Trochosira polychaeta: a colonial diatom from the late Cretaceous exhibiting two contrasting chain-linking mechanisms and a wide range of preservation.

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ABSTRACT

The fossil species *Trochosira polychaeta* Strelnikova, exhibits a wide range of preservational states that has led to contrasting interpretations with regard to its resting stage or vegetative cell status. Within shallow-buried, well preserved diatomites from the Alpha Ridge of the Arctic Ocean, a continuum of dissolution effects are documented and a vegetative cell status is clearly indicated. The chains are formed by a central linking process but complex marginal structures also constitute a complementary linking mechanism. The double linkage may have supported the integrity of the colonial chains and provided a mechanism for enhanced nutrient uptake. The presence of two distinct types of linking might also represent a stage in a transition from the Cretaceous when central linking structures were common, through the Cenozoic to the modern with more common linking through marginal structures.

KEYWORDS

Trochosira polychaeta; Cretaceous; diatoms; dissolution; chain linkage; transitional form

Introduction

The Cretaceous diatom record documents their evolution and radiation from isolated occurrences within shallow coastal or shelf sequences to fully oceanic diatomite deposition (Harwood & Nikolaev, 1995; Harwood et al., 2007). Many early Cretaceous forms are morphologically distinct from those found in younger deposits but, by the late Cretaceous, many modern morpho-genera are recognized that persisted relatively unaffected through the K-Pg extinctions (Harwood, 1988; Sims et al., 2006; Harwood et al., 2007). Diatoms are a dominant phytoplankton group in the modern ocean and play a key role in the marine biological carbon pump. However, the timing of onset of this key biogeochemical function and the elucidation of Cretaceous diatom ecology in general, is problematical due to both preservational issues as well as to the general sparseness of material. Exceptional preservation in a few key deposits such as the Marca Shale of California (Nikolaev et al., 2001) or the diatomites of western Siberia (Strelnikova, 1974) afford the opportunity to observe delicate and preservationally ephemeral features of the diatom frustule that may be critical for ecological interpretation.

Diatom adaptations present by the early Cretaceous included resting spore formation and the development of linking structures to form colonial chains (Gersonde & Harwood, 1990; Harwood & Gersonde, 1990). The ability to evaluate the extent and development of both of these attributes is critically associated with the degree of preservation. For example there has been a tendency to designate robust and/ or more hyaline frustules as resting spores. Likewise, the structures that link chains (often delicate spines or processes) are vulnerable and with some dissolution and/ or mechanical stress resulting in breakage, may disappear entirely. Mechanisms of chain formation in Cretaceous diatoms included central and marginal linking structures (Witkowski et al., 2011) although subsequent evolution through the Cenozoic appears to have favoured linkage by the marginal spines or processes that are common in modern chain-forming species (Gebeshuber & Crawford, 2006; Crawford and Sims, 2008).

The differentiation of diatom vegetative cells and resting spores has been contentious in fossil examples (Hargraves, 1986) and is especially difficult in Cretaceous sequences due to the generally poor state of preservation of biosiliceous microfossils (Harwood et al., 2007). An exception to this is the shallow buried Cretaceous sediment (CESAR 6 and Fl-437 cores) from the Alpha Ridge of the Arctic Ocean, that contains superbly preserved diatomaceous material (Barron, 1985; Dell'agnese & Clark, 1994; Davies et al., 2009). The preservation of delicate and lightly silicified parts of the frustule affords an excellent opportunity to make the distinction between resting spores and vegetative cells and to document mechanisms of chain formation. Furthermore, the laminated sediments of the CESAR-6 core represent a palaeo-sediment trap that preserves successive flux events permitting the identification of co-sedimented diatoms from which more robust ecological interpretations may be made of associated species (Davies et al., 2009). In this contribution we document one species, *Trochosira polychaeta* Strelnikova that has been assigned resting spore status by some earlier studies (Kitchell et al., 1986; Dell'Agnese & Clark, 1994). It is a particularly intriguing example in that it exhibits a wide range of preservation, even within the relatively excellently preserved diatoms of the Alpha Ridge floras. Moreover, it appears to exhibit two distinct mechanisms of chain formation, by both a central linking process and a complementary marginal structure.

Materials and Methods

Sediment samples were taken from the Alpha Ridge CESAR-6 core, interval 134 – 295 cm, held at the Bedford Institute of Oceanography (see Davies et al. 2009 for detailed core description and stratigraphy). On sampling, the perfectly curated archive half was still wet and resembled a near-surface modern core of deep-sea diatom ooze. Samples were taken with a cookie-cutter slab sampler. Slabs were sub-sampled and one part was embedded with resin from which polished thin sections (PTS) were prepared. These were carbon-coated and imaged using back scattered electron microscopy (BSEI) to provide detail of the lamina structure. Following lamina identification, the still moist, sediment counterpart to individual PTS was sub-sampled, mounted on SEM stubs, gently air dried, gold coated and topographically imaged using SEI (secondary electron imagery) or BSEI. This ensured the imaging of intact sediment surfaces, undisturbed since settling, allowing the delicate original features to be examined. In addition, samples from counterparts to PTS were prepared by taking peels using adhesive tape. Complementary samples were prepared for optical microscopy using an adaptation of the method of Scherer (1994) (C.S. Allen pers, comm. 2004). Most of the micrographs in the present figures derive from imaging of mounts of the original intact, undisturbed sediment. To counter problems of charging in secondary electron imaging mode, most of the images were taken in BSEI mode. Although the resolution of BSEI is less than SEI, the processes of disaggregating and remounting the material would likely have resulted in the disintegration of the delicate structures present. We emphasize that our aims here were to facilitate the best possible observation of the diatom ooze in its undisturbed state, hence BSEI was used. We did not set out to undertake a detailed study of, for example, the wall ultrastructure for taxonomic purposes, which will be the subject of another publication.

Results

Occurrence of **Trochosira polychaeta** *within the CESAR-6 core*

A total of 3,622 laminae comprising 1693 varves or annual lamina groups were measured from the CESAR-6 core. Diatom abundance counts are given in Davies et al. (2009). The most common and simplest annual sediment configuration comprised a relatively thin lamina of *Chaetoceros*-type resting spores and a thicker lamina of vegetative cells of various species interpreted as the result of spring and late summer/ early winter flux respectively (Davies et al., 2009). Of the vegetative cell laminae, 1259 were designated “mixed flora” whereas 323 were near-monospecific or near-monogeneric being dominated by individual taxa. Some 73 laminae dominated by *T. polychaeta* were recognized, however, it was also a component of numerous “mixed flora” laminae. A wide range of states of preservation were evident. Valve diameters are variable but typically lie within the range 14 – 40 μm (Sims [1988] gives 14 – 55 μm and Strelnikova [quoted in Sims, 1988] gives 11 – 25 μm).

