

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 gestreiften Schaaalen. Kiel in der Schaaalenansicht 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.

SPECIES	Length μm.	Width μm.	Fibulae no. in 10 μm.	Costae no. in 10 μm.	'Y'*	Source of information
<u>N. affinis</u>	33-90	6-9	6-9	very fine	?0	b c
<u>N. angularis</u>	60-200	6-15	2.5-5	31-32	+	a c e g
<u>N. brevistriata</u>	186	6	5-5.5	24	?	b
<u>N. cursoria</u>	70-90	7	6-10	very fine	0	a b e
<u>N. dilatata</u>	120-150	?	2-3	very fine	?	e
<u>N. distans</u>	120-370	?	1.5-5	?22-30	0 to ++	b c
<u>N. eximia</u>	180	22	1.5-2	22	?	b
<u>N. hyalina</u>	40-80	?	7-8	over 40	+++	b e f
<u>N. quarner- ensis</u>	165-190	9	2-3.5	30(+)	0/+	b c d e
<u>N. spathulata</u>	80-120	9	4-7	40-41	+++	a b c e f g
<u>N. subdil- atata</u>	117-162	10	2-3	very fine	+ / ++	b
<u>Nitzschia</u> sp.A (Eilat)	28	4.4	5-6	48	?0	g

* 'Y' = degree of 'spathulatiness' of valve poles
(see text).

a = Boyer (1927)

b = Cleve & Grunow (1880)

c = Cleve-Euler (1952)

d = Grunow (1862)

e = Peragallo & Peragallo (1897-1908)

f = Van Heurck (1880-5)

g = my observations

In our present state of knowledge, however, it is impossible to determine the validity of these claims, and so, for the purposes of this study, all the original 'species' have been retained: these are listed in Table 19, together with their dimensions, stria densities, etc.

For this thesis three species have been examined. N. spathulata (studied using LM, TEM and SEM) was obtained from intertidal sand at St. Martin's, Isles of Scilly. N. angularis, which has also been investigated by Cox (1975a) who used LM and SEM techniques, was found on the lower shore at Sandpoint, near Weston-super-Mare: it was examined with the LM only. Finally, a small form, measuring only 28 μm . in length, was found in material from a marine pond at Eilat, Israel. This diatom (studied with TEM only), which in this dissertation is called Nitzschia sp.A (Eilat), is smaller than any previously known member of the Spathulatae: it is just outside the lower limit reported for N. affinis (33 μm .), and also is slightly narrower and has slightly fewer fibulae per unit length than that species (see Table 19).

N. spathulata may be distinguished from other members of the section, except N. hyalina, by the presence of marked expansions of the valve at each pole, which give the ends of the frustule (seen in girdle view) spathulate outlines (F.217). Authors frequently ascribe this species to de Brébisson (e.g. see Grunow 1862, Cleve & Grunow 1880, Peragallo & Peragallo 1897-1908, Cleve-Euler 1952, Hustedt 1955), although de Brébisson never published a description of it. The first published account of N. spathulata is in W. Smith's (1853) 'Synopsis of British Diatomaceae', where he remarked, under 'N. spathulata, n. sp.', '"Nitzschia spathulata", cl. De Brébisson in literis cum speciminibus, Sept. 1852.' Smith was quite explicit in his introduction (op. cit., p.4) that 'the letters n. sp. denote that the species to which they are appended is believed to be now for the first time described.' It is unlikely, therefore, that Smith wished to ascribe the species to

de Brébisson, and even if he did the I.C.B.N. (1972) states clearly that the correct author citation 'is the name of the actual publishing author', i.e. W.Smith, although de Brébisson may be mentioned if desired, the citation then being 'Bréb. ex W.Smith': it would be simpler, however, to use 'Smith' only.

The valve is long and linear (some small frustules are shown in F.247-8). The raphe is often eccentric (F.818, 823), contrary to the statements of some authors, e.g. Peragallo & Peragallo (1897-1908). Among the St.Martin's specimens there is variation in the degree of eccentricity of the raphe and in some other characters, and while it may prove that there are several species present in this sample, N. spathulata may be similar to Hantzschia marina, H. virgata, etc., in exhibiting a considerable degree of infraspecific variation: it is interesting that these species occupy the same type of habitat.

Using the light microscope it is difficult to resolve the striae, since there are 40 or more in 10 μ m. (F.244-6, 249), but the SEM reveals that a type 1 valve construction is present throughout (F.818-31). Distal to the raphe, but near the entrance to the subraphe canal, the frets are of approximately the same depth as the transapical costae; nearer the distal margin, however, the frets become smaller whereas the costae remain of equal depth as before - this change is quite abrupt (F.822, 825-6, 828-9, 831). The poroids are small and contain hymena, placed near the outer surface of the valve, in which the pores are in hexagonal array (F.542, but see F.541).

