

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 Hendey (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

the Sigmoideae, and the second because of the characteristic central deflection of the raphe system in that group (F.289). Grunow's system of classification was used by Van Heurck (1880-5, 1896), Schütt (1896), Peragallo & Peragallo (1897-1908), Karsten (1928), and more recently by Cleve-Euler (1952) and Hendey (1964). At first Hustedt also considered these three groups to be distinct (e.g. see Hustedt 1914), but later he merged first the Sigmata (1930), and then the Obtusae (1956) with the Sigmoideae, so that the classification returned to its 1862 state! Hustedt's reason for combining the Sigmata and Sigmoideae was that these groups were distinguished from one another only by the degree of eccentricity of the raphe system, which he considered insufficient to justify their separation, although at the same time (1930) similar differences were thought enough for the separation of the sects. Bilobatae and Dubiae. In 1955 Hustedt described a new species, N. sigmaformis, which resembled N. sigma in the shape of the valve, but had the deflected raphe system characteristic of the Obtusae. At first (1955) this finding made no difference to Hustedt's thinking about sectional classification, but in the next year he stated that in view of the existence of such forms as N. sigmaformis (which he clearly considered to be intermediate between the 'Sigmata' and 'Obtusae'), the sect. Obtusae could no longer be maintained as separate from the sect. 'Sigmoideae'.

At one stage Hustedt had included another of Grunow's original sections of Nitzschia in the 'Sigmoideae', but the type species of this group, the Spectabiles (first mentioned by Grunow 1862, and see Cleve & Grunow 1880), was subsequently transferred to Hantzschia.

As a result of the changes made by Hustedt, the sect. Nitzschia is large, containing nearly 50 described species: these are listed, with dimensions, etc., in Table 20. Almost any Nitzschia which has a sigmoid frustule can be referred with confidence to the sect. Nitzschia sensu Hustedt (1956), provided that its valves do not possess the

TABLE 20

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Central defl- ection of raphe system	Eccent- ricity of raphe	Sigmoid in valve view?	Sigmoid in girdle view?	Source of information
<u>N. attenuata</u>	99	7	8	22	present	present	+	yes	?	Østrup (1913)
<u>N. austriaca</u>	12-22	1.8-2.4	12	26	absent	absent	+++	yes	no	Hustedt (1959a)
<u>N. clausii</u>	20-55	3-5	10-12	32-38	present	?	+++	yes	?	Hustedt (1930) Hustedt (1938)
<u>N. clausiiformis</u>	70-86	9-9.5	7-8	28-30	present	present	++	yes	?	Gandhi (1962)
<u>N. cryophila</u>	140	6	8	20	present	?	?	yes	?	Cleve (1883)
<u>N. diaphana</u>	70	6	14	26	present	?	0	yes	?	Cleve (1896)
<u>N. falcata</u>	75	4.5	11	very fine	absent	absent	+++	yes	?	O.Müller (1905)
<u>N. fasciculata</u>	45-95	3-6	4-7	30	absent	absent	+++	?yes	yes	Hustedt (1930)
<u>N. filiformis</u>	20-100	4-6	8-11	36	present	present	+++	yes	yes	Hustedt (1930) this thesis
<u>N. firthii</u>	200-380	9-11	4-5	very fine	absent	absent	+	?	?yes	Fuge (1937)
<u>N. flexa</u>	60-160	4-6	7-12	40-45	absent	absent	++	no	yes	Hustedt (1930) A.Schmidt Atlas
<u>N. flexoides</u>	40-103	3-3.5	14-16	over 45	absent	absent	++	no	yes	Geitler (1968b)
<u>N. fussiiformis</u>	163-170	4.8-5	10	? not visible	absent	absent	++	no	?	Pantocsek (1902)
<u>N. geitleri</u>	250-290	7	5-7	45	absent	absent	+	?	yes	Hustedt (1959b)
<u>N. habershawii</u>	300-400	?	6-7.5	28	absent	absent	+++	yes	yes	Boyer (1927) Peragallo & Peragallo (1897-1908)
<u>N. höhnikii</u>	95-116	5-6	6	20	present	present	++/+++	no	yes	Hustedt (1959c)
<u>N. hondoensis</u>	152	10	?	?	absent	absent	++/+++	yes	?	Hanna & Grant (1926)
<u>N. ignorata</u>	50-70	4	8-11	36	present	present	+++	yes	yes	Hustedt (1930)

TABLE 20 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Central defl- ection of raphe system	Eccent- ricity of raphe	Sigmoid in valve view?	Sigmoid in girdle view?	Source of information
<u>N. improvisa</u>	130-165	6-6.5	7	22-24	present	present	+ / ++	no	yes	Simonsen (1960)
<u>N. insecta</u>	50	3	12	22	present	present	+++	no	?no	Hustedt (1942)
<u>N. intercedens</u>	150-300	?	6-7	27-30	absent	absent	+++	yes	yes	Peragallo & Peragallo (1897-1908)
<u>N. irresoluta</u>	70	3	9-12	? (not visible)	?present	absent	+++	yes	yes	Hustedt (1942)
<u>N. knysnensis</u>	150-200	7-8.5	5-6	21-23	present	present	+ / ++	yes	?	Cholnoky (1963a)
<u>N. kurzii</u>	100-140	9	7	30-32	present	present	?	?	?	Cleve & Grunow (1880)
<u>N. laevissima</u>	115-170	6-6.5	6-8	40	present	absent	++	?yes	no	Grunow (1884)
<u>N. leucosigma</u>	100(130)	?	10-13	35-36	absent	absent	+++	no	yes	Benecke (1900) Lewin & Lewin (1967)
<u>N. maxima</u>	600-900	?	3-4	15-18	absent	absent	++	yes	?yes	Peragallo & Peragallo (1897-1908)
<u>N. mirabilis</u>	80-90	6.5-7	5.5	very fine	absent	absent	+++	no	yes	Cleve-Euler (1952)
<u>N. miramarensis</u>	140-150	5-6	5-6	20	present	present	++	yes	?	Hagelstein (1938)
<u>N. oblongella</u>	32-41	5.4	5-6	very fine	absent	absent	0	no	yes	Østrup (1910)
<u>N. obtusa</u>	35-350	4-13	5-11	26-36	present	present	++ / +++	yes	?yes	Cleve-Euler (1952) A. Schmidt Atlas
<u>N. parvula</u>	20-40	3-6	5-8	30-36	present	present	+++	yes	no	Hustedt (1930) Cleve-Euler (1952)
<u>N. parvuloides</u>	30-50	4	7-9	32-36	?present	absent	+++	yes	no	Cholnoky (1955)
<u>N. perlonga</u>	483-500	8-8.5	5	25	absent	absent	++	?yes	no	Pantocsek (1902)
<u>N. prolongata</u>	115-130	3.5-4	5-7	24	present	present	++ / +++	yes	no	Hustedt (1938)
<u>N. pseudosigma</u>	60-100	5	5-6(9)	very fine	absent	absent	+++	yes	yes	Hustedt (1938)

