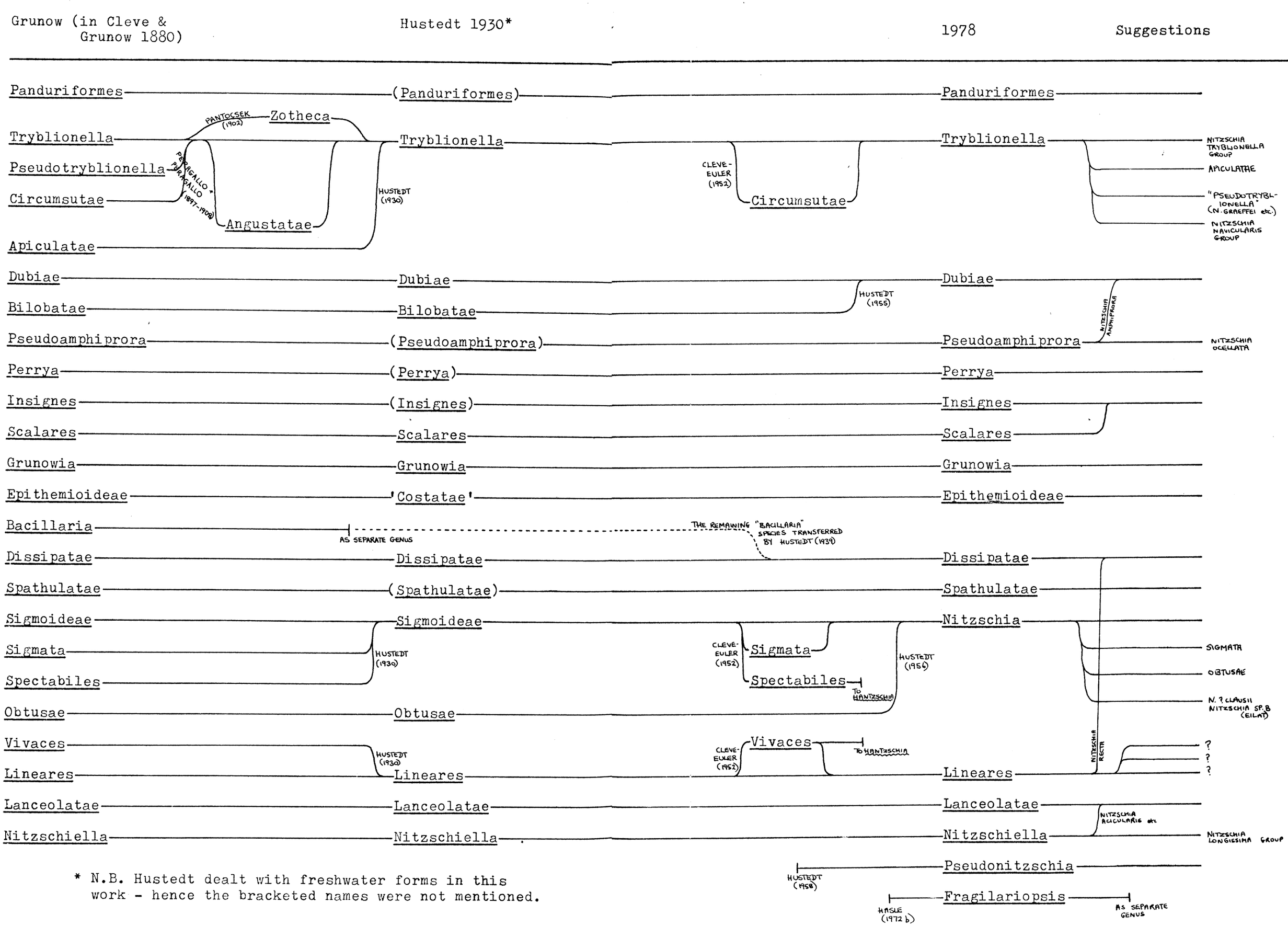
TABLE 25

Changes in the taxonomy of Nitzschia, 1880-1978



* N.B. Hustedt dealt with freshwater forms in this work - hence the bracketed names were not mentioned.

7: FINAL DISCUSSION

The foregoing account of the Nitzschiaceae has revealed certain inadequacies and errors in the present classification. Thus, some groups, e.g. Nitzschia sects. Dissipatae, Lineares and Nitzschia, appear to be heterogeneous collections of forms and need division, while elsewhere unexpected links have been detected between groups, e.g. (in Nitzschia) between the 'Sigmoideae' group (sect. Nitzschia), the sect. Spathulatae, N. recta and N. dissipata, all of which possess similar valve, raphe and subraphe structures.

