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Bryozoans from the Paraná Formation (Miocene), in Entre Ríos province, Argentina

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Abstract. Six species of bryozoans from the Paraná Formation are described herein. They were collected from the locality of Punta Gorda, close to the city of Diamante, in Entre Ríos province, Argentina. The specimens were found encrusting oyster shells in a bioclastic grainstone, representing a parautochtonous occurrence. The material described was referred to the following taxa: *Acanthodesia* cf. *sulcata* Canu (Membraniporidae), *Microporella* sp. (Microporellidae), *Schizoporella* sp. (Schizoporellidae), Schizoporellidae indet. and *Schizosmittina* sp. (Bitectiporidae), of the order Cheilostomata, and *Tubulipora* sp. (Tubuliporidae) of the order Cyclostomata. Of these, only the species included in *Acanthodesia* (but as *Membranipora*) had been previously described from the Paraná Formation. Therefore, the list of known bryozoan genera from this unit is enlarged from one to six. The genus *Schizosmittina*, previously known only from the Miocene of France and the Miocene to Holocene of Australasia, is recorded for the first time in South America.

Resumen. BRIOZOOS DE LA FORMACIÓN PARANÁ (MIOCENO), EN LA PROVINCIA DE ENTRE RÍOS, ARGENTINA. Se describen seis especies de briozoos pertenecientes a la Formación Paraná. Se recolectaron en la localidad de Punta Gorda, próxima a la Ciudad de Diamante, en la provincia de Entre Ríos, Argentina. Los especímenes fueron hallados incrustando las valvas de ostras en un grainstone bioclástico, conformando un depósito parautóctono. El material descripto se refiere a los siguientes taxones: *Acanthodesia* cf. *sulcata* Canu (Membraniporidae), *Microporella* sp. (Microporellidae), *Schizoporella* sp. (Schizoporellidae), Schizoporellidae indet. y *Schizosmittina* sp. (Bitectiporidae), del orden Cheilostomata, y *Tubulipora* sp. (Tubuliporidae) del orden Cyclostomata. De entre ellos, sólo aquél referido al género *Acanthodesia* (pero como *Membranipora*) había sido descripto anteriormente para la Formación Paraná. En consecuencia, la lista de géneros de briozoos conocidos para la mencionada unidad se incrementa desde uno a seis. El género *Schizosmittina,* anteriormente conocido tan solo para el Mioceno de Francia y el Mioceno al Holoceno de Australasia, es registrado por primera vez en América del Sur.

Keywords. Bryozoans. Paraná Formation. Miocene. Entre Ríos.

Palabras clave. Briozoos. Formación Paraná. Mioceno. Entre Ríos.

Introduction

The Paraná Formation was deposited during an important marine transgression which covered vast areas of Argentina, Uruguay, and southern Paraguay, southern Bolivia and southwestern Brazil. Although this unit shows a widespread subsurface distribution, exposed outcrops are restricted to the area along the left bank of the Paraná river, between the Nogoyá river in the south and the Feliciano river in the north (a distance of approximately 200 kilometers), in Entre Ríos province, Argentina. Equivalent to the Paraná Formation is the Camacho Formation, exposed along the left bank of the Río de la Plata, in southern Uruguay (see Sprechmann *et al.*, 2000 and references therein).

The earliest report on this unit is the work by A. d'Orbigny (1842), who measured a section at La Bajada, the original name of the locality where the modern city of Paraná lies. After him many authors studied different aspects of the geology and paleontology of this unit. Among these we can mention Darwin (1846), Bravard (1858), Burmeister (1876), Döering (1882), Borchert (1901), Ameghino (1906), Ihering (1907), Frenguelli (1920, 1947), Kantor (1925), Cordini (1949), Scartascini (1959), Camacho (1967), Yrigoyen (1969), Herbst (1971), Iriondo (1973), Aceñolaza (1976, 2000), Herbst and Santa Cruz (1999), Aceñolaza and Aceñolaza (2000), and Cione *et al.* (2000).