TABLE 20 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Central defl- ection of raphe system	Eccent- ricity of raphe	Sigmoid in valve view?	Sigmoid in girdle view?	Source of information
<u>N. quickiana</u>	70-105	6-7	4-6	37-38	absent	absent	+++	yes	?	Hagelstein (1938)
<u>N. rotula</u>	25-26	4	7-10	38-42	absent	absent	+++	yes	?	Carter (1966)
<u>N. schliephackeana</u>	75-130	8-9	4-5	24	?	?	?	yes	no	Von Schönfeldt (1913)
<u>N. sigma</u>	50-1000	4-15	7-12	22-30(+)	absent	absent	+++	yes	yes	Hustedt (1930) this thesis
<u>N. sigmaformis</u>	75-170	4-5	8-12	30	present	present	+++	yes	?	Hustedt (1955)
<u>N. sigmoidea</u>	160-500	8-14	5-7	23-26	absent	absent	++	no	yes	Hustedt (1930) this thesis
<u>N. subcohaerens</u>	14-45	3-7	9-18	over 30	absent	absent	+++	yes	yes	Cleve-Euler (1952)
<u>N. terryana</u>	200	?	7	25	?	?	?	no	yes	Boyer (1927)
<u>N. valida</u>	270-600	?	4-5	18-19	absent	absent	+++	no	?	Peragallo & Peragallo (1897-1908)
<u>N. vermicularis</u>	90-250	5-7	8-12	30-36	absent	absent	++	no	yes	Hustedt (1930) this thesis
<u>N. vidovichii</u>	100-140	?	8	24-25	present	present	+	no	yes	Peragallo & Peragallo (1897-1908) this thesis

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

- N. ?clausii: (LM, SEM) salt-marsh at Sandbay; the intertidal at Kilve, Somerset.
- N. filiformis: (LM, SEM) River Avon, at the Cumberland Basin, Bristol.
- N. flexa: (LM) material from drainage ditch at Walton in Gordano.
- N. ignorata: (LM, TEM) sediment from puddles at Sea Mills, Bristol; enrichment culture derived from sediment from the R. Wye at Brockweir.
- N. obtusa: (LM, SEM) sediment from Loch Darron.
- var. scalpelliformis: (LM, SEM) fossil sediment cores from the Santorini Islands; Arne creek.
- N. sigma: (LM, TEM, SEM) salt-marsh at Sandbay; tidal creek at Uphill, near Weston-super-Mare.
- N. sigma var.: (LM, TEM, SEM) sediment from puddles at Sea Mills, Bristol.
- N. sigmoidea: (LM, SEM) sediment from the Gloucester & Sharpness canal at Framilode; from a drainage ditch at Berkeley; from various prepared slides (B.M. 23316-7); enrichment culture derived from sediment from the R. Wye at Brockweir.
- Nitzschia sp.B (Eilat): (LM, TEM, SEM) fish-ponds at Eilat, Israel.
- N. vermicularis: (LM) material from drainage ditch at Walton in Gordano; the canal at Framilode.
- N. vidovichii: (LM, SEM) washings from Sargassum at Oahu, Hawaii.

extended apices characteristic of the sect. Nitzschiella.

In the course of the present study various species have been examined, and these are listed in Table 21, together with details of their sources and methods of examination. These species will be considered in turn, prior to a discussion of the taxonomy of the section.

The structure of N. sigmoidea is of especial importance since this species is the type of the genus, and also of the section. N. sigmoidea was first described by Nitzsch (1817), who named it Bacillaria sigmoidea. It received various other names from subsequent authors before Hassall (1845) designated it as the type of his new genus Nitzschia: he gave it the name N. elongata, but this was illegitimate since he ought to have used the earlier epithet of Nitzsch (see also I.C.B.N. 1972, p.247). Nitzsch's original material of 'Bacillaria sigmoidea' has apparently been lost, if indeed he ever made a permanent preparation of it, and so it will be necessary at some stage to select a neotype. Nitzsch's figures (1817, T.6 f.4-6) leave little doubt that his species is the same as N. sigmoidea sensu, for example, Hustedt (1930).

The sigmoid shape of the frustule in girdle view and its straightness in valve view are well shown in Nitzsch's illustrations (T.6 f.5a, b, 6). N. sigmoidea is a large form, up to 0.5 mm. long, easily distinguished from similar diatoms (e.g. N. vermicularis, N. flexa) by its coarser structure (F.322-4, 327-32, and see Table 20). The valve is  $\pm$  linear (F.333), with a moderately eccentric raphe system: it is acutely angled at the raphe, and obtusely, but quite abruptly, at the junction of distal mantle and valve face (F.836). The valve is quite deep, with the proximal mantle deeper than the distal (F.832, 836).

There is a type 1 valve construction in N. sigmoidea (F.832-3, 837, 839), as in all the members of this section. The transapical costae are much deeper than the frets, so that internally the frets are

difficult to observe (F.832), except near the valve apices (F.833, 835). The frets and costae delimit small, roundish poroids (F.837), in which there appear to be hymena lying flush with the outer surface of the valve: indeed, the hymena, frets and costae combine to make it appear as though the valve is covered externally with a 'skin' of silica (F.832, 834-5).

A quite unexpected discovery was that the valve possesses external, non-porose flaps of silica (F.832, 836, 838), like those of N. dissipata, N. spathulata, etc., although in favourably positioned valves the presence of these flaps can be detected by light microscopy (F.328). The external canals delimited by these flaps are more flattened in cross section than are those of N. spathulata, and do not open to the exterior at the poles (F.834-5). The edge of the flap is not fused to the valve, but is very tightly appressed to it (F.832, 838). The valve striae continue beneath the flaps, unbroken: in N. sigmoidea, unlike the other species in which such flaps have been found, there is no differentiation of that part of the valve which underlies the flap (F.839) - in N. recta, for example, the frets in this part are much larger than elsewhere (see F.886).

