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Recibido: 1 de agosto 2025 - **Aceptado:** 30 de septiembre 2025 - **Publicado:** 6 de noviembre 2025

Para citar este artículo: Juan López-Gappa, Débora Iturra, Leandro M. Pérez, Egly Pérez Pincheira, & Alberto C. Garrido (2025). A new species of *Cellaria* (Bryozoa, Cheilostomatida) from the late Danian (Paleocene) of Patagonia (Argentina). *Publicación Electrónica de la Asociación Paleontológica Argentina* 25(2): 183–190.

Link a este artículo: http://dx.doi.org/10.5710/PEAPA/30.09.2025.550

ISSN 2469-0228

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ARTÍCULO Año 2025 - 25(2): 183–190 PeAPA Publicación Electrónica ASOCIACIÓN PALEONTOLÓGICA ARGENTINA

A NEW SPECIES OF *CELLARIA* (BRYOZOA, CHEILOSTOMATIDA) FROM THE LATE DANIAN (PALEOCENE) OF PATAGONIA (ARGENTINA)

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Abstract. The cheilostome bryozoan genus *Cellaria* is characterized by articulated, dichotomously branching colonies, which are composed of cylindrical internodes joined by cuticular nodes. The genus includes over 130 species, with approximately 70 taxa ranging from the late Paleocene to the Holocene. This study describes *Cellaria daniana* sp. nov., based on material collected from the Roca Formation, upper Danian (Paleocene) of northern Patagonia, Argentina, making it the earliest known occurrence of the genus. The most distinctive feature of *C. daniana* sp. nov. is its vicarious avicularium, which lacks mandibular pivots and exhibits a distally depressed cryptocyst, resembling that of *C. stachi* from the Eocene of Victoria, Australia. *Cellaria stachi* shows a great morphological similarity with *C. daniana* sp. nov., supporting a close biogeographic connection between South America and Australasia during the Early Cenozoic.

Key words. Roca Formation. Neuquén Basin. Río Negro Province. Danian. Marine invertebrates. Bryozoan.

Resumen. UNA NUEVA ESPECIE DE *CELLARIA* (BRYOZOA, CHEILOSTOMATIDA) DEL DANIANO TARDÍO (PALEOCENO) DE LA PATAGONIA ARGENTINA. El género de briozoo queilostomado *Cellaria* se caracteriza por sus colonias articuladas, ramificadas dicotómicamente, compuestas por internodios cilíndricos conectados por articulaciones cuticulares. Incluye más de 130 especies, con aproximadamente 70 taxones registrados desde el Paleoceno tardío hasta el Holoceno. Este estudio describe a *Cellaria daniana* sp. nov. en base a material colectado en la Formación Roca, Daniano superior (Paleoceno) del norte de Patagonia, Argentina, representando el registro conocido más antiguo del género hasta la fecha. El rasgo más característico de *C. daniana* sp. nov. es su avicularia vicaria, que carece de *pivots* mandibulares y exhibe un criptocisto deprimido distalmente, similar al de *C. stachi*, del Eoceno de Victoria, Australia. *Cellaria stachi* exhibe una gran similitud morfológica con *C. daniana* sp. nov., sustentando una estrecha conexión biogeográfica entre Sudamérica y Australasia durante el Cenozoico Temprano.

Palabras clave. Formación Roca. Cuenca Neuquina. Provincia de Río Negro. Daniano. Invertebrados marinos. Briozoo.

THE BRYOZOAN genus *Cellaria* Ellis & Solander, 1786 comprises over 130 species (Bock, 2025), including approximately 70 taxa ranging from the latest Paleocene (Gordon & Taylor, 1999) to the Holocene (Di Martino *et al.*, 2025).

In Patagonia, *Cellaria* is represented by 12 poorly known specific or subspecific taxa described or recorded from the early Miocene (Canu, 1904, 1908). Additionally, *Cellaria* fragments found in upper Oligocene deposits of Santa Cruz Province (Patagonia) were attributed to the extant European species *C. fistulosa* (Linnaeus, 1758) by Ortmann (1902). Studies specifically focused on the fossil bryozoan fauna of the Paleocene Roca Formation (Canu, 1911; Brezina *et al.*, 2021) have not yet identified any representatives of *Cellaria*. As noted by Gordon & Taylor (1999), few studies have addressed Paleocene bryozoan faunas from the Southern Hemisphere (Canu, 1911; Brood, 1976;

Gordon & Taylor, 1999; Brezina *et al.*, 2021).

