

TABLE 11.

SPECIES	Length µm.	Width µm.	Fibulae no. in 10 µm.	'Striae'* no. in 10 µm.	Axial sternum	Degree of cent- ral constrict- ion of valve	Proportion of valve loculate	No. of poroids per loculus	Source of information
<u>N. areolata</u>	35-40	10-11	10	10	absent	++	50%	4-7	Helmcke & Krieger (1953-) Hustedt (1952)
<u>N. bisculpta</u>	133-170	50-62	5.5-6	12-13	present	+	60%	?	A.Mann (1925)
<u>N. constricta</u>	13-100	6-18	10-20	10-20	absent	+ / ++	?	?	Cleve-Euler (1952) Helmcke & Krieger (1953-)
<u>N. corpulenta</u>	30	12	8	14	absent	+++	?	?	Hendey (1957)
<u>N. ferox</u>	35	14	6-8	16	present	++	30%	?	Hustedt (1952)
<u>N. mollis</u>	30	5-6	22	21-23	absent	+	?	?	Hustedt (1952)
<u>var. africana</u>	13-18	5-6	18-24	24-25	absent	+	60%	2-4	Cholnoky (1959) this thesis
<u>N. panduriformis</u>	40-120	10-30	6-10	14-25	present	+ / ++	60%	several?	Cleve-Euler (1952) this thesis
<u>N. rorida</u>	23-45	9-11	10-12	24-27	present	+	30%	?	Giffen (1975) this thesis
<u>N. ruda</u>	?	?	?	?	absent	+	?	?	Cholnoky (1968a)
<u>Nitzschia</u> sp. (Scilly material)	15-25	6.5-8.5	10-12	21-22	absent	+	60%	2	this thesis

* i.e. transapical rows of loculi.

4.6.6.1 The section Panduriformes

The sect. Panduriformes was founded by Grunow (in Cleve & Grunow 1880) to include two species, N. panduriformis and N. constricta, and these are the most commonly encountered members of the group, although several related species have also been described (see later). Grunow (op. cit.) gave the following description of the group:

'Schaalen breit, in der Mitte zusammengezogen, mit stärkerer oder schwächerer Längsfalte, Kiel dem einen Rande sehr genähert, Kielpunkte sehr deutlich oder scheinbar fehlend. Punktirung wie bei Pleurosigma angulatum.'

Initially there was no indication of the taxonomic rank of the group (Grunow merely said 'Gruppe'), but by analogy with others of Grunow's infrageneric groupings, e.g. Pseudotryblionella, Epithemioideae, which were designated as sections in a companion paper (Grunow 1880), it is clear that Grunow intended sectional rank for the Panduriformes. In any case, Cleve (1883) used this grouping, clearly designating it a 'sectio'.

This is one of the few sections of Nitzschia which has not altered in its circumscription since 1880; hence the value of quoting Grunow's description in full. The two diagnostic features given by Grunow - the shape of the valve, and the arrangement of the 'Punkte' in quincunx - are those which have been used by subsequent authors, e.g. Van Heurck (1896), Peragallo & Peragallo (1897-1908) and Karsten (1928), and there is rarely any problem about the referral of diatoms to this group, given adequate material.

For a long time N. panduriformis and N. constricta, together with N. bombiformis when this was considered separate from N. constricta (e.g. by Grunow, in Van Heurck 1880-5, Pl.58 f.9, published 1881, but not in the text of the same work, by Van Heurck himself, published in 1885; also by Boyer 1927), were the only species placed in this group.

However, A.Mann (1925) described N. bisculpta from the Philippine and Hawaiian Islands, and Hustedt (1952) added N. areolata, N. ferox and N. mollis; his N. inducta may also belong here. Hendey (1957) described a species with markedly constricted valves from Freetown in W. Africa (N. corpulenta), and more recently Cholnoky (1968) and Giffen (1975) have described N. ruda and N. rorida respectively. Cholnoky (1956) found a new species of Nitzschia, N. oliffii, which resembles members of the Panduriformes in valve shape, and sometimes in the arrangement of the 'Punkte' (e.g. see Cholnoky 1956, Abb.4 f.117), but he stressed in a later paper (1963b) that the structure of the striae is not the same as in N. panduriformis etc.

