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Tasselia ordamensis: A biogenic structure of probable deposit-feeding and gardening maldanid polychaetes

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ABSTRACT

The internal structure and growth direction of well-preserved *Tasselia ordamensis* specimens from the Upper Cretaceous–Cenozoic of Antarctica and Tierra del Fuego are not compatible with its current interpretation as a domichnion/equilibrichnium trace fossil. Accordingly, its functional morphology and the likely ethology of the producer are revised. *Tasselia* is a protrusive structure composed of a lined inner tube surrounded by vertically stacked sediment disks and ending in a basal chamber. Each disk has two domains of active burrow fills. The micritic, outer burrow fill domain consists of radial petaloid elements containing abundant radiolaria, calcispherules, diatoms and plant debris. This domain was formed by excavation due to deposit feeding; thereby non-ingested particles remained in the chamber and ingested particles passed through the gut to the sediment surface. Microfossil-rich material was collected at the sediment surface, placed in the feeding chamber, and rearranged within the petaloid elements probably after pulsed delivery of organic matter. The wineglass-shaped inner burrow fill domain is enriched in coarser particles and its petaloid elements crosscut the outer burrow fill domain. This domain probably functioned as "culturing compartment" for bacteria and its secondary reworking implies some form of 'gardening' and feeding on these bacterial populations at depth. The concentric striae on the organic-lined inner tube and the vertically stacked series of sediment-disks suggest maldanid polychaetes as the producers of *T. ordamensis*.

1. Introduction

The peculiar biogenic structures studied by Tassel (1964) from Pliocene shallow marine deposits in the polder of Ordam, Belgium were named *Tasselia ordamensis* and interpreted as made by pogonophores (Heinzelin, 1964). However, the shallow water origin of these structures contradicted the deep-marine habitat of most pogonophores and Babin et al. (1971) found that the type material of *T. ordamensis* could be produced by shallow-water maldanid polychaetes. In particular these authors compared the trace fossil *T. ordamensis* Heinzelin with the very similar biogenic structure produced by the shallow-water polychaete *Maldane glebifex* Gruber: both biogenic structures have in common a nested series of mud-disks surrounding a central, organically lined tube ornamented with circular striations and regularly spaced annulations on its outer wall.

Even though *Tasselia ordamensis* was listed in the Treatise on Invertebrate Paleontology (Häntzschel, 1975) it remained poorly known possible because the overall morphology of the trace could be easily mistaken as an inorganic concretion. The same structure was informally described as a "pine-cone structure" from the Upper Cretaceous of Antarctica (Scasso et al., 1991) and formally defined as a new trace fossil from the Pleistocene of Italy (D'Alessandro and Iannone, 1993). Based on the observation of modern examples recovered from shallow to deep marine settings off NW Africa Wetzel and Bromley (1996) provided important evidence on the systematic, environmental conditions, functional morphology and producing organism of *T. ordamensis.* In a study of recent deep-water bottom samples in Canada, Dufour et al. (2008) analyzed the structure and composition of the consolidated biogenic structure of the polychaete *Maldane sarsi* Malmgren. Two- and three-dimensional reconstructions of this structure, based on CT scans (see Dufour et al., 2008, Fig. 1), clearly show the diagnostic features of *T. ordamensis*, supporting the assertion of Babin et al. (1971) that the producers of the trace fossil *Tasselia* were most likely maldanid polychaetes.

A major problem of this interpretation, however, is that current accepted ethology of *T. ordamensis* is not consistent with the mode of life of maldanid polychaetes. Thus, whereas *T. ordamensis* is interpreted as an equilibrium trace fossil made by suspension feeding organisms (D'Alessandro and Iannone, 1993; Wetzel and Bromley, 1996; Ponce et al., 2007), most maldanids are head-down, conveyor-belt deposit feeders that transport subsurface particles to the surface (Mangum, 1964; Fauchald and Jumars, 1979). In addition, some maldanids subduct also bottom particles to a feeding cavity at depth by 'hoeing' surface sediments (Levin et al., 1997). Dufour et al. (2008) concluded that the mud structure of *Maldane sarsi* has an increased amount of bacteria around the inner tube, suggesting that the worms

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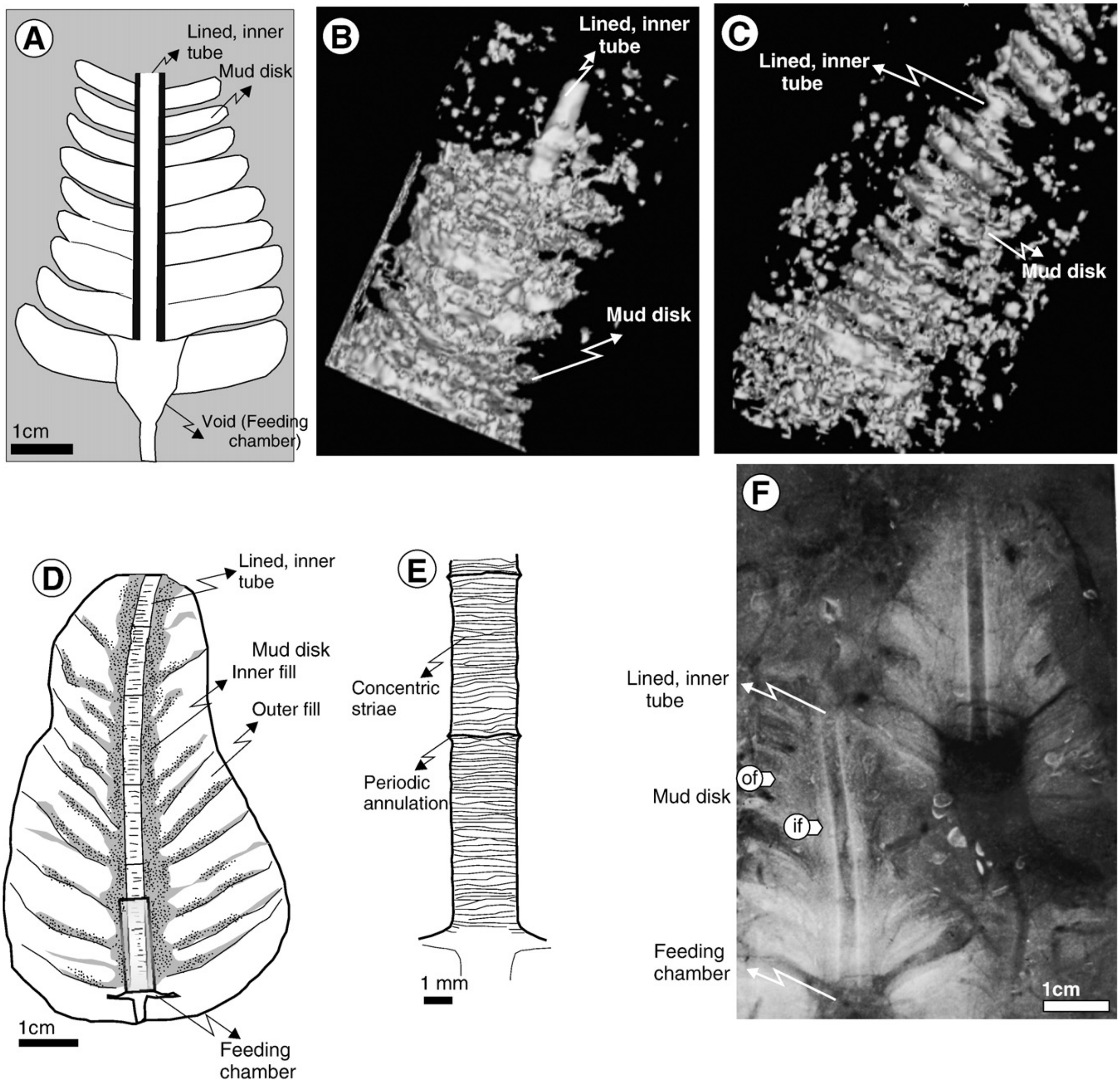


Fig. 1. Biogenic structures produced by maldanid polychaetes and *Tasselia ordamensis*. A: Schematic 2D reconstruction of the biogenic structure of *Maldane sarsi* (based on Dufour et al., 2008). B–C: 3D CT scans of the biogenic structure of *M. sarsi* generously provided by S. Dufour. D–E: Schematic reconstruction of *Tasselia ordamensis* after Tassel (1964) and Babin et al. (1971); D, whole structure, the rectangle marks the location of E; E, ornamented outer wall of the inner tube. F: X-ray radiograph (negative; mud–dark, sand–light) of modern *Tasselia ordamensis* from off Northwest Africa, (of), outer fill domain, (if), inner fill domain. Picture kindly provided by A. Wetzel.

may derive some nutritional benefits from this enhanced bacterial growth.

