



New trace fossils from the La Meseta Formation (Eocene) of Seymour Island, Antarctica

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Abstract: Trace fossils *Lockeia siliquaria* James, *Ophiomorpha nodosa* Lundgren, *Parataenidium seymourensis* isp. n., *Protovirgularia rugosa* (Miller and Dyer) and *Rhizocorallium jenense* Zenker have been described for the first time from the Eocene La Meseta Formation of Seymour (Marambio) Island, Antarctic Peninsula. Determinations of some trace fossils formerly described from this formation have been revised. The whole trace fossils association from the La Meseta Formation points to foreshore-off-shore environment as indicated by presence of the *Skolithos* and *Cruziana* ichnofacies, and to at least temporal normal salinity.

Key words: Antarctica, Eocene, trace fossils.

Introduction

Trace fossils are among the most important tool in recognition of many aspects paleoenvironments and their biota (e.g. Ekdale *et al.* 1984; Bromley 1996; Pemberton *et al.* 2001; McIlroy 2004). Almost 20 years ago this fact was acknowledged by Wiedman and Feldmann (1988), who in the Eocene La Meseta Formation of Seymour Island recognized burrows *Ophiomorpha*, *Muensteria*, *Diplocraterion*, *Skolithos*, *Helminthopsis*, “halo”, “rind” burrows, “enigmatic lobed rod” and borings *Zapfella*, *Oichnus*, and *Teredolites*. The cited authors concluded that the trace fossils together with sedimentary features point to a nearshore environment, generally above wave base, mostly above the normal wave base. Porębski (1995, 2000) made extensive sedimentological studies of the formation and recognized it as a complex stack of estuarine fill separated by high-relief tidal-ravinement surfaces. He mentioned and illustrated several trace fossils from different facies, which were determined at different taxonomic level as *Skolithos*, U-shaped forms “comparable with *Rhizocorallium* and *Diplocraterion*”, *Teredol-*

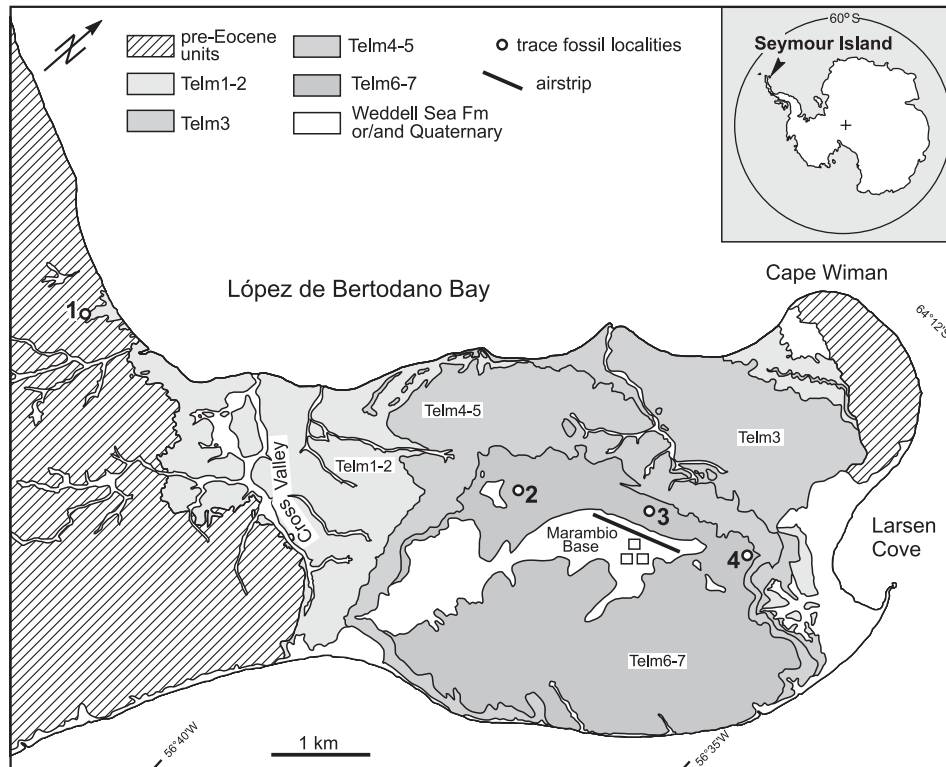


Fig. 1. Geological sketch map of the northern part of Seymour Island (simplified from Sadler 1988) showing the sites (1–4) where studied trace fossils were collected. Inset shows position of Seymour Island in the northern Antarctic Peninsula sector.

ites, *Ophiomorpha–Thalassinoides*, *Ophiomorpha*, *Diplocraterion polyupsilon* Smith, *Teichichnus*, *Trichichnus*-like strings, *Polykladihnus irregularis* Fürsich, *Scolicia*, and forms resembling *Arenicolites*. Bitner (1996a, b) described and illustrated epifaunal organisms (foraminifera, serpulids, cirripeds) and gastropod, phoronid, sponge and algal borings which were recognized on the brachiopod shells from the La Meseta Formation. Pirrie *et al.* (1998) studied high Mg calcite cements in *Teredolites* from the formation.

