This species bears many resemblances to species of the sect.

Insignes. The coarseness of the valve structure, the raphe structure, and the fibula morphology all suggest a close relationship with that group: indeed, the <u>Insignes</u> and <u>Scalares</u> are probably insufficiently distinct to justify their separation.

4.6.6.8 The section Grunowia

This is a small group, containing but eight described species, of which only two, N. sinuata and N. denticula, are commonly encountered or recognised. These were also the first taxa to be described, N. sinuata by W.Smith (1856), as 'Denticula sinuata', and N. denticula (as?) by Rabenhorst (1853, teste W.Smith 1856): the latter, however, has a complex nomenclatural history which is examined further below.

N. kittonii was published by H.L.Smith in 1878, while N. moissacensis, described by Héribaud, followed in 1903 (teste Hustedt 1927a).

N. denticuloides and N. subdenticula were described by Hustedt (1942), and finally Cleve-Euler (1952) separated N. solgensis from N. denticula, in which it had previously been classified as the var. delognei.

These species are listed, with their dimensions etc., in Table 17.

Smith (1856) gave an accurate drawing and description of the taxon now known as N. denticula, under the name 'Denticula obtusa Kutz.'

(compare Smith's Pl.34 f.292 with Hustedt 1930, f.780). Kutzing (1844), however, gave Echinella obtusa Lyngbye as a synonym of Denticula obtusa, whose author citation should therefore be '(Lyngbye) Kutz.': Smith's citation is inaccurate. Smith (op. cit.), however, had studied the Lyngbye material of 'Echinella obtusa', from Greville's collection, and he stated that this 'is different from the present' (i.e. N. denticula) 'and in fact belongs to the genus Diatoma, the zigzag arrangement of the frustules being perfectly distinct.' Smith considered that Kutzing's (1844) T.17 f.14 represented N. denticula (sensu Hustedt 1930).

SPECIES	Length um.	Width um.	Fibulae no. in 10 µm.	Costae no. in 10 µm.	Shape of valve	Extent of fibulae (% width valve)	Source of information
N. denticula	10-100	3- 8	5-8	14-20	linear/ linear-elliptical	70-100	Hustedt (1930) this thesis
N. denticuloides	40-60	4	8-10	17	linear	50	Hustedt (1942)
N. interrupta	10-54	3.8-6	5-8	14.5-20	lanceolate	40-50	Cleve (1883) Cholnoky (1957) Schoeman (1973)
N. kittonii	30 - 35	6.5	4 • 5 - 6	13-14	lanceolate	L ₊ O	Hagelstein (1938)
N. moissacensis	?	?	?	?	?	?	(see Hustedt 1927a)
N. sinuata	20-50	5-8	5-6	18	lanceolate, with characteristic central expansion	40	Hustedt (1930)
N. solgensis	10-20	3 - 4	6.5-7	24-25	lanceolate	4:O	Cleve-Euler (1952)
N. subdenticula	L _i O	8	6	10	lanceolate	50	Hustedt (1942)

not Echinella obtusa, but while this is possible, it seems unlikely since the valves illustrated by Kutzing had slightly protracted poles and in general resemble the valves of Diatoma vulgare var. producta illustrated by Hustedt (1930): in valves of N. denticula of the same size (40 µm. long) as Kutzing's forms protracted poles are not to be found. It is irrelevant, however, whether Kutzing meant the organism now called N. denticula or a species of Diatoma: the application of the epithet 'obtusa' must be determined from Lyngbye's material because Kutzing quoted Echinella obtusa as a synonym.

Therefore, when Grunow (1862) described 'Denticula kutzingii' (which is clearly identical to N. denticula sensu Hustedt 1930: compare Hustedt's f.780 with Grunow's T.12 f.15, 27) he did so quite legitimately. He took care to point out that 'Dent. obtusa Kutz.' was a species of Diatoma and that Smith's identification was wrong. It is not clear, however, whether Denticula kutzingii should be typified by Grunow's material, or by Smith's, or by Rabenhorst's slide 985 from the 'Algen Sachsens' series, since Grunow quoted both these other authors in his description (1862, pp.548-9).