The raphe is continuous from pole to pole. The raphe fissure is very deep, and opens externally onto the apex of a narrow ridge (as in some N. spathulata), which is visible in the light microscope as a plain strip of silica extending out from the subraphe canal walls (F.327-8, 838). Internally at the poles there are simple helictoglossae (F.833); externally the raphe fissure curves off and ends very near the valve margin (F.834-5).

There is a well-defined subraphe canal whose exterior walls are porose (F.836, 838). These poroids are arranged in transapical rows which represent extensions of the valve striae (F.837-9). Near the poles the slit into the subraphe canal becomes narrower transapically



(compare F.833 with 839), as in N. dissipata, N. recta and Nitzschia sect. Spathulatae.

The fibulae of N. sigmoidea are large in relation to the transapical costae, and must be classified as being of type vii (see section 4.6.3.5)(F.833, 837, 839). Proximally and distally the fibulae spring from longitudinal ridges, such that portulae are delimited at the inner sides of the interspaces (F.833, 839). At least on the distal side of the raphe, there is also a second longitudinal ridge, nearer to the raphe than the first and separated from it transapically by two or three poroids. At this level, then, there is a second, outer portula, though this is less well-defined than the other.

The cincture of N. sigmoidea has not been studied intensively, but appears to consist of several bands, each bearing several transverse rows of poroids (F.327).

The chromatophores are arranged as in the majority of Nitzschia species (a type 1 arrangement) and occupy most of the length of the diatom (F.320-1). The plates lie against one side of the girdle and one valve face, but frequently lobe under the raphe onto the other valve. The Bütschli globules are small (unpubl. obs.). The elongate nucleus, which lies centrally, next to a widening in the cleft between the chromatophores, was studied in detail by Lauterborn (1896), who noted several nucleoli to be present (op. cit., T.3 f.23).

N. vermicularis (F.323, 329-30) and N. flexa (F.324, 331-2) seem to be very similar to N. sigmoidea in valve construction. In these species also there is no sign of central raphe endings, and the fibulae are very like those of N. sigmoidea. The frustules are sigmoid only in girdle view, and in all three the valves hardly diminish in depth from centre to pole. Thus, since the cincture is of constant width, the frustule is as wide near the poles as elsewhere - in girdle view it is 'parallel-sided'. In N. flexa and N. vermicularis lines may be observed

with the light microscope (e.g. see F.330) which run parallel to the raphe: these almost certainly indicate the presence of external flaps. Other aspects of valve structure, together with the chromatophore arrangement, also suggest close links between these species and N. sigmoidea (for chromatophore data, see F.325-6, Pfitzer 1871, Heinz-erling 1908).

Hustedt (1930) stated that the transapical striae of N. flexa are 'Äusserst zart, kaum erkennbar.' Specimens of this species obtained from a ditch at Walton in Gordano, Co. Avon, had 44 striae in 10  $\mu\text{m}$ ., visible only with blue light, the condenser being oiled (obj. apert. N.A. 1.3)(F.332).

The specimens of N. sigma observed had 21 striae and 6-8 fibulae in 10  $\mu\text{m}$ . (F.302), while the smaller diatom, here called 'N. sigma var.', had 33-34 striae and 10-11 fibulae (F.303-4). The latter organism is quite common, but does not seem to correspond to any described taxon.

One of the most obvious features of both N. sigma and N. sigma var. is that their frustules are sigmoid in both girdle and valve aspects (F.299-300). This separates these diatoms from N. sigmoidea and its allies. Moreover, the valves (and cincture?) diminish in their per-valvar dimension from centre to pole, so that the frustule is not parallel-sided in girdle view (F.299, 840). The valve is relatively shallow (F.848, 850) and the proximal mantle is only feebly developed. The raphe system is strongly eccentric (F.302-4).

The valve construction, though of type 1, is dissimilar to that in N. sigmoidea. In N. sigma and N. sigma var. the frets are much more strongly developed than in that species, and are almost as deep as the costae (F.844-6, 848, 850). Furthermore, the frets are widely spaced, so that the poroids are easy to resolve with the LM, even in the more delicate N. sigma var. (F.302, 304). Each poroid opens to the interior of the valve by a small, transapically elongate aperture (F.845-6, 850).

The valve transapical costae are somewhat triangular in section, diminishing in width towards the exterior of the valve, while the frets appear to increase in width from inside to outside (F.845), so that the external aperture of each poroid is larger than the internal, and is oval, being only slightly elongated transapically (F.844, 848). There is no evidence that the areolae are appreciably constricted at the outside of the valve, and so, although each areola is quite deep, it cannot be termed a loculus (sensu Anon. 1975). Over the valve there is often a certain amount of variation in the relative thicknesses, depths, etc. of frets and costae: generally the frets are more feebly developed near the raphe and reach their maximum size relative to the costae near the apical plane (F.844). Such variation is more pronounced in N. sigma than in N. sigma var.

Each poroid of N. sigma contains a cribrum (F.543, 847), which can just be made out using the SEM. These cribra were illustrated by Hendey (1964, TEM observations), who failed, however, to note the hymena present in each of the circular or oval pores of this structure (F.543). The hymen pores are arranged in a subregular manner. In N. sigma var. there are no cribra; hymena are present, though, and in these the pores are again arranged subregularly, almost in hexagonal array (F.539). The lack of cribra in N. sigma var. lends credence to the hypothesis concerning the occurrence of these structures propounded during discussion of infraspecific variation in Hantzschia marina, provided, of course, that N. sigma var. is accepted to be very closely related to N. sigma. The cribra and/or hymena lie near the inside of the poroids (contrast N. sigmoidea).

In neither of the taxa under consideration are there any external flaps of silica (F.844, 848); nor is there a marginal ridge.

The raphe is without central endings. The external fissure opens onto the crest of a narrow ridge, which in N. sigma, but not in N. sigma var., is flanked on either side by grooves (F.842, 844). At the

poles, internally there are prominent helictoglossae (F.843, 849); externally the fissure continues past the helictoglossa with very little change in direction, and reaches almost to the margin of the valve pole (F.841, 851).

There is a well-defined subaphe canal, raised above the general level of the valve (F.841, 844, 848, unpubl. obs.). The poroids in the canal walls, for the latter are porose, are smaller than those of the valve face and their hymena lie nearer the outer surface of the valve. They are arranged in transapical rows, one row lying opposite each stria of the valve face (or proximal mantle): there are more poroids per row in the canal walls of N. sigma than in those of N. sigma var. (F.842, 848, 851, unpubl. obs.).

