

A few other points may be made.

Several matters suggest that N. amphibia is probably quite closely related to the sect. Grunowia. Thus, of all the Lanceolatae, N. amphibia is one of the most coarsely structured (cf. sect. Grunowia) with only 15-16 striae in 10 μm . (F.367-71). The poroids are large, and conspicuous even in the light microscope, and each contain a 'cribrum' in addition to the hymen: this cribrum is very similar to that found in N. sinuata. Moreover, the fibulae bear an exact spatial relationship to the transapical costae in both taxa, and the structure of the cincture also appears fairly similar (note the presence of warts on the bands of both N. amphibia and N. sinuata). On the other hand, it should be noted that N. amphibia differs from the Grunowiae in that central raphe endings are present, the striae become double within the subraphe canal, and the fibula morphology is much simpler.

N. amphibia is also similar to N. angustata (sect. Tryblionella). Valve, raphe and subraphe structure are very alike in these taxa, although a well-developed marginal ridge is present in N. angustata, but lacking in the other. Geitler has observed auxospore formation in both (see section 4.3) and found them to differ, but N. angustata's method of formation is like that of another member of the Lanceolatae, namely N. fonticola, and thus it is probable on several grounds that the relationship between N. angustata and the sect. Lanceolatae is very close.

4.6.6.15 The section Nitzschiella

As with various other sections of Nitzschia (e.g. Tryblionella, Grunowia and Perrya), this section was originally a separate genus, declared as such in 1864, by Rabenhorst. Subsequently Grunow (in Cleve & Grunow 1880) reduced it to the status of a subgroup of Nitzschia, and most authors have followed his example. Grunow had previously (1862)

Nitzschia sect. Nitzschiella

TABLE 24

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Eccent- ricity of raphe	Sigmoid in valve view?	Sigmoid in girdle view?	± cresc- ent shaped?	'X'*	Source of information
<u>N. acicularis</u>	50-150	3-4	16-20	60	absent	+++	no	no	no	++	Hustedt (1930) Hasle (1964)
<u>N. beagleana</u>	300-360	5.6	7-8	28	absent	+++	no	no	no	+	Patrick (1970)
<u>N. behrei</u>	220-250	5-6	6 (15 in rostra)	?over 40	absent	+	no	yes	no	+	Hustedt (1959c)
<u>N. brevirostris</u>	40	3-4	16	?over 40	absent	+++	no	no	no	++	Hustedt (1955)
<u>N. curvirostris</u>	350	?	5	very fine	?	+	no	no	yes	+++	Cleve (1878)
<u>N. decipiens</u>	32-36	2.7	7-9	44	present	+++	no	no	no	+	Hasle (1964)
<u>N. diversicostata</u>	180-225	?	5-6	very fine	?	0/+	no	no	±yes	+++	Brun (1894)
<u>N. droebakensis</u>	35-42	3	16-22	60	present	+++	yes	?	no	++	Hasle (1964)
<u>N. elegans</u>	45-85	2.5	13-16	28	present	+++	no	no	no	+	Hustedt (1956)
<u>N. gracillima</u>	165-259	3-5	7.5-9	?very fine	absent	+++	no	no	no	0	Heiden & Kolbe (1928)
<u>N. granii</u>	27-79	1.5-2	17-20	50	absent	+++	no	no	no	0	Hasle (1964)
<u>N. hummii</u>	150-240	5-6	7-10	30	absent	+++	no	no	yes	0	Hustedt (1955)
<u>N. incerta</u>	120-185	5.5	?	12.5-14.5	absent	+++	?yes	yes	no	0	Peragallo & Perag- allo (1897-1908) Cleve & Grunow (1880) as <u>N. incerta</u>
<u>N. incurva</u>	50-80	4.5	6-7	14.5	absent	+++	?yes	yes	no	0	
<u>N. irremissa</u>	45-65	3-5	18	?over 40	absent	+++	no	no	no	++	Cholnoky (1959)
<u>N. lecointei</u>	21-112	2.5-5	5-14	51-55	present	+++	no	no	no	0	Hasle (1964)
<u>N. longirostris</u>	100-115	4-4.5	10-14	36	absent	+++	no	no	no	0	Hustedt (1938)

* 'X' = degree of sharpness of transition between valve
'body' and rostra: '0' is a smooth transition.

TABLE 24 (contd.)

