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EUFLABELLA N. IGEN.: COMPLEX HORIZONTAL SPREITE BURROWS IN UPPER CRETACEOUS–PALEOGENE SHALLOW-MARINE SANDSTONES OF ANTARCTICA AND TIERRA DEL FUEGO

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ABSTRACT—Fine-grained sandstones and siltstones of Late Cretaceous to Eocene age in Antarctica and Tierra del Fuego yield an association of well-known shallow-marine trace fossils. Among them stick out complex spreite burrows, which are formally described as *Euflabella* n. igen. and subdivided into five ichnospecies with different burrowing programs and occurrences. As shown by concentrations of diatoms, radiolarians, foraminifers, and calcispheres in particular backfill lamellae, the unknown trace makers lived on fresh detritus from the surface as well as the burrowed sediment. In some ichnospecies, vertical sections show that the spreite is three-dimensionally meandering in upward direction and that upper laminae tend to rework the upper backfill of the folds underneath. This could mean a second harvest, after cultivated bacteria had time to ferment refractory sediment components, which the metazoan trace maker had been unable to digest before.

INTRODUCTION

The archetypal ichnofacies scheme (Seilacher, 1967) builds on recurrent groupings of ethologically similar trace fossils that record particular environmental conditions. A general consequence of this concept is that, through time, the same ichnofacies may be represented by different ichnotaxa that reflect similar behaviors corresponding to environmental conditions (Seilacher, 2007; MacEachern et al., 2010; Buatois and Mángano, 2011). Nonetheless, detailed studies of recurrent trace fossil suites typical for the *Cruziana* ichnofacies of Late Cretaceous to Cenozoic age have shown a more or less similar grouping of dominant ichnotaxa (e.g., Frey and Howard, 1985, 1990; MacEachern and Pemberton, 1992; Pemberton et al., 1992; MacEachern et al., 2010; Buatois and Mángano, 2011).

Most elements of that grouping are also found in distal shoreface to offshore deposits of Antarctica and Tierra del Fuego, including the ichnogenera *Asterosoma*, *Chondrites*, *Cylindrichnus*, *Nereites*, *Ophiomorpha*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Rhizocorallium*, *Rosselia*, *Schaubcylindrichnus*, *Scolicia*, *Taenidium*, *Teichichnus*, and *Thalassinoides* (Figs. 1–3; see also Scasso et al., 1991). However, a striking feature is the distinctive representation, in cases with absolute dominance, of trace fossils which are unknown, or poorly known, elsewhere in the world. In previous papers, we have already described some of these, including the ichnogenera *Paradictyodora* (Olivero et al., 2004), *Patagonichnus* (Olivero and López Cabrera, 2005), and *Tasselia* (Olivero and López Cabrera, 2010). The main objective of this paper is to describe another new group of distinctive trace fossils, which are well represented in the ~2400 m thick, Campanian–Maastrichtian shelfal mudstones and fine-grained sandstones of the Marambio Group, James Ross Basin, Antarctica and the ~500 m shelf deposits of the Leticia Formation, Austral Basin, Tierra del Fuego.

STRATIGRAPHICAL, PALEOENVIRONMENTAL, AND ICHNOLOGICAL FRAMEWORK

James Ross Basin, Antarctica.—At the northeast tip of the Antarctic Peninsula, the James Ross Basin includes the ~3-km thick marine succession of the Santonian to Danian Marambio Group (Figs. 1, 2). It contains three unconformity-bounded sequences punctuating the Santonian–Maastrichtian development of the shelf area that at the end of the Late Cretaceous extended for more than 100 km between the Antarctic Peninsula and the Weddell Sea (Olivero, 2012). The Marambio Group is highly fossiliferous, including a diverse and abundant invertebrate fauna of serpulids, crustacean decapods, echinoderms, gastropods, bivalves, ammonites, marine and terrestrial vertebrates, and plant remains (Macellari, 1988; Crame et al., 1991; Scasso et al., 1991; Marenssi et al., 1992; Pirrie et al., 1997; Olivero, 2012).

The Santonian–early Campanian N Sequence is interpreted as a shallowing deep-water deltaic succession, passing from prodelta, delta slope, and shallow marine deposits of the Santa Marta Formation, which are restricted to northwestern James Ross Island (Scasso et al., 1991). In southeastern James Ross Island, the shallow marine coquinas and cross-bedded sandstones of the upper Santa Marta Formation are replaced by age-equivalent, lower shoreface to outer shelf storm-influenced, graded sandstones and mudstones (Rabot Formation, Olivero, 2012). The middle part of the Rabot Formation (~70–200 m, Fig. 2) consists of intensely bioturbated and fossiliferous muddy fine-grained sandstones with hummocky cross-stratification and wave ripples (Marenssi et al., 1992; Martinioni, 1992; Pirrie et al., 1997). Dominant trace fossils are large forms of *Stelloglyphus* isp., *Euflabella singularis* n. isp., *Thalassinoides suevicus* and *Ophiomorpha annulata*. At Redonda Point, the upper interval of interbedded mudstone and sandstone (Fig. 2), preserving at least two horizons with graphoglyptid trace fossils, probably represent distal offshore settings (Olivero et al., 2010; Olivero, 2012).

In the southeastern part of the basin (Figs. 1, 2), the succeeding late Campanian to early Maastrichtian NG Sequence includes a shallowing transition from: 1) offshore mudstones; 2) offshore mudstones and distal tempestites; and 3) regressive, prograding delta-wedges, referred to the Hamilton Point, Sanctuary Cliffs, and Karlsen Cliffs members of Snow Hill Island Formation, respectively (Pirrie et al., 1997; Olivero, 2012).

The Sanctuary Cliff Member, ~200 m of mudstones and sandstones with hummocky cross-stratification, represents

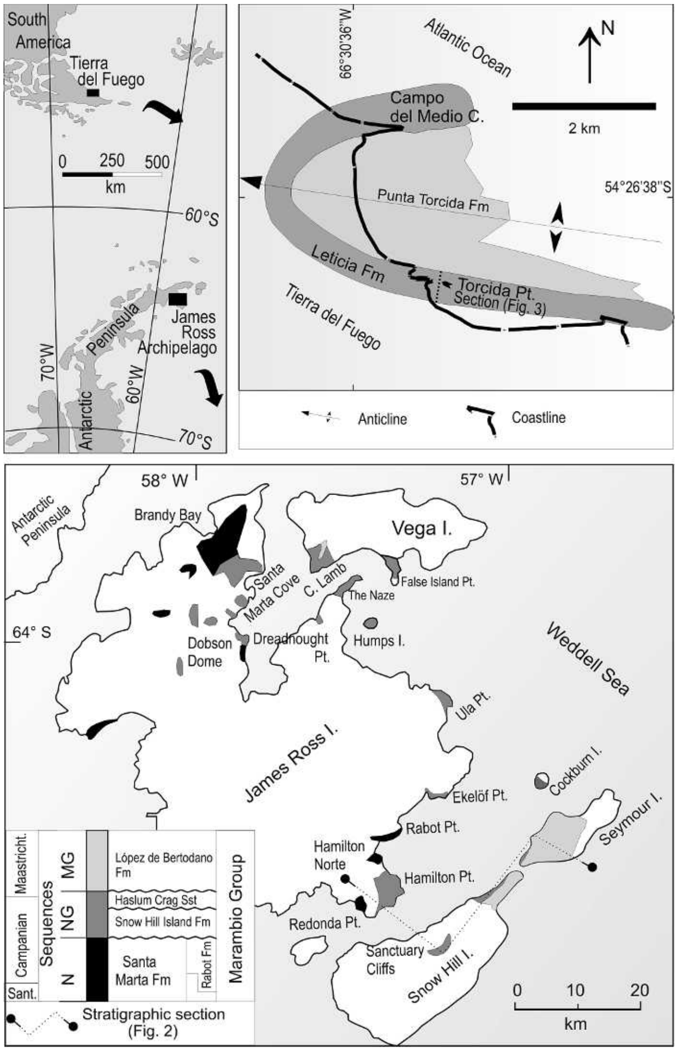

FIGURE 1—Studied areas and geological sketch maps of the James Ross archipelago, Antarctica and the Cabo Campo del Medio anticline, Tierra del Fuego.

sedimentation from suspension in low energy offshore settings and distal tempestites. The muddy fine-grained sandstone interval (~0–30 m; Fig. 2) is intensely bioturbated. Dominant trace fossils are *Euflabella multiplex* n. isp., *Stelloglyphus* isp., *Tasselia ordamensis*, *Ophiomorpha annulata*, and *Phycosiphon incertum*. The rest of the Member preserves thick, intensely bioturbated horizons dominated by *E. multiplex*, *T. ordamensis*, and *Paradictyodora antarctica* (Fig. 2).

The Karlsen Cliffs Member consists of regular alternations of bioturbated mudstone and very fine-grained sandstone beds arranged in coarsening and thickening upward packages, 3–7 m thick, deposited in prograding deltaic lobes (Olivero et al., 2008). The base of these packages contains abundant *Euflabella radiata* n. isp and the rest of the interbedded mudstones and thin sandstones is locally intensely bioturbated. Dominant trace fossils are *Nereites missouriensis*, *Schaubcylindrichnus coronus* (isolated tubes), *Teichichnus rectus*, and *E. radiata*; less common are *Ophiomorpha annulata*, *Tasselia ordamensis*, *Rhizocorallium* isp., *E. singularis*, and *Chondrites* isp. (Fig. 2).