This study describes a new species of *Cellaria* based on material collected from the Roca Formation, upper Danian (Paleocene) of northern Patagonia, Argentina, representing the oldest known occurrence of this genus to date.

GEOLOGICAL SETTING

During its maximum extent, the Neuquén Basin encompassed Neuquén, the southern part of Mendoza, and the western regions of Río Negro and La Pampa provinces. It was bounded to the north by the Sierra Pintada system and to the south by the Somuncurá or North Patagonian Massif (Uliana & Dellapé, 1981). The Cerro Azul 2 site is located in the northwestern part of Río Negro province, approximately 12 km S–SE of Lago Pellegrini (Fig. 1). At this locality, both the Jagüel and Roca formations have been identified. Research conducted near the study area has documented the presence of the Cretaceous/Paleogene (K/Pg) boundary. This is based on nannofossil (Musso *et al.*, 2012), ostracod (Ceolín *et al.*, 2015), and palynomorph (Pérez Pincheira & di Pasquo, 2021) assemblages.

Massive, laminated, slightly calcareous shales are present throughout most of the section (Fig. 2). From 16.5 m onward, coquinas and massive limestones appear, along with invertebrates such as *Ostrea wilckensi* Ihering, 1907, *Cubitostrea ameghinoi* (Ihering, 1902), and *Pycnodonte* (*Phygraea*) *burckhardti* Böhm, 1903. Above 30 m, carbonate mudstones and silty carbonate sandstones with horizontal and wavy lamination are observed. Sample S18—where colonies of the new species were found—consists of

Figure 1. Map of the study area. Abbreviations: **NB,** Neuquén Basin. Scale bar= 10 km.

massive to laminated carbonate shales with an opaque greenish colour (Fig. 2). This sample belongs to the Roca Formation and is attributed to the upper Danian, as it lies above the levels containing *O. wilckensi* (del Río *et al.*, 2011; Brezina *et al.*, 2017).

Paleoenvironment at the Cerro Azul 2 site

Towards the end of the Cretaceous, specifically during the Maastrichtian and into the early Danian, the Northern and Central Patagonia were submerged by an epicontinental sea that advanced from the Atlantic Ocean (Woelders *et al.*, 2017). This marine transgression caused the southern tip of South America to become an archipelago around the time of the K/Pg boundary (Aguirre-Urreta *et al.*, 2008). It covered much of the Patagonian region and extended westward to the foothills of the Andes in the area corresponding to the Neuquén Basin (Bertels, 1979). The advance of the sea over the continent is well documented in the stratigraphic record, particularly in the Jagüel and Roca formations (Carrera & Casadío, 2016), in the central sector of the basin near the mountain foothills.

The general climatic conditions prevailing during the transgressive event—which allowed the sea to advance from the South Atlantic in a northwesterly direction—suggest that the region experienced a warm and humid climate at that time, with normal marine salinity conditions in the epicontinental sea in the northern part of Río Negro Province, at least during the early Danian (see Woelders *et*

