



Bryozoan internal moulds from the La Meseta Formation (Eocene) of Seymour Island, Antarctic Peninsula

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Abstract: The loose, small zooecia of the cheilostome bryozoans have been discovered in the lowermost part of the La Meseta Formation on Seymour (Marambio) Island. They systematically include the representatives of Beanidae Canu *et* Bassler, Catenicellidae Busk, Savignyellidae Levinsen, and Calwelliidae MacGillivray. The bryozoan assemblage is comprised of separate, small-sized internal moulds dominated by distinct, boat-shaped zooecia belonging to *Beania*, scarce, unizoidal internodes tentatively included into a ditaxiporine catenicellid *?Vasignyella*, and representative of the family Savignyellidae. A few branched segments composed of multiseriate zooecia arranged back to back were tentatively incorporated into *?Malakosaria*. *Beania* marks the oldest fossil record, whereas representatives of Savignyellidae along with ditaxiporine catenicellid and *?Malakosaria* are for the first time reported from Antarctica. The relationship between the taxonomic composition, colony growth-patterns represented by membraniporiform/petraliform, catenicelliform and cellariform, along with associated biota and sedimentary structures of the La Meseta Formation implies nearshore environment, with considerable wave action, and warm climatic conditions.

Key words: Antarctica, Seymour Island, La Meseta Formation, Eocene, Bryozoans.

Introduction

Bryozoans from the La Meseta Formation (LMF) were reported by Gaździcki and Hara (1994) and later subsequently in the systematic works by Hara (2001, 2002). This moderately rich bryozoan assemblage comprised of forty-four species represented by cerioporine cyclostomes and cheilostomes, was systematically dominated by microporoideans, ascoporan umbonulomorphs and lepraliomorphs and documented from the rich bryozoan-bearing localities: ZPAL 1, ZPAL 5, ZPAL 11-12 of the Telm 1 (Hara 2001). The bryozoan assemblages were found in the sediments exposed in the north-eastern part of the island, in a sequence of shallow-water, deltaic and/or estuarine, poorly consolidated sandstones and siltstones, accumulated within an incised valley (Sadler 1988; Porębski 1995; Marensi *et al.* 1998; Marensi 2006; Tatur *et al.* 2011; Gaździcki and Majewski 2012).

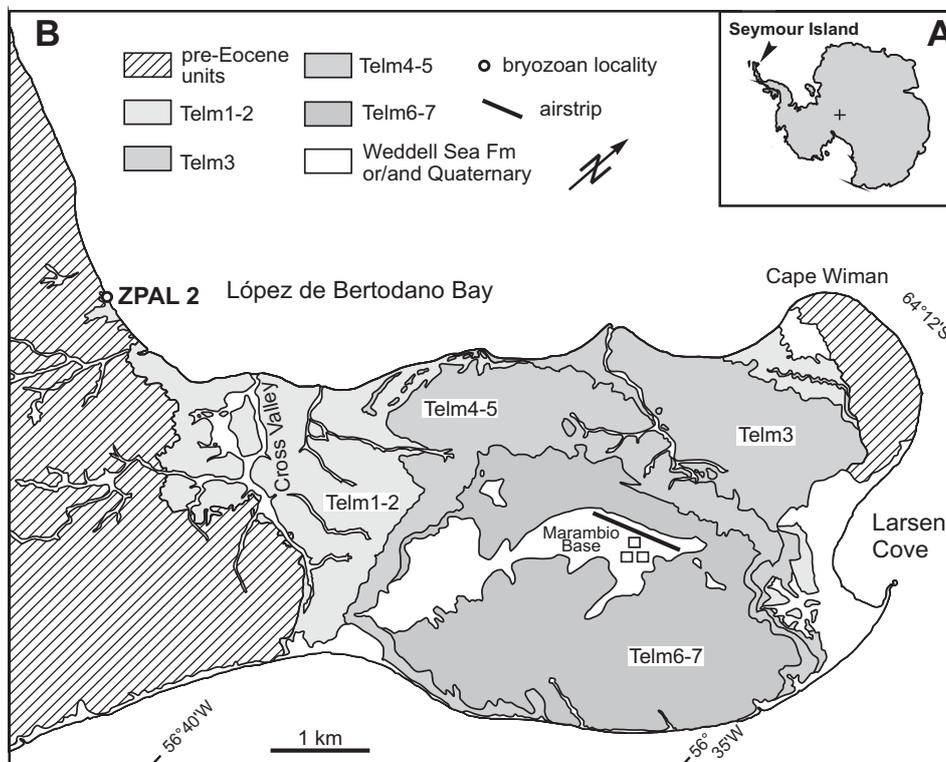


Fig. 1. Geological map of the Seymour Island showing locality of ZPAL 2 (Telm1) in the La Meseta Formation from where the bryozoans were collected (adapted from Gaździcki and Majewski 2012).

Bryozoans, described in this paper, preserved as internal moulds, accompanied by benthic foraminifera (Gaździcki and Majewski 2012) and ostracods (Szczechura 2001), were collected from the locality of ZPAL 2 (Figs 1–2). The strata, which represent the lowermost part of the La Meseta Formation, Telm1 (Sadler 1988) or Valle de las Focas Allomember *sensu* Marensi *et al.* (1998), are interpreted as early Eocene (52–54 Ma) in age (Dzik and Gaździcki 2001; Marensi 2006; López-Cabrera and Olivero 2011; Gaździcki and Majewski 2012).

The loosely scattered bryozoan zoecial moulds composed of unizoidal and bi-zoidal as well as branched multiserial internodes taxonomically belong to the genus of *Beania*, ditaxiporine catenicellid of the genus *?Vasignyella*, and representative of the Savignyelliadae and *?Malakosaria* sp. The reports on this kind of fossils are nearly completely absent among the palaeontological literature, however, bryozoans preserved as the internal moulds were the subject of earlier studies of Buge (1945).

The taxonomical analyses of the studied bryozoans moulds and their attribution to the relevant taxa, needed lots of comparative studies including the Recent materials.

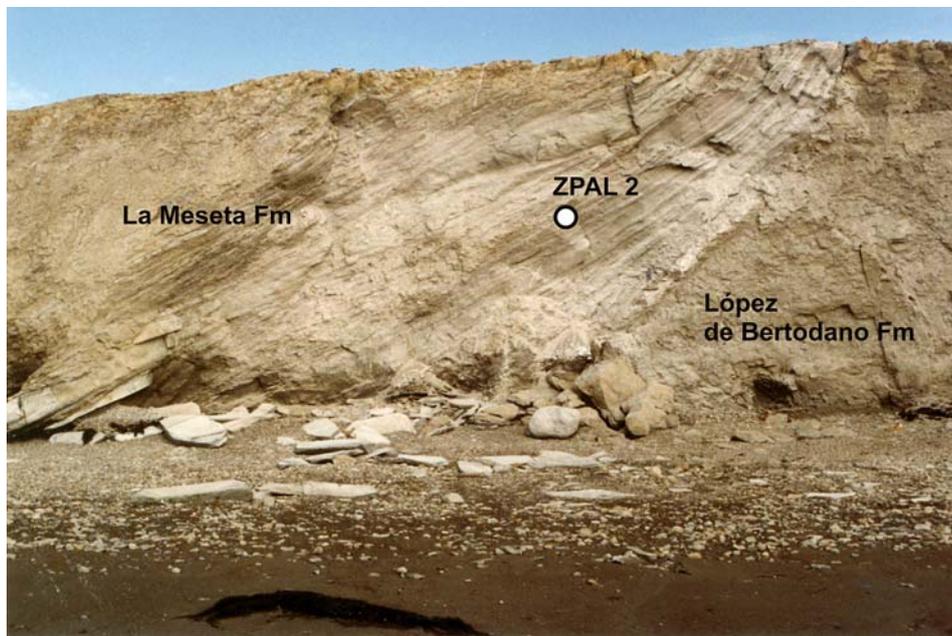


Fig. 2. Location of the bryozoan site ZPAL 2. Photographed by A. Gaździcki, 1994.

Apart from the detailed taxonomical descriptions of the bryozoans from the locality of ZPAL 2, this paper discusses their possible migration routes, origin and biogeographical importance including cosmopolitan genus of *Beania*, and the endemic austral genus of *Malakosaria*, strictly restricted to the Australasia. The occurrence of the ditaxiporine catenicellid represented by *?Vasignyella* sp. and the recognized here bryozoans of the family Savignyellidae shows their oldest fossil record in the Southern Hemisphere.