More importantly, however, it is felt that this study has revealed inadequacies in the thinking behind contemporary diatom classifications, even though the taxa recognized in these may still in many cases represent natural groupings. It seems clear from the writings of Hustedt (e.g. 1930, 1967), Hendey (1971), Hasle (1972b) and Von Stosch (1977, p.133) that diatom taxonomy is still dominated by 'essentialism', a philosophy which derives from such men as Plato and Aristotle, and which in taxonomy (where it is known as 'typology') led to

'1. the ontological assertion that Forms exist,

2. the methodological assertion that the task of taxonomy as a science is to discern the essences of species, and

3. the logical assertion concerning definition' (Hull 1965a), which is 'a restatement of the inherent essence or nature of a thing' (Popper, quoted by Hull).

It would be incorrect to accuse modern diatomists of holding to the first two tenets given above, but they are surely guilty of adhering to the last, which otherwise stated is 'definition by properties connected conjunctively which are severally necessary and jointly sufficient' (Hull 1965a). Groups so defined are termed 'monothetic' because the defining set of features is unique (Sneath & Sokal 1973). Thus,

Hasle (1964, 1965b) found that certain Nitzschia species had a similar valve structure to that of Fragilariopsis species, but did not form band-like colonies; the formation of such colonies, however, was the 'essential' character for that genus (see Hustedt 1958) and so Hasle concluded that, since the Nitzschia and Fragilariopsis species obviously belonged together, Fragilariopsis could not be upheld as a separate genus, and that 'band-like colonies' must be excluded from the definition of her new combination, Nitzschia sect. Fragilariopsis (1972b). The possibility that the 'Nitzschia' species could be included in Fragilariopsis without the need to 'demote' the latter did not receive attention. Schütt's (1896), Hustedt's (1927-66, 1930) and Karsten's (1928) systems of classification are all basically monothetic. The diatoms are divided into successively smaller and smaller groups, just as in an identificatory key: the groups themselves are defined by means of carefully selected characters (in the higher categories, usually frustule shape and symmetry) common to all the included forms. This procedure leads to a great stress on the primary characters, and a reluctance to consider as useful any characters whose distribution conflicts with the accepted system. Thus, Hustedt (1967) claimed that 'der Feinbau der Arten innerhalb grösserer Gattungen nicht konstant ist, sondern in mehr oder weniger zahlreichen Typen auftritt, die sich in vielen Gattungen wiederholen ... und daher als Gattungscharaktere nicht in Frage kommen, sondern nur zur Differenzierung auf kleinsttaxonomischem Gebiet herangezogen werden können', while Hendey (1971) stated that 'any arrangement made by virtue of similarity in electron microscope microstructure of the valve substance cuts across all other groupings whether they are based upon symmetry, physiology, ecology or reproduction pattern', and gave three examples where a classification according to EM structure would, in his view, lead to ludicrous taxonomic placings. The implication is that certain characters are inherently worthy to be used in classifi-

cation, while others are not. As further examples of this attitude may be quoted Hasle's (1972b) remark that 'the reduction of the raphe function ... is evidently no commonly used taxonomically distinctive character', and Von Stosch's (1977) claim that 'each of ... symmetry of valve pattern and colony formation would suffice in the Pennales to establish a separate genus.' Hustedt (1967) mentioned that in both Cymbella and Gomphonema there are some species with one row of pores between each pair of adjacent costae, and others with two rows, and he argued from this apparent case of parallelism that the use of valve structure in generic classification is illegitimate. For him the symmetry relationships of the cells were of overriding importance. But there is no logical reason why valve structure should not be used as the 'key character'. Indeed, observations such as those reported here concerning a 'Nitzschia-Gomphonitzschia' (see section 4.7.7), and those of Lauritis et al. (1967) or Geitler (1968c), suggest that symmetry itself may not be too safe a taxonomic criterion when used alone. It is noticeable that Hendey (1971) fails to apply to the traditionally-used symmetry the mode of argument he adopts with reference to valve structure: if he had, he might have remarked upon the 'ludicrous situation' of placing together Gomphonema, Licmophora, Gomphonitzschia and Surirella (in part) because all have heteropolar frustules.

