

Sieves and Flaps: Siliceous Minutiae in the Pores of Raphid Diatoms

by

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With 4 plates and 3 text figures

Abstract: A survey of pore structure in raphid pennate diatoms, exclusive of *Mastogloia* and the Eunotiaceae, suggests that the ultimate pore occlusions fall into two main groups. In one the occlusion takes the form of a delicate membrane occupying the whole pore; the membrane is of more or less uniform thickness and is perforated by round or elongate holes with minimum dimensions of 5-10 nm. Volae, cribra or other structures may also be present. In the other group the pores are closed by flaps that extend out from the pore wall, or from the bars of cribra. These two types are termed hymenate and volate pore occlusions respectively. The systematic implications of the distribution of pore occlusion types are discussed.

Introduction

Before the invention of the electron microscope we knew very little about the structure of the pores through the diatom frustule, except in coarsely-structured forms such as *Isthmia* Ag. and *Triceratium* Ehrenb. Some of the observations made by workers such as Lauterborn, Müller and Hustedt (see Hustedt 1927-66, Fritsch 1935) are quite remarkable, but of course even in the most expert hands the light microscope is incapable of resolving structures smaller than about 200 nm in diameter. It is not surprising, therefore, that the introduction of the transmission electron microscope (TEM) led to the discovery of a wealth of detail about the fine structure of the valve, detail docu-

mented in the Helmcke & Krieger Atlas (1953-) and in the works of Okuno, Desikachary and others (see Hendey 1959, 1971). This new information was sometimes used in systematics: particularly important contributions were made, for instance, by Hasle (1964, 1965a, b) on *Nitzschia* Hass., and Reimann & Lewin (1964) on *Cylindrotheca* Rabenh. The development of scanning electron microscope (SEM) techniques had a more profound impact on diatom taxonomy and I think it would be fair to claim that this instrument is now the preferred tool of workers in this field, except where small or lightly silicified forms are under consideration. The reasons for this are clear: the SEM allows the easy determination of surface morphology, which before required the laborious preparation and examination of replicas, and, because of its great depth of focus and apparently three-dimensional image, makes it fairly simple to investigate the spatial interrelationships of different frustule elements.

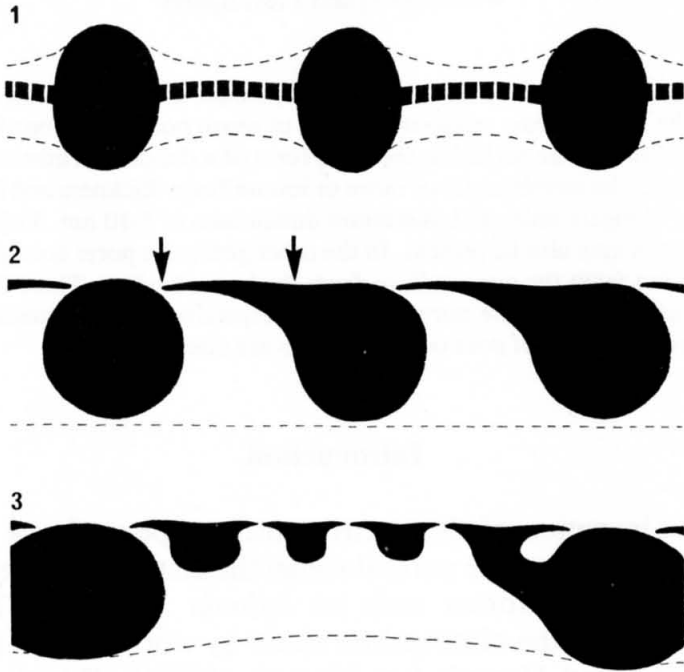


Fig. 1. Apical section of a part of a diatom possessing simple hymenate pore occlusions. Compare Fig. 13.

Fig. 2. Transapical section of a volate form, e.g. *Gomphonema*: the arrows indicate the extent of the volate occlusion. Compare Figs 20, 21, 27.