The upper part of the NG Sequence consists of forced regressive, cross-bedded tidal deposits of the Haslum Crag Sandstone, which records the incision, migration, and filling of

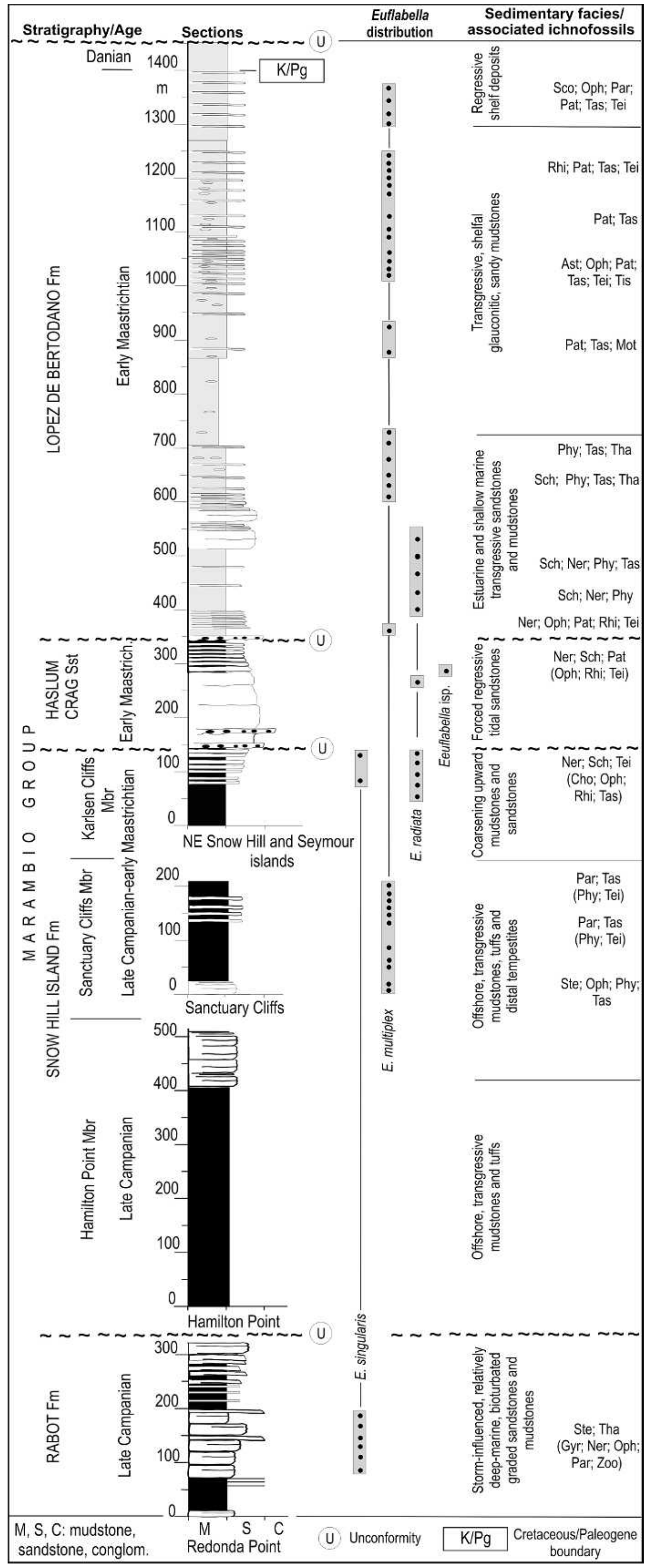

FIGURE 2—Section of the Upper Cretaceous Marambio Group in southeastern James Ross Basin, showing the distribution of *Euflabella* ichnospecies, ichnofossil associations, and sedimentary facies. See *Figure 1* for location and *Figure 3* key for ichnofossils.

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relatively large and deep subtidal channels (Olivero et al., 2008). The upper, fine-grained part of the channel fill is generally strongly bioturbated. Dominant trace fossils are *N. missouriensis*, *Patagonichnus stratiformis*, and *Schaubcylindrichnus* isp.; less common are *Ophiomorpha nodosa, Teichichnus* isp., *Rhizocorallium* isp. and *Nereites biserialis*. *Euflabella* is extremely rare in these deposits (Fig. 2). As a comment in passing, Uchman (1995) included *Neonereites* Seilacher (see Seilacher, 2007) in *Nereites* MacLeay and interpreted *N. biserialis* as a junior synomym of *Nereites missouriensis*. However, the central tunnel of the Antarctic material has the diagnostic double row of fecal pellets of *N. biserialis*. As this feature may be a useful taxobase at the ichnospecific level we provisionally use the combination *Nereites biserialis* to distinguish the Antarctic material from *N. missouriensis*.

In Snow Hill and Seymour islands (Figs. 1, 2) the MG Sequence is represented by the Maastrichtian to Danian López de Bertodano Formation, which includes from base to top: 1) shallow marine and estuarine tidal-channel mudstones and sandstones; 2) transgressive, glauconite-rich sandstones and mudstones; and 3) regressive, mudstones and sandy siltstones (Macellari, 1988; Olivero, 2012; see also Crame et al., 2004).

The basal shallow marine and estuarine tidal-channel deposits rest on a high-relief unconformity deeply incised into the Haslum Crag Sandstone (Pirrie et al., 1997). Trace fossil abundance and composition are highly variable in these deposits, with ichnofossils being more abundant and diverse toward the axial, subtidal portion of the estuary (Olivero et al., 2008). These deposits include large subtidal channels filled with thin alternation of mudstone and muddy very fine-grained sandstones. Dominant trace fossils are *Nereites biserialis*, *Phycosiphon incertum*, *Schaubcylindrichnus coronus*, *Thalassinoides suevicus* and *Euflabella radiata* (Fig. 2).

The basal estuarine deposits grade upward into transgressive, intensely bioturbated and highly fossiliferous, glauconite-rich sandstones and mudstones (Macellari, 1988; Crame et al., 2004; Olivero, 2012). Dominant trace fossils are *Euflabella multiplex*, *Patagonichnus* isp., and *Tasselia ordamensis*. Localized horizons also preserve *Asterosoma* isp., *Ophiomorpha annulata*, *Thalassinoides suevicus*, *Teichichnus rectus*, and *Tissoa* isp. in addition to a dense mottling. The uppermost regressive deposits (Macellari, 1988) preserve a similar trace fossil association, with the addition of localized abundance of *Scolicia prisca* and *Paradictyodora antarctica* (Fig. 2).

Austral Basin, Tierra del Fuego.—Here, the Paleogene marine sandstones and mudstones were deposited in successive foredeeps and satellite basins that developed during the forward propagation of the Fuegian thrust-fold belt. Accordingly, the *Euflabella*-bearing shallow marine and shelfal deposits of the late middle Eocene Leticia Formation reveal complex stratigraphical and structural relationships, interpreted as syntectonic deposits in a wedge-top depozone (Torres Carbonell et al., 2008; Torres Carbonell and Olivero, 2012). At the Atlantic shore of Tierra del Fuego, the Campo del Medio Cape anticline (Fig. 1) shows the best exposures of the Leticia Formation (Fig. 3). Its ~500-m thick deposits represent a transgressive-regressive cycle. It is characterized by basal and upper intervals of shallow marine, channelized sandstones with intervening, totally bioturbated and fossil-rich, very fine-grained shelfal sandstones and mudstones (Olivero and Malumián, 1999). The base of the Leticia Formation rests on a major unconformity in the turbidites of the early Eocene Punta Torcida Formation. Another unconformity separates the top of the Leticia Formation from the turbidites of the late middle to late Eocene Cerro Colorado Formation.

Within the Leticia Formation, the basal part (0–100 m interval; Fig. 3) consists of massive and parallel laminated thick sandstone beds and intercalated thin-bedded heteroliths. Tidal sedimentary structures, such as herringbone cross-stratification, flaser bedding and ripple cross lamination with mud drapes are preserved in some horizons. Within this interval there are few bioturbated horizons densely populated by *Diplocraterion parallelum*, *Asterosoma* isp., *Tasselia ordamensis*, *Gyrochorte comosa*, *Curvolithus simplex* and *Euflabella sinuosa* n. isp. (Fig. 3). Conversely, the middle part of the formation (230–440 m interval; Fig. 3) consists of totally bioturbated silty sandstones. Superimposed on a mottled background, recognizable trace fossils are *Chondrites* isp., *Macaronichnus* isp., *Palaeophycus heberti*, *Planolites montanus*, *Phycosiphon incertum*, *Schaubcylindrichnus coronus*, *Teichichnus rectus*, *Euflabella singularis*, *Ophiomorpha nodosa*, *Asterosoma* isp., and *D. parallelum*. *Euflabella radiata* was only recorded in a single sandstone bed, where it defines a pervasive ichnofabric. The shallow marine, channelized sandstones on top contain horizons with a dense ichnofabric of *Gyrochorte comosa* and *Curvolithus simplex* (López Cabrera et al., 2008).

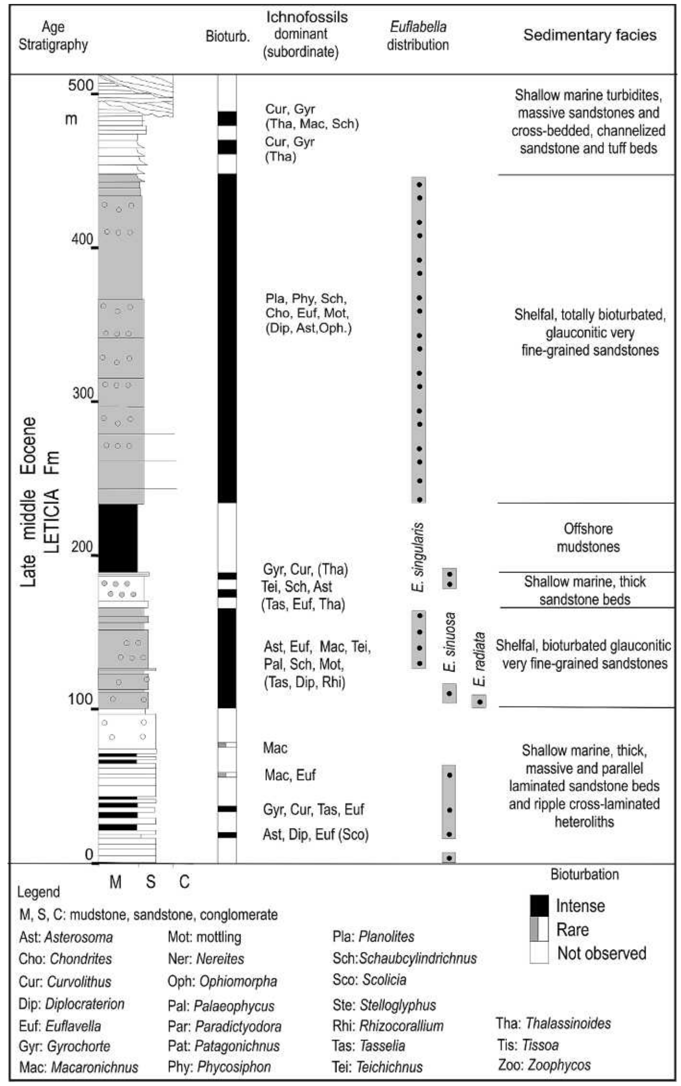

FIGURE 3—Stratigraphic section of the late middle Eocene Leticia Formation at the Cabo Campo del Medio Anticline, showing ichnofossils association, distribution of *Euflabella* ichnospecies, and sedimentary facies. See *Figure 1* for location.