Hull (1965a) stated that 'it is commonplace now to recognise what Adanson realised almost two hundred years ago that taxa names cannot be defined by sets of properties the members of which are severally necessary and jointly sufficient, for seldom is a property of any taxonomic value distributed both universally and exclusively among the members of a taxon.' With regard to the Bacillariophyta, Hull's comment is optimistic: the necessity for a non-Aristotelian, polythetic approach to taxonomy has not been explicitly recognized by more

than a very few diatomists. As research continues, however, it becomes less and less easy to define diatom taxa in the traditional, monothetic manner. Thus, forty years ago Hantzschia was said to be distinguishable from Nitzschia by the symmetry of the frustule about the median valvar plane (Hustedt 1930), but then Lauritis et al. (1967) and Geitler (1968c) found hantzschioid cells of Nitzschia spp.; Hustedt (1930) said of Hantzschia 'Kiel ... am ventralen, gewöhnlich konkaven Schalenrand gelegen', but some forms of H. amphioxys (q.v.) have the raphe on the dorsal side of the valve; Hustedt said 'Zentralporen vorhanden', but they are absent from H. segmentalis, H. spectabilis and H. vivax; and so one might continue.

In fact, taxa can only be defined satisfactorily in a polythetic manner, by 'sets of statistically covarying properties arranged in indefinitely long disjunctive definitions' (Hull 1965a): thus, the logical structure of the definition of taxon 'A' must be not '$A^{Def.}$ a.b.c.d' , where a, b, c and d are properties each of which is necessary and which together are sufficient for inclusion within 'A', but '$A^{Def.}$ a.b.c.d V b.c.d.e V a.c.d.f V ...' , where V indicates that a.b.c.d, b.c.d.e, etc. are alternatives - here no one property or set of properties is necessary for inclusion (Hull 1965a).

Let us go on to consider that basic unit of taxonomy, the species. It has been shown in this dissertation that several traditionally accepted diatom species (Hantzschia marina, H. virgata, etc.) vary considerably within themselves in several characters. But what is a species?

Two main approaches to this problem may be distinguished. Firstly, there is the 'phenetic' approach, where populations are compared on the basis of morphological, cytological, biochemical and other characters, and clusters of like forms recognized. From this 'we may regard as a species (a) the smallest (most homogeneous) cluster that can be

recognized upon some given criterion as being distinct from other clusters, or (b) a phenetic group of a given diversity somewhat below the subgenus category, whether or not it contains distinct subclusters' (Sneath & Sokal 1973). Secondly, there is the 'biological species concept', which may be explained via Simpson's (1943, quoted by Mayr 1957) definition of a species as 'a group of organisms so constituted and so situated in nature that a hereditary character of any one of these organisms may be transmitted to a descendant of any other.' As has already been pointed out (section 4.5.7), the latter concept is, so far, quite impracticable in the Bacillariophyta, even were it flawless in theory (but see Sokal & Crovello 1970): the complete life-cycle is known only for a tiny minority of species, and it is in just one of these, Cocconeis placentula, that sufficient information is available to enable some progress towards the use of crossing behaviour in taxonomy (see Geitler 1973 for references). In any case, there are considerable problems in the application of the biological species concept to certain cases - viz. allopatric, allochronic or asexual populations -, problems which led Hull (1965b) to propose a 'disjunctive definition' of species, which extends the biological definition to cover difficult cases. Thus, he defined species as populations that

'1. consistently interbreed producing a reasonably large proportion of reasonably fertile offspring, or

'2. consistently serially interbreed with synchronic populations producing a reasonably large proportion of reasonably fertile offspring, or

'3. do not fulfil either of the first two conditions but have not diverged appreciably from a common ancestry which did fulfil one of them, or

'4. do not fulfil any of the first three conditions because they do not apply but are analogous to populations which do fulfil at least one of the first three conditions.'

As can be seen, conditions 3. and 4., in contrast to the first two, involve the use of phenetic criteria, but even so it is clear that Hull's definition offers little improvement on more 'orthodox' biological species concepts when the Bacillariophyta are under consideration: since we have virtually no evidence about interbreeding among diatoms, we lack the 'standard' against which conditions 3. or 4. may be judged. It must be noted that Hull did not regard his definition as exhaustive; rather, it was intended to be an indefinitely long, disjunctive definition, allowing the possibility of alternatives other than those above. It is difficult, however, to see what alternative may be proposed which is both harmonious with the above and yet applicable in the Bacillariophyta.