Fig. 3. Apical section of a complex system, with cribrum-borne volae, as in *Achnanthes kuwaitensis*. Compare Fig. 22.

We should remember, however, that with diatom specimens the resolution of the SEM is only rarely better than 15 nm, and is inadequate to allow examination of the finer details of pore structure. Thus, while the utility of the SEM cannot be doubted, it is essential that in any systematic investigation TEM studies are undertaken wherever possible to supplement SEM-derived data. Perhaps it is because of an overreliance on the SEM in the last decade that the distinction I describe below has apparently remained unformulated, even though much of the information upon which it is based was available twenty years ago.

Methods

The TEM work was accomplished through the use of an AEI EM6G (University of Bristol) or a JEOL 100S (University of Edinburgh), operated at 60 or 80 kV. SEM observations were made with Cambridge S4a (Bristol) and S150 at 20 and 30 kV respectively. Specimen preparation was as described by Mann (1977).

Observations

My analysis is restricted to the diatoms traditionally classified in the Monoraphideae and Biraphideae (Hustedt 1927-66), i.e. the raphid pennate diatoms apart from the Eunotiaceae Kütz., which family exhibits several peculiarities in the anatomy of the raphe system, and in the presence of rimoportules in many members. I am also ignoring *Mastogloia* Thwaites, which has a complex valve structure quite unlike anything I have found elsewhere.

Within this large group there seems to be a fundamental division between what may be termed hymenate and volate types of pore occlusion. The first consists of a delicate siliceous membrane that extends across the whole pore (hence hymen); the membrane is of more or less uniform thickness, and is perforated by tiny round or elongate holes (Figs 1, 4-16, 18-19). The most familiar form of the structure, in which the holes are circular and approximately 5 nm in diameter, has been termed a *rica* by Ross *et al.* (1979). However, to the outsider

'hymen' is probably more intelligible than 'rica', this being to my mind an important consideration if we are to prevent diatom biology becoming an obscure branch of science, for initiates only. At the moment we can surely allow terminology to evolve as our knowledge increases, and so I suggest the general term 'hymenate pore occlusion' for any membrane of the type described, perforated by holes with a minimum dimension of 5-10 nm.

In the simplest type of volate occlusion the pore is closed by a flap of silica (vola: Ross & Sims 1972), attached to the wall of the pore by a fairly broad base and extending most of the way across it, leaving only a curved slit by which communication may be effected between outside and inside (Figs 2, 20-21, 27, 32). In other types there may be more than one flap per pore (Figs 17, 28-30), or the flaps may be borne on cribra (Figs 3, 22, 33-34), but in all cases the flap thins from base to free edge, and is non-porose.

Neither term is meant to imply homology of the structures to which it may be applied; both should nevertheless be useful for expediting communication. Pore occlusions in the valves and girdle bands of a single frustule usually have the same basic plan, although those of the bands are usually somewhat simpler. No case is known to me where volate and hymenate occlusions occur together in the same frustule (but see below).

The Hymenate Pore Occlusion

It is important to realize that my distinction between hymenate and volate occlusions applies only to the finest structures present in the pores. In several species where the ultimate siliceous occlusion is hymenate, the pores also contain volae, placed somewhat nearer the external apertures of the pores than the hymenes. These volae are rarely very extensive and are probably only analogous to the volate occlusions of *Epithemia* Bréb., *Gomphonema* Ehrenb., etc. *Nitzschia hungarica* Grun. and *Scoliopleura tumida* (Bréb.) Rabenh. are examples of forms with volae as well as hymenate occlusions, although the phenomenon occurs to a lesser or greater extent in a number of unrelated genera. Elsewhere, cribra or other structures may be present in addition to the hymen. Thus, in the larger forms of *N. sigma* (Kütz.)

