TABLE 12

Species of Nitzschia sect. Tryblionella studied during the present investigation, and their sources.

N. acuminata: (LM, SEM) salt-marsh at Ferrybridge, near Portland, Dorset.

N. angustata: (LM, SEM) sediment from river at Braemar.

N. apiculata: (LM, SEM) sediment from the (tidal) River Avon, at the Cumberland Basin, Bristol; salt-marsh at Sandbay.

N. circumsuta: (LM) Cleve & Möller slide 48.

N. debilis: (LM, TEM, SEM) Afon Bran bridge material; sediment from puddles at Sea Mills, Bristol.

N. hungarica: (LM, TEM, SEM) sediment from drainage ditch at Berkeley; Sea Mills puddles.

N. levidensis: (LM, SEM) Berkeley ditch material.

N. navicularis: (LM) River Avon, at the Cumberland Basin, Bristol; B.M. slides 18138
23285
23286

Nitzschia sp. ('Pseudotryblionella' group)(see F.210): (LM) Grunow slide 1559a, from the Vienna collection.

N. tryblionella: (LM, SEM) Berkeley ditch material.

TABLE 13

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	'Rippen' no. in 10 µm.	Extent of 'Rippen'	Strength of 'Rippen'	Width of axial sternum	Source of information
N. acuminata	50-90	13-17	12-16	12-16	present	0	0	0	++	Hustedt (1930) this thesis
N. acuta	40-100	11-18	?	14-15	?present	0	0	0	0	Cleve & Grunow (1880)
N. adducta	18-22	6-7	16-18	16-18	?absent	0	0	0	0	Hustedt (1955)
N. aerophila	14-30	5.5-6.5	10-14	26-30	present	0	0	0	+	Cholnoky (1960a, 1968b)
N. angustata	25-110	5-10	12-18	12-18	present	0	0	0	0	Hustedt (1930) this thesis
N. apiculata	20-50	5-8	17-20	17-20	present	0	0	0	+	Hustedt(1930) this thesis
N. ardua	23-36	5	20-22	?	?	0	0	0	?	Cholnoky (1961)
N. balatonis	22	8.5	?	16	?absent	0	0	0	0	Cleve & Grunow (1880)
N. bathurstensis	20-25	8-9	11-13	22-25	present	0	0	0	+/++	Giffen 1970b
N. bicuneata	72-77(95)	21-22(32)	6-7	13-14	?present	0	0	0	0	Cleve & Grunow (1880)
N. brightwellii	?	?	?	15	present	0	0	0	0	Cleve & Grunow (1880)
N. calida	34-43	9-10	10	?	present	17-19	complete	+	0	Cleve & Grunow (1880)
N. campechiana	61-100	23-26	3-4	22	present	+	short	+++	0	Cleve & Grunow (1880) Grunow (1880)
N. chutteri	15-19	6.5	?16-18	16-18	absent	0	0	0	+	Archibald(1966, 1971)
N. circumsuta	130-300	50-65	3.5	25-30	present	0	0	0	0	Hustedt (1930) this thesis
N. coarctata	70-125	22-26	?	6-7.5	?present	0	0	0	0	Cleve & Grunow (1880)
N. cocconeiformis	25-32	11-29	8	8	absent	0	0	0	+	Cleve & Grunow (1880) Grunow (1880)
N. conformata	22-28	6-8	12	?	present	+	complete	++	0	Hustedt (1952)

TABLE 13 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	'Rippen' no. in 10 µm.	Extent of 'Rippen'	Strength of 'Rippen'	Width of axial sternum	Source of information
N. davidsonii	38	12.5	5-6	11	?	0	0	0	?0	Cleve & Grunow (1880)
N. debilis	13-25	7-8	7-9	38-41	present	0/12-14	partial/ complete	0 to ++	+	Hustedt (1930) this thesis
N. didyma	48-55	12	3-4	20-24	present	+	short	+	?	Hustedt (1952)
N. divergens	15-25	4-6	10-12	?24	present	?24	?	?	0	Hustedt (1952)
N. graeffei	127-140	?	5	10	?present	0	0	0	0	Cleve (1878)
N. granulata	28-44	14-20	6.5-7	6.5-7	absent	0	0	0	++ (punctate)	Cleve & Grunow (1880)
N. halteriformis	48-55	18-22	6-8	?	present	7	complete	+++	0	Hustedt (1952)
N. hantzschiae-formis	43-51	8-9	?	?	?	?	?	?	+	Fritsch & Rich (1924)
N. hungarica	20-110	6-9	7-9	16-20	present	0	0	0	+	Hustedt (1930)
N. inducta	45-55	9-12	5-12	25-30	present	0	0	0	0	Hustedt (1952)
N. irritans	20-25	8-10	16	16	?	0	0	0	0	Cholnoky (1961)
N. jelineckii	70-140	21-23	5.5-7	12-15	present	0	0	0	0	Cleve & Grunow (1880)
N. lanceola	30-55	9-10	7.5-9	7.5-9	absent	0	0	0	0	Cleve & Grunow (1880) Hustedt (1955)
N. levidensis	18-54	9-14	12	?	present	9-13	complete	++	0	Hustedt (1930)
N. limicola	16	8.5	?	?16	?absent	?16	?	?	0	Cleve & Grunow (1880) Grunow (1880)
N. lionella	20-28	6-7	12	30	?absent	0	0	0	0	Cholnoky (1960a)
N. littoralis	45-130	18-30	4-8	12-13	present	0	0	0	0	Cleve-Euler (1952)
N. magnacarina	29.1	10	6	24-26	present	0	0	0	++	Hohn & Hellerman (1966)

