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 µm.), 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),

Nitzschia sect. Lineares

TABLE 22

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Eccentricity of raphe	Fibula morphology	Source of information
N. aestatis	44-50	4-5	12-17	? (not visible)	absent	++	thin, oblong-roundish	Giffen (1973)
N. aquaea	72-87	6-7.5	6.5-7.5	?40	?absent	?	?1 SRC	Cleve-Euler (1952)
N. arctica	130	14	8	25	present	+++	small	Cleve (1896)
N. bella	180-230	7-9	6-7	25-28	absent	+++	coarse: more than 1 SRC	Sovereign (1963)
N. chilensis	170-190	10	3	16-18	absent	++	coarse: more than 1 SRC	Hustedt (1927b)
N. claasseniae	60-70	4-5	8-9	38	present	++	?1 SRC	Cholnoky (1958)
N. fluminensis	120-160	13-15	3.5-5	14-16	absent	++	?1 SRC	Van Heurck (1880-5) Cleve & Grunow (1880)
N. fragilarioides	13-17	2.3	10	20	?	?	?	Cleve & Grunow (1880)
N. frickei	?	?	?	?	present	++	?1 SRC, but small	A.Schmidt Atlas
N. frigida	45-75	8-12.5	7-9(10)	over 35	present	?+	?1 SRC	Cleve & Grunow (1880)
N. garrensis	100-130	4-5	5-8	very fine	?absent	++	like that in N. recta?	Hustedt (1950)
N. hemistriata	45-50	9-10	6-7	36-37	absent	+/++	large	Hagelstein (1938)
N. ingenua	75-180	4-6	6-12	35	absent	++	1 SRC	Hustedt (1935, 1938)
N. islandica	94	12	6.5	19-20	absent	+/++	?1 SRC	Østrup (1918b)
N. kaikonkiensis	87	5	12-13	40	absent	++/+++	?	Woodhead & Tweed (1960)
N. lauenburgiana	130-150	6-7	11-14	23-26	absent	++	1 SRC	Hustedt (1950)
N. limes	66-84	8-9	12-13	12-13	?	++	1 SRC	Pantocsek (1902)
N. linearis	70-180	4-7	8-13	28-30(+)	present	++	usually 1 SRC	Hustedt (1930) Cleve-Euler (1952) this thesis

TABLE 22 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Eccentricity of raphe	Fibula morphology	Source of information
N. loczyi	109-110	7.5	3	14	absent	+/++	large, quadrate	Pantocsek (1902)
N. majuscula	200	19	3-3.5	14.5	absent	0	?1 SRC	Van Heurck (1880-5) Cleve & Grunow (1880)
N. parallela	60	4	6-9	28	absent	+/++	1SRC	Hustedt (1955)
N. perspicua	20-25	3.5-4	20	very fine	absent	+++	?	Cholnoky (1960b)
N. polaris	50-110	5-7	5-6.5	over 40	present	+	?	Grunow (1884) Cleve-Euler (1952)
N. pseudolinearis	100-120	7-8	8-11	22	present	++	1 SRC	Hustedt (1922)
N. recta	60-167	5-7	4.5-9	40	absent	++	large in relation to the costae; bar-like	Hustedt (1930), this thesis Cleve-Euler (1952)
N. rectiformis	35-55	5	5-8	very fine	absent	+++	as N. recta	Hustedt (1943)
N. reinhardii	111-142	8-9	6-8	23	?	?	?	Alexejenko (1931)
N. speciosa	150-180	?	7.5	23	absent	+	like that in N. recta, or N. sigmoidea	Hustedt (1945)
N. stefaninii	66-93	8	7	14	present	++	1 SRC	Frenguelli (1929)
N. sublinearis	40-75	4-6	13-15	35	absent	+++	small; no clear relationship to costae	Hustedt (1930) this thesis
N. subvitrea	70-90	9-10	5-7	30	absent	+	?1 SRC	Hustedt (1922)
N. suecica	70-180	5-6	11-12	22-24	absent	+++	?1 SRC	Cleve & Grunow (1880) Cleve-Euler (1932)
N. tenuis	120-170	2	11	30	present	++/+++	1 SRC	Hustedt (1950)
N. tenuissima	60-70	?	14	very fine	present	++	?1 SRC	Peragallo & Peragallo (1897-1908)
N. vacillata	40-55	6-7	10-15	over 40?	absent	+++	?	Giffen (1966)
N. vacua	75-80	5	5-8	over 40?	absent	++	coarse; large in relation to costae	Hustedt (1950)
N. vasta	30	5	6-8	15	present	+++	± like that in N. vitrea	Hustedt (1939)
N. vitrea	35-200	5-13	4-7	17-27	absent	+	large, quadrate	Hustedt (1930) Cleve-Euler (1952) this thesis