We must decide, therefore, what the aims of diatom taxonomy are to be and what methods are to be employed in attaining them. A 'biological classification' is not possible; a 'phylogenetic classification' is also out of the question - apart from any other reason, because of the inadequacy of the fossil record; we are left with phenetics and the type of species definition proposed by Sneath & Sokal (see above). Ecologists, physiologists, cytologists and others all need a system of classification which is sufficient for their different requirements, 'a general arrangement intended for general use by all scientists' (Sneath & Sokal 1973). This must be the diatom taxonomists' aim. Such a classification, called a 'natural classification' (ibid.), is based upon overall resemblance, taking into account as many characters as possible: 'experience shows that because resemblances or differences in a number of associated features in the plants making up a group are likely to apply to other of their features not considered in making the classification, a natural classification has a predictive value. Classification should therefore become more natural the more attributes we include in it' (Davis & Heywood 1963; see also Sneath & Sokal 1973).

Thus, in diatoms we must study all characters, not a select few; but are some characters inherently more important than others? (N.B. 'character' should be understood in the sense of Sneath & Sokal 1973, viz. 'a taxonomic character of two or more states, which within the study at hand cannot be subdivided logically, except for subdivision brought about by the method of coding'). Geissler (1970b) stated that 'Bei den Diatomeen hat sich aber immer wieder gezeigt, dass nicht alle Merkmale gleichrangig behandelt werden können. Kleine Differenzen im Rhaphenbau sind ohne Zweifel wichtiger als stärker auffallende Änderungen im Schalenumriss,' and therefore doubted the usefulness of numerical taxonomy, although she seemed to see hope in the modifications introduced by Kendrick (see Sneath & Sokal, op. cit.), which allow some weighting. Sneath & Sokal argue strongly, however, that character weighting should not be allowed; their arguments are worth quoting:

'1. If it cannot be decided how to weight the features, one must give them equal weight - unless it is proposed to allocate weight on irrational grounds.

'2. To create taxonomic groups, one must first decide how to weight the features that are to be employed for classifications. Therefore, one can use no criterion that presupposes the existence of these taxa. For example, one cannot choose the constant features - to know if they <u>are</u> constant one must first set up taxonomic groups, and these have not yet been established.

'3. The concept of taxonomic importance has no exact meaning. If 'importance' means 'important to me because I am interested in it,' this is only special pleading. If 'importance' means basic or fundamental, this can only mean that it sums up a number of other characters: if they are unknown, they are hypothetical; if known, the character is not single but multiple. If 'importance' means essential to survival, the taxonomy can estimate viability but not resemblance. If 'importance' means 'correlation with other features', then the added weight is due to these other features; where we observe the correlation breaking down, we do not regard the feature as important.

'4. If differential weighting is admitted, exact rules must be given for estimating it. One must know whether the weight to be given to the possession of feathers is twice or twenty or two hundred times that given to possession of claws, and why. We do not know of any method for estimating this, and even if such a method were to be developed we doubt if any systematist would have the patience to use it because of the hundreds of characters he would need.

'5. The nature of a taxonomy depends upon its purpose: a systematist could arrange living creatures in many ways but chooses one way because he thinks it is the best for some purpose. We hold the view that a 'natural' or 'orthodox' taxonomy is a general arrangement intended for general use by all kinds of scientists. ... It cannot therefore give greater weight to features of one sort, or it ceases to be a general arrangement. Being general, it is best for general purposes but is perfect for none.

'6. The property of 'naturalness' is, we believe, due to the high content of implied information that is possessed by a natural group ... The content of information is measured by the number of statements that can be made about its members: each statement has unit value, and whether we think them important or not is irrelevant.

'7. The use of many characters greatly evens out the effective weight that each character contributes to the similarity coefficient. Unless highly unequal weights are given to some characters, the very employment of many characters tends to make the taxonomy equally weighted.'

If, then, all admissable characters (an example of an inadmissable character being one which is a logical consequence of another) are to be used equally in the development of a classification, considerable problems are going to arise in the collection and analysis of data. There is no easy answer to the difficulties of collection: it is an inevitable problem of working with small organisms such as diatoms that information collection is lengthy and tedious. Indeed, diatoms are of a particularly unfortunate size and physiology in that they are not so large that the determination of morphological or chemical characters is simple, but not so small and 'vigorous' that their physiological habits may be investigated with ease (as with bacteria). It is

noticeable from the lists of numerical taxonomic studies provided by Sneath & Sokal (1973, Appendix A) that investigations of the larger plants and animals (especially the Spermatophyta, Chordata and Arthropoda) have been common, as have those of fungi, yeasts and bacteria, but that other groups, especially of unicellular, eukaryotic plants/animals have received hardly any attention at all. Nevertheless, there is no alternative, no short-cut: data must be collected. In the analysis of data, computer methods will undoubtedly be of service in the future. Unfortunately, time has not permitted the use of numerical taxonomic techniques during the present study, and analysis has had to be done by more subjective means. Before discussing some of the results obtained from this analysis, however, it would seem useful to consider some of the characters which may be usable in future taxonomic work.