W. Smith, and in some populations of *Hantzschia marina* (Donkin) Grun., there is a well-developed cribrum in each pore, lying in the same plane as the hymen. In *N. sinuata* (W. Smith) Grun. (Mann 1978), *N. denticula* Grun. (Fig. 26) and *N. amphibia* Grun. (Lange-Bertalot & Simonsen 1978, Mann 1978) more delicate cribra are present, external to the hymenes. These cribra, though fine, are still resolvable using the SEM: by contrast, all hymenes appear structureless when viewed with this instrument.

Cox's (1976) claim that 'the presence of a porous plate over the internal surface of a stria pore appears to be a constant feature of pennate diatoms' cannot be upheld, although this arrangement is probably characteristic of the majority of raphid species. In genera such as *Brachysira* Kütz. (see Round & Mann 1981), *Frustulia* Rabenh. (Cox 1975) and *Neidium* Pfitzer, and in some *Navicula* Bory species, e.g. *N. mutica* Kütz. and *N. perpusilla* (Kütz.) Grun., the hymenes do indeed lie more or less flush with the internal surface of the valve; in various others, e.g. *Navicula* subgenus *Navicula* they are placed only slightly nearer the valve exterior. Most of the Bacillariaceae (Nitzschiaceae of some authors: see Silva 1980), however, have valves in which the hymenes are close to, or flush with the outer surface of the valve. Variation may occur within species, as for instance in *Hantzschia amphioxys* (Ehrenb.) Grun. (Mann 1978), but this is uncommon.

Where the valve is chambered the hymen is sometimes at the inner aperture of the chamber (be it a loculus or an alveolus, sensu Ross *et al.* 1979), sometimes at the outer aperture. Thus, in *Pleurosigma* W. Smith (Fig. 14) and *Gyrosigma* Hass. the hymen occupies the inner, oval aperture, while the outer aperture, a slit, is quite without occlusion. The hymen occupies a similar position in the *Nitzschiae Panduriformes* Grun., and in the *smithii* group of *Diploneis* (including *D. smithii* (Bréb.) Cleve, *D. fusca* (Greg.) Cleve and the freshwater species): in other *Diploneis* species the structure can be somewhat more complex. *Trachyneis* Cleve provides a contrast. Here the striae consist of several alveoli, each of which opens to the inside by a single, large, unoccluded pore, and to the outside by a number of elongate slits containing hymenes. *Pinnularia* Ehrenb. and *Caloneis* Cleve are similar, except that there is only one alveolus per stria and the outer pores are circular (compare Figs 10 and 12); in some, if not all, species of these

genera, as in *Hantzschia virgata* (Roper) Grun. (Mann 1977, 1981) the hymenes lie more or less flush with the outer surface of the valve, so that in scanning electron micrographs intact valves appear almost structureless externally.

The diameters of the holes in the hymenes, or their widths where the holes are elongate, are virtually constant within a valve, and usually measure approximately 5 nm. In some species, e.g. *Amphora perpusilla* (Grun.) Grun., they are larger than this, but in acid-cleaned material it is often difficult to be sure that perforation size has not been increased through erosion during specimen preparation.

Hymenate occlusions may be classified according to the shape and arrangement of the perforations. As has already been mentioned, the perforations are usually circular in outline, but in a few cases, e.g. *Entomoneis* Ehrenb. (Fig. 19), *Anorthoneis* Grun. (Fig. 15) and *Cocconeis* Ehrenberg (Gerloff & Rivera 1979), they are linear, although it is common to find a few round holes in each hymen. *Navicula pusilla* W. Smith (Fig. 18) has similar occlusions.

With regard to the arrangement of the perforations three groups may be distinguished, though the boundaries between them are by no means clearcut. These three will be described in turn and a list given of taxa known to me that exhibit each type.

Hexagonal Array

In this group the holes are closely packed in a strict hexagonal array (Figs 5, 8, 11, 12), which usually has the same orientation throughout the hymen. The only exception found so far is in one population of *Hantzschia marina*, where two or more areas with different orientations may be distinguished in each poroid (Fig. 5), and I have suggested that in this diatom the hymen may be produced by the separate formation and subsequent assembly of several discrete blocks of lattice (Mann 1977).