In this work we present a new ethologic interpretation for *Tasselia ordamensis* based on the study of very well preserved material from the Upper Cretaceous of Antarctica and Cenozoic of Tierra del Fuego. Our new interpretation dissolves the above-mentioned discrepancies. The excellent preservation of the studied specimens shows the trace fossil in all details, for instance, a secondary reworked domain surrounding the central lined tube. This domain is also present in the type material, but it has been previously unnoticed. It provides a clue to deduce the variable nutritional strategies of the *Tasselia* producers.

2. Material and methods

The studied material includes more than 400 specimens of *T. ordamensis* from shallow- and deep-water Upper Cretaceous to Cenozoic marine deposits in Antarctica and Tierra del Fuego. Most of this material was studied directly in the field during the last decade. Selected specimens were collected and deposited in the invertebrate paleontological collections of the Centro Austral de Investigaciones Científicas (CADIC-CONICET, Ushuaia) under the numbers CADIC PI 90 to 102. Provenance of the Antarctic material is from relatively shallow-water deposits of the latest early Campanian Santa Marta and Rabot Formations (see Scasso et al., 1991; Olivero, 2007); the late Campanian to early Maastrichtian Snow Hill Island Formation at Snow Hill Island and Hamilton Point and Santa Marta Cove, James Ross Island; and the Maastrichtian López de Bertodano Formation at Seymour Island (Olivero et al., 2008). In Tierra del Fuego, *Tasselia* was recorded in the relatively deep-water deposits of the Maastrichtian Policarpo Formation (Olivero et al., 2003); turbidites of the early Eocene Punta Torcida Formation; marginal marine deposits of the mid-late Eocene Leticia Formation; turbidites of the Cerro Colorado

Formation (Olivero and Malumián, 1999; López Cabrera et al., 2008); and in deep-water deposits of the Oligocene Estancia María Cristina beds, early Miocene Cabo Ladrillero and San Pablo Beds (Malumián and Olivero, 2006; López Cabrera et al., 2008). We also studied the Wetzel's collection of *T. ordamensis*, including modern material from off NW Africa, housed at the Geologisch–Paläontologisches Institut der Universität Basel, Switzerland.

The morphological elements and internal structure of *Tasselia* were studied in longitudinal and transverse polished sections prepared from well-preserved material, covering the range of lithologies preserving the biogenic structure. The mineral composition, grain-size variation, and microscopic structure of different morphological elements were studied by means of oriented thin sections prepared from parts of the same polished samples mentioned above. Grain size and mineral composition were analyzed both in the host rock and the biogenic structure. Grain-size analysis was performed in thin sections following the Gazzi–Dickinson standard method trying to accomplish a minimum of 300 counts in each sample. Schematic drawings of morphological elements of the biogenic structure were prepared by tracing digital pictures on a computer. The orientation, polarity, and relationships of the trace fossil to bedding were observed by manual excavation and careful splitting of the sediment along and perpendicular to bedding planes.

3. Biogenic structures produced by maldanid polychaetes

3.1. Morphology and composition

Most maldanid polychaetes are interpreted as highly specialized burrowers feeding on organic particles buried in soft, fine-grained sediments. They excavate head downward cementing the surrounding materials together to form a fairly compact but variable structure. For example, the biogenic structure of *Maldane sarsi* (Fig. 1A–C) has a central tube with a thick lining and a thick outer envelope of mud; other species lack the outer envelope, so the structures consist only of an organic-lined tube and in some cases the tubes are no more than poorly consolidated burrows (Mangum, 1964; Day, 1967; Fauchald and Jumars, 1979; Rouse and Pleijel, 2001). Except for these broad observations, biological studies, however, generally do not include the description of the biogenic structure made by infaunal polychaetes and the neoichnology of the group is thus known imperfectly.

To the authors' knowledge, the only studies that have investigated with some detail the structure and composition of the biogenic structures made by maldanids are those of Babin et al. (1971) and Dufour et al. (2008). Babin et al. (1971) described the biogenic structure produced by the cosmopolitan polychaete *Maldane glebifex* Gruber. The structure has a pyriform shape and consists of a cylindrical inner tube covered with a thick wall of organic matrix ornamented with fine, concentric, irregular striae that alternate with stronger periodical annulations. This inner tube is surrounded by a compact envelope of foraminiferal-bearing sand particles, which in turn is surrounded by a thicker sediment disk made of aggretated layers of silt and sand particles. The inner tube continues in isolation in the lower part of the structure forming a long tail that probably reflects the rapid decay of the weaker sediment disk and differential preservation of the stronger inner organic-lined tube wall (Babin et al., 1971, planche 33, Figs. 1 and 2). Babin et al. (1971) compared this biogenic structure with the type material of *Tasselia ordamensis* and concluded that the latter is a homologous structure, produced also by maldanid polychaetes (Fig. 1D–E).

The polychaete *Maldane sarsi* Malmgren is also a cosmopolitan species, living in deep waters from the Artic to the Antarctic in muddy bottoms (Day, 1967). The biogenic structure of *M. sarsi* was studied in cores by means of axial tomodensitometry (CT scans) by Dufour et al. (2008). S. Dufour kindly provided some CT scans of the structure and these are reproduced here (Fig. 1B–C). These 3D scans and the accompanying 2D scheme (Fig. 1A) show that the biogenic structure of *M. sarsi* is remarkably similar to *Tasselia ordamensis*. Indeed, the X-ray radiographs of modern *T. ordamensis* structure, kindly provided by A. Wetzel (Fig. 1F), from off NW Africa (Wetzel and Bromley, 1996) show that the similarity with the *M. sarsi* structure is striking. The lined inner tube ending in a basal void, interpreted as a feeding chamber, and the surrounding sediment disks can be clearly recognized in these structures (see in addition the corresponding figures in Wetzel and Bromley, 1996 and Dufour et al., 2008). The internal structure of the mud disk cannot be seen in the CT scan figures of the *M. sarsi* structure (Fig. 1A–C), but it is clearly shown in the X-ray radiographs of *T. ordamensis* where the inner and outer burrow fill domains can be differentiated in the mud disk (Fig. 1F).

3.2. Burrow construction and feeding strategies

Maldanids polychaetes have a slender elongate body with reduced parapodia and simple capillary and hooked chaetae (Day, 1967). The general functions of the capillary chaetae include locomotion, stabilization during peristalsis, and sensing the environment, whereas the hooked chaetae function mainly as anchors (Merz and Woodin, 2006). As in most polychaetes the organic membrane lining the tube is made from mucus segregated at the anterior part of the worm. The tube grows by successive addition of strings of mucus while the animal rotates slowly inside the tube. Parapodia probably help to distribute uniformly the mucus and the operation is quite similar to the Indian method of making pottery (Barnes, 1974). The smooth, inner wall of the tube results from the up and down movement of the worm and the evenly mucus distribution by parapodia acting as brushes, whereas the external ornament of irregular striae probably reflects the successive addition of the strings during growth (Schweitzer et al., 2005) as well as the impression of sedimentary particles pressed against the outer tube wall (Thomsen and Vorren, 1984). The coarser annulations may reflect halts in growth as suggested by the illustrations of Tassel (1964), where these coarser annulations are located at the roof of the basal feeding chamber (Fig. 1 D–E).

Burrowing tubicolous maldanids have their anterior part within the substrate at the lower part of the inner tube. From the lower end of the tube the worm laterally excavates the substrate, ingests sedimentary particles and particulate organic matter; faecal residues are ejected to the sediment surface at the upper end of the tube (Mangum, 1964; Fauchald and Jumars, 1979). As the organism ingests the sediment, voids are left and the surrounding sediment collapses providing new material to the feeding worm (Fauchald and Jumars, 1979). The processes of loosening, excavation, and ingestion of sediments are carried out by means of eversion–inversion cycles of the proboscis (Kudenov, 1977). Particle selection occurs during ingestion; particles too large to enter through the pharynx are dropped off from the buccal mass. Thus, the size of the ingested particles depends in part upon the size of the worm, but apparently both small and large worms are always capable of ingesting particles smaller than fine-grained sand (Kudenov, 1977). Due to this selection process the largest non-ingested particles, generally coarser than medium-coarse grained sand, are left over and become concentrated at the bottom of the inner tube, there eventually forming a biogenic graded bed (Rhoads and Stanley, 1965).

Several maldanids of the subfamily Euclymeninae also transport freshly deposited surface particles down to the feeding cavity at depth by ‘hoeing’ surface sediments using their modified pygidium (Levin et al., 1997). Part of the subducted material is ingested and returned to the sediment surface as faeces and part of this material is left in the feeding cavity and probably redistributed into the sediment disks. The mechanics of this redistribution process is not well known, but according to Dufour et al. (2008) *M. sarsi* utilizes its cephalic plate to form disks of compacted sediment, cemented with mucus.