The age of the Paraná Formation has been a matter of great debate over the years and remains yet to

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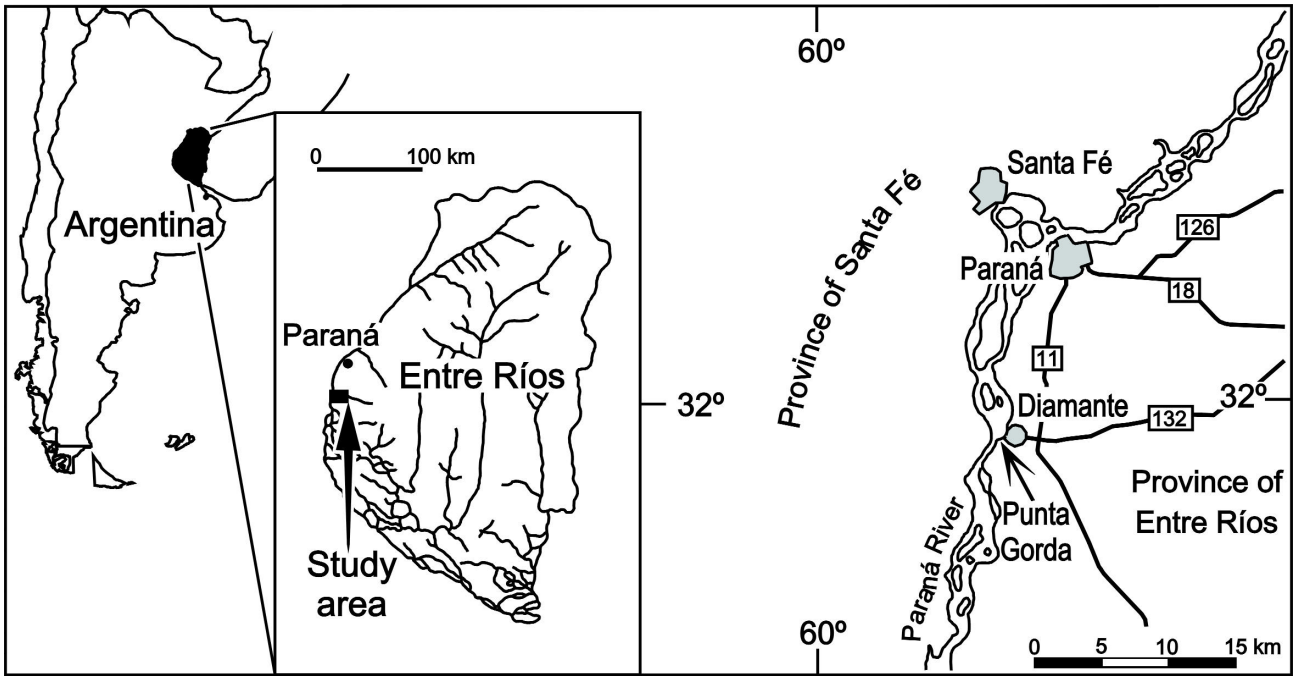


Figure 1. Location map of the studied area / *Mapa de ubicación de la localidad estudiada.*

be completely elucidated. However, most authors agree it was deposited during the Middle Miocene (Aceñolaza, 2000; Aceñolaza and Aceñolaza, 2000; del Río, 2000), or Late Miocene (Herbst and Zabert 1987; Cione *et al.*, 2000). Such a conclusion is based mainly on the fossil content and stratigraphic relations, as no radiometric data have been obtained. The fossils described from this unit are mainly molluscs, forams, ostracods, fish and whales, but none of them allows greater age precision. Stratigraphic correlation among the different localities has been further hampered by the nature of the exposures, which lack continuity and show a wide range of facies variation.

While several works have been published concerning the paleontology of vertebrates and invertebrates from the Paraná Formation, the only one to deal specifically with bryozoans was that by Canu (1908). He described and ilustrated material sent to him by F. Ameghino. Canu (1908) described three species from the locality of Paraná: *Membranipora bravardi* (p. 255, pl. III, fig. 1, 2, 3), *Membranipora cristallina* (p. 256, pl. III, fig. 12) and *Membranipora sulcata* (p. 257, pl. II, fig. 2). The genera *Cellaria* and *Discoporella* were reported by Closs and Madeira (1968) from subsurface sediments equivalent to the Camacho Formation at the northeastern corner of Uruguay.

The Paraná Formation includes green muddy-siltstones and muddy-sandstones with marine fossils, topped by a bioclastic limestone with fragments of bivalve (mostly oysters and pectinids) shells (Aceñolaza, 1976). The bryozoans studied herein were collected at the locality of Punta Gorda (32º04'16'' S 60º39'09'' W), near the city of Diamante, Entre Ríos, Argentina (see figure 1). Marengo (2000) studied the Paraná Formation and its microfossils based on data obtained from the well drillings in the Diamante harbor. He concluded that the Paraná Formation in the Diamante area was deposited in a shallow sea, with some intercalations of sediments of a transitional environment, probably of deltaic origin. The vertical variation in the microfaunas suggests the existence of two or three flooding events. The whole thickness of this formation in the Diamante area including marine and transitional facies, is 60 meters.

