

Species of the genus *Melicerita* Milne Edwards (Bryozoa, Cheilostomatida) in the Early Miocene of Patagonia (Argentina)

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SPECIES OF THE GENUS *MELICERITA* MILNE EDWARDS (BRYOZOA, CHEILOSTOMATIDA) IN THE EARLY MIOCENE OF PATAGONIA (ARGENTINA)

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Abstract. Species of the cellariid genus *Melicerita* Milne Edwards develop bilaminar flattened colonies consisting of alternate transverse rows of hexagonal zooids. In South America, its stratigraphic range extends from the Early Miocene to the Recent. Re-examination of the type material of *M. triforis* Ortmann from the Monte León Formation of Río Chalfá, and scanning electron microscope images of *M. ortmanni* Canu from the Early Miocene Chenque Formation, confirmed that the latter is a junior synonym of *M. triforis*. Vicarious avicularia are described for the first time in *M. triforis*. Lectotypes are herein chosen for both nominal species. *M. imperforata* sp. nov. is described from material obtained in the Monte León Formation (Early Miocene). It differs from all known *Melicerita* species in the size and shape of its vicarious avicularia, which are marginal and much larger than the autozooids. The Recent Magellanic species *M. temaukeli* Moyano and *M. blancoae* López Gappa share morphological similarities with *M. triforis*.

Key words. Cellariidae. Monte León Formation. Chenque Formation. Argentina.

Resumen. LAS ESPECIES DEL GÉNERO *MELICERITA* MILNE EDWARDS (BRYOZOA, CHEILOSTOMATIDA) EN EL MIOCENO TEMPRANO DE PATAGONIA (ARGENTINA). Las especies del género *Melicerita* Milne Edwards (Cellariidae) desarrollan colonias aplanadas bilaminares compuestas por hileras transversales alternas de zooides hexagonales. En Sudamérica, su rango estratigráfico se extiende desde el Mioceno Temprano hasta el Reciente. El examen del material tipo de *M. triforis* Ortmann de la Formación Monte León en el Río Chalfá, y de imágenes de microscopía electrónica de barrido de *M. ortmanni* Canu de la Formación Chenque (Mioceno Temprano), confirmó que esta última especie es sinónimo junior de *M. triforis*. Se describen por primera vez las avicularias vicarias de *M. triforis*. Se eligen aquí lectotipos para ambas especies nominales. Se describe a *M. imperforata* sp. nov. a partir de material obtenido en la Formación Monte León (Mioceno Temprano). Esta nueva especie difiere de todas las demás *Melicerita* por el tamaño y la forma de sus avicularias vicarias, que son marginales y mucho más grandes que los autozooides. Las especies magallánicas actuales *M. temaukeli* Moyano y *M. blancoae* López Gappa comparten similitudes morfológicas con *M. triforis*.

Palabras clave. Cellariidae. Formación Monte León. Formación Chenque. Argentina.

AMONG the anascan-grade cheilostomes, the family Cellariidae is characterized by a complete development of the cryptocyst, a calcareous reinforcement of the frontal surface which divides the body cavity into two compartments, the hypostegal and perigastric cavities. The cellariid cryptocyst lacks slots or holes for the passage of the parietal muscles, which resulted in the development of a peculiar hydrostatic mechanism for lophophore protrusion (Pérez & Banta, 1996). Another feature of this family is the existence of concealed ovicells, sometimes termed endotoichal, opening to the exterior by an independent aperture immediately distal to the maternal opesia (Cook *et al.*, 2018).

Although most cellariid genera are characterized by erect, articulated colonies composed of rod-like internodes linked by cuticular joints, colonies in the genus *Melicerita* Milne Edwards, 1836 have bilaminar flattened blades consisting of alternate transverse rows of hexagonal zooids (Hayward, 1995).

In South America, *Melicerita* is represented in the fossil record by the cenozoic species *M. triforis* Ortmann, 1900 and *M. ortmanni* Canu, 1908. The Recent South American species of this genus comprise *M. blancoae* López Gappa, 1981 and *M. temaukeli* Moyano, 1997 from the Magellanic region (López Gappa, 1981; Hayward & Thorpe, 1989; Hayward,

1995; Moyano, 1997a), *M. atlantica* Busk, 1884 from the continental slope off Argentina and Uruguay (Busk, 1884; Figuerola *et al.*, 2018; Ramalho *et al.*, 2022), and *M. brasiliensis* Vieira, Gordon, Souza & Haddad, 2010 from the Brazilian continental shelf and upper slope (Vieira *et al.*, 2010). *Melicerita* has a rich fossil history in the Palaeogene and Neogene of Australasia (Waters, 1882a, 1882b, 1883; MacGillivray, 1895; Brown, 1952, 1954, 1958; Powell, 1969), and today it reaches maximum diversity in the southern hemisphere (Hayward, 1995).

The aims of this study are to discuss the status and affinities of the fossil *Melicerita* introduced by Ortmann (1900, 1902) and Canu (1908), and to describe a new species of the genus based on material collected at Monte León Formation, Early Miocene of Atlantic Patagonia.

Institutional abbreviations. LIMF, Laboratorio de Investigaciones en Metalúrgica Física, Facultad de Ingeniería; MLP, Museo de La Plata “Francisco P. Moreno”, La Plata, Buenos Aires, Argentina; MNHN, Muséum National d’Histoire Naturelle, Paris, France; PRI, Paleontological Research Institution, Ithaca, New York, USA; UNLP, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.

METHODS

The specimens were coated with gold and images were obtained using a FEI ESEM Quanta 200 scanning electron microscope (SEM) at LIMF, UNLP. Measurements were taken from SEM photos with imageJ. Both this publication and the new taxon erected herein are registered in ZooBank and the resulting life science identifiers (LSID) are provided.

GEOLOGICAL SETTING

The Cenozoic marine units of Argentine Patagonia extend from the north of Río Negro Province to the extreme south of the South American continent in Tierra del Fuego Province. These stratigraphic units originated in cyclical eustatic changes and tectonic controls that brought about different transgressive events. At least five episodes of mean sea-level rise have been recorded since the Maastrichtian (Malumián, 1999).

