5: THE EPITHEMIACEAE

In order to help establish whether the present limits of the Nitzschiaceae are correct, or whether they should be altered so as to include other genera (or to exclude genera now classified within it), it is necessary to examine other groups of diatoms which appear to be closely related to it. Such a group is the Epithemiaceae, a family which includes three genera - Epithemia, Rhopalodia and Denticula. These taxa consist exclusively of forms possessing subtended raphes, and while it is true that another family, the Surirellaceae, also consists of such forms, the Epithemiaceae seems to be more akin to the Nitzschiaceae, especially since in the Surirellaceae the raphe system runs around the whole perimeter of the valve; (this property makes comparisons between these families difficult because of the lack of common reference points - e.g. it is at present impossible in the Surirellaceae to distinguish 'central' from 'polar' raphe endings). The Surirellaceae was given a certain amount of attention during this study, but no close links between it and the Nitzschiaceae were discovered and so it will receive no further consideration in this thesis.

The Epithemiaceae is traditionally separated from the Nitzschiaceae according to whether or not the raphe is borne on a keel (see Hustedt 1930, Patrick & Reimer 1966): keels are supposedly present in the latter, but absent in the other. Hustedt (1930) mentioned another criterion, namely the degree of development of the fibulae (his 'Kielpunkte'). Neither feature is satisfactory, however, since certain species of Denticula are no less keeled than some species of Nitzschia (e.g. N. vidovichii, sect. Nitzschia), while the other criterion is so vague as to be useless. In view of the deficiencies in the diagnosis of this group, it is necessary, before further discussion is attempted concerning the limits of the Nitzschiaceae, to give a short account of

frustule structure in each of the three genera of the Epithemiaceae.

5.1 Epithemia

It is logical to tackle this genus first since it is the type of the family. Epithemia is a genus of moderate size, containing 38 species according to Van Landingham (1969). Most often, these organisms are to be found growing on submerged vegetation or on wet sand (see Hustedt 1930, Round 1958a, b, c): they do not occur in salt water.

The structure of the frustule was studied in detail by three light microscopists - O.Müller (1898), Fricke (in A.Schmidt Atlas, T.249-52) and Hustedt (1928a). Since this, however, little further progress has been achieved, although some transmission electron micrographs have been published in the Helmcke & Krieger Atlas (1953- , T.80, 295, 506-9), while Schoeman & Archibald (1976-) have given an account of structure in E. sorex.

For this study, four species - E. argus, E. muelleri, E. sorex and E. zebra - have been examined using LM and SEM techniques, and one of these (E. sorex) has also been investigated using the TEM. Other species are also included in the discussion which follows, data for these being derived from the drawings and descriptions of Fricke (op. cit.) and Hustedt (1930).

With regard to the overall form of the frustule, Epithemia shows a resemblance to Hantzschia. In both, the frustule is dorsiventral, and 'spiegelsymmetrisch' about the median valvar plane, while the raphe system is usually nearer the ventral, than the dorsal valve margin (F.998, 1000, 1006). Unlike in Hantzschia, however, the valve apices are usually broad and bluntly rounded (F.1000, 1006, 1008, and see Hustedt 1930). There are never any 'shoulders' near the poles on the ventral side (contrast H. amphioxys, H. virgata, etc.), which is straight or slightly concave (slightly convex only in E. intermedia: see Hustedt 1930, f.732). Any constriction of the valve near the pole

(as is present, for example, in E. sorex) is because of variation in the
curvature of the dorsal, not the ventral margin (F.1000).

The species differ from one another in the shape of the valve,
the relative heights of the ventral and dorsal mantles, and the rel-
ative widths of the ventral and dorsal halves of the cincture. Thus,
some forms have almost straight valves (e.g. E. turgida: Hustedt 1930,
f.733-4), while others have strongly bent ones (e.g. E. hyndmanni: op.
cit., f.735), etc. In a complete frustule the two valve faces are
often not parallel to one another, because of cincture asymmetry and/or
differences in mantle height. This is exemplified in E. sorex (F.998),
whereas in other species, e.g. E. zebra and E. muelleri, the valve
faces are more or less parallel (F.1006; see also Fricke op. cit.,
T.249-52). In Hantzschia, however, although the cincture is often
asymmetrical, yet where valve faces may be distinguished these are
usually parallel (unpubl. obs.).

The valve construction is difficult to describe, but is perhaps
easiest to explain through reference to E. zebra (Text F.4D). In this
species the valve is pierced by transapical rows of 'areolae', each of
which is constricted at both the inner and outer surfaces of the valve,
and hence is loculate according to the definition given by Anon. (1975).
To the inside the 'areola' opens by a large circular foramen (F.1005,
1007, 1009), whereas externally there are four (sometimes more or less)
smaller holes, which are placed fairly regularly about a central 'boss'
of unperforate silica (F.1005, 1000-1, Text F.4D). These holes are
not closed by hymena, which structures might be expected to be present
if Epithemia was closely related to the Nitzschiaceae, but by flanges
of silica which extend out from the central boss. They are connected
to the boss over a wide base, and extend almost to the far margin of
the hole; they stop short of this, however, leaving a narrow, arcuate
slit (F.1010, Text F.4D, and see F.569, 1013-4). Similar pore occlusions

are to be found in some Gomphonema species (e.g. G. sphaerophorum;
Helmcke & Krieger 1953- , Pl.909), Raphoneis surirella (ibid., T.148),
and probably in Coscinodiscus nitidus (unpubl. obs.).