Morphology (Figs 1-22)

Marginal linking structures

In the best preserved examples, abundant intact, linked or semi-intact chains linking up to 4 cells are observed (Figs 1, 2). In these cases, initial disarticulation most commonly occurs between valves, rather than within the marginal structures, attesting to the relative strength of the inter-cell linkage. In detail, the marginal structure is compound (Figs 3, 4, 5, 6) and comprises a hyaline valve margin of about 1.5 μm with superimposed, buttress-like filaments spaced at 0.5 – 1 μm; next a highly porous zone (3-4 μm) over which the buttress-like filaments extend and connect with finer filaments. The filaments are contiguous but may merge or bifurcate across the transition. (Note that Sims [1988] describes the buttress-like filaments as "vertical strands or costae….. linked by finer costae"- her figs 15, 19, 21.) The final section is a hyaline zone (4-8 μm) punctured by rows of fine pores. The rows of fine pores may terminate or coalesce towards the mid-point between valves, resulting in some examples, in a more hyaline central section (Figs 3-5, 6, 7-10, 11). In other examples, the rows of pores are more continuous and, in frustules exhibiting partial dissolution of pores, the overall structure resembles a series of hyaline strips that appear to link across the mid-point between the siblings (Figs 8, 10, 18). The join between the marginal structures of adjacent cells is marked by an irregular welded suture (Figs 3, 4, 6, 7) which appears to be the next most susceptible to parting after the valves themselves (Figs 8, 11). In some examples there is a fine annular hyaline ridge just beyond the start of the rows of fine pores (Figs 7, 8). This ridge sometimes survives significant dissolution (Figs 12, 13) and is also clearly visible in figs 15, 19 and 20 of Sims (1988). We emphasize here that this view is in contrast to that of Sims (1988) who misinterpreted the marginal linking structures as girdle bands. We describe the distinct girdle, in detail, below. Sims' interpretation was likely due to the lack of fine preservation in her samples. Only in fig. 16 of Sims (1988) is a delicate cingulum remnant observed, where it is described as a "hyaline marginal ridge" of the valve.

Girdle

The remnants of a cingulum are most commonly observed between partly detached valves (Figs 3, 4, 9, 11, 12, 13, 20, 21, 22) and see also on the lower valve of fig. 16 of Sims (1988). From the valve margin, the cingulum comprises a 1 to 1.5 μm hyaline zone, succeeded by a zone of thin hyaline strips around 0.1 μm thick with similar spacing. These strips are invariably highly corroded and only in one instance are they observed to exceed 4 μm in length (Fig. 11). Where still attached to the valve, they are clearly external to, and separate from, the marginal structures described above (Fig. 12). The advalvar margin of these strips (Figs 9, 11) possesses a *pars interior* that inserts under the edge of the "parent" valve (Fig. 6). These girdle remnants resemble the girdle bands of *Skeletonemopsis morenoensis* Sims as imaged in fig. 6 of Sims (1994).

Central Linking Structure

A hyaline central linking process with a tri-radiate base is observed in examples where the marginal structure has been wholly or partly corroded (Figs 14-17, 19-21). It is also apparent as a shadow beneath the marginal structures in optical microscopy (Fig. 18). In some instances the process forms a tri-faceted rod with a pointed tip that inserts into a hyaline tri-radiate process with a connecting slot (Figs 14, 16, 20, 21) and see also figs 16 and 17 of Sims (1988). (Note that here we use the same descriptive terms as Sims, 1988.) In other cases, a clasp-type structure (Fig. 17) may link onto a flattened hyaline process, again with a tri-radiate base (Fig. 15) resulting in a shorter inter-valve separation. We note that Sims (1988) also documented two, apparently distinct central linking structure configurations (see Discussion, below).

Range of preservation states

The wide range of preservation states that track the progressive erosion and dissolution of *T. polychaeta* are illustrated in Figs 18-22 and schematically in Fig. 23. The most delicate and ephemeral structures are the cingula which are generally only present as remnant bases, with the fringe only preserved exceptionally (Figs 11-13). The first breaks within the chains evidently occur between valves of the same cell rather than between the linking structures.

Subsequent erosion affects the marginal structures, with a break appearing along the sutured join between the two valves and piecemeal loss of the more delicate elements (Figs 7-13; 19-22). Progressive erosion of the marginal structure reveals the central linking process (Fig. 19). With further degradation, all trace of the central process also vanishes (Fig. 22). The surface of the valve face may be covered by hyaline ridges or what Sims (1988) describes as “anastomosing costae with thickened knobs or verrucae at their junctions” (Figs 12-17 and 20-22; Sims, 1988, figs 16, 17, 20). These hyaline structures on the valve face also appear subjected to progressive erosion, culminating in an unadorned valve with radial areolae (Fig. 22). Sims (1988) also described this progressive erosion, noting that: “On eroded valves, the central linking mechanism is often missing, with little evidence to show that it had ever been present, apart from a few missing cribra.”.

Although there is a wide range in preservation types, it is common that within individual laminae, there is a more uniform state of preservation. This ranges from laminae with largely intact, still-articulated chains (Figs 1, 2) to laminae with only highly eroded frustules (Fig. 22).

Discussion

***Vegetative cell status and ecology of* Trochosira polychaeta**

The distinction between diatom resting spores and vegetative cells in the fossil record is important in the palaeoecological interpretation of ancient diatomaceous sediments. For example, the presence of abundant resting spores has been related to sedimentation from the spring bloom (McQuoid & Nordberg, 2006), and resting spore flux may be especially important in the export of fresh organic material to the sea floor (Salter et al., 2012; Rynearson et al., 2013). Earlier interpretations of *T. polychaeta* have assigned it resting spore status (e.g. Kitchell et al., 1986; Dell'Agnese & Clark, 1994). More recently, in a review of resting spore assemblages from the Lomonosov Ridge, Arctic Ocean, Suto et al. (2009) reasoned that although the valves of *T. polychaeta* were heavily silicified, the possession of numerous areolae might indicate vegetative cell status.

A number of criteria have been proposed to aid the distinction between resting spores and vegetative cells in the fossil record. The key identifying characteristics of vegetative cells that Gersonde & Harwood (1990) used were (1) weakly silicified valves; (2) a relatively large frustule volume; (3) a perforate basal siliceous layer leading to a relatively "permeable" valve structure; (4) the presence of connecting bands. In addition, Hargraves (1986) also noted the absence of girdle bands in spores. However, the preservation of delicately silicified material is a necessary prerequisite to the use of such criteria. In poorly preserved examples there is a selective bias towards more heavily silicified frustule elements so that there is a tendency towards spore identification.

From our study and that of Sims (1988), it is evident that *T. polychaeta* represents an example of a colonial vegetative cell. The preserved chains, the delicate linking structures and the presence of remnant girdle bands individually and collectively argue for a vegetative cell status. The co-occurrence of *T. polychaeta* with *Hemiaulus* Heiberg spp. within the vegetative laminae of the CESAR 6 core further supports a vegetative cell status. The fact that *T. polychaeta* and *Hemiaulus* spp. were sedimented concurrently and both are chain formers suggests a common ecological niche: one of adaptation to the stratified waters of the Cretaceous Arctic summer (Davies et al., 2009).

The wide range of preservation states in *T. polychaeta* is interpreted as representing the results of different stages of dissolution. From our extensive experience of diatom observations in surface and deep sediment traps, and in surficial laminated sediments that preserve successive flux events undisturbed by benthic activity, there can be significant variation in water column dissolution. This likely reflects the variable dissolved silica concentration in ocean waters, particularly at the termination of blooms when silica becomes depleted, or in stratified water columns where there may be sharp gradients in concentrations. It might be argued that, where only highly eroded *T. polychaeta* frustules are observed (Fig. 22), these may represent the formation of a resting stage, with the more lightly silicified vegetative frustule components having been discarded. However, even in such circumstances, significant remnants of the more delicate structures are present and the rows of fine areolae are consistent with vegetative stage status (cf. Suto et al., 2009).

There is a tendency towards consistent levels of preservation of *T. polychaeta* within individual laminae with co-location of largely intact, still-articulated chains, on the one hand (Figs 1, 2), to laminae with highly eroded frustules on the other (Fig. 22). Well-preserved and dissolved frustules may occur only mm apart, so that differential dissolution post-sedimentation is not possible. Since these near-monospecific laminae correspond to individual flux events (Davies et al., 2009), the differential preservation is likely due to differing dissolved silica water column concentrations post-bloom and prior to settling, reflecting seasonal differences in nutrient availability and water column structure.