The first fossil *Melicerita* recorded in Argentina was *M. triforis* Ortmann, 1900. Fragments of this species were collected by J.B. Hatcher between 1896 and 1899 on the

south bank of Río Chalfía (Fig. 1), a locality where the Monte Observación Member (*sensu* Parras & Cuitiño, 2018) of the Early Miocene Monte León Formation crops out intermittently (Cuitiño *et al.*, 2021). This member is lithologically similar to the stratigraphic successions which extend over Atlantic ravines in the type area of the Monte León Formation at Monte León National Park, although in this area the outcropping levels correspond to facies of deltaic deposits.

The Monte León Formation crops out mainly on the Atlantic coast of Santa Cruz Province, where its type locality is found (Parras *et al.*, 2012). This marine unit has a high taxonomic diversity of invertebrates, among which bryozoans make up one of the best-represented phyla. The type material of *Melicerita imperforata* sp. nov., and our specimens of *M. triforis* come from the locality ‘Cabeza de León’ (Fig. 1).

In its type area, the Monte León Formation consists of siliciclastic rocks in medium to fine sandy to silty beds, and has an approximate thickness of 47 m. Most of the sediments that make up this stratigraphic succession seem to have accumulated in a depositional environment characteristic of a shallow, low-energy marine platform, with a large contribution of volcanic materials (Malumián, 1999). This unit was dated as Early Miocene based on an isotopic study carried out by Parras *et al.* (2012). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio resulted in an age of 22.12 Ma at the base (Playa La Mina locality) and 17.91 Ma in the upper part of the stratigraphic succession (Las Cuevas locality), which correspond to the Aquitanian and early Burdigalian, respectively.

Melicerita is represented by *M. ortmanni* Canu, 1908 in the Chenque Formation, which crops out abundantly around the city of Comodoro Rivadavia, Chubut Province (‘Punta Borja’, Fig. 1). This unit is approximately 300 m thick (Cuitiño *et al.*, 2015) and has a lithology similar to that of the Monte León Formation. It is made up of siliciclastic material, mostly sandstones and shales, with levels of marine invertebrates and reef structures dominated by oysters. Isotopic analyses (Cuitiño *et al.*, 2015) estimated the age of this unit as 19.69 Ma at the base (Cordova-2 locality) and 15.37 Ma at the top of the stratigraphic succession (Antena-3 locality), *i.e.* Burdigalian to early Langhian. This temporal range partly overlaps with that of the Monte León Formation, being however slightly more recent.

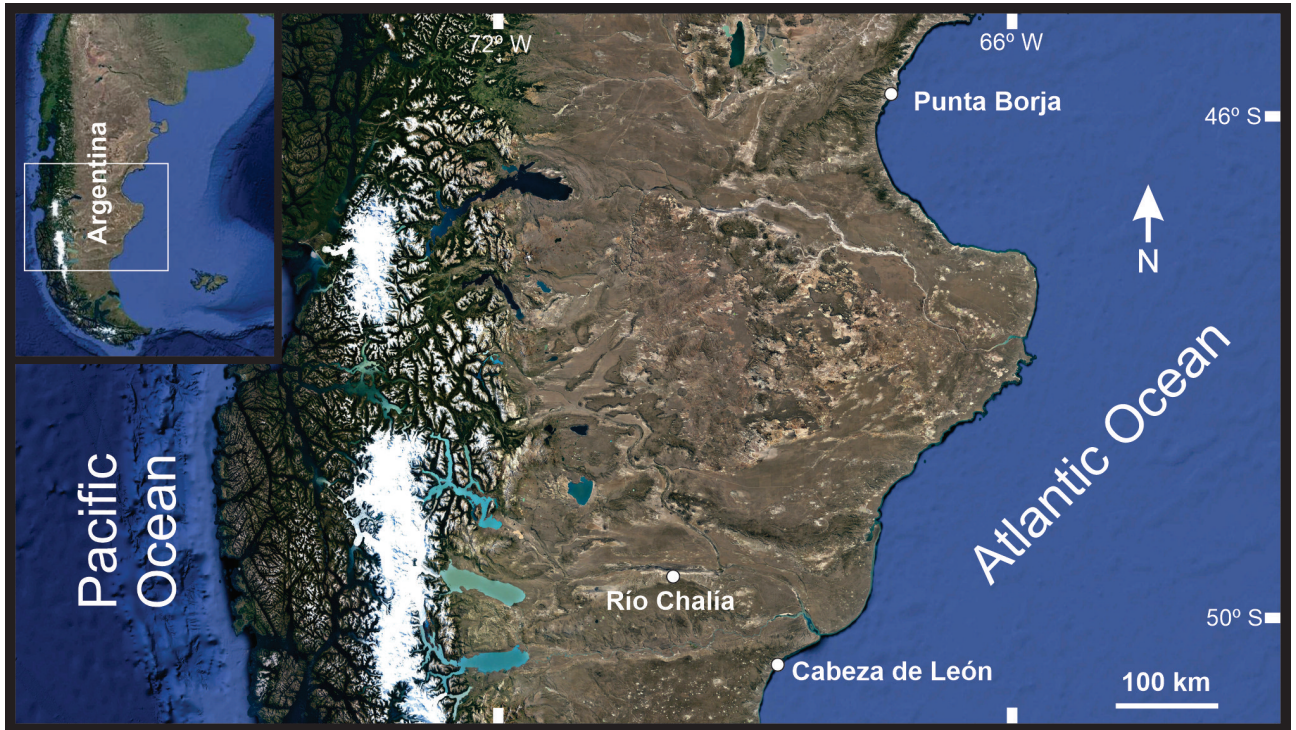


Figure 1. Study area showing the location of 'Punta Borja' (Chenque Formation), 'Cabeza de León' and 'Río Chalfía' (Monte León Formation) in Argentine Patagonia.

SYSTEMATIC PALEONTOLOGY

Order CHEILOSTOMATIDA Busk, 1852

Suborder NEOCHEILOSTOMINA d'Hondt, 1985

Superfamily CELLARIOIDEA Fleming, 1828

Family CELLARIIDAE Fleming, 1828

Genus *Melicerita* Milne Edwards, 1836

Type species. *Melicerita charlesworthii* Morris, 1843. Tertiary from Europe.

Melicerita triforis Ortmann, 1900

Figures 2, 3.1–3.4; Table 1

1900 *Melicerita triforis* Ortmann, p. 370.

1902 *Melicerita triforis* Ortmann, p. 65, pl. 13, fig. 3a, b.