TABLE 13 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	'Rippen' no. in 10 µm.	Extent of 'Rippen'	Strength of 'Rippen'	Width of axial sternum	Source of information
N. marginulata	60-110	11-18	9-11	19-23	present	0	0	0	+++	Cleve-Euler (1952)
N. mucronata	46.8-50	8.1-8.5	10-11	12	?	0	0	0	++	Pantocsek 1902
N. natalensis	32-40	11-13	8	38	?	0	0	0	+	Cholnoky (1960a)
N. navicularis	30-80	15-25	8	8	absent	0	0	0	+++ (punctate)	Hustedt (1930) this thesis
N. nicobarica	95-203	37-48	2.5-3	23-25	present	0	0	0	0	Cleve & Grunow (1880)
N. novaehollandiae	65-175	13-14	7-7.5	14-15	?present	0	0	0	?	Cleve & Grunow (1880)
N. partita	37	14	7	7	absent	0	0	0	+	Hustedt (1952)
N. persuadens	18-25	6-7	12	32	present	0	0	0	0	Cholnoky (1961)
N. perversa	42-46	22-26	?	?	present	11-12	partial	++	+	Cleve & Grunow (1880) Grunow (1880)
N. plana	155-290	20-26	3.5-8	16-22	present	0	0	0	+/++	Cleve-Euler (1952)
N. plicatula	50-60	7-8	10-12	18-20	present	0	0	0	+	Hustedt (1953)
N. ponciensis	24-28	4-5	16-17	27-30	present	0	0	0	+	Hagelstein (1938)
N. princeps	138.4	32.8	2	?	present	0	0	0	0	Hanna & Grant (1926)
N. pulchra	40-50	17	4-10	4-6: 12 (see Hustedt)	present	0	0	0	0	Hustedt (1952)
N. punctata	20-70	10-25	7-9	7-10	absent	0	0	0	0/+	Hustedt (1930)
N. rabenhorstii	217-225	20-22	8-9	17	?absent	0	0	0	0	Cleve & Grunow (1880) Grunow (1880)
N. salvadorina	135-155	26	3-4	16	present	0	0	0	+	Hustedt (1952)
N. sibula	30-36	7-8	10-12	22-25	present	0	0	0	++/+++	Giffen (1973)

TABLE 13 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	'Rippen' no. in 10 µm.	Extent of 'Rippen'	Strength of 'Rippen'	Width of axial sternum	Source of information
N. silicula	12-22	3.5-4.5	16	16	absent	0	0	0	0	Hustedt (1955)
N. subcostata	57-60	20	7	14-15	present	0	0	0	?0	Cleve & Grunow (1880)
N. subpunctata	15-20	5-6	16-18	22	absent	0	0	0	0	Cholnoky (1960a)
N. sulcata	115-125	20-25	4.5-5	11	?present	0	0	0	?0	Cleve & Grunow (1880)
N. tongatensis	58-138	9-10	5-6	19-22	present	0	0	0	0	Cleve & Grunow (1880)
N. tryblionella	60-150	16-35	7-9	20-21	present	5-8	complete	+/++	0	Hustedt (1930) this thesis
N. visurgis	30-40	12-14	6-9	35	present	+	?	?	0	Hustedt (1957)
N. zebuana	139	15	10-11	27	present	0	0	0	?	A.Mann (1925)

4.6.6.2 The section Tryblionella

Hustedt (1930) described this section thus:
'Kiel stark exzentrisch. Schalen mit mehr oder weniger deutlicher Längsfalte, Struktur in der Falte oft fehlend oder stark abgeschwächt. Symmetrieverhältnisse: drei gerade isopole Achsen; Zellkörper zur Valvarebene diagonalconsimil, zur Apikalebene diagonalsymmetrisch, zur Transapikalebene spiegelsymmetrisch; alle Hauptschnitte sind ebene Flächen. Vorzugsweise Salzwasserformen oder doch mehr oder weniger halophile Arten.'
The combination of a very eccentric raphe system and a longitudinal fold of the valve (which is straight) is sufficient to enable the referral of a specimen, taxon, etc. to this group.

