4.6.6.10 The section Dissipatae

Grunow (in Cleve & Grunow 1880) founded this section, giving as a description 'Aehnlich der vorigen beiden Gruppen' (i.e. the sects. Vivaces and Spathulatae) 'aber mit etwas weniger centralem Kiele, ohne Begleitlinien. Schaalen meist ziemlich klein, sehr z$\overset{a}{\underset{\wedge}{}}$rt gestreift. Andeutungen eines Centralknotens nicht vorhanden.' He referred three species to the group, viz. N. dissipata, N. media and N. acula. Hustedt (1930) considered that N. media cannot be distinguished from N. dissipata, and altered 'acula' to 'acuta', thinking that the former must have been a typographical error in Cleve & Grunow (1880); this practice has been followed by various diatom ecologists, e.g. Fjerdingstad (1950), Foged (1951) and Petersen (1943). As Cleve-Euler pointed out, however, there is little justification for such a change: 'acula' (Latin for 'little needle') is just as suitable as 'acuta' (Lat. 'pointed, acute') to describe this diatom. Cleve-Euler (1952) reduced N. acula to the status of a variety of N. dissipata (the two are certainly very similar), giving N. sphaerophora, which she had described in 1932, as the only other species of the group.

At various times, however, other species have been referred to the sect. Dissipatae, e.g. N. bacillariaeformis (Hustedt 1922) and N. terricola (Lund 1946). Hustedt (1939) transferred several species into the section which had previously been classified in the sect. Bacillaria, before the restitution of this taxon as a separate genus (see Cleve & Grunow 1880, Hustedt 1930), and in view of this transference it is worth quoting Hustedt's (1939) amplified description in full:

'Die Schalen der Dissipatae zeichnen sich durch einen zentralen oder nur wenig excentrischen Kiel und lanzettlich-kahnförmige Gestalt aus. Die Zellwand ist transapikal gestreift, die Streifen reichen bis unmittelbar an die Basis des Kiels, Längslinien beiderseits des Kiels

(die wahrscheinlich bei den betreffenden Arten die Grenzen zwischen Längsareas und dem strukturierten Teil der Schalen bedeuten) fehlen.'

Hustedt did not give an exhaustive list of the species involved in this change in taxonomy, but from the 1939 paper, and from a later paper on the marine littoral diatoms of Beaufort, N. Carolina (1955), it is clear that these included N. macilenta, N. longa, N. praelonga, N. socialis and N. linkei. More recently Cholnoky (1960a) described a new species, N. rufitorrentis, which he referred to this section on the grounds of the 'Symmetrieverhältnisse' of its cells. This species was not validly published, however, since no Latin description or diagnosis was supplied (I.C.B.N. 1972, Art.36). This was later rectified (1962), although the validity of the species is still questionable in view of the lack of a clear indication as to the nomenclatural type: in the 1960 paper he gave as a locality 'Seven Oaks-Tongaat 281' and noted (p.121) that material of the various samples used in the study had been deposited in Stockholm, London and Frankfurt, but whether this satisfies Article 37 of the I.C.B.N. is open to doubt.

Sovereign (1958), after consultation with Hustedt, published a new species, N. volcanica, which he referred to the 'subgenus Dissipatae'. No type was indicated, however, and hence the name is invalid: the combination 'Nitzschia subgen. Dissipatae (Grun.) Sovereign' is also invalid since it was mentioned only incidentally in the text (I.C.B.N. 1972, Art.34).

The apochlorotic diatom N. putrida was studied by Lewin & Lewin (1967), who stated that it belonged to the sect. Dissipatae (op. cit., p.366, and see Benecke 1900) or to the sect. Lineares (p.363). Giffen (1970b) described a new brackish water species, N. kowiensis, from a Salicornia marsh in S. Africa, while Hasle (1960, f.17) observed an unknown species of Nitzschia from marine phytoplankton which, except that it has much more closely spaced fibulae, appears to be very

similar to N. dissipata.

