

with Tryblionella, and so it might be better lost.

The species without central raphe endings (N. navicularis, N. granulata, N. cocconeiformis, N. punctata, etc.) require further study urgently: Pantocsek's grouping 'Zotheca' (see earlier) may well be valid.

A large number of species belong close to N. tryblionella: these will constitute the 'pruned' sect. Tryblionella since the above-mentioned species is the type.

4.6.6.3 The section Dubiae

In 1862 Grunow described a new grouping of Nitzschia species, giving as a diagnosis 'Frusteln in der Mitte mehr oder weniger zusammengeschnürt.' This group, the 'Constrictae' was not assigned a definite taxonomic rank and therefore does not have to be taken into account in questions of priority (I.C.B.N. 1972). Later (in Cleve & Grunow 1880) Grunow described the 'Dubiae' and 'Bilobatae', which groupings included several of the species formerly assigned to the 'Constrictae'. Again, however, the taxonomic rank was not specified, but in 1883 Cleve designated them sections. A problem arises, therefore, as to whether the authority for the sections Dubiae and Bilobatae is 'Grunow' or '(Grunow) Cleve', a problem which can be resolved only by establishing whether Grunow's paper entitled 'On Some New Species of Nitzschia' (published 1880), where sectional status is specified for certain, but not all, of Grunow's groupings, is a separate entity or only a part of the monograph contained in the Cleve & Grunow (1880) work.

Most authors have retained the sects. Dubiae and Bilobatae as separate, not only from each other (distinguishable on the basis of the degree of eccentricity of the raphe system - less eccentric in the Bilobatae), but also from other sections (e.g. see Schütt 1896, Peragallo & Peragallo 1897-1908, Cleve-Euler 1952, Hendey 1964). Hustedt also held this view at first (1930), but later (1955) he combined these

SPECIES	Length µm.	Width* µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Raphe eccentricity	Fibula morphology	Source of information
<u>N. adamata</u>	25-35	4-5	12-18	40	present	+++	1 SRC*	Hustedt (1957)
<u>N. adeliana</u>	36-47	4-4.5	11-12	30-34	present	++	?1 SRC	Manguin (1960)
<u>N. aestuarii</u>	40-66	9-12	14-16	30-32	present	++	1 SRC	Hustedt (1959c)
<u>N. bilobata</u>	80-150	12-14 (20 at widest)	5-7	17-19	present	0/+	1 SRC	Hustedt (1930) this thesis
<u>N. bremensis</u>	60-90	6-9	5-7	20	?	?+	?1 SRC	Hustedt (1930)
<u>N. commutata</u>	50-80	7-12 (12-17 at widest)	7-10	20-24	present	+ / ++	?	Cleve & Grunow (1880) Hustedt (1930)
<u>N. copiastriata</u>	46.7	7.9	9-10	32-34	present	++	?	Hohn & Hellerman (1966)
<u>N. custodis</u>	40-50	7-8	12-14	30-32	present	++	1 SRC	Cholnoky (1960a)
<u>N. dippelii</u>	80-110	?	4-5	42	present	0/+	Large: several SRCe	Hustedt (1930)
<u>N. dubia</u>	80-160	12-15	9-10	21-24	present	++	1 SRC	Hustedt (1930) this thesis
<u>N. dubiiformis</u>	40-50	5-7	16-18	very fine	present	++	1 SRC	Hustedt (1939)
<u>N. geniculata</u>	57	5	8-10	30	present	+	1 SRC	Hustedt (1938)
<u>N. hybrida</u>	45-90	8-9	8-10	21-25	present	0/+	1 SRC	Cleve & Grunow (1880) Hustedt (1930)
<u>N. hybridiformis</u>	60-93	6-8	5-10	35	present	+	1 SRC	Hustedt (1955)
<u>N. janei</u>	57-72	6-6.5	5-7	14	present	+	?1 SRC	Salah (1955)
<u>N. kittlii</u>	100-230	12-16	2.5-3.5	18-21	present	0/+	Large: 3-5 SRCE	Hustedt (1930)
<u>N. lacunarum</u>	65-75	6	7-8	30	present	?+	?1 SRC	Hustedt (1930)

* 'Width' = width of valve as this usually lies on the slide; the actual quantity measured depends upon the degree of eccentricity of the raphe.

* 'SRC' = subraphe costa.