In his 'Synopsis of British Diatomaceae' (Vol.1, 1853), W.Smith described a new genus of diatoms which he placed near Surirella and Campylodiscus, and for the next 26 years Smith's genus, Tryblionella (a diminutive of the Greek τρύβλιον = a cup, bowl: see Liddell & Scott 1968) was considered by all to be a separate entity, although it was gradually realised that its affinities lay with Nitzschia, not with the Surirellaceae (Grunow 1860, 1862, 1879; Rabenhorst 1864; Kitton 1873; etc.). By 1879, however, Grunow's 'long observation of this genus' (i.e. Nitzschia) 'had convinced him that the genus Tryblionella was not sufficiently distinct to warrant their separation'(note by Kitton in Grunow 1879), and in the following year this combining of the genera was formally proposed (Grunow 1880, Cleve & Grunow 1880), Tryblionella becoming a section of Nitzschia. While the majority of diatomists accepted Grunow's judgement (e.g. see Schütt 1896, Van Heurck 1896, Peragallo & Peragallo 1897-1908, Karsten 1928, Hustedt 1930), some have continued to uphold the validity of Tryblionella (e.g. Petit 1888, Pantocsek 1902, Von Schönfeldt 1913). Frenguelli considered Tryblionella separate even as late as 1942, but he was inconsistent in

his taxonomy, separating Tryblionella from Nitzschia in some works (1934, 1938b, 1942) but combining them in at least one (1938a).

The sect. Tryblionella has undergone several changes since it was described by Grunow (in Cleve & Grunow 1880). Peragallo & Peragallo (1897-1908) considered the sects. Circumsutae and Pseudotryblionella (see also Van Heurck 1880-5) to be insufficiently distinct from Tryblionella to justify their continued separation from it; this opinion was shared by Hustedt (1930), who also combined with this section the sect. Apiculatae (the sects. Circumsutae, Pseudotryblionella and Apiculatae were all described first by Grunow, in Cleve & Grunow 1880). These alterations have not met with universal acceptance: Cleve-Euler (1952) supported the inclusion of sects. Apiculatae and Pseudotryblionella in Tryblionella, but considered the Circumsutae distinct, while Hendey (1964) left Grunow's original scheme virtually unaltered. Grunow (in Cleve & Grunow 1880) separated the four sections mentioned above thus:

Tryblionella: 'Kiel sehr excentrisch, Schaalen meist wellig gefaltet, Kielpunkte undeutlich meist in gleicher Anzahl wie die Querstreifen.'

Apiculatae: 'Kiel sehr dem einen Rande genähert, Schaalen länglich linear oder in der Mitte etwas verdünnt, Querstreifen auf der Längsfalte matter wie auf dem übrigen Theil der Schaale oder fehlend. Punkte nicht in Quincunx.'

Pseudotryblionella: 'Kiel mehr oder weniger dem einen Schaalenrande genähert, Schaalen mit flacheren oder tieferen Längsfalten, über welche die Querstreifung gleichmässig wie im übrigen Theile der Schaale verläuft. Kielpunkte immer deutlich.

Circumsutae: 'Schaalen mit breiterer oder schmälerer Längsfalte ... , sehr excentrischem Kiele, deutlichen Kielpunkten und unregelmässig punktirter Oberfläche, welche ausserdem aber von zarten

regelmassigen Punktreihen durchzogen ist. ...'

Other authors have proposed divisions of Grunow's sect. Tryblionella. For instance, Peragallo & Peragallo (1897-1908) proposed the separation from it of a 'Groupe' Angustatae, containing N. angustata and N. marina, while Pantocsek (1902) described a new genus, Zotheca, to include N. navicularis, N. punctata, N. doljensis, N. coarctata and N. granulata. Neither suggestion has received much support, although Frenguelli used Pantocsek's grouping, either as a separate genus (1934), or as a ?section of Nitzschia (1926, p.68 - 'Nitzschia (Zotheca) granulata'). In this dissertation Hustedt's (1930) circumscription of the sect. Tryblionella will be used as a basis for further discussion.

Ten species have been studied during the present investigation; these are listed, together with the sites from which they were collected, in Table 12. This represents only a small fraction of the total number of species which have been described as belonging to this section (see Table 13), but most of the remainder are rare.

Several groupings may be distinguished within the ten species studied. The first includes N. tryblionella, N. debilis, N. levidensis and probably N. circumsuta. N. debilis has long been recognised to be closely related to N. tryblionella, and was included within it by Hustedt (1930) and Cleve-Euler (1952), as a variety. Later, however, Hustedt altered his opinion (e.g. see 1938, 1957); I believe he was right to do so, for reasons which are given below.

In both N. tryblionella and N. debilis, but especially in the latter, the valve is broad relative to its length (F.153-8, 165-6). It is undulate in transapical section and bears a very pronounced marginal ridge (F.717-9, 726). The valve construction is of type 3 (see section 4.6.2) in both, but there are minor differences between them. Thus, for instance, in N. debilis, in contrast to N. tryblionella, there are both axial and lateral sterna (F.159, 728, 730; contrast

F.165), although in the latter species the poroids are often more sparse in the region corresponding to the lateral sternum in N. debilis. Moreover, whereas in N. tryblionella the poroids are virtually invisible from the outside (F.718, 722-3), in N. debilis they are quite evident (F.726, 729); since the hymena (with subregularly arranged pores - F.535) were still present in the poroids of the N. debilis specimens examined, this is unlikely to be an artefact of acid cleaning. These features, taken together with differences in size and stria density (see Table 13), and with differences in raphe construction (see below) strongly suggest that a separation at species level is justified.