In E. sorex (F.569, 1000, unpubl. obs.) the construction is rather
different in that the areolae are not chambered, and the 'holes' descr-
ibed above are not arranged in fours as in E. zebra. These differences
from E. sorex, like the differences in valve shape, mantle heights, etc.,
will be useful in infrageneric classification. The type of pore occl-
usion (F.569), however, is identical to that described above, and to
that found in E. muelleri (F.1013-4) and E. argus (unpubl. obs.).

Müller's (1898) careful studies of E. hyndmanni suggest that this
species is very similar in structure to E. zebra, with four external
holes per areola (op. cit., T.26 f.1, 6), although Fricke's illustr-
ation (in A.Schmidt Atlas, T.249 f.10) suggests a rather more complex
arrangement. Fricke's illustrations of E. cistula, E. intermedia,
E. turgida (for which see also Helmcke & Krieger 1953- , Pl.508) and
E. reicheltii give no indication that valve constructions fundamentally
different from those already described occur in this genus.

Between the rows of areolae are transapically orientated costae;
in the SEM these are not obvious in the loculate forms, e.g. E. zebra
(F.1005, 1007, 1009). Certain costae are much enlarged, and project
into the cell lumen (F.1004, 1007): these are the prominent 'Rippen'
visible in the light microscope (see Hustedt 1930). The number of rows
of areolae intervening between adjacent 'Rippen' is often used as a
diagnostic character: thus, E. zebra may be distinguished from E. sorex/
E. hyndmanni/E. turgida by the presence between adjacent 'Rippen' of
4 or more rows of areolae in the first, but only 2-3 in the others
(Hustedt 1930).

There are no sterna on valve face or mantles; the rows of areolae
run unbroken from margin to raphe-sternum (F.1000, 1009, 1013).

There seems to be a remarkable constancy within Epithemia in

relation to raphe and subraphe structure. The raphe is borne on the outside of a tube, or canal, which opens to the inside of the valve by a series of oval portulae (F.1004, 1007). This tube is not raised above the general level of the valve, but lies in the thickness of the wall; the canal wall is not porose (F.1000, 1006, 1009, 1011). The more strongly developed transapical valve costae (the 'Rippen') continue unbroken across the tube internally (F.1004, 1007), a point which was apparently missed by Hustedt and Fricke (see their illustrations). There are often several portulae between adjacent 'Rippen', whereas there should be only one if the 'Rippen' were fibulae like those of Nitzschia sect. Grunowia: of the species illustrated by Hustedt (1930), only one, E. sorex, has a 1 : 1 correspondence of 'Rippen' and portulae. By definition, then, the fibulae are the plates of silica between adjacent portulae, whether or not these plates are traversed by costate thickenings. The fibulae run into one another, and it is not possible to define the limits of each exactly.

The raphe itself is quite uniform in structure throughout the species studied. Near the poles it is always placed near the midline of the valve, or near the ventral side (F.1000, 1008). As the centre of the valve is approached, however, the raphe-slit curves further and further towards the dorsal margin, so that in valve view the raphe system is in the form of a curvy 'V' (F.998, 1000, 1006, 1009, 1013). The degree to which the raphe approaches the dorsal margin at the centre varies within the genus: in E. argus and E. sorex the raphe comes very close to this margin, while in E. zebra and especially in E. intermedia the deflection is less (see Hustedt 1930).

Central raphe endings are always present (see Hustedt 1928a, 1930; Fricke, op. cit.). The electron microscope reveals that the external fissures are somewhat enlarged terminally into 'pores' (F.1000, 1009-10, 1013). Internally the raphe fissure is more or less continuous across

the centre (F.1007), although the centremost portion, which must be blind, is raised slightly in a structure which somewhat resembles a double helictoglossa. Both internally and externally the endings are noncoaxial-symmetrical.

At the poles the raphe ends internally in simple helictoglossae (F.1003), but these are impossible to see unless isolated valves are examined: the presence of girdle bands obscures it from view. There is no terminal fissure, the external fissure ending simply and without expansion, immediately above the helictoglossa (F.1000, 1008, 1014). This feature, which is common to all the taxa investigated with the SEM, was noted by Fricke in _E. hyndmanni_ (op. cit., T.249 f.6), a remarkable feat considering that he was using light microscopy.