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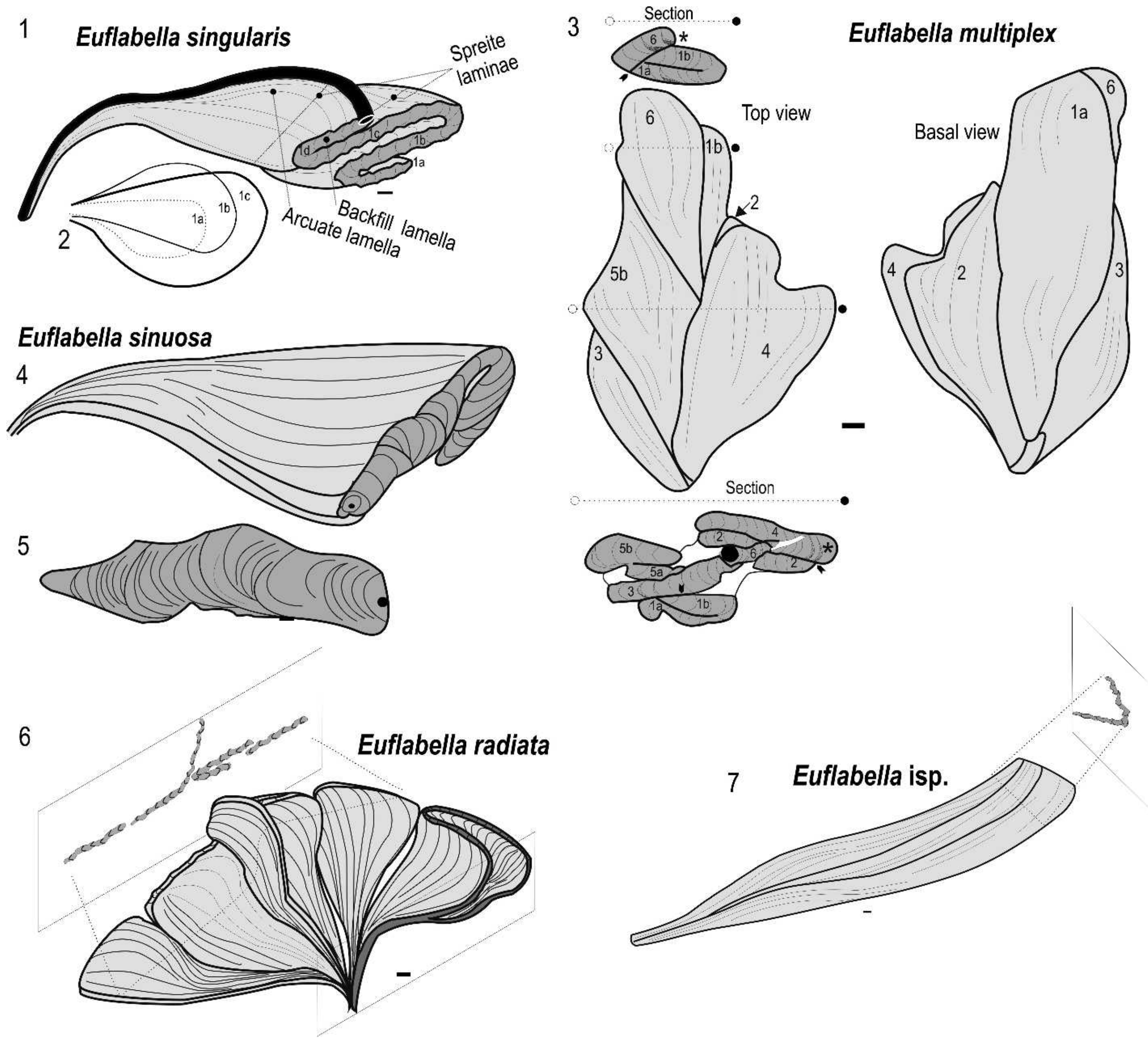


FIGURE 4—Schematic reconstruction of *Euflabella* ichnospecies. *1*, *2*, *Euflabella singularis*: *1*, showing the spreite body, the oblique to subhorizontal folded spreite laminae (1a, b, c, d), the gutter-shaped backfill lamellae, and the generating tube (marked in black); *2*, morphologies and relative sizes of successively superimposed laminae in bedding plane view, lamina 1d not shown for simplicity; *3*, *Euflabella multiplex*, upper bedding plane, vertical, and basal views, showing crosscutting relationships (arrows) among different limbs of folded spreite laminae (1 to 6), note geopetal structures (star symbol); *4*, *5*, *Euflabella sinuosa*: *4*, three- dimensional reconstruction; *5*, vertical cross section of the holotype CADIC PI 239, note changing directions of the spreite lamellae and disproportion between the thickness of the spreite and the diameter of the generating tube (black circle); *6*, *Euflabella radiata*, three- dimensional reconstruction and vertical off-axis and axial cross sections (rectangles); *7*, *Euflabella* isp., three-dimensional reconstruction and cross section. Scale bars=1 cm.

SYSTEMATIC ICHNOLOGY

The material described in this study is deposited in the paleontological collections of the Centro Austral de Investigaciones Científicas (CADIC-CONICET), Ushuaia, Tierra del Fuego, with the numbers CADIC PI 232 to 295.

Ichnogenus EUFLABELLA new ichnogenus

Type ichnospecies.—*Euflabella singularis* n. isp. from the Campanian–Maastrichtian of the James Ross Basin, Antarctica and the upper middle Eocene of the Austral Basin, Tierra del Fuego.

Other ichnospecies.—*Euflabella sinuosa* n. isp., *E. multiplex* n. isp., *E. radiata* n. isp., and *Euflabella* isp.

Diagnosis.—Horizontal to oblique burrows of sediment feeders, consisting of single or multiple spreite bodies arranged in linear or radial patterns. Each spreite body includes palmate spreite laminae with curved or sigmoidal backfill lamellation arising from an oblique to subvertical tube at the base. There may be only a single subhorizontal lamina or several, folded and partially superimposed laminae.

Etymology.—From the Greek *eu*, good, well, and the Latin *flabella*, fan, alluding to the elegant fan-like shape of the trace fossil in bedding plane view.

Remarks.—*Euflabella* n. igen. includes at least five new ichnospecies: *Euflabella singularis*, *E. sinuosa*, *E. multiplex*, *E. radiata* and *Euflabella* isp. (Fig. 4). In spite of their morphological disparity, all these ichnospecies share a common elementary spreite body. It consists of a single spreite lamina or multiple, folded subhorizontal to oblique laminae with straight to sigmoidal spreite lamellae (Fig. 4.1), as in *E. singularis* and *E. sinuosa*. The horizontal repetition of this elementary spreite body in linear or radial patterns produces the complex morphologies exemplified by *E. multiplex* and *E. radiata,* respectively. The growing direction of each lamina within the structure is generally indicated by a change in the geometry of the spreite lamellae. At the starting point, the spreite lamellae are more or less straight and then they change to a sigmoidal or markedly sinuous geometry (Fig. 4.1, 4.2). Preserved in full relief. The folded, subhorizontal laminae are mostly retrusively, rarely protrusively backfilled.

Euflabella n. igen. bears an apparent similarity with a number of ichnogenera, particularly with *Paradictyodora* Olivero, Buatois and Scasso, *Zoophycos* Massalongo, and some oblique forms of teichichnid burrows. This similitude is especially evident in incomplete specimens, particularly when only vertical cross sections are available. However, complete three-dimensional specimens of *Euflabella* are unique by the orientation and geometry of the burrow, as discussed in the ichnospecific descriptions.

Euflabella singularis new ichnospecies
Figures 4.1, 4.2, 5

Diagnosis.—*Euflabella* with a single spreite body consisting of commonly folded, subhorizontal to slightly oblique laminae. The generating tube has a similar diameter as the corresponding spreite.

Description.—Basically the burrow consists of several, commonly two to three, vertically superimposed and folded horizontal to oblique spreite laminae, which diverge from a common tube at the lower end and expand laterally at the distal side. Rarely the burrow has only a single or more than three laminae. At the point of lateral divergence, the laminae continue downward in a subcircular, oblique to subvertical tube. The laminae are 9 to 20 cm in length, 5 to 10 cm in width, and 0.5 to 1 cm in thickness.

In horizontal view, the margin of each lamina and the accompanying spreite lamellae is first straight, then gradually becomes more arcuate and finally develops a sigmoidal shape (Figs. 4.1, 4.2, 5.1, 5.2, 5.4, 5.6). In vertical view, the superimposed spreite lamellae with transversal back-fill generally indicate a retrusive (i.e., upwardly directed construction). In the last, uppermost lamina the generating tube is generally preserved. Its diameter is similar to the thickness of the spreite (Fig. 5.3, 5.5, 5.7).

Euflabella singularis is preferentially found in fine-grained sandstone and silty sandstone beds. The spreite material is the same as of the host sediment, but it is selectively sorted with the bulk consisting of alternating, curved layers of silt and very fine-grained sand particles. In contrast to the host sediment, minute aggregates of pyrite, as well as carbonized plant debris, are relatively abundant in the backfilled material, which tends to be darker in fresh cuts and lighter in weathered surfaces (Fig. 5).

