

HYALODISCOPSIS PLANA, A SUBLITTORAL CENTRIC MARINE DIATOM, AND ITS POTENTIAL FOR NANOTECHNOLOGY AS A NATURAL ZIPPER-LIKE NANOCLASP*

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Abstract. A small filamentous centric diatom, *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka, was collected from a subtidal *Macrocystis pyrifera* (L.) C. Agardh kelp forest off the coast of California. Valves are loculate and bear bifurcated, wrench-like marginal spines which establish a permanent connection between sibling valves. The overlapping spines, resembling a zipper, interconnect in such a way as to allow adjacent cells to potentially slide apart slightly, and the chain to flex with water movements. In external view a cluster of rugose granules adorns the center of the valve, with smaller granules sprinkling the rest of the surface. Internally the valve is hyaline (smooth) in the center, with faint ribs of silica radiating from the center. On the mantle and part of the valve face there are rows of pores in quincunx, occluded by rotae. On the external valve surface these rows of pores are interrupted by the spines. Rimoportulae are visible internally, located at about half the depth of the mantle, but cannot be distinguished on the exterior of the valve. Girdle bands are numerous, split and ligulate. This diatom species is very interesting from a nanostructural point of view: for nanoscientists *H. plana* is an exquisite example of a diatom that combines features such as naturally nanostructured surfaces, optimized micro- and nanomechanics, and elaborate energy dissipation devices. For the nanotechnologist this diatom is an invaluable source of inspiration for the design of micro-electromechanical systems (MEMS), design of nanoclasp, and functional microdevices in general. The current collaboration between physicists, (nano)engineers and biologists on *H. plana* may very well initiate inter- and transdisciplinary approaches in diatom science and technology, with mutual benefit for all fields involved.

Key words: chain-forming centric diatoms, interlocking nanodevices, nanotechnology, nanozippers, micro-electromechanical systems, nanoclasps

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INTRODUCTION

The sublittoral zone of marine coastal regions is undersampled as compared to the littoral and neritic zones, especially in the tropics and subtropics. One of us (MAT) found a rare chain-forming diatom in a sample containing various filamentous diatoms scraped from rocks within the Point Loma kelp beds [mostly *Macrocystis pyrifera* (L.) C. Agardh] off San Diego, California, U.S.A. The

valves fit the description of *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka reported in fossil and extant material from Japan and Russia (Kozyrenko 1971; Kozyrenko & Lastivka 1992; Kozyrenko & Makarova 1997; Olshtynska 1999). Here we report the presence of this species in a marine habitat in California, document its ultrastructure using scanning electron microscopy (SEM), and introduce it as a diatom with great potential for nanotechnology. We use standard terminology (Anonymous 1975; Ross *et al.* 1979).

* Dedicated to Dr. Kurt Krammer on the occasion of his 85th birthday

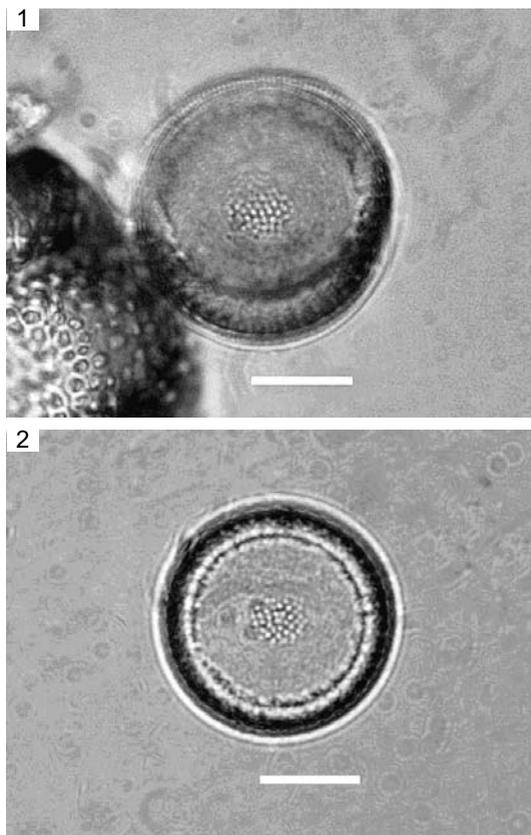
MATERIAL AND METHODS

Chains of diatoms, primarily *Biddulphia biddulphiana* (Sm.) Boyer (= *B. pulchella* Gray), were collected by SCUBA by C. Gramlich at 24 m depth off the San Diego coast at Point Loma on 27 October 2000. A small centric chain-forming diatom, rare in the sample, was singled out for observation. A subsample of material was rinsed to remove salts and to observe complete frustules and girdle bands. Another was acid-cleaned according to the von Stosch method (Hasle & Syvertsen 1996). Both samples were air-dried on cover slips. For light microscopy (LM) the specimens were mounted in Naphrax. For scanning electron microscopy (SEM) the cover slips were sputter-coated with Au/Pd and examined with a Hitachi S-2700 scanning electron microscope at accelerating voltage of 10 kV. For comparison to the genus *Paralia* (W. Sm.) Heib., specimens of *P. sol* (Ehrenb.) R. M. Crawford from the same Point Loma sample and *P. sulcata* (Ehrenb.) Cleve acquired with a plankton tow from St. Pete's Beach, Florida (25 October 2002) are illustrated.

OBSERVATIONS

LM. Valves are circular (diameter 22–53 μm in the sample investigated) with a heavily silicified outer margin. Large granules are clustered in the center of the valve (Figs 1 & 2). Careful focusing usually revealed central clusters of small dots at two levels of focus, indicating that two interconnected sibling valves were being observed. On a pair of valves in a tilted position, marginal bifurcating spines were just visible (Fig. 1). These could not be observed by LM when the valves were in the usual position lying flat on the cover slip (Fig. 2).