It will be remembered that in the Nitzschiaceae one band alone, the first, is in contact with the valve, except in those taxa with open bands, where the tip of the ligula of the second band may also lie adjacent to the valve. The pars interior of the first band in the Nitzschiaceae underlaps the valve margin, and sometimes also part of the valve itself, in which case it is usually modified to fit exactly under the valve costae and striae (e.g. as in _Hantzschia amphioxys_, _H. virgata_ var. _virgata_ or _Nitzschia sinuata_). In _Epithemia_, however, the first two or three bands all contribute substantially to the interlock with the valve (F.1012). The partes interiores of these bands (which are robust and heavily silicified) are much convoluted, so as to fit closely around the 'Rippen' and other structures of the valve (F.999, 1010). The first band of _E. sorex_ or _E. zebra_ extends only slightly under the 'Rippen'. The second extends further (F.999, 1001, 1004, 1010), and in _E. zebra_ the two halves of this band meet near the midline of the valve: they do not fuse (F.1005). The partes interiores do not extend into the lumen of the cell, nor do they underlap portions of the valve where areolae occur. Unpublished LM observations of _E. muelleri_ frustules suggest that the first three

bands may be involved in interlocking cingulum with valve, but further work is necessary before this is proven. Hustedt (1930) regarded these modifications of the partes interiores as septa ('Septen'), but this was an unfortunate appellation since these structures, closely appressed as they are to the 'Rippen' of the valve, hardly constitute a barrier or partition in the cell: it is no more justifiable that these should be called 'septa' than it would be to apply this term to the finger-like projections of the pars interior in Hantzschia amphioxys.

So far as I am aware, the Epithemiaceae is the only group of diatoms in which more than one band contributes to the interlocking between valve and girdle. The bond between these two parts of the theca is extremely strong, at least in E. sorex and E. zebra, where acid cleaning rarely separates more than a fraction of valves from their cingula; even fairly lengthy ultrasonication often fails to effect complete separation. Perhaps such rigidity of the frustule is a requisite of life in the habitats colonized by Epithemia, but diatoms of other genera with apparently weaker frustules (e.g. Gomphonema and Achnanthes species) grow abundantly in the same places.

The abvalvar bands are narrower than those nearer the valve (F.998, 1002), but their structure is otherwise ± unknown. Some observations of E. sorex suggest that certain of the abvalvar bands may each possess a single transverse row of pores, and Fricke (op. cit., T.249 f.12, 13) illustrated porose bands in E. cistula var. lunaris: this form, however, is unusual in other respects, and its frustule morphology is more like that of Rhopalodia. It would appear that the advalvar bands are usually closed (unpubl. obs.), but that open bands sometimes occur nearer the open end of the cingulum (F.1002, 1014).

The cytology of Epithemia species also provides a contrast to the Nitzschiaceae. As Mereschkowsky (1903a) noted, 'son endochrome est toujours composé d'une seule plaque ventrale, avec des bords très découpés, rétournant sur les valves.' Mereschkowsky's remarks were

based upon observations of E. sorex and another, unidentified species;
Pfitzer (1871) studied E. turgida, which also proved to have but one
chromatophore per cell.

5.2 Rhopalodia

As in Epithemia, the frustule is 'spiegelsymmetrisch' about the
median valvar plane, and exhibits dorsiventrality. It is separated
from Epithemia (with which it was once united) on the basis of valve
shape, and because the raphe is borne on a keel (F.1016, 1018). Most
often, Rhopalodia is found in the same types of habitat as Epithemia,
but unlike the latter it can occur in brackish or marine situations.

The valves of Rhopalodia species show a much greater variation
in shape than do those of Epithemia. Thus, for example, whereas in
Epithemia the valves are symmetrical about the median transapical plane,
in Rhopalodia this is not always so: Rh. hirundiformis and Rh. verm-
icularis are heteropolar (see Fricke op. cit., T.256 f.11-23), while
Rh. gibba and Rh. gibberula are isopolar, as in Epithemia (see Hustedt
1930).

The cincture may show pronounced dorsiventrality, as in Rh. musc-
ulus (F.1016, 1018, and Fricke op. cit., T.254 f.3, 4), or may be
almost symmetrical about the median valvar plane, as in Rh. hirundi-
formis var. turgida (ibid., T.265 f.4).

Three species, namely Rh. musculus, Rh. gibberula and Rh. parallela,
have been examined in the course of the present study, although much
further work will be necessary before detailed statements may be made
concerning the taxonomy of the genus.

Rh. musculus, which will be considered first, has a valve structure
very similar to that of Epithemia. The areolae, which are arranged in
transapical rows, with two rows between every pair of adjacent trans-
apical costae (F.1016), are each almost closed by a flap, there being
no sign of a hymen (F.570, 1015). The flap is joined to the wall of

the areola over a broad base, and obscures all but a narrow, arcuate slit, by which communication may be effected between cell and environment.

The raphe system is placed nearer to the dorsal margin of the valve than in Epithemia, but Rh. musculus resembles that genus in that the raphe, which liés almost in the midline of the valve at the pole, curves nearer to the dorsal margin as it approaches the centre (F.1016, 1018). Central raphe endings are present, but are not like those of Epithemia since, just before the centre, the external fissures are abruptly bent towards the ventral margin (F.1015).