Etymology.—From the Latin *singularis*, alone, a single object. It refers to the single spreite body that characterizes this trace fossil.

Types.—Holotype CADIC PI 232 (Fig. 5.1, 5.2) and paratype CADIC PI 235 (Fig. 5.4, 5.5) from the upper Campanian Rabot Formation, Redonda Point, James Ross Island, Antarctica.

Occurrence.—In addition to the type material, other examined specimens include: specimens CADIC PI 233–234, 235a and more than 100 specimens studied in the field from the Rabot Formation, upper Campanian, Redonda Point, James Ross Island, Antarctica; specimens CADIC PI 236; 237a, b, c and many specimens studied in the field from the Karlsen Cliffs Member of the Snow Hill Island Formation, lower Maastrichtian, Snow Hill Island, Antarctica; and specimens CADIC PI 238 and more than 50 specimens studied in the field from the Leticia Formation, upper middle Eocene, Austral Basin, Tierra del Fuego.

Remarks.—In bedding plane view, partial preservation of distal laminae with sigmoidal or strongly curved spreite lamellae (e.g., Fig. 5.2), as well as vertical cross sections of incomplete laminae, may be confused with some forms of *Zoophycos*. The folded laminae of *Euflabella*, however, are never present in *Zoophycos*. Loose specimens of *Euflabella singularis* may be confused with *Paradictyodora antarctica* (Olivero et al., 2004), but the latter is a vertical spreite burrow and the whole structure has a more squarish outline.

The oblique, basal part of *E. singularis* (e.g., the basal part of the holotype) (Fig. 5.1), may bear a distant resemblance with some oblique teichichinid burrows, such as *Teichichnus* isp. (oblique form) described by Frey and Howard (1985). They can be readily distinguished, however, by opposite trends in the shape of the spreite. In *E. singularis* (e.g., Figs. 4.1, 4.2, 5) the initial spreite lamellae are straight or slightly curved and change afterward to strongly sigmoidal or sinuous, in contrast to the oblique teichichnid burrow.

Euflabella sinuosa new ichnospecies
Figures 4.4, 4.5, 6, 7.1

Diagnosis.—*Euflabella* with a single spreite body bearing mainly subhorizontal and commonly folded laminae with sinuous spreite lamellae. The diameter of the generating tube is much smaller than the thickness of the corresponding spreite.

Description.—The basic morphology of the burrow is similar to that of *E. singularis*, but the thickness of each lamina is disproportionally larger than that of the generating tube. In addition, the spreite lamellae are arranged in irregular subsets of varying sizes and changing directions. Laminae are generally 15 to 30 cm in length, 10 to 15 cm in width, and 2 to 5 cm in thickness. When preserved, the corresponding generating tube is only about 0.5 cm thick.

On bedding planes, the surface of the trace may bear longitudinal striae (Fig. 6.1, 6.2) caused by minor folds of the spreite. In some specimens, the host rock around the upper part of the structure is also markedly deformed (Figs. 6.4, 6.6, 7.1). In vertical view, the superimposition of spreite laminae indicates an upward sequence. *E. sinuosa* occurs in full relief in fine-grained sandstones with micrite matrix. The backfill of the spreite lamellae consists of alternating sandy and micritic layers, the latter containing calcispheres, diatoms, foraminifera, and minute carbonized plant fragments (Fig. 6.5). Pyrite is also relatively abundant in the micritic lamellae. The vertically superimposed laminae are tightly folded with the upper limb reworking up to half of the thickness of the previous lamina (Figs. 6.4, 7.1)

Etymology.—From the Latin *sinuosa*, having many curves and turns. It refers to the many bends of the spreite lamellae that characterize this trace fossil.

Types.—Holotype CADIC PI 239 (Figs. 4.5, 6.1, 6.2) and paratypes CADIC PI 240–241 from the upper middle Eocene Leticia Formation, Tierra del Fuego, Austral Basin, Argentina.

Occurrence.—In addition to the type material, other examined specimens include CADIC PI 242–246 and more than 50 specimens studied in the field, from the Leticia Formation, upper middle Eocene, Tierra del Fuego.

Remarks.—In bedding planes (e.g., Fig. 6.3), the horizontal spreite laminae may resemble some forms of *Zoophycos*. In vertical cross sections, the bending and varying sizes of the spreite lamellae may also be confused with the backfill lamellae of *Teichichnus zigzag* Frey and Bromley, 1985. However, the vertical folding of the spreite readily differentiates *E. sinuosa* from *Zoophycos*, and *T. zigzag* does not have the folded laminae of *E. sinuosa*. The longitudinal striations on the surface of *E.*

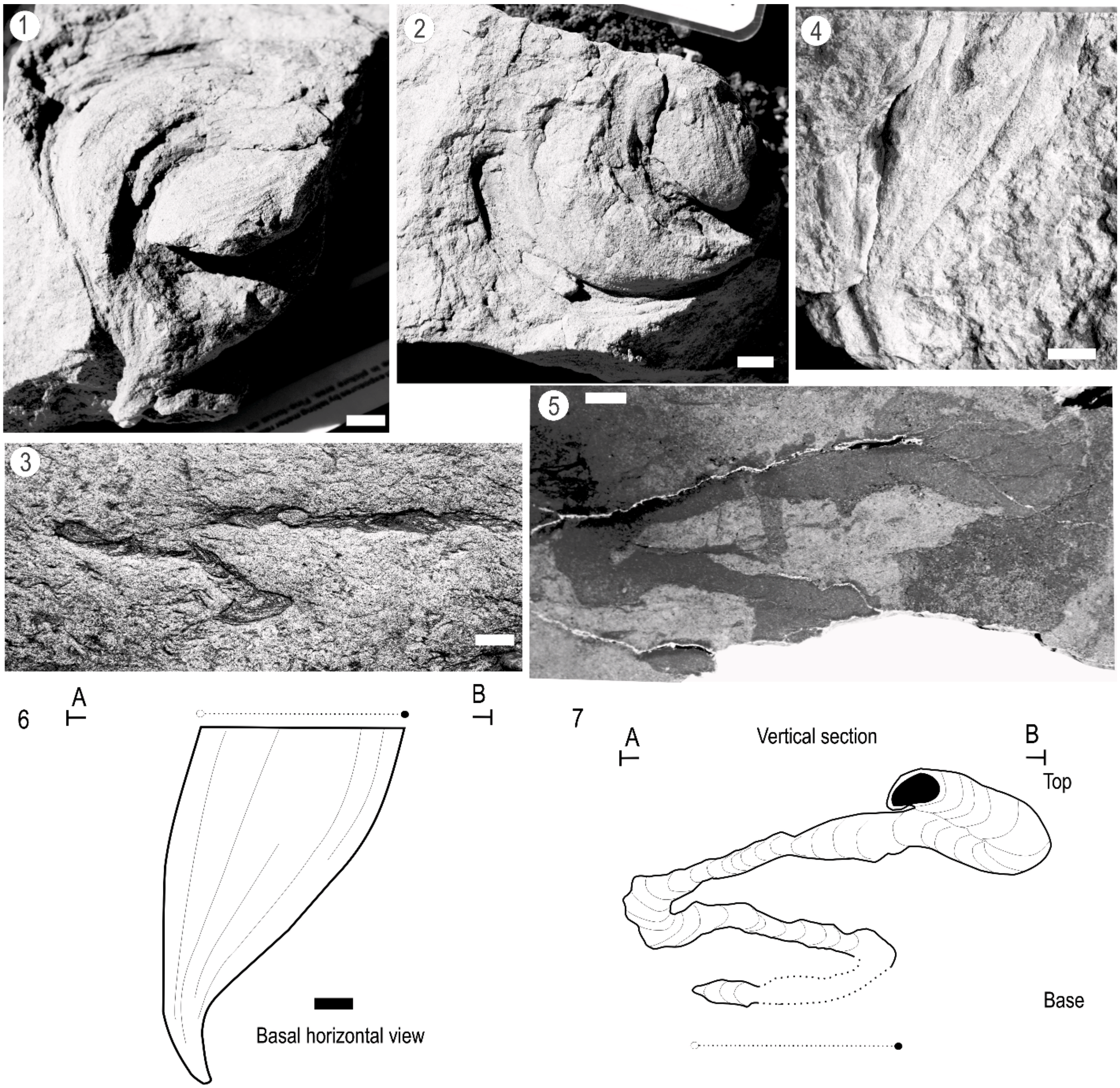


FIGURE 5—*Euflabella singularis. 1*, *2*, holotype CADIC PI 232: *1*, vertical to oblique view; *2*, bedding plane view, Rabot Formation, Punta Redonda, James Ross Island, Antarctica; *3*, vertical cross section showing three folded laminae, field specimen, late middle Eocene, Leticia Formation, Tierra del Fuego; *4–7*, paratype CADIC PI 235: *4*, *6*, basal bedding plane view and reconstruction; *5*, *7*, polished vertical cross section and reconstruction, Rabot Formation, Punta Redonda, James Ross Island, Antarctica. Scale bars=1 cm.

sinuosa are similar to those of the *Asterosoma* von Otto; but they lack the radial cracks of the latter.

EUFLABELLA MULTIPLEX new ichnospecies
Figures 4.3, 7.2–7.6, 8

Diagnosis.—*Euflabella* composed of multiple elementary spreite bodies arranged in linear patterns and with single or folded subhorizontal spreite laminae. Spreite laminae intercut older ones.