The outcrops at Punta Gorda consist of only a few calcareous beds close to the top of the Paraná Formation. They are overlain by Pliocene fluvial sands. The river level is commonly above the base of the calcareous beds, a fact that hampers observations and renders measurement of a complete geological section very difficult. The preservation of most calcitic fossils is very good but those with aragonitic shells are entirely missing or else represented only by moulds. Stratification and sedimentary structures are hidden by the erosive effect of the Paraná river. We present here a schematic section which shows the most important lithologies present at the exposure in Punta Gorda (see figure 2):

Base: not visible, as it is under the river level.

1. Medium-grained sandstone with horizontal stratification. Visible thickness: 1 m.

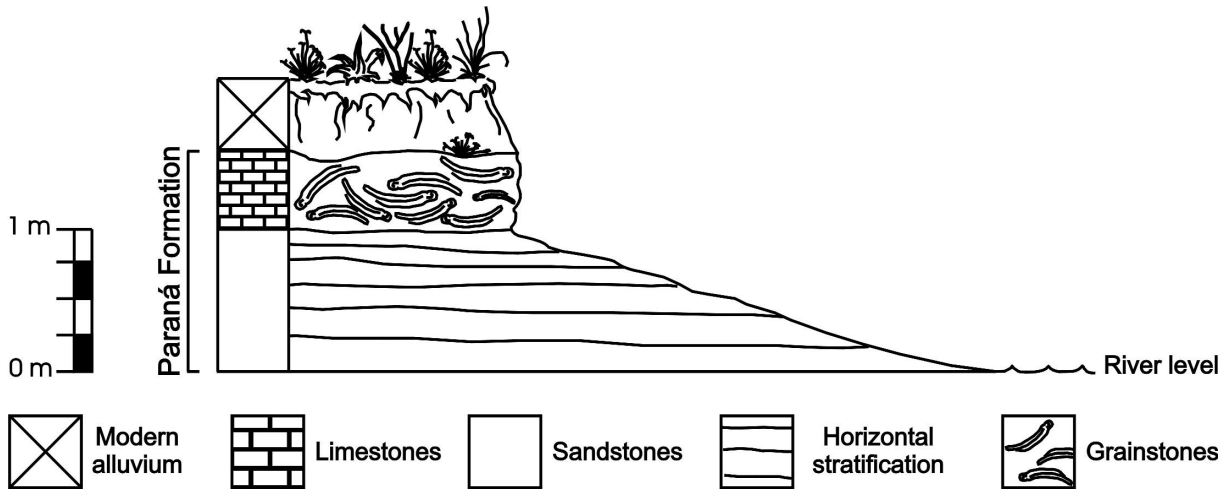


Figure 2. Schematic section showing the most important lithologies exposed at Punta Gorda / *Sección esquemática con las litologías más importantes observadas en Punta Gorda.*

2. Well-cemented grainstone with bioclasts and lithoclasts, without matrix. The bioclasts consist of fragments of marine invertebrates, such as bivalves, gastropods, bryozoans, balanids, annelids, sponges, echinoids, and foraminifera, bivalves being the most conspicuous. The larger bivalve shells commonly contain tubular borings filled by a cement of equant sparry calcite. Through the first 15 cm of this rock, the bioclasts are very-much fragmentary, but they are replaced upwards by a wide diversity of well-preserved fossils.

Petrographic analysis performed on samples of this bed shows that the lithoclasts are rounded to subrounded sand grains mainly composed of quartz, but there are also some feldspars present. The quartz clasts often show deformation ribbons, wavy extinction and grain boundary migration, revealing their metamorphic origin. Secondary silica growth is seen around some clasts. The most frequent feldspar is microcline, which is little weathered, with twinned crystals typical of plutonic rocks. Some clasts are composed of more than one crystal, showing textures commonly found in gneisses and migmatites. All these clasts have a homogeneous provenance, from an igneous-metamorphic complex.

The cementation observed consists of sparry crystals, both fibrous and more or less equant. The former are of marine phreatic origin while the latter precipitated when there was a change from a marine to a freshwater phreatic environment under conditions of weathering.

Top: covered by modern alluvium. The upper contact of this unit with the base of the Pliocene fluvial sands was not completely visible in the studied section.

Material and methods

The bryozoans were studied using a binocular microscope and some were photographed using a scanning electron microscope (SEM) at the Museo de Ciencias Naturales de La Plata (MLP), La Plata, Argentina. They were compared with congeneric specimens in the Colección Nacional de Paleoinvertebrados at the Invertebrate Paleontology Department of the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina, under catalogue number MACN-Pi 1910.