In this study material of several species has been examined: these species are N. panduriformis (forms approx. 60 x 15 μm ., with 6-7 fibulae and 12-13 'striae', i.e. transapical rows of 'Punkte', in 10 μm .), N. rorida (45 x 11 μm ., with 10-12 fibulae and 24-25 'striae' in 10 μm .), and a small form (15-25 x 6.5-8.5 μm ., with 10-12 fibulae and 21-22 'striae' in 10 μm .) which does not obviously belong to any described species, all from intertidal sand at St.Martin's, Isles of Scilly; and N. mollis var. africana (see Cholnoky 1959), from washings off Sargassum found growing on the south shore of Oahu Island, Hawaii, and from fish tanks at Eilat, Israel (specimens were 10-18 x 5-6 μm ., with 24-25 'striae' and a slightly lesser number of fibulae in 10 μm .).

N. rorida is almost certainly the same as N. panduriformis var. abrupta Peragallo & Peragallo (1897-1908, Pl.70 f.7, and compare F.143), found by them at Villefranche. It is a new record for Britain (see Hendey 1974).

It has been possible to study N. panduriformis, N. mollis var. africana (both samples) and the small unidentified Scilly form with the SEM, and in all the valve is of the type 5 construction described earlier (4.6.2). Thus, the distal parts of the valves in these species

are composed of hexagonal loculi, each of which opens to the outside by a large, more or less circular hole, unoccluded by hymen or other structure (F.140, 702, 705, 707, 716). The loculus opens to the interior of the cell by one or more poroids (F.708-12, 716), each closed by a hymen in which the pores are in hexagonal array (in the Scilly Nitzschia sp. and N. mollis var. africana: F.533-4). The hymena must be placed towards the outsides of the poroids since they are not evident in interior views of valves (F.708, and compare with F.704). In N. mollis var. africana there are two or three poroids per loculus (F.709, 716), while in the Scilly Nitzschia sp. there are only two, each pair being aligned in a strictly transapical direction (F.710). Light microscopic observations of N. panduriformis suggest that there are several poroids per loculus (F. 141); this may be an interference artefact, although alterations of the condenser height, diaphragm apertures, oiling the condenser, etc. made no difference to the image. Several (4-7) poroids per loculus are present also in N. areolata according to Helmcke & Krieger (1953- , T.191). These authors interpreted the structure correctly, except that they claimed that 'die hohen Kammern sind nach Innen weit geöffnet, nach aussen mit grossen Poren versehen', which, though possible, is unlikely in view of the type of structure demonstrated here to be present in other members of the Panduriformes.

Towards the raphe the external foramina (sensu Anon. 1975) of the loculi become larger, with a concomitant decrease in the height of the loculi, until near the raphe, in all the species studied with the SEM (and apparently also in N. areolata, Helmcke & Krieger, op. cit.), the valve becomes one-layered, with an external reticulum of costae (F.704, 707). In the forms of N. panduriformis observed here this change is abrupt, since the valve structure is interrupted by an axial sternum (which is apparently devoid of pores); only distal to this

sternum (the 'Längsfalte' of Cleve & Grunow 1880, and of Cleve-Euler 1952) is the valve loculate (F.139 and unpubl. obs.). In some of the larger varieties of N. panduriformis, however, (e.g. vars. lata, peralbata; see Peragallo & Peragallo 1897-1908, Pl.70 f.1, 2) and in N. biscalpta (A.Mann 1925, Pl.28 f.1, 2) it appears that the proximal half of the valve face may also be partly loculate (F.138).