TABLE 14 (contd)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Raphe eccentricity	Fibula morphology	Source of information
<u>N. lagunae</u>	100-110	7-8	10	?	present	+	1 SRC	Cholnoky (1960a)
<u>N. lesinensis</u>	85-105	?	3-6	14	present	0	?1 SRC	Cleve & Grunow (1880)
<u>N. lurida</u>	25-35	7-8	15-18	32-34	present	++	1 SRC	Cholnoky (1961)
<u>N. mitchelliana</u>	100-115	13-16	?	28-29	present	?	?1 SRC	Cleve & Grunow (1880) A.Schmidt Atlas
<u>N. nathorstii</u>	32-40	11	9	20	present	++	?	Cleve-Euler (1952)
<u>N. ngoziensis</u>	35-54	4-5	6-7	over 30	present	++	?	O.Müller (1905)
<u>N. pamirensis</u>	45-60	5-7	8-11	24	present	++	1 SRC	Hustedt (1922) as <u>N. ostenfeldii</u>
<u>N. pellucida</u>	55-70	?	13-14(17)	32(34)	present	?0	?1 SRC	Cleve & Grunow (1880)
<u>N. pretoriensis</u>	32-40	5-6	5-6	32-34	<u>absent</u>	?++	Large: 3-5 SRCe	Cholnoky (1957b)
<u>N. pseudohybrida</u>	25-45	3-6	10-16	40	present	+ / ++	1 SRC	Hustedt (1955) this thesis
<u>N. pseudostagnorum</u>	35-55	5-6	7-12	28-32	present	+ / ++	1 SRC	Hustedt (1956)
<u>N. pulchra</u>	100-160	19	8-12	18-24	present	++	1 SRC	Hustedt (1955)
<u>N. scherffeliana</u>	34	8.6	9-10	30-32	?	?	Large	Krenner (1926)
<u>N. seriens</u>	?	?	9-10	over 33	?	?++	?	Cleve & Grunow (1880)
<u>N. siberica</u>	106-118	14-15.5 (16-17 at widest)	9-10	33	?	?++	?1 SRC	Cleve & Grunow (1880)
<u>N. stagnorum</u>	30-60	6-10	7-9	26	present	+++	Small: no exact relationship to costae	Hustedt (1930) this thesis
<u>N. staurophora</u>	56-75	6 (8-9 at widest)	6-10	25-28	present	+	1 SRC	Giffen (1966)

TABLE 14 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Raphe eccentricity	Fibula morphology	Source of information
<u>N. subamphioxoides</u>	75-100	6-7	9-12	20	present	++	1 SRC	Hustedt (1959a)
<u>N. thermalis</u>	35-100	5-10	7-10	28	present	++/+++	?1 SRC	Hustedt (1930)
<u>N. thermaloides</u>	30-72	5-6	17-20	40	present	+	1 SRC	Hustedt (1955)
<u>N. valga</u>	18-40	4.5-6	12-16	very fine	present	++	?1 SRC	Cholnoky (1968a)
<u>N. vulpecula</u>	44-55	4.5-6	8-10	?*	present	+	?1 SRC	Giffen (1966)
<u>N. vulpeculoides</u>	70-95	6-8	7-9	30	present	++	?1 SRC	Giffen (1973) this thesis

* areolae in decussate rows: 17-18 oblique rows in 10 µm.

groups, noting that they 'merge into each other and in many cases it depends only on the interpretation of the observer whether the keel should be called more or less eccentric.' He observed further that 'it is often very difficult or impossible to decide whether a species belongs to the dubiae (sic!) or to the bilobatae, especially if only a few specimens are available, or if they are in an unfavourable position.' Therefore, he united the groups under the name 'Dubiae', giving as a diagnosis of the new group 'a moderately eccentric keel with distinct keel puncta and ... the valve ... more or less constricted in the middle.' After this, however, the 'sect. Dubiae (Grun.) Hust. ampl.' is mentioned again by Hustedt only once (1956), his subsequent papers (1957, 1959a, b, c) showing a reversion to his former practice. Nevertheless, I believe that Hustedt's alteration is probably justified, and that any division of the sect. Dubiae sensu Hustedt (1955) would not lie along the traditional boundary between 'Dubiae' and 'Bilobatae'. In the discussion that follows, the sect. Dubiae is taken to refer to both of Grunow's groupings.

