4.6 Nitzschia

4.6.1 Frustule

For a long time Nitzschia species were thought to be distinguishable from Hantzschia species by the symmetry of the frustule: if the raphes were situated on the same side of the frustule (Text 2E) then the individual was a Hantzschia, but if the raphes were opposed diagonally (i.e. the frustule was 'diagonalsymmetrisch' about the median valvar plane: Text 2B) then it was a Nitzschia. But while Hantzschia frustules appear to be constant in being 'spiegelsymmetrisch' with respect to the median valvar plane, some Nitzschia species can, apparently, form either hantzschioid or nitzschioid cells (see Round 1970a, Mann 1977). Lauritis et al. (1967) noted this dimorphism in N. alba, although it had been reported a long time before by Mereschkowsky (1903a) in N. lanceolata. Geitler (1968c) reported that hantzschioid cells of N. sigmoidea, N. palea, N. subtilis, N. kützingiana and N. flexoides exist commonly in natural populations, but in the present study very few hantzschioid cells of Nitzschia species have been observed. In N. communis, N. hantzschiana, N. amphibia, N. sinuata, N. debilis, N. mollis, N. hungarica, N. apiculata and several other species, hantzschioid cells do not appear to exist. One hantzschioid frustule of N. dubia has been found, but it is not known whether such frustules are of frequent occurrence in this taxon. Hantzschioid cells of Nitzschia species do not 'breed true': that is, a hantzschioid cell never divides to give two hantzschioid daughter cells. This feature, observed both by Lauritis et al. (1967) and by Geitler (1968c), is diagnostic, separating Nitzschia from Hantzschia (Round 1970a, Mann 1977).

Nitzschia frustules show an enormous variety of size and shape, which variety is discussed briefly in the next section and elsewhere. Some features, however, are more obvious in complete frustules, e.g.

the sigmoidity of N. sigmoidea, N. vermicularis and N. flexa. Some species have sharply angled valves (Text F.6H), which means that complete frustules of these forms tend to lie in 'girdle view': examples of this are found in N. sigmoidea, N. bilobata, N. vitrea and others. In other cases the girdle is very wide and here again complete frustules tend to lie in 'girdle view'. However, where the girdle is narrow in relation to the breadth of the valve and the valve is not sharply angled, frustules often lie in 'valve view', e.g. in many of the sect. Lanceolatae, N. tryblionella, N. navicularis, etc.

The cincture shows little overall dorsiventrality, being more or less symmetrical about the apical plane.

N.B. 'Apical plane' as this is applied in Nitzschia is explained in Text F.3A, B.

4.6.2 Valve morphology and anatomy

Within the constraints that the valve outline must be symmetrical about both the apical plane (since otherwise heterovalvy would occur - see Mann 1977) and the median transapical plane (although some marine planktonic Nitzschia species are slightly heteropolar), there is almost every conceivable variation in valve shape. Some forms are nearly circular in outline, e.g. N. perpusilla at the lower end of its size range (see Hustedt 1957, Abb. 100, 101), while at the other extreme are cells well over 500 µm. long, but only 7-10 µm. wide, e.g. Nitzschia sp.B (Eilat) (sect. Nitzschia). The valve may be sigmoid in valve view, or in 'girdle view', or in both. It may be constricted at the centre, as in N. panduriformis, or expanded, as in N. sinuata; the poles may be bluntly rounded (N. communis), extended into long rostra (N. acicularis), or capitate (N. capitellata). And many other variations could be listed.

In Nitzschia valve shape has traditionally been an important

criterion not only in the separation and identification of species, but also in the subdivision of the genus. Thus, the only feature separating the sect. Nitzschiella from the sect. Lanceolatae is that in the former the valves are 'very longly rostrate' (Van Heurck 1896), whereas in the latter they are not. Any lanceolate Nitzschia species with a strongly eccentric raphe system, providing that its fibulae are not appreciably extended across the valve face, can be placed in the sect. Lanceolatae. Further, following Hustedt's revisions of Grunow's classification of Nitzschia, virtually all sigmoid Nitzschia species are included within the sect. Nitzschia (i.e. the 'sect. Sigmoideae' of Hustedt 1957). This emphasis on shape sometimes leads to the grouping together of forms which otherwise show little resemblance to each other, and this will become apparent later.