In these two species the raphe runs more or less parallel to the proximal margin and is interrupted centrally (F.722, 727). Corresponding to this interruption, there is a wider separation of the median pair of fibulae (F.165, 725), but even so the central interspace is so deep and narrow that the central internal raphe endings cannot be seen in intact valves, using the SEM. The external central raphe endings of N. tryblionella are ± coaxial-symmetrical, with the fissures widening slightly at their ends (F.722). The subraphe canal is slightly constricted at this point (a feature which is visible in the light microscope), as it is also in N. debilis (F.160, 165, 718). In the latter, however, the external central raphe endings are abruptly deflected towards the distal margin and are thus noncoaxial-symmetrical (F.727). The polar endings of both are similar (F.723, 729-30, unpubl. obs.): a simple helictoglossa is present internally, while externally the raphe is slightly bent above the helictoglossa and continues into a short terminal fissure.

In both species the subraphe canal is quite well defined, and is raised above the general level of the valve (F.718-9, 726-7). At least in N. debilis the canal walls are perforate, there being one longitudinal row of poroids on each side of the raphe (F.727, 729): the

distal row is interrupted opposite the central raphe endings. Whereas in N. tryblionella the canal walls extend outwards so that the raphe opens onto the summit of a ridge (F.722), in N. debilis the canal walls seem to be more rounded.

The fibulae are of type ii or iii, those of N. debilis always being of the latter variety (F.730); in N. tryblionella the subraphe costae may be fused to a considerable extent, although the striae usually continue a little way into the fibulae (F.724-5, but see F.721). While the fibulae may each represent from 3 to 8+ subraphe costae, they are separated, one from another, by only 1 or 2 transapical costae; thus, the interspaces are very small (F.160, 165, 725, 730). The linear densities of the fibulae are the same in both species (7-9 in 10 µm.) even though the stria densities are quite different (see Table 13), which reflects the fact that, on average, each fibula of N. debilis contains more subraphe costae than does one of N. tryblionella.

The cincture is at present virtually unknown; the bands of N. debilis, however, appear to be without poroids (unpubl. obs.).

The chromatophores are arranged as in the majority of Nitzschia species (i.e. a type 1 arrangement), but whereas in N. tryblionella the chromatophores occupy virtually the whole length of the cell (F.166), in N. debilis there is a wide gap between the two plates centrally, each plate having a characteristic median extension towards the nucleus (F.148-52). The nucleus of N. debilis is more or less spherical, and is fairly small in relation to the width of the cell: the nucleoplasm stains very poorly with aceto-carmine (unpubl. obs.).

N. circumsuta, although it was originally placed in a different section from N. tryblionella by Grunow (in Cleve & Grunow 1880), probably belongs very close to that species. With its rounded outline and unconstricted centre (F.161), the valve is similar in shape to that of N. debilis or N. tryblionella, although it is much larger than

either of these. The fibulae are like those described above and appear striate in the light microscope, suggesting that they are of type iii (F.164); the subraphe canal is constricted at the centre (F.161, 164), and there is a wider separation of the median fibulae. Central raphe endings are present (F.164, and see Hustedt 1929). The valve is undulate in transapical section (unpubl. obs., and Hustedt 1930), and were it not for the absence of 'Transapikalrippen' (see section 4.6.2, valve construction type 3), Grunow's insistence on the separation of this taxon from N. tryblionella and its allies at sectional level would be incomprehensible. But the presence/absence of 'Transapikalrippen' is a poor criterion on which to base taxonomic judgements at this level: some valves of N. debilis possess only faint 'Transapikalrippen' or none at all, whereas others more nearly resemble N. tryblionella in bearing numerous costate thickenings (F.153-8) - the development of the 'Transapikalrippen' is very variable.

In N. circumsuta, as in N. tryblionella, the striae are unbroken by sterna (unpubl. obs.). Furthermore, Hustedt(1930) noted that the rows of poroids are 'meistens mit unregelmässig verteilten hyalinen Unterbrechungen, so dass bei schwächeren Vergrösserungen der Anschein einer verworrenen Punktierung hervorgerufen wird' (F.163), a phenomenon which is observable also in N. tryblionella (F.165).

The second grouping which can be recognised is one which conforms to Grunow's sect. Apiculatae, and includes N. acuminata, N. apiculata and N. hungarica. In these the valves are more or less linear, with slightly concave sides; this feature, together with the prominent axial sternum and the eccentricity of the raphe, makes members of this group easy to recognise.