Variation in separation of cells and in linking structures

There are variations in the separation of cells within *T. polychaeta* chains that appear to be driven by differences in the morphology of the central linking mechanism. Both Sims (1988) and this study document a relatively longer linkage involving the slotting of a tri-faceted spine into a tri-radiate slot, and a shorter link that involves a more flattened central process to which clasp-like joins are made by the opposing valve (Figs 14-17, and Sims 1988 figs 16, 17). Sims refers to the shorter join as “immature” but in modern diatoms, the connecting processes between cells may become shorter with silica limitation (Conway & Harrison, 1977). A similar limitation effect may exist in *T. polychaeta*. Computational studies suggest that a simple switch in environmental parameters might be sufficient to drive a change in the morphology of the structures that link diatom chains (Bentley et al., 2012).

The evolution of chain linking mechanisms: marginal linking, central linking and combinations of both

Chain formation appeared early within the evolutionary history of diatoms (Gersonde & Harwood, 1990; Crawford & Sims, 2008) and has evolved independently in several lineages of diatoms at different times since (Kooistra et al., 2007), yet its ecological significance remains a subject of debate. The most obvious utility of chain formation is that it keeps cells linked and so reduces dispersal (Crawford & Sims, 2008). It is also variously thought to provide resistance to predation (Smetacek et al. 2004), reduce sinking velocities (Takabayashi et al. 2006), enhance nutrient uptake (Musielak et al. 2009) and/ or aid sexual reproduction (Kooistra et al., 2007). Given this diversity in form and function, the Cretaceous was a period of much evolutionary experimentation, not least with regard to mechanisms of chain formation (Gebeshuber & Crawford, 2006).

Strelnikova (1971) originally designated the marginal linking structures of *T. polychaeta* as 'marginal spines' and hence, by analogy with the chain-linking mechanism of elongate marginal processes, assigned the species to the genus *Skeletonema* Greville (*Skeletonema polychaetum* Strelnikova). In studies restricted to optical microscopy, well preserved examples do, indeed, resemble *Skeletonema* (Fig. 18) but this resemblance does not survive SEM scrutiny. In the previous most detailed SEM-based description of samples (also from the Alpha Ridge) Sims (1988) described the marginal structures as girdle bands. However, examination of our samples, together with a re-assessment of Sims (1988, figs 15-21), clearly shows these to have formed between adjacent cells and not to represent part of an epi- or hypo-cingulum. Furthermore, we have identified separate features, external to the marginal linking structures, that appear to represent the remains of girdle bands (Figs 6, 11-13).

In the best preserved examples the marginal structures of adjacent valves of *T. polychaeta* are joined along an irregular 'welded' suture (Figs 3-5; 6, 7, 10). Two of the three other species of *Trochosira* documented by Sims (1988) (*T. mirabilis* Kitton and *T. coronata* Schrader & Fenner) possess marginal spines, but although they may overlap (in *T. mirabilis*), they are not joined, making *T. polychaeta* unique within the genus in this regard. The welded marginal structures of *T. polychaeta* appear to constitute a marginal linking mechanism that is distinct from the central linking structure. Why then would a diatom adopt two separate linking mechanisms? Gebeshuber & Crawford (2006) note that the central linking process or spine of *Trochosira* would have prevented twisting between cells but did not readily see how this could hold the valves together. Thus, it may be that the marginal welded linking structures of *T. polychaeta* helped maintain the integrity of the chain.

Was the development of marginal as well as central linking structures a "belt and braces" job designed to make chains stiffer and reinforce them against breakage? Several benthic diatoms such as the cymatosirids or *Ellerbeckia* R.M. Crawford possess both central and marginal linking structures, and it might be argued that the "double linking" strategy was adopted to reduce the likelihood of breakage in the turbulent environment of the benthic boundary layer. A combination of marginal and central linkages is also common in the Rutilariaceae (Witkowski et al., 2011). The conservative nature of this adaptation is exemplified by the tychopelagic genus *Paralia* Heiberg which has deployed both central and marginal structures from the late Cretaceous to the present (Crawford & Sims, 2008). Such arguments, however, cannot apply to *T. polychaeta* since it occupied a pelagic niche adapted to the stratified conditions of the Cretaceous Arctic summer together with several *Hemiaulus* species and *Rhizosolenia* Brightwell (Davies et al., 2009). In such stratified conditions nutrients are scarce in the surface and diatoms employ a range of strategies including symbiosis with N-fixing symbionts, mining nutrients from depth or reliance on episodic mixing events (Kemp & Villareal, 2013). Interestingly, numerical modelling of diatom nutrient acquisition suggests that more rigid chains encounter more nutrients (Musielak et al., 2009) so the double linking mechanisms may have given *T. polychaeta* a competitive advantage in this environment.

More broadly, could the development of marginal linkages have been a step on the way to changing from a central massive linking structure to a marginal linking mechanism closely resembling the marginal strutted processes of *Skeletonema* (Strelnikova's original taxonomic assignment)? From the Cretaceous through the Cenozoic there appears to be an evolutionary trend moving from dominant central linking towards more common marginal linking in diatom chain formation (Crawford & Sims, 2008; Gebeshuber & Crawford, 2006). It may be that *T. polychaeta* represents a transitional form in this trend. Much of this conjecture is necessarily speculative and it is clear that more research on the relationship between form and function in diatom chain linking mechanisms is required to address these issues. Quantitative studies of mechanical properties of different diatom chain configurations have only recently been initiated (Young et al. 2012) and such research will form an important foundation for further progress in this field.

Nomenclatural note

Although Tapia in Tapia & Harwood (2002) made a new combination *Trochosropsis polychaeta* for the subject of this article, we found no justification for this and have retained use of the name *Trochosira polychaeta*. The relevant nomenclatural details are as follows:

Trochosira polychaeta (Strelnikova) Simms 1988
Figs. 1-5; 7-22.
Trochosira polychaeta (Strelnikova) Simms 1988, p. 251, figs 15-21, 29-34.
Basionym: *Sceletonema polychaetum* Strelnikova 1971, p. 42, pl.1, figs 3-5.
Strelnikova 1974, p. 54, pl. 3, figs 3-7. – Barron 1985, p. 141, pl. 10.1, figs. 2-4
Synonymy: *Pyrgodiscus triangulates* Hajós and Stradner 1975, p.928, figs 11a, b; pl 18, figs 5, 6.
Trochosiropsis polychaeta (Strelnikova) Tapia in Tapia and Harwood 2002, p. 330, pl. 8, figs 3, 4.

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References

BARRON J.A. 1985. Diatom stratigraphy of the CESAR 6 core, Alpha Ridge, Arctic Ocean, In: Initial Geological Report on CESAR: the Canadian Expedition to Study the Alpha Ridge, Arctic Ocean. (Ed. By H.R. Jackson, P.J. Mudie & S.M. Blasco), pp. 137-148. Geological Survey of Canada, Paper 84-22. Ottawa.

BENTLEY K. CLACK C. & COX E.J. 2012. Diatom colony formation: a computational study predicts a single mechanism can produce both linkage and separation valves due to an environmental switch. *Journal of Phycology* 48: 716-728.

CONWAY H.L. & HARRISON P.J. 1977. Marine diatoms grown in chemostats under silicate or ammonium limitation. IV. Transient response of *Chaetoceros debilis*, *Skeletonema costatum*, and *Thalassiosira gravida* to a single addition of the limiting nutrient. *Marine Biology* 43: 33-43.

CRAWFORD R.M. & SIMS P.A. 2008. Some principles of chain formation as evidenced by the early diatom fossil record. *Nova Hedwigia* 133: 171-186.

DAVIES A., KEMP A.E.S. & PIKE J. 2009. Late Cretaceous seasonal ocean variability from the Arctic. *Nature* 460: 254-258.