The valves of all species are relatively broad (F.138-9, 143-6) and remarkably shallow (F.701, 707-11); they are undulate, so that the valve face is somewhat sigmoid in transapical section (F.707). The valve is acutely angled at the raphe, though not very strongly so, and thus the transapical section of the frustule is a parallelogram (F.701). There is in all cases a well-defined subraphe canal, raised above the general level of the valve. The canal walls are porose, with two or three poroids opposite each transapical 'stria' in N. mollis var. africana (F.704), but only one in N. panduriformis (unpubl. obs.). The poroids of the canal wall differ from those of the valve face, in that each of the former is surrounded externally by a raised rim of silica (F.704).

In all the taxa studied the fibulae have been found to be narrow, rib-like structures, which are usually very slightly extended onto the valve face (F.138-9, 141, 143-6, 708-11). Each is opposite a transapically orientated strip of silica which externally bears the transapical walls of the loculi (F.708). Although, because of the construction of the valve, the fibulae must be classified in the type vii category (see section 4.6.3.5), their form and arrangement are reminiscent of type i fibulae, e.g. those of N. linearis (sect. Lineares) or H. virgata.

Within the Panduriformes there is variation in the proportion of the transapical strips which bear fibulae: in N. areolata, N. constricta, N. mollis and its var. africana (F.146, 709) the vast majority of the

strips bear fibulae, whereas in N. biscalpta, N. corpulenta, N. ferox, N. panduriformis (F.138-9), N. rorida (F.143), N. ruda and Nitzschia sp.(Scilly)(F.144-5, 710) there are only about half as many fibulae as strips (N.B. for those species not observed during the course of this study, information about fibula spacing was derived from the original descriptions and illustrations - the relevant works have been cited above).

Externally the raphe is bordered on each side by thin ridges, which are continuous from pole to pole (F.701, 704, 706). The raphe itself, however, is interrupted centrally; here the ridges are set further apart than elsewhere, revealing a small, rounded knob (F.704) which presumably separates the two raphe fissures. The exact course of the central raphe endings is, however, difficult to determine. The central internal endings have not been observed (because of the particular morphology of Panduriformes valves), but the central interspace is always wider than the others (F.138-9, 141, 143-6, 709-10), whether the species has fibula spacings as in the N. areolata group or as in N. biscalpta etc. At the pole, internally there is a small, simple helictoglossa (F.709-11). The external fissure is bent very abruptly above the helictoglossa and then continues only a little farther (F.706). This terminal fissure may be directed toward either the distal (F.701, 706) or the proximal margin (F.705), and at the end is shallow and much expanded. The ridges bordering the external fissure stop just short of the position where the fissure becomes blind (F.706).

The cincture of N. mollis var. africana is composed of open bands of two types (F.701-3, 705). Thus, of the five bands present in the epicingulum, the first is wide and bears 2-5 transverse rows of poroids, while the others do not seem to be porose and are much narrower; the bands bear small warts externally, except on the ligulae (F.705). The distal half of the first band is wider, with more transverse rows of

poroids, than the proximal half (F.702). It seems clear that in vivo there must be a very close interlocking between the first band and the valve, since the pars interior of the first band bears a row of short, blunt projections, the linear density of which is equal to that of the transapical rows of loculi on the valve (F.702) - compare Hantzschia amphioxys, H. virgata vars. virgata and gracilis.

As noted above (section 4.6.5), Mereschkowsky (1901, 1903a) observed there to be a type 2 chromatophore arrangement in N. constricta, and a similar arrangement has been observed in the present study in two smallish members of the Panduriformes, probably closely related to N. constricta or to the Scilly Nitzschia sp. In these cells there was a single pyrenoid in each chromatophore (e.g. F.147).

Reaching conclusions about the taxonomy of this group is made difficult by the lack of information concerning many of the species. This is largely the result of their ecology, since most are to be found growing on marine intertidal sandflats or in some other marine benthic habitats, none of which have been worked adequately by diatomists; this last fact is well illustrated by the way in which Giffen, in a series of papers on marine intertidal sites in South Africa (1963, 1970a, b, 1971, 1973, 1975, 1976), has found it necessary to describe many new species from a variety of genera. Nevertheless, certain conclusions may be drawn from our present knowledge, and these are presented below.