New material was collected from the La Meseta Formation by one of us (A.G.) during the 1987–88, 1991–92 and 1993–94 Argentine-Polish Field Parties on Seymour Island. It contains, among others, the ichnogenera *Parataenidium* (with a new ichnospecies *P. seymourensis*), *Lockeia* James, *Protovirgularia* McCoy and *Rhizocorallium* Zenker, which are recorded for the first time in the La Meseta Formation. The new material and critical assessment of some determinations of trace fossils by Wiedman and Feldmann (1988) and Porębski (1995) have provided important details on the ichnology of the La Meseta Formation.

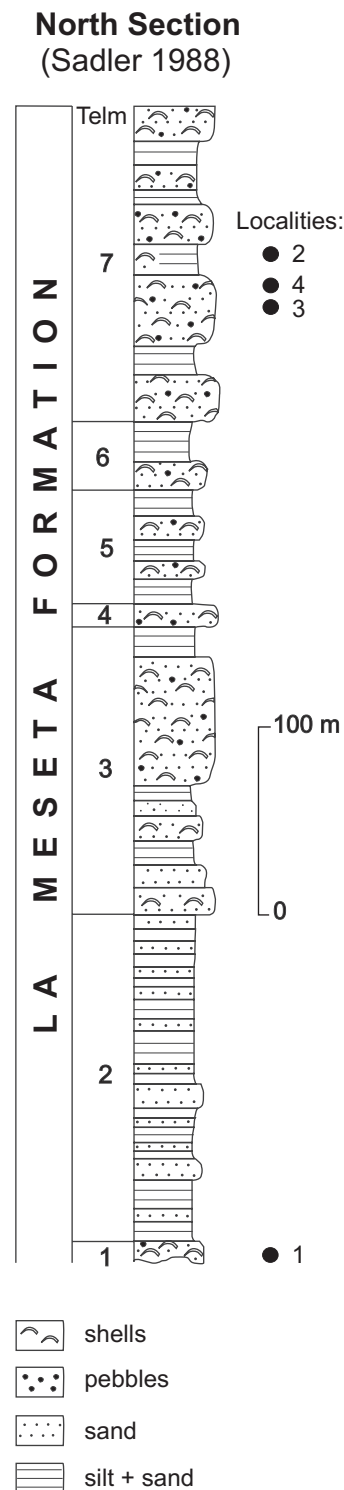


Fig. 2. Composite stratigraphic column of the La Meseta Formation (North Section) on Seymour Island showing distribution of main lithofacies and location of studied trace fossils. Section adapted from Sadler (1988).

The main aim of this paper is to describe and interpret the new trace fossil material and to interpret the trace fossil associations from the La Meseta Formation. The illustrated specimens are housed in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, under the catalogue number ZPAL Tf.2.

Geological setting

The stratified fossiliferous clastic sequence of the Eocene La Meseta Formation (up to 800 m thick) crops out in the north-eastern portion of Seymour (Marambio) Island located off the north-eastern tip of the Antarctic Peninsula (Fig. 1). The formation rests unconformably on either the Late Cretaceous López de Bertodano Formation or on the Paleocene Sobral and Cross Valley formations (Sadler 1988; Porębski 1995; Marensi *et al.* 1998). It is overlain by glacial marine deposits and a lodgment till (about 5 m thick) which indicates an age at the Eocene–Oligocene boundary (Ivany *et al.* 2006), and finally by the post-Late Pliocene Weddell Sea Formation (Gaździcki *et al.* 2004).

The La Meseta Formation was subdivided by Sadler (1988) into seven lithofacies units (Telm1–Telm7) and this division is accepted here (Figs 1, 2). For different subdivision schemes and their stratigraphic correlation see Marensi *et al.* (1998, fig. 4). The age of the lower part of the La Meseta Formation (Telm1–Telm2) is late Early Eocene based on marine palynoflora dominated by dinoflagellate cysts (Coccoza and Clark 1992). The uppermost part of formation (top of Telm7) according to $^{87}\text{Sr}/^{86}\text{Sr}$ isotope stratigraphy is the latest Eocene– earliest Oligocene (33.57–34.78 Ma) in

age (see Dingle and Lavalley 1998; Dutton *et al.* 2002; Ivany *et al.* 2006 see also Gradstein and Ogg 2004).