Sometimes the orientation of the array bears no apparent relation to that of other valve elements — this is the case in most of the Bacillariaceae, and in *Amphora perpusilla* (unpubl. obs.) — but in many species of *Navicula* subgenus *Navicula*, and in *Trachyneis aspera*

(Ehrenb.) Cleve, *N. perpusilla* and *Diploneis smithii*, where the hymen itself is elongate, the array is orientated strictly, with one of its three axes parallel to the long axis of the hymen (Figs 11-12).

Rhoicosphenia curvata (Kütz.) Grun.

Diploneis Ehrenb. spp.

Navicula perpusilla

N. pseudocomoides Hendey (Cox 1978)

N. delognei Van Heurck (Cox 1978)

N. digitoradiata Greg.

Stauroneis phoenicenteron Ehrenb.

Trachyneis aspera

Plagiotropis Pfitzer sp.

Amphora ovalis (Kütz.) Kütz.

A. perpusilla

Denticula tenuis Kütz.

many *Nitzschia* spp.

Hantzschia marina, in part

Bacillaria Gmelin

Centric Array

In the second group the perforations are ordered with respect to the centre of the hymen and hence, if a term is required, the arrangement may be said to be centric. Many *Cocconeis* species have hymenes of this type (e.g. see Gerloff & Rivera 1979, Fig. 29), although these of course have elongate perforations. Particularly good examples of centric arrays are found in *Nitzschia paeneperpetua* Mann (Fig. 7; Mann, in press).

Cocconeis spp.

Entomoneis spp.

N. paeneperpetua

N. dubia W. Smith

Regular Scatter

The third category includes forms in which the tiny pores are scattered across the hymen in a somewhat disorderly fashion. I thought at one time (1977) that the arrangement is random, but this is not so. If a statistical analysis is made it can be shown that the spacing is more regular than would be expected on the basis of a random distribution. A simple analysis is to determine the number of holes occurring within 'quadrats' placed at random on a large format reproduction of a micrograph of hymenes. If the holes are randomly distributed then the frequencies of quadrats containing 1, 2, 3, ... n holes, where n is the maximum number of holes possible per quadrat, should obey a binomial distribution: the Poisson distribution is inappropriate here since the density of holes clearly could not be much greater than it is

(see Greig-Smith 1957). In the absence of any other guide it seems most reasonable to take the maximum observed density of holes in a small part of the hymen as the maximum possible density, and to test the hypothesis that the observed frequency values could have come from a binomial distribution obtained by expansion of

$$\left[\frac{m}{n} + \left(1 - \frac{m}{n} \right) \right]^n ,$$

where m is the mean number of holes per quadrat. When this was done for *Hantzschia marina* hymenes of the type depicted in Fig. 1 the observed values fitted the appropriate binomial distribution with a probability of less than 0.025, being clustered much more closely about the mean than one would expect from a random scatter. Thus, even in species of this group there must be considerable control on the organisation of the hymen during valve deposition.

Achnanthes microcephala (Kütz.) Grun.

A. minutissima Kütz.

Amphipleura pellucida (Kütz.) Kütz.

Frustulia rhomboides (Ehrenb.) De Toni

Berkeleya rutilans (Trentepohl) Grun.

Brachysira spp.

Neidium bisulcatum (Lagerst.) Cleve

Pleurosigma angulatum (Quek.) W. Smith

Gyrosigma balticum (Ehrenb.) Rabenh.

Scoliopleura tumida

Navicula laevissima Kütz.

N. cocconeiformis Greg.

Pinnularia borealis Ehrenb.