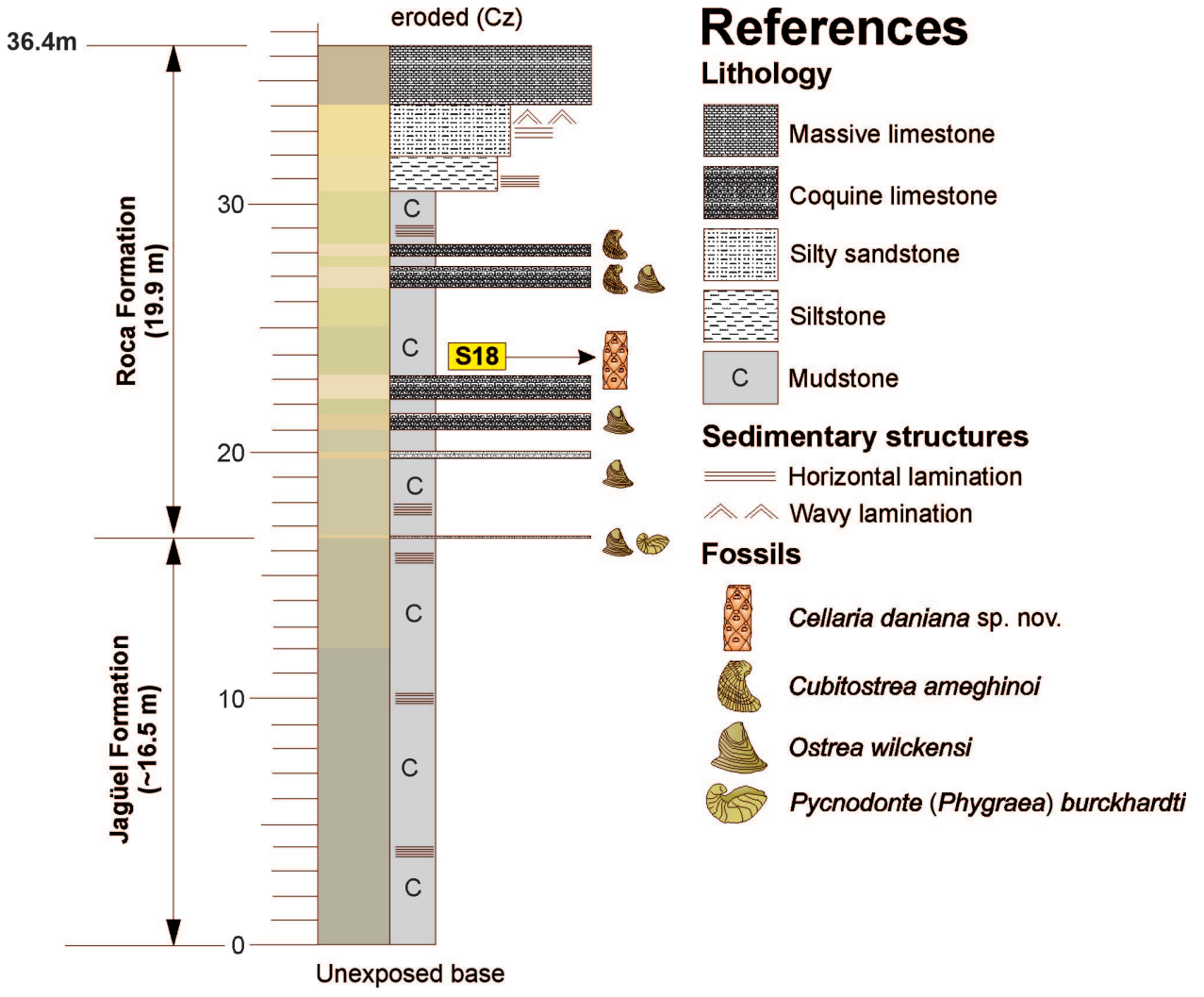

Figure 2. Stratigraphic profile of the study site. Abbreviations: **Cz,** Cenozoic.

al., 2017). The invertebrate fauna associated with *Cellaria daniana* sp. nov. suggests shifts in environmental energy and water depth within the basin. For instance, the bivalve *P.* (*P.*) *burckhardti*, which occurs in strata underlying the level where the new cellariid species was found (see Fig. 2), is characteristic of the central and western sectors of the basin, and is commonly associated with outer shelf facies, marked by low sedimentation rates (lower Danian; see Casadío, 1998). In contrast, above the level containing *Cellaria daniana* sp. nov. (Fig. 2), the bivalve species *O. wilckensi* and *C. ameghinoi*—the latter indicating a late Danian age (Casadío, 1998)—are present. These species are known for forming parautochthonous bioclastic accumulations and biostromes, deposited in shallow subtidal environments indicative of higher energy conditions (see Casadío, 1994).

These findings suggest that at the Cerro Azul 2 locality, the bryozoan assemblages found across various fossiliferous levels—alongside the associated macroinvertebrate fauna—reflect variations in environmental energy. These changes suggest a shallowing-upward trend in the stratigraphic succession analysed, and support an estimated late Danian age for the new species *Cellaria daniana* sp. nov. in this sector of the Neuquén Basin.

Sediments at the Cerro Azul 2 site were likely deposited in a shallow marine environment, characterized by intervals of high energy and elevated nutrient availability. This interpretation agrees with that proposed by Brezina *et al.* (2021), who stated that the preserved bryozoan assemblage indicates typical conditions of shallow proximal areas, with dominance of cyclostome bryozoans.