As stated in Chapter 1, diatom taxonomy has come to be based upon the morphology of the siliceous elements of the cell. No satisfactory reason has been put forward, however, why other characters should not be employed in addition to the traditional frustule characters. Indeed, Ross (1963) proposed a return to a more broad-minded approach to classification, while Geissler (1970b) has also admitted the possible usefulness of chromatophore number, etc. as supplementary characters ('ergänzende Merkmale'). Cytological characters are perhaps the most obvious candidates for use in future taxonomic work, and some of these are discussed below.

Chromatophore number, shape and disposition were employed in Petit's (1877) classification, and were studied in a wide variety of genera by Karsten (e.g. 1897, 1899) and Mereschkowsky (e.g. 1901, 1903a, b). Within the Naviculaceae the chromatophores can be very useful in identification and probably also in classification, although no recent schemes have incorporated such data. Thus, in living populations it is easy to separate Pleurosigma from Gyrosigma, even though the valve structure may not be discernible, since the first has contorted,

ribbon-like chromatophores, while the second has more substantial, straight, plate-like chromatophores (unpubl. obs.).

In the Nitzschiaceae there is not much variation in the chromatophores: Hantzschia cells usually have one type of arrangement, Nitzschia cells another. There are some taxa, however, which have exceptional arrangements, e.g. in Nitzschia sect. Panduriformes or N. longissima/ventricosa, and so chromatophore arrangement would appear to be of some taxonomic value within this family. It may be thought that the difference in plastid structure between Nitzschia and Hantzschia would also support the idea of using this data in taxonomy, but here a caution is necessary (see also Mann 1977). As Mereschkowsky (1903a) noted, 'l'endochrome évite l'organe de mouvement' (in this case, the raphe). This is especially evident in the Naviculaceae, but less apparent in those groups (Epithemiaceae, Nitzschiaceae, Surirellaceae, Amphiprora) whose members have fibulate raphe systems: nevertheless, Mereschkowsky's 'rule' seems to hold, at least in part, for the Nitzschiaceae. Now if this tendency is merely correlated with the presence of the raphe, and not a logical consequence of it, then the chromatophore shape may be legitimately used as a taxonomic character in addition to raphe extent and position. However, the form of the 'endochrome' may be developmentally related to the raphe system, and this would negate the use of certain aspects of chromatophore morphology as characters. Thus, if the same cytoplasmic factor is responsible both for the positioning of the raphe during valve deposition and for the absence of the chromatophore from beneath the raphe, then clearly it would be foolish to score 'raphe position' and 'chromatophore absence ... ' independently. Indeed, a differentiation of the cytoplasm underlying the raphe in Caloneis sp. and Navicula cuspidata has been noted by Miss L.A.Edgar (pers. comm.) both during and after valve deposition.

Even in the second case, however, by no means all chromatophore

characters would be rendered inadmissable: within taxa with similar raphe structure and positioning there is often much variation in the plastids - in number, location, lobing, size, etc. (e.g. in the Naviculaceae, see Mereschkowsky 1901, 1903a). But the caveat noted above must be borne in mind when considering Nitzschia and Hantzschia: how much of the difference between them in chromatophore morphology might be the result of the difference in frustule symmetry?

Within the Bacillariophyta the pyrenoid has received little study and has not been used in taxonomy, this situation contrasting markedly with that in the Chlorophyta (Lund 1962). Various characters may be distinguished which ought to be considered in future work: these include the number of pyrenoids per chromatophore, and their size, shape and position. Thus, in Nitzschia some taxa have several pyrenoids per chromatophore (see N. sigmoidea, section 4.6.5), while others (e.g. many members of the sect. Lanceolatae) have only one, although in this it is likely that the smaller Nitzschiae 'have no choice' - their plastids are too small to bear more than one pyrenoid. In Hantzschia the pyrenoid is situated between two plates of the chromatophore, joining them, whereas in Nitzschia this is rarely so (but see N. navicularis). In other genera, e.g. Diploneis and Pinnularia, pyrenoid characters show greater promise (see Tschermak-Woess 1953): sometimes, for instance, the pyrenoids are penetrated by invaginations of the cytoplasm (e.g. in Caloneis, Diploneis and Pinnularia; Tschermak-Woess op. cit., L.A.Edgar pers. comm.), while elsewhere (Hantzschia, Nitzschia) they are not.