P. gracillima Greg.

P. trevelyana (Donkin) Rabenh.

Caloneis bacillum (Grun.) Cleve

C. liber (W. Smith) Cleve

C. oregonica (Ehrenb.) Patrick

Hantzschia amphioxys

H. virgata

H. marina, in part
many *Nitzschia* spp.

Proboscidea insecta (Grun.) Paddock & Sims

The Volate Pore Occlusion

The simple type of volate occlusion described previously is widespread in *Gomphonema*. Except in a few cases each poroid contains a single volate occlusion, attached to one or other transapical side of the poroid (Figs 20, 27). *Gomphonema* pores have often been described as being reniform, but this is perhaps more a consequence of preparation procedures than a true description of structure. If the valves are at all eroded, as in Fig. 21, each occlusion is reduced to a larger or smaller stub, which represents the thick base of the vola: the pore will then

appear reniform, although it is not so in the sense in which this term may be applied to the poroids of *Hantzschia marina*. At least the smaller *Gomphoneis* species (*sensu* Dawson 1974) also have simple, volate occlusions.

In *Didymosphenia* M. Schmidt, Dawson (1973) has shown that each pore is occluded by several volae. A dendritic slit is left between their free edges and this may be seen from outside (Fig. 28) or inside (Fig. 29) — there is no trace of a hymen.

Cox (1976) claimed that hymenate occlusions are present in *Cymbella* Ag. species, although she did not illustrate these but instead *Navicula ramosissima* (Ag.) Cleve, in which she stated the structure to be 'inherently similar to pore sub-structure in *Cymbella*'. In view of Cox's opinion I have searched carefully for such occlusions in various species but have so far failed to detect any, even in samples that had been only gently cleaned with acid and in which species of other genera have intact hymenes. In *C. cymbiformis*, however, the internal aperture of each poroid is covered by a flap (Fig. 31), whereas externally the poroid opens by a narrow, unoccluded slit (see Krammer 1979). Other species also have volate occlusions, though the structure is nothing like as uniform as in *Gomphonema*.

Epithemia (Figs 17, 30) and *Rhopalodia* O. Müller species (Fig. 32) have fairly simple volate occlusions, although in some of the larger *Epithemiae* it is very difficult to work out the exact relationships between areolae and volae. The latter are always external.

More complex systems occur in some *Achnanthes* Bory and *Navicula* species. Most *Achnanthes* species have hymenate occlusions, but the larger forms, such as *A. brevipes* Ag., *A. coarctata* (Bréb.) Grun. and *A. kuwaitensis* Hendey, i.e. '*Achnanthidium*' of Hustedt (1927-66: it must be noted that this is not the correct name for the group — *vide* Patrick & Reimer 1966), and *A. longipes*, possess volate systems. Here, however, the volae are borne on cribra, each cribrum bar thinning out bilaterally into flaps that extend out towards adjacent cribrum bars (Fig. 3): in *A. coarctata* the flaps appear to have entire margins, but in *A. kuwaitensis* they are dissected (Fig. 22).

Navicula lyra Ehrenb. and other large lyrate species (but not the group clustered around *N. pygmaea* Kütz.) have fairly simple volate closures

at the inner apertures of the poroids. In *N. monilifera* Cleve a system of cribrum-borne volae is present (Figs 33-34), and in *N. scutelloides* W. Smith there are strange convoluted occlusions, very variable in form but basically volate in structure (Fig. 25).

A further variation occurs in some *Surirella* Turpin species, e.g. *S. ovalis* Bréb. and *S. cf. hybrida* Grun., where flaps extend out from opposite sides of each poroid, leaving only a slit for communication between exterior and interior (Fig. 23). *Surirella gemma* (Ehrenb.) Kütz., however, a species anomalous in a number of ways, has cribrum-borne volae, rather like those of *Achnanthes coarctata* (Fig. 24).

Discussion

The question now arises as to what significance this information has for systematics, physiology, or whatever. I will confine myself here to consideration of the relevance of pore structure variation in determining systematic relationships, although it is interesting to note that the holes through hymenes are of such a size that they must markedly affect the passage of large molecules into and out of the cell (compare the angiosperm data of Carpita *et al.* 1979).