SEM. A colony of four cells from the rinsed sample is illustrated (Figs 3–6). That this colony consists of four rather than two cells is indicated by the mantle of a valve seen between cells 3 and 4 (and presumably between cells 1 and 2; arrows, Fig. 3). The valve faces at both ends of the colony are fractured; probably this occurred as the specimen dried (the central parts of the valves are relatively thin) (Figs 5 & 6). Both ends of the colony were examined, and clusters of granules were apparent on the center of the valve faces (Figs 5 & 6). The frustules are irreversibly connected by overlapping

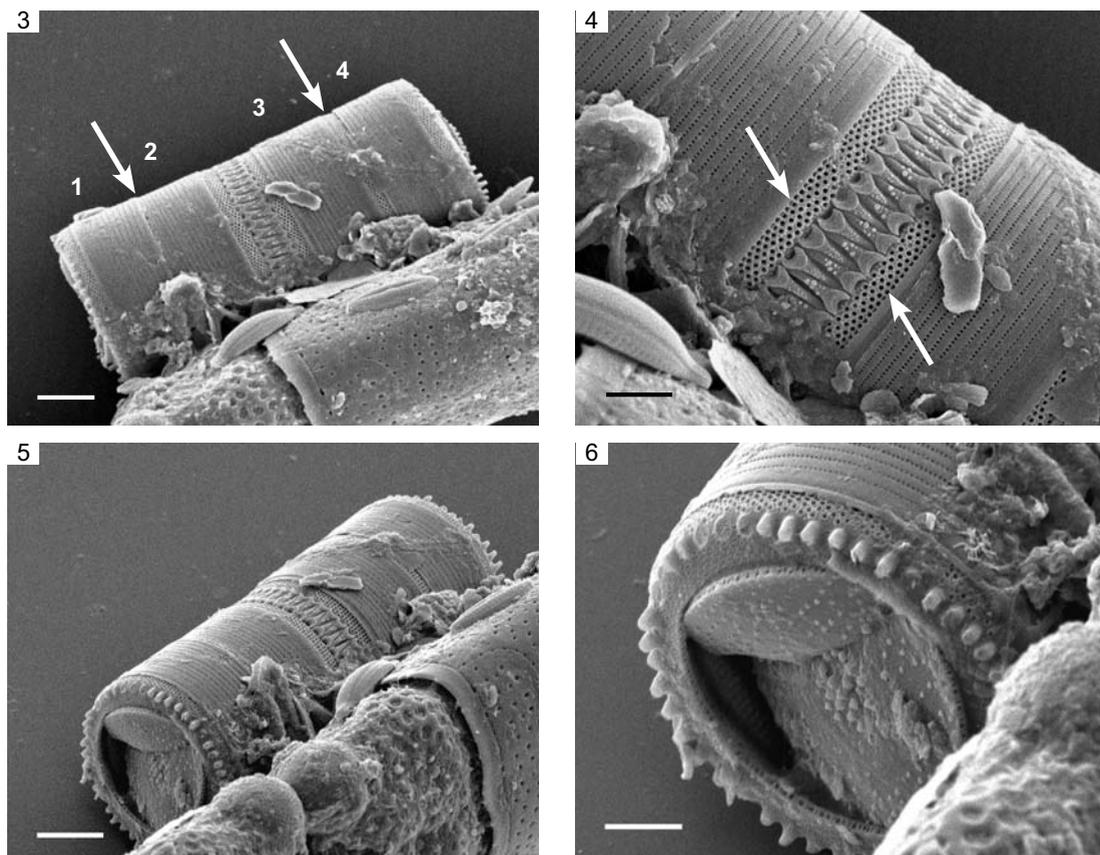


Figs 1 & 2. *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka, 1 – tilted valve, 2 – valve in flat position. All LM. Scale bars = 20 μm .

spines (Fig. 4). The marginal spines on the end valves on both sides of the colony are broken.

The narrow girdle bands are numerous, split and ligulate, and bear a single row of small, rectangular poroids (Figs 4 & 23).

Almost all of the specimens observed in the acid-cleaned sample were doublets, two sibling valves closely and apparently permanently interlocked face-to-face (Fig. 17). In order to view the external face of valves in SEM, singleton valves lying in the upright position were located (Figs 7–12). These specimens invariably had broken spines. These few specimens permitted the following observations. The cluster of central granules occupies about 1/5 to 1/3 of the diameter of the valve. Often the granules close to the periphery of the cluster have spines facing away