Only the overall plan and the superficialities of valve structure can be distinguished using the light microscope. Using electron microscopical techniques, however, it is possible to recognize several types of construction, and these are discussed below:

1. Alternation of single rows of poroids with transapical costae; striae of valve face not interrupted by sterna; marginal ridge sometimes present.

This type, also found in Hantzschia (the 'H. amphioxys type'), is widespread in Nitzschia: indeed, the majority of Nitzschia species exhibit this mode of construction, although there are many minor variations on the basic theme. The frets are almost always of less depth than the transapical costae, this being especially noticeable in N. sigmoidea. The poroids are each closed by a hymen, in which the pores may be arranged in one of several ways, namely -

a. hexagonal array (e.g. F.564)

b. centroid (e.g. F.537, 545-7)

c. subregular (e.g. F.538)

d. random (e.g. F.562)

In the first the pores are arranged very regularly such that each pore lies at an equal distance from each of its 6 immediate neighbours, which thus form an equilateral hexagon around the first. Such an arrangement has been noted above to exist in some Hantzschia marina cells. Many members of the sect. Lanceolatae possess hymena of this type (e.g. F.557-8, 561, 564).

The centroid types are those in which the pores are organised about the centre of the hymen, so that the hymen is ± radially symmetrical; the central part itself is often non-porose (F.545-8). This type may be subdivided into two groups, which intergrade. In the first the pores are arranged in concentric circles (F.545), while in the other the hymen is divisible into rather ill-defined radial sectors (F.546) within which the pores are arranged in hexagonal array; one of the three intersecting lines of the lattice is tangential to the hymen margin. It must be emphasized, however, that in this second group the pores are not so regularly arranged as in type a. above, and in many cases it is somewhat difficult to distinguish the sectors.

In the subregular type the pores are not arranged in a strict hexagonal array, but nor are they randomly distributed. There is a certain degree of regularity in the arrangement and on occasion some, but not all, of the pores may be arranged as in a.

Into the last group fall those hymena in which no ordering of the pores can be detected.

Throughout, the pores have a diameter of approx. 5 nm.

In addition to the hymen, the poroids may be partly occluded by other silica structures. The poroids of the larger forms of N. sigma (with approx. 21 striae in 10 μm.) are bridged by cribra, each pore of which contains a hymen (F.543). Cribra are also present in N. epithemioides (F.552), but in this species hymena have not yet been demonstrated.

In N. sinuata and N. amphibia, external to the hymen, is a strange structure which, for want of a better term, must be called a cribrum. It consists of a reticulate network of silica bars of different thicknesses, which delimits holes of various shapes and sizes (F.553-5). One bar, which runs in a transapical direction across the centre of the poroid, is usually more strongly developed than the rest. This reticulum is just discernible using the SEM (F.908), and appears to be pressed up against the outer surface of the hymen (as determined by careful focussing with the TEM).

2. Two or more rows of poroids between each adjacent pair of transapical costae; sterna not usually present; marginal ridge absent. (F.980-3).

Broadly speaking, this type is quite similar to the last. The poroids are again closed by hymena, in which the pores are arranged in one of the patterns described above (e.g. F.551).

Most of the species whose valves are thus constructed belong to the sections Fragilariopsis or Pseudonitzschia; it may be significant that these are both planktonic taxa. Quite often, while most of the costae may be separated by two rows of poroids, some adjacent pairs are separated by only one row.

3. Single rows of poroids present between adjacent costae; transapical costae little deeper than the frets; sterna and marginal ridge usually present.

In this type, exemplified in N. tryblionella and N. debilis, is the nearest approach among the Nitzschiaceae to a laminate construction of the siliceous framework (F.724): the valve more closely resembles a pleated silica sheet of uniform thickness, perforated by rows of small poroids, than it does the ribcage-like morphology of type 1.

A more or less axial sternum is often present, and sometimes also a lateral sternum, placed near the distal margin; neither is very clearly defined (F.728). There is a prominent marginal ridge (F.718-9, 729, 732). The poroids, which are very narrow (and consequently difficult to resolve with the light microscope) and lie in strictly transapical rows, are each closed by a hymen (F.535). The internal aperture of the poroid is often ringed by a shallow 'sill' (F.721, 724, 730).