DELL'AGNESE D.J. & CLARK D.L. 1994. Siliceous microfossils from the warm Late Cretaceous and Early Cenozoic Arctic Ocean. *Journal of Paleontology* 68: 31-47.

GEBESHUBER I.C. & CRAWFORD R.M. 2006. Micromechanics in biogenic hydrated silica: hinges and interlocking devices in diatoms. *Journal of Engineering Tribology* 220: 787-796.

GERSONDE R. & HARWOOD D.M. 1990. Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 1: Vegetative cells. In: *Proceedings of ODP, Scientific Results, 113.* (Ed. by P.F. Barker & J.P. Kennett) pp. 365-402. College Station, TX (Ocean Drilling Program).

HAJÓS M. & STRADNER R.H. 1975. Late Cretaceous Archaemonadaceae, Diatomaceae and Silicoflagellatae from the South Pacific Ocean, Deep Sea Drilling Project, Leg 29, Site 275. *Initial Reports of the Deep Sea Drilling Project*, 29: 913-1009. Washington D.C.

HARGRAVES P.E. 1986. The relationship of some fossil diatom genera to resting spores. In: *Proceedings of the 8th international diatom symposium* (Ed. by M. Ricard), pp. 67-80. Koenigstein: O. Koeltz: Koeltz Scientific Books.

HARWOOD D.M. 1988. Upper Cretaceous and lower Paleocene diatom and silicoflagellate biostratigraphy of Seymour Island, eastern Antarctic Peninsula. In: *Geology and Paleontology of Seymour Island, Antarctic Peninsula*, Geological Society of America Memoir 169. (Ed. by M.R. Feldmann & M.E. Woodburne) pp. 55-129. Boulder.

HARWOOD D.M. & NIKOLAEV V.A. 1995. Cretaceous diatoms: morphology, taxonomy, biostratigraphy. In: *Siliceous Microfossils*, (Ed. by C.D. Blome et al. (conveners)), Paleontological Society short course notes 8, pp. 81-106, pls 101-104.

HARWOOD D.M. & GERSONDE R. 1990. Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 2: Resting spores, Chrysophycean cycts, an endoskeletal dinoflagellate, and notes on the origin of diatoms. In: *Proceedings of ODP, Scientific Results, 113.* (Ed. by P.F. Barker & J.P. Kennett) pp. 403-425. College Station, TX (Ocean Drilling Program).

HARWOOD D.M., NIKOLAEV V.A. & WINTER D.M. 2007. Cretaceous Records of Diatom Evolution, Radiation, and Expansion. In: *Pond Scum to Carbon Sink: Geological and Environmental Applications of the Diatoms* (Ed. by S. Starratt), pp. 33-59. The Paleontology Society Papers 13, Paleontological Society.

KEMP A.E.S. & VILLAREAL T.A. 2013. High diatom production and export in stratified waters - A potential negative feedback to global warming. *Progress in Oceanography* 119: 4-23.

KITCHELL J.A., CLARK D.L. & GOMBOS A.M. 1986. Biological selectivity of extinction: A link between background and mass extinction. *Palaios* 1: 504-511.

KOOISTRA W.C.F., GERSONDE R., MEDLIN L.K. & MANN, D.G. 2007. The origin and evolution of the diatoms: Their adaptation to a planktonic existence. In: *Evolution of primary producers in the sea*. (Ed. by P.G. Falkowski & A.H. Knoll) pp 201-250.

MCQUOID M.R. & NORDBERG K. 2006. Composition and origin of benthic flocculent layers in Swedish fjords following the spring bloom - contribution of diatom frustules and resting stages. *Nova Hedwigia* 83: 1-16.

MUSIELAK M.M., KARP-BOSS L., JUMARS J.A. & FAUCI L.J. 2009. Nutrient transport and acquisition by diatom chains in a moving fluid. *Journal of Fluid Mechanics* 638: 401-421.

NIKOLAEV V.A., KOCIOLEK J.P., FOURTANIER F., BARRON J.A. & HARWOOD D.M. 2001. Late Cretaceous diatoms (Bacillariophyceae) from the Marca Shale member of the

Moreno Formation, California. *Occasional Papers of the California Academy of Sciences* 152, 119 pp.

RYNEARSON T.A., RICHARDSON K., LAMPITT R.S., SIERACKI M.E. POULTON A.J., LYNGSGAARD M.M. & PERRY, M.J. 2013. Major contribution of diatom resting spores to vertical flux in the sub-polar North Atlantic. *Deep Sea Research I* 82: 60-71.

SALTER I., KEMP A.E.S., MOORE C.M., LAMPITT R.S., WOLFF G. & HOLTVOETH J. 2012. Diatom resting spore ecology drives enhanced carbon export from a naturally iron-fertilized bloom in the Southern Ocean. *Global Biogeochemical Cycles* 26: GB1014, doi:10.1029/2010GB003977.

SCHERER R.P. 1994. A new method for the determination of absolute abundance of diatoms and other silt-sized sedimentary particles. *Journal of Paleolimnology* 12:171-179.

SMETACEK V., ASSMY P. & HENJES J. 2004. The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. *Antarctic Science* 16: 541-558.

SIMS P.A. 1988. The fossil genus *Trochosira*, its morphology, taxonomy and systematics. *Diatom Research* 3: 245-257.

SIMS P.A. 1994. *Skeletonemopsis* a new genus based on the fossil species of the genus *Skeletonema* Grev. *Diatom Research* 9: 387-410.

SIMS P.A., MANN D.G. & MEDLIN L.K. 2006. Evolution of the diatoms: insights from fossil, biological and molecular data. *Phycological Reviews* 45: 361-402.

STRELNIKOVA N.I. 1971. Species novae bacillariophytorum e sedimentis cretae posterioris in declivate orientali partis polaris ac praepolaris Montium Uralensium. Novosti Systematiki Nizshikh Rastenii, Botanicheskii Institut, Akademia Nauk SSSR, 8: 41-51.

STRELNIKOVA N.I. 1974. *Diatomei pozdnego mela*. Moskva: Nauka.

SUTO I., JORDAN R.W. & WATANABE M. 2009. Taxonomy of middle Eocene diatom resting spores and their allied taxa from the central Arctic Basin. *Micropaleontology* 55: 259-312.

TAKABAYASHI M., LEW K., JOHNSON A., MARCHI A., DUGDALE R., & WILKERSON F.P. 2006. The effect of nutrient availability and temperature on chain length of the diatom, *Skeletonema costatum*. *Journal of Plankton Research* 28: 832-840.

TAPIA P.M. & HARWOOD D.M. 2002. Upper Cretaceous diatom biostratigraphy of the Arctic archipelago and northern continental margin, Canada. *Micropaleontology* 48: 303-342.

WITKOWSKI J. , SIMS P.A. & HARWOOD D.M. 2011. Rutilariaceae redefined: a review of fossil bipolar diatom genera with centrally positioned linking structures, with implications for the origins of pennate diatoms. *European Journal of Phycology* 46: 378-398.

YOUNG A.M., KARP-BOSS L., JUMARS J.A. & LANDIS E.N. 2012. Quantifying diatom aspirations: mechanical properties of chain-forming species. *Limnology and Oceanography* 57: 1789-1801.

Figure Captions.

Figs 1-2. SEM images of *Trochosira polychaeta* chains. **Fig. 1.** Four cells in a chain with separation between valves, but with marginal structures still largely intact and linking successive valves (position of successive valves arrowed). **Fig.2.** Three chains, with lower chain linking four cells with valves and marginal structures intact. Middle chain shows separation of valves of central frustule and erosion of marginal structures in the top valve. Scale bars = 10 μm.