In this study N. dissipata and N. linkei have been examined using the LM, TEM and SEM. The first was found in a variety of samples, those studied most intensively being some samples of epipelon from Shearwater, Wilts; the other was obtained from the marine intertidal of a site in Cornwall (Tregantle), and Sandbay.

N. dissipata (sensu Hustedt 1930) is a fairly small diatom, 15-70 µm. long and 4-7 µm. wide (ibid.), which is lanceolate in shape (F.253-254). The valve is very finely structured, so that light microscopy usually reveals only the fibulae and two longitudinal 'lines' joining the fibula bases (e.g. see Hustedt 1930, f.789). The SEM reveals, however, that the valve has a type 1 construction (F.808-11). In fact, the striae may sometimes be resolved using the light microscope if the full aperture of an immersion lens (NA 1.3 or higher) is developed, and oblique illumination used to increase contrast: 40-44 striae in 10 µm. have been counted in the Shearwater specimens (F.253-4), and this agrees with counts made on other specimens (unpubl. obs.).

The valve is undulate in transapical section (F.810), but while it is sharply folded near the distal margin there is no marginal ridge (F.809, 811). In the light microscope, using bright-field or phase optics, two lines may just be distinguished which run parallel to, and close to, the two more prominent lines at the bases of the fibulae (F.253-4): like the more obvious lines, they each run from pole to pole. According to Grunow (in Cleve & Grunow 1880) and Hustedt (1939) - see their descriptions of the Dissipatae, given above - these lines, Grunow's 'parallelen Begleitlinien', are absent in the sect. Dissipatae, this matter separating the Dissipatae from the Spathulatae. Examination of N. dissipata with the electron microscope revealed that the structural basis for these 'lines' is the same in both taxa: two flaps of non-porose silica extend out, one from each wall of the subraphe canal,

enclosing two external 'canals' (F.809, 811; Text F.1 centre right). The margins of the flaps are closely appressed to the valve face, except that near the poles, where the flaps end, small openings are left into the canals (F.811). The reconstruction of the structure of N. dissipata in Helmcke & Krieger (1953- , Pl.920) is inaccurate.

From the exterior the valve has a smooth appearance (F.809, 811), which suggests that the hymena lie near the outside of the poroids (compare N. sigmoidea, N. recta, N. spathulata: sects. Nitzschia, Lineares and Spathulatae respectively). Helmcke & Krieger (1953- , Pl.918) and Cox (1975c) have both illustrated the hymena, which have a subregular pore arrangement.

The raphe is unbroken centrally. The specimen figured by Helmcke & Krieger (1953-) in T.89 (upper stereopair) possesses central raphe endings, but is not of N. dissipata (compare with their Pl.918-9, and with Schoeman & Archibald 1976- , 'Nitzschia dissipata (2)' f.5, 6). At the poles internally there is the usual simple helictoglossa (F.808). The terminal fissure is quite long and is more or less hook shaped, as noted by Okuno (in Helmcke & Krieger 1953- , text accompanying Pls. 918-20), its final part being more or less parallel to the valve margin at the pole (F.811). The terminal fissure can apparently be directed towards either the proximal (Schoeman & Archibald 1976- , (2) f.6) or the distal side (F.811).

A well-defined subraphe canal is present (F.810), although because of the presence of the flaps, its extent is not obvious from the exterior (F.809). As in all Nitzschia species with such flaps, the subraphe canal is raised above the general level of the valve. The outer wall of the canal is porose (unpubl. obs.).

The bar-like fibulae are massive relative to the size of each transapical costa, and the relationship between these two elements is obscure (F.808, 810; compare N. sigmoidea, sect. Nitzschia). Towards

the poles the opening into the subraphe canal is narrower, and hence the fibulae are shorter (F.808).

The cincture is virtually unknown, except that the first band has two transverse rows of poroids (see Cox 1975c, Pl.42a; Helmcke & Krieger 1953- , T.400).

As has already been noted (section 4.6.5), N. dissipata has a type 1 chromatophore arrangement (F.255), although Mereschkowsky (1903a) claimed otherwise. Geitler (1958) figured Bütschli globules at the ends of the chromatophores, but often these are not very obvious.