Certain of the transapical 'costae' are more strongly developed than the others (F.160, 165, 718, 726, 732), and these are the 'Transapikalrippen' noted and drawn by Hustedt (1930): in descriptions of taxa possessing this type of construction it is essential that it is clearly specified as to which structures, the transapical 'costae' or the'Transapikalrippen', are under consideration.

While the distinction into costae and frets is not marked, it is likely that this type is close to the first.

4. Two or three rows of poroids between adjacent transapical costae; a prominent axial sternum and a marginal ridge present. (F.739, 741).

Three species - N. acuminata, N. apiculata and N. hungarica - have been found to exhibit this type of construction. The sternum is very well defined and quite without perforation (e.g. F.171, 744, 746). The poroids are closed by hymena; in N. hungarica, in each poroid there are also two or three volae, which project into the poroid lumen (F.536): these are in a different plane from the hymen, but whether above or below is not known. The marginal ridge is a pitiful structure compared with that of N. tryblionella or N. debilis, a mere 'piping' at the junction of valve face and distal mantle (F.741-2). The transapical costae are strongly developed, and in N. hungarica they are often continuous externally across the sternum (F.733); this transapical thickening of the sternum is often detectable using the light

microscope. Internally the sternum is always smooth and without ridging (F.734, 740, 744).

5. Some part of the valve face loculate (sensu Hendey 1971); axial sternum sometimes present; no marginal ridge. (F.707, 709, 713).

This type seems to be restricted to the sect. Panduriformes. Only the distal half of the valve face is chambered (F.702, 707): towards the raphe the valve is only one-layered (F.704). The internal surface of the valve is smooth since the costae, which are so obvious externally on the proximal half of the valve face, do not project into the lumen of the cell (F.708-11). The poroids, each closed by a hymen (F.533-4), are usually grouped into twos or threes, and these groupings are arranged over the valve in quincunx (F.138-9, 144-6, 707, 709-10). Each chamber in the loculate part of the valve opens to the valve interior by such a group of two or more poroids; it opens to the exterior by a larger, circular aperture (F.702). From the inside of the valve it is not possible to say where the valve becomes loculate.

In some cases small flaps of silica are present, each attached to the outside of the inner wall layer near to a poroid (F.712). The flap extends above the poroid, 'overshadowing it': its purpose is unknown.

These five types of construction cover the vast majority of known Nitzschiae, but other types may exist. It has not yet been possible to study with the electron microscope various species, at present classified in the sect. Tryblionella, which may possess a valve structure not conforming to any of the categories described above. Thus, N. navicularis is quite like N. acuminata etc. (type 4), except that a marginal ridge does not seem to be present and the axial sternum is perforated, although the pores here are much smaller than those elsewhere in the valve (F.176-7). Surprisingly, these pores do not

appear to have been detected by previous workers since they are nowhere mentioned or illustrated (see Peragallo & Peragallo 1897-1908, Hustedt 1930, Cleve-Euler 1952, etc.), even though they are easily visible using bright field optics. This species, together with N. granulata which is similar in several ways (e.g. two rows of pores between adjacent costae marginally, one row centrally; similar shape and size), may well prove to exhibit a sixth type of construction. Likewise, N. cocconeiformis, N. punctata and various others will also need study (see sect. Tryblionella).

Some other features may be mentioned before attention is turned to the raphe and its associated structures. In a few taxa an external flap of silica, arising from the walls of the subraphe canal, extends some distance across the valve enclosing a passage or 'canal', which runs almost the whole length of the diatom, exterior to the plasmalemma (Text F.1, centre right). The free margin of the flap is closely appressed to the valve face (or proximal mantle), except at the poles where there is usually an opening. The transapical costae and valve poroids continue beneath the flap, although the poroids open only into the 'canal', but the flap itself is non-porose. In all cases flaps are present on both sides of the raphe, whether or not the raphe is eccentrically placed, and have been found only in taxa exhibiting a type 1 construction.

Externally, small warts or spines are present in some species, especially on the marginal strip. Here they are often organised into transapical rows, e.g. in N. hungarica (F.734) and N. linearis (F.895), whereas if present elsewhere on the valve they are scattered randomly. N. sinuata and some others have a single row of warts on the very margin of the valve (F.790).

4.6.3 Raphe and associated structures

see over/