The valve construction exhibited by N. acuminata etc. has already been described (section 4.6.2, valve construction type 4). The transapical costae are very obvious in the SEM, both externally and intern-

ally (F.733, 735, 740, 742, 744, 746); between them there are usually two or three rows of poroids (F.536, 737, 739-42, 746-9: sometimes one in N. hungarica, but then only in a fraction of the valve - F.736, 741). Helmcke & Krieger (1953- , T.88) illustrated a somewhat eroded specimen of N. apiculata in which there were three rows of poroids between adjacent costae, while in the valves of the same species figured by Schoeman & Archibald (1976-) there were three or four rows. The valve is undulate in transapical section (F.743, 746), with the axial sternum on an inward fold. The external face of the sternum bears small warts in N. hungarica and N. apiculata (F.736, 741-2), as does the marginal strip (F.734, 741-2; see also Schoeman & Archibald 1976- , 'N. hungarica' f.4, 9): N. acuminata is almost without these, at least on the axial sternum (F.746, 748). The poroids of N. hungarica possess volae, and the hymen pores are arranged subregularly (F.536).

The raphe opens onto the summit of a ridge, as in N. tryblionella or the sect. Panduriformes (F.736-7, 743, 745, 748-9). Central raphe endings are present but difficult to observe, externally because of the narrowness of the raphe fissure and the presence of flanges bordering the fissure (which flanges form the ridge noted above), and internally because of the narrowness and depth of the central interspace, even though this is wider than the other interspaces (F.171-2, 174, 739). In all three species the central raphe endings are slightly depressed (F.737, 749) - i.e. the subraphe canal is constricted as in N. tryblionella or N. debilis - and this is visible using the light microscope (F.175). At the pole the raphe ends internally in a simple helictoglossa (F.738, and unpubl. obs.). The terminal fissure is rather longer than in N. tryblionella or N. debilis, and curves off until it comes to run more or less parallel to the margin of the valve pole (F.736, 743, 745, 747). This curvature can be directed towards either the distal (F.745; 743) or the proximal side (F.747; 742) in N. acuminata and N. apiculata,

and probably also in N. hungarica. The flanges bordering the raphe externally vanish just before the beginning of the terminal fissure (F.736, 745, 747).

The fibulae are of type i or vii. In N. acuminata and N. apiculata each transapical costa, except the centremost, bears a fibula (F.171, 174-5, 740): thus, because the fibulae are small they are not easily distinguished with the light microscope - as Grunow (in Cleve & Grunow 1880) noted, 'Kielpunkte undeutlich oder fehlend'. The relationship between the fibulae and transapical costae is more obscure in N. hungarica (F.172-3, 739). Some costae bear fibulae, but in other cases a fibula may lie opposite a 'stria' (i.e. the rows of poroids between two adjacent costae)(see F.739, top right). In this species too, however, the fibulae are small and are never like those of N. tryblionella or N. debilis; because of their positioning they are more obvious in the light microscope than those of N. acuminata or N. apiculata.

There is a small subraphe canal which is raised above the general level of the valve (F.743, 748-9). The canal walls appear to be unperforate: the transapical rows of poroids continue into the interspace but do not extend beyond the outer edges of the fibula bases.

The cingulum consists of perhaps 4, nonporose bands: in N. acuminata and N. hungarica some of these bear spines on their abaxial margins and warts on their partes exteriores (unpubl. obs.). The first band in N. acuminata, which is open, bears a series of short, blunt projections (unpubl. obs.) which, in the intact frustule, underlap the valve costae as in Hantzschia amphioxys (q.v.).

The chromatophores of all are very similar and are arranged as in N. tryblionella etc. (type 1 arrangement), with each chromatophore extending virtually from centre to pole (F.168-70). Bütschli globules are not obvious in the N. tryblionella and N. apiculata groups.

Various other species appear to belong in this second group, and these are mentioned later. One published electron micrograph (Helmcke

& Krieger 1953- , T.397) was claimed by its authors to be of N. acuminata, yet the valve figured is under 20 µm. long, while Hustedt (1930) gives a minimum of 50 µm. for this species, and has a structure different from that described above: it clearly belongs in the 'Apiculatae', however, (on the grounds of valve shape, raphe position, presence of a well-defined axial sternum, presence of warts on the distal mantle, etc.) but in contrast to the species described above it has only one row of poroids between adjacent transapical costae.

N. angustata, which was originally described by W.Smith (1856) as a species of Tryblionella, has always, since its transfer to Nitzschia, been classified in the sect. Tryblionella, except by the Peragallo brothers (see before). Its structure, however, is quite dissimilar to that of any member of the section described so far. Although a marginal ridge is present in this species (F.750), as in the foregoing, the valve construction is of type 1; there are no sterna (F.750, 751, 755). Near the raphe, in the walls of the subraphe canal, the striae become double (F.754-5), just as in various members of the sect. Lanceolatae - e.g. N. fonticola (unpubl. obs., and see Lange-Bertalot 1977, T.8 f.5), N. acidoclinata (ibid., T.10 f.1, 2), N. amphibia (F.905, 907-9), N. hantzschiana (F.912-5, 919) and N. cf.hantzschiana (F.928-9). It is interesting, moreover, that in the last-mentioned species there is a well-developed marginal ridge as in N. angustata (F.924-5).