So far, observations have indicated that the dictyosomes will probably not be useful within the Nitzschiaceae. Elsewhere, or at higher taxonomic levels, however, the arrangement of these organelles should provide another character (see Gschöpf 1952). Especially notable are the paired Golgi structures in Pinnularia, Caloneis, Amphora and

Surirella (Gschöpf 1952, Drum 1966, my unpubl. obs.), otherwise known as 'Doppelplättchen' or 'Doppelstäbchen' (Heinzerling 1908, Lauterborn 1896, etc.).

In this dissertation it has been noted that the nuclei of some taxa (e.g. Hantzschia amphioxys, Nitzschia vitrea) stain strongly with aceto-carmine, while others (e.g. N. sinuata) give weaker reactions, sometimes taking up hardly any stain. While the staining technique requires some refinement, it seems that these differences in staining reaction reflect true differences in nuclear structure. Even in unstained, living cells it can be seen using light microscopy that in some taxa (Hantzschia spp., Navicula ?monilifera, Caloneis spp.) the nucleus is of a granular appearance whereas elsewhere it is ± homogeneous; it is in the 'granular' forms that stain is taken up most intensely, in such a way as to indicate that the chromosomes are more strongly condensed than is usual in eukaryotic interphase nuclei. EM observations of Caloneis (L.A.Edgar pers. comm.) agree with the LM work and suggest that these nuclei may be similar in structure to those of the Euglenophyta (see Dodge 1973). A further variation, in which there are two darkly staining 'plaques', one at each end of the interphase nucleus, is exemplified in some Navicula species closely related to N. cryptocephala, occurring in fresh- and salt-water (unpubl. obs.; see also Geitler 1951, Rudzki 1965).

Chromosome counts have been made on few diatoms, although Lauterborn (1896) was able to determine that 2n = 16 in Nitzschia sigmoidea, and Geitler (e.g. 1973) has made several counts. It is to be feared that in some cases accurate determination of chromosome number will be almost impossible since many diatom nuclei are small, and hence their chromosomes tiny, while the presence of the silica frustule makes adequate spreading of the metaphase plate difficult (unpubl. obs.).

The number of nucleoli per nucleus is probably a useful character:

TABLE 26

List of frustule characters which may be useful in taxonomic studies of the Nitzschiaceae.

1. Symmetry of the frustule about the median valvar plane.
2. Symmetry of the valve about the apical plane.
3. Symmetry of the valve about the median transapical plane.
4. Cincture width, relative to the frustule (measured at an agreed stage in the division cycle).
5. Length range.
6. Width range.
7. Shape of valve outline (several characters).
8. Position of raphe system on valve.
9. Course of raphe system (e.g. biarcuate).
10. Valve constructional type.
11. Linear density of costae.
12. Relative development of costae and frets, and variation in this across the valve (several characters).
13. Spacing of the frets.
14. Position of fret relative to costa.
15. Shape of poroid.
16. Size of poroid.
17. Rims around internal apertures of poroids (see Nitzschia tryblionella).
18. Position of hymen relative to poroid.
19. Hymen pore arrangement.
20. Cribra.
21. Volae.
22. Axial sternum.
23. Lateral sternum.
24. Warts on outer surface of valve.
25. Angling of valve at raphe.
26. Height of proximal mantle.
27. Height of distal mantle.
28. Marginal ridge.
29. Width of marginal strip.
30. Form of valve margin (e.g. wavy or straight).
31. Position of subraphe canal relative to general level of valve.
32. No. of longitudinal rows of poroids within the subraphe canal.
33. Doubling of striae within the canal.
34. Poroids between the helictoglossa and the valve margin at the pole.

35. Form of internal central raphe endings.
36. Presence of a 'knob' just distal to the int. cent. r.e.
37. Form of the external central raphe endings.
38. Form of the external polar raphe endings.
39. Interraphe distance.
40. External flaps of silica.
41. External flanges bordering the raphe fissure.
42. Fibula morphology (several characters).
43. Longitudinal ridges joining the fibula bases.
44. Cingulum structure (many characters).

there is one per nucleus in N. linearis, H. amphioxys and various others, but several in N. sigmoidea.

The Bütschli globules require further investigation in order to determine how much they are affected by environmental conditions, but preliminary observations indicate that within Nitzschia their size may be of use (small in N. sigmoidea, large in N. sigma, etc.).