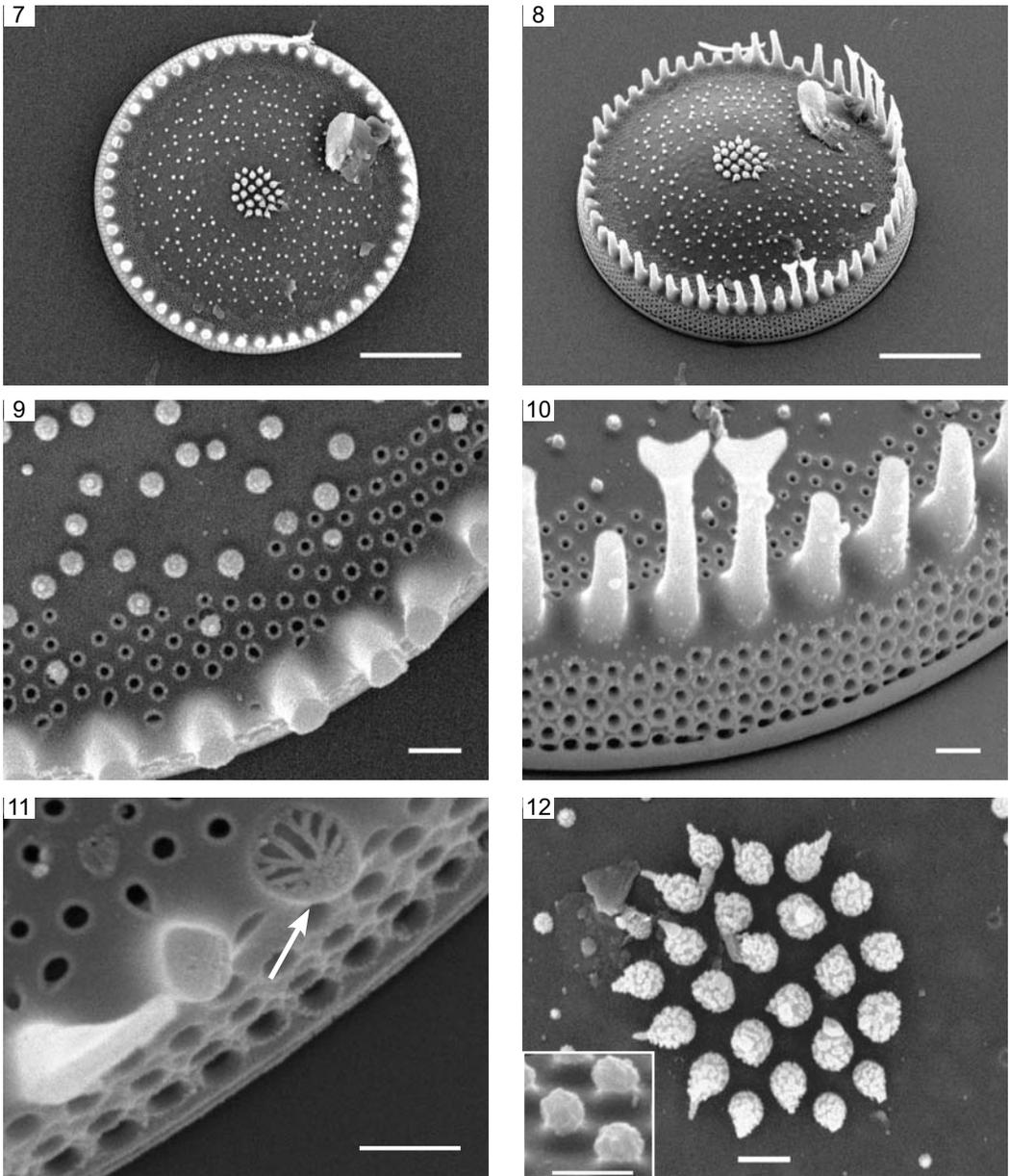


Figs 3–6. *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka filament. 3 – complete filament consisting of four cells apparently attached to filament of *Biddulphia biddulphiana* (Sm.) Boyer. (for clarification, arrows point to the demarcations between cells 1 and 2 and cells 3 and 4), 4 – detail of linkage of two cells (arrows point to the mantles of the connected cells), 5 – oblique view of filament, 6 – end of filament, showing broken marginal spines. All SEM. Scale bars: 3 & 5 = 10 μ m; 4 & 6 = 5 μ m.

from the center (Figs 7 & 12). Individual granules are elevated on pedestals (Fig. 12, inset). Smaller granules are scattered over the rest of the surface (Figs 7–9). Valves are disc-shaped; the valve face is slightly convex (Fig. 8), although one suspects that in a doublet (Fig. 17) the valves may be complementary (one convex, one concave), as in *Cocconeis* (Fig. 27b in Round *et al.* 1990). The valve face/mantle junction is somewhat rounded and nearly at right angles. The mantle is relatively deep. Spines measure 3.6–5.8 μ m long and are located on the valve face, curving gently upward (Fig. 10). There are *ca* 6 spines in 10 μ m. These bifurcate at their ends, producing a crescent (wrench) shape, and are smooth on the internal side

(Fig. 18). Close examination of spines broken at various levels reveals that they are basically solid except at their base (Figs 9–11). A spine broken at the base has a bilaterally symmetric pattern of loops (Fig. 11, arrow). This pattern may be related to the morphogenesis of the spines. Several rows of areolae are located along the valve margin just inside the ring of spines (Fig. 9). These continue onto the mantle but are not present, or are covered over, in the area from which the spines originate.

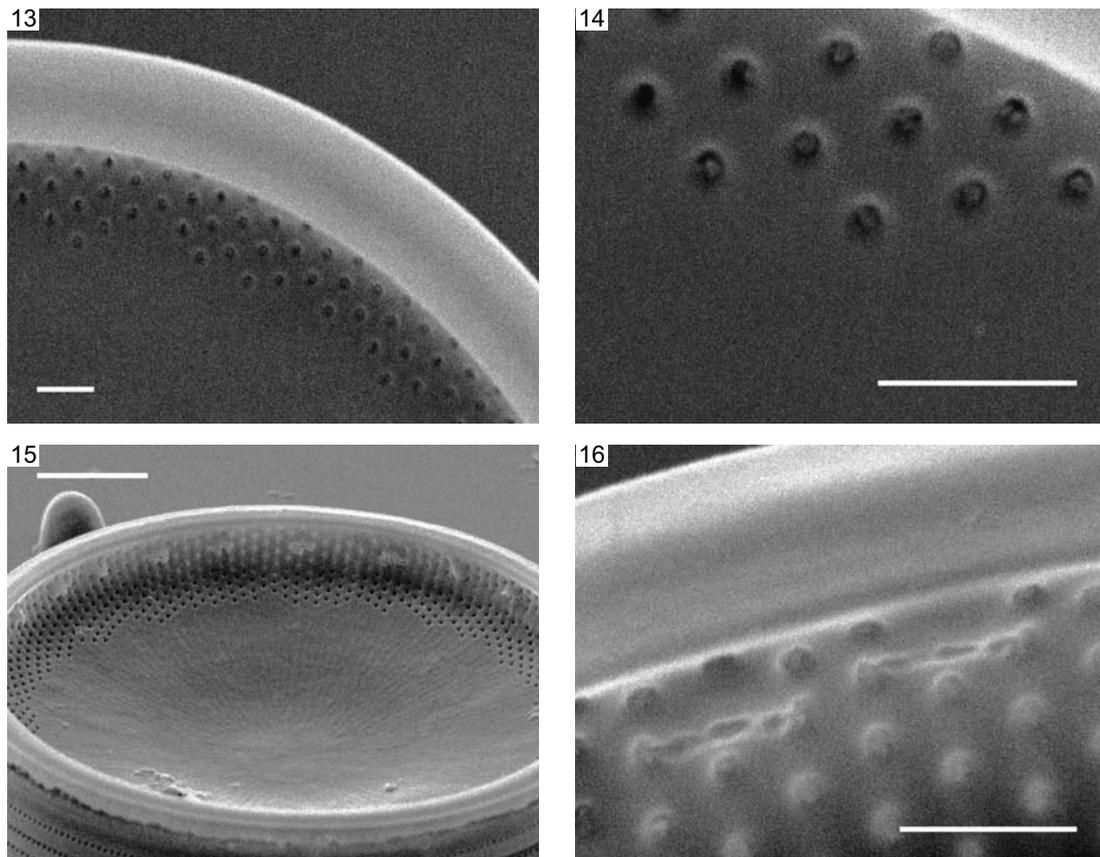
Internally the surface is smoothly concave without central processes (Figs 15 & 17). The valve is bounded by a thick hyaline rim (Fig. 13). The rows of pores seen in external view are also evident on the inside and form a continuous un-



Figs 7–12. *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka, 7 – external view, 8 – same valve as Fig. 7, tilted 45°, 9 – close-up showing broken spines, small granules and marginal pores, 10 – valve tilted 45°, with broken and unbroken spines, 11 – spines broken at two different levels and one unbroken spine (arrow points to spine broken at the base), 12 – central granules. Inset: central granules, tilted specimen. All SEM. Scale bars: 7 & 8 = 10 μ m; 9–12 = 1 μ m.

disturbed pattern even through the sites of origin of the external spines (Fig. 15). The pores are occluded with several small rotae (Fig. 14). When the specimen is tilted, processes come into view

that are 3–7 μ m apart (Figs 15 & 16). These are below the rim; they seem to bear no relationship to the external spines, and no obvious external structures correspond to these processes.