Bryozoans represented mostly by possibly loosely encrusting (membraniporiform), or unizoidal flexible articulated or rooted colonies (catenicelliform) from the base of the LMF are either taxonomically and morphologically different from the rich bryozoan assemblages recognized in the higher part of the Telm1 (*i.e.* locality ZPAL 1, see Hara 2001).

Material and methods

The studied bryozoans preserved as moulds were recognized in the residuum of the already sorted bulk sediment samples collected during a fieldwork carried out by A. Gaździcki during the Argentinian-Polish field parties on Seymour Island in the austral summer of 1993/1994.

Rock samples were collected from the locality ZPAL 2, north-east of the island (Fig. 1; Gaździcki and Majewski 2012, fig. 2), but detailed investigation was fo-

cused on a few samples taken from the base of the section (Fig. 2). Rock material (1.5 kg) was mechanically crushed and dissolved using the standard Glauber salt. Forty-eight individual zooecia and 3 segments recognizable as bryozoans were selected from the washed material through the series of sieves of a fraction greater than 63 μm , for further taxonomical examinations. Ultrasonic cleaning has been employed to remove weakly-adherent matrix. All described taxa have been examined and measured using a WILD M10 binocular microscope. Well-preserved specimens were investigated with a Philips XL-20 scanning electron microscope at the Institute of Paleobiology PAS (Warszawa), as well as at the Polish Geological Institute-National Research Institute (Warszawa) using a ZEISS-LEO 1430 SEM. The material illustrated on Figs 3–5 is back-scattered electron micrographs based on the nineteen selected specimens. Collection of the studied material abbreviated as ZPAL Br. XI/1-51 is housed at the Institute of Paleobiology of the Polish Academy of Sciences (Warszawa).

Systematic paleontology

Class Gymnolaemata Allman, 1856
 Order Cheilostomata Busk, 1852
 Suborder Neocheilostomatina d'Hondt, 1985
 Infraorder Flustrina Smitt, 1868
 Superfamily Buguloidea Gray, 1848
 Family Beaniidae Canu *et* Bassler, 1927
 Genus *Beania* Johnston, 1840

Type species: *Beania mirabilis* Johnston, 1840.

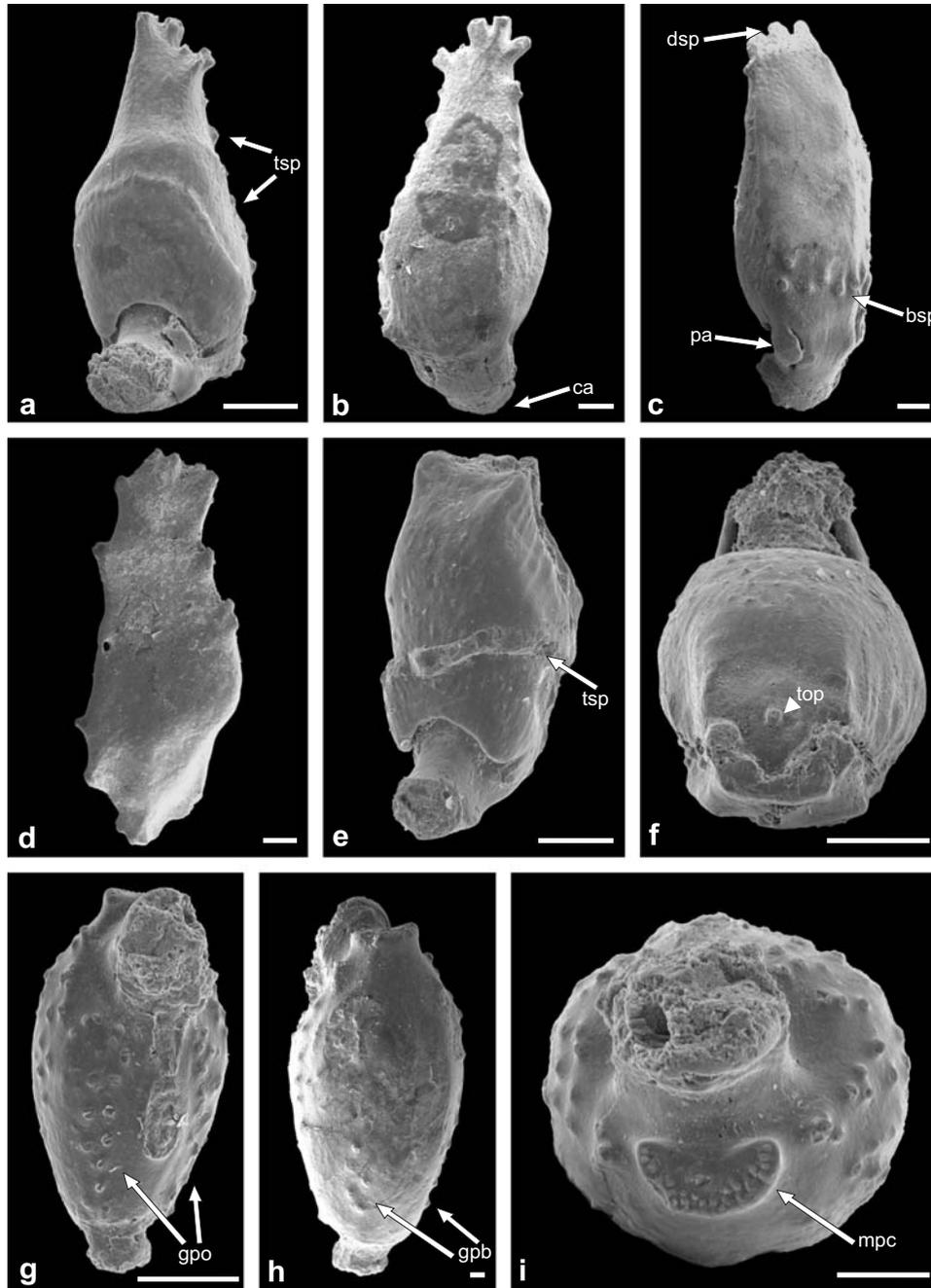
Beania cf. *mirabilis* Johnston, 1840
 (Figs 3a–c, 4c–f)

1840. *Beania mirabilis* Johnston, 1840: p. 272, text-figs 1–2.

2001. *Beania mirabilis*; López Gappa: p. 73–76, figs 1–2.

2010. *Beania mirabilis*; Ramalho, Muricy and Taylor: p. 503, fig. 3.

Fig. 3. **a–c.** *Beania* cf. *mirabilis*. **a.** Single, erect zooecium from the frontal side with an boat-shaped, convex basal portion and a row of marginal spines (tps) along the margin, scale bar 200 μm , ZPAL Br. XI/23. **b.** General view of a single zooecium from the basal side showing the lateral margins and the distal projections, and tubular connecting tube-caudae (ca), scale bar 100 μm , ZPAL Br. XI/22. **c.** Lateral view of a single zooecium showing a few distal (dsp) and proximal appendices (pa) and the traces of the basal radicles or spines (bsp), scale bar 100 μm , ZPAL Br. XI/25. **d.** *Beania* aff. *inermis*, a general view of the zooecium from the dorsal side, scale bar 200 μm . **e–f.** *Beania* cf. *mirabilis*. **e.** Frontal view of a moulded zooecium with a pair of preserved marginal spines (tsp), scale bar 200 μm , ZPAL Br. XI/26. **f.** A zooecium upside down showing its distal part, with two pairs of the distal spines, and opesium with a small process of the operculum (top), scale bar 200 μm , ZPAL Br. XI/3. →



g–i. *Vasignyella* sp. **g.** Frontal view of a unizoidal internode, showing the distally placed aperture, and two rows of the gymnocystal pores (gpo), ZPAL Br. XI/4, scale bar 200 μ m. **h.** Basal view of elongated zoecium with some pores (gpb) on the dorsal side, ZPAL Br. XI/36, scale bar 200 μ m. **i.** Distal part of the zoecium showing the occluded orifice and a mural pore-chamber (mpc), ZPAL Br. XI/4, scale bar 100 μ m. Seymour Island, La Meseta Formation (Eocene), ZPAL 2, Telm1.

Material. — 22 well-preserved internal moulds, and 12 specimens fragmentary preserved.