The silica elements of the cell provide a multitude of characters: those relevant to the Nitzschiaceae are listed in Table 26. Some of these have been used before, others are old characters modified, and the remainder are new, usually because they were formerly undetectable. Problems arise in the use of cincture elements to provide characters, since at this stage in our knowledge it is not possible to determine whether one is comparing like with like. If every diatom had the same number of bands comparisons would not be difficult, but as it is, if we compare 1^{st} band with 1^{st} band, 2^{nd} with 2^{nd}, etc., then frequently we will compare the most abvalvar band in one diatom not with the most abvalvar band in another, to which it is usually very similar, but with whatever band is 'numerically' equivalent to it: this would not appear to be very satisfactory. Moreover, we have no means of knowing, except by phylogenetic speculation, which bands are equivalent in cinctures with differing numbers of elements, and we cannot presuppose (as did Von Stosch 1975) that there are at most only two or three types of band present and force comparisons between these. The cincture promises to provide many taxonomic characters, but the distinguishing of these and their coding is likely to be the most difficult part of any projected taxonomic study.

Cellular functions provide another source of taxonomic data. Thus, colony formation (which is often correlated with the presence of morphological features such as linking spines, etc.) and the method of auxospore formation can provide additional characters. The problem

with reproductive characters is the difficulty of obtaining information.

Ecological, distributional and physiological data could also be used in systematics (Sneath & Sokal 1973). However, it is difficult to determine the ecological preferences, distribution etc. of a species or variety or higher taxon if this is not already adequately characterized. Thus, for the moment I recommend that ecological data are used only as a check on the validity of classifications based on the morphological, cytological and other features discussed above.

Future progress in diatom systematics depends, then, on the accurate analysis of the variation pattern on the basis of as many characters as possible. The effect of equal weighting, advocated above, will be to remove the bias towards certain characters shown in the present system: there are no special 'familial', 'generic' or 'specific' characters, and the variation pattern cannot be expected to follow set rules. Thus, it should not be surprising to us that within an apparently natural grouping such as the '*Obtusae*' group (*Nitzschia* sect. *Nitzschia*) there is considerable variation in the position of the raphe, from ± central in *N. vidovichii* to strongly eccentric in *N. filiformis*, whereas in other sections or genera, e.g. *Nitzschia* sect. *Fragilariopsis*, *Navicula*, *Diploneis* and *Pinnularia*, the raphe position is virtually constant; or that the internal polar raphe endings are monotonously alike throughout the Nitzschiaceae, but vary within *Cymbella*; or again that the internal and external central raphe endings are ± identical throughout the '*Nitzschiae Obtusae*' (see above), but vary within *Hantzschia virgata*; etc.

The finding of extensive infraspecific variation within *H. amphioxys*, *H. marina*, *H. virgata* and *H. distinctepunctata* forces the conclusion that each 'species' must be sampled very thoroughly before confident statements may be made about its taxonomy. It is not suffic-

ient to study only the type material, although this must be examined, of course, in order to determine the correct application of taxa names.

It is interesting that such a degree of infraspecific variation should occur within the species listed above, but apparently not within such taxa as Nitzschia communis. One suspects that there must be something atypical in the reproductive biology of these Hantzschiae that allows such a variation pattern to develop: perhaps they are largely apomictic, each morphologically distinct population representing a clone derived ultimately from a product of a rare sexual 'event'. Such thoughts are encouraged by the consideration that three of these species (H. marina, H. virgata and H. distinctepunctata) live in the same habitat, viz. marine intertidal sand, an environment subject to great and varied stresses - extremes of temperature and salinity, frequent burial and disturbance, etc: the species living here may not be able to 'afford the luxury' of producing ill-adapted (as well as successful) sexual recombinants, even if the stresses in fact allow conjugation. Polymorphy, as exhibited by these Hantzschiae, is frequently a feature of apomictic populations (Stebbins 1950). In the same habitat species of other genera also seem to show infraspecific variation, examples of these being Navicula lyra and Caloneis sp. To say that the taxa mentioned may not be species, but aggregates of species, does not solve the problem, since one still has to explain why the pattern of variation is as it is.

During the present study some interesting structures have been observed in members of the Nitzschiaceae, and these deserve attention apart from that due in relation to taxonomy. Several species (Nitzschia sigmoidea, N. recta, N. dissipata, members of Nitzschia sect. Spathulatae, and probably N. vermicularis and N. flexa) have been found to possess external, non-porose flaps of silica. These spring from near the raphe and extend some distance across the valve face, enclosing

canals which usually (but see N. sigmoidea) open to the surrounding medium near the valve apices: the canals are external to the cell plasmalemma and seem to be empty in vivo (L.A.Edgar, unpubl. obs. of Nitzschia sp.). The function of these structures, found also in a couple of marine littoral species of Navicula and in some Amphora species (unpubl. obs.), is unknown.