Figs 3-5. SEM images showing the marginal structures of *Trochosira polychaeta*. **Fig. 3.** Linked cells showing intact marginal structures between the lower two valves. Note the erosion of the marginal structures at the top that reveals the base of the central tri-radiate linking structure. **Fig. 4**. Detail of upper central portion of Fig. 3 showing the tripartite configuration of the marginal structures (arrows mark the boundaries): 1) a hyaline zone of about 1.5 μm with buttress like filaments; 2) a highly porous zone (3-4 μm) over which the buttress-like filaments extend and connect; 3) a hyaline zone punctured by rows of fine pores. Note the irregular suture with the marginal structure from the adjacent valve in the lower part. **Fig. 5.** Detail of structure of a valve linked in a more closely spaced chain with a proportionately shorter hyaline section. Scale bar represents 10 μm (Fig. 3), 1 μm (Fig. 4), 5 μm (Fig. 5).

Fig. 6. Sketch showing main elements of a more intact and well preserved example also displaying a remnant of a cingulum.

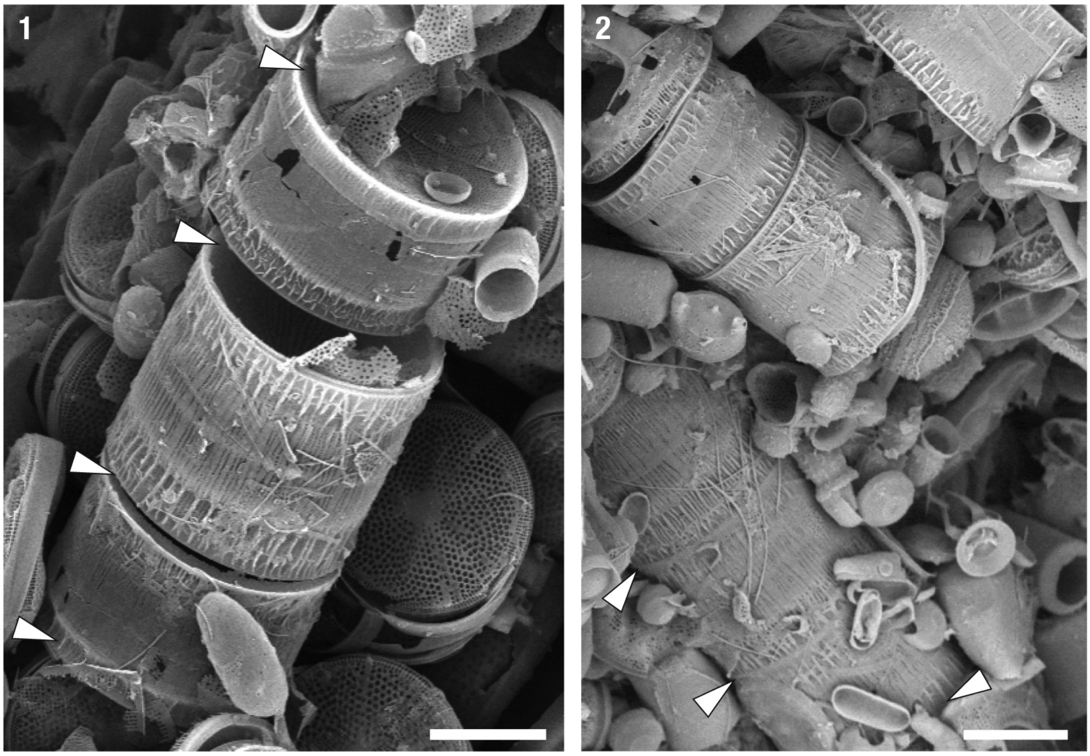
Figs 7-10. SEM images of *Trochosira polychaeta* showing detail of the marginal structures. **Fig. 7.** Two linked valves with marginal hyaline zone welded at the mid point. A prominent hyaline ridge (arrowed) is present and a part of the hyaline zone between this and the mid-point join has detached. **Fig. 8.** A more dissolved marginal structure in which many of the pore boundaries have gone giving the overall appearance of separate irregular hyaline strips. The prominent hyaline annular strip (arrowed) is also partly corroded but still clearly visible and an intact segment is present to the left. **Fig. 9.** Detached valves with the upper showing a largely eroded marginal structure. Extending from the lower valve, and in contrast to Figs 8 and 10, a more hyaline outer zone persists. The eroded basal part of a cingulum lies between the valves (arrowed). **Fig. 10.** Two connected valves showing a partly eroded marginal linking structure. The pore boundaries of the rows of fine pores in the central zones are mainly eroded giving the impression of a series of vertical hyaline strips or processes with many apparently still connecting the two cells. Scale bars represent 10 μm.

Figs 11-13. SEM images of *Trochosira polychaeta* showing detail of the remnant cingula. **Fig. 11.** A chain showing parting between valves and along the irregular mid-point suture of the marginal linking structure. Detached, eroded segments of cingula are arrowed. A relic still-attached cingulum is arrowed “A”. Remnants of delicate, thin hyaline strips around 0.1 μm thick with similar spacing are common, but, exceptionally, in the lowermost example, these are seen to extend for up to 5 μm. The cingula are clearly separate and distinct from the still-intact marginal linking structures. **Fig. 12.** Detached valves, the uppermost with a still attached cingulum from which the hyaline strips are largely eroded. On the left margin (arrowed), the cingulum is clearly external to, and separate from the remnant marginal structures which include the hyaline annular strip (seen intact in Figs 7 and 8). Note external openings of rimoportulae along the valve margin (three are arrowed). **Fig. 13.** Detail of still-articulated valves with cingulum remnant covering the upper valve with largely eroded hyaline strips. Openings of rimoportulae occur along the valve margin (arrowed). Scale bar represents 10 μm (Fig. 11), 5 μm (Figs. 12, 13).