1908 *Melicerita ortmanni* Canu, p. 272, pl. 4, figs. 1, 2.

Referred material. (1) *Melicerita triforis* Ortmann, 1900. Upper Río Chalfía, collected by J. B. Hatcher. PRI 66673 (three syntypes). The fragment illustrated in figure 3a of Ortmann (1902) is here chosen as lectotype (PRI 66673), the other

two fragments becoming paralectotypes (PRI 104824). (2) 'Cabeza de León', Monte León Formation, MLP 36485, 41 fragments. (3) Online SEM images of *Melicerita ortmanni* Canu, 1908, Collection Tournouër, MNHN (MNHN Collection, 2022). Set of five fossil specimens (syntypes). The specimen photographed in images som06516 through som06520 is here chosen as lectotype (MNHN.F.R53506), the other four fragments becoming paralectotypes (MNHN.F.A87403).

Description. Colony erect, bilaminar, ribbon-like, flat, with acute margins, dividing dichotomously, attached to the substrate by rhizoids. Maximum fragment size observed 11.06 × 6.27 mm. Alternating transverse rows of up to 25 autozooids immediately before a bifurcation. Autozooids hexagonal, longer than wide in some colony areas, as long as wide in others; autozoid margins straight, protruding. Cryptocyst granular, markedly concave, strongly depressed towards the centre (Fig. 2.1). Autozoid shape becoming irregularly hexagonal or pentagonal towards the colony margin, with the cryptocyst widening outwards (Fig. 2.2). Opesia located in distal half of autozoid, D-shaped or

slightly reniform in more central areas, becoming distinctly reniform towards the colony margin, its length comprising ~21% of autozoid length. Proximal margin of the opesia slightly upturned, changing from straight to strongly convex during ontogeny. Two pairs of condyles close to the lateral margins of the opesia (Fig. 2.1). Kenozooids marginal, with a small round subcentral foramen (Fig. 2.3). Occasional kenozooids may occur interspersed in transverse autozooidal rows, with one or sometimes two round foramina similar to those of marginal kenozooids (Fig. 2.4). Vicarious avicularia infrequent, occurring in groups near the midline of the colony (Fig. 2.5), similar in size and shape to autozooids, replacing them in transverse rows, with a broad U-shaped sinus limited by a pair of bicuspid condyles in the proximal margin of the opesia, and a distal pair of small condyles in the distal margin (Fig. 2.6). Ovicelled zooids similar in size and shape to autozooids (Fig. 3.1); ovicell aperture D-shaped to subtriangular, with concave proximal border, located at the extreme distal end of the zooid; cryptocyst granules near the proximal margin of the ovicell aperture longitudinally aligned (Fig. 3.2). Two cribrate areas (often broken, Fig. 3.3) communicating the ovicell with the hypostegal cavity occur lateroproximally to the ovicell aperture. The occurrence of rhizoids in the basal part of the colony is evidenced by the presence of swollen cameras with a proximal rounded orifice in the proximal end of each autozoid. The opesia of the rhizoid-bearing autozooids becomes partially occluded by the development of proximal

