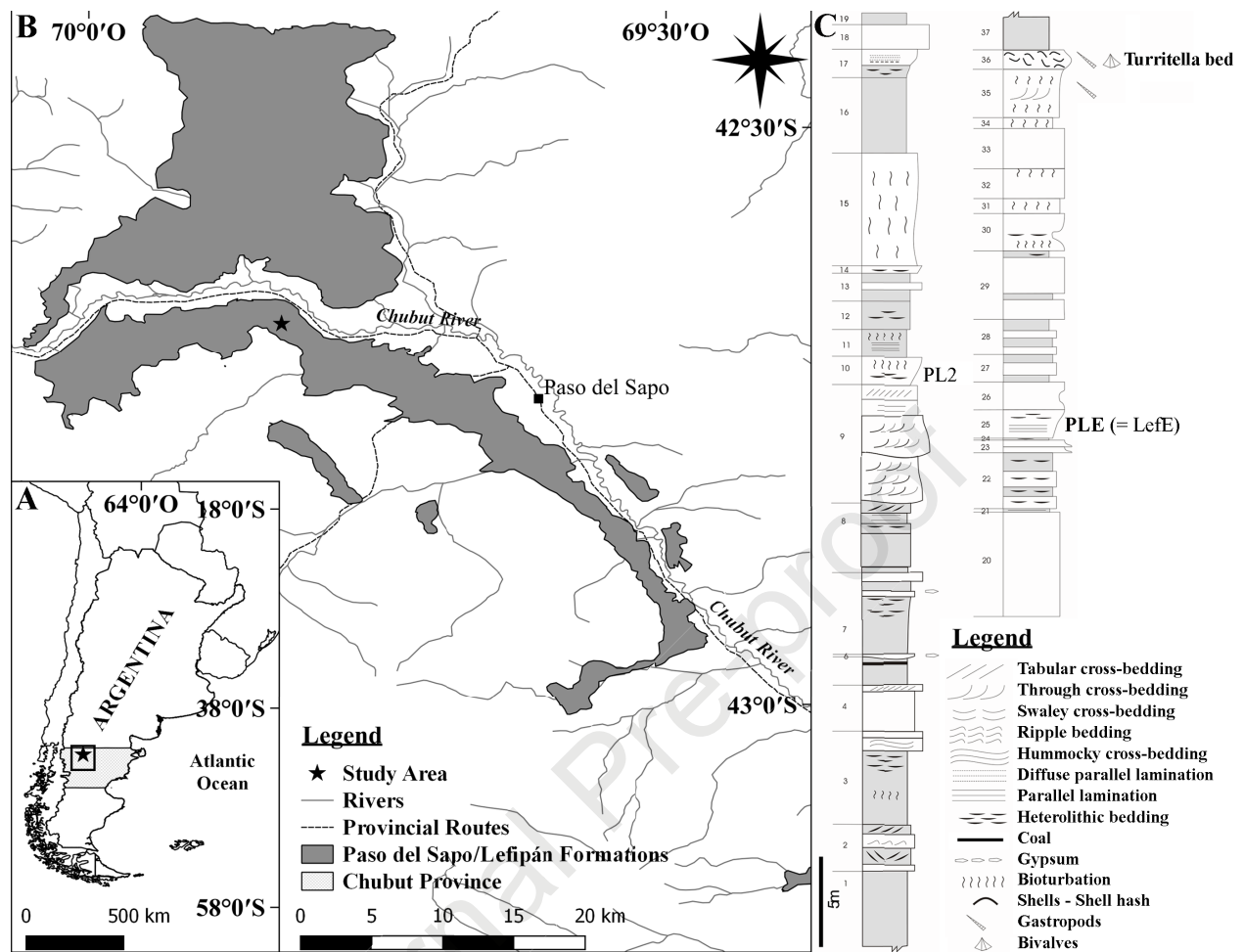
Figure 4. Digital camera photographs and scanning electron micrographs of selected specimens of *Conopeum foliorum* n. sp. encrusting a dicot leaf remain. A. General view of leaf specimen completely overgrowth by numerous bryozoan colonies; (1) MEF-PI 7102-1 (Paratype), (2) MEF-PI 7102-2 (Paratype), (3) MEF-PI 7102-3 (Paratype), scale bar = 10 mm. B. SEM detail of the specimen MPEF-PI 7102-1 (Paratype) in (A), scale bar = 0.5 mm. C. Detail view of early astogeny of specimen MPEF-PI 7102-1 (Paratype) in (B); showing ancestrula (*) and periancestrular zooids, scale bar = 0.05 mm. D. SEM detail of an autozoid (up left in B), scale bar = 0.1 mm. E. SEM detail of specimen MPEF-PI 7102-1 (Paratype) (down left in B); showing elongate rectangular autozooids arranged in a brick-wall pattern and row bifurcation, scale bar = 0.2 mm. F. SEM detail of early astogeny of specimen MPEF-PI 7102-2 (Paratype) in (A); showing ancestrula (*) and periancestrular zooids, scale bar = 0.01 mm.