When Grunow (in Cleve & Grunow 1880) transferred <u>Denticula kütz-ingii</u> to <u>Nitzschia</u> he changed the specific epithet to 'denticula', explaining his reasons thus - 'Ich habe den Artnamen dieser häufiger Art, die von <u>Nitzschia</u> nicht getrennt werden kann, wegen <u>N. Kutzingiana</u> Hilse umändern mussen.' But the I.C.B.N. (1972, and see Stafleu & Voss 1975, Voss 1976) does not forbid the use of the genitive (<u>kutzingii</u>) and the adjectival (<u>kutzingiana</u>) forms of the same word for different species of the same genus (I.C.B.N. 1972, Art.75), although it discourages this practice (ibid., Rec.23A). A 'N. <u>kutzingii</u>' was, however, described by Rabenhorst (1864), although according to Lange-Bertalot (1977) this was a later synonym of <u>N. pusilla</u>; so, Grunow was correct in changing the name to <u>N. denticula</u>, but for the wrong reasons!

Hagelstein (1938) stated that 'N. Denticula minor and N. Heideni are apparently synonymous with N. Kittonii. The first taxon was described by Cleve (1883) who 'accepted the determination as a variety of N. Denticula ... only on the authority of Mr. Grunow. Indeed, the lanceolate shape of the valve in this taxon, together with the fact that the fibulae do not extend across the whole of the valve, sets it apart from N. denticula. According to Hustedt (1927a) N. denticula var. minor is also identical to Denticula interrupta Reichelt and so, because Hustedt considered this organism to be sufficiently distinct from N. denticula to warrant separation at specific level, and because Reichelt's epithet takes precedence over N. heidenii (Meister) Hustedt (for which see A. Schmidt Atlas, T.351), Hustedt proposed the combination N. interrupta (Reichelt) Hust. If Hagelstein was correct, however, the correct name of this organism is N. kittonii. It is instructive, therefore, to compare descriptions of N. kittonii with those of N. interrupta. Hagelstein illustrated two valves of N. kittonii which were lanceolate, with dimensions of $30/35 \times 6.5 \mu m$. and 4.5-6 fibulae and 13-14 striae in 10 µm. For N. interrupta, Schoeman (1973, following Cholnoky and Hustedt) gave 10-54 x 3.8-6 µm., with 5-8 fibulae and 14.5-20 striae in 10 μ m.: the valve shape is similar to that of N. kittonii. Boyer's (1927) description of N. kittonii, however, agrees almost exactly with that of N. interrupta given above, and thus it is possible, but non-proven that these two taxa ought to be combined, as suggested by Hagelstein. Further progress is not possible without a greater knowledge of these forms and examination of H.L. Smith's type material.

Rabenhorst (1864) founded a new genus, <u>Grunowia</u>, to include <u>Denticula sinuata</u> and <u>D. tabellaria</u>, but he designated no type for the genus and thus one must be selected. Since the latter species has often been considered to be merely a variety of the former (e.g. by

Hustedt 1930, Cleve-Euler 1952) it is clearly not suited to serve as the type of <u>Grunowia</u>. I suggest, therefore, that <u>G. sinuata</u> is selected as the type of <u>Grunowia</u>, and hence <u>N. sinuata</u> as the type of <u>Nitzschia</u> sect. <u>Grunowia</u>. The demotion of <u>Grunowia</u> to sectional status within <u>Nitzschia</u> was suggested by Grunow (in Cleve & Grunow 1880), and his view has been shared by most authors; Pantocsek (1902) and Frenguelli (1934), on the other hand, retained it as a separate genus.

Hustedt (1930) gave as a description of the group 'Kiel wenig ausgeprägt, stark exzentrisch. Kielpunkte rippenartig in die Schalenfläche verlängert, Rippen aber nicht durchlaufend oder doch an Stärke allmählich abnehmend. In mancher Beziehung den <u>Denticula-Arten ähnlich</u> und auch als solche beschrieben.'

For this thesis two species, <u>N. sinuata</u> and <u>N. solgensis</u>, have been studied with the LM, SEM and TEM, while another, <u>N. denticula</u>, has been studied with the LM only. <u>N. sinuata</u> var. <u>sinuata</u> and <u>N. solgensis</u> were found in material collected from the underside of the bridge over the Afon Bran at Llandovery, Dyfed, while <u>N. sinuata</u> var. <u>sinuata</u> was also obtained from among dense growths of blue-green algae (<u>Dichothrix compacta</u>) growing on limestone cliffs at Burrington Combe, in the Mendip Hills. <u>N. denticula</u> was studied from a slide of '<u>Denticula</u> obtusa Sm.', No.30 in the Eulenstein type slide series: this had been made from W.Smith's original Penzance material (see W.Smith 1856, p.19).