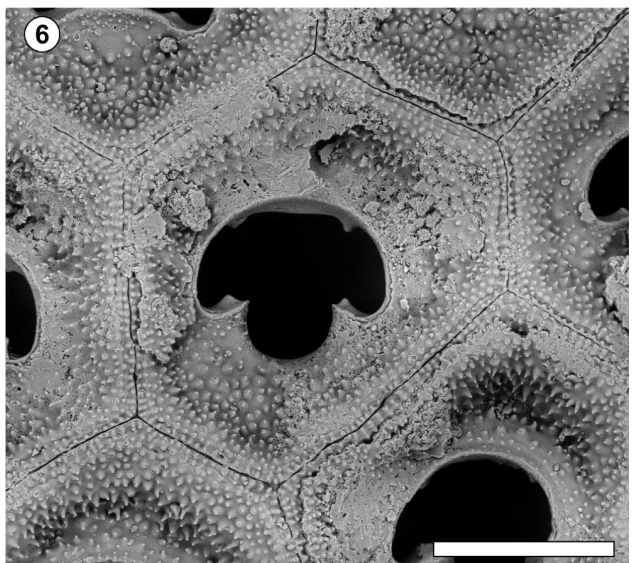
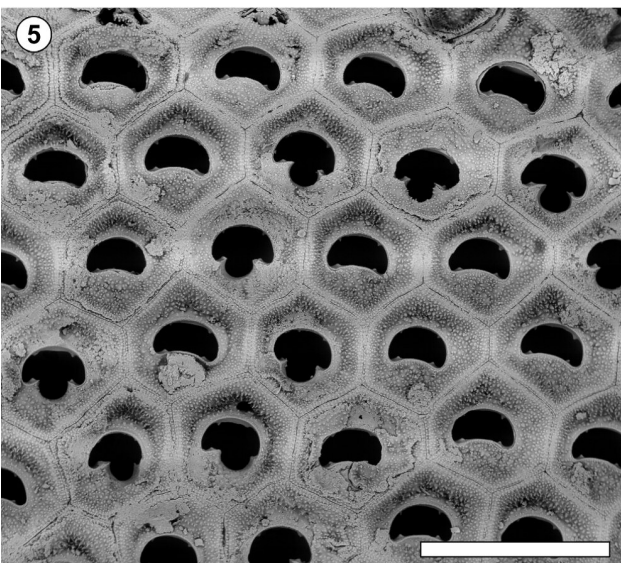
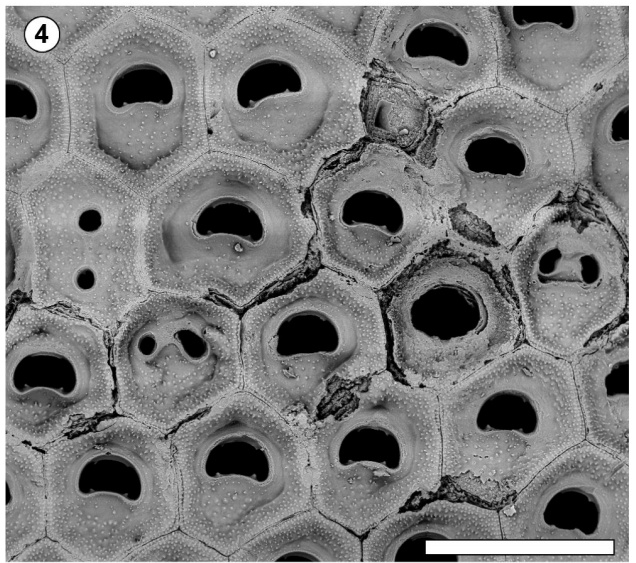
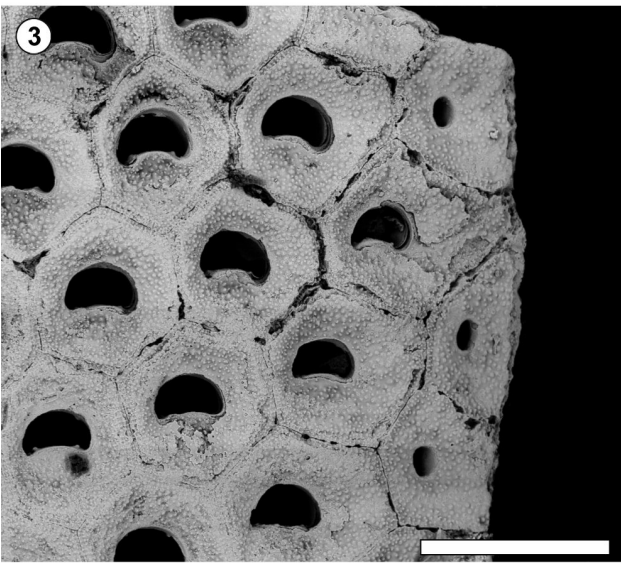
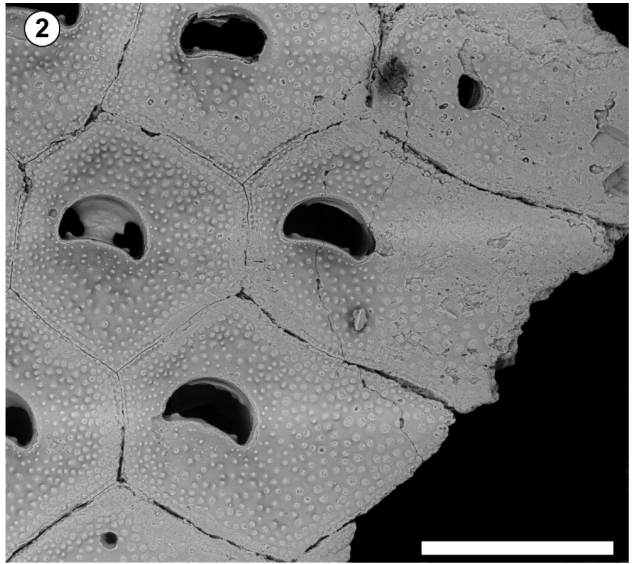
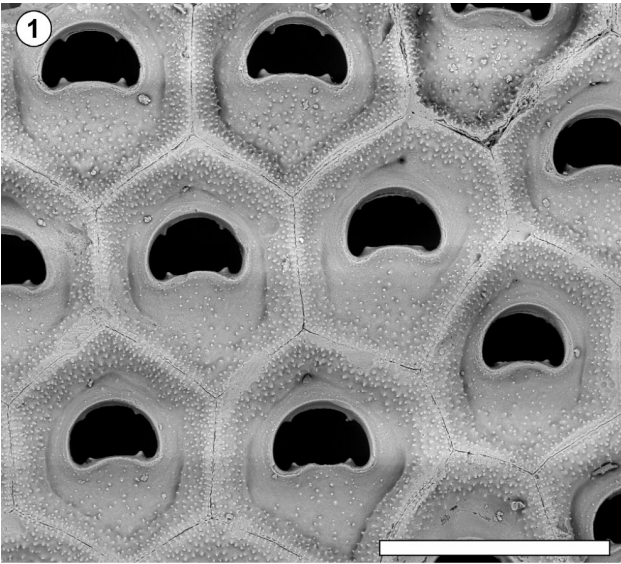
and distal calcareous tabs, leaving eventually a pair of lateral subcircular to irregular orifices (Fig. 3.4). Ancestrula unknown.

Remarks. The cribrate areas in the cryptocyst of the ovicelled zooids are delicate structures that are rarely preserved intact. It is more common to find them broken, as is shown in Figure 3.1 and 3.3. They were misinterpreted as avicularia by Ortmann (1900, 1902), a fact that led Canu (1908) to the unnecessary introduction of his new species *M. ortmanni*, while including with doubts Ortmann's species as a possible senior synonym. These structures link the ovicell cavity with the hypostegal space, and are not a constant feature of the genus. Their probable function could be to facilitate the transfer of oxygen to the embryo. They have been found in several southern hemisphere species, such as *M. blancoae* from the Magellanic region (López Gappa, 1981; Hayward & Thorpe, 1989; Hayward, 1995; Moyano, 1997a), *M. chathamensis* Uttley & Bullivant, 1972 and *M. knoxi* Uttley & Bullivant, 1972 from New Zealand and the Chatham Islands (Uttley & Bullivant, 1972; Gordon, 1986), *M. obliqua* (Thornely, 1924) from Antarctica (Hayward & Thorpe, 1989; Hayward, 1995) and *M. brasiliensis* from Brazil (Vieira *et al.*, 2010). According to the SEM images taken from the syntypes of *M. ortmanni* stored in André Tournouër's collection at the MNHN (image som06520; MNHN Collection, 2022), cribrate areas were also present in the material collected at 'Punta Borja', although they were unnoticed by Canu (1908).

TABLE 1 - Measurements of *Melicerita triforis* (μm , $n = 10$)

	Autozoid length	Autozoid width	Opesia length	Opesia width
Mean	420	287	88	160
Minimum	399	264	84	151
Maximum	443	299	95	168
Standard deviation	15	10	4	6

Figure 2. *Melicerita triforis* Ortmann, 1900, MLP 36485. **1**, General aspect of autozooids. Note the distal and proximal pairs of condyles; **2**, Colony margin, showing one marginal kenozooid and pentagonal autozooids with their cryptocyst widening outwards; **3**, Kenozooids with rounded foramina at the colony margin; **4**, Kenozooids with two foramina interspersed in transverse autozooidal rows; **5**, Several vicarious avicularia near the midline of autozoid rows; **6**, Close-up of a vicarious avicularium. Scale bars, **1**= 400 μm ; **2**= 300 μm ; **3–5**= 500 μm ; **6**= 200 μm .