The external raphe fissure is bordered by two flanges, but these are discontinuous at the centre, as is the raphe (F.755). Only the external central raphe endings have been observed, and these do not correspond to those in any of the N. tryblionella or N. apiculata groups. The terminal fissure is short and deflected to one side (F.754).

The subraphe canal is well differentiated and set above the general level of the valve (F.754-5; unpubl. obs.). A fibula is borne on each transapical costa (?except the centremost) and thus, since the

fibulae are small, they are not very obvious in the light microscope (unpubl. obs.; Hustedt 1930).

It can be seen that N. angustata fulfils the requirements of Grunow's diagnosis of the sect. Tryblionella (quoted on p.158), and so it is not surprising that Grunow classified it here. Various points indicate, however, that it belongs closer to the Lanceolatae than to the Tryblionellae, and these are discussed below.

Firstly, the shape of the valve (± linear, with bluntly rounded apices; see Hustedt 1930, and F.750), although it would allow of a fairly close relationship with the Tryblionellae, is more akin to that encountered in many of the sect. Lanceolatae, e.g. N. amphibia or N. communis (F.367-71, 434-5): the var. acuta (Hustedt 1930, f.768), with its protracted apices, is especially similar to the Lanceolatae.

Secondly, the valve structure of N. angustata is much more like that of certain Lanceolatae, especially N. cf.hantzschiana, than that of N. tryblionella or N. apiculata or other members of the sect. Tryblionella. In particular, the doubling of the striae near the raphe sets N. angustata apart from the Tryblionellae.

Thirdly, in contrast to most of the sect. Tryblionella, N. angustata has a relatively deep valve and the frustule is as wide, or wider, pervalvarly as it is transapically.

With particular reference to Grunow's diagnosis of the sect. Tryblionella, it may be noted that in N. angustata the folding of the valve face is only slight (F.751), being little more than in some Lanceolatae. In N. angustata each transapical costa bears a fibula, but while this is rare in the Lanceolatae it is not unknown (e.g. in N. karrooensis, Cholnoky 1959, Abb.7 f.301). Thus, even those characters which encouraged Grunow to place N. angustata in the sect. Tryblionella would appear to permit a classification nearer the Lanceolatae.

The chromatophores of this species have not yet been studie

detail: Van Heurck's (1896) illustration shows, however, that they are of the usual Nitzschia type.

The cincture consists of open bands. In the mature cingulum there are four bands, all of which have different morphologies although the second and third bands are quite similar (F.752-3). The first band has a single transverse row of poroids, lying at the junction of the pars exterior and pars interior (F.751-5). This band is quite broad and bears small warts on its pars exterior; these are more closely spaced towards the abvalvar margin.

The second and third bands are extremely narrow for most of their length (F.751, 754). The second bears a prominent ligula centrally which closes the opening between the ends of the first band (F.753). The ends of the second band are narrow and unexpanded (F.754). The third band also bears a prominent ligula centrally, but in addition it bears an antiligula, so that it partly closes the opening left by the fourth band as well as closing that left by the second (F.754). The ends of the third band are slightly expanded (F.753).

The last band is most unusual in that it is wider than any of the others (F.751-3): this phenomenon has not been observed in any other species of Nitzschia. It bears a single transverse row of what appear to be longitudinally (sensu Von Stosch 1975) elongated poroids, each closed by a hymen - confirmation of this awaits TEM examination. The fourth band, like the first, bears small warts.

Few comparisons are possible between the cinctures of N. angustata and other Tryblionellae because of the paucity of information concerning the latter. Nevertheless, it may be pointed out that the perforate nature of the first band in N. angustata separates this species from N. debilis or N. acuminata, and suggests a link with the Lanceolatae and some other Nitzschia species. Some similarities exist between the cinctures of N. angustata and N. sinuata (see sect. Grunowia, and F.790).

A fourth group may be distinguished, including N. navicularis and probably also N. granulata (although this has not been observed during the present study). The valve of N. navicularis is very broad relative to its length (Hustedt 1930 gives dimensions of 30-80 x 15-25 µm.) and is 'elliptisch bis linear-elliptisch mit mehr oder weniger stumpf gerundeten, nicht vorgezogenen Polen' (ibid.; see F.176). It is, therefore, fairly similar in shape to N. tryblionella or N. debilis, though perhaps a little more rounded at the poles.

Some aspects of the valve structure of N. navicularis have already been described (section 4.6.2). There are a few similarities to the valves of the N. apiculata group - the presence of a well-defined axial sternum, the presence of more than one row of poroids between adjacent costae (F.176-7) - but other characters point to a wide separation of these groups. Thus, the axial sternum in N. navicularis is porose, and the structure is much more coarse than in N. apiculata etc. There is no sign of a 'central nodule' in N. navicularis: the raphe is continuous from pole to pole (F.176-8). Correlated with this is the fact that all the transapical costae bear fibulae, even the centremost (F.176, 178). The shape of the valve and the chromatophores with their prominent pyrenoids (F.179-83) also indicate that a close relationship with the 'Apiculatae' is unlikely.