The sect. Dubiae is large, containing around 50 species, the majority of which are listed together with their dimensions etc. in Table 14. During the present study eight species have been investigated, namely N. bilobata (LM), obtained from a tidal creek at Uphill, near Weston-super-Mare; N. dubia (LM, TEM, SEM), from ± freshwater puddles at Sea Mills, Bristol, and from a ditch at Berkeley, Co. Avon; N. subamphioxoides (LM, TEM, SEM), from the puddles at Sea Mills, and also from a subaerial 'streak' of diatoms on the walls of Carreg Cennen Castle, near Llandeilo, Dyfed (my specimens of this species are somewhat smaller than those of Hustedt 1959b, being in some cases only 43 µm. long, yet from the valve shape, fibula and stria densities etc. an identification as N. subamphioxoides seems possible); N. stagnorum (LM) from a puddle at Sea Mills; N. vulpeculoides (LM, SEM) and N.

pseudohybrida (LM) from intertidal sand at St. Martin's, Isles of Scilly; an unidentified species (LM), from intertidal mud at Sandpoint, which will be referred to as Nitzschia sp. (Severn); and a second unidentified species (SEM), obtained from washings off Sargassum sp. from Hawaii, which will be called Nitzschia sp. (Hawaii).

N. bilobata is a moderately large diatom (see Table 14) with a nearly central raphe system. Intact frustules and isolated valves almost always lie in girdle view (F.184), this reflecting the fact that the valve is very acutely angled at the raphe. The valve height alters considerably along the apical plane, being least at the centre and poles: thus, the valve, and hence the frustule too, is constricted at its centre - it is 'bilobate' (F.184).

The valve is of a type 1 construction, the poroids being visible (with some difficulty) in the light microscope (F.187). There are no sterna, but there is a very wide valve margin (F.184, 186, 188; see also Hustedt 1930) exceptional in Nitzschia. There is often a disturbance of the stria pattern centrally - the centremost stria may fork near the valve margin, or the central striae may be missing (F.184, 188).

The raphe is interrupted centrally (F.187), the endings being coaxial-symmetrical: usually correlated with this is a wider separation of the median fibulae. Light microscope observations suggest that the internal fissures end in raised, helictoglossa-like structures (F.184). Flanges are present on each side of the raphe, as for example in N. spathulifera or N. sigmoidea (sects. Insignes and Nitzschia respectively), so that the raphe opens externally onto the crest of a narrow ridge (F.186, 188). The light microscope does not reveal the details of raphe structure at the poles, but it seems that a submarginal helictoglossa is probably present internally (F.184, 186).

The fibulae are bar-like structures, each equivalent to a single subraphe costa (F.184, 186, 188-9). The bases of the fibulae seem to be

joined by longitudinal ridges (F.188), although confirmation of this will have to await SEM examination. The fibula nearest each pole is somewhat larger than the others, and is almost circular in girdle view (F.184-6, 189), while the remainder of the fibulae are much extended perivalvarly: this is correlated with the fact that the polar fibulae alone join the valve margins, not the valve faces (F.189).

The cincture is broad and consists of many bands (at least 5 per cingulum - F.185, 187). Each of at least the first three bands bears a single transverse row of poroids, placed near the junction of pars exterior and pars interior (F.187).

The chromatophores are two in number, arranged as in the majority of Nitzschiae, i.e. disposed symmetrically ('spiegelsymmetrisch') about the median transapical plane (unpubl. obs., and see Karsten 1899).

N. dubia, like N. bilobata, has a strongly angled valve and tends always to lie in girdle view (F.190, 193). The raphe system is more eccentric than in N. bilobata but there is, nevertheless, a considerable portion of the valve on the proximal side of the raphe (F.190). The frustules may apparently be nitzschioid or hantzschoid (observations on the Berkeley sample).

The valve is of a type 1 construction, the poroids again being resolvable using the light microscope, but only with difficulty (F.191-192, 762-3). The poroids are round and quite large in relation to the frets and transapical costae (F.537, 763). Each poroid is closed by a hymen, placed near the outer surface of the valve (unpubl. obs.); the hymen pores are in a centroid (concentric) to subregular arrangement (F.537). There are no sterna and the marginal strip is narrow (F.191-2).

The raphe is interrupted centrally (F.191) but the central interspace is not markedly different from the others in size or shape. The central raphe endings are coaxial-symmetrical (unpubl. obs.), and it appears that the internal fissures terminate in a structure resembling

a double helictoglossa (F.191). The external polar raphe endings have not been observed; internally there is a simple, submarginal helictoglossa (F.762).

The fibulae represent single subraphe costae (F.190-3, 762-3). Surprisingly, this is more obvious in the LM than it is in the SEM (in spite of the greater resolution of the latter) owing to the presence of longitudinal ridges joining the fibula bases (F.762). There seem to be two such ridges on each side of the raphe, so that portulae are delimited at two levels (unpubl. obs.). These constrictions of the interspace are only slight, however, compared with those in Nitzschia sp.(Hawaii)(see later).

The cincture is virtually unknown, but is much narrower than that of N. bilobata (compare F.193 with 185).

There are two chromatophores, arranged as in N. bilobata (unpubl. obs.; Pfitzer 1871, Karsten 1899).