The vicarious avicularia, not described by Ortmann (1900, 1902) for *M. triforis* or by Canu (1908) for *M. ortmanni*, are similar to those of *Melicerita temaukeli* Moyano, 1997a, which have a U-shaped proximal sinus and occur near the midline of autozoid rows. *Melicerita triforis* also strongly resembles *M. blancoae* López Gappa, 1981 due to the presence of marginal kenozooids with a round foramen and cribrate areas in the cryptocyst of the ovicelled zooids, but differs from this species in the presence of vicarious avicularia (absent in *M. blancoae*).

Geographic and stratigraphic occurrence. The type material of *M. triforis* was collected by J. B. Hatcher at Upper Río Chalfía (Monte León Formation, Early Miocene, see Cuitiño *et al.*, 2021), Santa Cruz Province, Argentina (Fig. 1). Our material comes from the same formation, at ‘Cabeza de León’, Monte León National Park. The type material of *M. ortmanni* was collected at ‘Punta Borja’, Chenque Formation.

***Melicerita imperforata* sp. nov.**

Figures 3.5–3.6, 4.1–4.6; Table 2

LSID urn:lsid:zoobank.org:act:8D1ECC96-670A-4243-9522-0C9B2FD14086

Derivation of name. The species name is derived from the Latin adjective *imperforatus*, imperforate, alluding to the absence of cribrate areas in the ovicelled zooids.

Diagnosis. *Melicerita* lacking marginal kenozooids. Cribrate areas in the cryptocyst of the ovicelled zooids absent. Giant vicarious avicularia, with blunt distal ends and wide spatulate

rostra, ca. 50% longer than autozooids, located on colony margins.

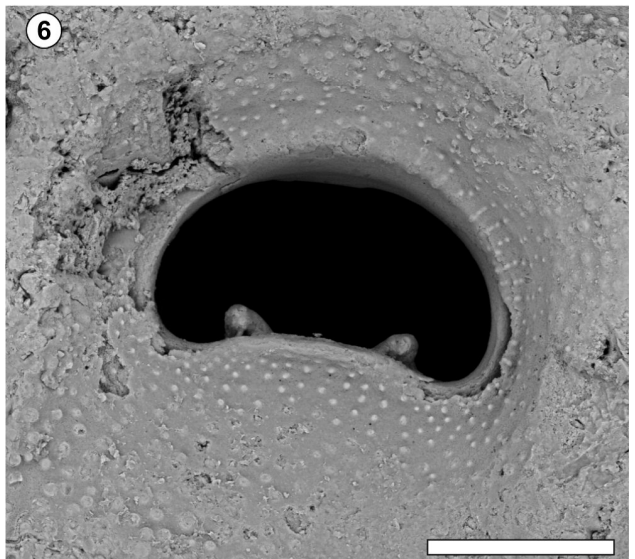
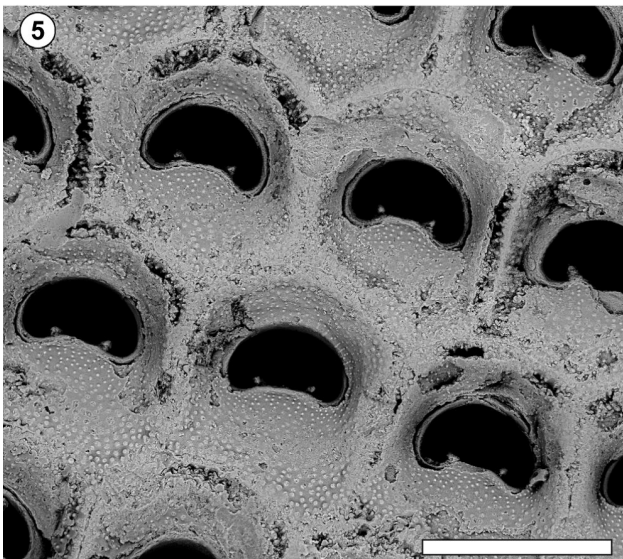
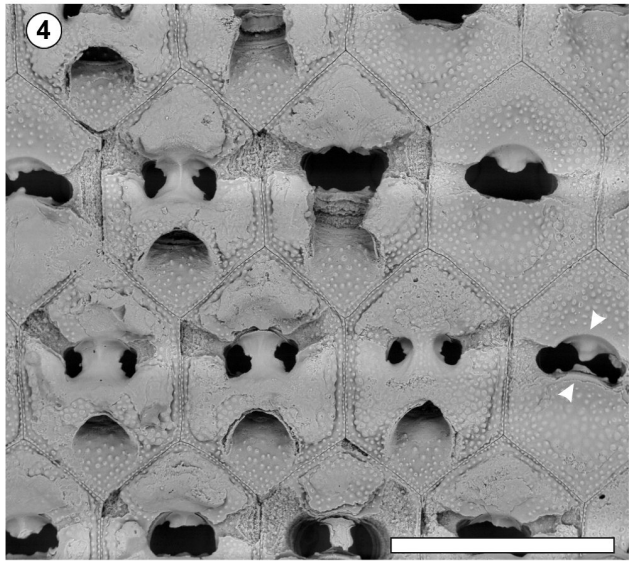
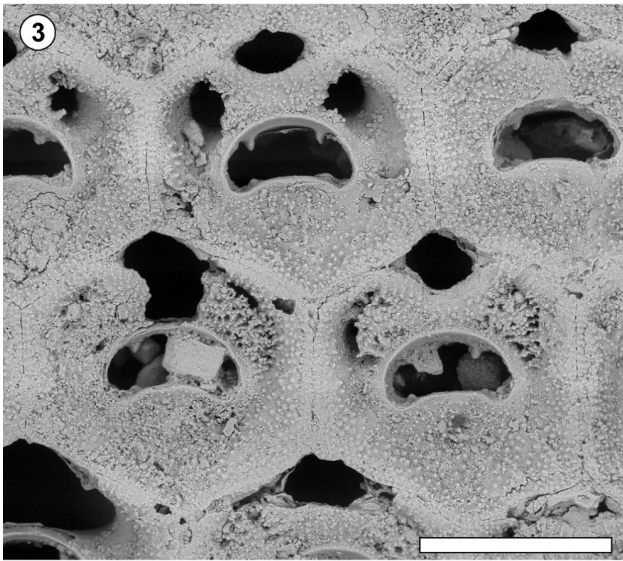
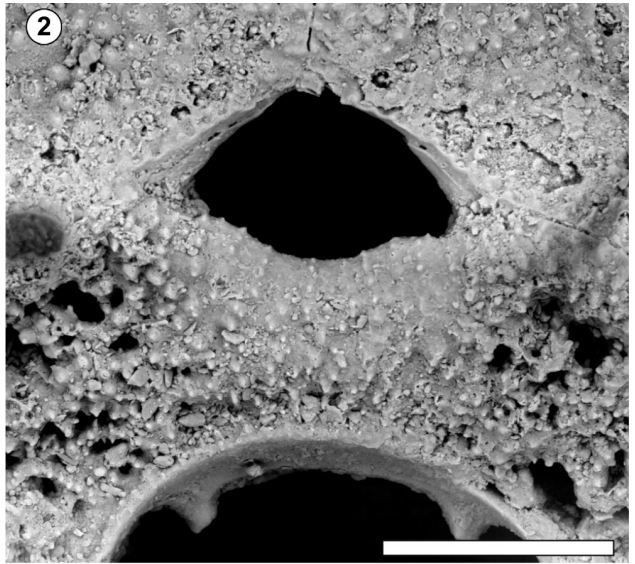
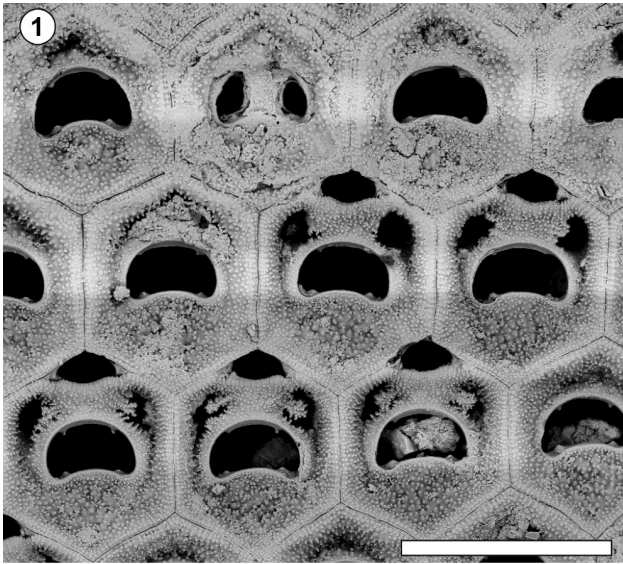
Type material. Holotype: MLP 36486. Paratypes: MLP 36487, 51 fragments.