Description.—Adjacent, successive elementary spreite bodies with single or folded laminae are commonly arranged in a divergent pattern, with the longest axis of each set forming an acute angle as in the holotype. The mainly linear backfilling results from the addition of successive pairs of these divergent spreite bodies away from their common origin, i.e., protrusively (Figs. 4.3, 7.2–7.5, 8.1–8.4). Besides this elegant divergent pattern, there are specimens that enlarge the structure by adding successive spreite bodies one in front of the other, with markedly curved distal culminations (Figs. 7.4, 7.5, 8.6, 8.7). In other specimens, the spreite bodies are nearly parallel and progressively added side by side (Figs. 7.6, 8.9). Dimensions of the whole structure vary from about 10 to 25 cm in length, 4 to 10 cm in width, 1 to 2 cm in thickness, while the final tubes are only 0.8 to

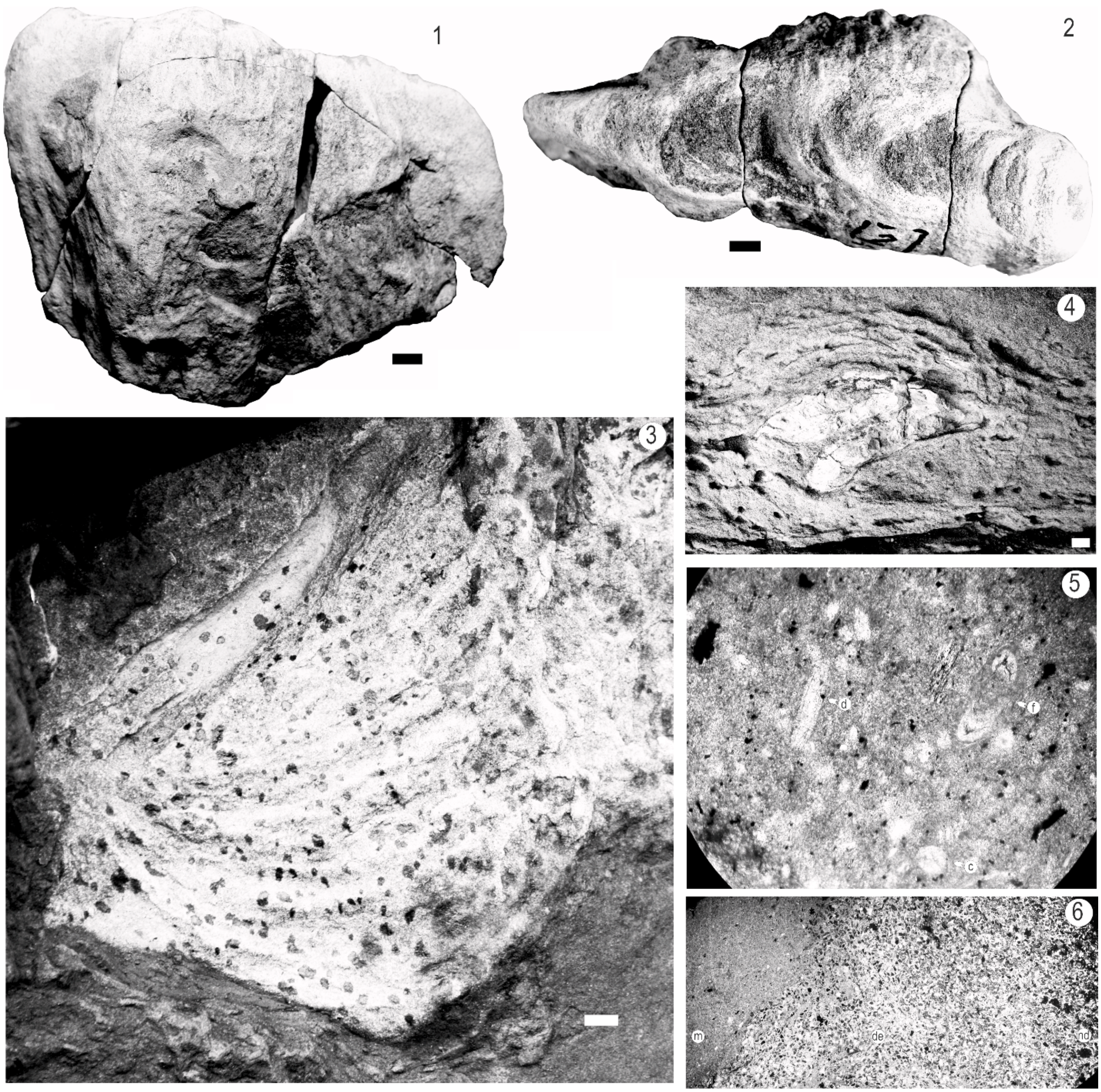


FIGURE 6—*Euflabella sinuosa* from the late middle Eocene, Leticia Formation, Tierra del Fuego. *1*, *2*, holotype CADIC PI 239: *1*, upper bedding plane view; *2*, cross section; *3*, upper bedding plane view of a field specimen; *4*, vertical section of a field specimen, note bedding deformation of host sediment; *5*, *6*, thin sections of specimen CADIC PI 242: *5*, microfossil-rich micrite layer of the spreite lamellae diatom length ∼0.2 mm; *6*, contact between the micrite spreite layer and host rock, showing deformed and non-deformed zones, largest sand grains in the host rocks ∼0.2 mm. Scale bars=1 cm. Abbreviations: f=foraminifer; d=diatom; c=calcisphere; m=micrite spreite layer; de=deformed zone; nd=non-deformed zones.

1.5 cm in diameter. The total length of the holotype is about 20 cm.

The folded spreite laminae are vertically piled; in the holotype there are at least six of them. In vertical cross section, geopetal backfill and mutual cross-cutting relationships indicate that the structure grew in an upward direction, i.e., retrusively. All of the intercutting relationships and reworking of previous laminae is systematic and occurs between successive arms of the same spreite as well as between different ones (Figs. 4.3, 7.2, 7.3, 7.5, 8.2, 8.5).

Euflabella multiplex is preserved as full relief in sandy mudstones with micritic matrix. The transversal back-fill lamellae consist of alternating layers of micrite and very fine-grained sand particles. The micrite layers generally preserve abundant pyrite, forams and calcispheres (Fig. 8.8). Commonly, other trace fossils (including *Phycosiphon incertum*, *Patagonichnus* isp., *Teichichnus rectus*, and *Paradictyodora antarctica*) cross-cut and in cases almost wipe out *E. multiplex* (Figs. 7.2, 7.3, 8.7, 8.10).

Etymology.—From the Latin *multiplex*, manifold, composed of

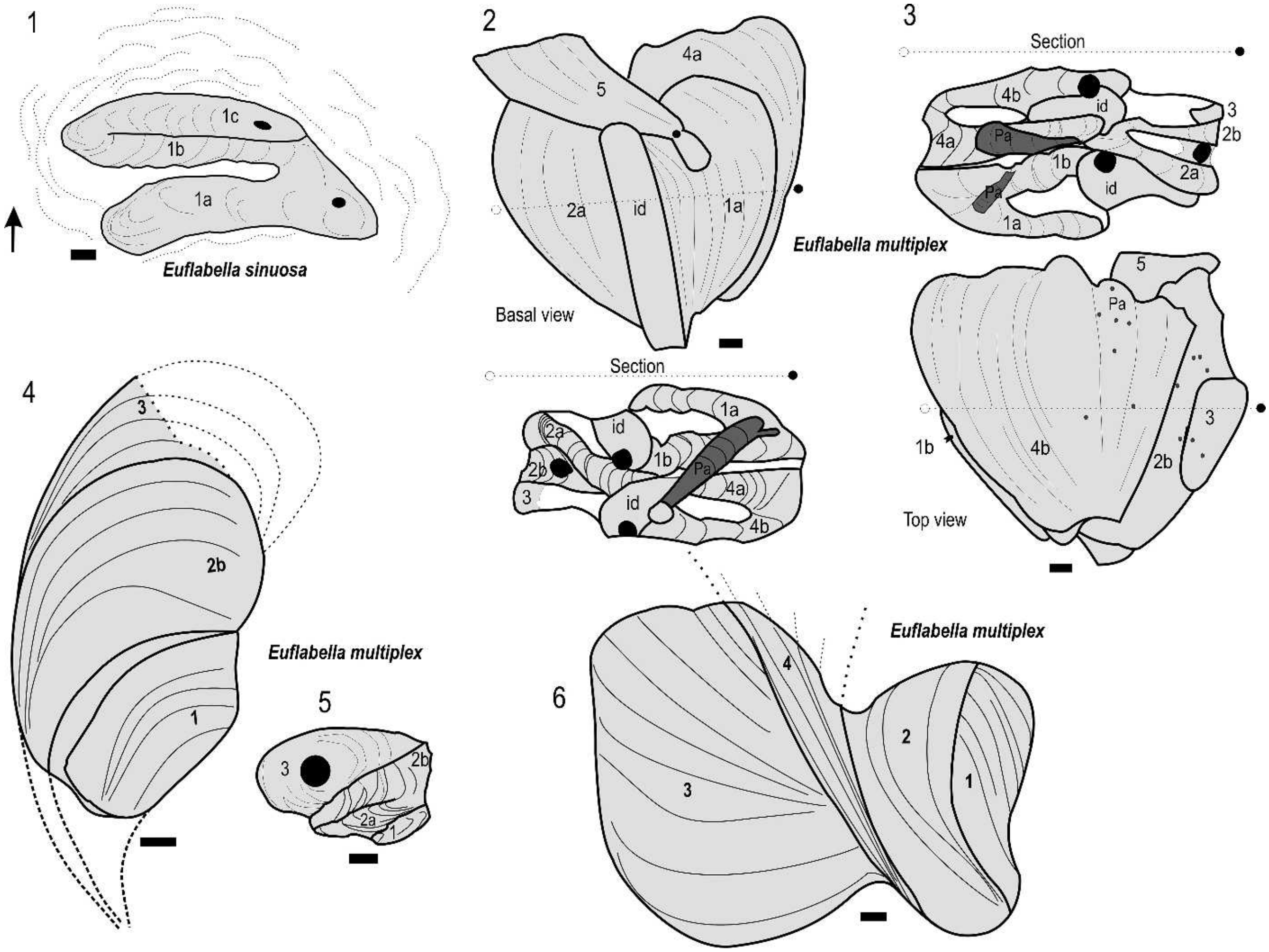


FIGURE 7—Internal structures in *E. sinuosa* and *E. multiplex*. *1*, *E. sinuosa* illustrated in *Figure 6.4*, note retrusive character and reworked middle limb (1b); *2*, *3*, *E. multiplex*, basal and upper bedding plane views with sections, note reworking of older laminae by later ones (id) as well as by other ichnofossils (Pa=*Patagonichnus* isp.), specimen CADIC PI 248, López de Bertodano Formation, Seymour Island, Antarctica; *4*, *5*, *E. multiplex*, late Campanian, Sanctuary Cliffs Member, Snow Hill Island Formation, Sanctuary Cliffs, Antarctica; *4*, upper bedding plane view showing enlargement by successive frontal addition of new spreite bodies, CADIC PI 250; *5*, vertical cross section of a similar specimen, CADIC PI 253; *6*, *E. multiplex*, upper bedding plane view showing enlargement by successive side by side addition of new spreite bodies, specimen CADIC PI 252, upper Maastrichtian, López de Bertodano Formation, Seymour Island, Antarctica. Scale bars=1 cm.

many individuals or elements, alluding to the multiple spreite bodies that characterize this ichnospecies.