The La Meseta Formation preserve an exceptional record of Eocene shallow-marine ecosystems (Feldmann and Woodburne 1988; Stilwell and Zinsmeister 1992; Gaździcki 1996, 1998, 2001; Dzik and Gaździcki 2002). Moreover the geochemical analyses made on the fossil bivalve shells (*Cucullaea*, *Eurhormalia*) from the formation indicate a considerable climatic cooling event during the sedimentation of the upper part of the formation (Gaździcki *et al.* 1992; Dutton *et al.* 2002; Ivany *et al.* 2004, 2006). This cooling event can be correlated with the late Eocene–early Oligocene glaciation in Antarctica (Barrett 1996, see also Birkenmajer *et al.* 2005).

The studied trace fossil collection comprises 11 specimens. They were collected from four localities (Figs 1, 2). The assemblage of *Lockeia siliquaria* and *Protovirgularia rugosa* was found in the Telm1 unit at locality 1 (*Bill Hill*, see Gaździcki and Tatur 1994, fig. 1). The remaining specimens were collected from the Telm7 unit: *Ophiomorpha nodosa* at locality 2, *Rhizocorallium jenense* at locality 3; and *Parataenidium seymourensis* isp. n. at locality 4.

Synopsis of ichnotaxa

Ichnogenus *Lockeia* James, 1879

Diagnosis. — Bilaterally symmetrical, elongated, commonly almond-shaped, rarely triangular or heart-shaped outline with smooth margin, preserved commonly as hypichnial mounds, commonly with a distinct median crest. Vertical spreite can be present (after Rindsberg 1994; modified by Schlirf *et al.* 2001).

Remarks. — *Lockeia* is commonly interpreted as a bivalve resting trace (Seilacher and Seilacher 1994) occurring in marine and various non-marine environments since ?Late Cambrian (Fillion and Pickerill 1990). Moreover, small crustaceans can be potential producers of *Lockeia* (Bromley and Asgaard 1979; Pollard 1981). For further discussion see Mángano *et al.* (2002).

Lockeia siliquaria James, 1879

(Fig. 3)

Material. — A dozen specimens on a sandstone slab (17 × 19 cm).

Diagnosis. — Thin, elongate, to stout, generally high-standing, almond-shaped, smooth hypichnial ridges, with strongly arcuate to almost obtuse terminations; occasionally showing vertical spreite (after Schlirf *et al.* 2001).

Description. — Smooth, hypichnial and epichnial, predominantly straight, variously oriented, densely aggregated, almond-shaped mounds with pointed or rarely obtuse terminations. They are 13–19 mm long and 5–8 mm wide. The mounds are preserved in full relief in a fine-grained sandstone bed that is 10–25 mm



Fig. 3. Trace fossils from the La Meseta Formation. *Lockeia siliquaria* James, 1879 (some indicated as *Lo*), *Protovirgularia rugosa* (Miller and Dyer, 1878) (*Pr*), and transitional forms between *Lockeia* and *Protovirgularia* (*Prt*). Specimen ZPAL Tf.2/1, locality 1, Telm1.

thick and shows graded bedding. They extend out up to 3 mm above slightly undulating bedding plane. Most of the mounds display flat top, which, in contrast to the bedding plane, is not covered with reddish muddy film but show whitish sandstone. This suggests that such a top is a parting surface. Some of the mounds overlap laterally. There are very elongated ridges with at least one pointed termination. Some of them display lateral chevron ribs. There are forms ranging from *Lockeia* to *Protovirgularia*, which occurs in the same bed.

Remarks. — According to the older literature, the more stout forms can be referred to *Lockeia amygdaloides* (Seilacher, 1953) and the narrower forms to *Lockeia siliquaria* James. However, Seilacher and Seilacher (1994) and Schlirf *et al.* (2001) treated them as the morphological variants of *L. siliquaria* James, because they occur in the same beds together with transitional forms between these two ichnospecies. The same is true for the material from the La Meseta Formation. Herein, forms transitional to *Protovirgularia* occur as well, but we prefer to separate these two ichnogenera, which represent two different ethological groups, *i.e.* cubichnia and repichnia, respectively.