The subraphe canal is raised above the general level of the valve (F.1015) on a distinct keel, but, as in Epithemia, the external canal walls are non-porose. Each transapical costa is continuous across the back of the subraphe canal, and forms a single fibula; the outer edges of the fibulae are developed into flanges, which combine with those of adjacent fibulae to delimit oval portulae (F.1017). Certain of the transapical costae are more strongly developed than the others, and this is reflected in the degree of development of the fibulae, some of which are more robust than the remainder.

The cincture is composed of several (6 or 7) bands, all of which are perforate (F.1018-9; see also Fricke op. cit., T.254 f.3,4). The method by which the bands interlock with the valve is not known.

There is one chromatophore per cell, as in Epithemia, and this has a much lobed margin (F.518-20). Mereschkowsky (1903a) recorded a like chromatophore structure in Rh. gibba (his 'Epithemia gibba').

In Rh. parallela and Rh. gibberula the valve is again traversed by costae, some of which are more strongly developed than the rest (F.1020, unpubl. obs.). The pore structure is not known, although Helmcke & Krieger's (1953- , T.395) TEM work on Rh. gibberula suggests that the pores are closed by flaps, although it is clear that the

structure is far more complex than in Rh. musculus.

Both species have a valve which is sharply angled at the raphe, but there is no sign of a keel (unpubl. obs.). Central raphe endings are present, but, at least in Rh. parallela, do not take the same form as is described above. The subraphe canal opens to the interior of the valve by oval or elongated portulae (F.1020), and the external canal walls are porose. In Rh. parallela all the valve transapical costae are continuous below the raphe, whereas in Rh. gibberula only some, the more strongly developed 'Rippen' (Hustedt 1930), are so (F.1020). Portulae are present between only some of the subtending costae in Rh. parallela (unpubl. obs.).

Turning to other, previously published information, there is no indication that hymena are present anywhere in Rhopalodia (see Helmcke & Krieger 1953- , T.81, 184, 396): the valve construction would appear to be of the type present in Epithemia.

The genus is more diverse than Epithemia, containing a wider range of variation in valve outline, raphe and subraphe structure: thus, for example, Rh. gracilis, unlike all other species of Rhopalodia and Epithemia, does not possess central raphe endings (Fricke op. cit., T.255 f.22-32). Within Rhopalodia there seem, in fact, to be two distinct groups of species. The first, including Rh. musculus and Rh. gibberula, consists of forms which have strongly 'dorsiventral' cinctures and strongly bent valves, and which live in brackish or marine habitats. Of these, as has already been noted, Rh. musculus is quite similar to Epithemia, except in its ecological preferences. The second group comprises the majority of Rhopalodia species, and includes Rh. gibba, Rh. parallela, Rh. gracilis, Rh. vermicularis and Rh. hirundi-formis. These have approximately linear, straight valves, an almost symmetrical cincture, and occur in freshwater. It seems likely that the genus will require subdivision (perhaps even division) along this

line of demarcation, although Müller subdivided the genus according
to the symmetry relationships about the median transapical plane, i.e.
separating heteropolar from isopolar forms (see Hustedt 1930); this
would appear, however, to be a rather artificial classification.

There do not appear to be any close similarities between Rhop-
alodia and any of the genera of the Nitzschiaceae. Instead, the
affinities of this genus seem to lie with Epithemia, as has always
been thought to be the case.

5.3 Denticula

According to Van Landingham (1969), the genus Denticula contains
approximately the same number of species as Epithemia, but in the last
few years several new species have been described by Schrader (see
Schrader 1973b) from fossil sediments. Denticula contains marine as
well as freshwater species: the former are planktonic, whereas the
latter occupy habitats similar to those occupied by freshwater Epi-
themia or Rhopalodia species, but with a greater extension into sub-
aerial niches.

Most species of Denticula have a valve outline which is exactly,
or almost symmetrical about the apical plane (e.g. F.506, 511, 513).
The raphe system may be central or eccentric. With regard to other
characters, it is possible to distinguish three groupings within
Denticula, and these will be considered, each in turn.

The first group contains the type species of the genus, D. elegans
(designated the type by Boyer 1927), as well as D. tenuis, D. parva,
and probably also D. linearis and D. bacillum. Of these, D. tenuis
and D. elegans have been examined during this study, the former with
LM, TEM and SEM, the latter with LM and SEM only. All of these species
are restricted to freshwater habitats.

