

which in some ways resembles N. sigma (Hustedt 1955), except that it is not sigmoid, but arcuate. N. rostrata was not illustrated by Grunow, and has apparently not been found since the original description (in Cleve & Grunow 1880): its taxonomic position is therefore unknown.

On the basis of the above findings it is suggested that the sect. Nitzschiella be retained to include N. longissima and its allies, that the N. acicularis group is best transferred into the sect. Lanceolatae (or placed in a separate section very close to that group, if it proves that there is a discontinuity in the spread of variation which might be used as a taxonomic boundary), and that N. lorenziana (sensu lato), N. subcurvata and N. granii be transferred to other sections as indicated above. N. lecointei, N. decipiens and the four species mentioned in the previous paragraph require study urgently.

N. ventricosa probably belongs closer to N. longissima than might be expected from the dissimilarities in subraphe structure. The size and shape of the valve, the structure of the raphe itself, the valve construction, and the type and arrangement of the chromatophores all suggest that such a link is likely. The same arguments apply to Nitzschia sp.C (Eilat). The relationship between N. ventricosa, N. epithemoides and Gomphonitzschia clevei (Hustedt 1929, T.3 f.1a, b) may also be close, however, and should be studied: all have very similar subraphe constructions.

4.6.6.16 The section Pseudonitzschia

This section, like the sect. Fragilariopsis (q.v.) was until recently a genus in its own right, founded by Peragallo & Peragallo (1897-1908). Few authors mentioned or used this genus, however, except Heiden & Kolbe (1928) and Frenguelli (1938b). Cupp (1943) referred typical Pseudonitzschia species to Nitzschia, while the grouping was

not even mentioned by Karsten (1928). Hustedt (1958), after an examination of material brought back by the 1938/39 German Antarctic Expedition, came to the conclusion that Pseudonitzschia should be reduced to sectional status within Nitzschia (unlike Fragilariopsis, which he retained as a separate genus), an opinion shared by Hasle (1965a), who made a detailed light and electron microscopical (TEM) study of 15 Pseudonitzschia species.

Hustedt's (1958) main thesis was that in Nitzschia, Pseudonitzschia and Fragilariopsis one could trace a series of forms in which there is a progressive loss of raphe function. Thus, most Nitzschia species are fully motile, with a fully developed raphe system; Pseudonitzschia species have a much reduced raphe, while in Fragilariopsis the process is complete: 'Rhaphe-reduktion morphologisch mehr oder weniger vollkommen, in bezug auf die Eigenbewegung vollkommen.' Furthermore, these three stages or groups could be distinguished on the basis of colony formation - Fragilariopsis species form band-shaped colonies, Pseudonitzschia species form chain-like colonies (see section 4.4), while most other Nitzschia species are solitary.

Many of the sect. Pseudonitzschia are delicate forms, lightly silicified with very fine structure. Thus, the SEM often has very little to add to what has already been noted using the TEM (by Hasle 1965a). In the course of the present study four species have been examined, namely N. seriata (LM, TEM, SEM), N. lineola (LM, TEM, SEM), N. pseudo-delicatissima (LM, TEM, SEM) (= 'N. delicatula' of Hasle 1965a: see Hasle & Mendiola 1967, Hasle 1976), and a species (LM, SEM) which does not fit well any of the descriptions given by Hasle (1965a): this diatom (F.355) is rhombic-lanceolate in outline, 60 μm . long, 4 μm . wide (at the centre), with 14-15 fibulae and 24 transapical costae in 10 μm . All were obtained from sample 'F 65.26' of the Dept. Agriculture & Fisheries for Scotland Marine Laboratory at Aberdeen.

In view of Hasle's detailed study, it is not worth describing the above or any other species in depth, and so only a few points will be made prior to a discussion of the section's taxonomy.

Firstly, it may be noted that the poroids of sect. Pseudonitzschia species are like those of other members of the Nitzschiaceae in that they possess hymena: this has been established in N. seriata (F.549), N. lineola (unpubl. obs.) and N. pseudodelicatissima (F.550). The hymen pores are arranged in strict hexagonal array. The hymena, which were not noted by Hasle (1965a), are placed near the outside of each poroid, so that the valve exterior appears smooth (F.975).

N. seriata (F.352-4, 549, 974) and Nitzschia sp. (F.355, 975-6) both have more than one row of well-defined, circular poroids between each pair of adjacent transapical costae. The other two taxa have only one row of poroids between costae, but each poroid is subdivided into 2-3 (N. lineola: F.973) or 2-4 (N. pseudodelicatissima: F.550, 971-2) sectors by delicate strips of silica, hardly thicker than the portions of hymen they separate (F.968, 970). The strips which run across the poroids transapically are usually more strongly developed than the others.

As in the sect. Fragilariopsis, terminal fissures are absent, while the internal fissures end in simple helictoglossae (F.971, unpubl. obs.). These are often placed quite far back from the valve poles - perhaps a consequence of the shallowness of the valve (F.968, 970, 974-976).

The valve is not acutely angled at the raphe (F.975, unpubl. obs.), which is itself always strongly eccentric (F.352-9). The fibulae are not extended across the valve, but are small, often inconspicuous structures: there are approximately half as many fibulae as costae (N. pseudodelicatissima, F.970-2; N. lineola, F.358, 973; Nitzschia sp., F.355) or virtually the same number (N. seriata, F.352-4, 974), but

there is no exact spatial relationship between these two elements. Pronounced longitudinal ridges link the fibula bases both proximally and distally.