These three taxa may at once be separated from each other by the shape of the valve. N. sinuata var. sinuata (hereafter referred to as 'N. sinuata') has a very characteristic double constriction of the valve such that the valve outline is undulate (F.215). N. denticula, on the other hand, has a linear (F.225; Hustedt 1930, f.780) or linear-elliptical valve (F.226), while N. solgensis valves are lanceolate (F.231-3). The last, moreover, is considerably smaller than the others.

Viewed with the oil immersion lenses of a light microscope, the valves are conspicuously punctate (F.215-20, 225-6, 231-3), even in N. solgensis where the striae are relatively densely packed (24-26 in 10 µm.). The electron microscope reveals that the valve construction is of the normal Nitzschia type (type 1 - see section 4.6.2), the transapical costae being very slightly deeper than the frets (F.783-4, 791, 798-9, 800). In N. sinuata and N. solgensis the poroids are more widely spaced, and more irregularly positioned, in the distal half of the valve face, beyond the limits of the interspaces (q.v.)(F.218-9, 232-3); in the latter species the striae tend to be interrupted near the midline of the valve, so that sometimes an ill-defined axial sternum may be distinguished (F.233, 799, 802). Within the interspaces the poroids are always very regularly arranged, as they are over the whole valve of N. denticula (F.225-6).

The valves of all three species are heavily silicified. The marginal strip is especially strongly developed for <u>Nitzschia</u> and projects slightly into the cell at the poles, making SEM observation of the helictoglossa difficult (F.791-2, 798). The valve is sharply angled near the distal margin so that there is a small, but well-defined distal mantle (F.801): in <u>N. sinuata</u> there is also a prominent marginal ridge (F.782, 784). Poroids are not present in the distal mantles of either species. The valve margin in <u>N. sinuata</u> bears a line of irregularly spaced small warts (F.783, 790).

The poroids are closed by hymena in which the pores are in hexagonal array (F.553-4, 556): in N. sinuata there is also a coarser structure which lies against the hymen and resembles a cribrum (F.553; this is also described elsewhere - see section 4.6.2).

The raphe is eccentric, though not greatly so (less, for example, than in the sect. <u>Lanceolatae</u>)(F.782, 801). The valve is not strongly angled at the raphe in <u>N. sinuata</u>, nor are there flanges or ridges

bordering the raphe fissure (F.783-4). In $\underline{\text{N.}}$ solgensis the valve is more sharply angled at the raphe, but again the raphe fissure is not bordered: in this species the raphe is more eccentric than in $\underline{\text{N.}}$ sinuata and the proximal mantle is slightly concave (F.801).

The raphe-slit is continuous from pole to pole in all three species (e.g. F.783-4). At the poles, internally there is a simple helicto-glossa (F.792, 802); externally there is a moderately long terminal fissure which may be directed towards either the proximal (F.787-8, 801) or the distal margin (F.785-6), both fissures of a single valve, however, being turned in the same direction (F.785-8). The terminal fissure is bent abruptly at its midpoint so that it takes the form of a circumflex accent, while its junction with the remainder of the external fissure is marked by another bend.

Type iv fibulae are present, although the various species of the group differ in the details of fibula morphology (F.216-9, 225-8, 791, 798-9, 802-3). The oval portulae are quite easily seen with the light microscope in suitably orientated valves of N. sinuata and N. denticula (F.218, 226, 228), and it is strange that no one appears to have noted them before: they are just as obvious as the portulae of <u>Denticula</u> tenuis or <u>D. elegans</u> (F.511, 513), which were depicted by Hustedt nearly fifty years ago (1930, f.723-5). In <u>N. solgensis</u>, because of its more delicate structure, the portulae are much more difficult to distinguish.

bar, wider than the transapical costa which bears the fibula, which bar, on the proximal side, is fused to the proximal mantle immediately adjacent to the marginal strip; distally it extends to the midline of the valve face where a web of costate thickenings extend out onto the valve (F.789, 791-2). The effect of the presence of these bars and the associated 'webs' is to delimit a second level of portulae at

the inner boundaries of the interspaces. Each bar is connected to the outer flanges (see section 4.6.3.5) by a thin membrane of silica (F.791); compare <u>Denticula tenuis</u> (Chapter 5). In <u>N. denticula</u> the fibulae are simpler, and are extended across virtually the whole width of the valve (F.225-6). Those of <u>N. solgensis</u> are usually very similar to the fibulae of <u>N. sinuata</u> (F.798-9, 802), although occasional valves may be found which have more extended, <u>N. denticula</u>-type fibulae (F.803).