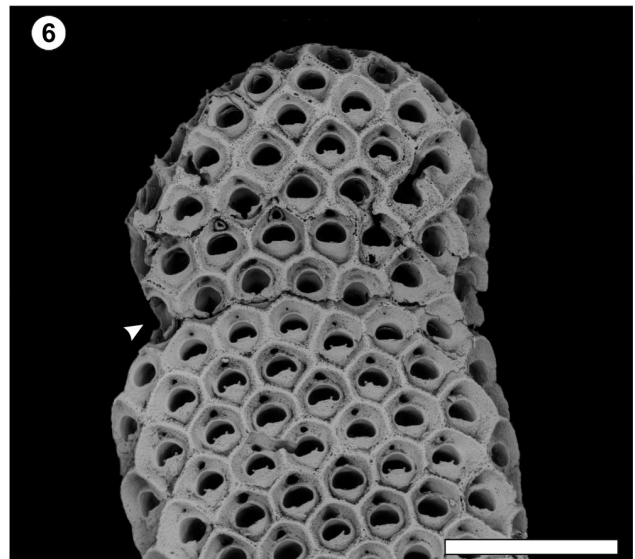
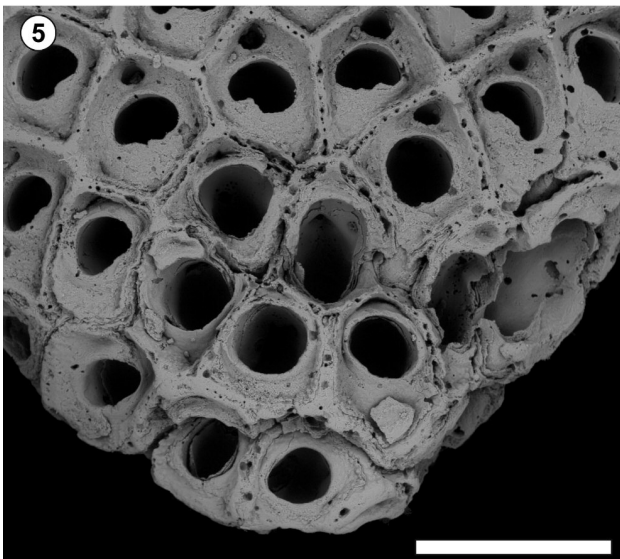
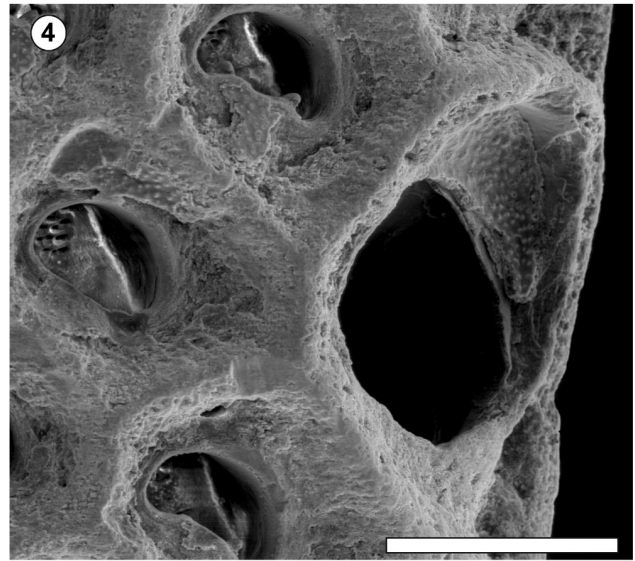
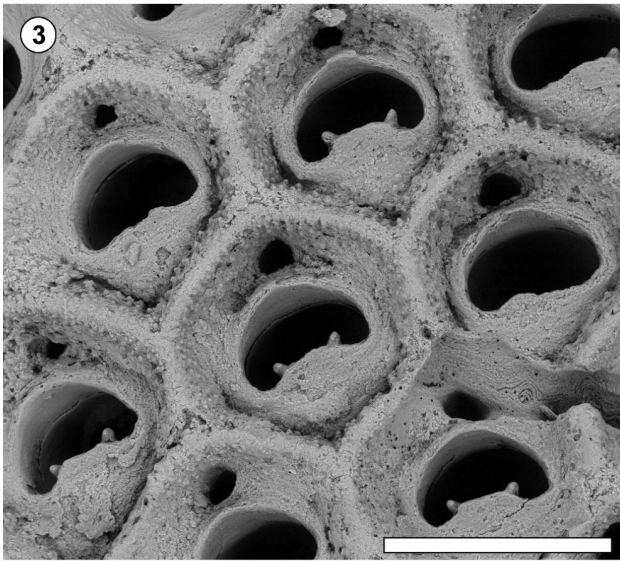
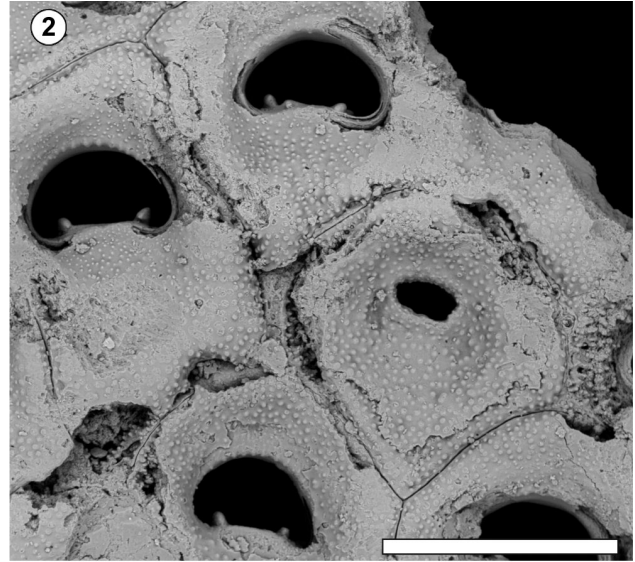
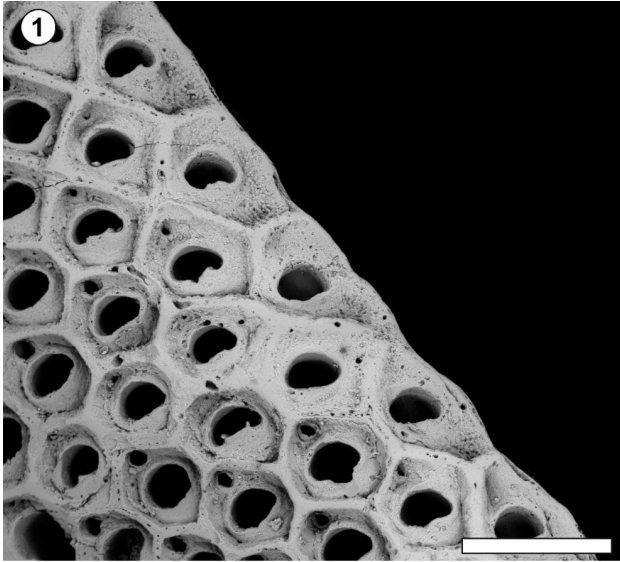
Description. Colony erect, bilaminar, bifurcating dichotomously. Maximum fragment size observed: 11.46 × 5.33 mm. Alternating transverse rows of up to 16 autozooids. Autozooids hexagonal, slightly longer than wide; autozoid margins straight, protruding (Fig. 3.5). Cryptocyst granular, markedly concave, strongly depressed towards the centre; cryptocyst granules radially aligned near the distal margin of the opesia (Fig. 3.6). Marginal autozooids irregularly pentagonal (Fig. 4.1). Opesia subcentral, reniform; its length comprising ~28% of autozoid length. Proximal margin of the opesia slightly upturned, changing from straight to convex during ontogeny. Only one proximal pair of condyles present (Fig. 4.2). Kenozooids with a small rounded or elliptical foramen may occasionally occur interspersed in transverse autozoid rows (Fig. 4.2). Marginal kenozooids absent. Ovicelled zooids extremely abundant, similar in size and shape to autozooids; ovicell aperture small, rounded or transversely elliptical, located between the opesia and the distal end of the zooid; cribrate areas absent (Fig. 4.3). Vicarious avicularia rare, large, rhombic, with blunt distal end and wide spatulate rostrum, ca. 50% longer than autozooids, located on colony margins (Fig. 4.4). Rhizoid-bearing autozooids not observed. Colony during early astogeny fan-shaped (Fig. 4.5). Ancestrula unknown.