Two thin sections were made in order to study the petrography of the deposit.

Discussion

All the bryozoans found are encrusting colonies, sheet-like in *Microporella* sp., *Acanthodesia* cf. *sulcata* (Canu, 1908), *Schizoporella* sp. and Schizoporellidae indet., mainly disc-shaped in *Schizosmittina* sp., and lobe- to disc-shaped in *Tubulipora* sp. (Hageman *et al.*, 1998). In almost all the specimens studied the left valves of the oyster *Crassostrea rhizophorae* (see del Río and Martínez, 1998, p. 55, pl. 18, fig. 3 and pl. 24, fig. 6) served as a substrate. However, there are some situations in which parts of the colonies are on epibionts which share the same oyster shell as the substrate. These include balanids and serpulids. The bryozoans are seen to grow on the inner side of the shells rather than on the outer surfaces. In fact, the colonies that are on the outer surfaces of the shells are often growing in the spaces left between other epibionts, or else began their growth from the inner side. Specimens of *Tubulipora* sp. are the only bryozoans that are found entirely on the outer sides of

shells which lack any other epibionts. Thus, it may seem that *Tubulipora* sp. had a certain preference for the outer surfaces of the oyster shells while the cheilostomes had it for the inner surfaces.

A great competition for space on the oyster shells is seen among the bryozoans as well as between them and the other epibionts. In the first case, some examples of flank overgrowth (Jackson, 1979) can be seen; for instance of *Acanthodesia* cf. *sulcata* Canu over *Microporella* sp. and *Acanthodesia* cf. *sulcata* Canu over *Schizoporella* sp. (see figure 4.A). In addition, there are colonies that began their growth directly on top of another colony (fouling), such as *Schizosmittina* sp. over *Schizoporella* sp. (see figure 4.H).

The fact that the cheilostome colonies are found in the inner rather than on the outer sides of the left oyster valves, may indicate that in most cases these colonies were initiated after the death of the bivalve. The rest of the epibionts, such as cyclostomes, serpulids and balanids are typically found on the outer side of the shell, indicating that the oyster shells may have been also colonized while the animal was still alive. The left valves of the oysters are appropriate substrates for colonization by bryozoans because their weight and convex shape prevent the valves from being easily transported and rolled over the sea bottom. In the same way, when the valves lay with their convexity pointing upwards, the strong concavity of their inner surface generates a protected environment suitable for larval settlement, and subsequent growth of the whole colony. Although this is the most stable hydrodynamic condition for the left valve of the oysters, some were found totally turned over with the concave side upwards. While the diversity of bivalves is fairly high in this outcrop, bryozoans were found in no other valves than the left valves of *Crassostrea rhizophorae* (Reeve, 1873). It is important, however, to note that the right valves of this oyster are very scarce in this locality. The hydrodynamic conditions present during the deposition of these sediments were probably the main factor involved in the sorting of the oyster shells.

This deposit is a hydrodynamic accumulation of valves in which the fossils present are parautochtonous. The bivalve shells are all disarticulated, but are very well preserved and show no other signs of significant reworking. Some of the fossils found, such as the gastropod *Crucibulum argentinum* (Philippi, 1893), can be associated with high energy conditions. The presence of deep and shallow burrowing bivalves, together with an irregular echinoid of the genus *Monophoraster,* are indicative of a soft bottom environment. In addition, the relative abundance of the lithoclasts found in these rocks suggests significant proportion of more or less loose sand among the sediment on the bottom. The absence of matrix can be explained by the energetic transportation of clasts, and does not mean that there was no mud in the system. It can be inferred that the valves were accumulated mainly after the death of the organisms (at least those inhabiting a soft bottom environment), as the grainstone so generated implies the formation of a hard bottom. The presence of echinoids, pectinids and the bryozoans described herein suggests water with normal salinity (35‰).

Systematic descriptions

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMATA Busk, 1852
Suborder ANASCA Levinsen, 1909
Family MEMBRANIPORIDAE Busk, 1854