Of course, systematic relationships cannot be determined from the distribution of the states of one character. Even if several characters can be derived from the 'ultimate pore occlusion' it is still clear that in one sense the latter has no direct systematic significance, since in order to determine relationships in these distinctly cryptogamic plants we have to rely entirely upon a phenetic approach, employing overall similarity as the measure of kinship. Thus pore structure provides only a small part of the evidence one would need in order to make out a substantial case for systematic proximity.

Nevertheless, one might expect that in a natural classification hymenate forms would tend on the whole to be grouped with hymenate forms, and volate with volate. The distribution of different pore occlusion types, then, is a challenge to us to look again at the classification of raphid diatoms, to see whether any of our current ideas need revision.

In several ways pore structure serves merely to strengthen arguments

already put forward on the basis of other characters. Thus Cox's (1976) suggestion that the Gomphocymbellae is a natural group is supported by the presence of volate occlusions in *Gomphonema*, *Gomphoneis*, *Didymosphenia* and *Cymbella*, and the uniformity of construction in *Epithemia* and *Rhopalodia* confirms the validity of the Epithemiaceae Grun., *sensu* Simonsen (1979). Simonsen's reappraisal of his earlier view that the Epithemiaceae are connected with the Bacillariaceae appears to have been wise: certainly the pore occlusions in the two groups are quite different. In this connection it is relevant to note that Lange-Bertalot (1980) has described a new species of *Nitzschia*, *N. leistikowii*, with an areola structure 'similar to that found in the genus *Gomphonema*'. This species appears, then, to have volate occlusions, although in other respects it is a 'respectable' member of the *Nitzschiae Lanceolatae* Grun. Volae are found in addition to hymenes in several *Nitzschia* species, e.g. *N. hungarica* and a member of the *Panduriformes* that I call *N. mollis* Hust. var. *africana* Cholnoky, and in such forms it is easy to miss the hymenes, especially in harshly cleaned material: until recently I believed *Scoliopleura* Grun. to lack hymenes for similar reasons. Assuming that hymenes are indeed absent, two points may be made. The only difference between *N. leistikowii* and *N. frustulum* (Kütz.) Grun. is said to be the pore structure. If so I think it doubtful that the two should be separated, since a single character is insufficient to differentiate species. The other point is that other evidence, e.g. raphe disposition, fibula structure and valve structure, indicates clearly that any resemblance to the Epithemiaceae in the type of pore occlusion can only be a result of convergence.

Convergence can probably be invoked too to explain the resemblance between the pore occlusions of the Epithemiaceae and those of the gomphocymbelloid diatoms. It is perhaps no coincidence that volate occlusions are more widespread in attached forms than in more active, epipelagic species. *Gomphonema*, *Cymbella*, *Epithemia* and *Rhopalodia* are well known as components of the haptobenthos, while *Achnanthes brevipes* and its relatives are also epiphytic or epilithic. Outside the raphid diatoms volate occlusions may be found in *Rhaphoneis* Ehrenb. species and *Psammodiscus nitidus* (Greg.) Round & Mann (1980), and these too are attached forms. It must be admitted, however, that the correlation between habitat and pore

occlusion type is by no means complete: *Rhoicosphenia* Grun. and *Cocconeis*, for instance, are attached, but possess hymenes, while *Navicula lyra* and *Surirella gemma* are epipellic and have volae. Nevertheless the correlation is interesting and illustrates well the fact that in most cases we have no idea what all the siliceous bric-a-brac actually does *in vivo*.