N. subamphioxoides, which was first described in 1959 (by Hustedt 1959a), but which from my observations seems nevertheless to be quite common, is similar to N. dubia in valve shape, in the disposition of the raphe system, and in the width of the marginal strip (F.203-6, 756). The valve construction is also like that of N. dubia, except that the round poroids are quite small relative to the costae and frets (F.538, 757). The poroids are clearly visible using the light microscope (F.206: Hustedt 1959a stated 'Transapikalstreifen kräftig ... deutlich punktiert') and each contain a hymen, placed near the outer aperture of the poroid, with pores in a subregular (almost hexagonal) array (F.538).

Central raphe endings are present, and are coaxial-symmetrical (F.758): internally the slits end in a 'double helictoglossa' (F.760). The internal fissure ends at the pole in the usual simple helictoglossa (F.761), while externally the raphe continues to near the margin of the valve without much deflection (F.759). N. subamphioxoides does not

possess prominent flanges bordering the raphe as in N. bilobata (F.203-4).

Most of the fibulae are bar-like structures, each equivalent to a single subraphe costa (F.203-6, 757, 760-1). Some, however, are fused in pairs or occasionally in larger aggregates, although the fusion is almost always incomplete (F.757). The central interspace is wider apically than most of the others, but within it there are often one or more siliceous 'stumps', each placed where a fibula base might otherwise be (F.757, 760). These structures are reminiscent of the knobs near the central raphe endings of some Hantzschia species (H. virgata, H. marina), except that in these the knobs are on the distal side of the raphe, whereas in N. subamphioxoides they are developed more fully on the proximal side. As in N. dubia there is a tendency towards the formation of portulae at two levels (F.760). Sometimes, however, the longitudinal ridges are hardly evident, as in some of the Carreg Cennen specimens.

The cincture is of approximately the same width relative to the valve as in N. dubia (compare F.205 with 193). LM observations show that the first band bears a single transverse row of poroids, placed near the junction of pars exterior and pars interior (F.205).

The chromatophores are like those of N. bilobata and N. dubia (unpubl. obs.)

N. stagnorum has been studied only with the light microscope; this is unfortunate since it seems that this species differs in several respects from those taxa described above and from most other species traditionally referred to the sects. Dubiae and Bilobatae.

Isolated valves usually lie in valve view (F.207), and the raphe is quite strongly eccentric. The valve is almost imperceptibly constricted centrally, although central raphe endings are nevertheless present; the central interspace is larger than the others (F.207-8).

The valve construction is probably of type 1, although the poroids cannot be resolved using the light microscope; the marginal strip is narrow. The structure of the raphe is not discernible using light microscopy, but there is no deflection of the raphe system centrally and so it is likely that the central endings are coaxial-symmetrical: a slight thickening of the valve at each pole probably betrays the presence of a helictoglossa (F.209).

The distal fibula bases are joined by a prominent longitudinal ridge, which interrupts the course of the transapical valve striae (F.208); it is not yet known whether there is a ridge proximally. The fibulae themselves are of various sizes: often they are wider than the transapical costae. They are quite short transapically and do not seem to be in any exact spatial relationship to the costae (F.207-9). Indeed, the form of the fibulae and the degree of eccentricity of the raphe suggest that this species belongs closer to the sect. Lanceolatae: it is, however, more robust than most forms belonging to that group.

N. stagnorum has a type 1 chromatophore arrangement (Heinzerling 1908).

N. pseudohybrida, a very delicate form found in the epipsammic fraction of the St. Martin's intertidal sand sample (F.202), and Nitzschia sp.(Severn)(F.194) are similar to N. bilobata/N. dubia/N. subamphioxoides, with their centrally constricted valves (in girdle view), central raphe endings, and thin, bar-like fibulae each consisting of a single subraphe costa. The poroids of Nitzschia sp.(Severn) are obvious (using the LM) over the greater part of the valve distal to the raphe, but nearer the raphe they become less so. Moreover, in the part of the valve face nearest the distal margin the poroids are spaced very irregularly (F.194), a feature which does not appear to occur in any other species of this section.

The raphe system of Nitzschia sp.(Severn) is moderately eccentric,

as is that of N. pseudohybrida (see also Hustedt 1955, Pl.15 f.3, 4).

N. vulpeculoides was first described by Giffen (1973). The valve is quite strongly constricted centrally (in girdle view) and has an eccentric raphe system (F.195). As Giffen noted, the poroids are arranged in decussate rows (F.196-7, 201), but while in the sect. Panduriformes a similar arrangement of the 'puncta' reflects the loculate nature of the valve (see elsewhere), in N. vulpeculoides there is a normal type 1 construction (F.764-7). The poroids are closed by hymena which lie flush with the outer surface of the valve (F.766). There are no sterna and the marginal strip is not particularly wide (F.767).