The fibulae of both taxa are very similar and seem to represent single subaphe costae, although the exact relationship between fibulae and costae is obscured by the morphology of the fibulae themselves, since, as in N. sigmoidea, portulae are formed at two levels (F.843, 845-6, 849-50). The inner portulae are formed at the inner edges of the fibulae: they are delimited by flange-like extensions of the fibulae and by two longitudinally orientated ridges, joining the proximal and distal fibula bases. These portulae are oval or somewhat rectangular in shape - contrast N. sigmoidea, where the interspaces are much larger relative to the fibulae, so that the portulae are usually rectangular and often broader in the apical direction than in the transapical. Between the inner and outer portulae each fibula narrows abruptly (F.846, 850) to the width of a single transapical costa, as in N. sinuata and Nitzschia sp. (Hawaii)(sects. Grunowia and Dubiae). The outer portulae are formed in a similar fashion to the inner, but are a little smaller.

The cincture of N. sigma is composed of open bands, which are unperforate (F.842).

The chromatophores are similar to those of N. sigmoidea in extent

and positioning (F.308-9, 315). In N. sigma the chromatophore margin is frequently extensively lobed (F.309-12), and most of the frustule is underlain by plastid. It has already been mentioned (section 4.6.5) that N. sigma (and N. sigmoidea) each possess several elongate pyrenoids: in N. sigma var. there is probably only one per chromatophore. Both N. sigma and N. sigma var. possess large, prominent Bütschli globules (F.308-10, 315).

The two chromatophores are separated centrally by a narrow cleft which is sometimes wider at its centre (F.308-10, 313, 315). The nucleus is located just above this cleft and projects into the cell lumen (F.313): in girdle view it is more or less circular in outline. The nucleoplasm is granular and stains quite well with aceto-carmin (F.314).

A sigmoid species of Nitzschia having almost the same shaped and sized valves as N. sigma var. (compare F.319 with 303-4) was often found in salt marsh samples. It could easily be separated from N. sigma by the presence of central raphe endings, and from its dimensions, striation density, etc. (48 x 5.5  $\mu\text{m}$ . with 12-13 fibulae and 29 striae in 10  $\mu\text{m}$ .) it seems likely that it belongs in N. clausii; the identification, however, is not certain.

Another species whose identity is not known was found in a sample from Eilat, Israel. The extreme length of this form (around 700  $\mu\text{m}$ .) puts it outside the size ranges of most of the sect. Nitzschia: those species which do attain such lengths, viz. N. maxima, N. sigma, do not agree with the Eilat form in other characters, e.g. linear densities of fibulae and striae, presence of a central nodule. This species will be referred to as Nitzschia sp.B (Eilat).

N.?clausii is sigmoid in valve view (F.319) and also in girdle view. The valve is quite shallow, as in N. sigma (F.857, unpubl. obs.). In the proximal half of the valve face the costae project outwards much further than the frets, while distally the costae and frets are of

the same height (F.856). The poroids are elongated transapically, and are closed by hymena, placed centrally or perhaps slightly nearer the inner ends of the poroids (F.856-7).

There are no external flaps of silica (F.856), and the valve is not very strongly angled at the raphe, which is strongly eccentric. In some cases there is a partial marginal ridge (F.859).

N. ?clausii has a 'central nodule', visible using the LM (F.319), and a wider separation of the median pair of fibulae. Therefore it is not surprising that the SEM reveals that the raphe is interrupted centrally (F.857-8), the endings being coaxial-symmetrical both internally and externally. Internally there is a structure resembling a double helictoglossa.

The external fissures are not bordered by flanges. At the pole the terminal fissure extends to near the valve margin, where it bends abruptly and then continues parallel to the margin for a short distance (F.859). It is not yet known whether distal and proximal curvatures are both to be found: so far, only distal curvatures have been observed. Internally there is a simple helictoglossa (F.860).

The fibulae are of type vii (F.857). Longitudinally orientated ridges join the fibula bases both proximally and distally, but, in contrast to N. sigmoidea and N. sigma, portulae are formed at only one level. The fibulae are broad in the apical direction, but quite thin (F.857, 860).

There is a well-defined subraphe canal, raised slightly above the general level of the valve (F.856, 858-9). The walls of this canal are porose, with one small, round poroid opposite each transapical stria (F.856-9).

Some at least of the bands bear one transverse row of poroids, placed near the junction of pars interior and pars exterior (F.859, unpubl. obs.).

The chromatophores are similar to those of N. sigma (F.316, and see also Pfitzer 1871).

Nitzschia sp.B (Eilat) is a remarkable form since although the valve may be around 700  $\mu\text{m}$ . in length, it is not more than 10  $\mu\text{m}$ . wide. The frustule is linear, hardly diminishing in depth or width until near the poles, and it is only here that there is any curvature, giving the frustule a sigmoid twist in girdle and valve views (unpubl. obs.).

As in N.?clausii, the valve is quite shallow (F.852-3). The valve is not sharply angled at the raphe, but bluntly rounded (F.854). It is constructed of transapical costae and frets (a type 1 construction), with no sterna nor marginal ridge. The frets are of the same depth as the costae, these elements together delimiting round poroids (F.853). There are 7 fibulae and 26 costae in 10  $\mu\text{m}$ ., with 26-27 poroids in 10  $\mu\text{m}$ . transapically (F.317-3). Towards the distal margin it often appears from the outside as though the poroids are more widely spaced than elsewhere (F.854-5), but this is probably a consequence of the curvature of the valve, since internally there is no such change in spacing (F.852). The hymena, which are placed approximately centrally in the poroids, are of the centroid type, with the pores arranged in concentric circles about the centre of the hymen (F.545, 548). The area immediately around the centre is non-porose, but it is no thicker than the remainder of the hymen.

The raphe is interrupted centrally (F.317), the endings being coaxial-symmetrical both internally and externally, as in N.?clausii: the ends of the external fissures, which lie in a slight depression of the valve surface, are somewhat expanded, while the internal fissures end in a 'double helictoglossa' (F.852, 854). The central interspace is larger than the others, both transapically and apically (F.317). Near the poles the raphe veers away from the proximal margin (F.318), and comes near to the distal margin before curving around the valve apex until it points back along the valve: the terminal fissure is thus

in the form of a hook (F.855).

The fibulae are similar to those of N. ?clausii, except that they often extend past the longitudinal ridges onto the valve face or proximal mantle (F.853). These extensions are short, and take place along one or several transapical costae; thus it may be that each fibula represents one or more fused subraphe costae. The interspaces are circular or oval in outline, as viewed from the valve interior, and of variable size.