In some cases, however, the distribution of pore occlusion types seems to indicate relationships that are not recognized in the current classification. Perhaps the most controversial inference is that the larger species of *Achnanthes*, i.e. *A. brevipes*, *A. longipes*, *A. coarctata*, *A. kuwaitensis* and others of this group, in which volate occlusions are present, may not be at all closely related to the other members of the Monoraphideae, *sensu* Hustedt (1927-66). Their affinities appear to lie instead with some of the naviculoids, especially *Navicula monilifera*, *N. humerosa* Bréb., *N. latissima* Greg., *N. scutelloides* and *N. lyra*. A few authors have suggested already that these *Achnanthes* species are misclassified. Mereschkowsky (1903) placed them, but not the other *Achnanthes* groups, with *Scoliotropis latestriata* (Bréb.) Cleve in the 'Scoliotropideae', and Cleve too considered that in a natural system the monoraphids might fall into several quite unrelated groups (Cleve 1894-5). Certainly these *Achnanthes* stand out by their size, coarse structure and possession of a peculiar chromatophore arrangement (see Mereschkowsky 1901, 1903), and, while other *Achnanthes* species, *Cocconeis* and *Anorthoneis* have offset, noncoaxial internal central raphe endings (like those of *Hantzschia*: compare Mann 1977, Figs 40, 60 and 79 with the illustrations of Gerloff & Rivera 1979), the large *Achnanthes* have coaxial endings. At least in two cases, moreover, viz. *A. brevipes* and *A. coarctata*, the central internal raphe ending is shaped like a shepherd's crook, as in *N. monilifera*, *N. humerosa* (Cox 1977) and *N. lyra*. The terminal fissure is well developed here, whereas in most other monoraphids the raphe ends almost directly above the helictoglossa. Thus, although considerably more work needs to be done, pore structure suggests a possible link between two groups often classified in different orders, a link in some measure supported by other lines of evidence. It is certain in any case that these forms do not belong in the same genus as species such as *A. microcephala* (the type of *Achnanthes*) or *A. lanceolata* Bréb.

There are other cases where pore structure suggests that taxa have been misclassified. It does not appear likely, for instance, that *N. pusilla* and *N. cocconeiformis* belong in the same group as *N. monilifera*, *N. punctulata*, *N. humerosa* and *N. latissima*, although all are placed in the same subgenus or section by Patrick & Reimer (1966) and Hustedt (1927-66): raphe structure as well as pore type suggests a need for revision.

The pore occlusions give several clues concerning the origins and interrelationships of the fibulate ('canal-raphe') diatoms, viz. the Entomoneidaceae Reimer, Auriculaceae Hendey, Epithemiaceae, Bacillariaceae and Surirellaceae Kütz. Firstly, it is not likely that *Entomoneis* (= *Amphiprora*, *sensu* Hustedt 1930, etc.), with its elongate hymen pores, fibulae and sigmoid twist, is at all closely related to *Plagiotropis* (= *Tropidoneis* Cleve): Mereschkowsky (1903) came to the same conclusion from a study of the 'endochrome'. There is also little indication that *Entomoneis* is more than distantly related to *Nitzschia*.

As Paddock & Sims (1977) have pointed out, the valve structure of many *Entomoneis* species is similar to that of *Auricula*: both *A. amphitritis* Castr. (Paddock & Sims 1980) and *A. flabelliformis* Voigt, for instance, have biseriate striae, as in *E. alata*, and it would be interesting to know if they too have elongate hymen perforations. *Proboscidea insecta*, until recently classified in *Auricula*, possesses round-pored hymenes, and, with its uniseriate striae and narrow, rib-like fibulae, would seem to be more akin to the Bacillariaceae than are most other fibulate groups.

Links between *Auricula*, *Rhopalodia* and *Epithemia* have been suggested by Simonsen (1979) and Paddock & Sims (1980). Pore occlusion evidence is not available, but it is interesting that all have isogamous reproduction (Geitler 1932) and all have but a single chromatophore per cell (unpubl. obs.; Mereschkowsky 1901, 1903).

The presence of hymenes with hexagonal arrays in *Simonsenia delognei* (Grun.) Lange-Bertalot lends no support to the idea that there is a 'systematic interrelationship between the Nitzschiaceae and Surirellaceae' (Lange-Bertalot 1979), but more evidence is necessary before we can eliminate this possibility. *Simonsenia* is clearly a member of the Bacillariaceae, though a strange one, and on balance I do not believe it likely that this family is at all closely related to the Surirellaceae.