The sect. Panduriformes may be characterized by the partly loculate valve; the panduriform outline of the valve; the narrow, rib-like fibulae and their relation to other valve elements; the distinctive external central raphe endings; and probably the chromatophore arrangement. In the light microscope the two features of greatest importance for the referral of species to this group are the loculate valve, which is reflected in the arrangement of the 'Punkte' in decussate

rows (F.138-9, 143-6), and the valve shape. These must be taken in conjunction since other species of Nitzschia, e.g. N. vulpeculoides (Giffen 1973, Pl.3 f.63-65; see also F.196-7, 764), have similar arrangements of 'Punkte' (although these represent not loculi, but poroids), while N. punctata var. coarctata and various others of the sect. Tryblionella have similarly shaped valves, but do not have decussate striae. Moreover, the group is, broadly speaking, internally consistent with respect to the ecology of its component species.

There is one species, however, which seems to have affinities with the Panduriformes, yet does not have a loculate valve. This is a very small (10 x 5 μm .) form which was found in the epipsammic fraction from intertidal sand at St.Martin's, Isles of Scilly. It has an ovate-lanceolate valve (F.714) which is hardly constricted centrally, but it has external central raphe endings and ridge-bordered external raphe fissure just as in the Panduriformes (F.715). The valve, however, is more or less laminate, with a type 1 valve construction; the trans-apical costae are feebly developed, being noticeable only near the raphe and near the distal margin (F.714-5). The valve is very delicate and thus it is difficult to resolve the striae with the light microscope, though there are only approx. 35 in 10 μm . (unpubl. obs.). The poroids are closed by hymena, which are raised above the surface of the valve (F.715): the hymen pores are in hexagonal array. There is a well-defined subraphe canal as in the Panduriformes, and the fibulae are slender, rib-like structures which each represent single subraphe costae (unpubl. obs.). The identity of this species is not known, but according to presently accepted criteria it must belong to the sect. Lanceolatae.

Within the Panduriformes, species are to be distinguished from each other on the basis of valve size (and to a lesser extent valve shape), the presence/absence of an axial sternum, the proportion of

the valve which is loculate, and, of course, the linear densities of fibulae and transapical 'striae'. In future other characters, such as the structure of the cincture, the number of poroids per loculus, and the mean spacing of the fibulae, calculated in a manner similar to that in Hantzschia (this character taking the place of a separate fibula linear density measurement), will probably be useful. The information available concerning the morphology of members of the Panduriformes is summarized in Table 11.

N. biscalpta is probably quite close to N. panduriformis, both taxa having axial sterna and approx. half as many fibulae as transapical rows of loculi; N. biscalpta, however, is much larger. N. panduriformis itself contains a wide range of forms (see Peragallo & Peragallo 1897-1908, Pl.70 f.1-6, 11-13; and F.138-9), and may represent more than one species.

N. constricta is very ill-defined. Classically it was separated from N. panduriformis on the basis that the fibulae are not obvious (Cleve-Euler 1952 - 'Kielpunkte undeutlich'), but without clarification this diagnosis is hardly satisfactory; a clear description of this species has not been given, and it will be necessary to examine many samples and the type material before the true nature of this species can be established. It seems likely that both N. mollis and N. areolata have been identified as N. constricta by many authors: indeed, it is likely that all three belong near one another, in view of their fibula arrangement and their lack of axial sterna (F.144-6).

N. corpulenta, N. ruda and the Scilly Nitzschia sp. are intermediate between the N. constricta and N. panduriformis groups, in that their fibula arrangement is that of N. panduriformis while there is no axial sternum.

N. ferox and N. rorida form a separate series: here only a small part of the valve is loculate (F.143).

N. mediterranea may also belong here (see Cholnoky 1961, f.70).