Central raphe endings are present and are coaxial-symmetrical (F.766): there is a slight thickening of the silica between the internal endings (F.764). The median fibulae are widely separated (F.195, 198, 200-1). At the pole, internally there is a simple, submarginal helictoglossa (F.196, 199, 768), while externally the raphe bends abruptly where the inner and outer fissures separate, and then carries on to near the valve margin (F.765).

The fibulae are slender, rib-like structures (F.196-201, 764), similar to those in Hantzschia virgata vars. intermedia or gracilis. Each is of the same thickness as a transapical costa, and probably represents a single subraphe costa (F.197, 200), although any such relationship is masked by the presence of two longitudinal ridges, one on each side of the raphe, which join the proximal and distal fibula bases (F.200, 764, 767). These ridges are not very high, but they completely interrupt the transapical valve striae, each of which is represented beyond the ridges by one or two poroids. A subraphe canal cannot be said to be present in this species (F.764, 766: contrast N. subamphioxoides).

The cincture and cytology are unknown.

It has not yet been possible to attempt an identification of

Nitzschia sp.(Hawaii) since this diatom has been observed only with the SEM. This is a fairly small diatom with an almost central raphe system (F.769). The valve is robust and of a type 1 construction, with round poroids, each closed by a hymen lying \pm flush with the external surface of the valve (F.770-1). The marginal strip is fairly narrow (F.771-2).

The raphe is interrupted centrally, the internal fissures ending in a prominent 'double helictoglossa' (F.770). At the pole the raphe ends internally in a simple helictoglossa lying along the mid-line of the valve (F.773), while externally the terminal fissure curves away until it comes to run parallel to and close to the polar valve margin (F.771).

At first sight the fibulae appear to be quite unlike any of those described above (F.773), but a closer examination suggests that they may not be so remarkable. Flange-like developments of the fibulae, together with longitudinal ridges (2 on each side of the raphe) combine to delimit oval portulae at two levels (F.770, 772-3), as in N. dubia and N. subamphioxoides. Between these levels, however, each fibula is abruptly constricted to the width of one transapical costa. I suggest, therefore, that here too each fibula is equivalent to a single subraphe costa, and that the differences between Nitzschia sp.(Hawaii) and N. dubia etc. is one of degree, not kind. The two median fibulae are more widely separated than are the remainder.

Of the eight species examined, then, seven are similar to one another in valve, raphe and subraphe structure. N. stagnorum, on the other hand, may belong elsewhere than in the sect. Dubiae.

Turning to the other species of the section it is clear that most closely resemble N. bilobata, N. dubia, etc. There is no indication that any of the species have anything other than a type 1 valve construction, although each will have to be examined using the electron microscope before this can be confirmed. The raphe is usually eccentric,

but not as much so as in some other sections (e.g. Lanceolatae, Fragilariopsis), and is interrupted centrally. The height of the valve usually alters over the length of the diatom, being least at the centre and poles: thus the frustule or valve appears constricted centrally in girdle view. In most cases the fibulae are equivalent to single subraphe costae (see Table 14).

There are some species, however, which differ from the majority, and these in particular require further study and may require transference elsewhere. Thus, N. kittlii (Hustedt 1930, f.776), N. dippelii (see Hustedt 1930), and N. scherffeliana (Krenner 1926, T.11 f.84) all have large, square or rectangular fibulae (as seen in girdle view) like those of N. vitrea (see Nitzschia sect. Lineares), although otherwise they seem to resemble N. dubia etc. quite closely. N. pretoriensis (Cholnoky 1957b) also has large fibulae, but shows a further similarity to N. vitrea in that the raphe is unbroken centrally (op. cit., T.4 f.110): it seems likely that these two species are more closely related to each other than either is to any member of the sect. Dubiae.

N. commutata is also of uncertain position: preliminary observations indicate, however, that its subraphe structure is unlike that of typical sect. Dubiae species.

On the whole, however, the sect. Dubiae, sensu Hustedt (1955), seems to be a most satisfactory grouping of species: there is no obvious break in the spread of variation which might indicate the need for subdivision or division.

4.6.6.4 The section Pseudoamphiprora

Grunow founded this section (in Cleve & Grunow 1880) to include N. ocellata and N. amphiprora (Cleve's 'Amphiprora nitzschioides' of 1873). Cleve (1883), Schütt (1896), Peragallo & Peragallo (1897-1908),