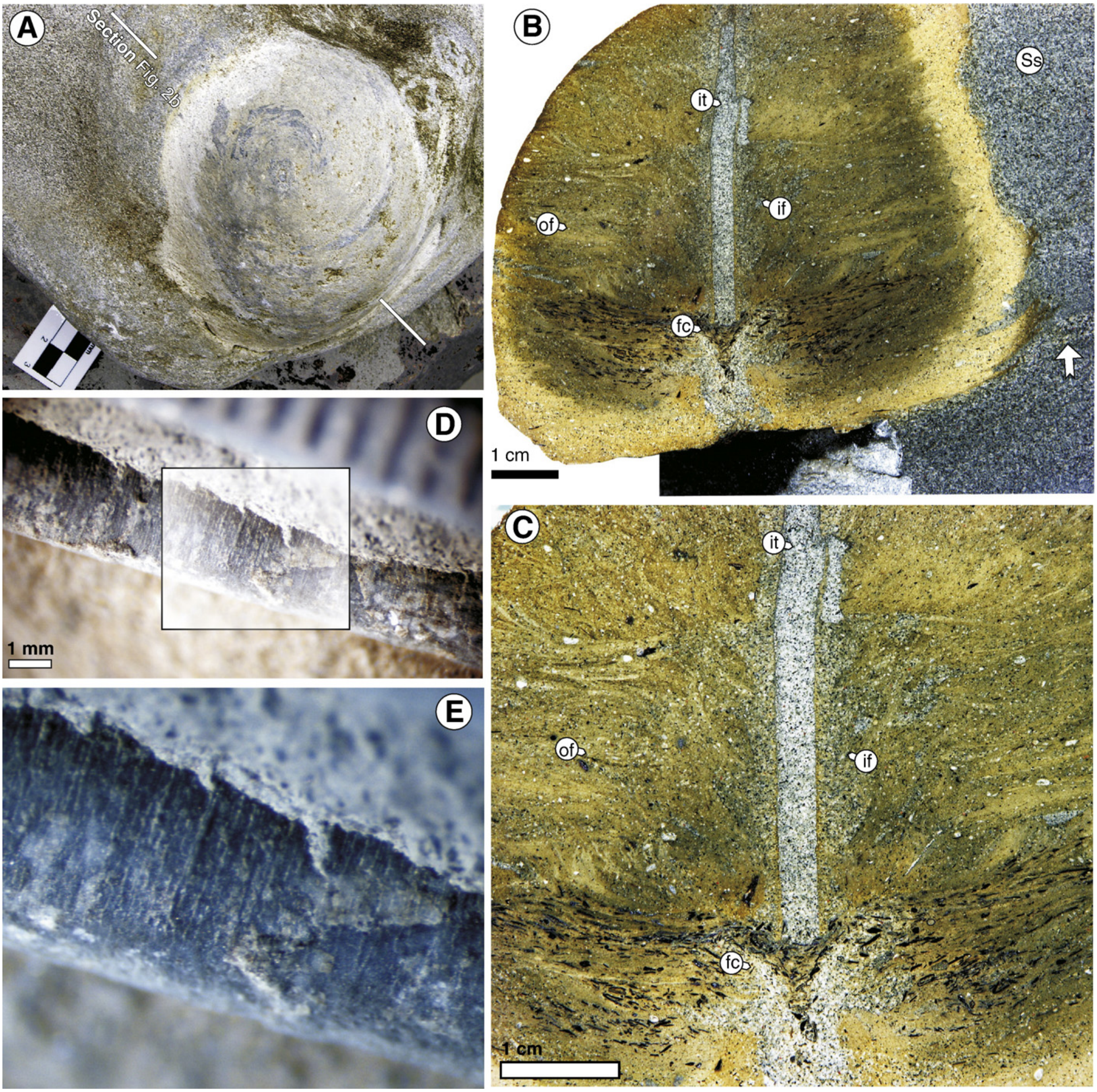


Fig. 2. Morphological elements of *Tasselia ordamensis*. A–C: Specimen preserved in fine-grained sandstone (A), polished section of the same structure (B) and enlarged basal part (C); inner tube (it), basal feeding chamber (fc) and inner (if) and outer (of) burrow fill domains. Note the different composition and sharp boundary between the burrow fill and the fine-grained sandstone (Ss), the non-deformed lamina at the burrow boundary (arrow), and the high concentration of comminuted plant debris in the feeding chamber and burrow fill. A, bedding plane view, B–C vertical sections, specimen CADIC PI 90 early Miocene Cabo Ladrillero beds, Tierra del Fuego. D–E: General (D) and detailed (E) picture of irregular striae and annulations on the wall of the lined, inner tube, specimen CADIC PI 98, late Campanian, Gamma Member, Santa Marta Cove, James Ross I., Antarctica.

Maldanid polychaetes are known to enhance aerobic activities along a narrow zone surrounding the inner tube and both, subduction of organic material by hoeing and irrigation probably stimulate microbial activity (Levin et al., 1997). In *M. sarsi*, the zone of the mud-disk surrounding the inner tube has higher concentrations of Fe and Mn than the surrounding zones, which probably results from precipitation due to oxidation by tube irrigation. Organic carbon and bacterial growth are also enhanced in this narrow, aerobic zone and the worms may derive some nutritional benefit from this enhanced bacterial growth. *M. sarsi* may therefore practice a form of bacterial 'gardening' and feed on bacterial populations at depth (Dufour et al., 2008).

4. The trace fossil *Tasselia ordamensis*

4.1. Morphology, grain-size and composition

Tasselia ordamensis is a broadly pear-shaped structure. Typical morphological elements include an axial lined tube that continues downward into a basal chamber (cf. Babin et al., 1971; D'Alessandro