MATERIALS AND METHODS

Twenty-three samples were collected during the survey of a ~36.4 m-thick stratigraphic section encompassing the Jagüel and Roca formations at Cerro Azul 2 (Fig. 2). The samples were processed with a 30% hydrogen peroxide solution to disaggregate the sediment and allow for initial cleaning. The residue was examined under a stereomicroscope, and bryozoan colonies were manually extracted. These colonies were subsequently re-immersed in a 30% hydrogen peroxide solution and further cleaned in an ultrasonic bath for several minutes.

The type material was sputter-coated with gold–palladium, and imaging was conducted using a Zeiss Gemini 360 scanning electron microscope (SEM) at the *Museo Argentino de Ciencias Naturales* (MACN), and a FEI ESEM Quanta 200 at the Scanning Electron Microscopy and Microanalysis Service of LIMF (*Departmento de Ingeniería Mecánica, Facultad de Ingeniería, Universidad Nacional de La Plata*). Measurements were taken from SEM images using ImageJ version 1.54g (Schneider *et al.*, 2012).

All examined material is housed in the Paleoinvertebrate Collection of the *Museo Regional de Cinco Saltos* (MCS-Pi), Río Negro Province, Argentina. The authors J. López-Gappa, D. Iturra, and L. M. Pérez were responsible for the systematic section of this paper and are to be considered the taxonomic authors for the newly described species.

SYSTEMATIC PALEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMATIDA Busk, 1852
Suborder FLUSTRINA Smitt, 1868
Superfamily CELLARIOIDEA Fleming, 1828
Family CELLARIIDAE Fleming, 1828

Genus *Cellaria* Ellis & Solander, 1786

Type species. *Farcimia sinuosa* Hassall, 1840. Eastern North Atlantic and Mediterranean seas, Recent.

Diagnosis. Colony erect, branching dichotomously, attached to substratum by chitinous rhizoids; internodes cylindrical, linked by chitinous nodes. Opesia barely larger than the operculum, with a pair of condyles in the proximal corners and sometimes with an opposing pair of denticles on the distal border. Avicularia interzooidal, interposed between autozooids in a longitudinal series, or vicarious.

Cellaria daniana López-Gappa, Iturra & Pérez sp. nov.
Figures 3.1–5, Table 1

LSID urn:lsid:zoobank.org:act:D2F59D39-A1DC-49A8-81F5-996C4A08B0A6

Derivation of name. The specific epithet refers to the Danian, the age of the formation in which the type material of this species occurred.

Diagnosis. Colony consisting of 7–8 alternate longitudinal series of zooids. Opesia-orifice with one pair of well-