The valve construction in this group is very similar to that in

Nitzschia sect. Grunowia (q.v.) and consists of single transapical rows
of poroids alternating with transapical costae (F.513, 1022-5, 1030).
The poroids are round, and contain hymena in which, in D. tenuis, the
pores are in hexagonal array (F.567-8). As in N. sinuata, the hymena
are placed not quite centrally in the poroids, but very slightly
nearer the outside surface of the valve (F.1023-4). Helmcke & Krieger's
illustration of D. tenuis (1953- , T.182) suggests that cribra similar
to those of N. sinuata and N. amphibia may be present in some popul-
ations of this species, but they were absent in the two populations
studied for this thesis. There is no sign whatsoever of flaps like
those which close the areolae of Epithemia or Rhopalodia species.

In D. tenuis the raphe is borne on a shallow, blunt-topped ridge
(F.1024-5), which might, perhaps, be termed a keel, although Hustedt,
by placing Denticula in the subfamily Epithemioideae (1930, p.379),
claimed that the raphe is 'nicht deutlich gekielt'. Distal to the
raphe there is an inward fold of the valve, so that the distal half of
the valve is sigmoid in transapical section. In D. elegans the raphe
is slightly more eccentric, is not raised on a keel, and lies at the
junction of valve face and proximal mantle (F.1029-30, 1033).

Hustedt (1928a) could not find central raphe endings in D.
tenuis (although he observed them in D. vanheurckii, D. valida and
D. thermalis), but believed that this was 'wahrscheinlich infolge
ihrer Zartheit.' Indeed, he considered (1930) that all the members of
the Epithemiaceae possess central raphe endings ('Zentralporen wohl
immer vorhanden, obgleich oft sehr schwer nachweisbar'), and figured
these in D. elegans (op. cit., f.725a) and D. tenuis (f.724b). But
in fact, neither D. tenuis, nor D. elegans, possess such endings: in
scanning electron micrographs the raphe may be followed from pole to
pole, and it is continuous (e.g. F.1030).

At each pole the raphe ends internally in a simple helictoglossa

(unpubl. obs.), while externally the fissure continues past this for some distance, as a blind groove (F.1024-5, 1033; contrast Epithemia). In D. tenuis this terminal fissure, whose separation from the remainder of the external fissure is marked by a sharp bend, follows a course similar in form to a circumflex accent (compare Nitzschia sect. Grunowia); the terminal fissure of D. elegans is somewhat simpler. Both terminal fissures of a single valve curve in the same direction, but this may be towards either the proximal (F.1025), or the distal margin (F.1024). Preliminary studies indicate that if the epitheca has distally directed fissures, the hypotheca will have proximally directed ones (F.1029).

A subraphe canal may be distinguished, but this is not raised above the general level of the valve: the extent of the canal is not determinable from external views alone (F.1025, 1030; compare sect. Grunowia). The exterior canal walls bear two longitudinal rows of poroids, one on either side of the raphe, each poroid being opposite a transapical stria (F.1023).

As in Rhopalodia and Epithemia, certain of the transapical valve costae are much thickened in the pervalvar plane, and are continuous beneath the raphe (F.1022-3): these heavily silicified structures have been termed 'pseudosepta' (Simonsen & Kanaya 1961, Anon. 1975). Intervening between each pair of 'pseudosepta' is one oval or subrectangular portula, as in Rh. gibberula, and so the 'pseudosepta' may also be termed fibulae. It can be seen that this subraphe structure is similar not only to that in Epithemia and Rhopalodia, but also to that in Nitzschia sect. Grunowia, from which it differs only in the degree by which the fibulae are extended across the valve. In D. tenuis, as in N. sinuata, each fibula is wider towards its inner edge than it is centrally, so that the fibula may be said to consist of three parts, viz. -

i. a solid bar which connects margin to margin (compare N. sinuata and N. solgensis, in which, however, the bar connects margin to valve face),

ii. a thinner 'membrane' of silica connecting this bar to the trans-apical valve costa immediately beneath, and to

iii. the flanges, which form the back of the subraphe canal and delimit the portulae.

The most advalvar row of cingulum elements in both D. tenuis and D. elegans are so adapted that in vivo they fit exactly around the fibulae (F.512). Thus, the bands bear a series of short projections (which are more like folds in D. tenuis), each corresponding to the position of a fibula (F.1028). In D. elegans the two sides of the cincture almost meet along the midline of the valve, but they do not quite achieve this, since the central part of each fibula is developed into a prominent boss which separates the two projections (F.1031-2). In contrast to Epithemia, only the first row of cingulum elements is involved in the bonding between valve and cingulum.

The most remarkable feature of the D. tenuis/elegans cincture is that it contains half-bands. Thus, instead of possessing a single 'valvocopula' (sensu Von Stosch 1975), these taxa have two half-bands, which each run along one side of the valve, from pole to pole (F.1029 and unpubl. obs.). The valvocopular half-bands of D. tenuis each bear a single transverse row of poroids (which contain hymena like those of the valve), which lies at the junction of the pars interior and pars exterior (F.1026, 1028). At least in D. elegans, a second row of half-bands is also present, adjacent to the first. Here again, the junctions between the bands lie at the poles, and it seems that the gaps between the bands of both the valvocopular, and the second series must be closed by ligulae borne by the third or subsequent bands: the third band is continuous around at least one pole (unpubl. obs.). The bands of D. elegans, in contrast to those of D. tenuis, seem to be quite

unperforate (F.1029, 1032): the valvocopular half-bands bear large flattish warts (cf. N. sinuata). This appears to be the first record of half-bands in a raphid diatom.