TABLE 2 - Measurements of *Melicerita imperforata* sp. nov. (µm, n = 10)

	Autozoid length	Autozoid width	Opesia length	Opesia width
Mean	352	329	99	182
Minimum	334	319	90	171
Maximum	374	360	110	198
Standard deviation	11	13	6	9

Figure 3. 1–4, *Melicerita triforis* Ortmann, 1900, MLP 36485. 1, Ovicelled zooids with broken cribrate areas; **2,** Close-up of ovicell aperture. Note the aligned cryptocyst granules; **3,** Broken and intact cribrate areas; **4,** Rhizoid-bearing autozooids. Note the proximal and distal tabs before meeting (arrowheads); **5–6, *Melicerita imperforata* sp. nov. Holotype, MLP 36486. 5,** General aspect of the autozooids; **6,** Close-up of the opesia, showing the proximal condyles and the cryptocyst granules. Scale bars, 1= 500 µm; 2, 6= 100 µm; 3, 5= 300 µm; 4= 400 µm.





Remarks. *Melicerita imperforata* sp. nov. differs from all other *Melicerita* species in the size and shape of its vicarious avicularia, which are larger than the autozooids.

In the examined material from Cabeza de León, the fragments of this species have a darker hue than those of *M. triforis*.

Geographic and stratigraphic occurrence. *M. imperforata* sp. nov. was only collected at 'Cabeza de León', Monte León National Park.