Types.—Holotype CADIC PI 247 (Figs. 4.3, 8.1–8.3), paratypes CADIC PI 248 (Fig. 7.2, 7.3) and CADIC PI 249, 252 (Figs.7.6, 8.9) from the upper Maastrichtian of the López de Bertodano Formation, Seymour Island, Antarctica, and CADIC PI 250 (Fig. 7.4), 251 (Fig. 8.7), 253 (Fig. 7.5) from the late Campanian, Sanctuary Cliffs Member of the Snow Hill Island Formation, Snow Hill Island, Antarctica.

Occurrence.—In addition to the type material, other examined specimens from the James Ross Basin, Antarctica are CADIC PI 254–273. Moreover, more than 100 specimens have been studied in the López de Bertodano Formation (Maastrichtian); CADIC PI 274–290 and more than 70 specimens studied in the field come from the Sanctuary Cliffs Member of the Snow Hill Island Formation (upper Campanian of Snow Hill Island); and CADIC PI 291–292 come from the Maastrichtian Karlsen Cliffs Member of the Snow Hill Island Formation, Snow Hill Island.

Remarks.—The repetition of spreite bodies, arranged in divergent, side by side or one in front of the other patterns result in different morphologies in bedding plane view. But these patterns are transitional and co-occur in the same bed. Thus they are all included in the same ichnospecies.

When fully preserved, *E. multiplex* is highly distinctive. If only part of the structure is available, the diagnostic features can be recognized in bedding plane view by discordant spreiten (Fig. 8.9) and in vertical cross section by intercutting of the laminae (Figs. 4.3, 7.2, 7.3, 7.5, 8.2, 8.5).

EUFLABELLA RADIATA new ichnospecies
Figures 4.6, 9

2001 *Zoophycos* isp.; OLIVERO and LÓPEZ CABRERA, p. 62 (part.)

2008 *Paradictyodora* isp., conical form; OLIVERO, PONCE, and MARTINIONI, p. 15

Diagnosis.—*Euflabella* composed of multiple elementary spreite bodies arranged in a radial pattern and with single or folded, subhorizontal to oblique spreite laminae.

Description.—The trace fossil is characterized by crowded, radially arranged spreite bodies, present in variable numbers, from two or three to many more, covering half to almost a whole circle. All of them radiate from a common center and in variable dispositions. Commonly, the initial part of the spreite is oriented oblique to subvertical and then changes to subhorizontal, followed again by an oblique tip. Other specimens show a more horizontal orientation throughout. The radial elements spread mostly in a single plane; rarely are they disposed in two different levels. In all observed specimens the radial elements follow either a dextral (e.g., Fig. 9.1, 9.2) or a sinistral (e.g., Fig. 9.4, 9.5) growth; but this direction is always uniform within a single specimen.

Etymology.—From Latin *radiata*, radiating from a center.

Types.—As complete Antarctic specimens are almost impossible to retrieve due to the friable nature of the host rock, the field specimen illustrated in Figure 9.2 has been chosen as the holotype. The partially recovered specimens CADIC PI 293 (Fig. 9.3) and CADIC PI 294–295 are designated paratypes. The type material is from the Karlsen Cliffs Member of the Snow Hill Island Formation, lower Maastrichtian, Snow Hill Island, Antarctica.

Occurrence.—In addition to the type material, more than 100 specimens were studied in the field within the Karlsen Cliffs Member of the Snow Hill Island Formation; a few specimens come from the Haslum Crag Sandstone (lower Maastrichtian), Snow Hill Island, Antarctica; about 25 specimens from the Maastrichtian López de Bertodano Formation from Snow Hill and Seymour islands; and many specimens from the Leticia Formation (upper middle Eocene), Tierra del Fuego, Argentina.

Remarks.—In bedding plane view, specimens in which radiating spreite bodies fill almost a whole circle may resemble *Zoophycos* and particularly *Spirophyton*. The cup-shaped spreite laminae of *Spirophyton*, however, are continuously lamellated in the horizontal plane and are piled up in a corkscrew (e.g., Seilacher, 2007, pl. 39) instead of being composed of several spreite laminae at a single level. The upper middle Eocene specimens from the Leticia Formation, previously classified as *Zoophycos* isp. (Olivero and López Cabrera, 2001) and now ascribed to *E. radiata* (Fig. 9.5), illustrate this point.

Partial, off-axis vertical sections of *E. radiata* may be difficult to distinguish from similarly oriented sections of conical forms of *Paradictyodora antarctica*. However, axial vertical sections of *E. radiata* are very distinctive and can be recognized by the characteristic folded laminae (Figs. 4.6, 9.6). Furthermore, in bedding plane view the multiple, adjacent radial spreite bodies of *E. radiata* are very diagnostic.

Euflabella radiata commonly occurs in high density in a single fine-grained sandstone bed and the resulting ichnofabric is very characteristic (Fig. 9.1).

EUFLABELLA isp.
Figures 4.7, 10

Description.—Large, elongate, complex spreite structure consisting of two folded laminae with an open V-shaped cross section (Fig. 4.7). The lamellae originate from a central point at the base of the structure and spread distally with an oblique orientation to the bedding plane. Each lamina shows a complex pattern, consisting of imbricated packages of sigmoidal lamellae, the thickest part of which alternates between proximal and distal positions in successive sigmoidal packages. The structure grows upward (i.e., retrusively) and the oblique laminae are about 65 cm long and 9 cm wide.

Occurrence.—Two field specimens from the Haslum Crag Sandstone, Maastrichtian, Snow Hill Island, Antarctica.

Remarks.—Only two specimens were observed, but this paucity may be related to the exceptional conditions required to preserve such a large structure in the relatively friable Haslum Crag Sandstone. At first glance, *Euflabella* isp. may be compared with the large teichichnid burrow referred to as *Teichichnus sigmoidalis* by Seilacher (2007, plate 41, p. 121). However, in *Euflabella* isp. there are at least two folded laminae, the structure is retrusive, and the sigmoidal packages are imbricated in a complex pattern. None of these features are present in *T. sigmoidalis*, thus the Antarctic material is considered as a different ichnospecies of *Euflabella*.

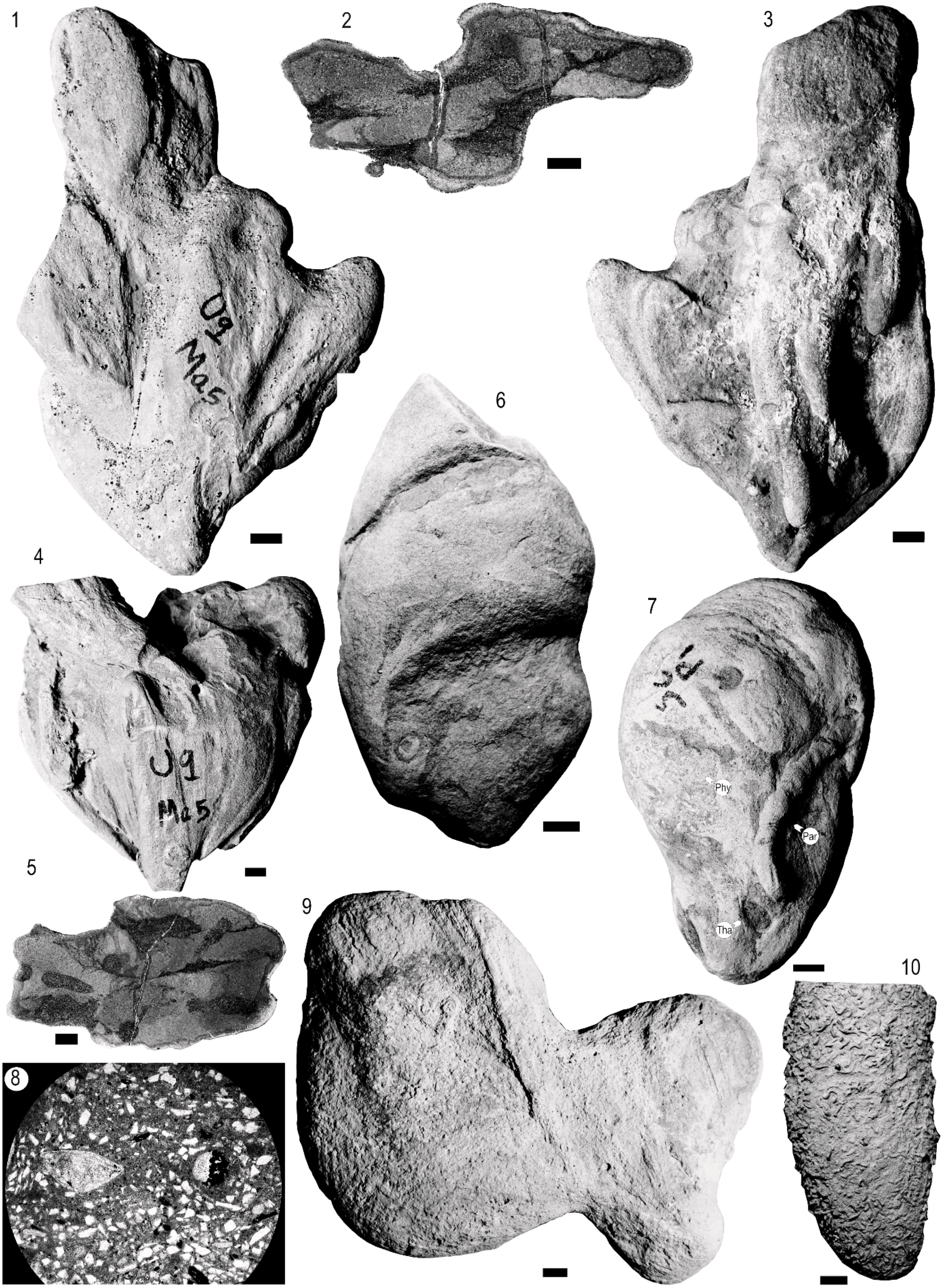
CONSTRUCTIONAL MORPHOLOGY AND ETHOLOGY

The complex pattern of subhorizontal, folded spreite laminae of *Euflabella* is interpreted to result from a combined translation and backfill of an elongated, cylindrical generating tube, including 1) horizontal displacement; 2) short U-turns in the vertical plane; and 3) transversal backfill. The lower end of the generating tube was subvertical, whereas the upper end was more or less parallel to bedding. While the lower end remained fixed in the sediment, the rest of the generating tube first moved along the bedding plane, then made a short retrusive U-turn in the vertical plane to finally re-start a new horizontal displacement in the opposite direction. As a consequence of this back and forth horizontal movement and the combined U-turns, the spreite of *Euflabella* was built (Fig. 4.1).