Genus ***Acanthodesia*** Canu and Bassler, 1920

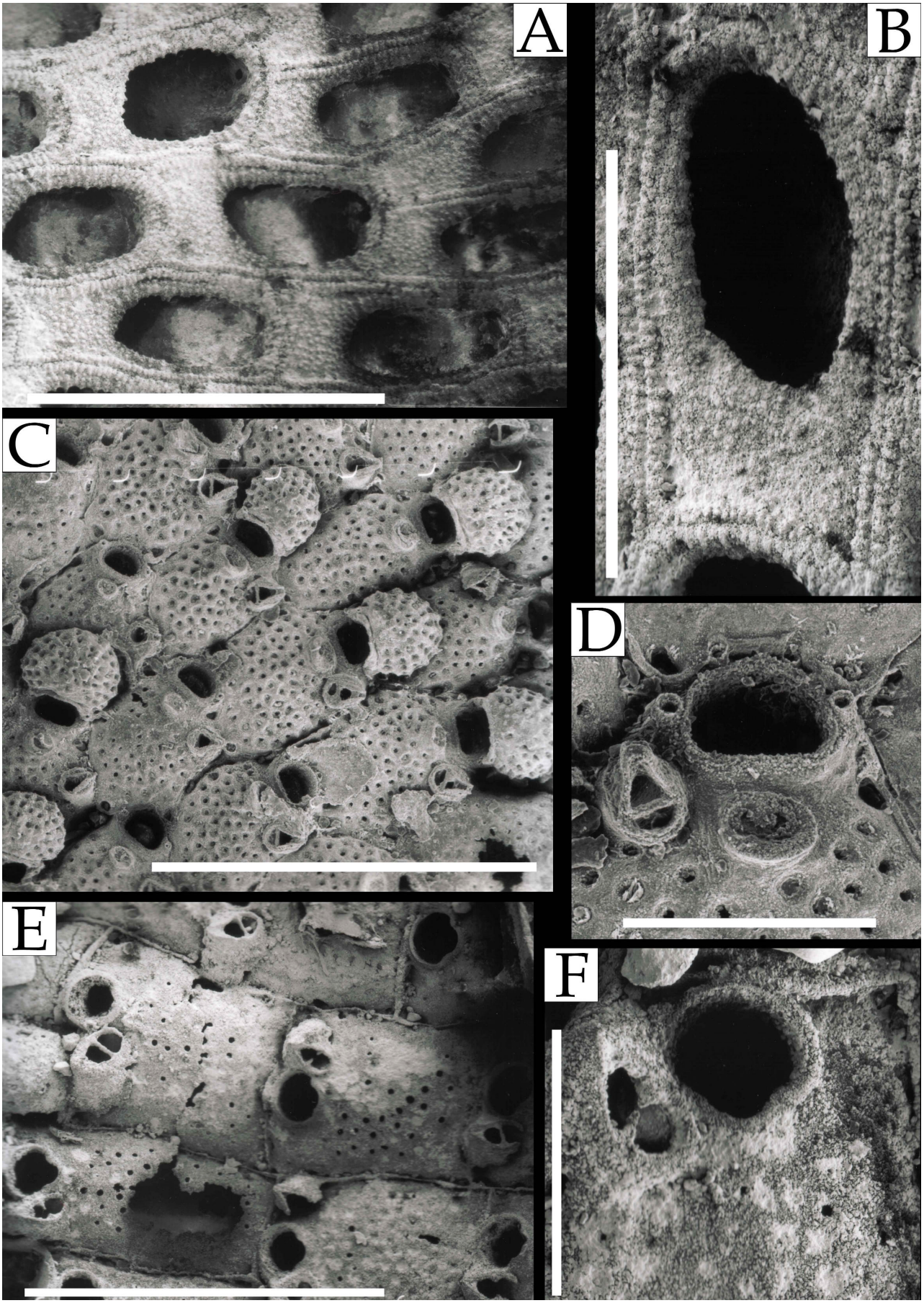
Type species. *Flustra savartii* Audouin, 1826.

Acanthodesia cf. ***sulcata*** (Canu, 1908)
Figures 3.A-B and 4.A

cf. 1908 *Membranipora sulcata* Canu, p. 257, pl. 2, fig. 2

Material. Fragments of colonies. MLP 13471 to 13476.
Description. Zoarium large, unilaminar and encrusting. Zooids elongate, distal edges convexly rounded and proximal edges somewhat concave. They are separated by a marked groove, either side of which is a raised boundary wall ornamented by small tubercles. The zooids have a conspicuous cryptocyst, slightly convex, and granulated. Opesiae elliptical and elongated longitudinally; mural rim, with minute denticles pointing inwards.
Remarks. In his original description of *Membranipora sulcata*, Canu (1908, p. 257) mentioned the possibility of finding ovicells, and the presence of intercalated hexagonal avicularia, very elongated and with rounded median opesiae. These last two features could not be identified by us in the studied specimens, or in those originally described by Canu and