Ichnogenus *Ophiomorpha* Lundgren, 1891

Diagnosis. — Simple to complex burrow systems lined at least partially with agglutinated pelletoidal sediment (after Howard and Frey 1984, modified by Uchman 1998).

Remarks. — This is one of the most common trace fossils known since the Permian, mostly from shallow-marine environments. It is produced in modern environments by callianassid crustaceans such as the recent *Callichirus major* (former *Callianassa major*), which usually produce a system of shafts and galleries in sandy sediments. Claw elements of *Callichirus* were found in infillings of *Ophiomorpha* from Eocene erratic blocks of East Antarctica (Schweitzer and Feldmann 2000). The ethology of this trace fossil is not fully understood: deposit and/or suspension feeding are considered for its tracemakers (see Ekdale 1992 for discussion). There are also deep-sea species of *Ophiomorpha*, e.g. *Ophiomorpha rudis* (Książkiewicz, 1977), which tracemakers probably fed on plant detritus matured by microbes (Uchman 1995; Tchoumatchenco and Uchman 2001).

Ophiomorpha displays transitions within the same burrow system to forms referred to *Spongiomorpha* Saporta (1887), *Thalassinoides* Ehrenberg (1944) and *Gyrolithes* Saporta (1884). Schlirf (2000) included all of these ichnogenera in *Spongiomorpha* Saporta, but this decision is seldom followed.

Ophiomorpha nodosa Lundgren, 1891

(Fig. 4)

Material. — Seven specimens.

Diagnosis. — *Ophiomorpha*, whose burrow walls consists predominantly of dense, regularly distributed discoid, ovoid, or irregular polygonal pellets (after Frey *et al.* 1978).

Description. — A fragment of straight tube with a wall covered with ovoid to irregular pellets. The tube is about 95 mm long and 17–18 mm in the diameter of the exterior. The pellets are up to 3 mm long and up to 2 mm wide.

Remarks. — The trace fossil described as *Ophiomorpha* Lundgren from the La Meseta Formation by Wiedman and Feldmann (1988, figs 2.1, 2.2) belong to this ichnospecies. Probably, the same concerns forms illustrated by Porębski



Fig. 4. *Ophiomorpha nodosa* Lundgren, 1891. Specimen ZPAL Tf.2/2. locality 2, Teln7.

(1995). *O. nodosa* Lundgren is one of the most common shallow-marine trace fossils and is produced mostly by callianassid shrimps (Frey *et al.* 1978; Ekdale 1992). It is most typical of the Skolithos ichnofacies (Frey and Seilacher 1980; Pemberton *et al.* 2001), but also occurs in deeper shelf tempestites (Frey 1990; Frey and Goldring 1992).

Ichnogenus *Parataenidium* Buckman, 2001

non 1859. *Eione*; Tate [not seen; *nomen nudum* according to Häntzschel (1975, p. W112; junior homonym of *Eione* Rafinesque 1814 (Mollusca) according to Rindsberg (1994, p. 53)].

?non 1961. *Petromonile*; Casey: p. 600. [*?nomen nudum*].

?non 1967. *Cylindrichnus*; Bandel [junior homonym of *Cylindrichnus* Toots in Howard 1966 (trace fossil) according to Bandel (1973)].

?non 1973. *Margaritichnus*; Bandel: p. 1002.

2001. *Parataenidium*; Buckman: p. 84.

Type ichnospecies. — *Parataenidium mullaghmorensis* Buckman, 2001.

Emended diagnosis. — Horizontal to subhorizontal trace fossils, which are composed of short, commonly densely packed and imbricated protrusions running up from a common, smooth basal cylinder. In horizontal section, the topmost part of some specimens gives an impression of a meniscate filling.

Remarks. — A lot of taxonomic problems concern this ichnogenus (see the synonymy list). *Eione* Tate, 1859, under which this trace fossil was described (*e.g.* Maples and Suttner 1990; Ainsworth and Crowley 1994; Głuszek 1998), is treated as a *nomen nudum* (Häntzschel 1975, p. W112) or junior homonym of a mollusc (Rindsberg 1994, p. 53), and therefore must be rejected. Application of the ichnogenus *Petromonile* Casey, 1961 (Rindsberg, 1994) is very problematic. It was applied for *Siphonia benstedii* Bensted (1862, p. 335) and own material, in both cases from the Early Cretaceous of England, by Casey (1961). The material by Bensted (1862, pl. 18) is known only from drawings, which do not give clear information about nature of *Siphonia benstedii* Bensted. Casey's (1961) material, which was considered as "probably infilled feeding burrows" (Casey 1973 in Häntzschel 1975, p. W187), gives the same problem and *Petromonile* was put by Häntzschel (1975,