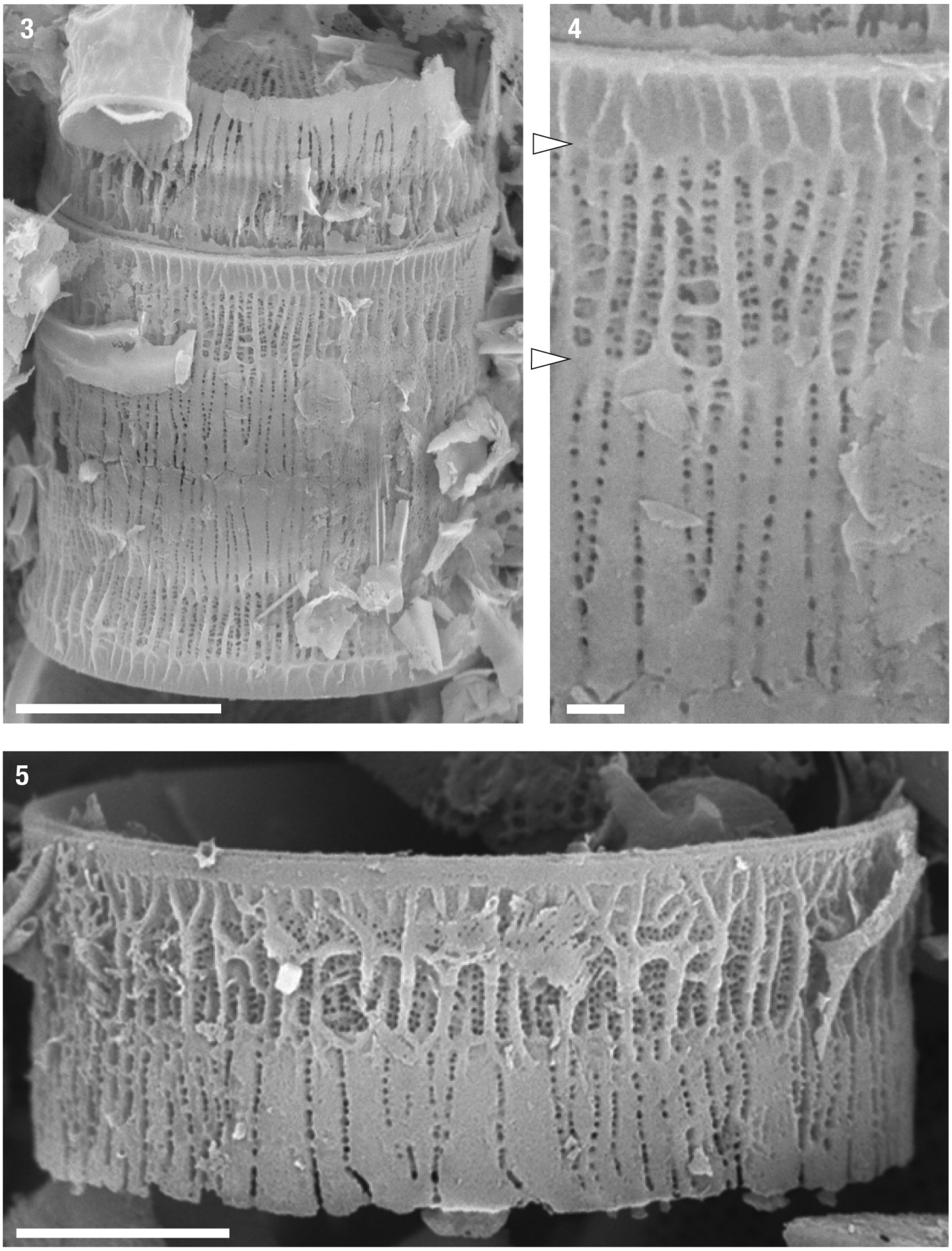
Figs 14-17. SEM images of *Trochosira polychaeta* showing detail of the central linking processes. **Fig. 14.** Valve view showing tri-radiate linking process. Note also the pattern on the valve face, well described by Sims (1988. fig. 17) as "thickened knobs (verrucae) linked by hyaline strands". **Fig. 15.** Detail showing a different form of the central process with a tri-radiate base but with a flattened area and no tapered rod. **Fig . 16.** Central process in the form of a tri-radiate tapered rod with tip arrowed – "T". Note the clasp of the once-linked cell is still attached (arrowed). **Fig. 17.** Central process in the form of a tri-radiate base but with clasp-like terminal structures. Scale bars represent 10 μm.

Figs 18-22. Images of *Trochosira polychaeta* showing progressive erosion. **Fig. 18.** Optical micrograph showing two linked valves. Note the central dark shadow representing the central linking mechanism. The marginal structures resemble marginal spines but there is a discontinuity at the mid point between the two valves with only a minority appearing to be contiguous across this, on detailed inspection. **Figs 19-22:** SEM images. **Fig. 19.** Two linked valves with the marginal structures partially broken and eroded allowing a direct view of the central linking process. Note the resemblance to the marginal linking processes of *Skeletonema*. **Fig. 20, 21**. Valves with marginal structures entirely gone, linked by central processes of differing thickness. In Fig. 21, the tri-faceted rod of the lower valve inserts into the enveloping tri-radiate hollow process of the upper valve. The valve surfaces are covered with thickened knobs or verrucae and linking hyaline strands (cf Sims; 1988, figs. 16-17). Note the girdle band remnants between the two disarticulated valves in the upper right of Fig. 20 and the still-attached cingulum in Fig. 21. **Fig. 22.** A near-monospecific concentration of valves with marginal and central linking structures eroded. The two paler valves, centre and left are internal views and the others are external showing partial to complete erosion of the hyaline annular ribs and verrucae. Scale bars represent 10 μm.

Fig. 23. Schematic cartoon showing the effects of progressive dissolution and fragmentation in *Trochosira polychaeta*. Step 1 shows initial breakage in marginal structures (Fig. 7); Step 2 shows progressive erosion of pores so that the marginal structures start to resemble isolated processes (Figs. 8, 10); In step 3 the marginal structure is sufficiently eroded to reveal the central linking process (Fig. 19); All marginal structures have gone in step 4, with central process and a linked valve fragment (Fig. 21); all linking structures have vanished in 5, with hyaline material covering the valve face (Fig. 14, 16, 20, 21) and in 6, the valve coverings have been eroded to reveal the rows of areolae (Fig. 22).