In N. spathulata there are external, non-porose flaps of silica (F.815-6, 818, 820, 824, 826; Text F.1 centre right), very like those in N. dissipata, N. sigmoidea or N. recta (see sects. Dissipatae, Nitzschia and Lineares respectively). These spring from near the raphe and delimit two 'canals', external to the plasmalemma, one on each side of the raphe. The flaps do not seem to be as closely appressed to the

valve face as in some other species (e.g. N. dissipata, N. recta), although this may be an artefact of acid cleaning. The valve trans-apical costae are more or less abruptly bent where the open margin of the flap abuts onto the valve face, and it is here also that the frets change in depth (F.820, 826). As in N. dissipata (F.811), the canals open to the interior of the cell by poroids containing hymena (F.820, 826), and to the exterior at the poles (F.815-6).

The raphe-slit is uninterrupted centrally. The structure of the slit seems to vary within the population of 'N. spathulata' studied. In some cells (apparently those with a larger terminal expansion of the valve - i.e. more spathulate) the raphe-slit is deep, and opens onto the crest of a ridge (F.824, 826). In these, moreover, the raphe is more central and the valve is \pm acutely angled at the raphe. Other valves are not acutely angled at the raphe, have no ridge, and have a more eccentric raphe system: here the slit seems to be more oblique to the valve surface than in the first group (F.820).

At each pole there is a prominent helictoglossa, which is placed slightly to one side of the valve apex (F.819, 821, 829). The external fissure is bent abruptly (F.816), not above the helictoglossa, but some way before it (see also the Eilat species), while the terminal fissure is \pm hook-shaped and ends close to the valve margin (F.815-6): its exact course varies among the St.Martin's specimens, in the same manner as in Hantzschia marina (q.v.)(unpubl. obs.). Near the poles the raphe fissure opens onto the very summits of the spathulate extensions (F.816).

The fibulae also show variation within 'N. spathulata'. In one group, corresponding to the forms where the valve is not appreciably angled at the raphe, the fibulae spring proximally from small bosses of silica, while the distal bases are somewhat extended across the valve (F.244-5, 820, 822-3). This extension is usually along one transapical

costa and so each fibula may perhaps be regarded as equivalent to a single subraphe costa (see section 4.6.3.5, type i). These fibulae are deeper near their distal bases than they are proximally.

In a second group the fibulae are more nearly symmetrical since they are no deeper distally than proximally, and are extended across the valve towards both margins. However, while proximally the extension is along one transapical costa, distally a fibula may extend along one, two, or even three costae (F.825, 828). But again, in view of the morphology of the proximal fibula base, it is possible that each fibula represents a single subraphe costa.

In yet a third group, which corresponds to those forms where the raphe-slit opens onto the crest of a ridge and where the valve is acutely angled at the raphe, both fibula bases are similar and resemble the proximal bases of the first group (F.249, 827, 830-1). It is not possible, therefore, to determine the relationship between fibulae and costae in this group (at least, not from mature valves), and so the fibulae must be classified as being of type vii.

The subraphe canal is well developed (F.816, 820, 825). The openings into the canal from the interior of the cell, i.e. the interspaces, are not of constant size along the length of the diatom, but are considerably narrower transapically near the poles (F.819-23), just as in N. dissipata and N. recta. Immediately before the valve apex, however, beyond the last fibula, the slit leading into the subraphe canal suddenly widens out to occupy the whole width of the valve.

The cincture is unknown, except that some of the bands bear several (more than 5) transverse rows of poroids (unpubl. TEM obs.).

The chromatophores of N. spathulata have already been described (see section 4.6.5) and have an arrangement and structure which conform to those of type 1 species. Each chromatophore lies against one side of the girdle, with one or two lobes extending 'onto' the valves (F.250-2).

The nucleus lies centrally, between the two plastids.

N. angularis has a \pm rhomboidal valve outline and a virtually central raphe system (F.242): its valve is much shallower than that of N. spathulata (compare F.242 with 243, and see Cox 1975c, Pl.42f, g, h). The construction of the valve is very similar to that of N. spathulata, with external flaps of silica, hymena near the outsides of \pm circular poroids, etc.: the grooves noted by Cox (1975c, legend to Pl.42f) to be present on the outside of the valve represent the junctions between the margins of the external flaps and the valve face.

The transapical costae are not as closely spaced as in N. spathulata, and it is possible to see them in the light microscope without the need to oil the substage condenser to the slide - there are approx. 32 striae in 10 μ m. in the Sandpoint specimens. The poroids themselves are also resolvable with the LM, but are difficult to draw.

The raphe-slit does not open onto the crest of a ridge (Cox 1975c), and is continuous from pole to pole. The helictoglossa appears to be placed at the very apex of the valve, and is submarginal (F.243).

The fibulae are much wider than the transapical costae (F.249), and the relationship between these two structural elements is obscure. The fibula bases are like those in the third group of N. spathulata (see Cox 1975c, Pl.42g, h). There is a well-defined subraphe canal (T.B.B.Paddock, pers. comm.). As in N. spathulata, towards the poles the interspaces become much narrower transapically (Cox 1975c, Pl.42h).

The cincture is composed of several bands, at least some of which bear several transverse rows of poroids, as in N. spathulata (F.243).

The chromatophores have already been described in some detail (section 4.6.5).