N. linkei does not possess the exterior flaps of N. dissipata, nor does it have similar fibulae (F.989-91). Most importantly, however, it forms short colonies of the type found in Bacillaria paxillifer (unpubl. obs., and see Van der Werff & Huls 1957-). Thus, since this feature, together with the central position and structure of the raphe, etc., is diagnostic of Bacillaria, it is proposed that N. linkei should be transferred into that genus; it will not, therefore, receive any further attention here. There is no indication that it is closely related to N. dissipata.

Largely as a result of the changes Hustedt (1939) made in its circumscription, this section has come to contain a wide variety of forms, many of which bear little resemblance to one another, beyond their common possession of central or only slightly eccentric raphe systems. Clearly, however, N. acula is close to N. dissipata, if it is not to be considered as a variety of that species: the illustrations and analysis given by Hustedt (1930) and Cleve-Euler (1952) leave no doubt in this.

N. terricola also appears to be closely related to N. dissipata, this proximity being supported (as Lund 1945 noted) by the position of the raphe and the invisibility of the striae. The fibulae are 'large

relative to the size of the valve' (ibid.) and are reminiscent of those of N. dissipata, while the entrance into the subraphe canal narrows from centre to pole as in that species (ibid., f.15Q). Lund also noted a resemblance between N. terricola and N. recta, which, as will be seen later (see sect. Lineares), adds further support to a classification near N. dissipata! There is no indication of a central break in the raphe - Lund's figures show no 'central nodule', nor any differentiation of the central interspace.

N. sphaerophora (Cleve-Euler 1932) and Hasle's 'Nitzschia sp.' (1960, f.17) are like N. dissipata in the positioning of the raphe, the fibula morphology, and the invisibility of the striae. They too seem to lack central raphe endings, and probably belong close to N. dissipata.

The above agree in many respects, but none of the other taxa referred to the Dissipatae by Hustedt and others, except perhaps N. bacillariaeformis (Hustedt 1922, T.10 f.48-50), can be classified here.

N. putrida has a raphe which is uninterrupted centrally, and its raphe system is only slightly eccentric (Lewin & Lewin 1967, f.2), but it lacks the external flaps of N. dissipata. Moreover, the valve construction appears to be unusual, with poorly developed or non-existent frets, and the fibula bases are joined by longitudinal ridges of silica: it should be noted in this connection that the more obvious longitudinal lines visible in light micrographs of N. dissipata (F.255, and figured, for example, by Hustedt 1930) represent the edges of the slit into the subraphe canal, not ridges like those of N. putrida or members of the sect. Lanceolatae.

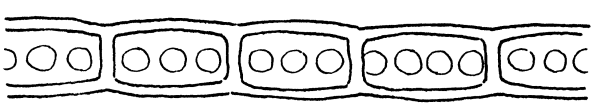
Beyond the fact that its raphe system is nearly central, N. volcanica bears little resemblance to N. dissipata and its allies. Hustedt's drawings (in Sovereign 1958) show a linear or linear-lanceolate diatom with a relatively coarsely structured valve (20-22 striae

in 10 µm., striae 'delicate punctatae'). The raphe is probably interrupted centrally since the central interspace is usually somewhat larger than the others (Sovereign 1958, f.69-74, 77, but apparently not in f.75-76). Moreover, the fibulae are quite different from those of N. dissipata and seem each to represent several fused subraphe costae: they are much larger than the interspaces, the opposite being true of N. dissipata.

Giffen (1970b) noted that the 'keel' of N. kowiensis is 'somewhat constricted in the middle'; in other Nitzschia species (e.g. N. linearis, N. debilis) such a constriction of the subraphe canal is associated with the presence of central raphe endings. In this, therefore, and in the strong silicification of the subraphe canal walls mentioned and illustrated by Giffen, N. kowiensis differs from N. dissipata. Moreover, the great width of the frustule in girdle view, relative to its width in valve view, also argues against classification near N. dissipata: N. kowiensis probably belongs nearer to the sects. Dubiae or Lineares.