The complex backfill structure suggests that *Euflabella* is a dwelling-feeding burrow, i.e., a fodinichnion produced either by an elongated worm-like organism or by the elongated organ of some other invertebrate, which systematically mined the sediments searching for food. In this regards, it is interesting to note that the similar, but vertically oriented, spreite of *Tursia flabelliforme* D'Alessandro and Fürsich, 2005 has been interpreted as produced either by the siphon of a tellinid bivalve or a worm-like organism, such as *Arenicola* (D'Alessandro and Fürsich, 2005). Subsequently, Serpagli et al. (2008) considered *Tursia* as a synonym of *Paradictyodora* and found compelling evidence that *T. flabelliforme* was probably produced by a tellinid bivalve. In their specimens, from the Pliocene of the Northern Apennines, a tubular structure preserved at one end of the spreite is interpreted as the fossilized impression of the exhalant siphon, whereas the rest of the spreite was interpreted as resulting from the movement of the inhalant siphon (Serpagli et al., 2008). Nonetheless, the systematic and regular mining program, which results in the complex horizontal spreite structures of *Euflabella* rule out a tellinid bivalve as the tracemaker. In addition, the vertically meandering fan structure of *Tursia flabelliforme* is never regular and its lamellar structure is only occasionally preserved (D'Alessandro and Fürsich, 2005). This is in marked contrast with the regular and well-defined vertical spreite observed in the type material of *Paradictyodora* (cf. Olivero et al., 2004). Hence, *Tursia* and *Paradictyodora* can still be considered as separated ichnogenera.

Though the complex spreite of *Euflabella* clearly points to a fodichnion, there are some variations in the general bauplan that may be related to particular feeding strategies. The bauplans of different *Euflabella* ichnospecies are mainly expressed by different phobotactic (see Raup and Seilacher, 1969) behaviors. Thus, whereas the construction of the successive folded laminae in *E. singularis* and *E. radiata* follows a positive phobotactic behavior (i.e., younger laminae never cross-cut previous ones) the opposite is the rule in *E. multiplex* and *E. sinuosa*.

In *E. singularis* and *E. radiata*, the composition of the backfill in the spreite is similar to that of the host rock (e.g., Fig. 5.3), suggesting that both traces were produced by deposit-feeding organisms that sorted out the sediments, ingesting the organic-rich material adhering to the fine-grained particles and backfilling the rejected coarsest particles.



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In *E. sinuosa* and *E. multiplex* the material backfilled in the spreite is partly similar to the host rock; but it also includes a dense aggregation of diatoms, foraminifers, and calcispheres, which are not evident in the host rock (Figs. 6.5, 8.8). They are a secondary addition; i.e., the tracemakers of *E. sinuosa* and *E. multiplex* fed on host sediments as well as on microorganisms and detritus from the surface. The systematic reworking of previous backfill is a striking feature, particularly in *E. multiplex* where the upper parts of previous laminae have been extensively reworked (Figs. 4.3, 7.2, 7.3, 7.5). We interpret this as a king of gardening, in which bacteria were cultivated in the upper part of each lamina. The site-selectivity of the reworked area, which is restricted to the upper part of older laminae makes autocoprophagy, as envisaged in the cache model for *Zoophycos* (Bromley, 1991), very unlikely in *Euflabella*. A similar feeding strategy, combining deposit feeding, surface detritus feeding, and bacterial gardening has postulated for *Tasselia ordamensis* De Heinzelin (Olivero and López Cabrera, 2010), which is commonly associated with *E. sinuosa* in Tierra del Fuego (Fig. 3) and with *E. multiplex* in Antarctica (Fig. 2).

PALEOENVIRONMENTAL DISTRIBUTION

In the Marambio Group, Antarctica, and the Leticia Formation, Tierra del Fuego, *Euflabella singularis*, *E. multiplex*, and *E. radiata* are found in shelfal fine-grained silty sandstones deposited under relatively low-energy conditions. In contrast, *Euflabella* is absent or very rare in relatively higher-energy settings, such as channeled tidal deposits of the Haslum Crag Sandstone or the upper part of the Leticia Formation (Figs. 2, 3).

Euflabella singularis is generally abundant in organic-rich, shelfal storm-influenced to offshore deposits. Associated ichnofossils are dwelling-feeding and grazing structures (Figs. 2, 3). *Euflabella multiplex* is very abundant in the transgressive offshore mudstones and distal thin-bedded tempestites of the Sanctuary Cliffs Member and the López de Bertodano Formation, where it is commonly associated in the same bed with *Tasselia ordamensis* (Fig. 2). *Euflabella radiata* is dominant in event shelfal fine-grained sandstones (Figs. 3, 9.5) or at the base of prodelta parasequences (Figs. 2, 9.1–9.3; see Olivero et al., 2008). Locally, it is also found in prodelta, thin-bedded alternations of silty sandstones and mudstones in the Karlsen Cliffs Member or in distal subtidal settings of the López de Bertodano Formation (Fig. 2).

Integrated ichnological and sedimentological data (Macellari, 1988; Olivero et al., 2008; Olivero, 2012; this study) indicate that *Euflabella singularis*, *E. multiplex*, and *E. radiata* are typical elements of the *Cruziana* ichnofacies. The associated trace fossils (Figs. 2, 3) generally characterize offshore to lower shoreface successions elsewhere in the world (e.g., MacEachern and Pemberton, 1992; Pemberton et al., 1992; Buatois and Mángano, 2011).

In contrast to the other ichnospecies, E. *sinuosa* is found in different sedimentary facies, consisting of massive or parallel laminated thick sandstone beds with localized horizons of heteroliths, current ripples and herringbone cross-stratification. The latter bear a low-diversity ichnofauna that represent a mixing of different ethologies (Fig. 3), including domichnia (*Diplocraterion*), fodinichnia (*Asterosoma*), traces of motile carnivourous/scavenging (*Curvolithus*), deposit feeders (*Gyrochorte*) and trophic generalists (*E. sinuosa*, *Tasselia*). In addition to the sedimentary facies, the general low degree of bioturbation and mixing of elements of the *Skolithos* ichnofacies and impoverished *Cruziana* ichnofacies suggest rather stressed environments in shallow subtidal, sand-rich settings (cf. Buatois and Mángano, 2011 and the bibliography therein).

CONCLUSIONS

Euflabella n. igen. is established for a group of very distinctive zoophycid feeding burrows in the Upper Cretaceous and Eocene shelf deposits of Antarctica and Tierra del Fuego. *Euflabella* consists of single or multiple spreite bodies arranged in linear or radial patterns. Each spreite body includes folded spreite laminae with curved or sigmoidal backfill lamellation arising from an oblique to subvertical tube at the base. Five new ichnospecies of *Euflabella* are distinguished: *E. singularis* has a single spreite body consisting of commonly folded, subhorizontal to slightly oblique laminae; *E. sinuosa* also has a single spreite body, but it bears sinuous spreite lamellae, which are disproportionally thicker than the size of the generating tube; *E. multiplex* and *E. radiata* consist of multiple elementary spreite bodies, but with different spatial arrangements being linear in the former and radial in the latter; and *Euflabella* isp. is a poorly represented large structure with imbricate bundles of sigmoidal spreite lamellae.

The complex structure of *Euflabella* results from the lateral dislocation and backfill of a cylindrical generating tube, including: 1) horizontal displacement; 2) short vertical U-turns; and 3) transversal backfill. The lower end of the generating tube was subvertical, whereas the upper end was more or less parallel to bedding. While the lower end remained fixed, most of the generating tube first moved along the bedding plane, then made a short retrusive vertical U-turn and finally started a new horizontal displacement in the opposite direction. As a consequence of this back and forth horizontal movement and the combined vertical U-turns, the spreite lamina of *Euflabella* was built.

