valve, the type of colony formed, and the delicacy of their structure (relative to Fragilariopsis).

A numerical taxonomic study would be of great help in this whole part of the Nitzschiaceae. While Hasle (1965b) is probably right in her claim that the Pseudonitzschia group is somewhat transitional between Nitzschia (sensu stricto) and Fragilariopsis, there remains a possibility that Pseudonitzschia might be better classified as a separate genus containing two subgenera, one corresponding to the 'N. seriata complex' (more closely related to Fragilariopsis), the other corresponding to the 'N. delicatissima complex' (closer to Nitzschia).

4.6.6.17 The section Fragilariopsis

In 1913 (in A.Schmidt Atlas, T.299) Hustedt founded the genus Fragilariopsis for the diatom previously called 'Fragilaria antarctica' or 'Fragilaria castracanei' (= Fragilariopsis kerguelensis: see Hasle 1965b), since he considered that its structure, with two rows of clearly visible poroids between each pair of adjacent costae, was too dissimilar to that of other Fragilaria species to permit its inclusion in that genus.

Subsequently, further species were described, or transferred from Fragilaria (e.g. by Hustedt 1958), and Van Landingham (1971) listed 14 species for the genus. Hasle (1965b) investigated 13 species in detail using light and transmission electron microscopy, and provided a key for the identification of these.

The classification of Fragilariopsis near Fragilaria was called into question through the finding (by Helmcke & Krieger 1953- , T.187-189) in 1954 of a raphe-slit in Fragilaria cylindrus, which was at the same time transferred to Fragilariopsis because of its valve structure.

In fact, Hustedt had already suggested (1952, teste 1958) that a canal raphe might be present in Fragilariopsis species - 'man bei einer genauen Untersuchung der Schalen den Eindruck hat, dass beide Schalenränder einander nicht völlig gleichen ... , so dass die Möglichkeit besteht dass sich an einem Schalenrand eine feine Kanalraphe befindet' (Hustedt 1958, quoting 1952) - and he later (1958) demonstrated canal raphes in several Fragilariopsis species. It became clear through this work, confirmed by Hasle (1965b, 1968b), not only that Fragilariopsis was not closely related to Fragilaria, but also that its true affinities lay with the Nitzschiaceae. As soon as this was recognized, however, authors began to have difficulties in finding characters on which to separate Fragilariopsis from Nitzschia itself, since there appeared to be few differences in valve structure between the former and certain species of the latter, especially of the sect. Pseudonitzschia. Hustedt (1958) maintained the separateness of Fragilariopsis, placing great emphasis on the formation of band-like colonies (see section 4.4). Paasche (1961) objected to this - 'difficulties are bound to arise ... where colonies are not formed or where the connection between the cells is so weak that the colonies tend to break up in preserved plankton samples' - stating that Hustedt's opinion would be untenable 'unless differences can be established in the valve structure which might serve as reliable marks of distinction between Fragilariopsis and Nitzschia.' Hasle at first (1965b) made no comment on this problem, but later (1972b) came to the conclusion that colony type does not justify separation at generic level: she therefore reduced Fragilariopsis to the status of a section of Nitzschia (see also Hasle 1974). Her emended diagnosis (1972b) is worth quoting in full:

'Valves broad and elliptical-linear-lanceolate in outline, or more or less linear. Apical axis isopolar or heteropolar. Canal raphe eccentrically situated, number of transapical ribs (costae) the same or

occasionally slightly greater than that of keel puncta, pseudonodulus absent or present. Intercostal membrane (stria) perforated by two alternating rows of poroids, occasionally one or more than two rows.' The colony type was excluded from her diagnosis, enabling the transfer into the section of N. sicula and N. americana etc., species of Nitzschia which possess a valve construction similar to that of Fragilariopsis, yet which do not apparently form colonies.

No voices have been raised in opposition to Hasle's alterations, but it is my contention that the validity of Fragilariopsis as a separate genus has not been disproved. Before discussing this, however, it is necessary to consider further the morphology of 'Fragilariopsis' frustules.

Four species have been examined during the present study, namely N. obliquecostata (LM), N. castracanei (LM)(= Fragilariopsis linearis: see Hasle 1972b), N. curta (LM, TEM, SEM) and N. cylindrus (LM, SEM), all from the underside of pack-ice at Signy Island, South Orkneys.