p. W186–187, fig. 109) in “unrecognized and unrecognizable genera”. Thus, it can be treated as probable *nomen nudum*. *Cylindrichnus reptilis* Bandel, 1967 from the Carboniferous of Kansas displays some of the diagnostic features of *Parataenidium*, such as row arrangement of barrel-like structures on the upper bedding surface. However, Hakes (1976) worked on similar material, which was also obtained from the quarry where the holotype of *C. reptilis* Bandel was found, and noted that some of the structures are isolated, and sectioning of some specimens (but not the holotype) did not prove connections between the barrel-like structures in the bed. The doubts were confirmed by Lockley *et al.* (1987). Moreover, the ichnogenetic name *Cylindrichnus* was used earlier by Toots in Howard (1966). Therefore, a new ichnogenus *Margaritichnus* Bandel, 1973 was introduced. Probably, all the complications resulted in a new ichnogenus *Parataenidium* Buckman, 2001 being introduced. It seems that the material of *Margaritichnus* Bandel requires further analysis, and further study will probably result in new taxonomic decisions, but at the present time the ichnogenus *Parataenidium* Buckman is most useful.

The emended diagnosis is close to the diagnosis of *Petromonile* by Rindsberg (1994, p. 53) but this latter does not include horizontal forms and the diagnosis does not address the horizontal section at the top. In the diagnosis by Buckman (2001), a discontinuity between the upper and lower part of the trace fossil is stressed. This feature, however, cannot be easily recognized, and therefore is abandoned. A more descriptive diagnosis is proposed.

Parataenidium was produced by an unknown organism, which processed sediment and produced the structure mainly by backfill action (Seilacher 1990). The lower part is attributed mostly to locomotion and the upper part to feeding (Buckman 2001). This trace fossil was known hitherto only from Paleozoic shallow-marine sediments (*e.g.* Marintsch and Finks 1982; Lockley *et al.* 1987; Maples and Suttner 1990; Głuszek 1998; Buckman 2001), except for the problematic *Petromonile* from the Lower Cretaceous of England (Casey 1961). Thus, the specimen from the Seymour Island shifts its upper stratigraphic range up to the Eocene.

Parataenidium seymourensis isp. n.

(Fig. 5A–C)

?1988. Enigmatic lobed rod; Wiedman and Feldmann: p. 537, fig. 2.7.

Holotype: Specimen ZPAL Tf.2/3, figured in Fig. 5.

Type horizon: Telm7, La Meseta Formation; Eocene.

Type locality: Locality 4, Seymour Island, Antarctic Peninsula.

Derivation of the name: From the type area – Seymour Island.

Material. — One specimen, which is a holotype.

Diagnosis. — *Parataenidium* with very short conical protrusions.

Description. — A curved subcylindrical structure built of fine-grained sandstone. Its base is almost smooth, with weak transverse undulations, which is related probably to internal structure. The upper part shows short, imbricated protrusions.