Unfortunately, it has not yet been possible to study the chromatophores of these two species. Geitler (1953) stated, however, that in D. tenuis 'jede vegetativer Zelle enthält zwei kleine plattenförmigen Chromatophoren, die nach Art der Nitzschien in Richtung der Apikalachse übereinanderliegen und gürtelständig sind.' This structure contrasts strongly with that found in Epithemia and Rhopalodia.

Electron microscope studies of D. parva, D. linearis and D. bacillum will be necessary before it is possible to prove conclusively whether these species belong near D. tenuis and D. elegans. Hustedt's illustrations of D. parva (1942, Abb.266-73) suggest, however, that central raphe endings are not present in this species, and that the fibula structure is like that described above: moreover, the valve structure appears similar and the raphe is eccentric, as in D. tenuis or D. elegans.

One further matter must be mentioned. In this group of Denticula species the frustules are 'diagonalsymmetrisch' about the median valvar plane, and the valves are symmetrical in outline about the apical plane, as in Nitzschia: contrast Epithemia and Rhopalodia.

The second group of species, which will be called the 'Sumatran' group since most of the taxa belonging to it were described or mentioned by Hustedt (1935, 1938) in his studies of the fossil and recent diatom flora of Sumatra, consists, like the first group, of freshwater forms. The species included here are D. vanheurckii; D. amphicephala, D. lanceolata, D. pelagica, D. rhynchocephala and D. robusta (all described by Hustedt 1935); D. bicuneata, D. elongata, D. lata and D. spathulifera (described by Hustedt 1938).

Several of the Sumatran group have valves which are asymmetrical

about the apical plane: examples of this include D. vanheurckii
(Fricke, in A.Schmidt Atlas, T.266 f.21, 24), D. rhynchocephala
(Hustedt 1935, T.4 f.26), D. lanceolata (ibid., f.28), D. pelagica var.
intermedia (ibid., f.31a), D. elongata (Hustedt 1938, T.37 f.1, 3, 5-6)
and D. robusta (ibid., f.7-11). In these, and in the symmetrical forms
(D. amphicephala, D. bicuneata and D. lata), there is also a greater
or lesser deflection of the raphe centrally, as in Epithemia. Hustedt
(1930, p.380) said of Denticula 'Zellkörper zur Valvarebene diagonal-
consimil (infolge der transapikalen, aber entgegengesetzten Verschieb-
ung der Raphe).' In this case the asymmetrical Sumatran forms ought to
be heterovalvar, one valve having a ventrally deflected raphe system
and the other having a dorsally deflected raphe system. But this does
not occur. Hustedt (1938, T.38 f.1-18) illustrated many valves of D.
vanheurckii, but none had a raphe system which was deflected other than
towards the dorsal margin. It must be concluded, therefore, that the
asymmetrical Sumatran species are 'hantzschioid', i.e. they are
'spiegelsymmetrisch', not 'diagonalconsimil' about the median valvar
plane. The ± symmetrical Sumatran taxa must await further study, but
on the basis of other characters it may be predicted that they too will
prove 'hantzschioid'.

Hustedt (1935, 1938) illustrated the valves of the Sumatran species
in much the same way as he always depicted Epithemia spp. (for example,
compare his 1938, T.39 f.18-20 with f.21-23), and he noted that (1935,
p.169) 'Transapikalrippen von Längrippen gekreuzt. Membran daher
areoliert.' It seems likely, therefore, that the valve construction in
these Denticulae is similar to that in Epithemia.

The raphe always possesses central endings according to Hustedt
(1935, 1938), and while he was in error concerning the raphe structure
of D. tenuis and D. elegans, there is no reason to doubt his observ-
ations of the larger, more robust Sumatran forms. In 1928 (a) Hustedt

depicted central raphe endings in D. vanheurckii, and the truth of
his illustrations is borne out by those of Fricke (op. cit., T.296
f.22, 25). Furthermore, Hustedt's later drawings (1935, 1938) are
virtually self-confirmatory since not only are central raphe endings
shown, but also a differentiation of the central interspace.

The polar raphe endings are unknown.

Certain of the transapical valve costae are developed into stronger
'Rippen', which seem to be continuous beneath the raphe, whereas the
remainder of the costae are interrupted (see Hustedt 1935, 1938).
Between each pair of 'Rippen', however, are several portulae - compare
Epithemia, contrast D. elegans, D. tenuis, D. parva, etc.

The cincture is poorly known, though it does not consist of half-
bands (ibid.). Hustedt did not describe the chromatophores.