The frustules are nitzschioid, with a fairly narrow cincture (e.g. see Hustedt 1927-66, f.662, 665; 1958, Abb.6; Paasche 1961, Pl.1b; Hasle 1965b, Pl.2 f.3, 6, 7, Pl.4 f.18). The valves are of various shapes, linear to almost circular, but all are fairly broad, and usually with very bluntly rounded apices; none are capitate (F.360-6, 977, 980). In common with the species of one other group within the Nitzschiaceae, viz. Gomphonitzschia, Fragilariopsis species often have heteropolar frustules. This is never very pronounced, but shows itself in a slight widening of one pole relative to the other: thus, in a ± linear-valved species such as N. curta (F.360-1) the sides of the valve are at a slight angle to one another instead of being parallel. Heteropolarity was noted by Hasle (1965b) to be present in five species, viz. N. paaschei (= F. atlantica), N. kerguelensis, N. obliquecostata (F.362), N. ritscheri and N. curta, the other eight species studied being isopolar (e.g. see F.366). However, in the Signy material some specimens

of N. cylindrus were also found to be heteropolar (F.365, but see F.363-364).

The valves are quite heavily silicified and are traversed by a series of transapical costae, which are widely spaced relative to the size of the diatom (F.362-6, 977-83): even in the smallest species, N. pseudonana, which is only 4-20 µm. in length, there are only 18-22 costae in 10 µm. (Hasle 1965b). The raphe system is strongly eccentric, lying at the junction of valve face and proximal mantle; there is also a well-defined distal mantle (e.g. F.983).

Between a pair of adjacent costae there are usually two rows of poroids, each row being immediately adjacent to the margin of a costa (a type 2 construction - see section 4.6.2)(F.362, 366, 981-3). Where the rows are packed close together, e.g. in N. cylindrus, the poroids of the two rows are often placed alternately (F.979): this is found also in N. kerguelensis, N. ritscheri and N. angulata (= Fragilariopsis rhombica)(see Hasle 1965b). Quite often, however, the strip between adjacent costae may bear one or three rows of poroids. N. cylindrus may exhibit considerable variation in this matter, even within a single valve (F.978-9). None of the species classified in Fragilariopsis by Hasle (1965b) have valves in which single rows of poroids alone are found: even in N. separanda the 'striae' become double near the distal margin.

The transapical costae do not project externally, and thus the outside surface of the valve is fairly flat and smooth (F.983; Hasle 1968b).

Each poroid is closed by a hymen. The hymen pores are circular, as in other Nitzschia species, and are arranged in various ways - hexagonal array (N. curta, N. kerguelensis in part), subregularly (N. ritscheri), or in ± centroid array (N. kerguelensis in part) (for N. curta, see F.551; for the remainder, see Hasle 1965b, Pl.6).

The raphe is not bordered by flanges, and is very simply constructed (unpubl. obs.). In most species the raphe runs unbroken from pole to pole (e.g. F.360-6). Hasle (1965b) found, however, that of the thirteen species she examined, three, namely N. paaschei, N. grunowii (= F. oceanica) and N. vanheurckii, possessed central raphe endings. In these the central interspace is somewhat larger than the others. The inner fissure ends at the pole in a simple helictoglossa (F.978), while externally there appears to be no terminal fissure, the outer fissure ending immediately above the helictoglossa (see Hasle 1965b, 1968b, 1972b).

Close to the raphe, one on each side of it, run two longitudinal ridges, from which spring the fibulae (F.360-6, 978-9, 982). The fibulae are not large and sometimes lie opposite transapical costae, so that they are often very inconspicuous; it is not surprising that the existence of the raphe remained unsuspected for so long (F.360-6, 981). The relationship between costae and fibulae is often inexact (F.366, 978-9, 982), but even so the linear densities of these elements are virtually identical within a single valve, except in N. vanheurckii (see Hustedt 1958, Hasle 1965b). The fibulae are never extended across the valve.

Because of the presence of ridges joining the fibula bases, there may be said to be a subraphe canal, although this is not set above the general level of the valve (unpubl. obs., and see Hasle 1968b, 1972b). The canal walls are not porose.

Little is known of the cincture of sect. Fragilariopsis species. Hasle (1965b) noted that the bands of N. grunowii each have several rows of poroids, while N. curta and N. cylindrus have only one row at least on the first band, as in some other Nitzschia species, e.g. N. sinuata, N. amphibia, N. cf.hantzschiana, N. linearis, N. bilobata, etc.

There is a similar paucity of information concerning the cytology

of these species. In N. grunowii, however, Hustedt (1927-66, f.662c) noted two chromatophores per cell, arranged symmetrically about the median transapical plane, just as in the majority of Nitzschia species.

The account given above summarizes our knowledge of cell structure in the sect. Fragilariopsis (excluding from consideration, for the present, those species transferred into the section by Hasle 1972b, viz. N. sicula and N. americana). This information is mostly the same as that available to Hasle (1972b), who stated that 'in discussions of the taxonomic position of the genus Fragilariopsis three characters have traditionally been of importance, viz. -

i. the structure of the raphe

ii. the structure of the membrane between the silicified ribs ...

iii. the type of colony.'