In conclusion, it appears that with regard to the ultimate pore occlusion raphid diatoms have only a very limited number of 'options'. The majority of species have sieve-like membranes, with tiny, round or elongate perforations; the remainder have unperforate, flap-like closures. These two I term hymenate and volate pore occlusions respectively, with no implication that all the structures in either category are necessarily homologous, although I think it unlikely that the round-pored hymen has arisen more than once. Many taxa are remarkably uniform in their pore structure: all *Brachysira* species, for instance, have hymenes with round pores in a regular scatter. In other cases, e.g. *Hantzschia marina*, the arrangement of hymen perforations may vary within a single species. So, just as with every other character, it is impossible to generalize about the taxonomic worth of the ultimate pore occlusion. The variation in pore structure within the raphid diatoms is interesting, however, and suggests that some of the more curious suggestions made by Cleve (1894-5) and Mereschkowsky (1903) may not be as far from the truth as has been assumed in the last half-century: their ideas are certainly worth careful, unprejudiced consideration.

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Explanation of Plates

Plate 1

Hymenate occlusions of valve pores (TEM). Figs 4-6. *Hantzschia marina*. — Figs 4, 6. Populations from Tregantle, Cornwall: hymen pores in regular scatter, $\times 71,000$. — Fig. 5. Population from Aberdeen Beach, Scotland: hexagonal array, $\times 79,000$. — Fig. 7. *Nitzschia paenepetua*: centric array, $\times 85,000$. — Fig. 8. *N. sinuata*, $\times 76,000$. — Fig. 9. *Proboscidea insecta*, $\times 65,000$. — Fig. 10. *Pinnularia gracillima* Greg., $\times 80,000$.

Plate 2

Hymenate and volate (Fig. 17) occlusions of valve pores (TEM). Fig. 11. *Navicula digitoradiata*, $\times 59,000$. — Fig. 12. *Trachyneis aspera*, $\times 34,000$. — Fig. 13. *Neidium bisulcatum*, $\times 58,000$. — Fig. 14. *Pleurosigma angulatum*, $\times 65,000$. — Fig. 15. *Anorthoneis excentrica*, $\times 61,000$. — Fig. 16. *Diploneis bombus*, $\times 68,000$. — Fig. 17. *Epithemia sorex*, $\times 46,200$. — Fig. 18. *Navicula pusilla*, $\times 63,000$. — Fig. 19. *Entomoneis alata*, $\times 43,000$.

Plate 3

Figs 20-25. Volate occlusions of valve pores (TEM). — Fig. 20. *Gomphonema acuminatum* var. *coronatum*, $\times 31,000$. — Fig. 21. *G. gracile*, $\times 57,000$. — Fig. 22. *Achnanthes kuwaitensis*, $\times 60,000$. — Fig. 23. *Surirella* cf. *hybrida*, $\times 51,000$. — Fig. 24. *S. gemma*, $\times 43,000$. — Fig. 25. *Navicula scutelloides*, $\times 61,000$. — Figs 26, 27. Scanning electron micrographs of valve exteriors. — Fig. 26. *Nitzschia denticula*. Delicate cribra visible in the poroids, $\times 32,000$. — Fig. 27. *G. acuminatum*, near basal pole, $\times 19,500$.

Plate 4

Scanning electron micrographs. Figs 28, 29. *Didymosphenia geminata*. — Fig. 28. Exterior showing dendritic slits (arrow) beneath rings of spine-like projections, $\times 27,000$. — Fig. 29. Interior, $\times 14,700$. — Fig. 30. *Epithemia mulleri*. Valve exterior near pole, $\times 6,700$. — Fig. 31. *Cymbella cymbiformis*. Valve interior with volate occlusions, some of which (arrowheads) are slightly displaced, $\times 19,000$. Fig. 32. *Rhopalodia musculus* (Kütz.) O. Müller. Valve exterior and central raphe endings, $\times 14,300$. — Figs 33, 34. *Navicula monilifera*: cribrum-borne volae. — Fig. 33. Exterior, $\times 14,600$. — Fig. 34. Interior, $\times 13,400$.