Figs 1-2



Figs 3-5

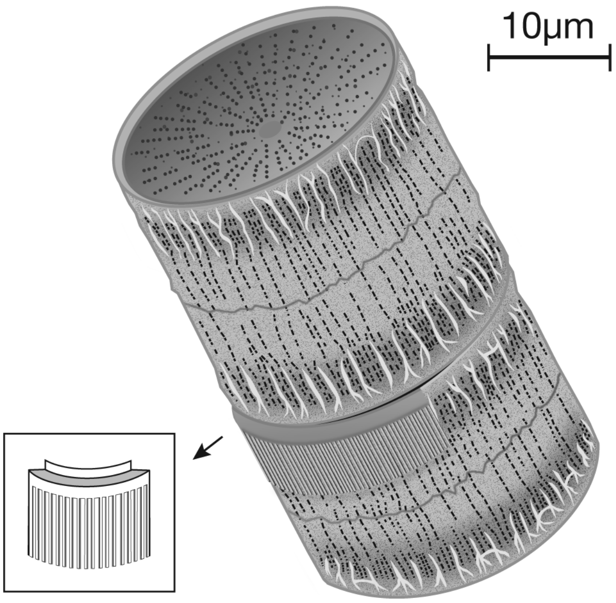
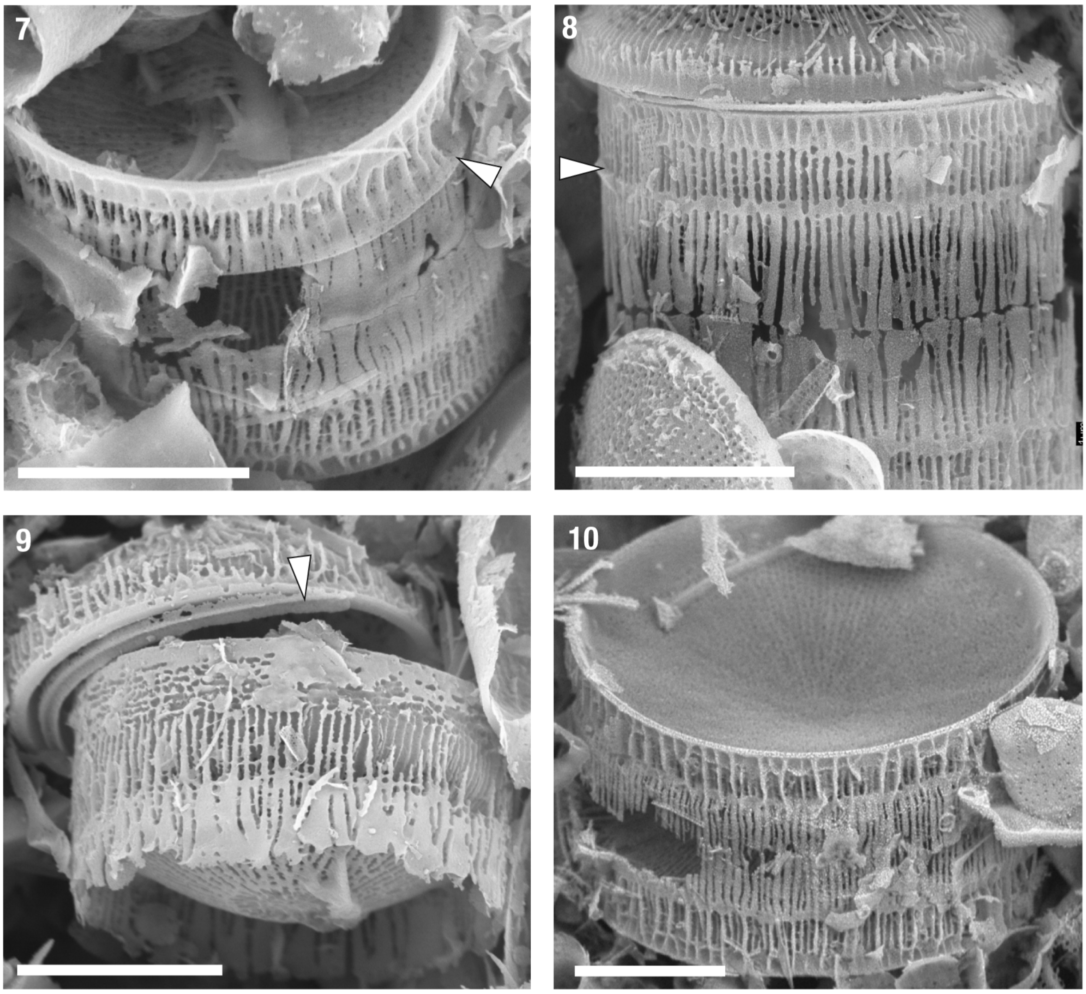
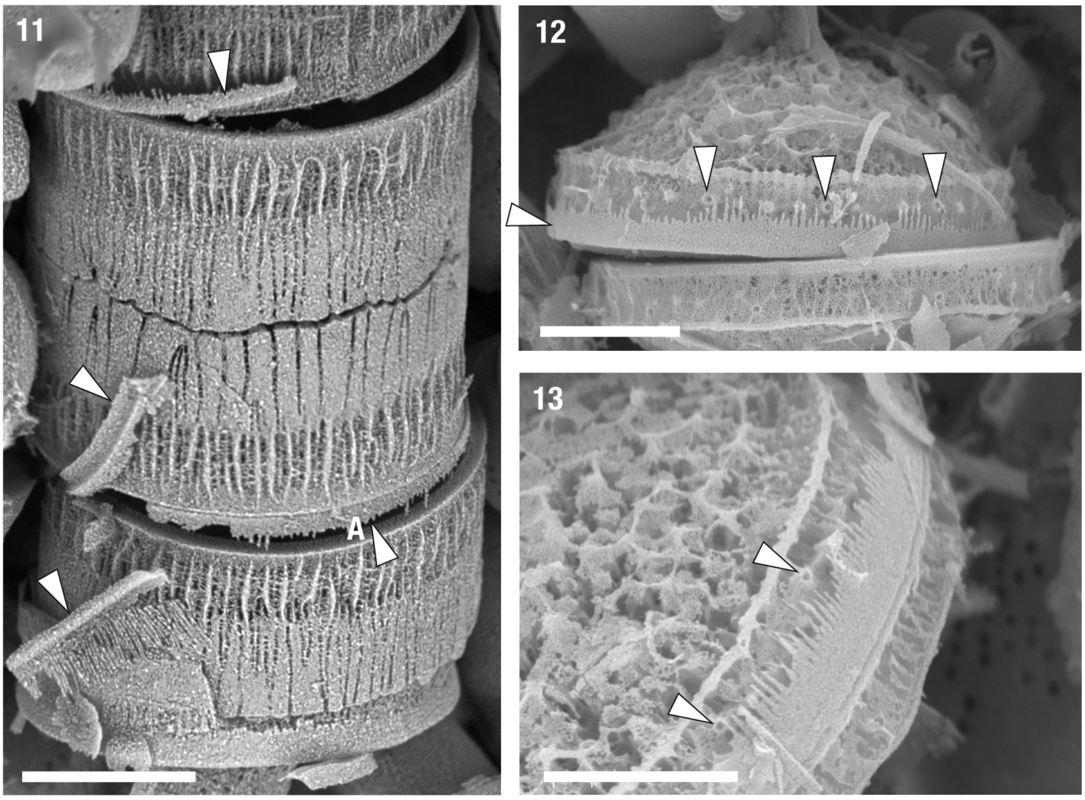