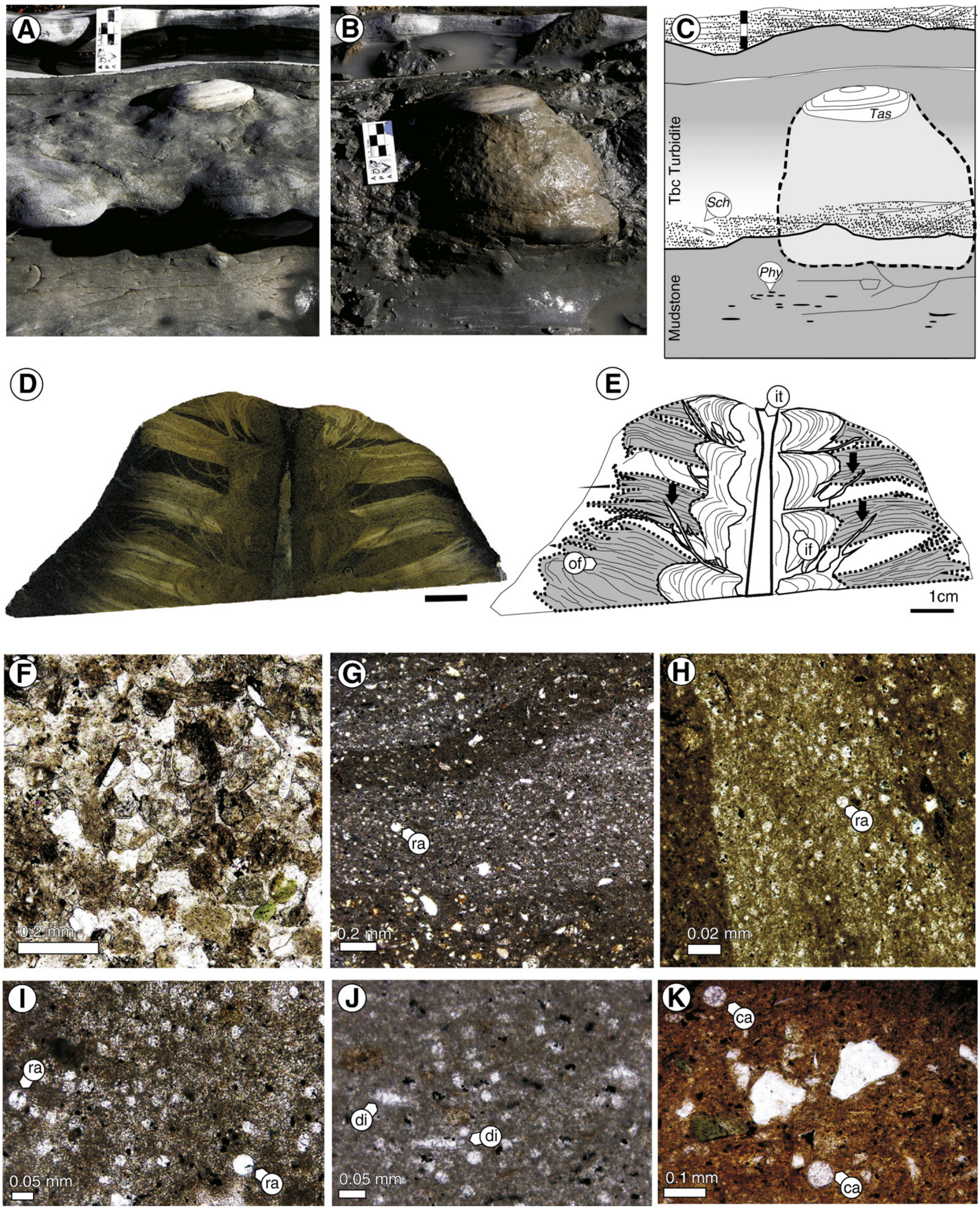


Fig. 3. Stratinomy, structure and composition of *T. ordamensis*. A–C: specimen cutting through two turbidite beds, after (A) and before (B) excavating it, and (C) schematic reconstruction. *Tasselia* (Tas), *Schaubcylindrichnus* (Sch), *Phycosiphon* (Phy). D–E: polished vertical section of the same specimen; lined, inner tube (it), outer (of) and inner fill (if) domains, note that lamellae of the inner fill domain cross-cut at several levels the outer fill domain and interdisk areas (arrows). F–J: thin sections of the turbidite and *Tasselia*; vertical section of the T_{bc} division (F), longitudinal (G, H) and transversal (J, I) views of the outer burrow fill with dense concentrations of calcified radiolarians (ra) and diatoms (di). A–J, specimen CADIC PI 91 CCa Member, Cerro Colorado Formation, late Middle Eocene, Tierra del Fuego; K: vertical thin section of the outer burrow fill with abundant calcispherules (ca), specimen CADIC PI 99, late Campanian, Gamma Member, Santa Marta Cove, James Ross I., Antarctica.

and Iannone, 1993; Wetzel and Bromley, 1996) and is surrounded by a structured burrow fill, which consists of two zones defining an inner and an outer burrow fill domain.

The axial inner tube has a circular cross-section, the diameter of which remains approximately constant (i.e. between 2 and 3 mm) along the length of the tube (Figs. 1F, 2A–C, 3A–B and 4A–B). The inner tube is lined with a thick wall, probably made of organic material (Babin et al., 1971), but in the studied specimens it was dissolved or replaced by calcite or a mixture of calcite and isotropic calcium phosphate, sometimes with agglutinated silt or very fine-grained sand particles. Diagenetic, fine-grained pyrite is common around the tube lining and proximal burrow fill (Fig. 5G–I). The external part of the lining shows transverse, irregular, narrow-spaced concentric striations interrupted periodically by coarser annulations (Fig. 2D–E). Where the organic wall is lost, this ornamentation is seen as impressions into the surrounding burrow fill (cf. Babin et al., 1971).

The basal chamber has a crude wineglass shape, the filling material of which differs from that in the surrounding burrow, particularly if the structure is preserved in fine-grained sandstones (Fig. 2). The lower part of the basal chamber is connected to a vertical shaft directed downwards and of similar diameter than that of the lined tube, but this shaft is not lined (Fig. 1 F; cf. Wetzel and Bromley, 1996).

The burrow fill is packed into several distinct, concave-upward, sediment disks, which could be vertically stacked in direct contact one on the bottom of the other or separate by a thin layer of undisturbed host sediment (Figs. 1, 2A–C and 3–5). As has been previously noticed (Tassel, 1964; Heinzelin, 1964; Babin et al., 1971) the central, concave-upward part of each sediment disk points downward and the diameter of successive sediment disks increases downwards. The sediment disks bear a distinct internal structure, which in vertical sections seems to be formed by subparallel planar laminae (D'Alessandro and Iannone, 1993; Wetzel and Bromley, 1996). However, in fact they consist of crowded, vertically stacked, discrete arched and flattened petal-like subcylindrical elements, the diameter of which is larger, but roughly similar to that of the lined tube. The arrangement of the internal structure in discrete, subparallel petaloid elements is evident in well preserved sediment disks (Fig. 4). Based on the composition, geometry, and crosscutting relationships of the internal elements within each sediment disk, the burrow fill is divided into an outer and an inner burrow fill domain.

The outer burrow fill domain differs from the host sediment with respect to both, grain-size and composition of particles. This is readily evident when *Tasselia* is preserved in fine-grained sandstones. The biogenic structures preserved in clean, well-sorted fine-grained sandstones have an outer burrow fill domain that is dominantly composed of micrite being relatively enriched compared to the host sediment in microfossils, mostly calcified radiolaria and diatoms, calcispherules, and tiny carbonaceous plant debris (Figs. 2, 3 and 5A–E). The internal structure of the outer burrow fill domain has a characteristic geometry defined by radially arranged subhorizontal to oblique petal-like structures. In horizontal view, the petal-like elements consist of distally expanding furrows bordered by slightly raised margins (Fig. 4C–F). In fine-grained sandstones there is a relative concentration of the coarsest grains along the raised margins and also at the base of the central furrow. In vertical radial sections these petal-like structures define subparallel curved lines, that converge to the basal part of the sediment disk (Figs. 2B, 3D–E, 4A–B, I and 5A). As seen in vertical sagital sections, the cross-section of each flattened, subcylindrical petal is lenticular (Fig. 4G–H).

The boundary between the outer burrow-fill domain and the host sediment is sharp, with no evidence of reorientation of particles or biogenic induced compressional deformation of the primary lamination of the host rock (Fig. 2B). Conversely, the coarser particles within the outer burrow fill domain are clearly reoriented, with their long axis parallel to the length of the petaloid elements (Fig. 2C, 5B). The boundary between the outer and inner fill domains is also neat, with clear evidence that the laminae of the inner fill domain cross-cut the outer fill domain (Figs. 3D–E and 4A–B and I). Commonly, the outer fill domain is also cut by other biogenic structures (Fig. 4G–H); in addition to a dense mottling the trace fossils *Paradictyodora antarctica*, *Chondrites intricatus*, *Zoophycos* isp., and *Phymatoderma granulata* are recognized.

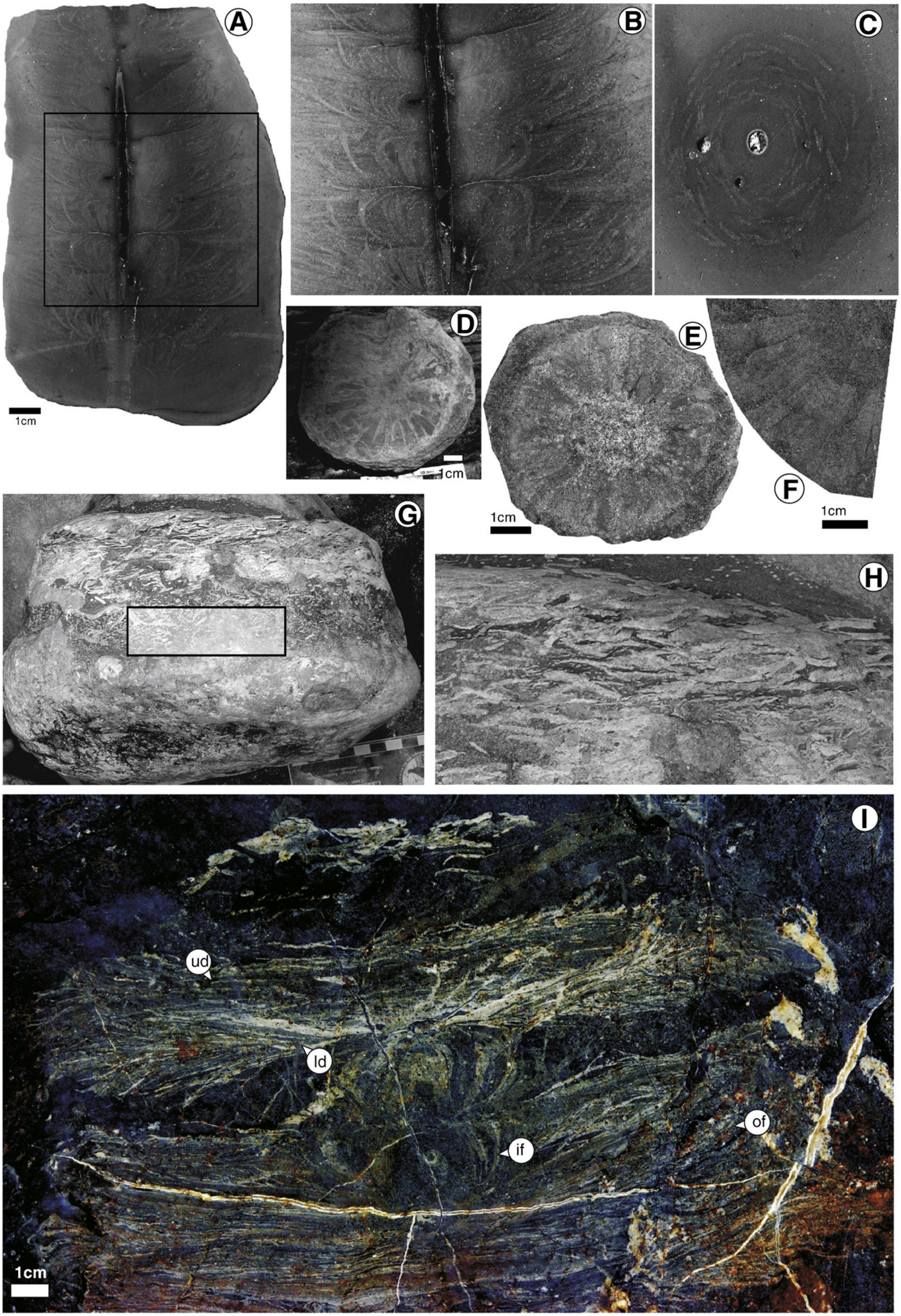
The inner burrow fill domain has a higher concentration of coarser particles than both the outer burrow fill domain and the host sediment (Fig. 5F). For *Tasselia* preserved in mudstones, the contrast in grain size between the outer and inner fill domains is not so strong. As exemplified by specimens of *Tasselia* from the early Eocene mudstones of the Punta Torcida Formation there is a subtle difference in the particle size and composition. Thus, whereas the outer burrow fill domain is dominantly composed of clay particles, the inner burrow fill domain is dominated by silt particles; also the inner burrow fill domain has a different, diagenetic reddish hue, probably due to higher iron content in the inner fill domain (Fig. 4A–C). When the trace fossil is preserved in fine-grained sandstones, the contrast between the outer and inner burrow fill domains is conspicuous. In this case, the higher concentration of coarser particles in the inner burrow fill domain, generally medium- to upper fine-grained sand, usually makes a strong contrast with the dominant micrite composition of the outer burrow fill domain, particularly if the coarser particles are glauconite grains. Grain size analysis of fine-grained sandstone from the late Campanian of Antarctica (Fig. 5F) shows that in the host rock the population of medium-grained sand particles is very small (<5%; about 30% of which are glauconite) and in the inner burrow-fill domain medium-grained particles are relatively concentrated, c.12%, with c. 70% of the coarsest population consisting of glauconite grains.