Figs 13–16. *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka, 13 – interior view of marginal area, 14 – detail of marginal pores, 15 – interior views showing rimoportulae, tilted 60°, 16 – detail of rimoportulae, valve tilted 60°. All SEM. Scale bars: 15 = 10 μm ; 13, 14 & 16 = 1 μm .

Granules of several sizes are present on the outer surface of the spines (Fig. 19). The spines are topped by a structure that closely resembles a single open-ended wrench (or spanner). The crescent-shaped distal portion of the wrench-like spines bears a ridge separating it from the shaft (arrowed, Fig. 19). The valve pairs are found with the heads of their spines far apart (Fig. 20) at an intermediate position (Fig. 21) or juxtaposed (Fig. 22), depending on the relative positions of the sibling valves. The regularly alternating, opposite orientation of the spines is occasionally interrupted (Figs 17 & 21).

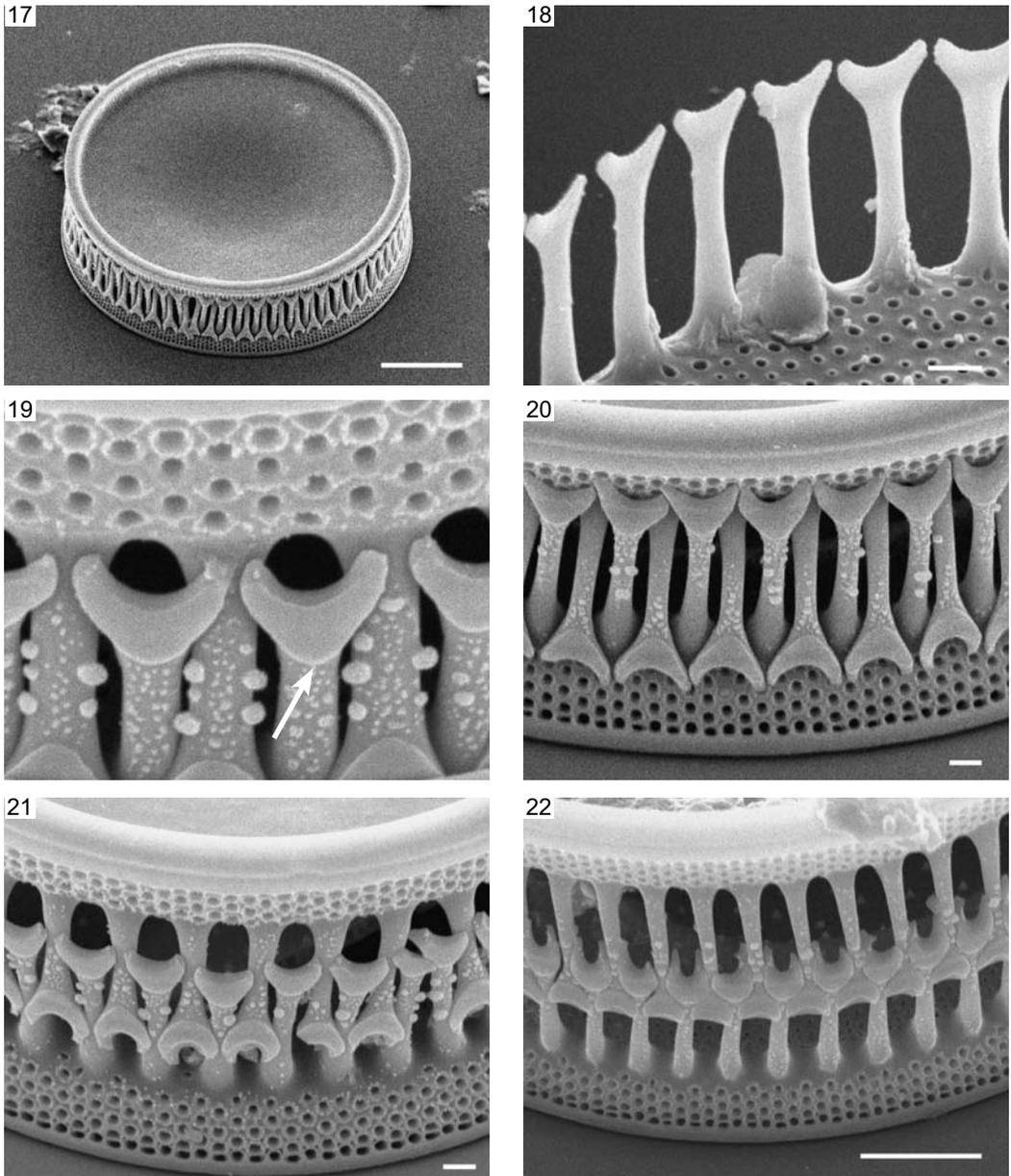
Sometimes, evidently during sample preparation, the girdle bands slipped to a position where they were associated with pairs of connected sibling valves (e.g., Fig. 23) rather than between valves of the

same cell in the normal position within the frustule as in Figure 4. Those cases yielded more information, showing the girdle bands to be numerous, split, ligulate, and possessing a single row of pores.

Fractured valves clearly show the loculate nature of this species (Figs 24–26). A valve with the rim detached (Fig. 24) and a section through the mantle (Fig. 25) demonstrate that the chambers of the mantle are deeper than those of the valve face (Fig. 26). The loculi continue into the central, hyaline portion of the valve.