Measurements. — The length of the zooecium (min. 0.48 mm, max. 1.2 mm); the width of the zooecium 0.54–0.66 mm; the width of the distal part 0.40–0.48 mm, the width of the basal part (connecting tube) – 0.25 mm; the length of the opesium 0.20–0.24 mm, the width of the opesium 0.22–0.32 mm.

Description. — Zooecia boat-shaped, ranging from oblong (Fig. 3a–b) to more or less oval-shaped (Fig. 2c, e–f), some of them tapering distally (Figs 3a–c, 4c–e) or they are truncated (Fig. 3c, e–f); longer than wide, mostly expanded in the middle part (Fig. 3a–b), convex from the lateral view (Figs 3a–b, e–f, 4c–d). Marginal spine bases, rather closely-spaced, occur along the lateral margins of zooecia, in a number varied from 8 to 10 on each side of the zooecium (Figs 3a–b, 4c–d). In one specimen a pair of marginal spines, which overarches the front of zooecium is met at the midline (Fig. 3e). The orificial rim possesses the distal, distinctive spines, giving a fork-like appearance (Fig. 3a–c). The proximal basal spines well-seen on the dorsal side of the zooecium; in some zooecia they occur in a number of six (Fig. 3c), or they also could be very small and indistinct. The frontal wall in some specimens occupies only two-third of the whole length of zooecium (Fig. 4c). The opesium is more or less quadrangular in shape, placed terminally. A small process of the operculum in one zooecium is visible (Fig. 3f). The oblique stripes along the lateral walls may occur in some zooecia, as well as the central part of the frontal wall may be punctured (Fig. 3e–f). The proximal end of zooecium possesses a relatively short and thick tubular connecting tube (caudae) of a thickness of 0.25 mm, placed centrally (Figs 3a–c, e–f, 4c–d), with two lateral appendices closely attached (Figs 3b–c, f, 4c–d, f), arranged parallel to the main axis of the zooecium. On the dorsal proximal end of some zooecia there are seen two holes, which probably represented the places after the supporting rootlets for fixation to the substrate. Avicularia and the ovicells are not observed.

Remarks. — *Beania mirabilis* Johnston, 1840 has previously been described by many authors from the Recent seas (Harmer 1926; Hastings 1943; López Gappa 2001; Ramalho *et al.* 2010), the only fossil record of *Beania* described as *B. bermundezi* Lagaaij was reported from the Upper Eocene of Cuba (Lagaaij 1968a). The zooecia included here to *Beania* cf. *mirabilis* indicate the closest similarity of the morphological features to the type species of *Beania mirabilis*, such as the shape of the zooecium, which is oblong or boat-shaped (Figs 3a–c, e–f, 4c–e); a possession of the quadrangular terminal opesium, and the presence of the dilated frontal surface and nine to ten pairs of marginal spines. On the other hand *Beania* cf. *mirabilis* differs from the type of *B. mirabilis* in a few features such as the larger width of zooecia, in a thicker basal proximal part of zooecium, as well as in the larger number of the marginal spines.

Recently described species of *Beania mirabilis* from Brazil (Ramalho *et al.* 2010) shows the presence of five pair of the marginal spines, which overarched the frontal membrane (Ramalho *et al.* 2010, p. 503). The author stressed that the num-

ber of the spines in *B. mirabilis* seems to be highly variable, what was also observed by other authors cited (Tilbrook *et al.* 2001). The zooids of *B. mirabilis* from Ponta Delgada (The Azores) are connected by stolons and they show the general outline of the zooecia similar to the material studied, however, *Beania mirabilis sensu stricto* differs from *Beania cf. mirabilis* by having smaller size of the zooecia (Lopez Gappa 2001, p. 74–75, fig. 9). Tilbrook *et al.* (2001) in his description of *Beania cf. mirabilis*, who examined the type specimens of the Johnston and Norman collections noticed, that the number of the marginal spines is a very variable feature showed by this species, and they may vary from 6–16 pairs. *B. mirabilis* Johnston and *B. alaskiensis* Osburn (Osburn 1952, p. 171, pl. 26, figs 6–7) shows slightly longer zooecia that were seen in *B. mirabilis* described by Ramalho *et al.* (2010), however, both species show streaking similarity in the form of zooecia to the *Beania cf. mirabilis* from the locality ZPAL2 of the La Meseta Formation (see Marcus 1944, p. 1, 60, 63, Est. XII, and XIII). Having a single, dispersed zooecia, it is difficult to reconstruct precisely the manner of budding of the colony, but certainly the zooecia were in a single series; they might be repent or loosely encrusting. In some specimens the connecting tubes are so short that at the first view they may appear to be wanting; in others the tubular portion may be as long or longer as the body of the zooecium. The connective tube in the specimens studied is very characteristic, extremely thick in comparison to another species of *Beania*. *Beania alaskiensis* Osburn (Osburn 1952, p. 171, figs 6–7), described from Alaska similarly as the specimens studied, shows comparatively thick connective tubular stalks, which are rather short, and elongated, as well as the terminal spines are present, similarly to the specimens studied (Fig. 2a–b). Another species of *Beania* such as *B. mirabilissima* Vieira, Migotto and Winston, 2010 also bears some similarity to the specimen studied in a general shape of the zooecium, and in the possession of the two pairs of the oral spines as well as in the presence of 6–10 pairs of the lateral, marginal spines (Vieira *et al.* 2010a).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), ZPAL 2, Telm1.

Beania aff. inermis (Busk), 1852

(Fig. 3d)

1854. *Diachoris inermis* Busk: pl. 72, figs 1–2.

1943. *Beania inermis*: Hastings: p. 411–412.

1995. *Beania inermis*: Hayward: p. 149–150, fig. 117.

Material. — 1 complete and 2 incomplete internal moulds.

Measurements. — Length of the zooecium 1.17–1.25 mm, the width of the zooecium 0.37–0.45 mm; the width of the opesium 0.18 mm, the length of the opesium 0.12–0.15 mm; the width of the tubular extension in the proximal part (connecting tube) – 0.12 mm.

Description. — Zooecium oval in shape (Fig. 3d), higher than wide. Frontal surface extensive, long, slightly punctured, occupying almost all frontal side of the zooecium; four blunt oral spines present at the distal extremities of the opesium, which is almost rectangular in shape. Along both sides of the lateral margins there are three to five small, short acute spines; they are not evenly spaced around its basal periphery; as well as not of the same length. The dorsal side slightly concave, a little bit uneven (Fig. 2d). A tubular extension of the basal part, is rather short and placed basally of a thickness of 0.12 mm. No avicularia and ovicells were observed.

Remarks. — The studied specimens reveals some similarities with *Beania inermis* (Busk), 1852 described by Hastings (1943, p. 411–412) from the South Atlantic Ocean and later on by Hayward (1995, p. 149–150, fig. 117B) by having a similar outline of the zooecium; the possessing of short marginal spines spaced around its basal periphery as well as by the same number of the distal spines. *Beania inermis* described by Hayward (1995, p. 149–150), from the East Falkland shows the presence of marginal spines, but also is often without them, contrary to the another subspecies of *B. inermis* var. *unicornis* described by Hastings (1943, p. 414–413, fig. 33A). The number of lateral spines and the size of zooecia are distinctive features, which distinguish two species *B. inermis* and *B. inermis* var. *unicornis*. The typical for *B. inermis* is that the colonies may form coherent sheets of closely packed repent zooids, and they are fixed by the rootlets. The very limited number of the specimens studied as well as the state of the preservation of the moulded zooecia unable to reconstruct a form of the colony (as a coherent sheet of closely packed repent zooids). Moreover, the presence of the 6 connecting tubes, which occur in the Recent material are not preserved in the fossil record. Avicularium has also not been observed. It is interesting that *B. hyadesi* Jullien originally described by Calvet (1909, p. 13–14), which is tentatively included into the synonyms of *B. inermis* (Busk), see Hastings (1943, p. 411–412), proved the only Antarctic record recognized further south from the Palmer Archipelago (Hayward 1995).

Another species of *Beania magellanica* (Busk) 1852 is similar to the specimens studied by a general outline of the zooecia, forming a reticulate sheet, each with six connecting tubes spaced around the basal periphery, however, *B. magellanica* has not marginal and distal spines and its zooecia are shorter than in *Beania* aff. *inermis*. Contrary, this species has a circumpolar distribution in Subantarctic regions, but it does not extend into Antarctic waters (Hayward 1995, p. 151, fig. 118; Hastings 1943, p. 415, fig. 34C).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), ZPAL 2, Teln1.