The geometry and internal structure of the inner burrow fill domain differ markedly from that of the outer fill domain. In horizontal transverse sections, subcircular areas with concentrated coarser particles or with dense lenticular structures, representing the cross-section of the petaloid elements, defines the inner fill domain (Fig. 4C). The petaloid elements are short, subvertical and strongly arched; each set of discrete petaloid elements are mostly confined within the sediment disk, cross-cutting the subhorizontal petaloid structures of the outer fill domain and, if present, also the interdisk layer of undisturbed host sediment. These features of the inner fill domain are conspicuous in vertical axial sections (Figs. 3D–E and 4A–B and I).

4.2. Stratinomy, substrate and population density

The original orientation of the trace fossil is vertical, with a marked polarity given by the preferred position of the widest part at the base of the structure. The tendency to enlarge the structure toward the basal part is clearly seen in vertical polished sections of specimens preserved in fine-grained sandstones. In this case the original, lateral termination of each sediment disk is preserved (Figs. 2B, 3D–E and 5A), ruling out the possibility that the basal enlargement of the structure could be a diagenetic artifact controlled by the preferential disintegration of mucus, or any other cementing material in the upper part of the biogenic structure (cf. Wetzel and Bromley, 1996). In some cases the structure is recorded with its long axis in subhorizontal position (Fig. 6), but it is always clear that these odd orientations correspond to reworked, parautochthonous specimens (cf. Wetzel and Bromley, 1996).

In agreement with previous studies (Tassel, 1964; Babin et al., 1971; D'Alessandro and Iannone, 1993; Wetzel and Bromley, 1996) all in situ specimens of *Tasselia* were recorded in mudstones (e.g. Fig. 4A–C) or in fine- to very fine-grained sandstones (e.g. Figs. 2A–C, 3D–E, 5A–D and 6), but they have not been recorded in medium- or coarse-grained sandstones. In turbidite beds, *Tasselia* occurs commonly confined within the muddy division, but we also have clear evidence that the biogenic structure can cross-cut two turbidite beds (Fig. 3A–C).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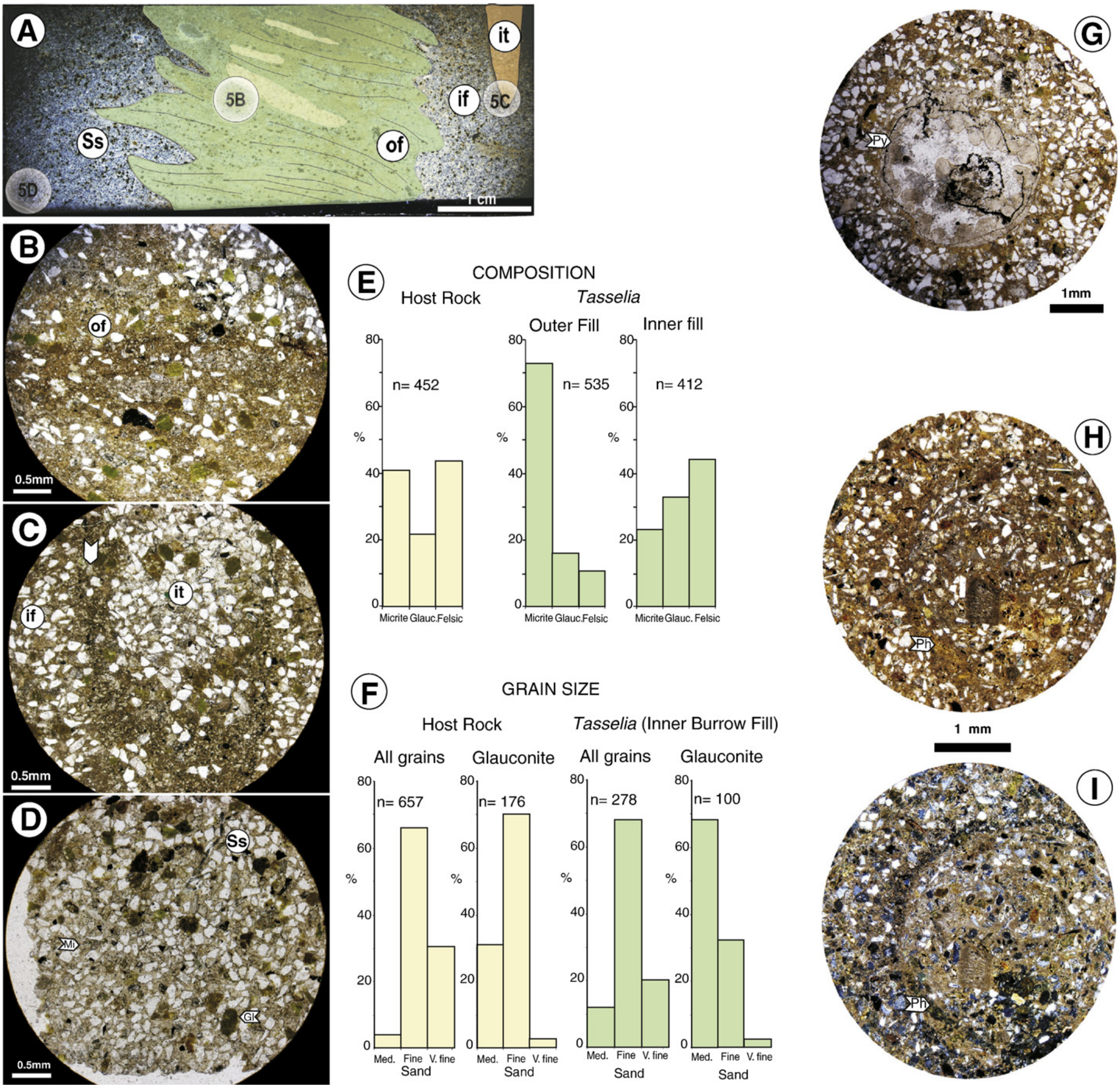

Fig. 5. Grain size and composition of the substrate and *T. ordamensis*. A: vertical thin section including *Tasselia* and the substrate (Ss) with location of pictures 5B, 5C, and 5D, the inner tube (it), and inner (if) and outer fill domains (of). B: micritic outer fill domain with coarsest particles concentrated at the bottom of laminae. C: inner tuber and surrounding inner fill domain, white arrow indicates the calcite-replaced tube wall. D: fine-grained, glauconitic (Gl) sandstone with micrite (Mi) cement. E: comparative percentage of micrite, glauconite (Glauc.) and felsic components in the host rock and *Tasselia*. F: grain-size distribution in the host rock and inner burrow fill domain, note higher concentration of coarse grains in the inner burrow fill domain. A–F, specimen CADIC PI 94, Snow Hill Island Formation, Gamma Mbr., Santa Marta Cove, James Ross Island, Antarctica. G–I: transverse thin sections of the inner tube and inner burrow fill domain. Lined tube replaced by calcite, with pyrite (Py) inside the tube and coating the wall (G). Tube wall with agglutinated particles cemented by amorphous calcium phosphate view in parallel (H) and crossed nicols (I). (G) specimen CADIC PI 95 and (H, I) specimen CADIC PI 96, both from the late Campanian Snow Hill Island Formation, Gamma Mbr., Santa Marta Cove, James Ross Island, Antarctica.