Figure 3. Scanning electron micrographs of selected bryozoans/ *Fotografías de microscopio electrónico de barrido de ejemplares seleccionados de briozoos.* **A-B. *Acanthodesia*** cf. ***sulcata*** (Canu, 1908). **A.** Group of zooids, MLP 13472, scale bar = 1000 µm/ *Grupo de zooides, MLP 13472, escala = 1000 m.* **B.** Zooid, MLP 13474, scale bar = 400 µm/ *Zooide, MLP 13474, escala = 400 m.* **C-D. *Microporella*** sp., MLP 13483. **C.** Group of autozooids, including ovicells and avicularia, scale bar = 1000 µm/ *Grupo de aoutozooides, junto con ovicelas y avicularias.* **D.** Detail of the primary orifice, the ascopore, an avicularium, and the four oral spines, scale bar = 200 µm/ *Detalle del orificio primario, el ascoporo, una avicularia, y las cuatro espinas orales, escala = 200 m.* **E-F. *Schizoporella*** sp., MLP 13474. **E.** Group of autozooids, including avicularia, scale bar = 1000 µm/ *Grupo de autozooides, incluyendo avicularios, escala = 1000 m.* **F.** Detail of the primary orifice and an avicularium, scale bar = 200 µm/ *Detalle del orificio primario y una avicularia, escala = 200 m.*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housed in the Colección Nacional de Paleoinvertebrados at the Invertebrate Paleontology Department of the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina, under catalogue number MACN-Pi 1910.

Acanthodesia has been considered by some authors as a synonym of *Biflustra* d'Orbigny, 1852. However, this is an unresolved problem, as the critical early growth stages of the type species of *Biflustra* (*Biflustra ramosa*) are unknown. Therefore the important issue of the presence or not of a twinned ancestrula can not be established in this genus. A twinned ancestrula is diagnostic of the Family Membraniporidae and occurs in the type species of *Acanthodesia* (*A. savartii*). Whereas most people have previously assumed that *Biflustra* has a twinned ancestrula and is a senior synonym of *Acanthodesia*, it is quite possible that *B. ramosa* has a single ancestrula. Therefore *Biflustra* should perhaps be regarded as a distinct genus (P. Taylor, personal communication).

Suborder ASCOPHORA Levinsen, 1909
Family MICROPORELLIDAE Hincks, 1879

Genus ***Microporella*** Hincks, 1877

Type species. *Escharia ciliata* Pallas, 1766.

Microporella sp.
Figures 3.C-D

Material. Fragments of colonies. MLP 13477 to 13483.
Description. Colony encrusting. Zooids with a convex frontal shield, evenly perforated by circular pores. Orifice elliptical, wider than long, with a straight proximal rim; four oral spines. Ascopore crescent-shaped, located close to the orifice surrounded by a raised wall. Avicularia adventitious, generally single, rarely paired, placed proximolaterally to the orifice and/or laterally to the ascopore, with complete cross-bar (when preserved), with a short triangular rostrum pointing distolaterally and an open tip. Ovicell globular and prominent, evenly porous, the pores aligned radially near the perimeter.
Remarks. The material clearly shows the characters typical of the genus *Microporella*, i.e. a perforated frontal wall, a distinct ascopore, the presence of adventitious avicularia, a semicircular orifice with oral spines. However, specific identification is not possible until more material becomes available.

Family SCHIZOPORELLIDAE Jullien, 1883

Genus ***Schizoporella*** Hincks, 1877

Type species. *Lepralia unicornis* Johnston in Wood, 1844.