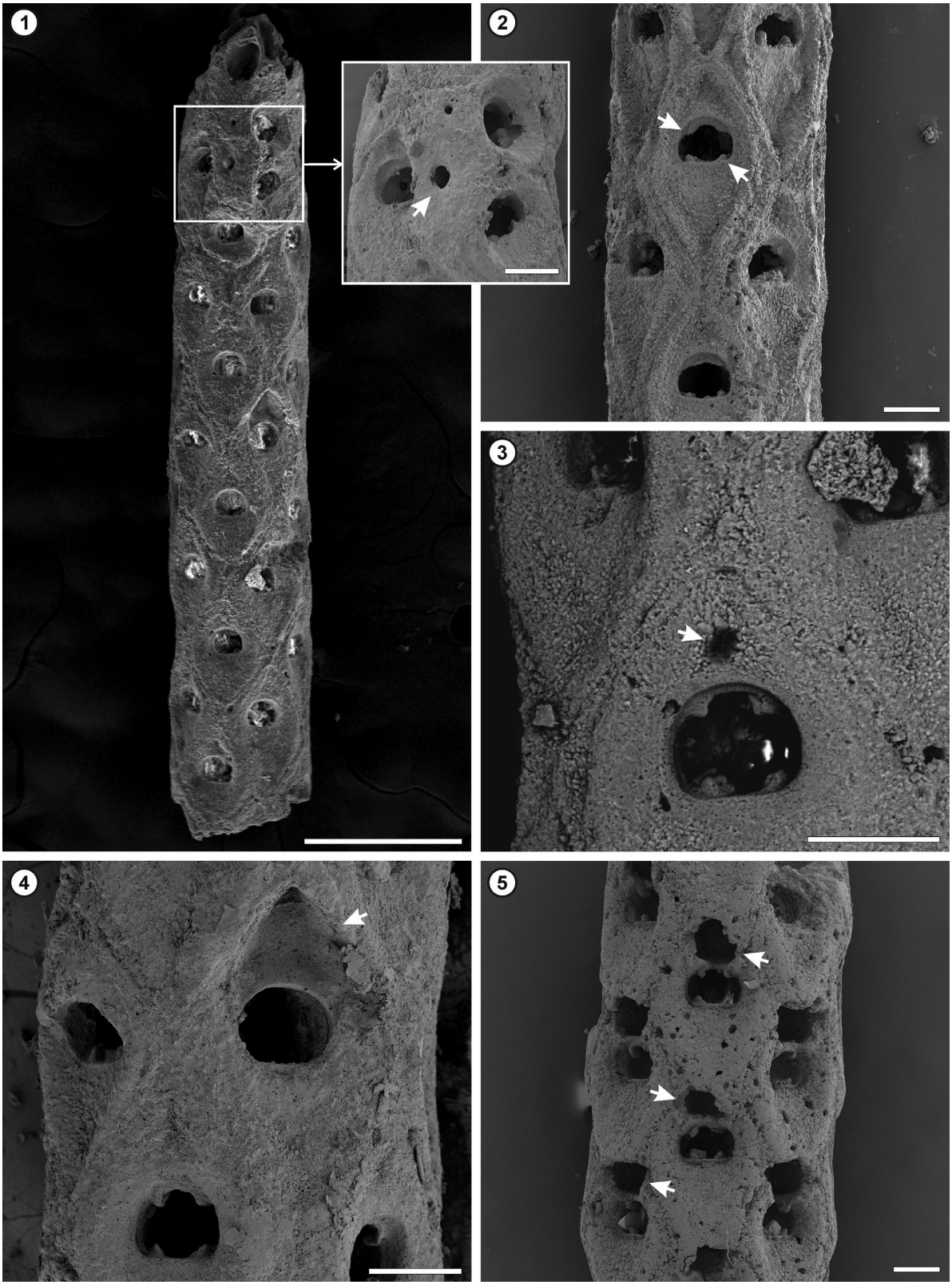

Figure 3. ***Cellaria daniana*** sp. nov. **1,** internode; the inset shows a detail of a kenozooid (arrow); **2,** close-up of autozooids. The proximal condyles as well as the distal ridge and teeth are arrowed. **3,** ooeciopore (arrow). **4,** vicarious avicularium (arrow). **5,** zooids with broken ovicells (arrows). Components 1, 3 and 4 correspond to the holotype (**MCS-Pi 1**) while components 2 and 5 to the paratype (**MCS-Pi 2**). Scale bar= 500 µm in 1; scale bar= 100 µm in 1 inset and 2–5.

developed proximal condyles; distal teeth connected by a conspicuous, concave ridge. Avicularia vicarious, about the same size of autozooids; opesia subcircular, without condyles or mandibular pivots; rostrum lanceolate, with acute tip, pointing distally; rostral cryptocyst depressed, concave, with a distal pore.

Type material. Holotype, one incomplete internode 2.57 mm long, MCS-Pi 1. Paratypes, MCS-Pi 2, four internodes (1.57, 1.51, 1.37, and 0.94 mm).

Description. Colony erect, jointed, composed of slender, subcylindrical, straight internodes (diameter 417–514 µm) consisting of 7–8 alternate longitudinal series of zooids (Fig. 3.1). Autozooids usually rhombic, longer than wide (363–487 µm long × 233–281 µm wide), with acute proximal and distal corners (Fig. 3.1). Lateral corners of neighbouring zooids almost in touch (Figs. 3.2, 3). Zooidal margins with straight, well-marked sutures. Cryptocyst granular, centrally depressed area tapering proximally. Opesia-orifice large, transversely D-shaped, wider than long (72–95 µm long × 101–127 µm wide). One pair of well-developed proximal condyles; distal teeth connected by a conspicuous, concave ridge (Fig. 3.2, 4). Kenozooids rare, located between autozooids, near the tip of a longitudinal series, with a circular opening for the attachment of a rhizoid (Fig. 3.1 inset). Avicularia vicarious (one per internode in the holotype), about the same size of autozooids (420–425 µm long × 227–0.248 µm wide); opesia subcircular, without condyles or mandibular pivots; rostrum lanceolate, with acute tip, pointing distally; rostral cryptocyst depressed, concave, with a distal pore (Fig. 3.4). Some autozooids with a small circular ooeciopore distal to the opesia-orifice, close to the distal zooidal corner (Fig. 3.3), others with endotoichal ovicells with broken roofs (Fig. 3.5). Ancestrula and early astogeny not observed.