Fig. 4. Petaloid elements of *T. ordamensis*. A–C: specimen preserved in mudstones, general (A) and detailed (B) view in longitudinal section showing the lined inner tube and the subvertical lamellae of the inner fill domain cross-cutting the subhorizontal ones of the outer fill domain. Transverse section (C) showing cross-sections of petaloid elements in the inner burrow fill domain, specimen CADIC PI 92, Punta Torcida Formation, Early Eocene, Tierra del Fuego. D–F: upper (D, F) and lower (E) plan views of individual sediment disks showing discrete, petaloid elements. D, specimen CADIC PI 93, early Miocene Cabo Ladrillero beds, Tierra del Fuego. E–F, specimen CADIC PI 100, late Campanian Snow Hill Island Formation, Gamma Mbr., James Ross Island, Antarctica. G–H: General (G) and detailed (H) views of lenticular sections of petaloid elements on the outer surface of *Tasselia*. Note dense *Chondrites* cross-cutting *Tasselia*, field specimen, upper Eocene, Cerro Colorado Formation, Punta Gruesa, Tierra del Fuego. I: Slightly oblique and off center vertical section showing the outer (of) and inner fill domains (if) lamellae. The upper disk consists of two amalgamated disks with the lower (ld) one cross-cutting the lamellae of the upper one (ud), field specimen, lower Oligocene, Maria Cristina beds, Punta Gruesa, Tierra del Fuego.

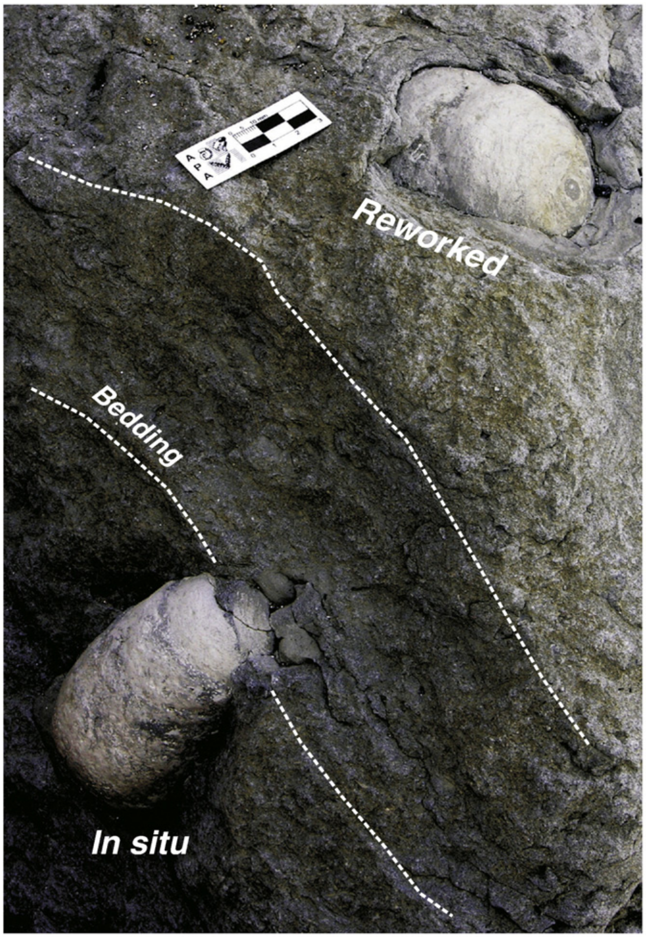

Fig. 6. In situ and reworked *T. ordamensis*. Field specimens in fine-grained sandstones of the late Middle Eocene Leticia Formation, Punta Torcida, Tierra del Fuego.

Specimens of the ichnogenus *Tasselia* commonly occur in high abundance restricted to particular horizons. The abundance of *Tasselia* in the Campanian, shallow-water deposits of the Santa Marta Formation, Antarctica or in the relatively deep-water Eocene turbidites of the CCb Member of the Cerro Colorado Formation, Tierra del Fuego, is explosive, with hundreds of specimens recorded in restricted horizons. Remarkable high-density concentrations of tens of *in situ* specimens in a very small area were recorded in the Miocene Cabo Ladrillero beds of Tierra del Fuego and in the Campanian of Antarctica. In the latter case, the estimation based on the number of specimens (8) within an area of 0.014 m^2 gives an average density of about 550 specimens per square meter (Fig. 7).

4.3. Stratigraphic distribution and associated trace fossils

In the geological record *Tasselia ordamensis* is mostly known from Upper Cretaceous and Cenozoic shallow-marine and deep-water deposits in Europe, Antarctica, and Tierra del Fuego. With the exception of few doubtful mentions the trace is not recorded in the Paleozoic. The biogenic structure was recorded in modern sediments off NW Africa, and could be widely distributed in present oceanic settings (see below).

The European record is restricted to the Cenozoic. It includes deep-water slope turbidites from the Eocene of Spain, characterized by low diversity trace fossil assemblage with *Thalassinoides*, *Ophiomorpha rudis* and ?*Tasselia* isp., whereas *Chondrites intricatus* and *Phycosiphon incertum* occur in associated marlstones (Uchman, 2001). In Poland, displaced *Tasselia* disks have been observed in Eocene turbidite deposits (T_{c-e}) in the Carpathians (Wetzel and Uchman, pers.comm., 2008); these *Tasselia* are penetrated by *Chondrites*. In Italy, *Tasselia* was recorded in Salento, in Pliocene–Pleistocene inner shelf silt and very fine-grained sandstone associated with *Thalassinoides*, *Gyrolithes*-like structures and *Palaeophycus* (D'Alessandro et al., 2004) and in similar facies in the Pleistocene of Sicily (D'Alessandro and Iannone, 1993). The type material is from the upper Pliocene, shallow water Merksem Sand, Belgium (Tassel, 1964; Heinzelin, 1964).

Tasselia ordamensis is also known from modern cores taken from c. 5 to 820 m water depth off NW Africa; co-occurring traces are *Helicodromites*, *Palaeophycus*, *Phycosiphon*, *Scolicia*, *Skolithos*, and *Trichichnus* (Wetzel and Bromley, 1996). Similar, modern biogenic structures attributed to maldanid polychaetes have a cosmopolitan distribution (Day, 1967; Dufour et al., 2008). In addition *Tasselia* has been observed in rather soft muddy sediments off Vietnam in 20 to 30 m water depth co-occurring with *Palaeophycus*, *Planolites*, and *Thalassinoides* (Wetzel, pers. comm., 2009).

In Austral regions the earliest record of *Tasselia ordamensis* dates back to shallow-water Campanian (Antarctica) and deep-water Maastrichtian (Tierra del Fuego) deposits. In Tierra del Fuego, the record of *Tasselia* is from the Maastrichtian up to the Lower Miocene (see Section 2). Co-occurring trace fossil assemblages are dominated by fodinichnia or mixed assemblages of domichnia and fodinichnia (Scasso et al., 1991; Olivero et al. 2003, 2004; López Cabrera et al., 2008).

In North America, reworked isolated tubes similar to the inner tube of *Tasselia* were described in Paleocene–Eocene turbidites from California (Farmer and Miller, 1981). Doubtful, Paleozoic mentions of *Tasselia* include Permian glaciolacustrine deposits of the Patterson Formation, Australia (Jackson and Van De Graff, 1981) and Ordovician marine deposits in the Sahara (Babin et al., 1971).

5. Interpretation of *T. ordamensis*

5.1. Protrusive burrow fill

Tasselia ordamensis was interpreted as a domichnion/equilibrium structure probably made by suspension feeder or microcarnivore organisms (D'Alessandro and Iannone, 1993; Wetzel and Bromley, 1996). The thick sedimentary envelope around the central tube was thought as a sediment lining built to stabilize the structure within a softground or soupground (Wetzel and Bromley, 1996), and the resulting cumulative structure was interpreted to grow up retrusively, in equilibrium with high sedimentation rates (Ponce et al., 2007).