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Central raphe endings	Eccent- ricity of raphe	Sigmoid in valve view	Sigmoid in girdle view	±cresc- ent shaped	'X'	Source of information
<u>N. longissima</u>	30-500	3-8	5-27	14-60	present	+++	yes/no	no	yes/no	+++	Cleve-Euler (1952) Hasle (1964)
<u>N. lorenziana</u>	65-235	3-5	6-8.5	14-20	absent	+++	yes	yes	no	0	Hustedt (1930) Cleve-Euler (1952)
<u>N. nyassensis</u>	153-487	2-4	15-16	?40	absent	++	no	no	no	0	O.Müller (1905)
<u>N. rostellata</u>	50-100	4-5	10-12	30	absent	+++	no	no	no	++	Hustedt (1956)
<u>N. rostrata</u>	60-140	4-9	?	20-26	?	?	no	no	yes	?	Cleve & Grunow (1880)
<u>N. rousselinii</u>	60-90	4-5	12	36	absent	+++	no	no	no	++	Maillard (1977)
<u>N. spiculoides</u>	60-95	2.5-4.5	12-16	over 40	present	+++	no	no	no	+	Hustedt (1949)
<u>N. spiculum</u>	70-100	1.5-2.5	14-16	over 40	present	+++	no	no	no	0.	Hustedt (1949)
<u>N. subacicularis</u>	30-42	2.5	14-16	33	absent	+++	no	no	no	++	Hustedt (1938)
<u>N. subcurvata</u>	47-90	1.5-2	12-15(+)	44-49	absent	+++	no	no	yes	0	Hasle (1964)
<u>N. transvaalensis</u>	70-90	4-5	14	?over 40	present	+++	yes	?	no	+++	Cholnoky (1958)
<u>N. ventricosa</u>	100-650	9-20	3-10	26-27	present	+ / ++	no	no	no	+++	Cleve & Grunow (1880)

included the 'Nitzschiella' species within Nitzschia as members of a group named 'Ceratoneis', presumably because one of these species, N. closterium (later transferred to Cylindrotheca by Reimann & Lewin 1964), when originally described, was included in Ceratoneis (by Ehrenberg 1841, teste Patrick & Reimer 1966).

No other sections have been combined with, or separated from the sect. Nitzschiella, although Hustedt (1938, 1955, 1956) noted an intergradation between this section and the sect. Lanceolatae. The diagnosis of the group is the same as it was in 1864, when Rabenhorst stated 'Frustula sicut in Nitzschia, sed apices valde attenuati vel applanati, elongati et nonnumquam torti.' The group is quite large, containing over 30 species, some of which are very poorly known and have therefore been omitted from Table 24 (q.v.). Few species are commonly reported except N. acicularis, N. longissima and N. lorenziana. Hasle (1964) described the structure of seven species of the sect. Nitzschiella in the course of a LM and TEM study of marine planktonic Nitzschia species.

In this study four species have been examined, namely N. acicularis (LM, SEM), obtained from a ditch at Berkeley, Co. Avon, and from an enriched culture derived from sediment of the R. Wye at Brockweir; N. longissima (LM, SEM), found in samples from fishponds at Eilat, Israel; N. ventricosa (LM, SEM), from washings off Sargassum from Oahu, Hawaii; and an unknown, apparently undescribed form (LM, TEM, SEM), found in the same sample as Nitzschia sp.B (Eilat) (see sect. Nitzschia). The last will be referred to as Nitzschia sp.C (Eilat).

The valve of N. acicularis is straight, and may be said to consist of three sections. The central section, occupying approximately half of the total length of the diatom, is almost linear; at each end of this part the valve diminishes in width fairly abruptly into the end sections, also linear, which therefore appear as thin rostra

(Latin; 'beaks')(F.343). As will be noted from Rabenhorst's diagnosis (see above), it is this valve shape which is diagnostic of Nitzschiella. The valve is shallow, with a strongly eccentric raphe system lying at the junction of proximal mantle and valve face (F.343, 967).

The valve construction is of type 1, with no sterna or other interruptions of the striae (F.967; see also Hasle 1964, Pl.11 f.8, 9). The valve is very delicate and finely structured: the striae cannot be resolved using the light microscope. Hasle's studies (op. cit.) indicate that the rows of \pm circular poroids are sometimes (at least) at a slight angle to the transapical plane.