Beania sp.
(Fig. 4a–b)

Material. — 1 complete zooecial mould and 3 separate distal parts.

Measurements. — The length of the zooecium 1.65 mm, the length of the distal part 0.62–0.85 mm, the width of the zooecium in the proximal part 0.33–0.40 mm, the width of the zooecium in the distal part 0.18–0.25 mm; the width of the opesium 0.08–0.09 mm, the length of the opesium 0.04–0.05 mm; the width of tubular extension in the basal part 0.24 mm;

Description. — Zooecium club-shaped, long and slender, in its distal part concave forming a sort of a shallow gutter of a max. depth ranging from 0.10 to 0.22 mm, bordered along the whole length by the bases of the marginal spines or spiny processes (Fig. 4a–b), in a number of 14. From the lateral view, the proximal part of zooecium, close to the connecting tube is boat-shaped and convex, of a much greater depth than in the distal part, ending by a pair of erect, blunt spines at the extreme distal end (Fig. 4a). The lateral walls of zooecium are striated in the proximal part. The length of the distal narrow part of zooecium is two-third of the whole length of the zooecium, bearing a distinctive 5 to 7 pairs of the marginal spines (Fig. 4b). The tubular extension of the basal part of zooecium of a thickness of 0.24 mm is placed medioproximally, bearing two small appendices from its both sides. In the basal part of the dorsal side of zooecium there are two concave small holes, which may be associated with the presence of the basal connecting rootlets. A few small basal spines in a number of 5–7 are placed dorsally in the proximal part of the zooecium.

Remarks. — A very characteristic feature of the studied specimens is a club-shaped zooecium, with a narrow elongated distal part, terminated by a pair of spines. There is also a great difference in width and the length of zooecium between its proximal and distal parts, where the distal part bears from 5 to 7 marginal spines. The studied zooecial moulds in respect to their shape, and particularly because of their very long distinct, distal parts are not comparable to any other species of the genus *Beania* Johnston known from the literature (Hastings 1943; Hayward 1995; Tilbrook *et al.* 2001; Tilbrook 2006; Ramalho *et al.* 2010; Vieira *et al.* 2010a). *Beania* sp. differs from both described here specimens of *Beania* cf. *mirabilis* and *Beania* aff. *inermis* by having different morphological shape, larger length and smaller width of the zooecial moulds, as well as in smaller size of the opesium. In view of the very scarce material (one complete zooecium and 2 separate distal parts), preserved as moulds available from the La Meseta Formation the specific determination is deferred.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), ZPAL 2, Telm1.

Family Catenicellidae Busk, 1852
Subfamily Ditaxiporinae Stach, 1935
Genus *Vasignyella* Gordon, 1989

Type species: *Catenaria otophora* Kirkpatrick, 1890.

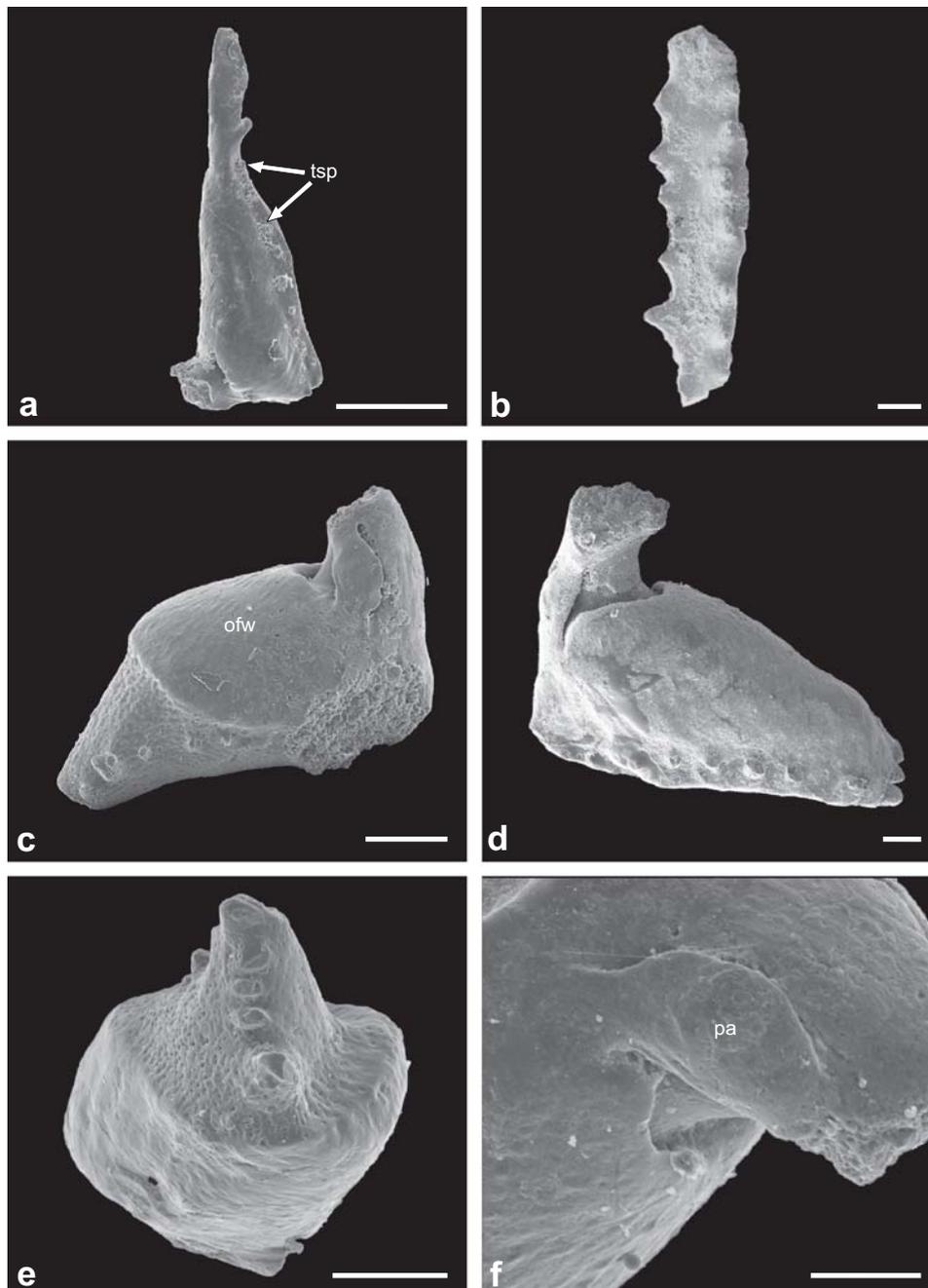


Fig. 4. **a–b.** *Beania* sp. **a.** Club-shaped zoecium from the frontal view with a row of distinctive, marginal spines (tps), ZPAL Br. XI/16, scale bar 100 μ m. **b.** Gutter-shaped upper part of the zoecium from the dorsal view bordered by a row of marginal spines, ZPAL Br. XI/41, scale bar 100 μ m. **c–f.** *Beania* cf. *mirabilis*. **c.** Lateral view of the zoecium showing the basally convex boat-shaped portion of the frontal wall (ofw) and a row of marginal spines, ZPAL Br. XI/5, scale bar 200 μ m. **d.** Lateral view of the →

?Vasignyella sp.
(Fig. 3g–i)

Material. — 3 single zooecia preserved as moulds.

Measurements. — Length of zooecium 0.80–0.88 mm, width of zooecium 0.36–0.40 mm; width of the zooecium in the distal part 0.32–0.34 mm, width of the zooecium in the proximal part 0.34 mm; width of the basal stalk 0.15 mm; length of the aperture 0.20–0.24 mm, width of the aperture 0.18–0.20 mm.