DISCUSSION

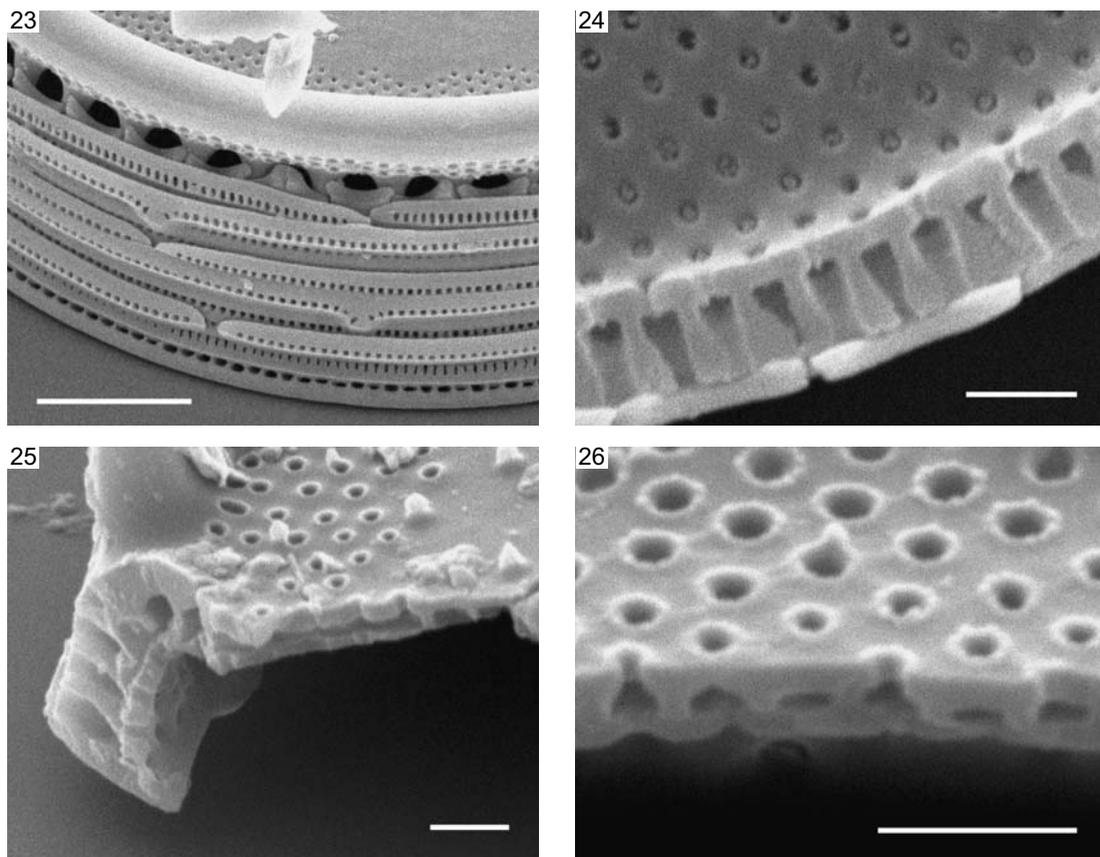
The most notable features in *Hyalodiscopsis plana* are the unique wrench-shaped, overlapping, inter-



Figs 17–22. *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka, all tilted 45°. 17 – sibling valves, general view, 18 – detail of interior of spines, 19 – detail of distal ends of spines. Arrow points to ridge of wrench-like distal ends; 20–22 – varying degrees of separation of spines of sibling valves: 20 – spines impinging on adjacent valves (note how the perforations sometimes engage the spine tips), 21 – spines slid to halfway positions, 22 – spines slid to yield maximum distance between sibling valves. All SEM. Scale bars: 17 & 22 = 10 μm ; 18–21 = 1 μm .

locked spines connecting the cells into colonies. The spines are generally bilaterally symmetric, as in a turnbuckle wrench (Fig. 31). Their arrangement

resembles the similarly shaped teeth or elements of a zipper (Fig. 32). During valve morphogenesis these must be produced simultaneously on newly



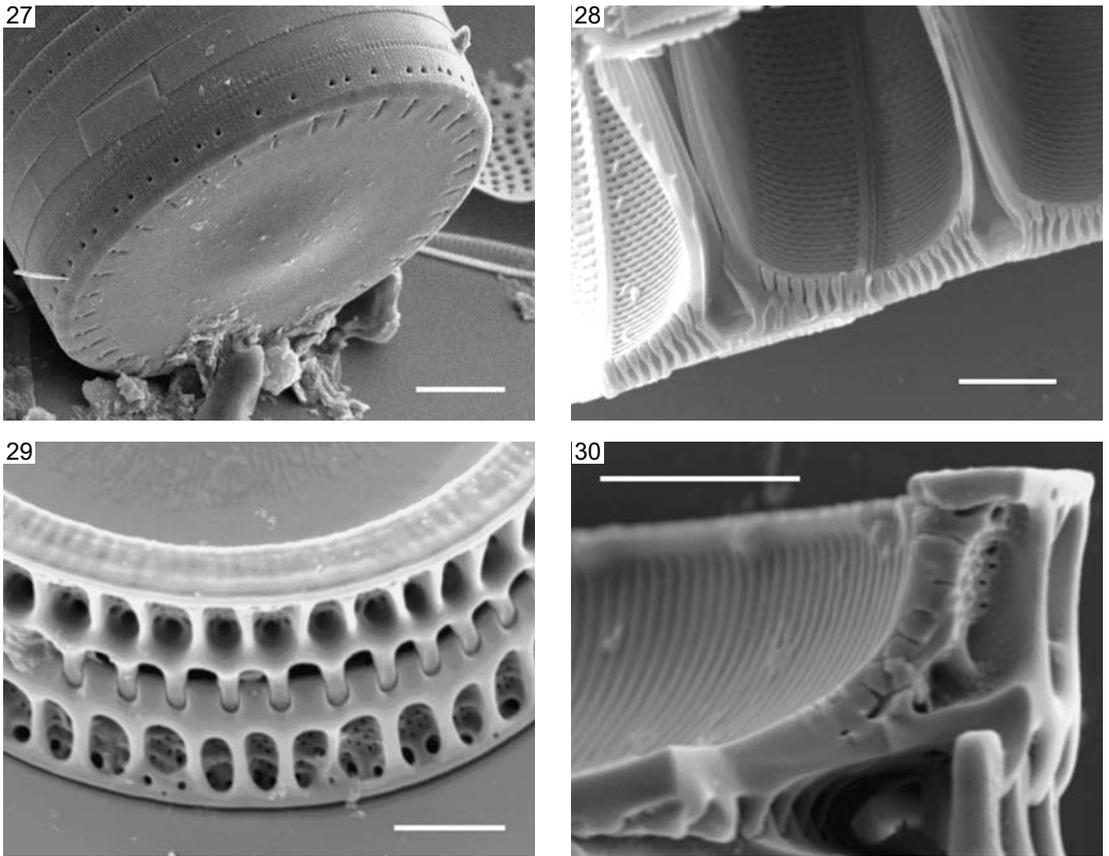
Figs 23–26. *Hyalodiscopsis plana* (Kozyr.) Kozyr. & Lastivka, 23 – girdle bands, tilted 45°, 24 – section through mantle of fractured valve, 25 – section through margin of fractured valve, tilted 45°, 26 – section in region of marginal pores on valve face, external surface at top, tilted 45°. All SEM. Scale bars: 23 = 5 μm ; 24–26 = 1 μm .