Euflabella is certainly a fodinichnion; however, variations expressed by phobotactic behavior and composition of the filling material, indicate multiple feeding strategies. Whereas *E. singularis* and *E. radiata* are positively phobotactic, i.e., younger laminae never cross-cut previous ones, the opposite is the rule in *E. multiplex* and *E. sinuosa*. The systematic reworking of previous laminae probably reflects gardening, with the upper part of each lamina being used to culture bacteria. Also, the backfill of *E. multiplex* and *E. sinuosa* contains many diatoms, forams, and calcispheres, which much less common in the host rock. This suggests that the tracemakers of *E. sinuosa* and *E. multiplex* fed also on microorganisms deposited as detritus at the sediment surface. Both the producer of *Euflabella sinuosa* and *E. multiplex*, appear to represent trophic generalists, adapted for deposit feeding, surface detritus

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FIGURE 8—*Euflabella multiplex*. *1–3*, holotype CADIC PI 247: *1*, upper bedding plane view; *2*, vertical cross section (see *Figure 4.3*); *3*, basal view, Maastrichtian, López de Bertodano Formation, Seymour Island, Antarctica; *4*, *5*: lower side and inverted cross section (see *Figure 7.2*); CADIC PI 248, Maastrichtian, López de Bertodano Formation, Seymour Island, Antarctica; *6*, *7*, upper side, bedding plane view: *6*, CADIC PI 250; *7*, CADIC PI 251, note intersection by *Thalassinoides* (Tha), *Paradictyodora* (Par), and *Phycosiphon* (Phy); Sanctuary Cliffs Member, Snow Hill Island Formation, Upper Campanian, Sanctuary Cliffs, Antarctica; *8*, thin section of micrite spreite lamella enriched in silt-grains, foraminifers and calcispheres partly coated by pyrite (diameter of calcispherule 0.24 mm), CADIC PI 256, López de Bertodano Formation, Maastrichtian, Seymour Island, Antarctica; *9*, *10*, upper side, bedding plane view; *9*, CADIC PI 252; 10, CADIC PI 254, almost totally reworked by *Phycosiphon incertum*; López de Bertodano Formation, Maastrichtian, Seymour Island, Antarctica. Scale bars=1 cm.

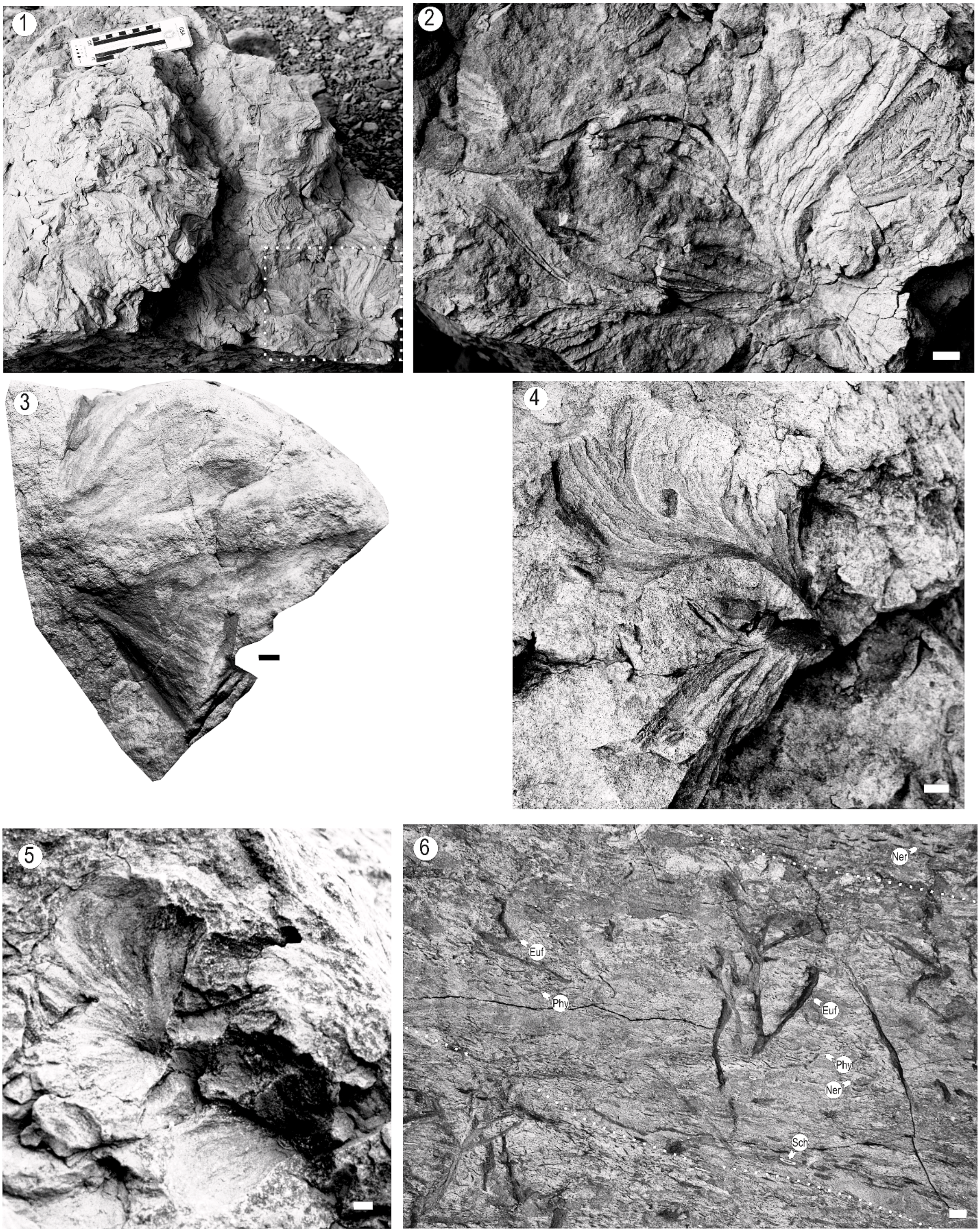

FIGURE 9—*Euflabella radiata*. *1*, *2*, upper side of field specimens, in bedding plane view: *1*, large slab showing the typical *E. radiata* ichnofabric; *2*, close-up of the holotype, Maastrichtian, Karlsen Cliffs Member, Snow Hill Island Formation, Snow Hill Island, Antarctica; *3*, basal view of paratype CADIC PI 293, Maastrichtian, Karlsen Cliffs Member, Snow Hill Island Formation, Snow Hill Island, Antarctica; *4*, field specimen, upper side, Maastrichtian, Karlsen Cliffs

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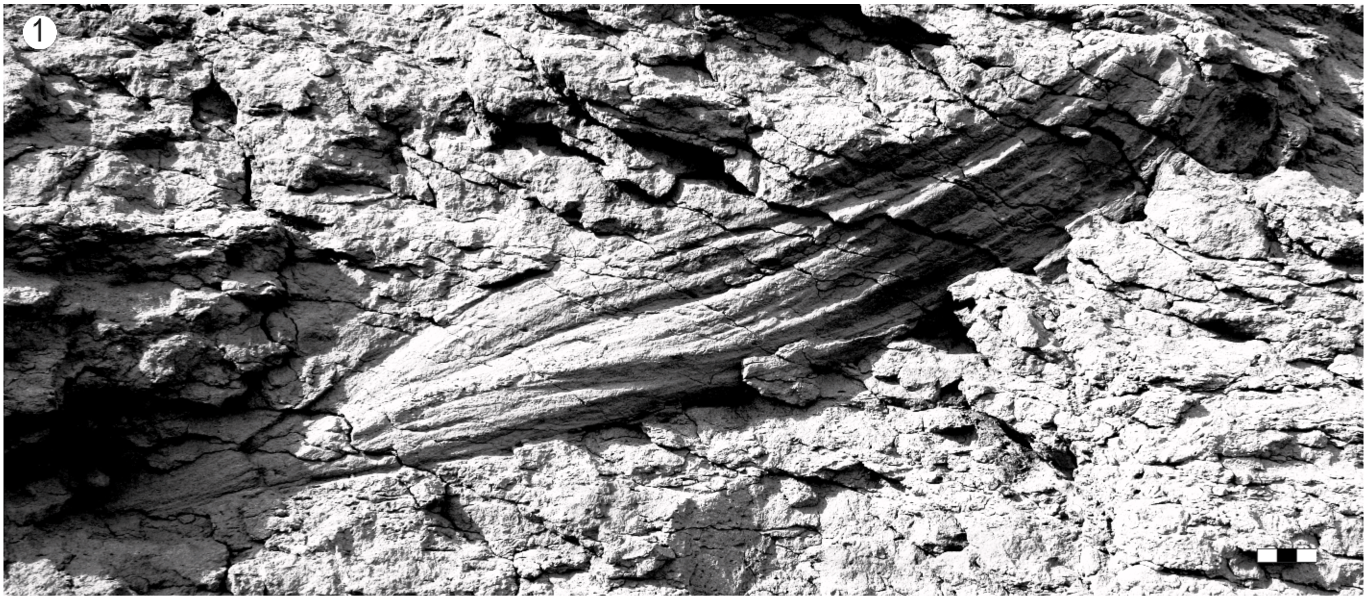

FIGURE *10*—*Euflabella* isp. Vertical view of the large, slightly oblique field specimen, reconstructed in *Figure 4.7*, Haslum Crag Sandstone, Snow Hill Island, Antarctica. Scale bar=3 cm.

feeding and gardening. This behavior most probably reflects a strategy to cope with fluctuating food resources.

In Antarctica, *E. singularis*, *E. multiplex*, and *E. radiata* are the dominant trace fossils in most of the ~2400 m thick, Campanian-Maastrichtian shelfal mudstones and fine-grained sandstones of the Marambio Group. *Euflabella singularis* is also widely distributed in the ~350 m thick, shelfal very fine-grained sandstones of the Leticia Formation. Both in Antarctica and Tierra del Fuego, these traces are associated with typical trace fossils of the Late Cretaceous-Paleogene *Cruziana* ichnofacies in lower shoreface-offshore successions.

In contrast to the other ichnospecies, *E. sinuosa* occurs only in Tierra del Fuego and in different sedimentary facies and associated with different suites of trace fossils. The sedimentary facies and ichnology suggest rather stressed environments in shallow subtidal, sand-rich settings, where elements of the *Skolithos* and an impoverished *Cruziana* ichnofacies may co-occur.

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Member, Snow Hill Island Formation, Snow Hill Island, Antarctica; *5*: field specimen seen from the top, late middle Eocene, Leticia Formation, Tierra del Fuego; *6*, vertical section of densely bioturbated sandy siltstones; two thin beds (dotted line) show a dense ichnofabric of *Phycosiphon incertum* (Phy), *Nereites biserialis* (Ner), and *Schaubcylindrichnus coronus* (Sch) that is cross-cut by *E. radiata* (Euf), Maastrichtian, López de Bertodano Formation, Snow Hill Island, Antarctica, field photograph. Scale bars=1 cm.

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