The third group which may be distinguished within Denticula
comprises the marine, planktonic species. These have frustules which
are diagonally symmetrical about the median valvar plane (Simonsen &
Kanaya 1961), with valves which are symmetrical in outline about the
apical plane. The raphe is quite strongly eccentric, lying at the
junction of valve face and proximal mantle (Simonsen & Kanaya 1961,
Hasle 1972b, f.8).

This group has been revised by Simonsen & Kanaya (1961) and
Schrader (1973a, teste 1973b), who listed nine species of which only
one, D. seminae, is known not to be extinct. This species has been
studied, using the SEM, by Hasle (1972b).

The valve of D. seminae is linear with bluntly rounded apices
(see Simonsen & Kanaya 1961, Pl.1 f.26-29). Across it run transapical
costae, some of which are more strongly developed than others (Hasle
1972b, f.8): these stronger and weaker costae are the 'pseudosepta'
and 'secondary pseudosepta' of Simonsen & Kanaya. Near the distal
margin the weaker costae are somewhat thickened, projecting further

into the lumen of the cell than they do elsewhere (Hasle 1972b; compare f.3 with f.8).

Between the costae is an 'intercostal membrane', which bears several irregular transapical rows of poroids: the valve structure is not interpretable in terms of an alternation of single transapical rows of poroids with transapical costae, as is found in D. tenuis and most Nitzschia species, and nor is it like the structure in Epithemia. Rather, it appears that the valve construction is akin to that of some species of Nitzschia sect. Fragilariopsis (see Hasle 1965b), except for the greater development of some costae in D. seminae.

There is no sign of central raphe endings in any of the illustrations given by Simonsen & Kanaya (op. cit.), Hasle (1972b) or Schrader (1973b). Hasle (op. cit.) did not illustrate the polar endings.

The fibulae are small, rib-like structures, often but not always placed opposite the valve costae (an exact correspondence is not possible since there are more fibulae than costae - Hasle 1972b, f.8). The fibula morphology suggests a link with Nitzschia sect. Fragilariopsis (q.v.), and would support a separation of these species from the D. elegans group.

It is difficult to determine the girdle structure from the information published so far. Simonsen & Kanaya (1961) supply a diagram which summarizes their conception of the structure of the girdle 'septum' present in these species, but it is hard to reconcile their interpretation with Hasle's (1972b) scanning electron micrographs. On Simonsen & Kanaya's view, the septum is formed from one or more girdle elements, and consists of a complete, closed band, whose sides are connected to each other transapically by several 'crossbars', each of which corresponds to, and fits over one of the more strongly developed valve costae. Thus, it would resemble D. tenuis and D. elegans except that, in contrast to these and Epithemia, there is no break in

the crossbar in or near the apical plane: according to Simonsen &
Kanaya 'each crossbar is connected with the septum at both ends, i.e.
with two sutures',but 'when isolated septa are seen, they have almost
always lost their crossbars.' Hasle (1972b, f.8) illustrated a valve
of D. seminae in which the septum, including the crossbars, was absent,
and so it would appear that the crossbars are not part of the valve
(but see below), but in view of their position, and their detachability
from the remainder of the septum, can they be considered to be part of
the cincture? Since in diatoms there is, so far, no information to
suggest the existence of any siliceous elements besides valve and
cingulum, it is important to determine the nature of these crossbars.
If the possibility that they belong to neither valve nor cingulum is
discounted, then there appear to be two likely explanations of the
observed phenomena.

Firstly, it is possible that the crossbars are part of the valve,
analogous to the 'knobs' borne by the fibulae in D. elegans: they
would, in this case, be connected to the more prominent valve costae
by membranes of silica, as in D. elegans or D. tenuis. The sutures
noted by Simonsen & Kanaya would represent the margin of the first
band's pars interior. Hasle (1972b, f.4) illustrated an isolated
band of D. seminae and this had a pars interior which was clearly
adapted to fit around the cross bars: this would be the first band if
the above hypothesis is correct. This first explanation explains
Simonsen & Kanaya's observation that detached septa are almost always
without crossbars, but is perhaps less satisfactory when consideration
is given to Hasle's f.8, in which is shown a valve without crossbars:
this could be derived from the suggested structure only through
considerable erosion, unless the valve illustrated was incompletely
silicified (see section 4.3).

Alternatively, the septum may be a composite structure, formed
from the first two bands of the cingulum. Here, the crossbars would

be borne by the first band, whose pars exterior would have to be very
narrow since it is not visible in Hasle's f.3, although this might be
because of the low magnification employed. The 'sutures' would represent
the junction of the second band with the first. Thus, Hasle's f.3
would represent a valve with the first, but not the second band in
place, while f.8 would represent the situation where the cingulum
was entirely missing. On this hypothesis there is no explanation for
Simonsen & Kanaya's observation concerning isolated septa, unless the
first band disintegrates easily.

In either case it is clear that the cincture of D. seminae is
unlike that found in the other groups of Denticulae.