forming sibling valves, permanently locking the frustules of the two daughter cells together. Until this species is cultured, the timing of formation of the spines relative to the valves they hold together will remain unknown. There appear to be no separation valves in *Hyalodiscopsis plana*: of six single valves observed on the external side, all had broken spines. The single colony observed also possessed ends with broken spines. All other specimens in the cleaned sample consisted of two sister valves attached face-to-face, arising from adjacent cells. When seen in an untilted position, only the inner part of the uppermost valve is visible in SEM. Tilting brings the other valve and spines into view. The lack of separation valves and the presence of broken spines on all single specimens

suggests that the mode of colony formation is mechanical fragmentation of filaments.

The ability of the spines on sibling neighboring cells to slide past each other (Figs 19–22) suggests that the filaments are flexible. For example, we estimate that the spines of the 38.3 μm inner diameter specimen in Figures 17 and 20 may slide as much as 7.2 μm , allowing a possible tilt of 10.6°, so that a chain of 33 cells could bend in a full circle. This condition may confer a selective advantage if the colonies are epiphytic or epilithic in a turbulent habitat. That there is a limit to this flexibility is implied by the broken spines (and evident fragmentation) found on either end of the colonies.

At first glance *Hyalodiscopsis* Kozyr. & Lastivka resembles *Paralia* (W. Sm.) Heib., especially



Figs 27–30. 27 & 28 – *Paralia sol* (Ehrenb.) R. M. Crawford, Point Loma, California: 27 – end of colony, 28 – section through fractured colony. 29–30 – *Paralia sulcata* (Ehrenb.) Cleve, St. Pete’s Beach, Florida: 29 – pair of sibling valves, 30 – detail of section through a pair of sibling valves. All SEM. Scale bars = 5 μ m.

in girdle view, and both appear to be found in similar habitats. In fact, *Paralia sol* (Ehrenb.) R. M. Crawford was found in the same sample as *Hyalodiscopsis* (Figs 27 & 28). *Hyalodiscopsis* differs from *Paralia* in several important respects. Both form colonies with permanently interlocking spines, and most *Paralia* species have girdle bands with slits. However, *Paralia* is not loculate but rather has peripheral channels as in *Paralia sol* (Figs 27 & 28) and *Paralia sulcata* (Figs 29 & 30). Also, *Paralia* does not possess central granules but has a smooth (Crawford *et al.* 1990; Round *et al.* 1990; Sims & Crawford 2002) or ridged (Garcia 2003) central surface. In *Paralia* the spines interlock as in a jigsaw puzzle, interdigitating rather than overlapping as in the spines of *Hyalodiscopsis*

(Crawford 1979; Round *et al.* 1990). The rimoperculae of *Paralia* are generally on the rim of the valve (Fig. 30) or just below it (Garcia 2003), while those of *Hyalodiscopsis plana* are located at a distance from the thickened rim (Fig. 13). Additionally, *Paralia* exhibits heterovalvy and separation valves, whereas all valves of *Hyalodiscopsis* observed in this study have an identical structure and the colonies seem to lack separation valves.

Little is known of the fossil genus *Strangulonema* Grev. (Round *et al.* 1990). Its furcated spines resemble those of *Hyalodiscopsis plana*. From the illustrations of Round *et al.* (1990), which are of eroded specimens, it does not appear to have a loculate structure but the spines appear to be permanently interlocked. Round *et al.*



Fig. 31. Manufactured turnbuckle wrench. <http://www.rceasy.com/wp-content/uploads/2007/08/79277.JPG>, with permission of RCEasy – News on Radio Control Ca.

(1990) were unable to determine if this genus has processes, so only further study can determine if it is related to *Hyalodiscopsis*.

The structure of the processes is puzzling. They appear to have struts, or supports on either side (Fig. 16), but do not seem to have satellite pores (as do fuloportulae). Thus, the marginal processes seen in *Hyalodiscopsis* must be rimoportulae (cf. Schmid 1994).

Nanozippers have been synthesized at the molecular level (Ray *et al.* 2006; Kholmanov *et al.* 2009), and of course the double helix of DNA itself is a nanozipper both in its replication (Watson & Crick 1953) and winding/unwinding (Abdel-Monem *et al.* 1976), as are protein leucine zippers (Landschulz *et al.* 1988), collagen zippers (Engel & Prockop 1991), and cadherin zippers involved in cell-cell adhesion (Weis 1995). *Hyalodiscopsis* may be the first known natural nanozipper whose teeth (rimoportulae) are made of solid material (Bogdanski *et al.* 2004), though as a zipper it is permanently zipped. Perhaps if the silica were replaced atom for atom (Sandhage *et al.* 2002; Drum & Gordon 2003; Gordon 2010) by a more pliable material, a real opening and closing nanozipper could be made from *Hyalodiscopsis* valves.