The raphe is not interrupted centrally (F.343 and unpubl. obs.): the polar endings have not been observed in the present study and were not illustrated by Hasle (op. cit.).

The fibulae are small structures, but large in relation to the 'transapical' costae (F.967 and unpubl. obs.). The fibula bases are joined by longitudinal ridges on both the proximal and distal sides of the raphe, and this has the consequence that a subraphe canal may be distinguished. The canal walls are porose, with one poroid opposite each transapical stria (see Hasle op. cit., Pl.11 f.8). The fibulae are somewhat irregular in size and spacing, and bear no definite spatial relationship to the costae (F.967). In all, the subraphe structure is very similar indeed to that found in various species of the sect. Lanceolatae (e.g. N. communis, N. hantzschiana and N. palea) and in N. sublinearis.

The cincture is unknown.

N. acicularis has two chromatophores per cell, arranged as in most Nitzschia species (i.e. a type 1 arrangement: F.337 and see Mereschkowsky 1901, Heinzerling 1908). The chromatophores do not extend into the rostra.

N. longissima, N. ventricosa and Nitzschia sp.C (Eilat) are

similar in shape to N. acicularis, except that the rostra are much longer relative to the central portion - in N. longissima, for example, the central section is only about one-fifth of the total length: also the central part is usually more fusiform in shape (F.338, 340, 344). These three diatoms are much larger than N. acicularis, and more coarsely structured, but all have a type 1 valve construction (F.955-8, 961-6). In the rostra the valve face is almost non-existent, the raphe system occupying virtually the whole width of the valve (F.338, 341, 348).

N. longissima is more finely striate than the other two species, the Eilat specimens having around 40 striae in 10 μm . (F.339). The poroids, which are somewhat irregularly spaced, are circular and contain hymena, which are placed near the external apertures of the poroids (F.955, unpubl. obs.). As has already been mentioned (section 4.6.5), different authors have recorded a very wide range of stria densities for this species, and it is possible that the Eilat specimens are not typical. It may be noted, however, that Hasle's (1964) specimens appear to have been very similar to those studied here.

The raphe system in N. longissima is strongly eccentric. The raphe is interrupted centrally (F.338-9, and see Hustedt 1929), where there is also a constriction of the subraphe canal (F.955). The central endings are coaxial-symmetrical: internally there is a very prominent 'double helictoglossa' (F.956), while externally the fissures expand slightly as they approach the centre (F.955). The polar raphe endings have not been observed, but one of Hasle's illustrations (op. cit., Pl.11 f.3) suggests that a terminal fissure is present.

The fibulae, which are large in relation to the transapical costae, but shallow in a direction perpendicular to the raphe-sternum, are of various sizes, and are irregularly spaced (F.338, 957). They are often oblique to the transapical plane, and frequently fuse with

one another to a lesser or greater extent. They are joined at their bases by longitudinal ridges running one on each side of the raphe, and parallel to it (F.338, 956-7). The subraphe canal is well defined, and raised above the general level of the valve (F.955). The transapical striae are interrupted by the longitudinal ridges, but continue beyond them into the subraphe canal: each stria (of proximal mantle or valve face) is represented within the canal by two or three poroids (F.956-7, unpubl. obs., and see Hasle 1964, Pl.5 f.6). The raphe-sternum widens opposite the central raphe endings and here there are only one or two poroids opposite each stria: the longitudinal ridges become smaller centrally, so that the central interspace is larger not only in the apical direction, but also in the transapical (F.956).

The cincture is quite wide: each cingulum consists of several bands, which appear to be porose judging by the striations visible in scanning electron micrographs (F.955).

The chromatophores of this species have already been described and discussed (see section 4.6.5): the Eilat specimens had numerous small chromatophores per cell, unlike the diatoms drawn by Cupp (1943).

N. ventricosa has a lower stria density than the last (see Table 24), but the striae are very difficult to observe. The poroids are circular or somewhat oval (F.958): hymena have not yet been detected, but the specimens examined were broken and appeared somewhat eroded.

The raphe system is only slightly eccentric (F.340, 961); as in N. longissima, central raphe endings are present, these being coaxial-symmetrical (F.342, and see Hustedt 1929). The external fissures widen considerably at the centre (F.958), while internally there is a prominent 'double helictoglossa' (LM observations - F.342 - confirmed by Dr.F.E.Round's unpublished SEM data). At the poles the raphe ends internally in a submarginal helictoglossa (unpubl. obs.): externally there is a terminal fissure, which curves off towards one side of the

valve (F.960).