Description. — Zooecium unizoidal, oval-shaped more or less claviform in shape, slightly resembling amphora-like, tapering in the proximal and distal parts (Fig. 3g). The frontal area of zooecium is very slightly convex, the dorsal side distinctly keeled, convex, the width of zooecium equals approximately twice of the length (Fig. 3g–h). Primary orifice terminal, slightly longer than wide, highly raised (Fig. 3h), situated almost at the summit of zooecium, with a lower margin slightly sinuate (Fig. 3g). The frontal wall obviously penetrated by many small pores, which are distributed in four longitudinal series; two on each side of mid-line, symmetrically on the frontal wall, closer to the lateral margins; some pores seen along the lateral margins, particularly on the distal part of zooecium (Fig. 3g). Two lines of very small pores, close to the lateral margins occur on the dorsal side of the zooecium, they show a linear arrangement and they may represent a small internal spot of calcification (Fig. 3g–i). Series of very faint longitudinal ridges are seen on the frontal side and along the middle part of the dorsal side of zooecium. The proximal basal portion of zooecium possesses a short relatively thick, basal stalk of a maximum thickness of 0.15 mm (Fig. 3h). A distinct, semi-circular rosette-plate of the length of 0.18 mm and width of 0.09 mm, serving for the connection with the another zooecium (Fig. 3i) shows a granular structure, and is placed on the dorsal side of zooecium.

Remarks. — The frontal wall of the specimen illustrated on Fig. 3g–i, is obviously penetrated by many small pores, which may be associated with a gymnocystal pores, in more or less regular linear arrangement. The shallow excavation, seen in the middle of the frontal wall, and having fairly uneven texture, is possibly a place not infilled by sediment and thus not flush with the inner frontal surface that was later dissolved, because we deal with the moulds (Fig. 3g). The presence of the small pores seen on the dorsal side of the specimens, may represent the internal spots of calcification, and they are the same which are seen on the frontal wall. The *Vasignyella* (Gordon, 1989), was previously the sole one in the catenicellid bryozoan subfamily Vasignyellinae of the nearest generic relative of the extinct *Ditaxiporina* Stach, 1935 (subfamily Ditaxiporinae), with a nearly-identical auto-

boat-shaped zooecium, showing a row of marginal spines, scale bar 100 µm, ZPAL Br. XI/2. e. View of the distal part of a zooecium with the paired marginal spines at the distally placed area of the orifice, scale bar 200 µm, ZPAL Br. XI/31. f. Detail of the proximal part of a zooecium showing a short connecting tube, with one appendix from the lateral view (pa), ZPAL Br. XI/37, scale bar 100 µm. Seymour Island, La Meseta Formation (Eocene), ZPAL 2, Teln1.

zooidal morphology, but with most multizoooidal internodes. In a subsequent revision of multizoooidal catenicellids, Gordon and Braga (1994) noticed a striking similarity of zooids of *Vasignyella otophora* to those of species of *Ditaxiporina* Stach, 1935, which ranges from the Eocene in Europe to the Early Oligocene of Arkansas. Most *Ditaxiporina* species have multizoooidal internodes, but one *D. septentrionalis* (Waters 1891), has uni-, bi-, tri-, and multizoooidal internodes (Waters 1891, p. 5–6, pl. 1, figs 1–8) and shows almost the same amphora-like shape of the zooecium, with slightly keeled dorsal wall, the similar length of zooecium, the highly elevated orbicular aperture, similarly to the specimens studied. The distinct difference between the specimen studied and the type-material of *C. septentrionalis* presented by Waters (1891) from Montecchio Maggiore (N Italy) of the Priabonien (Eocene) is the occurrence of the pores on the dorsal side of the specimen studied. Moreover, the size of the aperture in the specimen studied is larger as in the *C. septentrionalis* (Waters 1891, pl. 1, figs 1, 6, see also Braga 1963, p. 41).

The genus *Vasignyella* Gordon, 1989 with the type species of *Catenaria otophora* Kirkpartick, 1890 (Kirkpartick 1890, p. 17–18, pl. 5, fig. 1a–c), shows the arrangement of the zooecia in the single series, which are slender with the frontal wall punctured, but the dorsal surface is smooth; on the lateral surface there are three characteristic mural pore-chambers. The type species of *Vasignyella* – *C. otophora* is similar to the specimens studied, but the type material does not show the pores on the dorsal wall. Unfortunately, Kirkpartick (1891) has not specified the magnification of the *C. otophora* (Kirkpartick 1890, p. 17–18, pl. 5, fig. 1a–c). Lagaij (1968a) described the specimens from the Middle Miocene of Madura Island, and Indonesia as *Savignyella otophora*, but Lagaij (1968a) noticed the lack of lateral pore-chambers and the ovicells. The specimen studied but also *S. otophora* described by Laagaij (1968a) have similar shape and size of the zooecium. Moreover, the Laagaij's record (1968a) is extremely important due to extending of the known stratigraphical range of this genus into the Miocene. *Ditaxiporina bifenestrata* Cheetham (Cheetham 1963, p. 485–488), is composed of long, slender internodes with zooecia arranged in two alternating series, its frontal wall possesses the tubular frontal pores tending to be aligned in four longitudinal series, similarly as the specimen from the locality of ZPAL 2 of the La Meseta Formation but differs from the LMF specimens in having twice smaller size of the width and the length of the zooecia and apertures. The lack of the few morphological features such as avicularia, and not very well-seen characters around the orificial periphery, the possession of the pores on the dorsal side, and the lack of the characters of the ovicell make the generic identification uncertain, although assignment to the subfamily Ditaxiporinae Stach, 1935, is relatively secure and strongly confirm the catenicelloidean origin. Therefore, the generic identification of this species is difficult and its assignment to the only recently occurring *Vasignyella* genus is very tentative.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), ZPAL 2, Telm1.

Family Savignyellidae Levinsen, 1909

(Fig. 5a–e)

Material. — Two internal moulds; one specimen numbered ZPAL Br. XI/28 figured on Fig. 5a, and three bi-zooidal moulds with two specimens illustrated on Fig. 5b–e.

Measurements. — Length of the zooecium 0.53–0.90 mm, width of the zooecium width 0.17–0.32 mm; width of aperture 0.12 mm, length of aperture 0.04–0.11 mm; length of a mother zooecium 0.50–0.67 mm, length of the budding zooecium 0.22–0.40 mm, width of the budding zooecium 0.18–0.20 mm, length of the ovicelled zooecia 0.40 mm, width of the ovicelled zooecia 0.20 mm; the diameter of the stolon 0.025–0.032 mm.

Description. — Zooecia preserved as internal moulds, forming a separate elongated internodes; or composed of bi-zooidal nodes, arranged in linear series of two zooecia jointed to one preceding zooecium, at the back of the oral opening (Fig. 5a), one of them (daughter zooecium) is budding from the dorsal side of the mother zooecium (Fig. 5b–e).

Zooecium narrow proximally, expanding in the middle part and then narrowing in the distal part (Fig. 5a–b). The frontal surface of zooecium slightly convex (Fig. 5a) or flat (Fig. 5b), perforated by a few scattered distinct pores, mostly in the proximal part of the zooecium and with 7–8 larger pores, seen along the lateral margins of zooecium (Fig. 5a). The dorsal side convex with two indistinct lines of very small pores. Along margins of zooecium, there are 3–5 distinct mural pore-chambers; in its middle part there are two larger pores, placed disto-laterally. On the dorsal side, there are two lines of very small pores running longitudinally (Fig. 5a). Orifice roughly circular, small-sized, a little wider than long, placed distally, with a raised peristome, the proximal ridge – that must give a sinus (Fig. 5a), or could be very small, semicircular placed terminally, with no sinus (Fig. 5b, d). Two small lateral holes which are seen along both sides of the orifice (Fig. 5a). A new zooecium originated from the dorsal side (Fig. 5a–d). Ovicell hyperstomial, large, bulbous, situated terminally (Fig. 5e), with a centrally placed small tabula (Fig. 5b, d). In one internode stolon originated from the basal surface of the primary zooecium (Fig. 5c).

Remarks. — Levinsen (1909), who erected family Savignyellidae included two genera *Savignyella* along with *Halysisis*, which both form threadlike, slightly calcified branches, with only one zooecium per segment. In the studied material the most common are pairs of zooids, where the daughter zooid is produced from a dorsal side of the mother zooecium (Fig. 5b–c), however, the single separate unizoooidal internode also occurs (Fig. 5a). The studied specimens are characterized by the possession of the flat or slightly convex frontal surface, on which there are a few scattered pores; the distal wall has two rows of the pores. The lateral

pores in a number of 7–8 are very low, so they also may represent ?lateral scars, or the ?connecting pores to the lateral zooids.