The other species of the marine group are similar to D. seminae
in valve and girdle structure. All appear to have unbroken raphes and
possess several transapical rows of poroids between each pair of costae.
These poroids are often in quincunx (Simonsen & Kanaya 1961, Pl.1),
and it would seem that, as in D. seminae, the whole intercostal membrane
must be regarded as equivalent to the stria of D. tenuis: compare
Helmcke & Krieger's (1953-) illustrations of D. lauta (Pl.504-5), which
belongs in the marine group, with those of D. tenuis (T.182).

Nothing is known concerning the cytology of these species.

These, then, are the three groups, separable from one another on
the grounds of their valve, raphe and girdle structure, and by their
symmetry relationships. In view of the close similarities between the
D. elegans group and Nitzschia sect. Grunowia, and the differences
between it and Epithemia, it would seem that this group (and hence
'Denticula', since D. elegans is the type species) must be transferred
into the Nitzschiaceae. The Sumatran group should be separated from
Denticula and left in the Epithemiaceae, either as part of Epithemia,
or as a new genus. The marine group seems nearer to the Nitzschiaceae
than to the Epithemiaceae, but further studies, especially of pore

structure, are necessary.

Two species of Denticula, D. thermalis and D. costata, do not fit comfortably into any of the above groupings. D. costata is like the Sumatran species in its raphe structure, but its valve does not appear to be constructed as in that group (see Hustedt 1938, T.36 f.13-15). Perhaps the differences between D. costata and, for example, D. vanheurckii are like those between Epithemia sorex and E. zebra - differences of degree, not kind: the cincture structure is apparently uniform between D. costata and the Sumatran species.

D. thermalis is somewhat of an anomaly. Its symmetry relationships and structure are similar to those of D. elegans, except that between every pair of adjacent transapical costae there are two rows of poroids (F.506). Certain of the transapical costae are much thickened, and are continuous beneath the raphe: since there is only one portula between each pair of these costae, they may be regarded as fibulae (F.506-7). The subraphe structure is therefore like that of D. tenuis or D. elegans. Hustedt (1928a) illustrated central raphe endings in D. thermalis, but I have been unable to confirm this (using light microscopy): certainly, the valve is very slightly constricted centrally (as seen in 'girdle' view) and this may indicate a central interruption of the raphe (F.507).

Unlike D. tenuis and D. elegans, D. thermalis does not possess half-bands. The first band is open, but occupies the whole perimeter of the valve (F.508). Otherwise, it has the same morphology as the two valvocopular half-bands of D. elegans, with narrow projections extending quite far along the fibulae (F.509).

On balance, D. thermalis seems to belong with D. elegans and its allies, but further investigation is undoubtedly necessary.

What, then, is the relationship between the Epithemiaceae and the Nitzschiaceae?

If the suggested changes in the taxonomy of Denticula are implemented, then it would seem that there are few similarities between the members of the two families beyond their common possession of a fibulate raphe system. Thus, while the Nitzschiaceae have a hymenate pore structure, the Epithemiaceae have what may be termed a 'volate' system (; Anon. 1975 defined 'vola' as 'one of the elements of a velum that consists of a number of separate elements projecting from the wall of an areola'). The valves of Epithemia, Rhopalodia and the Sumatran 'Denticula' species are mostly asymmetrical in outline about the apical plane, while the frustules are 'spiegelsymmetrisch' about the median valvar plane: such symmetry relationships are found in only a few of the Nitzschiaceae (Hantzschia, Cymbellonitzschia and Allonitzschia), and these otherwise give no indication of being closely related to members of the Epithemiaceae. The raphe system in the latter family is usually positioned closer to the dorsal margin at the centre of the valve than it is nearer the poles: such a deflection of the raphe is present only in Nitzschia sect. Nitzschia (the Obtusae group), and again no other evidence suggests a close relationship of these taxa. Central raphe endings are always to be found in the Epithemiaceae (with the sole exception of Rhopalodia gracilis), whereas these are lacking in many of the Nitzschiaceae, e.g. Denticula (the D. elegans group), Nitzschia sects. Grunowia and Spathulatae, N. sigmoidea and its allies, Hantzschia spectabilis, H. vivax, H. segmentalis, Cylindrotheca gracilis, Cyl. signata, Bacillaria, etc. The subraphe construction also provides contrasts. The cytology of the Epithemiaceae is not well known, but present knowledge indicates that whereas in the Nitzschiaceae there are at least two chromatophores per interphase cell, in the Epithemiaceae there is only one. As checks on the validity of the rearrangements proposed in the taxonomy, it may be predicted that D. elegans will prove to possess two chromatophores per cell,

while the Sumatran 'Denticula' species 'should' have only one. Avail-
able information concerning auxospore formation supports the continued
separation of the Nitzschiaceae from the Epithemiaceae, the transfer
of D. tenuis out of the latter family, and the retention of D. van-
heurckii within it (see section 4.3).

It is interesting that the systematic changes suggested above
would, if implemented, bring the taxonomy of Denticula back to what
it was in 1862, when Grunow included this genus in his newly founded
family, the 'Nitzschiae'.