The elements (see Section 4.1) suggest, however, that the *Tasselia* structure was formed in a different way. The cross-cutting relationships between morphological elements of the outer and inner fill domains clearly indicate that the structure is formed protrusively, i.e. in downward direction (Figs. 3D–E and 4A–B, I). This is also evident from the stratinomy of the structure, as in the case of Fig. 3A–C. In this case, obviously the construction of the structure started at the muddy division of the T_{bc} turbidite and finished at the muddy division of the previous turbidite, cross-cutting the sandy division of the initial substrate.

The morphology of the petaloid elements and the internal structure of the thick sedimentary envelope indicate a burrow fill resulting mainly from deposit feeding and reorganization of sedimentary particles within the substrate. Since compressional features should be expected in the fabrication of a sediment lining, the observed neat and sharp burrow boundary, lacking any evidence of compression or splitting of primary lamination in the substrate (Fig. 2B) is more consistent with a burrow fill. Nonetheless, an additional stabilizing function for this thick burrow fill is very likely as *Tasselia* is typically found in substrates that probably were soft during its construction.

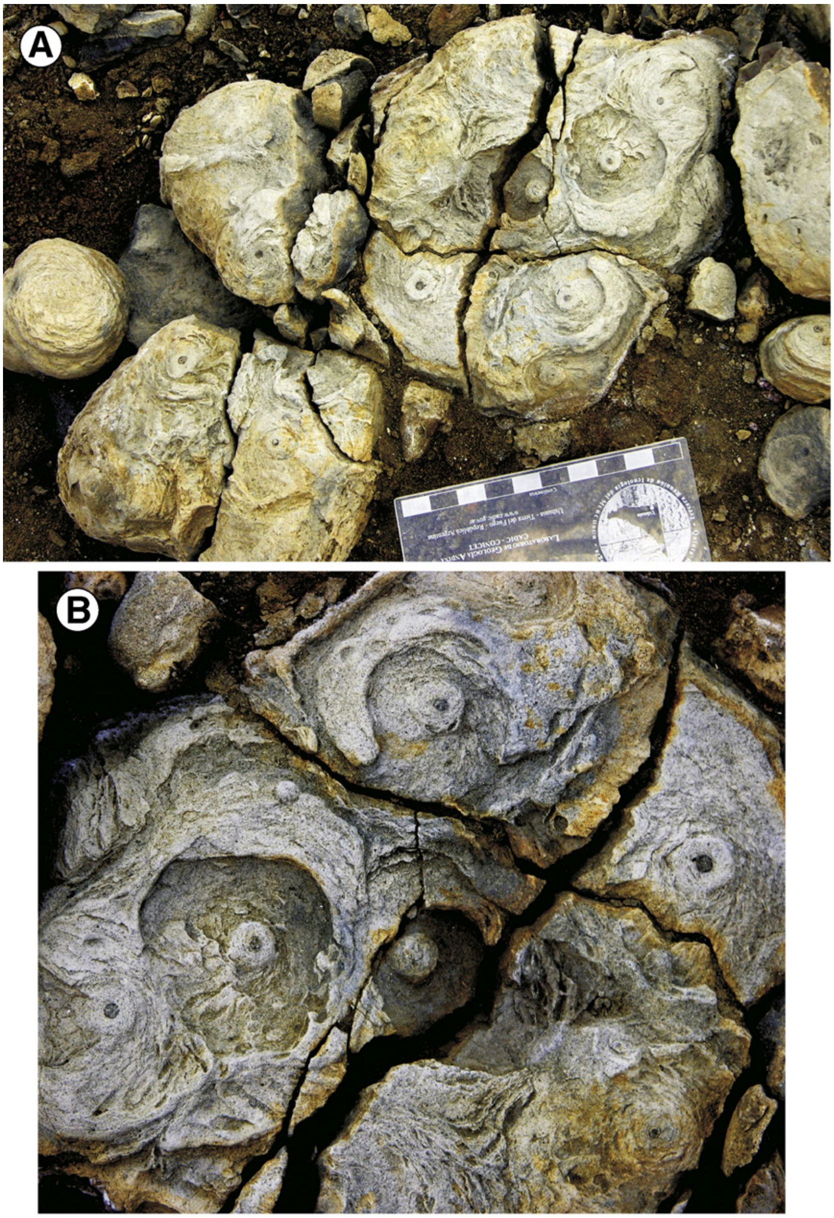

Fig. 7. Density of *T. ordamensis*. General (A) and detailed (B) upper bedding plane views of crowded specimens in a single bed. Field photographs of the slab CADIC PI 97, early Campanian Santa Marta Formation, Beta Mbr., Brandy Bay, James Ross Island, Antarctica.

5.2. Construction of the structure and feeding strategies

Based on the morphology, structure and composition of the internal elements, the active burrow fill is interpreted to have originated from different nutritional strategies, including deposit feeding, detritus feeding, and possible microbial gardening (Fig. 8). The interpreted main processes during the production of the *Tasselia* structure are described for simplicity when already several burrow fill disks have been produced (Fig. 8A). Then the lower end of the central lined tube is located at the roof of the basal chamber and the fill in the innermost part of sediment disk above the chamber functions as "culturing compartment", not being reworked yet. The production of the structure continues with the active excavation of the substrate at the level where the next burrow fill disk will be formed, and hence the basal feeding chamber is shifted downward (Fig. 8A). Because the composition of the substrate and the burrow fill material is different (Section 4.1, Fig. 5E), the trace maker probably fed on organic material that is mainly associated with fine-grained particles, digesting the organic compounds and ejecting the sediment particles to the surface (deposit feeding mode, Fig. 8A). The coarsest particles, medium-grained sand, probably too large to be ingested by the organism were left at the bottom of the excavation chamber and/or concentrated by gravity in the central part, eventually forming part of the inner fill domain at a later stage (e.g. Figs. 2B and 5F).

Most of the excavated chamber of the burrow is filled with micrite and densely packed plant debris and microfossils, including radiolarians, diatoms, and calcispherules (Figs. 2B–C and 3G–K). This material, particularly the microfossils are absent in the host-sediment or not present in such abundance as in the burrow fill, suggesting that this material was subducted from the surface to the bottom of the structure (detritus feeding mode, Fig. 8B). The dense concentration of plant material in particular levels of the active burrow fill and the absent of such material in the adjacent levels of the host sediments clearly indicate that this material was not sorted during the excavation of the burrow. This material was definitely rearranged within the burrow by the producer as indicated by enrichment of the