The zooids are basally flat, distal communication scar shows, that they were linked to a parent zooid, and to a daughter zooid. According to Levinsen (1909) the node with an ovicell, is never a single zooecium, and there are often many zooecia with ovicell in a node. The node may, however, be only one ovicelligerous zooecium followed by the ordinary zooecium, from the distal end of the older zooecium, and a new zooecium arises in the median line (Levinsen 1909, p. 273). The same pattern of the origin of a new zooecium is seen in the specimen from the La Meseta Formation (Fig. 5b, d).

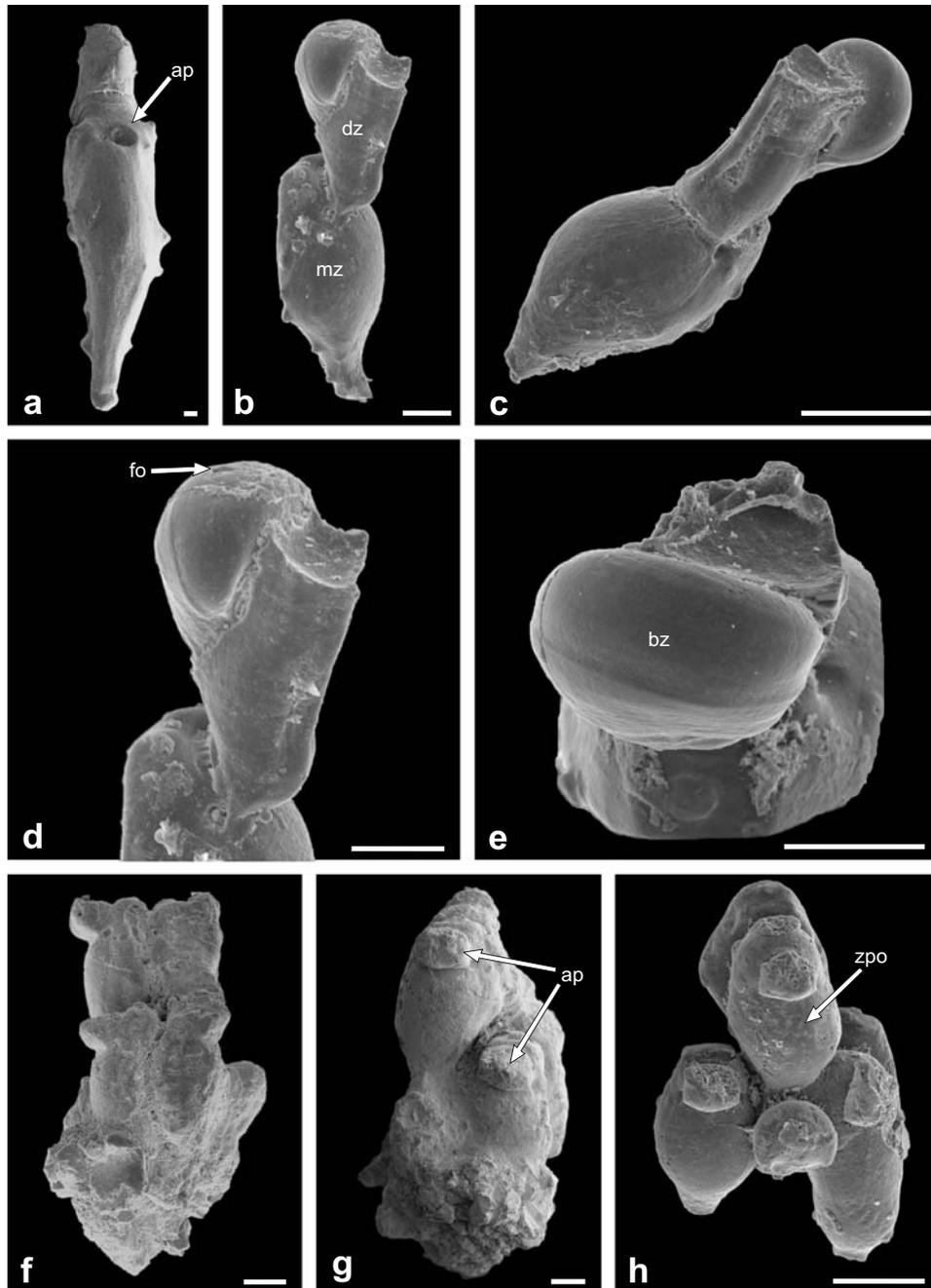
The specimen illustrated on Fig. 5a shows small differences between a specimens illustrated on Fig. 5b–e, where the first one has a smaller size of the zooecia but larger apertures; its frontal wall is slightly convex, but not so flat then in the specimens illustrated on Fig. 5b–e, as well as the morphology of the aperture differs between the specimens illustrated on Fig. 5a and Fig. 5b–e. The ovicell which is well-seen in a few specimens budded from the dorsal side of the mother zooecium seems to be recumbent. The dorsal budding pattern, strongly support the connection of these unizoidal moulds to the family Savignyellidae.

Particularly, the specimen illustrated on Fig. 5a, together with such features as the presence of the raised peristome, the scattered frontal pores, two longitudinal lines of pores on the dorsal surface, as well as the budding pattern from the dorsal side, the possession of the rosette-plates (2 or 3), in the distal part of the dorsal side, seems to be similar to the representatives of the family Savignyellidae.

The presence of the slightly sinuated orifice in the La Meseta specimens makes similar them to the genus *Savignyella*, as well as the ovicells in a genus *Halysisis* are more recumbent than those seen on Fig. 5b–e. The *Catenicella* sp. illustrated by Braga (1963, p. 41, tav. 4, figs 6 and 8) and later included into Savignyellidae (Braga 2008, p. 82, pl. 10, fig. 116), shows the same budding pattern as the specimens from the La Meseta Formation. The main distinguishing features, between the specimens presented by Braga and those from the La Meseta Formation are the larger size of the aperture, the presence of the larger number of pores and the avicularia, which are barely seen, but they are present in the specimens illustrated on Fig. 5a.

According to personal communication of Gordon (2010), the specimens presented by Braga (1963, p. 41) described as *Catenicella* sp. and later included into the family Savignellidae (Braga 2008, fig. 116), may represent the new genus.

Fig. 5. **a–e.** Savignyellidae. **a.** Frontal view of the single zooecium showing slightly sinuate aperture (ap) and a proximal broken part of a daughter zooecium, scale bar 20 μ m, ZPAL Br. XI/43. **b.** View of the mother zooecium (mz) from the dorsal side with the budded zooecium (dz), scale bar 200 μ m, ZPAL Br. XI/28. **c.** Budding zooecium, scale bar 200 μ m, ZPAL Br. XI/39. **d.** Budding zooecium showing its upper part with a foramina (fo), scale bar 100 μ m, ZPAL Br. XI/28. **e.** Upper view of a budded zooecium (bz), scale bar 100 μ m, ZPAL Br. XI/39. **f–h.** ?*Malakosaria* sp. **f.** Segment of a few →



zoecia arranged back to back, scale bar 200 μm ZPAL Br. XI/. **g.** Segment composed of six zoecia showing the apertures (ap), arranged alternately back to back, scale bar 100 μm , ZPAL Br. XI/6. **h.** Triad of the back to back zoecia from the frontal view showing the apertures and a few pores (zpo) or shallow depressions, scale bar 200 μm , ZPAL Br. XI/1. Seymour Island La Meseta Formation (Eocene), ZPAL 2, Telm1.

Having only a very scarce documentary material, it could be assumed that the studied La Meseta specimens are close to the representatives of the family Savignyellidae, or they may represent an ancestry line of the closely related taxa within the Savignyellidae. Zooecia described herein and illustrated on Fig. 5 show the characteristic zooidal flexure similarly to that observed in the family Savignyellidae and Vasignyellidae (Lagaaij 1968a, pl. 12, figs 8 and 11; Vieira *et al.* 2007, p. 53, fig. 4, p. 54, fig. 8).

Occurrence. — La Meseta Formation; Lower Eocene, Seymour Island, ZPAL 2, Teln1.

Family Calwelliidae MacGillivray, 1887

Genus *Malakosaria* Goldstein, 1882

Type species: *Malakosaria sinclairii* (Busk, 1857).

?*Malakosaria* sp.

(Fig. 5f–h)

Material. — 3 segments composed of a few back to back zooecia preserved as moulds.