Hasle did not directly discuss the first point in relation to Nitzschia, but did remark that 'the reduction of the raphe function implied in loss of motility is evidently no commonly used taxonomically distinctive character.' Tradition, however, would not seem an adequate reason why this character should not be used. It may be significant that in Fragilariopsis species, unlike most other Nitzschia species except those belonging to the sect. Pseudonitzschia, the outer raphe fissure does not continue past the helictoglossa. With regard to the central raphe endings, other groups besides the sect. Fragilariopsis show internal divisions between species with endings and those without (e.g. Rhopalodia, Hantzschia, Nitzschia sects. Lanceolatae, Pseudonitzschia, etc.).

The second character, the structure of the intercostal 'membrane', was also not discussed by Hasle, except in relation to species of Nitzschia sect. Pseudonitzschia and the genus Pseudoeunotia. Hasle noted that her earlier investigations (1965b) had shown that in the majority of Pseudonitzschia species the intercostal membrane is perf-

orated by two rows of poroids, and that this construction is also present in Pseudoeunotia; she used these similarities between Fragilariopsis and other groups as arguments against the validity of Fragilariopsis as a separate genus. She did not mention, however, that by far the majority of Nitzschia species have completely different valve constructions (see section 4.6.2). While the structure of the intercostal membrane does indeed seem to ally Fragilariopsis to Pseudonitzschia, it argues against close links with other Nitzschia species.

In her conclusion to the 1972b paper Hasle stated that since Pseudonitzschia had already been reduced to the status of a section of Nitzschia (by Hustedt 1958), with the implication that 'colony type did not warrant any higher rank', then Fragilariopsis should also be rejected as a separate genus. But equally, might one not argue that Fragilariopsis and Pseudonitzschia should both be given generic status: after all, similar colonies are not formed by other species in the Nitzschiaceae. A single character cannot be used in this way, to uphold or deny the validity of a genus. One other factor which seems to have influenced Hasle in her thinking (e.g. see Hasle 1972b, p.113) is that after death, during fossilization, cells may become detached from one another so that it is no longer possible to say whether colonies were originally present. But surely characters should never be excluded from consideration merely because they are indeterminable in fossilized specimens? Diatom classification must be based on as complete a knowledge of the organisms as is possible using contemporary methodology: fossil diatoms must then be fitted into the classificatory scheme as best they may. With reference to colony formation, this is clearly a useful character in this group, though the formation of band-shaped colonies must not be thought of as an obligatory requisite for membership of Fragilariopsis.

Various characters make it possible to separate a 'Fragilariopsis' grouping from 'Pseudonitzschia' or Nitzschia (sensu stricto). It is a

simple matter to go through recent literature on fossil marine diatoms (e.g. Schrader 1974a, b, 1976) and, by visual inspection of the micrographs, classify the Nitzschia (sensu lato) species into 'Fragilariopsis' and 'true Nitzschia' types, even though in these cases no information is available concerning colony formation. This separation, which I believe valid, is not based upon the presence or absence of any one feature, but upon the overall appearance of each of the forms. It is possible, however, to rationalize this apparently subjective judgment, and to distinguish those characters which form the basis for it.

Many of these characters were listed by Hasle (1972b) in her diagnosis of the sect. Fragilariopsis. The valves are shallow, and broad in relation to their length: they usually have blunt, rounded ends, and are hardly ever capitate (but see N. sicula var. rostrata: Schrader 1976, Pl.2 f.31). Many are linear (e.g. N. maleinterpretaria, N. pusilla Schrader, nom. illeg., N. evenescens, N. januaria, 'Nitzschia sp.14': ibid., Pl.2), and there is a tendency towards heteropolarity (e.g. in N. efferans, N. claviceps: ibid., Pl.2 f.1-6). Present in all are ± heavily silicified transapical costae, which are often rather irregularly spaced, a consequence perhaps of the type of valve construction present (see above); there are several fossil species with only one row of poroids between adjacent costae, but on other grounds these taxa belong close to more typical 'Fragilariopsis' species. The raphe system is strongly eccentric, and the raphe is rarely interrupted centrally. The fibulae are small, and usually of the same linear density as the transapical costae.