N. granulata also has no central break in the raphe (Hustedt 1929), and there is in this species, as in N. navicularis, an exact equivalence of fibulae and transapical costae. An axial sternum, as such, is not distinguishable in N. granulata, but the central part of the valve, with its single rows of poroids (the remainder of the valve face bears paired rows as in N. navicularis - see Peragallo & Peragallo 1897-1908, Pl.69 f.20), is probably equivalent to the sternum of N. navicularis.

How, then, do other species of this section relate to the groupings

distinguished above, and thus what conclusions may be drawn concerning the taxonomy of the section?

A large number of species may be referred to the N. tryblionella group with some confidence. N. levidensis (F.167, 731-2) and N. calida, which have often been considered to be varieties of N. tryblionella but should probably be separated from it for reasons like those given for N. debilis, nevertheless belong very close to N. tryblionella (see Hustedt 1930, 1957). Various other species are similar, if the available illustrations are accurate: these are N. brightwellii (Ralfs in Pritchard 1861, Pl.8 f.7), N. littoralis (Cleve-Euler 1952, f.1438), N. perversa (Grunow 1880, Pl.12 f.6; Frenguelli 1938b, f.22), N. visurgis (Hustedt 1957, Abb.43) and N. princeps (Hanna & Grant 1926, Pl.21 f.8). N. plana has traditionally been placed near N. apiculata (e.g. see Cleve & Grunow 1880), but its structure - for instance, the ill-defined nature of the axial sternum - suggests a link with N. tryblionella (see W.Smith 1853, Pl.15 f.114; Cleve-Euler 1952, f.1433; Hendey 1964, Pl.39 f.7). N. zebuana may also belong here (see A.Mann 1925, Pl.28 f.7).

N. campechiana and N. nicobarica, which were placed in the sect. Pseudotryblionella by Grunow (in Cleve & Grunow 1880), are probably to be placed in the above group in view of their possession of certain features, e.g. closely spaced rows of small poroids, folded valve, fibulae large in relation to the transapical costae and of the same shape as those of N. tryblionella, valve shape, etc. (see the illustrations of N. campechiana and N. nicobarica in Grunow 1880, and compare with Hustedt's 1930 drawing of N. tryblionella). Moreover, in N. campechiana certain of the transapical costae are thickened into short 'Transapikalrippen' (see Grunow 1880, Pl.13 f.16a, b; A.Mann 1925, Pl.28 f.4, 5). 'Transapikalrippen' are present in N. halteriformis also (Hustedt 1952, f.26), but here, unlike in N. campechiana, they traverse

the whole width of the valve. The fibulae of this species are very similar to those of N. tryblionella.

Two species, N. umbilicata and N. conformata, were said by Hustedt (1949 and 1952 respectively) to be close to N. levidensis (= 'N. tryblionella var. levidensis' in these papers), but the first is apparently synonymous with N. calida (Schoeman & Archibald 1976-), while the second requires further study. N. magnacarina (Hohn & Hellerman 1966, Pl.2 f.13), N. sibula (Giffen 1973, f.59, 60) and N. bathurstensis (Giffen 1970b, f.67-69) are apparently also of this group.

The N. apiculata group is somewhat smaller, containing, in addition to the above, only N. marginulata, which has a very wide axial sternum and relatively closely spaced transapical costae (Cleve-Euler 1952, f.1434); N. aerophila, the smallest member of the group, with even more densely packed costae than the last (see Table 13); and perhaps a couple of others. Hustedt (1935) described a new species, N. rugosa, which he placed near N. hungarica, but the appearance of its valve leads me to doubt this classification since an axial sternum is not evident and the valve is too sharply constricted at the centre: it would seem to belong nearer to the sect. Dubiae. Conversely, N. plicatula, which was thought by Hustedt (1953) to be closely related to N. commutata of the sect. Dubiae, almost certainly belongs in the N. apiculata group (ibid., f.1, 2, and Cholnoky 1960a, f.292-5). Indeed, if the structure of N. plicatula is like that of the 'Apiculatae', then it will be difficult to maintain its separation from N. hungarica since their dimensions, stria densities, etc. are almost identical.

As noted above, N. granulata seems to belong near N. navicularis. N. punctata may also be closely related to these - it too lacks central raphe endings and has a 1:1 relationship of fibulae to transapical costae - but it differs from them in nowhere having two rows of poroids

between adjacent costae. There is an axial sternum (Peragallo & Peragallo 1897-1908, Pl.69 f.22-25; Hustedt 1930, f.762), although this is non-porose and ill-defined. N. subpunctata (Cholnoky 1960a, f.314) and N. hustedtiana (= N. punctata formae minores: see Cholnoky, op. cit.) are supposed to be closely related to N. punctata, but their small size (N. subpunctata, for example, is only 15-20 x 5-6 µm.) suggests that the possibility should be explored that they may belong in the sect. Lanceolatae. Certain other species also lack central raphe endings and may belong near N. punctata: these are N. adducta (Hustedt 1955), N. balatonis (Cleve & Grunow 1880), N. lanceola (Van Heurck 1880-5), N. lionella (Cholnoky 1960a) and 'Tryblionella querandina' (Frenguelli 1938b).