but not mentioned in Grunow (1880), there is a problem concerning the author citation of the Lineares since the status of this group was not specified in the former paper, nor in Grunow (1862). Cleve (1883) seems to have been the first to assign it sectional status (see also sect. Dubiae).

The sect. Lineares is a large group, containing around 40 species (Table 22), few of which are ever recorded, however, except those described in Hustedt (1930), namely N. linearis, N. recta, N. sublinearis and N. vitrea. These four species are also those which have been examined during the present study. The first (studied with LM, TEM and SEM) was found at various sites, e.g. on the underside of the bridge over the Afon Bran at Llandovery, Dyfed; on the walls of Carreg Cennen Castle, Dyfed; in an enrichment culture derived from material from the R. Wye near Brockweir; etc. N. recta (LM, SEM) was found in a ditch at Walton in Gordano, Co. Avon, and in the epipelon of Shearwater, Wilts. N. sublinearis (LM, SEM) was studied from cultures derived from rivers in the Bristol area, while N. vitrea (LM, SEM) was found in a subaerial 'streak' of diatoms on the underside of the vault of a culvert at Bigsweir, Gwent.

N. linearis, the type species of the group, first described and illustrated by W.Smith (1853, p.39 and Pl.13 f.110), has a linear valve with a quite strongly eccentric raphe system. In girdle view the frustule is often slightly bilobate (F.270, 274 and Hustedt 1930, f.784), though not to the same extent as in the members of the sect. Dubiae; in larger frustules this feature is scarcely apparent (F.263).

The valve construction is of type 1 (F.268-9, 892-6). The costae project above the frets both internally and externally; the poroids, which are elongated transapically, contain hymena in which the pores are arranged subregularly (F.540). The hymena are not visible in SEM micrographs of internal or external aspects of the valve (in cases

where, from TEM observations, hymena are known to be present), and so presumably they lie approximately centrally in the poroids. There are no sterna in N. linearis (F.264, 268, 893), nor in the other three species (F.886, 890, 901), and while the valve is quite sharply bent at the junction of valve face and distal mantle (F.893), marginal ridges are absent.

Although there is a well-defined subraphe canal, raised above the general level of the valve (F.893, 896), the striae continue virtually without interruption, past the bases of the fibulae, right up to the narrow raphe-sternum: the canal walls, then, are perforate.

The raphe-slit opens onto the crest of a narrow ridge (F.896, 898), as in N. sigmoidea, N. spathulifera, etc. (see sects. Nitzschia, Insignes respectively). This ridge is visible in the light microscope (F.271): it is somewhat higher near the poles than centrally. At the centre of the valve the subraphe canal is abruptly constricted, a feature which is obvious using light microscopy, and is often useful in identification (F.263-4); here the raphe is interrupted (F.265, 898). The internal endings are like those of many Nitzschia species, being in the form of a 'double helictoglossa', and are coaxial-symmetrical, as are the external endings (F.894, unpubl. obs.). The interraphe distance is small and the raphe-slit narrow, so that the external endings are often difficult to see, even with the SEM.

At the poles, internally there is a simple helictoglossa (F.266-7, unpubl. obs.), while externally the terminal fissure curves off (apparently towards either the distal or the proximal side - unpubl. obs.), the final portion of it running parallel to the polar valve margin (F.896-7).