Of the 'Bacillaria' group of species transferred by Hustedt, N. longa has a subraphe structure which at once separates it not only from N. dissipata and its allies, but also from all other known Nitzschia species. Hustedt (1955) described this construction as follows: 'Between the strong primary keel puncta at the base of the border canal, faint secondary keel puncta are intercalated, thus dividing the broader primary openings into more or less smaller ones' (see Hustedt's Pl.16 f.1), viz.

(redrawn after Hustedt 1955)



It is difficult to see how to describe this structure in terms of fibulae, interspaces, etc. Perhaps the 'primary keel puncta' should be regarded as fibulae, with several portulae present between each pair of adjacent fibulae; alternatively, the 'secondary keel puncta' could be termed fibulae. Each portula is opposite a transapical stria. This structure is in some ways reminiscent of Epithemia (q.v.), and the relationship between these taxa should be investigated. Hustedt's illustration indicates that the raphe is not interrupted centrally, and that the valve may be sigmoid.

It is unlikely that N. praelonga belongs in the Dissipatae in view of its coarse structure (16 striae in 10 µm.) and the apparent absence of flaps, which should, if present, be obvious in such a large diatom. The subraphe structure seems to be more like that of N. putrida than N. dissipata (Cleve 1881, Peragallo & Peragallo 1897-1908). N. macilenta also little resembles N. dissipata (see Peragallo & Peragallo, op. cit.).

The heterogeneity of the sect. Dissipatae, sensu Hustedt (1939), was perhaps inevitable, given the vagueness of his description. Any Nitzschia species with a central or slightly eccentric raphe system and a fairly flat, shallow valve, but lacking other distinguishing features, must in Hustedt's system be referred to the Dissipatae: it is a 'dustbin' group. The absence of longitudinal lines ('Längslinien', 'parallelen Begleitlinien') near the raphe was used by Grunow (in Cleve & Grunow 1880) and Hustedt (1939) to distinguish this group from the Spathulatae, but as has been shown, the type species, N. dissipata, does possess such lines, which indicate the presence of external flaps. Indeed, it may now be asked whether there is any difference between the Dissipatae (sensu stricto) and the Spathulatae, a question which may be resolvable with the aid of numerical taxonomic techniques. The species excluded from the Dissipatae, e.g. N. longa, N. praelonga, etc.,

must be found other homes, although at present there are no obvious places for them.

4.6.6.11 The section Spathulatae

'Aehnlich der Gruppe Bacillaria, aber mit meist sehr zart gestreifen Schaalen. Kiel in der Schaalenansicht meist von 2 parallelen Begleitlinien eingefasst. Die meisten Formen dieser Gruppe bilden eine zusammenhängende Kette, in welcher die Abscheidung von Arten sehr schwierig ist. Andeutungen eines Mittelknotens nie bemerkbar?' (Grunow, in Cleve & Grunow 1880).

The 'Spathulatae' was one of the groupings recognised by Grunow (1862) in his first taxonomic review of Nitzschia. The taxonomic rank of the group was not indicated, however, and it was not until 1883 that sectional status was specified, by Cleve. In 1862 Grunow placed four species in this group, namely N. spathulata, N. quarnerensis, N. distans and N. hyalina. Later (in Cleve & Grunow 1880) he transferred N. angularis to the Spathulatae, which species, together with N. fluminensis and N. lanceolata, he had formerly (1862) placed in the 'Angulares'; in 1880 (op. cit.) Grunow also described several new species - N. affinis, N. eximia, N. subdilatata and N. brevistriata - and transferred Bacillaria cursoria into Nitzschia sect. Spathulatae. Peragallo & Peragallo (1897-1908) have since added N. dilatata, but apart from this the group has not increased in size since Grunow's 1880 monograph (in Cleve & Grunow).

Certain internal changes have been suggested: N. quarnerensis was made a variety of N. distans by Grunow (in Cleve & Grunow 1880), a practice followed by the Peragallos (1897-1908) and Cleve-Euler (1952), while N. hyalina was considered to be a variety of N. spathulata by Van Heurck (1880-5) and the Peragallos (op. cit.). In addition, Van Heurck demoted N. affinis to varietal status within N. angularis.