In N. cocconeiformis, the valve is ± elliptical, with broad 'striae' "composed of rows of very minute puncta (forming transverse and oblique lines as on Pleurosigma angulatum, 26 in 0.01 mm.) interrupted by a central, linear lanceolate, blank space" (Grunow 1880). There is no 'central nodule' and there is a 1:1 relationship between the transapical costae and the fibulae. The structure of the intercostal 'membrane' is unique, but N. cocconeiformis is probably fairly closely related to N. navicularis in view of the raphe and subraphe structure, and the presence of an axial sternum. The diatom described by Meister (1932, f.38-9) as 'Disconeis belawani' is almost certainly N. cocconeiformis: the fibulae are evident on the left-hand sides of the valves illustrated.

There is at least one further grouping within the sect. Tryblionella sensu Hustedt (1930), and this comprises four species - N. graeffei, N. jelineckii, N. rabenhorstii and N. salvadorina - together with various other forms (e.g. N. subcostata and N. bicuneata) when these are considered distinct from N. jelineckii and N. graeffei, and a few

very poorly known species (e.g. N. sulcata)(see Cleve & Grunow 1880, pp.74-77). One species of this group has received attention during the present study, this being found on Grunow's slide 1559a, obtained from the Naturhistorisches Museum, Vienna (F.210-3).

In these species the valve structure seems to be much closer to the 'true Nitzschia' type, i.e. type 1. Transapical costae alternate with single rows of pores. The valves are broad and usually linear, with no central constriction; in a few, however, the valve is ± panduriform (F.210). The fibulae are thin and appear to represent single subraphe costae: the interspaces are broad relative to the fibulae, this providing a contrast with the groups described above (F.210-2, and see Grunow 1863, T.5 f.4; 1880, Pl.12 f.1, 4; Hustedt 1952, f.27). N. salvadorina is unusual in that the striae are 'spatio hyalina medio longitudinali irregulariter definito interruptae' (Hustedt 1952). Whether this may be termed a sternum is doubtful: certainly N. graeffei, N. rabenhorstii and N. jelineckii are without sterna or other interruptions of the striae, although the valve is usually folded (see F.210, 213).

A few species originally placed in the sect. Tryblionella do not belong in any of the groupings described; but some of these undoubtedly belong elsewhere in Nitzschia. Thus, on the grounds of its raphe and valve structure, N. marina may be placed in or near the sect. Fragilariopsis (see Hustedt 1958), and N. creticola should probably follow it. Cholnoky (1957a) placed his new species N. rautenbachiae in the Tryblionellae, but there was little justification for this, as he later recognised (1970): no suitable position has yet been found for this species or the similar N. pseudocarinata. Hustedt's (1952) illustration of N. pulchra suggests that this may have a loculate valve, in which case it might best be transferred to the sect. Panduriformes, even though the 'puncta' are not in decussate rows: the form of the fibulae

supports this suggestion. It is possible that part of the valve of N. inducta may also be loculate (see Hustedt 1952, f.17). N. silicula surely belongs in the sect. Lanceolatae (see Hustedt 1955, Pl.16 f.19, 20).

Various other species have been described, but their taxonomic positions are unguessable: these include N. divergens (Hustedt 1952); N. limicola (Cleve & Grunow 1880, Grunow 1880); N. ardua, N. irritans and N. persuadens (Cholnoky 1961). The illustrations of diatoms claimed to belong to this section are often very poor, which may reflect the difficulty of interpretation of structure in these forms where the LM alone is used.

Thus, concerning the taxonomy of the section Tryblionella (sensu Hustedt 1930) certain changes appear to be in order. Hustedt and others have grossly oversimplified the situation by amalgamating Grunow's four sections (Tryblionella, Apiculatae, Pseudotryblionella, Circumsutae) into one. The result is an extremely heterogeneous collection of forms which must be split into several sections, if not genera.

Grunow's sect. Apiculatae emerges as a valid grouping of species united by their possession of a well-defined axial sternum, similar valve and raphe structure, etc. They should be separated from the sect. Tryblionella. Hustedt's opinions concerning the sect. Circumsutae, however, are justified: its separation from Tryblionella cannot be entertained.

Grunow's Pseudotryblionella contains some forms which belong in the N. tryblionella group, but also others, viz. N. graeffei etc., which do not and themselves form a natural grouping. Grunow specified no type for this section and thus his name might, perhaps, be applied to the latter group, with N. jelineckii or some other as the type, and including N. graeffei, N. rabenhorstii and N. salvadorina. Grunow's name may be misleading, however, in its slight implication of a link

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