There is a fairly well-defined subraphe canal, which is not raised above the general level of the valve (F.852, 854). Externally the junction of canal wall and valve face is marked by a line of transapically elongate pores, which appear to be the external openings of the first row of poroids on the valve face, i.e. that row immediately adjacent (internally) to the distal longitudinal ridge (F.854). Proximal to the raphe there is another line of elongate pores, which are the external openings of the first row of poroids on the proximal mantle. Within the subraphe canal there is one longitudinal row of poroids on each side of the raphe: these poroids are usually slightly smaller than those of the valve face - there is one poroid inside the canal opposite each transapical stria (F.853-5).

The cincture and cytology of Nitzschia sp.B (Eilat) are unknown.

N. obtusa, N. obtusa var. scalpelliformis, N. filiformis, N. vidovichii and N. ignorata may be dealt with together since they are very similar in form and structure. Before entering into a discussion of these forms, however, it is necessary to make two points, concerning the identification of N. obtusa and N. ignorata.

A great variety of different forms is referred to N. obtusa (see Hustedt 1930, Cleve-Euler 1952) and it is by no means clear that all these belong together. Hence the var. scalpelliformis is treated separately in this account, while 'N. obtusa' is taken to refer to some



long and narrow (110 x 4  $\mu\text{m}$ .) forms with strongly sigmoid, linear valves and bluntly rounded apices (F.287-92, 361).

A form with 9-11 fibulae and around 40 striae in 10  $\mu\text{m}$ . (F.305-6), observed in samples from a puddle at Sea Mills, Bristol, has been tentatively identified as N. ignorata. It is somewhat smaller than Hustedt (1930) allows for this species (32-35 x 3.3  $\mu\text{m}$ . as against 50-70 x 4), with finer striation (Hustedt's forms had 'etwa 36 in 10  $\mu\text{m}$ .'). Lund (1946) described some diatoms from soil which he referred to N. ignorata, and these had 34-38 striae in 10  $\mu\text{m}$ . and were only 31-44  $\mu\text{m}$ . in length, so perhaps the Sea Mills specimens are not exceptional. I have found some other forms, again with 10-12 fibulae and around 40 striae in 10  $\mu\text{m}$ ., and with a shape like that of the Sea Mills specimens, but measuring only 20 x 3  $\mu\text{m}$ . (F.307), in an enrichment culture derived from a sediment sample from the R. Wye, near Brockweir. These also would seem to belong near N. ignorata.

All the taxa of this group, except N. vidovichii, are sigmoid in valve view (F.289, 297, 305-7, unpubl. obs.), although in N. filiformis this can be difficult to detect. N. vidovichii is quite straight in valve view, but resembles the other species in being sigmoid in girdle view (Grunow 1862, T.18 f.32). The valve shape of N. obtusa has already been described; the valves of N. obtusa var. scalpelliformis and N. ignorata (F.305-7) are  $\pm$  linear, with fairly acute apices, while N. filiformis is linear-lanceolate with bluntly rounded poles (F.297). N. vidovichii is linear or linear-lanceolate with broad apices (F.293-5).

In all, the valves are fairly shallow, and are without sterna or marginal ridges (F.862-6; 867, 869; 873, 876; 880-1). The raphe may be nearly central (N. vidovichii, F.293-6) or eccentric (N. obtusa and var. scalpelliformis, N. filiformis, N. ignorata: F.289, 297, 305, etc.), but in either case the valve is not acutely angled at the raphe.

Throughout, the valve construction is of type 1 (F.865-6, 869,

871, 873, 877, 880-1, 885). There is variation between the species, however, in the relative development of costae and frets, in the shape of the poroids, etc. In N. obtusa and its var. scalpelliformis the frets are of only slightly less depth than the costae: both come to the same level externally (F.865-6; 867, 869). The poroids are slightly elongated transapically. The hymena were absent from the valves of both these taxa, and so their position is unknown. In N. obtusa the external aperture of each poroid is slightly smaller than the internal (compare F.865 with 866). N. filiformis is similar to N. obtusa, except that the external aperture of each poroid is even smaller relative to the internal aperture (compare F.880 with 881): the internal apertures are again elongated transapically. The hymen lies near the inner end of each poroid (F.880, 883).

The construction of N. vidovichii is somewhat different. Here the frets are considerably smaller than the costae, and lie nearer the outside of the valve than the inside (F.873, 877). The poroids are small relative to the costae and are  $\pm$  round (F.873, 875), except near the valve apex. From the inside of the valve it is difficult to distinguish anything except the massive transapical costae: only in fractured valves is it possible to determine the valve structure accurately (F.877). The hymena have not been observed.

The structure of N. ignorata is known only from TEM observations, which indicate that the internal apertures of the poroids are elongated transapically, while the external apertures are more circular, and slightly smaller (F.544, 885, unpubl. obs.). The hymena lie near the internal apertures and have a subregular arrangement of pores, or a more or less centroid pattern in the circular poroids of the subapical canal walls (F.544).

As mentioned before, the members of Grunow's sect. Obtusae were distinguished from other sigmoid Nitzschia species by their possession

of a raphe system which is deflected centrally, towards the distal margin. All the taxa under consideration have such deflected raphe systems (e.g. F.289, 293), although the deflection is more or less obvious, depending on the species; in N. filiformis and N. ignorata (which are in any case small diatoms) the deflection is small, but nevertheless present (F.297, 305-6, 879, 885). The deflection is correlated with the presence of noncoaxial-symmetrical central raphe endings. The internal central endings (F.863, 870-1, 880), apart from their lack of 'coaxialness', are very similar to those of N. ?clausii or Nitzschia sp.B (Eilat), or many other Nitzschia species, but the external endings are very characteristic, unlike those of any other member of the Nitzschiaceae except, perhaps, N. debilis (F.865, 875, 881, 885). These have already been described (section 4.6.3.3), but it may be noted that the 'central fissures' always end along striae of the valve face, usually along the central pair (e.g. F.865). The fissures thus interrupt the normal pattern of costae and frets, and are underlain by a non-porose extension of the raphe sternum which is often visible in the light microscope (F.290, 292, 296, 298).

At the poles the internal raphe fissures end in simple helictoglossae (F.862, 872, 876, 884). However eccentric the raphe-slit is over most of its length, the helictoglossae always lie in the apical plane: thus it may be observed that in N. obtusa and N. filiformis, where the raphe is for the most part strongly eccentric, near the poles it becomes less so, moving from its position close to the junction of proximal mantle and valve face onto the latter (F.291, 297, 862, 864, 882, 884).