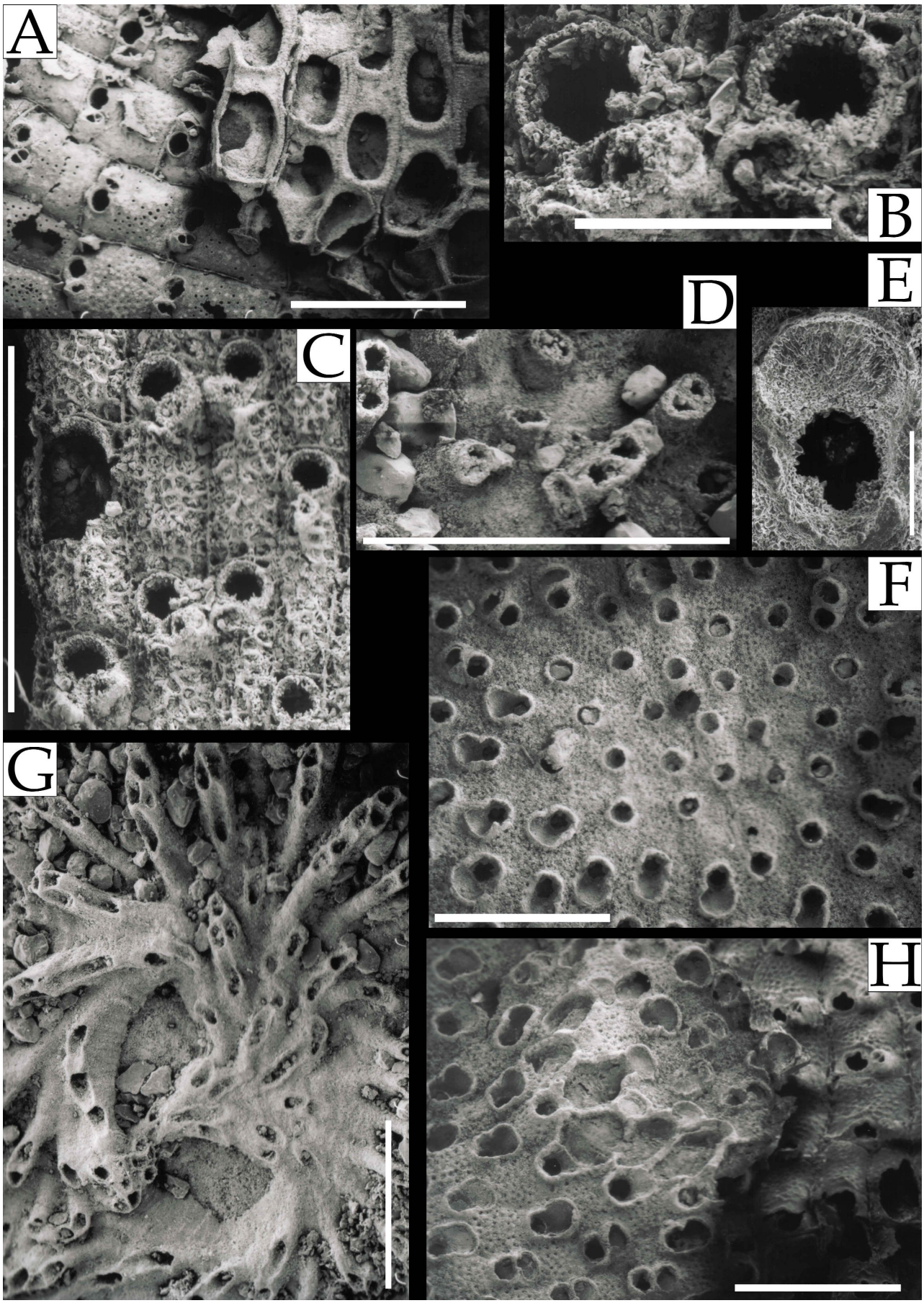
Schizoporella sp.
Figures 3.E-F, 4.A and 4.H

Material. Fragments of colonies. MLP 13474, MLP 13484 to 13488.
Description. Colony encrusting. Zooids elongated or rounded quadrate in outline, with distinct zooidal boundaries marked by a thin raised wall, and a convex frontal shield, perforated by numerous large circular pores. Orifice semicircular with a thick rim, and a U-shaped sinus and two small condyles. Avicularia adventitious, single, rarely paired, located laterally of the orifice, the short triangular rostrum directed distolaterally; cross bar complete.
Remarks. The characters observed do not permit the specific identification of these specimens. However, the presence of a semicircular orifice with a proximal sinus and two condyles, along with the adventitious avilcularia lateral to the orifice, clearly allow its inclusion in *Schizoporella*.

Schizoporellidae indet.
Figures 4.B-C

Material. Fragments of colonies. MLP 13489.
Description. Zoarium encrusting. Zooids rectangular, very elongated, with a convex frontal shield, densely perforated by large polygonal to irregularly shaped pores. Orifice almost circular, with a small "U" shaped sinus. Laterally to the sinus are two small "denticles" directed distally. Orifice somewhat elevated over the frontal shield, with a thick rim. Avicularia adventitious, single, with