Okuno (in Helmcke & Krieger 1953- , Pl.710-1) has illustrated a form which he identified as N. angularis var. affinis; the structure of this form appears to be very similar to that of N. angularis itself.

Nitzschia sp.A (Eilat) has a linear-elliptical valve outline, and a central raphe system (F.812). Its valve construction is like that of N. spathulata. As in that species, there is an abrupt change in the size of the frets where the free margin of an external flap abuts onto the valve face: indeed, not only do the frets change in depth relative to the transapical costae (as judged by a change in opacity to electrons) but they also change in spacing, being much more densely packed nearer the valve margins (F.813). The transapical costae become narrower at this junction, and thus two discrete structural organisations may be distinguished, these occurring on the same valve, viz.

- i. (nearer the raphe, 'within' the external flaps). Costae wide relative to the frets, both, however, being ± heavily silicified. Circular/oval poroids present. Frets not ordered apically.
- ii. (elsewhere). Distance between costae approx. equal to the width of each costa. Frets lightly silicified, costae moderately so. Poroids slit-like, elongated in the apical direction. Frets ordered into strict longitudinal rows.

Again the raphe is unbroken centrally. At the poles it appears to end internally in simple helictoglossae, while the external fissure, which is abruptly bent some distance before the helictoglossa, continues to near the valve margin where it is again bent abruptly: it then runs around the valve pole for a little way, parallel to the margin (F.813). Both endings of a single valve are directed towards the same side (F.812).

The fibulae are similar to those in N. angularis, except that they are thinner (relative to the transapical costae). The subraphe canal walls are porose, and the slit into the canal from the cell interior narrows towards the valve poles, just as in N. angularis and N. spathulata.

The cincture and cytology of the Eilat species are unknown.

An examination of the relevant literature suggests that no valve morphology fundamentally different from those described above can be expected to occur within the sect. Spathulatae as it now stands. The '2 parallelen Begleitlinien' observed by Grunow (see above) and considered by him and others to be diagnostic of this section, seem always to be correlated with the presence of external flaps (since they may also be seen in suitably orientated valves of N. sigmoidea, N. dissipata and N. recta), and must represent the edge of the flap and/or the slight change in valve structure (F.242, 244-5, 249). Central raphe endings do not occur in any of the Spathulatae, and there are always few fibulae in relation to the number of transapical costae.

There are few obvious breaks in the pattern of variation within this section. Such features as the degree of eccentricity of the raphe, the fibula morphology, the relative development of costae and frets, the structure of the raphe-slit, etc., may help in the separation of species, when used in combination with more conventional parameters, e.g. fibula and stria densities. Cleve-Euler (1952) stated that 'Nitzschia distans, angularis, affinis u. spathulata bilden eine zusammenhängende Formenreihe ohne fixierte Grenzen.' While she may have been unduly pessimistic, Cleve-Euler's remarks illustrate the difficulties encountered in this group. I suspect, however, that when the habitat in which these species dwell (the marine littoral) has been investigated more fully, the taxonomy of this group will become much less problematic.

There are a couple of other species, N. incrustans and N. martiana, hitherto assigned to other sections of Nitzschia, which may belong in the Spathulatae. Giffen, who has illustrated both of these (1971), shows them as having virtually central raphe systems, as in N. angularis, with fibulae which are large in relation to the striae (see also Peragallo & Peragallo 1897-1908). There are no central constr-

ictions etc. of the subraphe canal, nor any sign of a 'central nodule', while near the poles the interspaces are narrower transapically, just as in the Spathulatae. Neither Giffen nor the Peragallo brothers illustrated the '2 parallelen Begleitlinien', but it is easy to miss these in delicate or narrow valves. N. martiana occurs in mucilage tubes, as does N. angularis: it was in fact the type of Agardh's genus Homoeocladia, which included many of the tube-dwelling Nitzschia species (see I.C.B.N. 1972 for details of typification). Thus, in view of similarities in morphology and habitat preference, it seems likely that these species are closely related to the Spathulatae: certainly there is, at present, no other satisfactory place for them. Other, as yet undescribed, species may also be referred to this section, e.g. that illustrated in F.817, found in a sample from the underside of pack-ice at Signy Island, South Orkneys.

4.6.6.12 The section Nitzschia

This is the 'sect. Sigmoideae' sensu Hustedt (1956). The name 'Sigmoideae' is incorrect, however (though it is more familiar to most diatomists than 'Nitzschia'), since this group includes the type species of the genus, N. sigmoidea (see I.C.B.N. 1972). Only Hendeby (e.g. 1964) has commonly used 'Nitzschia' instead of 'Sigmoideae'.

The sect. Nitzschia as circumscribed by Hustedt (1956) includes three groups which had previously been thought distinct, namely the sects. Sigmoideae (sensu Cleve & Grunow 1880), Sigmata and Obtusae. A grouping called the 'Sigmoideae' was first recognised in 1862, by Grunow, who included in it N. sigma and N. obtusa (the types of the Sigmata and Obtusae) as well as N. sigmoidea. Later (in Cleve & Grunow 1880) Grunow separated the Sigmata and Obtusae from the Sigmoideae, the first on the ground that the raphe is somewhat more eccentric than in