The taxa vary inter se in the length and course of the terminal fissure. Thus, while N. obtusa var. scalpelliformis (F.868) and N. vidovichii (F.874) have ± hooked fissures like that of Nitzschia sp.B (Eilat), in N. obtusa (F.864) and N. filiformis (F.882) the outer fissure is merely deflected a little near its end. In N. filiformis

distal and proximal curvatures have been noted (unpubl. obs.): both are probably present in the other taxa also, but so far only proximal curvatures have been noted in N. obtusa var. scalpelliformis, and only distal in N. obtusa and N. vidovichii.

In all of these species the fibulae are broad apically, much wider than the transapical costae, and spring both distally and proximally from longitudinal ridges. In N. obtusa it seems that each fibula is composed of occasionally two, usually three fused subraphe costae: this is suggested by the slight extension of each fibula past the distal, or proximal, longitudinal ridge, along two or three transapical costae (F.862-3, 866). In N. obtusa var. scalpelliformis (F.867, 871-2) and N. filiformis (F.880, 884) the fibulae are similar to the above, although the relationship between fibulae and costae is less obvious. N. vidovichii, on the other hand, has such strongly developed longitudinal ridges that the fibulae to a large extent lose their individuality (F.876-8). All have porulae at only one level, and while the fibulae are wide apically, they are thin in a direction perpendicular to the raphe sternum. The interspaces are oval or circular in outline.

A subraphe canal may be distinguished, but, as in Nitzschia sp.B (Eilat), it is not set above the general level of the valve. Indeed, in N. vidovichii the canal is somewhat depressed, and the transapical costae of the valve face (proximal and distal halves) continue without interruption or deflection right up to the raphe-sternum (F.873, 875-6, 878).

On the distal side of the raphe, at the junction of valve face and subraphe canal wall, is a line of transapically elongate 'pores' or grooves (these were noted by Cox 1975c, in N. filiformis) (F.865, 869, 881). Into each groove open one poroid of the valve face and one poroid of the canal wall (F.883 and unpubl. obs.). In the canal wall, opposite each groove, there is also another poroid, of the same size

or slightly smaller than the poroids of the valve face (F.864-5, 868-9, 881-2): each distal stria, then, is represented within the canal by two poroids, one opening directly to the exterior of the valve, the other opening into the groove (see also N. ignorata, F.885). N. vidovichii is slightly different in that both poroids of the canal wall open into the groove (which is less well defined because of the relative heights of costae and frets in this species: F.873, 875). In N. filiformis the grooves merge into one another slightly near the centre of the valve (F.881).

Proximal to the raphe the structure appears similar (e.g. F.381), but it is not clear how many poroids enter the grooves, which are much smaller than those on the distal side. As might be expected from the almost central position of the raphe in N. vidovichii, there is little difference in this species between the proximal and distal sides (F.873, 875).

In all, the canal walls are rounded and lack ridges bordering the raphe (contrast N. sigmoidea, N. sigma).

The first bands of N. vidovichii (F.873, 875-6) and N. filiformis (unpubl. obs.) each bear one transverse row of poroids, placed near the junction of pars interior and pars exterior; the pars interior of N. vidovichii has an entire margin (F.876). Along the valve margin of N. vidovichii is a row of short, transapically orientated ridges: perhaps these have something to do with the interlock between valve and first band.

Type 1 chromatophore arrangements are present in N. obtusa (Mereschkowsky 1903a), N. obtusa var. scalpelliformis and N. filiformis (unpubl. obs.), and N. vidovichii (Mereschkowsky 1901, 1903a).

Thus, on the basis of frustule and valve shape and symmetry, valve, raphe and subraphe structure, and cincture structure (as far as this is known), it seems possible to distinguish four groupings among

the species described above. These are

1. N. sigmoidea, N. vermicularis and N. flexa: this group corresponds to Grunow's sect. 'Sigmoideae'.
2. N. sigma and N. sigma var., representing Grunow's sect. Sigmata.
3. N. obtusa, N. obtusa var. scalpelliformis, N. filiformis, N. ignorata and N. vidovichii, which were all formerly contained in Grunow's sect. Obtusae.
4. N. ?clausii and Nitzschia sp.B (Eilat), which represent a grouping of sigmoid Nitzschia species which has not been recognised previously.

A review of the literature suggests that there are no other major lines of variation within the sect. Nitzschia besides those listed above. Many of the species referred to this section are poorly described; given below is an account of most of the species traditionally ascribed to the sect. Nitzschia, with comments on their probable taxonomic positions.

N. flexoides was described by Geitler (1968b), who found it growing in the mucilaginous masses produced by the ciliate Ophrydium versatile. It is sigmoid only in girdle view, and has a shape like that of N. sigmoidea. It lacks central raphe endings and would seem to belong in the N. sigmoidea group.

N. falcata, described by O.Müller (1905) and referred to the sect. Sigmoideae, sensu Grunow, is strangely twisted; perhaps it is an abnormal form of some other diatom - Müller found it only once.

N. fussiiformis has valves with extended apices, as in the sect. Nitzschiella (see Pantocsek 1902, T.10 f.256). Pantocsek's illustration does not show the valve as being sigmoid, and there is no mention in his description of any sigmoidity in the frustule. He stated clearly, however, that this species belongs in the 'sect. Sigmoideae' (sensu Grunow); until type material can be examined, no further comment is possible.

In 1937 Fuge described a large sigmoid species of Nitzschia which he named N. firthii. He found this in Chinese canned fish and concluded from this that it must be marine, although the species found with it (including Bacillaria paradoxa, N. obtusa, N. sigma, N. granulata and Gyrosigma fasciola) would allow of a brackish habitat. N. firthii has an almost central raphe system, with no sign of central raphe endings. It appears from Fuge's f.1 that the frustule is sigmoid in girdle, but not in valve view, as in N. sigmoidea. Moreover, the fibulae are large and widely spaced in relation to the transapical costae, and so a classification near N. sigmoidea would seem quite likely. A very similar diatom, N. geitleri, was found by Hustedt (1959b) in plankton from the Neusiedler See in Austria. The waters of this lake have a strange chemistry (ibid.), and allow the growth of brackish water diatoms, e.g. Rhopalodia gibberula, Bacillaria paradoxa, N. sigma, as well as fresh-water forms, e.g. N. dissipata, N. acicularis, N. sigmoidea, etc., so it is not inconceivable that N. firthii could grow here. The dimensions of the valves, the delicate valve structure, the position of the raphe, etc., all support a combining of Hustedt's N. geitleri with N. firthii (see Table 20).