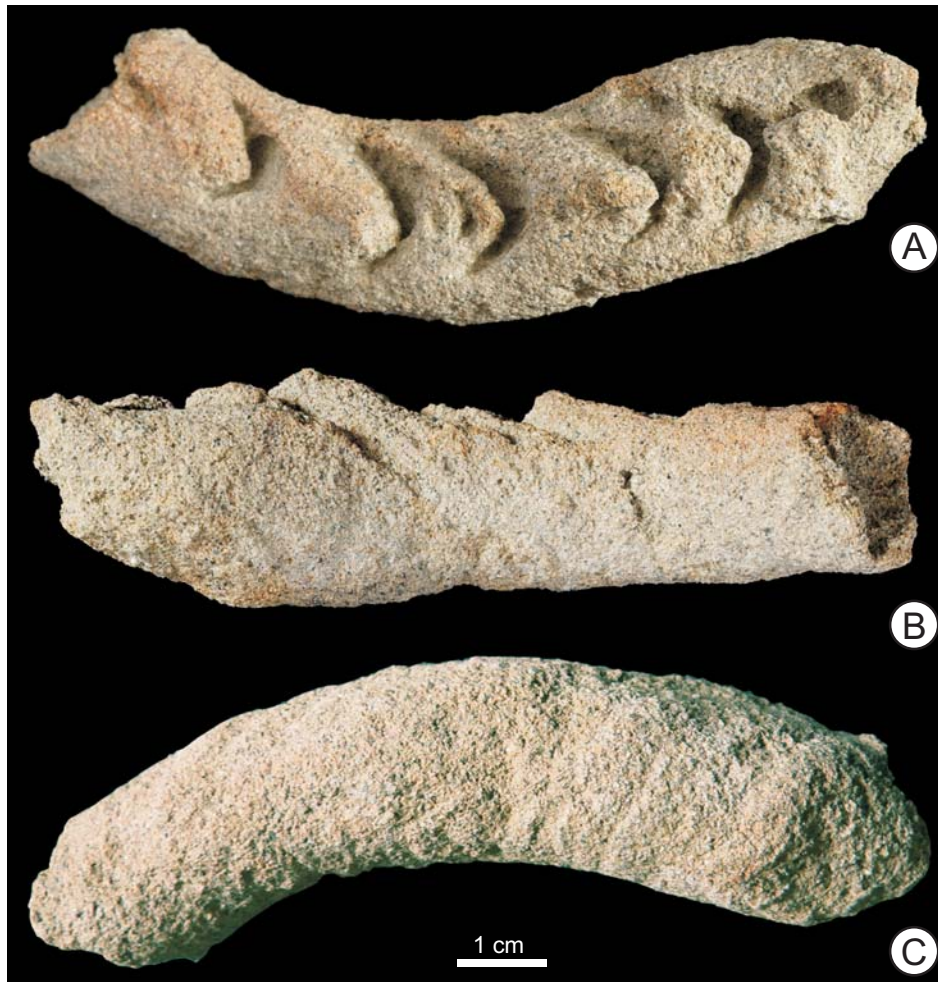


Fig. 5. *Parataenidium seymourensis* isp. n., holotype. A. Top view. B. Side view. C. Bottom view. Specimen ZPAL Tf.2/3, locality 4, Teln7.

sions, inclined at the angle of about 45° . The protrusions look like flattened, tilted, partly invaginated cones. The whole structure is about 110 mm long, 23–24 mm wide, 23–30 mm high. Tips of the protrusions are 13–22 mm apart. The protrusions are 22–24 mm long and separated by depressions, which are up to 3 mm wide in the middle part.

Remarks. — So far, two ichnospecies of *Parataenidium* are recognized. *P. moniliformis* (Tate, 1859) is characterized by the protrusions with globular, barrel-like terminations (Buckman 2001). *P. mullaghmorensis* Buckman, 2001 is typified by strongly oblate, imbricated wedge protrusions, with distinctly meniscate upper part separated from the lower part. The third, new ichnospecies, *P. seymourensis* is distinguished by its conical protrusions.

The “enigmatic lobed rod” described and illustrated by Wiedman and Feldmann (1988, fig. 2.7) belongs to *Parataenidium*, but is smaller (8 mm in diameter) and details of its upper part are not illustrated.

The depressions between protrusions resulted from weathering of probably more fine-grained material. This suggests strong processing of sediment in the upper part of the burrows typical of this ichnogenus (Buckman 2001). It is not excluded that the meniscate trace fossil from the La Meseta Formation determined as *Muensteria* (Wiedman and Feldmann 1988, p. 535, fig. 2.4) represent the uppermost part of the trace fossil.

Ichnogenus *Protovirgularia* McCoy, 1850

Diagnosis. — Horizontal or subhorizontal cylindrical borrows, trapezoidal, almond-shaped, or triangular in cross-section, distinctly or indistinctly bilobed. Internal structure, if preserved, is formed by successive pads of sediment that may be expressed as ribs on the exterior. Ribs arranged in chevron-shaped, biserial pattern along external or internal dorsal part. Occasionally with smooth mantle covering the structure and/or oval mound-like terminations of the trace (after Uchman 1998).

Remarks. — Seilacher and Seilacher (1994) revised *Protovirgularia* and proved its molluscan origin by neoichnological experiments. They expanded the previous diagnosis of this ichnogenus, which was limited to keel-like trace fossils covered with chevron-markings open in one direction (Han and Pickerill 1994), by including full-relief trace fossils in *Protovirgularia*, previously described under different ichnogenera (see Uchman 1998 for review). Mángano *et al.* (2002) proposed exclusion of the smooth forms out of *Protovirgularia* and inclusion them in *Lockeia* James. However, this is very problematic because the smooth forms represent repichnia and *Lockeia* represents cubichnia. *Protovirgularia* occurs in various marine environments (Mángano *et al.* 2002 for review).

Stratigraphic range. — Arenig (Fillion and Pickerill 1990) – Miocene (Bayer 1955; D’Alessandro 1982).