Discussion. Some fragments of *M. imperforata* sp. nov. show growth-checks (Fig. 4.6), suggesting that this species underwent seasonal variations in growth rate, like in *M. obliqua* (Thornely, 1924) (Winston, 1983; Brey *et al.*, 1998; Bader & Schäfer, 2004) and *M. chathamensis* (Key *et al.*, 2018). Growth-checks are evidenced by transverse constrictions (Fig. 4.6) and from the zooids of the first rows after the growth-check being morphologically different than those located before the constriction (Fig. 4.6).

Fragments of *M. triforis* and *M. imperforata* sp. nov. occur together in the Monte León Formation and are not easy to

distinguish at first glance. Differences between the two species are summarized in Table 3, the most striking being the presence of marginal kenozooids and cribrate areas in ovicelled zooids in *M. triforis* (both absent in *M. imperforata* sp. nov.).

Melicerita triforis and *M. temaukeli*, together with the Antarctic *M. flabellifera* Hayward & Winston, 1994, are the only species of the genus with fully vicarious sinuate avicularia. Sinuate avicularia are also present in the Australasian *M. angustiloba* Tenison-Woods, 1862, but they are smaller than the autozooids (see Gordon, 1986).

The Recent species of *Melicerita* have a widespread bathymetric distribution, ranging from the continental shelf to the upper slope (40–1675 m, Tab. 4). The fine grain-size and the high degree of bioturbation of the sedimentary rocks of the Monte León Formation, however, suggest an inner-shelf, normal salinity, shallow water environment (Parras *et al.*, 2020).

In conclusion, our study shows that *Melicerita ortmanni* Canu, 1908, from the Early Miocene Chenque Formation, is

TABLE 3 - Differences between *Melicerita triforis* and *M. imperforata* sp. nov.

	<i>M. triforis</i>	<i>M. imperforata</i> sp. nov.
Colony width	Up to 25 autozooids	Up to 16 autozooids
Colour of fragments	Whitish	Darker
Autozooid size	~0.42 × 0.29 mm	~0.35 × 0.33 mm
Relative size of opesia	~21% of autozooid length	~28% of autozooid length
Condyles	Two pairs	One proximal pair
Marginal kenozooids	Present	Absent
Size of vicarious avicularia	Same size as autozooids	Much larger than autozooids
Location of vicarious avicularia	Between autozooids	Marginal
Shape of ovicell aperture	D-shaped to triangular	Round to transversely elliptical
Cribrate areas	Present	Absent

Figure 4. *Melicerita imperforata* sp. nov. 1–3, 5, 6 Paratypes, MLP 36487; 4, Holotype, MLP 36486. 1, Marginal autozooids; 2, Kenozooid. 3, Ovicelled zooids. Note the conspicuous proximal pair of condyles; 4, Vicarious avicularium; 5, Early astogeny; 6, Growth-check (arrowhead). Note the different morphology of the zooids before and after the growth-check. Scale bars, 1= 500 µm; 2–4= 300 µm; 5= 500 µm; 6= 1 mm.

a junior synonym of *M. triforis* Ortmann, 1900, from the Monte León Formation of Río Chalía, and that *M. imperforata* sp. nov. is a second representative of the mainly austral genus *Melicerita* in the Early Miocene of Patagonia.

TABLE 4 - Bathymetric ranges of the Recent species of *Melicerita*

Species	Bathymetric range (m)	Source
<i>M. alternans</i> d'Hondt & Gordon, 1999	435	d'Hondt & Gordon (1999)
<i>M. angustiloba</i> Tenison-Woods, 1862	78–786	Powell (1969), Wass & Yoo (1983), Gordon (1986)
<i>M. (Henrimilnella) articulata</i> d'Hondt & Gordon, 1999	360	d'Hondt & Gordon (1999)
<i>M. atlantica</i> Busk, 1884	1098–1577	Busk (1884), Figuerola <i>et al.</i> (2018)
<i>M. biseriata</i> Souto in Souto & Albuquerque, 2019	1073	Souto & Albuquerque (2019)
<i>M. blancoae</i> López Gappa, 1981	74–780	López Gappa (1981), Hayward & Thorpe (1989), Moyano (1997a, 1997b, 2000)
<i>M. brasiliensis</i> Vieira, Gordon, Souza & Haddad, 2010	100–480	Vieira <i>et al.</i> (2010)
<i>M. chathamensis</i> Uttley & Bullivant, 1972	168–507	Uttley & Bullivant (1972), Gordon (1986), Key <i>et al.</i> (2018)
<i>M. depressa</i> De Blauwe & Gordon, 2014	595–602	De Blauwe & Gordon (2014)
<i>M. digeronimoi</i> Rosso, 1992	123–681	Rosso (1992), Gutt <i>et al.</i> (2000)
<i>M. ejuncida</i> Gordon, 1986	132–1675	Gordon (1986), d'Hondt & Gordon (1999)
<i>M. flabellifera</i> Hayward & Winston, 1994	40–628	Hayward & Winston (1994), Gutt <i>et al.</i> (2000)
<i>M. knoxi</i> Uttley & Bullivant, 1972	530–549	Uttley & Bullivant (1972)
<i>M. latilaminata</i> Rogick, 1956	96–367	Rogick (1956), Moyano (1968, 1969), Androsova (1972), Hayward & Thorpe (1989), Gutt <i>et al.</i> (2000), López de la Cuadra & García Gómez (2000)
<i>M. (Henrimilnella) laurifolia</i> d'Hondt & Gordon, 1999	360	d'Hondt & Gordon (1999)
<i>M. lingulata</i> Liu & Hu, 1991	450–602	Liu & Hu (1991), De Blauwe & Gordon (2014)
<i>M. obliqua</i> (Thornely, 1924)	136–634	Thornely (1924), Livingstone (1928), Vigeland (1952), Rogick (1956), Androsova (1972), Winston (1983), Hayward & Thorpe (1989), Gutt <i>et al.</i> (2000), Bader & Schäfer (2004)
<i>M. robusta</i> Liu & Hu, 1991	270	Liu & Hu (1991)
<i>M. subantarctica</i> d'Hondt, 1984	55	d'Hondt (1984)
<i>M. temaukeli</i> Moyano, 1997	430–780	Moyano (1997a, 1997b, 2000)
<i>M. transversa</i> De Blauwe & Gordon, 2014	595–602	De Blauwe & Gordon (2014)

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