Hasle (1965b, 1972b) mentioned some other taxa, viz. N. sicula, N. americana, N. barbieri and N. peragallii, which are very similar to species of the sect. Fragilariopsis in valve morphology, yet until 1972 were not placed in that group since, as far as is known, they do not form colonies. Hasle's (1972b) solution to this problem was to exclude 'ribbon-shaped colonies' from the diagnosis of the group:

'species previously regarded as belonging to the section Lanceolatae Grun. like N. sicula and N. americana will then fit into the diagnosis of Fragilariopsis.' Hasle implies, therefore, that each of the characters listed in the diagnosis for a group must be shared by all members of that group: Hasle's sect. Fragilariopsis is to be understood as a 'monothetic' group, i.e. one 'formed by rigid and successive logical divisions so that the possession of a unique set of features is both sufficient and necessary for membership in the group thus defined' (Sneath & Sokal 1973, who claim that 'the disadvantage of monothetic groups is that they do not yield "natural" taxa, except by a lucky choice of the characters used for division'). In a monothetic group, therefore, great emphasis is to be placed on each of the characters listed in its diagnosis. Hasle's diagnosis, however, is inadequate since it fails to distinguish Fragilariopsis from members of the sect. Tryblionella, and because certain of the characters are meaningless. Taking her characters one by one:

1. 'Valves broad and elliptical-linear-lanceolate in outline, or more or less linear.'
   The valves of N. navicularis or N. granulata or N. hungarica (all of the sect. Tryblionella) fit this description, as does that of N. communis (sect. Lanceolatae).
2. 'Apical axis isopolar or heteropolar.'
   Not diagnostic!
3. 'Canal raphe eccentrically situated, .. '
   Fulfilled also by many other Nitzschia species, especially members of the sects. Tryblionella and Lanceolatae, such as those mentioned above.
4. ' ..number of transapical ribs (costae) the same or occasionally slightly greater than that of keel puncta, .. '
   Such an arrangement is found in the sect. Tryblionella, e.g. in N. navicularis, N. granulata, N. apiculata, etc.

5. ' ..pseudonodulus absent or present.'

   Not diagnostic!

6. 'Intercostal membrane (stria) perforated by two alternating rows of poroids, occasionally one or more than two rows.'

   Does not separate sect. Fragilariopsis from sect. Tryblionella, in particular N. navicularis, N. apiculata.

It should also be noted that this diagnosis also fails to separate Fragilariopsis from Pseudonitzschia satisfactorily. If, however, Hasle's diagnosis is reworded, and understood to refer to a polythetic group, i.e. one in which 'organisms are placed together that have the greatest number of shared character states, and no single state is either essential to group membership or is sufficient to make an organism a member of the group' (Sneath & Sokal 1973), then it becomes satisfactory. Thus, I suggest that inclusion within 'Fragilariopsis' be determined by reference to the following character states:

1. valves broad in relation to their length
2. valves elliptical-linear-lanceolate or linear
3. valve apices broad and bluntly rounded
4. apical axis heteropolar
5. valve shallow
6. valve face ± flat, not folded
7. valve not acutely angled at the raphe
8. raphe system strongly eccentric
9. central raphe endings not present
10. terminal fissure absent
11. linear density of transapical costae approx. equal to L.D. of fibulae
12. relationship between costae and fibulae not exact
13. fibulae small, not extended across the valve
14. subraphe canal walls without poroids
15. subraphe canal not raised above general level of valve
16. 2 rows of poroids between each pair of adjacent costae
(17. costae irregularly spaced)
18. marginal ridge absent
19. axial sternum absent
20. formation of band-shaped colonies

It is essential to remember that none of the above is necessarily common to all Fragilariopsis species, and that no Fragilariopsis species necessarily possesses all the above properties. A species of this group should, however, exhibit a larger number of these character states than a member of any other group. The exact number required for inclusion within Fragilariopsis cannot be determined at present, although this may be possible in the future, using numerical taxonomic techniques.

The distinction between this group and any other seems clearcut, and I see no reason why generic status should not be awarded to Fragilariopsis. Hasle's (1972b) argument for the rejection of the genus was one advocating consistency in the treatment of apparently similar taxonomic problems. Thus, since Pseudonitzschia had been demoted to sectional rank (by Hustedt 1958, Hasle 1965a), Fragilariopsis ought to follow suit. But if all characters are given equal weight (a matter which has been much discussed in recent years, and which seems to be the only safe procedure in taxonomy, in the absence of any indication of how to 'weight' characters objectively - see Sneath & Sokal 1973, pp.109-13), then the question of consistency does not arise since colony formation, the character traditionally considered most important in the Pseudonitzschia-Fragilariopsis group, is just one of many other characters, each of which plays an equal part in the development of the classification. In the approach recommended above there is no problem in accommodating N. sicula, N. americana, etc., or the fossil species (e.g. N. reinholdii, N. miocenica, N. indica, N. fossilis, N. cylindrica, etc. - see Schrader 1974a, b, 1976) in Fragilariopsis.