FUTURE WORK

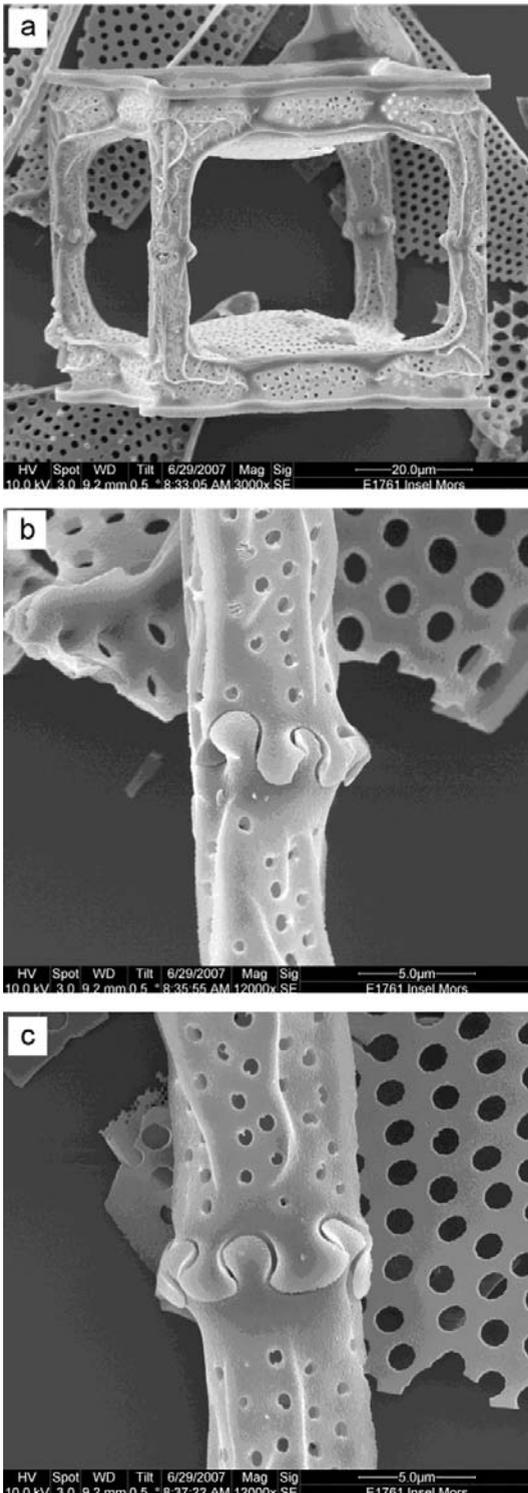
Hyalodiscopsis plana raises many questions important to diatom nanotechnology, some common to diatoms in general, some originating from its apparently unique structure. For example, Figure 23 shows a stack of girdle bands, presumed by many investigators to hold the valves together. Yet it is not clear how this is accomplished mechanically. While the girdle bands overlap, what is it that keeps them from slipping off each other? Are

they under tension? This could be investigated by measuring the 3D shape of a girdle band *in situ* and then taking it off, perhaps by carefully crushing the attached structures, to see if its radius decreases on release. If so, is there a difference between its inner and outer silica, such as has been demonstrated for valves and raphes (Crawford *et al.* 2009)? Its mechanical behavior would then be analogous to a bimetallic strip such as is used in thermostats and nanotubes (Wang *et al.* 2008). It would be good to know whether it is mechanically prestressed under tension, as are the setae on gecko feet (Autumn *et al.* 2000).

While much effort has been devoted to studying the morphogenesis of costae and punctae in diatom valves using molecular and computer simulation techniques (Gordon & Drum 1994; Parkinson *et al.* 1999; Lenoci & Camp 2006; Gröger *et al.* 2008; Hildebrand 2008; Kröger & Poulsen 2008; Lenoci & Camp 2008; Brunner *et al.* 2009;



Fig. 32. Closeup of a modern manmade zipper. From http://en.wikipedia.org/wiki/File:Reissverschluss_Helix.jpg, reproduced under a GNU Free Documentation License.



Crawford *et al.* 2009; Gordon *et al.* 2009), scant attention has been paid to other features of diatom silica (Pickett-Heaps *et al.* 1994; Pickett-Heaps 1998; Pickett-Heaps & Klein 1998). The coordinated overlapping of the wrench-like marginal spines needs to be followed during morphogenesis. As the size of these features is comparable to the wavelength of light, it may be necessary to use methods of *in vivo* soft x-ray micro-computed tomography to follow their development (Jacobsen 1999; Donoghue *et al.* 2006; Zschech *et al.* 2008; Abramson *et al.* 2009) and/or methods to be developed for molecular tomography of cells (Chen & Chen 2008).

The fracture patterns of diatoms hold potential for nanotechnology applications in general. Tailored points of fracture should be of great interest and relevance to those working with man-made micro- and nanomachines, for production and recycling. There is a need for microscale machines that break in a certain predetermined way. In *Hyalodiscopsis plana* there seems to be precisely such a tailored location of mechanical failure for the valve faces (Figs 5 & 6). In terms of nanotechnological applications and devices, diatoms might be used, for example, as encapsulated transporters for pharmaceuticals or the like in nanomedical applications (Gordon *et al.* 2009). With a little mechanical stimulus, as from a small actuator, diatom pharmaceutical transporters could be opened and the content would be released. In the case of *H. plana* it even appears that the valve faces do not leave the cells when broken loose but are still stored in the cells (Fig. 6); in nanomedicine this might carry the benefit of minimizing 'waste' in the body.

Mechanical stability studies of these diatoms should build upon and extend previous micro-mechanics work (Hamm *et al.* 2003). Preferably an environmental SEM should be used, since the

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Fig. 33. SEM images of *Solium exsculptum* Heib., an Eocene fossil (45 million years old) from a deposit at Mors, Denmark. b & c show the linking structures in more detail. Scale bars: a = 20 µm; b & c = 5 µm. The sample is from the Hustedt Collection in the Alfred Wegener Institute, Bremerhaven, Germany, # E1761, with permission of Friedel Hinz and Richard M. Crawford.

thin layer of metal from the sputter coating of the samples for conventional SEM studies would of course alter the results.

The wrench-shaped spines that connect the sibling cells (Figs 3–5 & 17–22) have potentially very useful nanomechanical properties. As already suggested (Crawford & Gebeshuber 2006; Gebeshuber & Crawford 2006; Gebeshuber 2007), such nanoclasps might serve as energy dissipation devices, since they seem to allow for tiny movements of the sibling cells relative to each other, and for slight curvature of the chain. Micromechanical experiments to measure the degree of movement possible in various directions would yield valuable information on the function(s) of nanoclasps.