The fibulae are narrow structures, each one representing a single subraphe costa (F.264-71, 894), although occasionally partial fusion may occur between adjacent subraphe costae. There may be a trace of a longitudinal ridge running between the distal fibula bases, but this

is never well developed (F.893-4). Each transapical costa that bears a fibula widens slightly near the fibula base, just as in Hantzschia virgata var. virgata.

The epicingulum consists of at least five, open bands (F.895, 897). In some of these there is a single transverse row of pores (F.270-1, 904), but this seems to be on the pars interior of each band, since the pores are never obvious in scannong electron micrographs of intact thecae or frustules (F.895, 897). The pars exterior of each band bears vermiform thickenings of silica (F.895, 904), a feature which has not been observed in any other species of Nitzschia, while the abvalvar margin bears 'teeth', which may perhaps have some function in holding the bands in place relative to one another in vivo.

The chromatophores are of the normal Nitzschia type, and occupy most of the cell length (F.272-4). The nucleus is slightly oval (F.274, 278) or elongated apically (F.275), and lies centrally, between the two chromatophores (which may lie against opposite sides of the girdle: F.276). The interphase nucleus stains poorly with aceto-carmine (F.278); as might be expected, however, the daughter nuclei of a recently divided cell stain rather more intensely (F.277). A single nucleolus can usually be seen (F.278).

The frustule of N. recta is not at all bilobate in girdle view, but is linear (F.256). The valve also is linear, or somewhat lanceolate in the shortest cells (F.257). Using bright field light microscopy, the valve appears almost structureless, except for the prominent fibulae (F.257). In fact, the striae, although very fine, may be resolved, there being 38-40 in 10 μm. (F.258-9).

The valve construction is of type 1 (F.886-8). Over most of the valve the costae are deeper than the frets, but near the raphe they are of the same depth, so that here, but not elsewhere, the poroids are quite obvious from the inside of the valve (F.886). Externally the

costae and frets come to the same level (F.888). The poroids themselves are round, and seem to contain hymena, placed near their external apertures (F.888). As a result of the relative positions of costae, frets and hymena, the outside surface of the valve presents a more or less smooth, structureless aspect. The structure of N. recta, then, is unlike that of N. linearis but is very reminiscent of sects. Spathulatae and Dissipatae (sensu stricto), and the 'Sigmoideae' group in the sect. Nitzschia. This similarity is reinforced by the presence in all these and in N. recta of external flaps of silica (F.259, 888, unpubl. obs.).

The raphe, which is unbroken centrally, opens onto the crest of a narrow ridge, as in N. sigmoidea or N. linearis (F.888). At the poles, internally there are simple helictoglossae (F.887); the external endings are unknown.

There is a well-defined subraphe canal, with porose walls, raised above the general level of the valve. The entrance into this canal diminishes in width from centre to pole, becoming very narrow just before it widens out again beneath the helictoglossa (compare F.886 with 887).

The fibulae are large in relation to the transapical costae, and no definite spatial relationship between these two elements can be distinguished (F.886).

Cincture and cytology are unknown.

Thus, N. recta bears many resemblances to other Nitzschia species with external flaps: its valve, raphe and subraphe structure all indicate a link with the 'Sigmoideae' (see sect. Nitzschia), the sect. Spathulatae, and in particular with N. dissipata (compare F.886-8 with 809-11, 818-39). There is little to suggest a close relationship with N. linearis.

N. sublinearis is a smaller and more delicate diatom than either

of the preceding (see Table 22). The valve is linear (F.260), and the raphe is very strongly eccentric (F.261-2, 890). The frustule is not constricted centrally either in girdle or valve view (unpubl. obs.).

The valve is shallow and of a type 1 construction, the costae being deeper than the frets (F.889-91). There are no sterna, nor external flaps. The poroids, which are ± circular in outline, contain hymena, in which the pores are arranged subregularly (Helmcke & Krieger 1953- , Pl.922).