Østrup's N. oblongella (1910) is a small form, sigmoid in girdle but not in valve view. Though it has only 5-6 fibulae in 10  $\mu$ m., the striae are very fine, a situation uncommon in the N. sigma, N. obtusa and N. ?clausii groups. There is no sign of central raphe endings, and thus a classification in the 'Sigmoideae' would seem likely.

Apart from N. schliephackeana, which is known to me only from the rather poor description in Von Schönfeldt (1913) and needs further investigation, no other forms seem to be referable to the 'Sigmoideae'.

Turning now to the N. sigma group, it is probable that N. habershawii, N. intercedens, N. maxima, N. valida and N. pseudosigma are all very close to N. sigma: indeed, N. habershawii and N. intercedens

are sometimes considered to be varieties of N. sigma (Peragallo & Peragallo 1897-1908). All have a similar frustule shape, valve construction and fibula morphology, if the drawings by Peragallo & Peragallo (op. cit.) and Hustedt (1938) are accurate.

N. fasciculata is very similar to N. sigma in frustule shape (compare Hustedt 1930, f.815a, b with 813), but differs in fibula morphology and in the arrangement of the 'puncta', which are strictly in quincunx. There are no central raphe endings and on the whole this species would seem to fit comfortably into the 'Sigmata'. The 'puncta' are probably poroids, not loculi (cf. N. vulpeculoides, sect. Dubiae).

N. hondoensis was said by its authors, Hanna & Grant (1926), to belong 'to a group of which N. sigma ... is the more familiar', and certainly their illustration (Pl.21 f.5) supports this contention. This diatom needs further study to determine the ranges of the stria and fibula linear densities, since this information was not provided in the original description.

The apochlorotic species N. leucosigma was illustrated (TEM and LM) by Lewin & Lewin (1967). Their f.3 shows that this diatom is straight in valve view, while f.4 and 5 show it to be strongly sigmoid in girdle view. At first sight this would appear to suggest that this species is related to N. sigmoidea, but the valve is without external flaps and a close examination of the girdle aspect shows that this form resembles N. sigma in that the frustule tapers in its perivalvar dimension, from centre to apex. There are no central raphe endings. The fibulae seem to be simpler than those of N. sigma or N. sigma var., but nevertheless this species is probably best placed in the 'Sigmata' as, indeed, was suggested by Lewin & Lewin.

Cleve-Euler's N. mirabilis (1952) is not well illustrated. It does not appear to possess central raphe endings, but the valve construction and fibula morphology cannot be guessed. It is sigmoid only in girdle view, and while Cleve-Euler placed it in the 'Sigmata', its



true position may be elsewhere.

N. quickiana was described by Hagelstein (1938) from a mangrove swamp at Miramar in Porto Rico. Hagelstein, unlike Hustedt, did not separate the species of Nitzschia into sections, and he made no comments about the taxonomic position of his new species. Nevertheless, his description and illustration (a photograph, Pl.8 f.14) give several clues to its affinities. The frustule is sigmoid in valve view (the valve outline being similar to that of N. sigma), the raphe system is strongly eccentric, and there is no sign of central raphe endings. The valve construction seems to be very similar to that of N. sigma, except that the transapical costae are more closely spaced (37-38 in 10  $\mu$ m.). The poroids can be resolved with the light microscope and form oblique as well as transapical rows: there are 28 oblique rows in 10  $\mu$ m. From Hagelstein's figures for the spacings of the transapical and oblique rows, it seems likely that the poroids are elongated transapically since even if the 'oblique' rows were in fact aligned parallel to the apical plane, the distance between adjacent frets would be 1.36x the distance between adjacent costae. Hagelstein also noted that 'at intervals there are more strongly emphasized striae, which break the striae into a series of sections'; the same phenomenon may be noted in some forms of N. sigma (unpubl. obs.). There is no indication that central raphe endings are present. The fibulae are large relative to the costae and appear to resemble those of N. sigma more than those of N. sigmoidea or N. obtusa. It is fairly clear from Hagelstein's micrograph that portulae are formed at the inner edges of the fibulae, as in N. sigma, and that these portulae are somewhat oval in outline. In all, N. quickiana would seem to belong in the 'Sigmata'.

N. subcohaerens was classified in the sect. Sigmata sensu Grunow by Peragallo & Peragallo (1897-1908) and Cleve-Euler (1952). This species grows in mucilage tubes (teste Grunow 1879) and requires study. It is a fairly small form (see Table 20), sigmoid in valve and girdle

views. It does not appear to possess central raphe endings, but perhaps these could have been overlooked in such a small diatom.

N. terryana is known to me only from the description in Boyer (1927) who placed it in the 'Sigmata'. There is insufficient information in this description to permit any speculation concerning its position.

There are many species which, by their possession of a centrally deflected raphe system, may be thought likely to belong near N. obtusa. These vary from forms in which the raphe is nearly central (N. improvisa and N. knysnensis) to those where the raphe is strongly eccentric (N. parvula and N. sigmaformis). Valve structure, raphe structure, and fibula morphology seem to be very similar in N. h hnkii (Hustedt 1959c, T.1 f.6, 7), N. improvisa (Simonsen 1960, T.2 f.19-20a), N. knysnensis (Cholnoky 1963a, f.92), N. miramarensis (Hagelstein 1938, Pl.8 f.4, 5) and N. prolongata (Hustedt 1938, T.41 f.28): these species also resemble the forms described in detail above, belonging to the N. obtusa group. The illustrations of N. miramarensis and N. improvisa show the interruption of the striae opposite the central raphe endings. In all these species the fibulae are broad relative to the transapical costae, as in N. obtusa. In N. sigmaformis the fibulae are perhaps a little more slender (Hustedt 1955, Pl.16 f.2, 3), but otherwise the valve and raphe structure of this diatom are as in the above.

 strup (1913) described a new species, N. attenuata, which must apparently be classified in the N. obtusa group because of its centrally deflected raphe system.  strup's illustration is not detailed enough to allow of further discussion, except to note that its raphe is not very eccentric.

N. clausiiformis (Gandhi 1962, T.125 f.57) is not sufficiently distinct from N. obtusa var. scalpelliformis (to which Gandhi notes a resemblance) to justify separation at specific level. The dimensions of the valves and the linear densities of fibulae and striae fall

within the ranges allowed in N. obtusa by Hustedt (1930), and Gandhi's two diagnostic characters separating N. clausiiformis from N. obtusa - 'more clearer striae and the apices constricted and subcapitate' - are surely inadequate: the apices of diatom valves are often very variable within a species as a result of size diminution during vegetative division (see, for example, Lund's 1946 series of valves of N. hantzschiana).