Protovirgularia rugosa (Miller and Dyer, 1878)

(Fig. 3)

Material. — A few specimens on a sandstone slab (17 × 19 cm).

Diagnosis. — Commonly short *Protovirgularia* terminated by smooth *Lockeia*-like body. Chevron markings strong (after Seilacher and Seilacher 1994; modified by Uchman 1998).

Description. — Hypichnial, straight to slightly curved ridge, almond-shaped in cross section, covered with oblique side ribs symmetrically girding the ridge. The ridge is at least 55 mm long and terminated by *Lockeia siliquaria* James. It is 5–7 mm wide and about 5 mm high. The ribs are about 1 mm wide and 3–5 mm apart. The ridge cross-cuts another ridge, which is 60 mm long, 5–7 mm wide and

7–9 mm high. This ridge is almost smooth, but indistinct oblique ribs can be still seen. Short, pointed ridges with a flat top and side ribs, up to 50 mm long, are transitional forms to *Lockeia siliquaria* James.

Remarks. — The ribs were produced by the cleft foot of bivalves anchoring in sediment during their locomotion (Seilacher and Seilacher 1994). Judging from cross-cutting relationships, the almost smooth ridge, which resembles *Uchirites triangularis* Macsotay, 1967 that was included in *Protovirgularia* by Uchman (1998), was produced earlier than the ridge with well expressed ribs. It can be supposed that the poor preservation of ribs in the former one is related to substrate consistency, which became more stiff in time, and the cleft terminations of the bivalve foot is better imprinted in case of the younger specimen.

Seilacher and Seilacher (1994, p. 11) interpreted this ichnospecies as “cubichnial version of *Protovirgularia* [...] always found at the bases of sandy tempestites. So it makes sense that escape was in response to storm sand sedimentation”. *P. rugosa* occurs from Devonian (Dahmer 1937) to Miocene (D’Alessandro 1982).

Ichnogenus *Rhizocorallium* Zenker, 1836

Diagnosis. — U-shaped spreiten-burrows, parallel or oblique to bedding plane; limbs more or less parallel and distinct; tube diameter : diameter of spreite >1:5 (after Fürsich 1974).

Remarks. — *Rhizocorallium* is interpreted as a structure produced by suspension feeding (only short oblique, retrusive forms) or by deposit feeding organisms, mostly crustaceans (Fürsich 1974; Schlirf 2000). It occurs mostly in shallow marine deposits, however it ranges from the deep-sea (Uchman 1992) to marginal marine settings (e.g. Farrow 1966; Hakes 1976), or even non-marine deposits (Fürsich and Mayr 1981).

Stratigraphic range. — Cambrian (Seilacher 1955; Jensen 1997) – Miocene (Fürsich and Mayr 1981; Uchman *et al.* 2000) and probably Pleistocene (Hong 1997; Virtasalo *et al.* 2004).

Rhizocorallium jenense Zenker, 1836

(Fig. 6A–B)

Material. — Two specimens.

Diagnosis. — More or less straight, short U-shaped spreiten-burrows, commonly oblique to bedding plane and occasionally vertically retrusive (after Fürsich 1974).

Description. — Tongue-like structures encircled by marginal tunnel, and filled with spreiten. The marginal tunnel is 19–12 mm wide, and the whole structure is 50–60 mm wide. It is slightly wider distally. The tongue is at least 110 mm long. The spreiten display sandstone of slightly different grain-size arranged in arcs, which are up to 10 mm wide. The arcs form undulations on the spreiten surface.

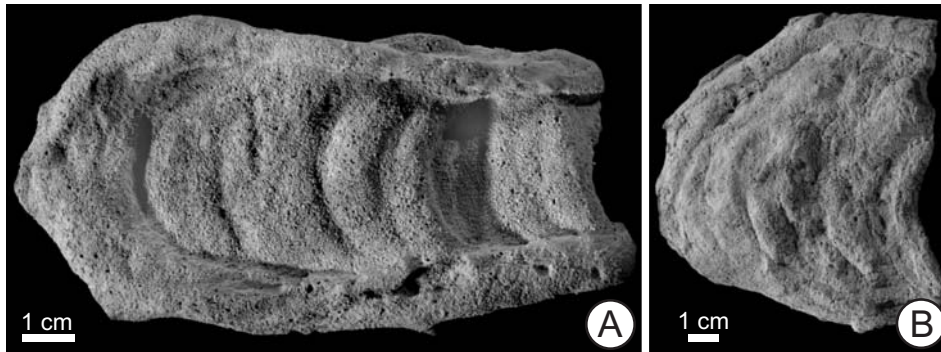


Fig. 6. *Rhizocorallium jenense* Zenker, 1836. A. Specimen ZPAL Tf.2/4. B. Specimen ZPAL Tf.2/5. Locality 3, Teln7.