The fibulae are of type viii (see section 4.6.3). In the central section of the valve the fibulae represent single subraphe costae, and are usually extended across the whole width of the valve, although some traverse only half the valve, from raphe system to one margin (F.342). The outer edge of each fibula (i.e. that part nearest the raphe) is extended into flanges which extend towards adjacent fibulae in much the same fashion as has been described for N. sinuata (sect. Grunowia), so that oval portulae are delimited: between certain of the fibulae, however, there is no opening into the subraphe canal, the 'interspaces' being blocked by thin membranes of silica (F.342)(cf. N. epithemioides, sect. Epithemioideae).

In the rostra the subraphe structure is rather different, and perhaps this is inevitable given the virtual absence of anything (valve face, distal or proximal mantle, etc.) except the raphe system. Here the fibulae each appear to consist of several subraphe costae, which are fused into a bundle resembling a sheaf (F.341, 959). Again some fibulae are joined by thin membranes of silica: indeed, the proportion of such blocked interspaces is much greater in the rostra than in the 'body' of the valve.

There is a well-defined subraphe canal which is raised above the general level of the valve (F.961), and constricted centrally (F.958). The transapical striae are interrupted by the flanges and longitudinal ridges associated with the fibulae, but each is represented within the canal by two or three poroids (F.961, unpubl. obs.).

The structure of the girdle is unknown.

According to Mereschkowsky (1903a), N. ventricosa has numerous small chromatophores like those of N. longissima (in part).

Nitzschia sp.C (Eilat) is a more robust diatom than the last, although it has slightly more transapical striae per unit length

(F.345, compare with 342). The raphe system is eccentric, but not greatly so (F.344). The poroids are circular (F.964-6): hymena have not yet been demonstrated.

Central raphe endings are present and are coaxial-symmetrical (F.344-5). The internal fissures terminate in a remarkable, beak-like 'double helictoglossa' (F.346, 962, 964), which is far larger than any other such structure found to date. The external endings are expanded, and set in a depression formed by a constriction of the subraphe canal (F.965). The polar endings have not yet been observed using the SEM: the light microscope reveals, however, that a prominent helictoglossa is present internally (F.348).

While the raphe structure is clearly quite similar to that of N. longissima or N. ventricosa, the subraphe structure is unlike that of any other member of the Nitzschiaceae. It is as though a narrow, thin silica strip, in which a single row of circular holes had been punched, were to be cemented in place beneath the raphe (F.344-8, 962-3, 966); or, the construction may be likened to that of N. sinuata or N. ventricosa, but with the costate part of each fibula removed. In the central part of the valve the holes through the 'fibular plate', which might be termed portulae or interspaces, are more widely spaced than in the rostra (F.344, unpubl. obs.). The centremost portula is larger than any other (F.344-5, 962). According to the classification of fibula morphologies outlined earlier (section 4.6.3.5), Nitzschia sp.C (Eilat) has type vi fibulae.

Again there is a well-defined subraphe canal, raised above the general level of the valve (F.965). Each transapical stria is represented within the canal by about 4 poroids (F.966).

Cincture and cytology are unknown.

Although the descriptions given above cover only 4 out of 30+ species, it appears from a survey of the literature that these 4

demonstrate most of the features relevant to a discussion of the taxonomy of the sect. Nitzschiella.

Only one species, N. diversicostata, is similar to N. ventricosa, with fibulae extended across the whole width of the valve. Indeed, it is not clear what the distinction between these taxa is, since their size ranges, linear densities of fibulae, etc. overlap. Brun, however, who described N. diversicostata, was clearly aware of the existence of N. ventricosa (described by Kitton 1873) since he mentioned it in the original description of the other (1894). Boyer (1927) suggested that the taxa are distinguishable by the degree of irregularity in the spacing of the fibulae (more irregular in N. diversicostata), but this on its own would not justify separation at specific level.

Of the species studied by Hasle (1964), N. droebakensis is like a smaller version of N. longissima (ibid. - 'The valvar structure as resolved in the electron microscope is nearly identical with that of N. longissima'); N. granii and N. subcurvata seem to belong nearer the sect. Pseudonitzschia (q.v.), while N. decipiens and N. lecointei (ibid., Pl.11, 12), both with ± lanceolate valves, do not resemble other members of the sect. Nitzschiella very closely, and should, perhaps, be placed elsewhere.