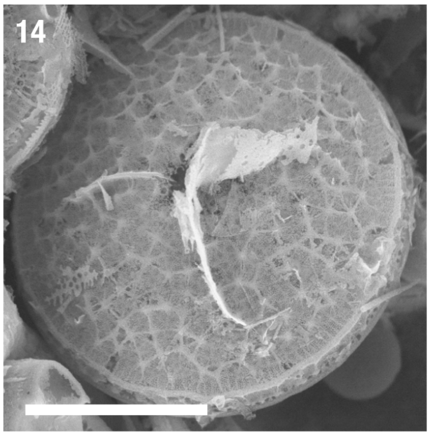
Figure 6

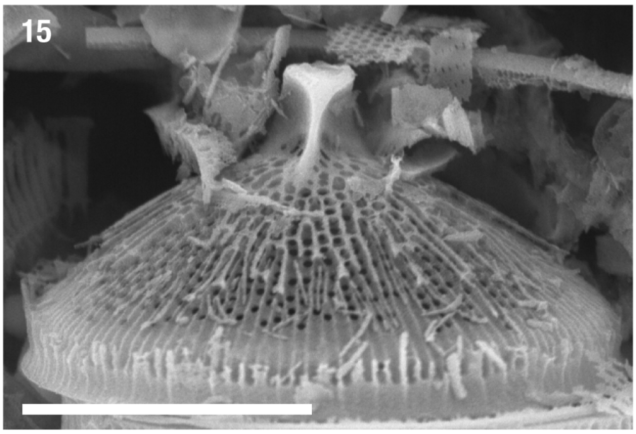


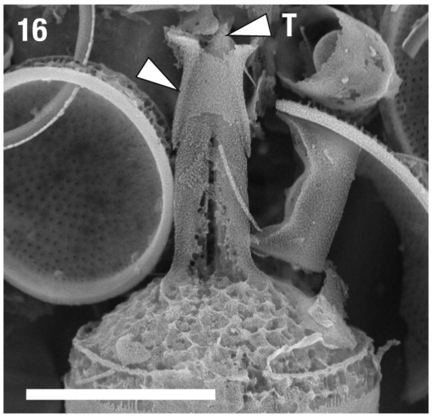
Figs 7-10

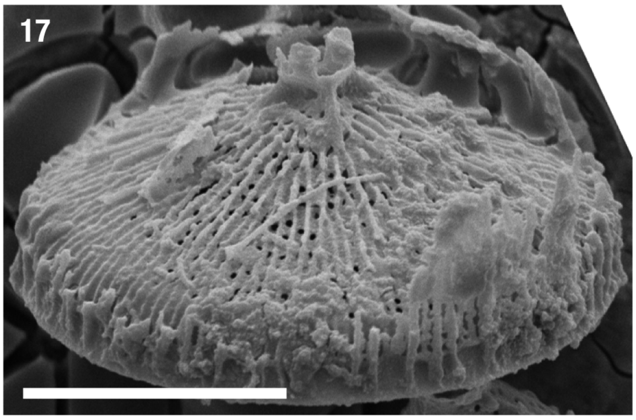


Figs 11-13

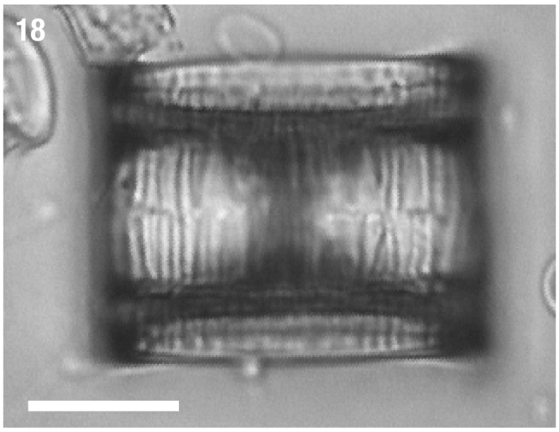


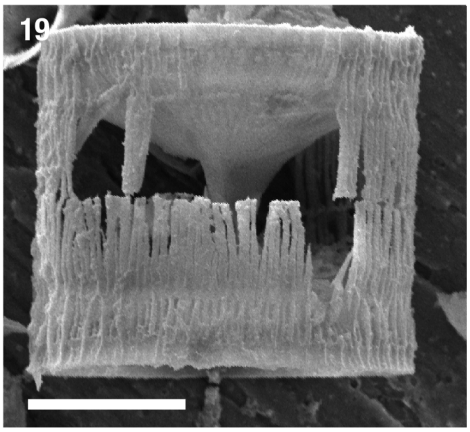


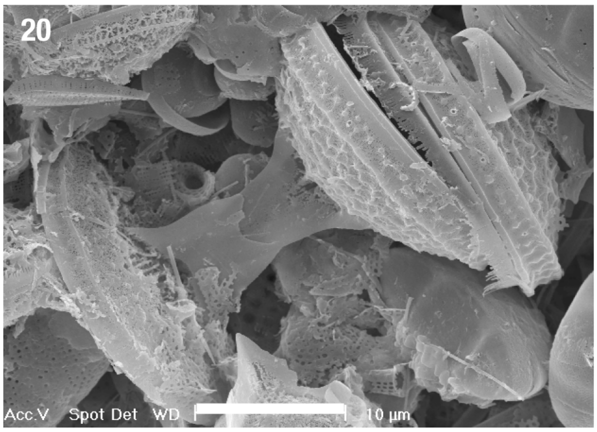


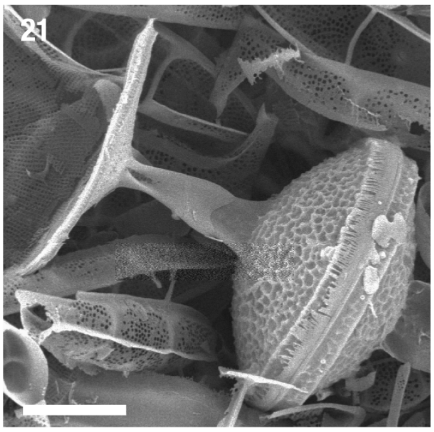


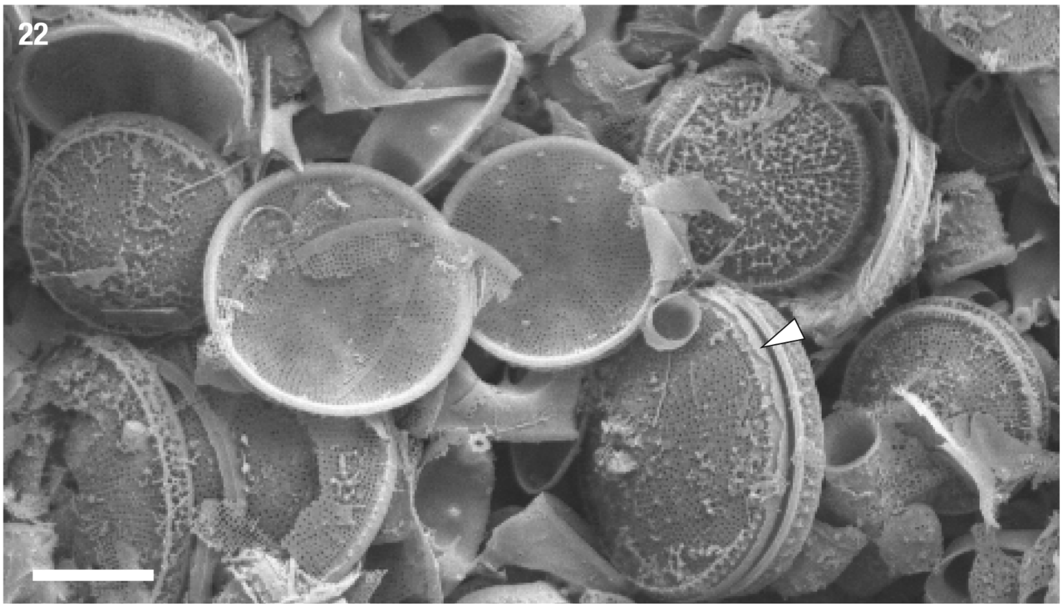
Figs 14-17











Figs 18-22

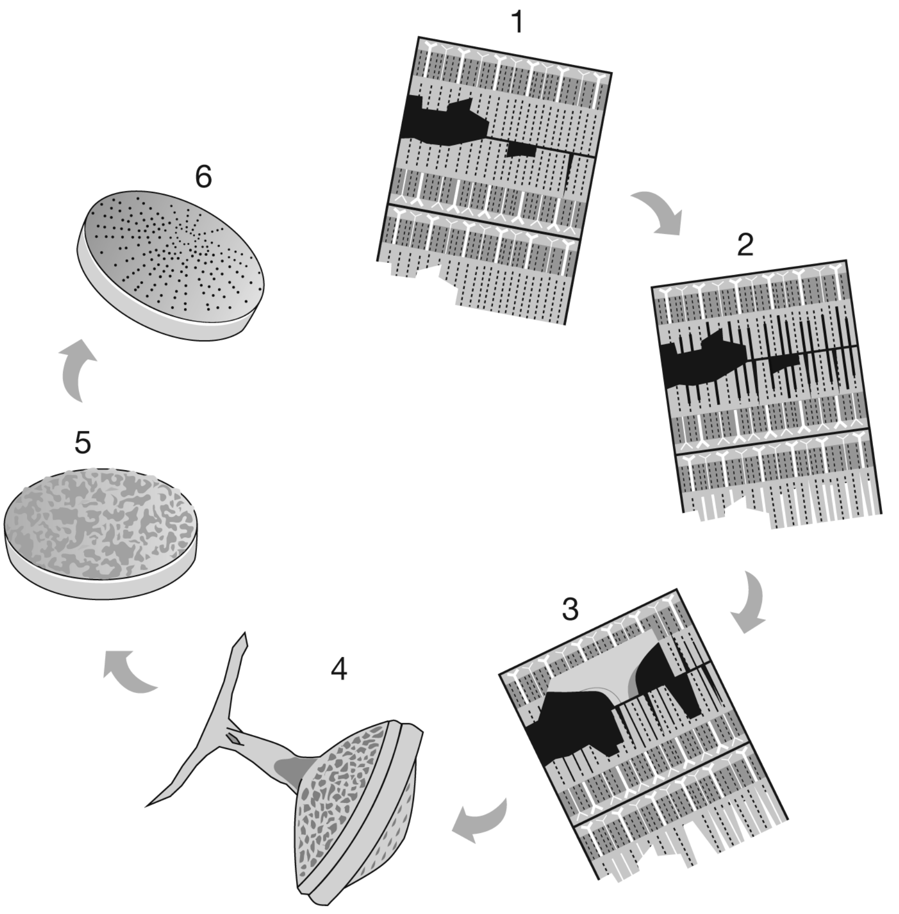


Figure 23