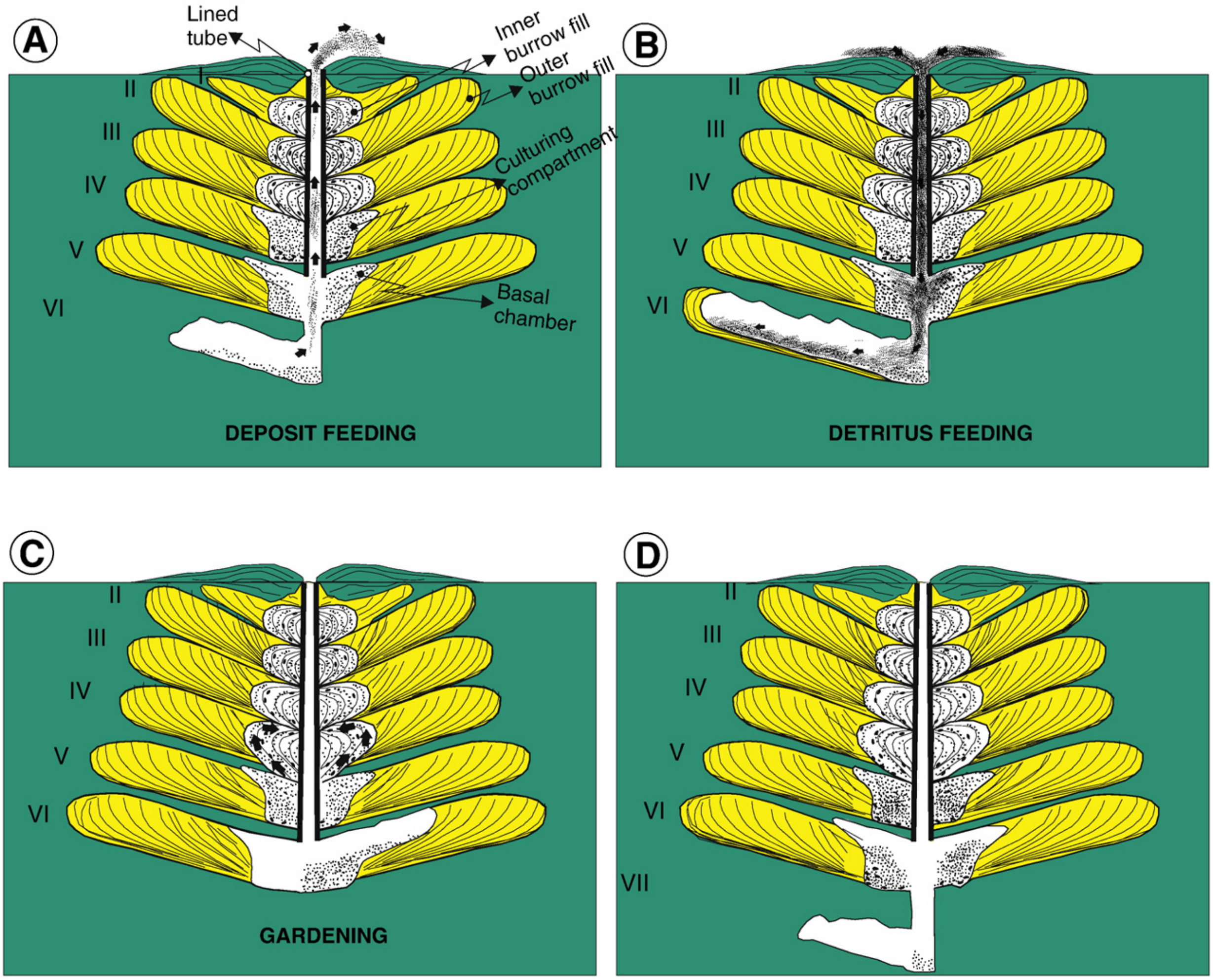

Fig. 8. Schematic reconstruction of *T. ordamensis* and feeding strategies of the producer. A: After an initial stage with five (I to V) sediment disks the lined tube ends at the roof of the basal chamber and the fill in the "culturing compartment" of disk IV still was not reworked. The active excavation of future sediment disk VI is associated with deposit feeding, ejection of sand particles to the surface (arrows) and concentration at the bottom of the excavation of particles too large to be ingested. B: The excavated part of the structure is retrusively filled with nutritious material (detritus feeding) subducted from the surface (arrows). C: The material filling the "culturing compartment" at sediment disk IV is reworked in the narrow zone (arrows) of the inner fill domain, the laminae of which cross-cut the outer fill domain. Reworking of sedimentary particles in the previous feeding chamber, strongly suggests culturing and gardening of microbial organisms. D: A new cycle of excavation and filling of a sediment disk starts. The cartoons are not necessarily in sequential order.

subducted particles in specific levels (Fig. 2B–C) and the peculiar morphology of the petaloid elements (Fig. 4D–H). The arrangement of the internal laminae of each petaloid element, as seen in vertical sections (Figs. 4A,I and 8), indicates that the outer burrow fill domain started at the outer margin of the excavation and continued toward the central part of the burrow, ruling out that this material was radially compressed by the producer. The structure and composition of the outer fill domain thus imply a detritus feeding mode when the producer dragged surface material to a feeding cavity before ingestion. The repeated enrichment of densely packed microfossils and plant debris in discrete levels within the structure probably reflects pulsed delivery of organic matter to the seafloor, followed by rapid subduction and redistribution by the trace maker. Pulsed delivery of organic matter to the seafloor is a widespread phenomenon and the food is generally rapidly consumed by the benthos, particularly if it consists of labile organic material, such as that associated with particulate matter derived from phytoplankton cells (phytodetritus) clumped together by bacteria and organic slimes (Quijón et al., 2008). Hoeing, downward transport and probably caching of organic matter is the expected response to pulsed phytodetrital inputs (Levin et al., 1997).

After excavation and production of a burrow fill disk (e.g. Fig. 8 disk VI), a new feeding chamber is formed. The material filling the previous feeding chamber now functions as "culturing compartment" and is situated above. Then the "culturing compartment" is reworked in a narrow zone that constitutes the inner fill domain (Fig. 8C). The activity of the producers reworking the relatively coarse material next to the axial tube is expressed by the remarkable structure of the inner fill domain, while its petaloid laminae clearly crosscut the outer burrow fill domain (e.g. Figs. 2B–C, 3D–E, 4A–F, I). This reworking activity was repeatedly conducted by the producer, probably just after abandonment of the previous feeding chamber, during or after constructing a new feeding chamber below, but before formation of a new disk below and enlargement of the lined tube. The remarkable structure of the inner fill domain, which originates from reworking of the sedimentary particles stored in the previous feeding chamber, strongly suggests culturing and gardening of microbial organisms (gardening mode, Fig. 8C).

The inferred main ethological category of *Tasselia* as a fodinichnion is consistent with the commonly associated trace fossils, which are dominated by biogenic structures made by deposit feeders (see Section 4.3) and with the record of *Tasselia* in modern settings characterized by organic-rich muddy sediments (Wetzel and Bromley, 1996).

5.3. Identity of the trace-maker

Due to divergent taphonomic selection rarely a trace fossil and its producer are found together, as in the superb examples of Solnhofen mortichnia (Seilacher, 2008). In a few cases, however, the identity of the trace maker can be deduced from particular fingerprints, as in the trace fossil *Cruziana* made by trilobites (Seilacher, 2007). This latter approach can be applied to the trace fossil *Tasselia*, which includes features that on the whole can be considered diagnostic fingerprints of maldanid polychaetes. These include the association of the organic-lined inner tube, with sizes and microstructures typical of some annelid polychaetes including maldanids, and the morphology and internal structure of the thick sediment cover, typical of maldanids. The high-density population of the *Tasselia* structure, c. 550 specimens per m^2, is also common in annelid polychaetes and several genera in the Maldanidae are known to colonize the seafloor in high numbers, reaching generally several hundred specimens per square meter (Mangum, 1964; Levin et al., 1997, Dufour et al., 2008).

Lined tubes are made by several marine invertebrates, but apparently the characteristic ornamentation on the outer wall bearing irregular, fine striae interrupted by regularly spaced, coarser annulations are typical of burrowing tubicolous polychaetes that build their membranous tube by successive additions of strings of mucus (Barnes, 1974; Schweitzer et al. 2005; Thomsen and Vorren, 1984). Similar structures, albeit of larger size and different morphologies, are known from the fossil record and assigned to annelid polychaetes (Howell, 1962; Schweitzer et al. 2005; Thomsen and Vorren, 1984, and the bibliography therein). In particular, the ornamentation of the irregular tubes from the Eocene La Meseta Formation, Antarctica (Schweitzer et al., 2005) is similar to the irregular striae of the inner tube of *Tasselia*. These Eocene ornamented tubes were compared with similar structures known in extant polychaetes of the families Ampharetidae, Maldanidae, Sabellidae and Trichobranchidae (Schweitzer et al., 2005).

The analysis of different guilds in polychaete families based on food, feeding habits, and locomotion patterns suggest, however, that only maldanids successfully occupied the burrowing, subsurface deposit feeding, sedentary, and non-jawed guild (Fauchald and Jumars, 1979), and thus are possibly capable of building biogenic structures such as *Tasselia*. Indeed, the only known extant biogenic structures homologous to the vertically stacked series of sediment-disks of the trace fossil *Tasselia* result from the feeding activity of burrowing and sedentary maldanid polychaetes, such as *Maldane glebifex* (Babin et al., 1971) and *M. sarsi* (Dufour et al., 2008).

6. Conclusions

In addition to an axial lined tube and a basal feeding chamber, the morphological elements of *Tasselia ordamensis* include a burrow fill arranged in vertically stacked sediment disks. Each sediment disk includes an outer and an inner burrow fill domain structured into radially arranged petaloid elements. The laminae of the petaloid elements of the inner burrow fill domain sharply crosscut the internal structure of the outer burrow fill domain and interdisk layers of undisturbed host sediment.

The crosscutting relationships between the outer and inner fill domains indicate a protrusive structure. This, in addition to the internal morphology and crosscutting relationships of the outer and inner fills domains, indicates that *Tasselia ordamensis* is a fodinichnion, not a domichnion/equilibrium structure made by suspension feeders as was previously thought.

The active burrow fill of *Tasselia* was originated through deposit feeding, detritus feeding, and probably gardening strategies of the producer. During deposit-feeding, the producer organism excavated the burrow ejecting non-digested particles to the surface. The excavation was filled with fine particles, plant debris and microfossils subducted from the surface (detritus feeding) and redistributed into the excavation originating the structured outer fill domain. After building a new feeding chamber, the previous one functioned as a “culturing compartment” for microbes; hence, the reworking of the inner fill material inside this compartment probably represents a gardening activity.

The structure and composition of the biogenic structures of the extant polychaetes *Maldane glebifex* Gruber and *Maldane sarsi* Malmgren are remarkably similar to those of *Tasselia ordamensis.* Particular fingerprints allowing inferring maldanids as the producer of the trace fossil *T. ordamensis* are the circular striations and regularly spaced annulations on the outer wall of the inner tube and the vertically stacked series of sediment disks.

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