For nanotechnology applications we should know more about the micromechanical properties of the girdle bands. An upscaled mechanical model of a diatom from plastic or some other elastic material, or perhaps from glass, or a multiscalar finite element representation (Ghanbari & Naghdabadi 2009; Sauer 2009; Ilic *et al.* 2010) that represents the shapes and perhaps some of the mechanical properties of the real diatom would provide a platform for addressing some very basic unanswered questions about diatoms. Are the girdle bands under tension? Why doesn't the whole diatom fall apart? In *Hyalodiscopsis plana* the girdle bands are not quite complete circles. As seen from Figure 23, in *Hyalodiscopsis plana*, whose cells have many girdle bands, the location of the gap in the girdle bands varies in angular position. This increases the mechanical stability of the cell. However, in some species the bands are complete circles (e.g., *Isthmia* C. Agardh). In most species the girdle bands are nearly complete circles (as in *Hyalodiscopsis plana*), but in *Ditylum* J. W. Bailey species the girdle bands are not even bands but merely scales (von Stosch 1975; Round *et al.* 1990). The sites where the ligula and antiligula meet do seem to be spaced around the cell.

Another question is whether the location where the girdle bands are slightly thicker, and where pores are absent (Fig. 23), is exactly opposite the gaps in the incomplete circles.

The rather large pores of the mantles and overlapping spines are visible above the bands between

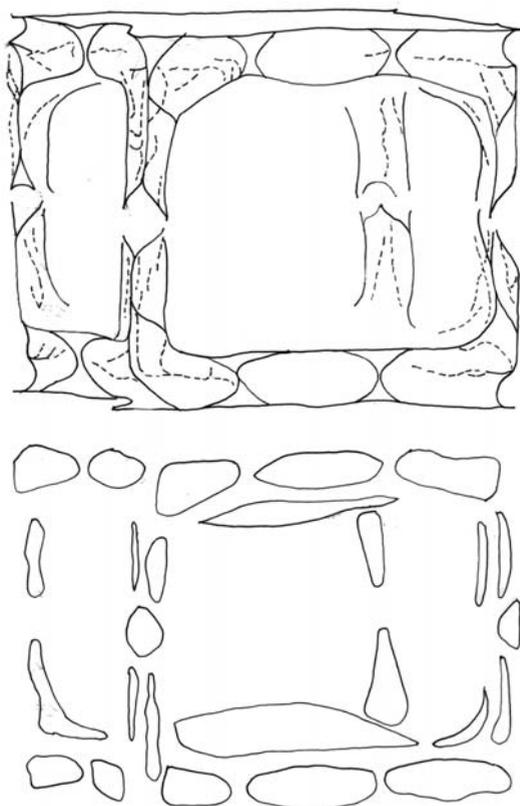


Fig. 34. Top: primary structure of *Solium exsculptum* Heib., as far as discernable (dark regions interpreted as reinforced main structural elements; dashed lines indicate secondary ribs reinforcing the thin plates). Bottom: scheme of approximate extension of thin plates, enabling exchange by interspersed holes. From Gebeshuber *et al.* (2010) with permission from Nova Science Publishers.

the two central cells of the colony and, somewhat occluded by girdle bands, a valve mantle can be seen between two outer cells (Fig. 4, arrows). The mantle is the side of the valve with the roundish pores (cf. numbers in Fig. 3, arrows in Figs 3 & 4).

The pattern of the overlapping spines may be related to their morphogenesis. Also, the pattern looks highly optimized; this might be checked by calculating mechanical stability versus material saving.

The absence of areolae where the spines are inserted also points to mechanical optimization (cf. Fig. 10). A micromechanical optimization study of

Solium exsculptum Heib. identified reinforcement ribs, primary and secondary structures, and various other micromechanical optimizations in this fossil diatom (Figs 33 & 34) (Gebeshuber & Crawford 2006; Gebeshuber 2007):

‘The most obvious characteristic about the structure of *Solium exsculptum*, its rectangular shape, cannot be explained yet. Between the main ribs the silica structure is extremely thin and interspersed with pores. In these fragile plate-like structures, secondary stiffening by small, undirected ribs can be observed. These reinforcement structures prevent the buckling that flat shells are prone to. The flange structure around the rim, which obviously belongs to the primary structure, is interesting – perhaps it helps in the attachment of the valves or serves as an attachment structure for the cell membrane (Fig. 33). The primary structure of *S. exsculptum* consists of the dark areas that can be distinguished in Figure 33 (for sketch see Fig. 34 top). These are reinforcement ribs, delivering the main force transmission areas. In the primary structures there are no holes in the amorphous silica (Fig. 34 top). But there are reinforcement ribs. The whole structure is made from thin material. Plates or shells without ribs would be prone to buckling. The silica structure might be so thin since many pores are needed; the mechanical stiffness comes from the reinforcement ribs. Less material is needed if thin material and reinforcement ribs are used. There are no reinforcement ribs on the top and bottom part of the *Solium* Heib. image – only the holes. Inside this top and bottom parts resides the cytoplasm, it might provide enough mechanical support to prevent mechanical damage. Altogether the structural differentiation is very material efficient’ (Gebeshuber *et al.* 2010).

Given the known strength of diatom silica (Hamm 2005; Wee *et al.* 2005; Hamm & Smetacek 2007), it should be possible, using a finite element simulation, to predict the force needed to break the overlapping spines, and compare this to the forces generated in turbulent shear conditions (Nikora *et al.* 1997; Brindley Alías *et al.* 2004; Patel *et al.* 2004; Cozar & Echevarria 2005; Winder & Hunter 2008). The flexibility of *Hyalodiscopsis plana* may

be an advantage over rigid chain colonial diatoms in turbulent waters, both mechanically and in terms of access to diffusing nutrients (Karp-Boss *et al.* 1996; Pahlow *et al.* 1997; Karp-Boss & Jumars 1998). *Hyalodiscopsis plana* combines the advantages of spacing between cells in the chain and bending, conforming to ‘...the evolutionary trend in diatom chain formation toward non-touching cells. Details of spacing within chains will alter the way that turbulence and bending “pump” nutrient replete water between the cells of chains’ (Karp-Boss *et al.* 1996).

The small filament lengths of 2 to 4 cells may reflect the scale of this turbulence. Light piping of filaments (Gordon *et al.* 2009; Neethirajan *et al.* 2009) may help *Hyalodiscopsis plana* survive ‘a fluctuating light regime ... in turbulent waters’ (Lavaud *et al.* 2007).

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