The raphe is unbroken centrally, but is not bordered by flanges as in N. recta or N. vitrea (unpubl. obs.). At the poles there are the usual helictoglossae internally (F.891), while each terminal fissure is fairly short, but strongly hooked either to the proximal or the distal side (unpubl. obs.).

The fibulae spring proximally and distally from longitudinal ridges (F.261-2, 889, 891, unpubl. obs.). They are mostly broader than the transapical costae, but are nevertheless small: they bear no clear relation to the transapical costae and exhibit a variety of widths even within a single valve (F.261-2, 889-91). The fibulae are very shallow in a direction perpendicular to the raphe sternum, and altogether they resemble those of many Lanceolatae more than they do those of N. linearis, N. recta or N. vitrea.

Cincture and cytology are unknown, except that a type 1 chromatophore arrangement is present (unpubl. obs.).

N. vitrea is in some ways similar to N. linearis, e.g. in the eccentricity of the raphe (compare F.282-3, 901-3 with 267, 270, 893-4), possession of a well-differentiated distal mantle (F.902-3), appearance of the valve externally, etc., but other features suggest that the kinship is not close.

The overall shape of the frustule is rather like that of N. recta, except that the cincture is wider: there is no central constriction

(F.284).

The valve is of a type 1 construction (F.899-903) and is somewhat coarsely structured (F.279-80). The costae are very little deeper than the frets, and the poroids, which are somewhat elongated transapically, are easily visible both internally and externally (contrast N. recta) (F.899, 903). Hymena would appear to be present at the inner ends of the poroids (F.899-900, unpubl. obs.). There are no external flaps (F.902-3). The subraphe canal is prominent, as in N. linearis, raised above the general level of the valve (F.902-3).

The raphe is bordered externally by flanges (F.279, 282, 902), which are strongly developed in the larger forms of the species. There are no central raphe endings (F.279, 282, unpubl. obs.). A simple helictoglossa is present internally at each pole (F.900): the course of the terminal fissure is the same as in N. linearis, turning distally or proximally (unpubl. obs.).

Each fibula is composed of 2-4 fused subraphe costae and, as well as being broad in the apical direction, is very deep, so that in 'girdle view' it appears square or shortly oblong (F.279-84, 899). The massiveness of the fibulae is a feature which, coupled with the overall shape of the valve, makes N. vitrea one of the most easily recognisable species of Nitzschia. There seem to be longitudinal ridges joining the fibula bases, although fracture sections will be necessary to confirm this: at any rate, the interspaces are oval, as viewed from the inside of the valve (F.899-901).

The walls of the subraphe canal are porose, the valve striae continuing over them, leaving only a narrow raphe-sternum: each stria is represented within the canal by two or three poroids (F.902-3, unpubl. obs.).

The cingulum consists of 8 open bands, each of which is a little narrower than the next advalvarly (F.902-3 - in these micrographs the eighth bands can just be seen, but are not numbered). The bands do not

bear vermiform thickenings but do each possess a single row of small warts or teeth on the abvalvar margin. As in N. linearis, exterior views of intact cinctures or cingula obtained using the SEM give no indication of pores, but light microscope observations show that some type of perforation is present (F.280): it would appear, therefore, that it must be the pars interior, not the pars exterior, which is porose.

Two chromatophores are present per cell, disposed symmetrically, one on each side of the median transapical plane as in most Nitzschia species (F.285). The nucleus, placed centrally between the two chromatophores, stains strongly with aceto-carmine (F.288). The nucleoplasm does not stain uniformly, however, but appears 'granular': in the smaller specimens of N. vitrea (?var. salinarum) found in the Bigsweir sample this granularity was especially evident (F.286-7). A single nucleolus can sometimes be seen (F.285). Bütschli globules are not prominent in this species.

These four species, then, are distinct from each other and differ in many ways: they do not appear to form a natural grouping. It is difficult to discuss other species of this section, in some cases because no good illustrations are available, in other cases because the small size or light silicification of the diatom has made observation of detail virtually impossible. Thus it is pointless to comment upon the taxonomy of N. chilensis, N. fragilarioides, N. islandica, N. kaikonkiensis, N. reinhardi and N. suecica (see Table 22) without examination of specimens.