Remarks. — Widening in the distal part can reflect ontogenic grow of the tracemaker, similarly to some *Diplocraterion* (Bromley and Hanken 1991). Porębski (1995) referred some U-shaped forms with spreite to *Rhizocorallium* but not illustrated them.

Discussion

The described ichnotaxa enlarge and refine the hitherto known trace fossil association from the La Meseta Formation. Wiedman and Feldmann (1988) determined *Ophiomorpha*, which we ascribed to *O. nodosa* Lundgren. It is possible that *Muensteria*, described by the cited authors is the upper part of *Parataenidium*. However it is, *Muensteria*, which lumps forms of different affinity, is not recommended for further use (Mikuláš and Uchman 1996). The enigmatic lobed rod of Wiedman and Feldmann (1988) probably belong to *Parataenidium*, for which a new ichnospecies *P. seymourensis* was recognized on the basis of the new material. The trace fossil determined as *Helminthopsis* Heer by Wiedman and Feldmann (1988) displays meniscate filling, and what is a typical feature of *Taenidium* Heer (D'Alessandro and Bromley 1987). The “halo” burrow by Wiedman and Feldmann (1988, fig. 2) is probably a concretion structure around a tubular trace fossil. The wood borings determined by the cited authors as *Teredolites* Lymerie contain long curved tubes typical of *Teredolites longissimus* Kelly and Bromley (1984). The borings perpendicular to the log course, which are illustrated by Porębski (1995, his fig. 8) and those which were studied by Pirrie *et al.* (1998) can belong to *Teredolites clavatus* Leymerie, 1842. Determinations of *Diplocraterion* and *Skolithos*, and the borings *Zapfella* De Sain Seine and *Oichnus* Bromley, and the forms illustrated by Porębski (1995) do not pose problems. The ichnotaxa described in this paper *Lockeia siliquaria* James, *Protovirgularia rugosa* (Miller and Dyer) and *Rhizocorallium jenense* Zenker are added to the list of trace fossils.

All the trace fossil association (*Diplocraterion* isp., *Lockeia siliquaria*, *Polykladichnus*, *Teichichnus*, *Scolicia*, *Ophiomorpha nodosa*, *Parataenidium seymourensis* isp. n., *Parataenidium* isp., *Protovirgularia rugosa*, *Rhizocorallium jenense*, *Skolithos* isp., *Taenidium* isp., *Teredolites longissimus*, *Oichnus* isp., *Zapfella* isp.) point to shallow marine environments. *Diplocraterion*, *Ophiomorpha nodosa* and *Skolithos* are typical members of the Skolithos ichnofacies, which typifies fore-shore-middle shoreface environments with sandy substrate. *Rhizocorallium jenense*, *Taenidium*, *Scolicia*, *Teichichnus*, *Protovirgularia* and *Lockeia* are common in the Cruziana ichnofacies, which typifies lower shoreface-offshore settings. However, members of the Skolithos ichnofacies can occur in tempestites in range of the Cruziana ichnofacies (Pemberton *et al.* 2001). Wiedman and Feldmann (1988) concluded that the La Meseta Formation deposits accumulated generally above wave base, mostly above fairweather wave base, including tidal environment. However, the trace fossils typical of the Cruziana ichnofacies show that at least some parts of these deposits was accumulated very close to or below fairweather wave base (*cf.* Pemberton *et al.* 2001), which is consistent with sedimentological interpretations by Porębski (1995). In particular, the strongly bioturbated sediments with *Teichichnus* points to a lower energy environment below normal wave base, maybe with a lowered salinity (compare Pemberton *et al.* 2001). Porębski (1995, p. 79) suggested that low diversity of trace fossils can be caused by lowered salinity for at least part of the formation. However, salinity fluctuations are possible, but the diversity (14 ichnogenera) is generally not different from diversity in other Cenozoic shallow-marine formations. The presence of *Scolicia*, which is produced by stenohaline echinoids, shows that at least locally the salinity was normal. The occurrence of *Scolicia* in a heteroliotic facies, which was interpreted as a tidal channel fill (Porębski 1995, p. 38), is rather unusual, because this trace fossil is rather typical of deeper environment in range of the Cruziana ichnofacies.

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