Because of the fibula morphology it is possible to distinguish a subraphe canal, although this is not raised above the general level of the valve: from the outside of the valve the extent of the subraphe canal is not apparent (F.784, 800-1). The canal walls are perforate, one longitudinal row of poroids lying on each side of the raphe (F.216-217, 219, 792, 797-9, 803, etc.).

The epicingulum of N. sinuata consists of four bands (F.790) which are similar in their morphologies to those of N. angustata (sect. Tryblionella). The first band, which is also the widest, bears a single transverse row of small round poroids, which marks the junction between the pars exterior and pars interior (F.217, 781, 793-4). The second and third bands are similar to one another, unperforate, and much narrower than the first (F.790). The second band, like the first but unlike the third or fourth, bears numerous small warts on the pars exterior. The fourth band is just a little narrower than the first and bears a single transverse, of longitudinally (sensu Von Stosch 1975) elongate poroids. All the bands are open, the ligula of the second closing the gap left by the first, etc. (unpubl. obs.).

The first band of N. sinuata deserves special consideration. The pars interior of this band is wider than the marginal strip of the valve, and hence in vivo the edge of the pars interior lies not against the plain, smooth inner side of the marginal strip, but against the fibulae and/or the transapical costae. Thus it is perhaps not surprising

that the distal half of the pars interior is regularly crimped, the periodicity of the small pleats corresponding to that of the valve transapical costae, while on the proximal side there is, in addition to the smaller pleats, a series of large pleats which in vivo fit around the fibulae (F.793-5). At the poles, where the fibulae extend across the whole width of the valve, the distal half of the band also bears a few large pleats (F.795).

The first band of <u>N. denticula</u> is very similar to that of <u>N. sinuata</u> and is open (F.229-30). Otherwise, however, the cinctures of <u>N. denticula</u> and <u>N. solgensis</u> are unknown.

The chromatophores of N. denticula (see Mereschkowsky 1903a),

N. sinuata and N. solgensis have a type 1 arrangement (e.g. see F.221222). In N. sinuata the chromatophores extend into the interspaces
and thus the chromatophore margins are crenulate (F.221-2, 224). The
chromatophores sometimes lie to one side of the cell, against the
girdle, or they may be more central. Butschli globules are present,
but often not very conspicuous (F.222, 224). The nucleus lies centrally,
between the chromatophores, and is quite small: the nucleoplasm is
fairly homogeneous and stains very poorly with aceto-carmine (F.223).
In the Burrington Combe specimens of N. sinuata the cytoplasm was
packed with small granules.

The particular valve, raphe and subraphe structure found to be present in the sect. Grunowia serve both to confirm the internal consistency of the group, and to separate the section from any other, although some links with other taxa can be detected (e.g. with N. angustata or N. amphibia). Within the section, however, three subgroupings may be distinguished. Firstly, there are taxa with linear or linear-elliptical valves, and fibulae which extend transapically across more than half of the valve face: N. denticula and N. denticuloides belong to this group. The latter is very similar to the more frequently

reported N. denticula and may well be only a variety of it, since in its dimensions, stria density, etc. it falls within the limits of N. denticula (see Table 17, and Hustedt 1930, 1942).

No sinuata and its varo tabellaria, which requires study in order to confirm that it is not sufficiently different from the type to warrant its separation at species level, constitute the second group. Here, the valve is expanded centrally and the fibulae take the form described in detail above.

In the third group there is a similar fibula morphology to that in N. sinuata, but the valve outline is lanceolate or linear-elliptical. The taxonomy of this group is most confused. There seems to be a whole series of forms (species?) of similar shape and structure, differing only in the linear densities of striae and fibulae. Thus, there is a range from the coarseness of N. subdenticula through N. kittonii/interrupta to the delicacy of N. solgensis. Authors often call similar or identical diatoms in this group by quite different names: thus, for instance, Foged (1959, Pl.12 f.11) illustrated a diatom which is almost certainly N. solgensis, but called it N. heidenii (i.e. N. interrupta) var. pamirensis. Biswas (1964) described N. solgensis-like individuals as N. sinuata var. denticuloides, while Gandhi (1960) described a new variety of N. denticula, var. rostrata, which in fact seems to belong nearer N. kittonii. Much work is necessary on these forms; possibly all form part of a single series, representing a highly variable species, similar in the breadth and continuity of variation to Hantzschia marina or H. distinctepunctata.

4.6.6.9 The section Epithemioideae

'Kiel mässig exzentrisch. Kielpunkte mehr oder weniger in Rippen verlängert, die vom Kiel aus beide Schalenteile in transapikaler