Figure 5. Digital camera photographs and scanning electron micrographs of selected specimens of *Conopeum foliorum* n. sp. encrusting a dicot leaf remain. A. General view of leaf specimen MPEF-PI 4795 overgrowth by numerous bryozoan colonies; and showing insect-damage (down left), scale bar = 20 mm. B. SEM detail of the specimen MPEF-PI 7106 (Paratype); showing encrusting, multiserial colonies with radial growth pattern, ancestrula (*) and periancestrular zooids, scale bar = 1 mm. C. Detail view of early astogeny of specimen MPEF-PI 7106

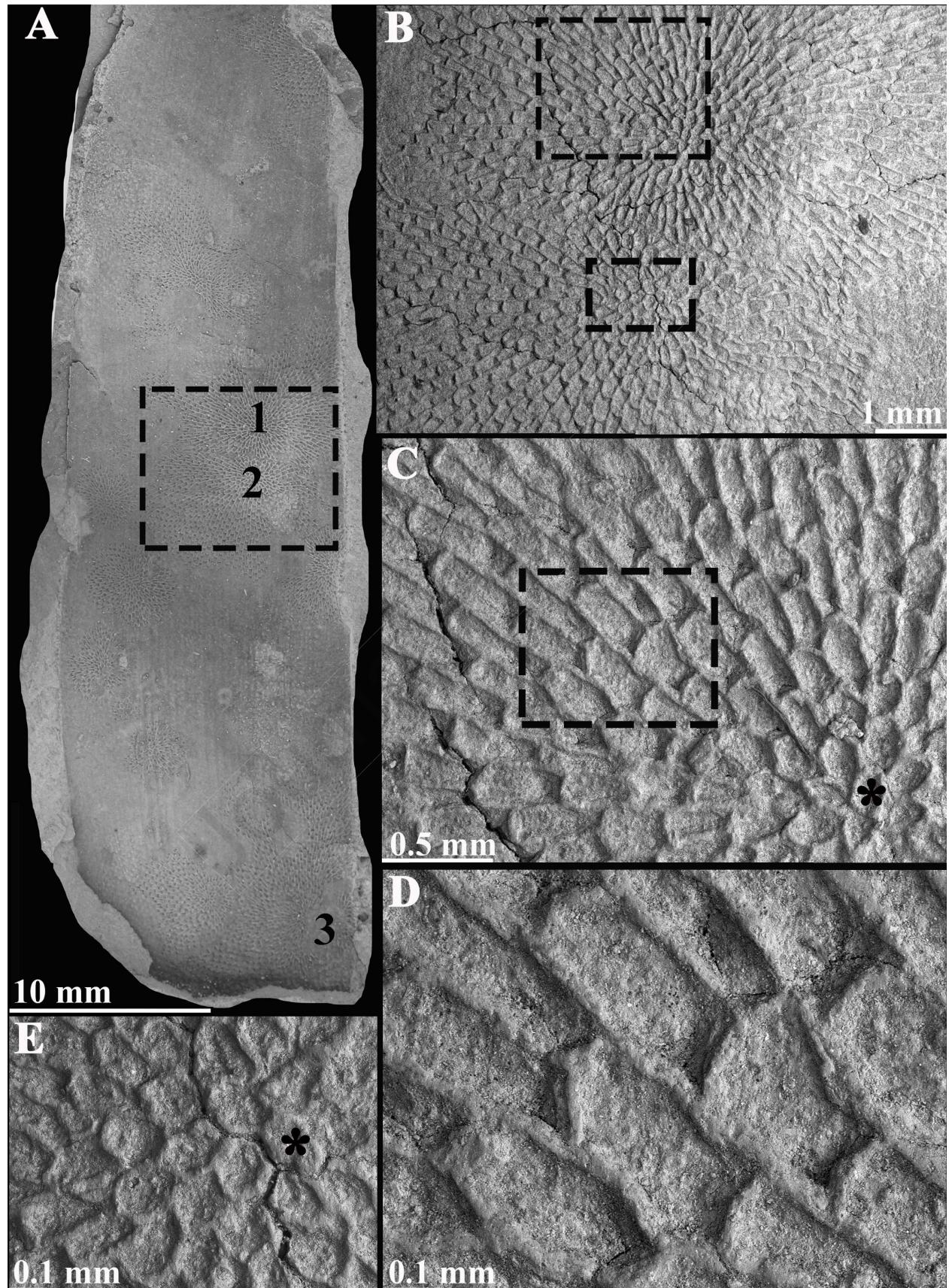
541 (Paratype); showing ancestrula (*) and periancestrular zooids, scale bar = 0.2 mm. D. SEM detail
542 of an autozoid (in B), scale bar = 0.1 mm. E. SEM detail of specimen MPEF-PI 7106 (Paratype)
543 (up left in C); showing elongate rectangular autozooids arranged in a brick-wall pattern and row
544 bifurcation; arrows point to rounded granules, scale bar = 0.2 mm.

Table 1. Measurements of *Conopeum foliorum* n. sp. taken from the type material (i.e. holotype and paratypes; n = 7). Values are expressed in mm; CV in %.

	Mean	SD	CV	MIN	MAX	N
ZL	0.392	0.045	11.426	0.290	0.509	175
ZW	0.201	0.039	19.511	0.129	0.271	175







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