Measurements. — Length of zooecia 0.50–0.62 mm, the width of zooecia 0.25–0.35 mm; the length of aperture 0.10–0.13 mm, the width of aperture 0.15–0.17 mm; the width of the segment from the frontal view 0.62–0.67 mm, the width of the segment from the lateral view 0.37–0.42 mm, the length of the segment 1.0–1.05 mm; the length of ovicell 0.22 mm, the width of ovicell 0.20 mm.

Description. — Segments are composed of six to eight zooecia (Fig. 5f–h), forming a part of a branch of a width of 0.67 mm from the frontal view. Zooecia are disposed in the overlapping alternated pairs, back to back (Fig. 5f–h), arranged in longitudinal rows, each comprising from 2 to 3 alternate series of zooecia, situated at the same plane (Fig. 5f–h). Zooecia are claviform, elongated, tapering proximally, with a short narrowed proximal part; in the middle part the zoecium increases in width towards the aperture and slightly become narrower in the distal part (Fig. 5f–h). The frontal wall of zooecia rather smooth with only some visible pores mainly in the proximal part of zoecium, below the aperture (Fig. 5h), and along the margins (Fig. 5f), which may be associated with the multiporous plates. Basal surface flat. Aperture, rather large, subcircular, longer than wide, with distinctly marked margins (Fig. 5g–h), the lower lip rather straight, slightly bended in the proximal direction, surrounded by a raised border (Fig. 5g–h). Two transversely oval uniporous rosette-plates are barely seen in the proximal part of aperture. Ascopore not seen. Avicularia wanting. One segment with a large ovicell is present (Fig. 5h).

Remarks. — The described specimens are tentatively included into the ?*Malakosaria* genus, and they resemble the *Malakosaria sinclairii* (Busk), in a few

morphological and almost all morphometrical features such as: a branch width, a zooidal dimensions, apertural sizes as well as in a very similar shape of the zooecia. *Malakosaria atlantica* described recently by Vieira *et al.* 2010b off São Paulo and Parana is similar in a few morphometrical features to the specimens studied, however, the pattern of arrangement of the zooecia, which form two independent rows of paired zooecia is different from the La Meseta specimens, which shows 2 to 3 rows of zooecia in the same plane, directed at the right angles to the zooecia of the successive row. The zooecia seen from the lateral sides are arranged back to back to each other (Fig. 5f).

The branches of the ?*Malakosaria* from the La Meseta Formation are equal throughout their length similarly as in *M. sinclairii*. Goldstein, who erected the genus *Malakosaria* along with a new species of *M. pholaramphos* (Goldstein 1882), showed a very similar pattern of the arrangement of zooecia, which are only slightly longer and wider than in the La Meseta specimens. The morphology and the sizes of the aperture of *M. pholaramphos* agrees well with the studied specimens form of the La Meseta Formation. Having just a very scarce and fragmented material without the full morphological features such as *i.e.* lack of avicularium, which was not observed in the studied moulds, the generic identity is unclear and provisional assignment to the ?*Malakosaria* is based mainly on the superficial as well as partly on the morphometrical resemblance to the *Malakosaria* genus.

Occurrence. — La Meseta Formation, Lower Eocene, Seymour Island, ZPAL 2, Telm1.

Palaeoenvironmental implications

Bryozoan assemblage in the lowermost part of the La Meseta Formation (Telm1, ZPAL 2) comprises exclusively taxa forming either separate, individual zooecia or segments composed of rows of zooecia, which were either loosely attached or erect flexible (Figs 3–5). They are all characterized by their small sizes belonging to forms, which in a living state build articulated internodes consisting of unizoooidal zooecia connected by chitinous joints.

Three types of the colony growth forms – membraniporiform/petraliform, cellariform, and cateniceiform, can be distinguished among the bryozoans in the studied biota (Stach 1936; Smith 1995; Hageman *et al.* 1997). The dominant colony growth-pattern is represented by *Beania*, whose loosely attached colonies reveal either petraliform or membraniporiform types. The cateniceiform growth-form represented by the loose zooecia of ditaxiporine cateniceid of the genus ?*Vasignyella* and savignyellids is generally used as a proxy for marine environment of a high wave/current energy or a rapid sedimentation rate, where the ability to slough sediment is a great advantage (compare Lagaij and Gautier 1965). The internode which consist mostly of separate jointed zooecia allow to follow the motion of water with a

little risk of breaking the colony, because of its extreme flexibility (Figs 2g–i, 4; Stach 1936; Wass 1977; Rosso 2009; Taylor and James 2013).

A few segments found in the studied material referred to the ?*Malakosaria* in a living state form free, flexible branches or joints belonging to the cellariiform growth-pattern, which usually choose clayey, sandy bottoms attached to the substrate by their basal rootlets (Fig. 5f–h).

Considering the living habitat of the *Beania* genus it should be pointed that this taxon is generally limited to the shallow-seas, intertidal or littoral zones, as well as to the variety of substrata including algae, shells of other bryozoans and a range of inorganic and organic hard substrate and is mostly restricted to the subtropical and tropical zones (Hayward 1995). The first data on the presence of the Eocene algal microplankton dominated by dinoflagellates, acritarchs along with chlorophyta from the La Meseta Formation (Telm1) was described by Coccozza and Clarke (1992).

Factors which contributed to the origin of the loose, articulated small zoecia, connected by joints possessing rhizoids or system of stolons, which help them to be attached to the substrate, are defined by a high availability of sand/mud substrate, shallow-water, and nearshore environment (Hageman *et al.* 1998). According to Cook (1979) an assemblage containing large numbers of well-preserved, minute colonies, which all developed rooting systems early in astogeny, is typical for a very short time of colonization of the minute colonies, which were originally a part of sessile microfauna directly inhabiting the sea bottom (Cook 1979).

In this context, ecologically, the rootlets of the colonies often called “sand fauna” were attached or involved with clusters of foraminifera-rich mud or sand grains. They always occur in the shallow water, where a great variety of substrate is available for the rooting attachment (Lagaaij 1968b; Cook 1979; Gordon and d’Hondt 1991). This statement could easily be adapted to the Eocene La Meseta biota where the biocenoses composed of bryozoans, benthic foraminifera and ostracods occur at the very base of the sandy, transgressive series in the lowermost part of Telm1 (Szczechura 2001; Gaździcki and Majewski 2012).

The taxonomic composition of the Early Eocene biota from the very base of the Telm1 at the locality of ZPAL 2 on Seymour Island, may indicate similar environmental setting like in some modern marine communities. For instance, the Recent Atlantic Brazilian intertidal setting could be comparable to that of the La Meseta Formation. It is a 3 meters deep and have natural substrata of coral reefs and sandstone banks, where the presence of the similar composition of the bryozoans like *Vasignyella* co-occurring with other taxa including *Beania*, *Savignyella* and *Catenicella* have been found (Vieira *et al.* 2007).

The very common feature of the studied bryozoan assemblage is the possession of the slightly or little calcified skeletons. Consequently, they can accommodate most of stress upon them by elastic deformation and flexibility of their skeletons, when an absence of calcification or light calcification occur (McKinney and Jackson 1989).

Biogeographical remarks

Bryozoans recovered from the base of the La Meseta Formation (ZPAL 2, Telm1) show the presence of a few cheilostomes represented by the families of Beaniidae Canu *et* Bassler, Catenicellidae Busk, Savignyellidae Levinsen, and Calwelliidae MacGillivray, which apart from the first and the latter ones are recognized in Antarctica for the first time.

Beania Johnston, the most common bryozoan remains in the studied assemblage is the oldest fossil record of this genus referring to *Beania bermundezi* from the Middle and Upper Eocene of the Jabaco Formation in Cuba (Lagaaij 1968a, p. 349–350, pl. 11, figs 11–14; Cheetham 1972). Lagaaij (1968a, p. 349) in his studies provided a very convincing evidence that *Beania* already existed in the Eocene of the Caribbean province.

Family Catenicellidae Busk is represented by the specimens included tentatively to ?*Vasignyella*. The oldest fossil remains of the catenicellid bryozoans are known from the Maastrichtian of Jamaica and the late Paleocene (Thanetian) of Europe and they are represented by the earliest-known genus of *Caberooides* Canu, 1908, which achieved a Tethyan – wide distribution by the Ypresian, ranging geographically from the NE Atlantic to Cheetham Island (New Zealand) and stratigraphically from the Upper Paleocene (Thanetian) to Upper Eocene (Priabonian), see Gordon and Braga (1994, p. 60).