N. transvaalensis (Cholnoky 1958) would appear to be very similar to N. longissima and, indeed, falls within the presently accepted limits of that species. N. curvirostris (Cleve 1878) has the valve shape of N. longissima/N. ventricosa/Nitzschia sp.C (Eilat), and is similar to the last in the positioning of the raphe: Cleve's illustration (1878, T.3 f.21) suggests, however, that the subraphe structure is more similar to that of N. longissima. N. behrei (Hustedt 1959c, T.1 f.1-3), also with a near central raphe, may belong near N. longissima but its valve is not sharply differentiated into 'body' and rostra. This species is sigmoid in girdle view, and the possibility remains that it may

belong in the 'Sigmoideae' group of the sect. Nitzschia.

N. lorenziana, together with N. incurva and N. incerta if these are considered distinct from N. lorenziana (as was done, for example, by Hustedt 1959c), bears little resemblance to other members of the sect. Nitzschiella and seems to belong nearer N. sigma (see sect. Nitzschia): N. lorenziana and its allies are sigmoid in both valve and girdle views, a feature not shown in other Nitzschiellae.

Several species are apparently close to N. acicularis. These include N. beagleana, N. brevirostris, N. irremissa, N. longirostris, N. rostellata, N. rousselinii and N. subacicularis (for references see Table 24). All these have a valve shape like that of N. acicularis, a strongly eccentric raphe system, and acicularis-type fibulae. All lack central raphe endings, except, perhaps, N. subacicularis, which in the original illustration (Hustedt 1938, T.41 f.12) was portrayed without, but later (Hustedt 1956, Abb.74) was shown with endings, judging in both cases by the presence/absence of a differentiation of the central interspace. N. elegans, N. spiculum and N. spiculoides are like N. acicularis, but almost certainly possess central raphe endings.

The N. acicularis group includes species which are very similar indeed to many species of the sect. Lanceolatae. In fact, the only distinction between these groups seems to be in the shape of the valve, and even here, as Hustedt noted several times (1938, 1955, 1956), there are many intermediate forms. Thus, for instance, N. graciloides (sect. Lanceolatae) is almost identical in shape to the longer cells of N. elegans (sect. Nitzschiella) (see Hustedt 1959c, T.1 f.4, 5 and 1956, Abb.71-73 respectively). N. subacicularis and N. spiculum are also particularly close to the Lanceolatae.

N. gracillima and N. nyassensis seem to be like N. acicularis, but require much further study. N. hummii is a coarsely structured diatom

which in some ways resembles N. sigma (Hustedt 1955), except that it is not sigmoid, but arcuate. N. rostrata was not illustrated by Grunow, and has apparently not been found since the original description (in Cleve & Grunow 1880): its taxonomic position is therefore unknown.

On the basis of the above findings it is suggested that the sect. Nitzschiella be retained to include N. longissima and its allies, that the N. acicularis group is best transferred into the sect. Lanceolatae (or placed in a separate section very close to that group, if it proves that there is a discontinuity in the spread of variation which might be used as a taxonomic boundary), and that N. lorenziana (sensu lato), N. subcurvata and N. granii be transferred to other sections as indicated above. N. lecointei, N. decipiens and the four species mentioned in the previous paragraph require study urgently.

N. ventricosa probably belongs closer to N. longissima than might be expected from the dissimilarities in subraphe structure. The size and shape of the valve, the structure of the raphe itself, the valve construction, and the type and arrangement of the chromatophores all suggest that such a link is likely. The same arguments apply to Nitzschia sp.C (Eilat). The relationship between N. ventricosa, N. epithemoides and Gomphonitzschia clevei (Hustedt 1929, T.3 f.1a, b) may also be close, however, and should be studied: all have very similar subraphe constructions.

4.6.6.16 The section Pseudonitzschia

This section, like the sect. Fragilariopsis (q.v.) was until recently a genus in its own right, founded by Peragallo & Peragallo (1897-1908). Few authors mentioned or used this genus, however, except Heiden & Kolbe (1928) and Frenguelli (1938b). Cupp (1943) referred typical Pseudonitzschia species to Nitzschia, while the grouping was