A subraphe canal may be distinguished, but it is not raised above the general level of the valve (F.975); the canal walls are not porose (F.971-3: cf. sect. Fragilariopsis).

Hasle's (1965a) illustrations demonstrate another point. She noted that the valve is slightly asymmetrical with respect to the apical plane in some species (N. seriata, N. subpacifica, N. heimii; and see F.352, 355), but in this case, if the frustules are nitzschioid, hetero-valvy must be exhibited, with some valves being raphid on the less convex side, others on the more convex side. This does indeed occur, and is well shown in Hasle's Pl.10: here f.1-4, 6-7 show valves of N. subpacifica with the raphe on the less convex side, while f.5, 8 show the other type of valve. It is also worth note that in Hasle's illustrations other taxa (N. pseudoseriata, N. pungens, N. fraudulenta and N. subfraudulenta) seem to have asymmetric valves: this requires confirmation, but if so, then this character is common to all of the 'N. seriata complex' (Hasle 1965a, following Proshkina-Lavrenko, divided the section into two parts, which she called the 'N. seriata' and 'N. delicatissima complexes').

As a result of her studies, Hasle (1965a) came to the conclusion that members of the sect. Pseudonitzschia may be characterized thus: 'Marine plankton species. Cells united into chains by overlapping of cell ends. Frustules strongly elongated, linear to lanceolate in girdle view, mostly linear to lanceolate in valve view, in some species asymmetric with respect to the apical axis. Transapical ribs one or more (apparently never more than two) to each keel punctum. Canal raphe markedly eccentric. Outer canal wall without poroids.'

This description would appear to be quite adequate, though one might add 'subraphe canal not elongated above the general level of the valve'

and 'poroids with cribra, or several rows of poroids between trans-apical costae.'

The differences between sect. Pseudonitzschia species and other Nitzschiae seem to be less pronounced than those between sect. Fragilariopsis and the latter. Several species at present classified in the sect. Nitzschiella bear very marked resemblances to certain Pseudonitzschia forms, except that they do not form stepped colonies. Thus, N. granii (sect. Nitzschiella) resembles N. cuspidata (sect. Pseudonitzschia) in the morphology of the cribra, in having a strip of non-porose silica (which might, perhaps, be termed a very thin lateral sternum) at the junction of valve face and distal mantle, and in having one row of poroids between adjacent costae, and subraphe canal walls without poroids. N. subcurvata (sect. Nitzschiella) is another species which seems to be close to Pseudonitzschia, and it may be significant that both N. granii and N. subcurvata are delicate forms, very long in relation to their width, like the species of the 'N. delicatissima complex'. Hasle (1964) noted that 'the structure of the valve and the canal raphe of N. granii as revealed in the electron microscope is nearly identical with that of N. subcurvata and of some species of the "N. delicatissima" complex (which, however, have a pseudonodulus), all very delicate plankton forms.'

There is, of course, no reason why N. granii and N. subcurvata should not be transferred to Pseudonitzschia if this group is understood to be polythetic, since in this case stepped-colony formation would not be essential for group membership. The distinction between Pseudonitzschia and other sections of Nitzschia needs further study.

Certain members of the sect. Pseudonitzschia closely approach sect. Fragilariopsis species in some respects, especially in valve and raphe structure. This is particularly evident from Hasle's (1965a, Pl.4) illustrations of N. seriata and N. pseudoseriata: these species may be separated from Fragilariopsis, however, by the shape and size of the

valve, the type of colony formed, and the delicacy of their structure (relative to Fragilariopsis).

A numerical taxonomic study would be of great help in this whole part of the Nitzschiaceae. While Hasle (1965b) is probably right in her claim that the Pseudonitzschia group is somewhat transitional between Nitzschia (sensu stricto) and Fragilariopsis, there remains a possibility that Pseudonitzschia might be better classified as a separate genus containing two subgenera, one corresponding to the 'N. seriata complex' (more closely related to Fragilariopsis), the other corresponding to the 'N. delicatissima complex' (closer to Nitzschia).

4.6.6.17 The section Fragilariopsis

In 1913 (in A.Schmidt Atlas, T.299) Hustedt founded the genus Fragilariopsis for the diatom previously called 'Fragilaria antarctica' or 'Fragilaria castracanei' (= Fragilariopsis kerguelensis: see Hasle 1965b), since he considered that its structure, with two rows of clearly visible poroids between each pair of adjacent costae, was too dissimilar to that of other Fragilaria species to permit its inclusion in that genus.

Subsequently, further species were described, or transferred from Fragilaria (e.g. by Hustedt 1958), and Van Landingham (1971) listed 14 species for the genus. Hasle (1965b) investigated 13 species in detail using light and transmission electron microscopy, and provided a key for the identification of these.

The classification of Fragilariopsis near Fragilaria was called into question through the finding (by Helmcke & Krieger 1953- , T.187-189) in 1954 of a raphe-slit in Fragilaria cylindrus, which was at the same time transferred to Fragilariopsis because of its valve structure.