Figure 4. Scanning electron micrographs of selected bryozoans/ *Fotografías de microscopio electrónico de barrido de ejemplares seleccionados de briozoos.* **A.** Colony of ***Acanthodesia*** cf. ***sulcata*** Canu, 1908, MLP 13474, overgrowing one of *Schizoporella* sp., MLP 13474, from the flank, scale bar = 1000 µm/ *Una colonia de* Acanthodesia *cf.* sulcata *Canu, 1908, MLP 13474, sobrecreciendo a otra de* Schizoporella *sp., MLP 13474, por el flanco, escala = 1000 m.* **B-C. Schizoporellidae indet.**, MLP 13489. **B.** Detail of two primary orifices and avicularia, scale bar = 200 µm. Note the presence of the two "denticles" at each side of the proximal rim, at the right/ *Detalle de dos orificios proximales y avicularias, escala = 200 m. Nótese la presencia de los dos "dentículos" a cada lado del seno proximal, hacia la derecha.* **C.** Group of autozooids with avicularia, scale bar = 1000 µm/ *Grupo de autozooides con avicularias, escala = 1000 m.* **D.** Detail of ***Tubulipora*** sp., where an ooeciopore is visible just below the center, MLP 13493, scale bar = 1000 µm/ *Detalle de Tubulipora sp., donde se observa un oecioporo justo debajo del centro, MLP 13493, escala = 1000 m.* **E-F. *Schizosmittina*** sp., MLP 13486. **E.** Detail of the primary orifice and the inner region of a broken ovicell, scale bar = 100 µm/ *Detalle del orificio primario y la región interna de una ovicela rota, escala = 100 m.* **F.** *Central area of a colony, scale bar = 1000 m.* Note that ovicells are absent before more or less the fourth concentric row counting outwards from the center of the colony/ *Área central de una colonia, escala = 1000 m. Nótese que no se observan ovicelas antes de aproximadamente la cuarta fila concéntrica, contando hacia fuera del centro de la colonia.* **G.** Flabellate lobes of *Tubulipora* sp. showing uniserial and pluriserial fascicles of zooids, MLP 13493, scale bar = 1000 µm/ *Fascículos uniseriales y pluriseriales de zooides, conformando lóbulos con forma de abanico, MLP 13493, escala = 1000 m.* **H.** Margin of a colony of *Schizosmittina* sp. growing over one of ***Schizoporella*** sp., MLP 13486, scale bar = 1000 µm/ *Margen de una colonia de* Schizosmittina *sp. creciendo sobre otra de* Schizoporella *sp., MLP 13486, escala = 1000 m.*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complete cross bar (badly preserved), located proximolaterally of the orifice close to the median axis of the zooid, the rostrum raised distally and directed laterally.

Remarks. Only a small portion of a colony was found, but this is quite well preserved. There are no ovicells present. This specimen has not been assigned to any genus in particular, but the above mentioned "denticles" along with the perforations in the frontal shield seem to be good characters for any future determination.

Family BITECTIPORIDAE MacGillivray, 1895

Genus ***Schizosmittina*** Vigneaux, 1949

Type species. *Schizosmittina planovicellata* Vigneaux, 1949.

Schizosmittina sp.
Figures 4.E-F and 4.H

Material. Fragments of colonies. MLP 13486, MLP 13490 to 13492.

Description. Colony encrusting. Zooids with a flat to slightly convex frontal shield, evenly perforated by numerous subcircular pores. Boundaries between zooids poorly defined. Orifice subcircular, sloping inward, with a wide U-shaped sinus and two conspicuous lateral condyles. The orifice is completely surrounded by a more or less circular peristome. Ovicell fused with the peristome, subimmersed but raised over the frontal shield.

Remarks. The ovicells are not fully developed until more or less the fourth generation from the origin of the colony. However, the ovicells are not well preserved and all of them are abraded so that the aperture seems to be double. Some zooids have lost their frontal shield, showing more clearly their hexagonal shape. The sloping orificial sinus suggests that this species belongs in *Schizosmittina*, as does the form of the ovicell and peristome. No avicularia were observed in the studied specimens, but its absence is a possibility mentioned in the revised diagnosis of *Schizosmittina* (Gordon, 1994). This genus was previously known only for the Miocene of France and the Miocene to Holocene of Australasia (Gordon, 1994).

Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder TUBULIPORINA Johnston, 1847
Family TUBULIPORIDAE Johnston, 1838

Genus ***Tubulipora*** Lamarck, 1816

Type species. *Tubulipora transversa* Lamarck, 1816.

Tubulipora sp.
Figures 4.D and 4.G

Material. Two colonies. MLP 13493 and MLP 13494.

Description. Colony encrusting, showing an overall more or less discoidal shape but becoming divided into several flabellate lobes. Zooids elongated, with a clear tendency to be grouped in uniserial and pluriserial fascicles. Apertures connate, longitudinally elongated, often quadrangular in shape. Gonozooid lobate, the ooeciopore transversely elliptical, slightly bowed and adnate to the proximal edge of a fascicle.

Remarks. The colonies are small discs little more than 5 mm in diameter. They somewhat resemble *Tubulipora plumosa* Harmer, 1898 (see Harmelin, 1976, plate 31, figure 4).

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