N. diaphana was described by Cleve (1896), and possesses a central raphe system with a distinct central nodule. On the basis of the presence of the latter, Cleve referred this species to the N. obtusa group, but since the raphe system is not at all deflected, this conclusion must be held in some doubt until SEM studies can be undertaken. If the distinctive external central endings of the raphe characteristic of the 'Obtusae' were to be found, Cleve's conclusions would seem quite plausible, but otherwise N. diaphana would seem better placed near N. ?clausii and Nitzschia sp.B (Eilat).

Cholnoky's N. parvuloides (1955) also has a central nodule, although this is not evident in his illustrations (1955, f.72-3), but again there is no central deflection of the raphe system, and so a classification near N. obtusa seems unlikely. This species and N. parvula require study, and may belong near N. ?clausii.

N. kurzii was placed in the sect. Obtusae by Grunow (in Cleve & Grunow 1880), but this species is not well known.

N. perlonga was poorly illustrated and described by its author, Pantocsek (1902), and there seems to be no particular reason why he placed it in the Obtusae.

Hustedt (1942) described a new species of the sect. Lanceolatae, N. insecta, which had a central deflection of the raphe system 'die auf eine Annäherung an die Gruppe der Nitzschiae obtusae hindeutet.' In view of the great variation in the degree of sigmoidity within the N. obtusa group, from the strongly sigmoid forms, e.g. N. sigmaformis,

through such types as N. filiformis, to N. vidovichii, which is straight in valve view and only slightly sigmoid in girdle view, it seems more satisfactory that N. insecta should be placed in the 'Obtusae'. Hustedt did not mention whether he had observed this diatom in girdle view, and so it may be that this species will yet be found to exhibit some degree of sigmoidity: unlike N. vidovichii, however, the raphe is strongly eccentric. N. amplexans, also described by Hustedt (1957), may belong in the 'Obtusae' for similar reasons. It too has a strongly eccentric raphe system.

Besides N. diaphana and N. parvuloides, there are a couple of other forms which may belong near N. ?clausii and Nitzschia sp.B (Eilat). The first, N. laevissima, was described by Grunow (1884). It has a frustule which is sigmoid in valve view only, and a raphe which is almost certainly interrupted centrally - Grunow noted and illustrated a 'central nodule' and a wider separation of the median pair of fibulae (op. cit., T.1 f.65, 66). There is no central deflection of the raphe system.

The other species, N. irresoluta, described by Hustedt (1942), is fairly similar, but smaller and more strongly sigmoid. Again, there is always a wider separation of the median fibulae, indicating the presence of central raphe endings.

Finally, N. lorenziana must be mentioned, although it is usually placed in the sect. Nitzschiella (e.g. by Hustedt 1930). The valve poles can hardly be said to be protracted in the same way as those of N. acicularis or N. longissima, however, and N. lorenziana is sigmoid in both girdle and valve views. There is no sign of central raphe endings, and the raphe is strongly eccentric. The valve is, in fact, very similar to that of N. sigma, except that it is much thinner (compare Hustedt 1930, f.813 with 820). The striation of the valve is coarse (contrast

most Nitzschiellae) and it would seem likely that this species is closely related to the 'Sigmata'.

Thus, from a light and electron microscopical study of various species, together with a review of other species described as belonging to the sect. Nitzschia, it seems that four groupings may be distinguished. Three of these correspond to groupings previously recognised by Grunow (in Cleve & Grunow 1880) and named by him the 'Sigmoideae', 'Sigmata' and 'Obtusae', and it is suggested that these should be reinstated as sections of Nitzschia, although the first must be called 'sect. Nitzschia' since it contains the type. This section, containing species with external flaps of silica and a fairly characteristic raphe and subraphe structure, may be more closely related to the sects. Dissipatae (sensu stricto) and Spathulatae than to other groups of sigmoid Nitzschia species. The members of the 'Sigmoideae' all have uninterrupted raphes: the remainder of the sigmoid Nitzschia species lacking central raphe endings seem to fit fairly comfortably into the 'Sigmata'.

The 'Obtusae' reemerges as a valid grouping. As was explained earlier, Hustedt combined the sect. Obtusae with the other sigmoid groups largely because of the similarity in valve shape between N. sigmaformis and N. sigma. But valve shape is a poor criterion to use on its own in so comparatively weighty a matter as the combination or separation of all but the smallest taxonomic categories. Who would combine Gomphonema with Licmophora just because their frustules have the same shape? To do so would be to ignore almost all other evidence - e.g. the presence/absence of a raphe, the valve structure, the structure of the girdle, etc. The shape of a diatom is certainly of importance in classification, but does not in itself constitute sufficient grounds for Hustedt's change.

The fourth grouping has not previously been recognised. Perhaps

it will prove not to be a natural grouping: confirmation or denial of this awaits examination of N. laevissima and N. irresoluta, and more detailed studies of N. ?clausii and Nitzschia sp.B (Eilat).

N. austriaca must also be mentioned. This tiny diatom (12-22 x 1.8-2.4  $\mu\text{m}$ .), described by Hustedt (1959a), is sigmoid in valve view, but not in girdle view. Its raphe does not seem to be interrupted centrally, and but for the sigmoid twist of the valve, it might be classified in the sect. Lanceolatae. Possibly it belongs in the 'Sigmata', although it is very small for a member of that group.

#### 4.6.6.13 The section Lineares

'Kiel wenig exzentrisch. Zellen linear, in der Mitte wenig oder gar nicht eingezogen. Kielpunkte stets deutlich, nicht in die Schalenfläche verlängert.' (Hustedt 1930).

When this group was first described, by Grunow (1862) it comprised not only those forms which are included within it today, but also the species which were later separated into the Lanceolatae or Dissipatae. The first remodelling of the Lineares took place in 1880 (Cleve & Grunow), when the two other groups mentioned above were erected. Then, in 1930, Hustedt combined the Vivaces (another of Grunow's groupings, dating from Cleve & Grunow 1880) with the Lineares, a practice which has not been followed by all subsequent authors, among the dissenters being Cleve-Euler (1952) and Hendey (1964). Strangely, even Hustedt was not consistent in his treatment of the Vivaces, since in 1955 he recognised it as separate: with the transfer of the type species of the Vivaces, N. vivax, to Hantzschia (by Hustedt 1959a), however, this problem has been 'solved'. In the present study the remaining species of the Vivaces are considered under the Lineares.

As with other sections described by Grunow in Cleve & Grunow(1880),