Braga (1963) in his contribution to the systematic revision of the Reuss' (1868–69) and Waters' (1891–92) bryozoan faunas from Veneto (NE Italy) of the Upper Eocene–Lower Oligocene strata described two *Catenicella* species (Braga 1963, p. 40–41), of which one *Catenicella* sp. should be probably referred to a ?new genus of Savignyellidae and it shows a close similarity with the La Meseta specimens (Braga 2008, figs 116, 116a; compare with Fig. 5). Braga (1987) considered a Tethyan origin for the most of the Australian clades, however, this was largely based on stratigraphically and geographically limited data from the Southern Hemisphere. On the other hand catenicellids or ?savignyellids well-represented in the Paleogene deposits of Veneto (NE Italy) are found in increasingly younger deposits in the Indopacific basins, but they also live in the tropical seas (Braga 1987).

Nevertheless, catenicellids have a long history in the Australasian area from the Middle Eocene (the earliest fossil record), and they are commonly found in the Oligocene to the Recent (Brown 1958; Cockbain 1971; Schmidt and Bone 2001, 2003).

The representatives of the savignyellids present in the La Meseta Formation should be considered as the earliest known fossil record in Antarctica, which until now have only been found as far as in the NW Tethys (Braga 2008; Gordon and Braga 1994). The inconspicuous species of Savignellidae as a fossil, have been documented from the Upper Miocene of Caribbean, West Atlantic of Venezuela as

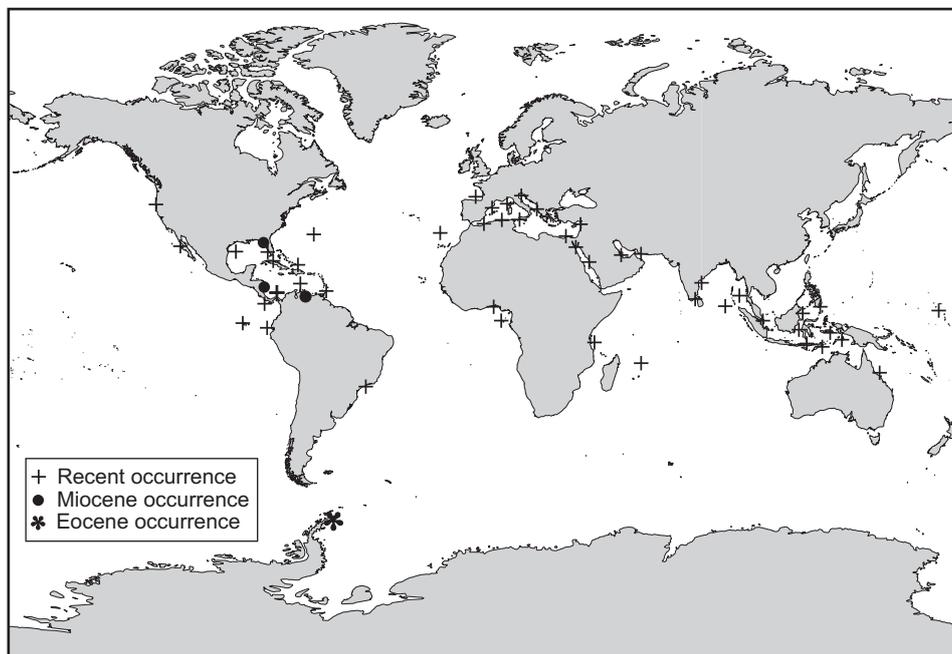


Fig. 6. Scheme showing the world distribution of the *Savignyella lafontii* (Audouin), a type species of *Savignyella*, marking the earliest fossil record of the family Savignellidae (asterisk) in the Early Eocene of Antarctica.

well as from Florida and in the Middle Miocene of Indonesia, up to the Mio-Pliocene of Nicaragua, where they are widely distributed in the tropical-warm temperate latitudes (Fig. 5a–e; Lagaaij 1968a, p. 353). In this context the occurrence of the potential representatives of the savignyellid bryozoans in the La Meseta Formation, dated on the basis of dinoflagellates as the late Early Eocene, predates the Tethyan occurrences (Cocozza and Clarke 1992).

Lagaaij (1968a) was the first who presented a range of the small-sized jointed forms, which build the articulated colonies, with internodes, consisting of one or a few zooecia, each connected by chitinous joints and with a radicate or stolonate base, which had an equally wide distribution in the Miocene. One of it was a Middle Miocene fossil from Madura Island (NE Java, Indonesia), which closely resembles *Vasignyella otophora* (Kirkpartick), as well as the specimens from the LMF (Fig. 5a) and thereby it may probably extend the known stratigraphical range (compare Lagaaij 1968a, pl. 12, figs 10–11).

A widespread marine, shallow-water *Savignyella lafontii* Levinsen, 1909 documented from the Late Miocene of Venezuela and Florida (Lagaaij 1968a), has a wide tropical-warm, temperate Recent distribution, extending throughout the Indopacific realm, Australia and the tropical and warm temperate Atlantic (Bermuda) to E. Florida, and southwards to the Gulf of Mexico, Caribbean, Brazil, Egypt, and W Africa (Fig. 6).

From the biogeographical point of view, the austral genus referred herein tentatively to the ?*Malakosaria* sp., is the first and the oldest fossil record of this genus from Antarctica, however, family Calwelliidae was already noted from the glacio-marine Miocene strata of the Cape Melville Formation, King George Island, South Shetlands (Hara 1997, 1998).

The Indo-West Pacific (IWP) has frequently been regarded as an evolutionary centre of origin along with the Atlantic, Caribbean and E Pacific but owing to the increasing volume of evidence there may be a homogenous, with the Early Cenozoic, pan-tropical (Tethyan) fauna, that has been disrupted by a series of essentially Neogene tectonic and climatic events (Crame 2001). This is in agreement with the studied biota from the La Meseta Formation, where the closely related taxa occur in the younger strata of the tropical and temperate-warm areas along the equator (Lagaaij 1968a; Gordon and Braga 1994).

On the other hand, the bryozoan fauna studied herein represents the new fossil records, and it could be an excellent biogeographical framework pattern, which is also confirmed by other groups of invertebrates discussed by many authors during the last century (Feldmann and Woodbourne 1988; Gaździcki 1996, 2001; Crame 1994; Dzik and Gaździcki 2001).

Conclusions

The most common elements in the studied bryozoans are small, inconspicuous, narrow elongated zooecia, preserved as moulds, separated after death, forming internodes or single zooecia as well as segments composed of a few zooecia (Figs 3–5).

They are described as *Beania* cf. *mirabilis* Johnston, *Beania* aff. *inermis* (Busk), *Beania* sp. and ?*Malakosaria* or alternatively they may represent a new genera associated closely with Savignyellidae but also one taxon belongs to the subfamily Ditaxiporinae, which has been tentatively classified as ?*Vasignyella* sp.

Analyses of the dominant colony growth-forms in conjunction with the depositional conditions of the lowermost part of the LMF (Telm1), show that the shallow-water assemblage has been controlled mostly by a combination of the depth gradient and substrate nature, which are key parameters controlling a biosystem inhabited by bryozoans and foraminifera (Gaździcki and Majewski 2012).

Beania Johnston and *Malakosaria* Goldstein, representatives of the family Savignyellidae and ditaxiporine catenicellids occur in the Recent seas and they predominate in the Indo-West Pacific, Atlantic and Southwest Pacific and Australasia. Presence of the new bryozoan records in the Eocene of the La Meseta Formation (Hara 2001, 2002), shows that Antarctic was an important centre of origin of bryozoan taxa during the Paleocene–Eocene cheilostome turnover (Zinsmeister and Feldmann 1984; Bottjer and Jabłoński 1988).

Bryozoans included here in the Ditaxiporinae (Catenicellidae) and Savignyellidae cast a new light on the migration routes and the evolution, and they predate the early Late Eocene catenicelloidean stock of NW Tethys as well as amphi-Atlantic distribution.

Remarkable attention should be paid on the climatic regime of the studied bryozoans represented by the taxa, which in the present day are widely distributed in the tropical-warm temperate latitudes and interpreted as deposited in the shallow-water settings (Tilbrook *et al.* 2006; Vieira *et al.* 2007).

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