There are several species which appear to be close to N. linearis. N. pseudolinearis and N. stefaninii resemble each other and N. linearis in valve and frustule shape, raphe construction and fibula morphology (Hustedt 1922, Pl.10 f.43-44; Frenguelli 1929, T.49 f.22-23). Indeed, these taxa seem to differ only quantitatively, e.g. in the

linear densities of striae and fibulae, in length and breadth, etc. N. tenuis is also close to N. linearis and was for a long time included within it as a variety (e.g. by Hustedt 1930, but see Hustedt 1950). N. claaseniae, N. frickei and N. tenuissima probably also belong here, as may N. arctica (for references see Table 22).

Many species do not possess central raphe endings, as judged by a lack of a 'central nodule' and/or any differentiation of the central interspace. Of these, only N. vacua (Hustedt 1950, f.11-13) seems likely to be closely related to N. sublinearis, while only N. loczyi (Pantocsek 1902, T.10 f.264) can confidently be placed near N. vitrea. N. hemistriata seems to have large, coarse fibulae like those of N. vitrea, but Hagelstein (1938, Pl.8 f.1) illustrated this diatom in valve view only, and so no conclusions can yet be reached.

N. aestatis, N. bella, N. garrensis and N. rectiformis probably belong near N. recta. These taxa would not, of course, have been referred to the Lineares had 'Längslinien' been observed, and thus there is no indication so far that these species have external flaps. The illustrations of Giffen (1973) and Hustedt (1943, 1950, and in Sovereign 1963) suggest, however, that these species have a valve, raphe and subraphe structure similar to that of N. recta. Hustedt's photographs of N. speciosa (1945, T.43 f.1-3) suggest that this species also, although much more coarsely structured than N. recta, is nevertheless closely related to it. Here, in fact, the raphe structure and fibula morphology are very reminiscent of N. sigmoidea (sect. Nitzschia), another species with external flaps.

Various other species have been described which do not resemble any of the four species studied in detail. Thus, N. ingenua, N. lauenburgiana, N. parallela and N. subvitrea all have thin, bar-like fibulae like N. linearis, but do not possess central raphe endings. N. polaris does not much resemble any other species, except N. vasta:

both have large fibulae relative to the size of the transapical costae (but not as large, and not of the same shape, as those in N. vitrea) and possess central raphe endings.

Certain taxa seem to belong in other sections or genera. Thus, N. limes (Pantocsek 1902) is very similar to N. angustata, while N. fluminensis and N. majuscula, with their almost central raphes, resemble species of Bacillaria (see Peragallo & Peragallo 1897-1908, Pl.71-2). N. vacillata seems to belong in Hantzschia (see Giffen 1966, T.62 f.98-99).

The sect. Lineares, then, is in a chaotic state, and greatly in need of revision.

4.6.6.14 The section Lanceolatae

'Kiel stark exzentrisch. Schalen in der Regel lanzettlich mit mehr oder weniger deutlichen Transapikalstreifen.' (Hustedt 1930).

The sect. Lanceolatae was erected by Grunow (1880, and in Cleve & Grunow 1880) to include various small Nitzschiae which he had formerly placed in the Lineares (see Grunow 1862). Even in 1880 this section included nearly twice as many species as did each of the next largest sections, Tryblionella and Pseudotryblionella, and since this time the growth of the Lanceolatae has far outstripped that of any other group. Many new taxa have been described, especially by Hustedt (over 90 species) and Cholnoky (about 40 species), so that the section now contains over 300 described 'species'. It is not surprising that Frenguelli (1943) wanted to change the name of this group to 'Eunitzschia' (i.e. 'true Nitzschia').

Since 1880 no one has suggested any changes in the circumscription of this vast section: indeed, only recently (Lange-Bertalot 1977) has there been any attempt at taxonomic revision. Diatoms belonging to the sect. Lanceolatae are widespread in all types of freshwater and