Remarks. The vicarious avicularium of *C. daniana* sp. nov. lacks mandibular pivots, and consequently, there is no distinct rostral foramen separated from the avicularian opesia. This new species most closely resembles *Cellaria stachi* Brown, 1958, from the Glenaulin Clay (upper Eocene) of Victoria, Australia, as both exhibit a distinctive type of vicarious avicularium with a distally depressed cryptocyst. However, the avicularia of *C. stachi* possess a proximal sinus in the opesia, an absent feature in *C. daniana* sp. nov.

No avicularia have been reported in the four *Cellaria* species described from the latest Paleocene to earliest Eocene of the Chatham Island (Gordon & Taylor, 1999). While vicarious avicularia are present in some of the Miocene Patagonian *Cellaria* species described by Canu (1904, 1908), none display a distally depressed cryptocyst adjacent to the opesia, as seen in *C. daniana* sp. nov.

Three late Cretaceous cellariid species of uncertain taxonomic status, originally assigned to *Cellaria* by d'Orbigny (1851), were later transferred to *Cellarina* d'Orbigny, 1851 by Canu (1900), a preoccupied genus name subsequently replaced by *Cellarinidra* Canu & Bassler, 1927. Therefore, the present study documents the oldest confirmed occurrence of the genus *Cellaria* to date.

Geographic and stratigraphic occurrence. Late Danian (Paleocene), Cerro Azul 2 site, Roca Formation, Río Negro Province, Argentina.

TABLE 1 – Measurements (µm) of *Cellaria daniana* sp. nov.

	Internode diameter	Autozooid length	Autozooid width	Opesia length	Opesia width	Avicularium length	Avicularium width
Mean	449	437	258	84	109	423	238
Minimum	417	363	233	72	101	420	227
Maximum	514	487	281	95	127	425	248
Standard deviation	38	44	15	6	10	4	15
N	5	10	10	10	10	2	2

DISCUSSION

The morphological similarity between *C. daniana* sp. nov. and *C. stachi* supports the hypothesis of a closer biogeographic connection between Patagonia and Australasia during the Paleocene than exists today. This connection may have facilitated the dispersal of larvae or colonies via rafting on floating substrates, a process observed in extant species (Achilleos, 2021). Notably, such dispersal could have taken place within the paleogeographic context of the Gondwanan breakup, which began in the Early Jurassic (~180 Ma; McLoughlin, 2001) and concluded near the end of the Eocene, approximately concurrent with the establishment of the modern Antarctic Circumpolar Current (Håkansson *et al.*, 2024). Following the final fragmentation of Gondwana, bryozoan faunas across these formerly connected landmasses became increasingly widespread (Håkansson *et al.*, 2024).

Previous studies have suggested that faunal affinities between Australasian and Patagonian bryozoans persisted at least until the early Miocene (*e.g.*, Casadío *et al.*, 2010; Pérez *et al.*, 2015; López-Gappa *et al.*, 2023). The complete opening of the Drake Passage during the early Oligocene, along with the associated reorganization of the global ocean circulation and the definitive onset of the Antarctic Circumpolar Current (Lawver & Gahagan, 2003), led to the formation of a new marine corridor between the bryozoan faunas of the southeastern Pacific and Atlantic Patagonia (Hedgpeth, 1969; Moyano, 1997).

The discovery of *Cellaria daniana* sp. nov. in the Roca Formation (upper Danian) confirms the presence of the family Cellariidae in northern Patagonia during the early Paleocene, approximately 5 million years after the K/Pg extinction event, representing the oldest known occurrence of the genus. This new species contributes to the diversity of Cheilostomatida in the Roca Formation and extends the stratigraphic range of *Cellaria* back to the onset of the Cenozoic.

ACKNOWLEDGEMENTS

The material was photographed by Fabián Tricárico and a team of SEM operators at MACN and LIMF, respectively. A doctoral fellowship of CONICET to Débora Iturra is acknowledged. This study was financed by National Geographic Society grant NGS-92822R 22. We thank Bjorn Berning, an anonymous reviewer and the editorial staff of PE-APA for improving an earlier version of this manuscript.

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LSID urn:lsid:zoobank.org:pub:B55389F3-C11F-44D9-A9BD-5AE73711E1C0

doi: 10.5710/PEAPA/30.09.2025.550

Recibido: 1 de agosto 2025
Aceptado: 30 de septiembre 2025
Publicado: 6 de noviembre 2025