All sufficiently well studied species of Nitzschia, Hantzschia and Bacillaria have been found to possess hymena. The arrangement of the hymen pores varies, but their size is ± the same throughout. Except for the raphe-slit (and the junctions between the girdle bands?), these pores must represent the route by which all nutrients, exported metabolites, etc. enter or leave the cell, presuming that the silica is quite impermeable to these. The function of the hymen, however, is unknown; is it, perhaps, a mechanical necessity, providing support for the plasmalemma given the higher osmotic pressure of the cytoplasm relative to that of the environment (Guillard 1962) and the absence of a contractile vacuole?

Within the raphid pennate diatoms the 'ultimate' pore occlusions seem to fall into two distinct types. The first is the hymen, found not only in the Nitzschiaceae, but also in many Navicula species (but ?not in N. lyra), Amphora, Gyrosigma, Pleurosigma (F.571-3), Amphipleura (Cox 1975a), Frustulia (ibid.), Berkeleya (Cox 1975b) and many other genera (see Helmcke & Krieger 1953-). As has already been noted (Chapter 3), in Cocconeis and Anorthoneis the plates closing the areolae are slightly different, with elongated, not round pores, and this is true also in Amphiprora (q.v.): in both these and Diploneis (which has a further slight variation - F.574), however, the pore occlusion is hymenate. In the second type the occlusions are 'volate' (see Chapter 5), and communication between cell and environment is conducted via narrow, usually arcuate slits between vola and vola, or between vola and areola wall. Such occlusions are found in Epithemia, Rhopalodia,

some Gomphonema species and probably Navicula lyra. A modification of this type where the volae extend out not from the areola wall, but from the bars of a cribrum, is found in those Achnanthes species (A. coarctata, A. brevipes, etc.) classified in the Achnanthidium group, while within the centrics and araphid pennates volate occlusions are to be found in Coscinodiscus nitidus and Raphoneis spp. (unpubl. obs.). There appear to be no intermediates between the volate and hymenate types; it is interesting, though perhaps coincidental, that the volate taxa are for the most part sedentary forms.

Within the Bacillariophyta it is often difficult to relate structure to function; two examples have been given - external flaps and pore occlusions - where the purpose of a structure is not yet known. Elsewhere a function is easier to detect: for example, the pore fields and ocelli of Gomphonema, Striatella, etc. are clearly related to the ability of these taxa to form mucilage stalks or pads. With regard to the raphe, this has long been known to be involved in locomotion, although the exact mechanism of motility remains a mystery. Several matters may be mentioned, however, which derive from the present study and may have a bearing on the elucidation of this mechanism.

It has been noted that the internal polar raphe endings are virtually uniform within the Nitzschiaceae: whatever the species, there is always a simple helictoglossa. Moreover, this structure is ± identical in most other raphid diatoms, only varying when there is in the vicinity a pore field through which mucilage is extruded: thus, the internal polar endings of Cymbella species are often hooded (Cox 1976). It would appear, therefore, that the helictoglossa is an essential part of the raphe, and that its morphology is probably highly relevant to raphe function. Also, terminal fissures seem to be essential for anything but the slowest movement: thus they are absent from those taxa - Nitzschia sects. Fragilariopsis and Pseudonitzschia, Epithemia, Eunotia, etc. - which are only slowly, or non- motile, but present in

other groups. The central raphe endings are more variable both internally and externally; perhaps, therefore, their morphology is less relevant to the basic mechanism of motility. Indeed, many of the Nitzschiaceae have been found to lack central raphe endings. Outside this family this phenomenon is to be noted in very few organisms: central raphe endings are present in all of the Naviculaceae and Epithemiaceae (sensu stricto, see below) except Rhopalodia gracilis, while in the Surirellaceae there are always two sets of endings per valve. In the last group, however, it must be pointed out that the raphe-slits do run unbroken from pole to pole, and thus they should, perhaps, be regarded as functionally equivalent to those Nitzschiaceae without central raphe endings. Is it a coincidence that central raphe endings are absent only from taxa with fibulate raphe systems? If the central raphe endings are not essential for motility itself, then perhaps their function is in part mechanical - a necessary truss between the two sides of the valve in those diatoms without fibulae. It is noticeable that in the larger Navicula species the central raphe endings are usually well separated and the raphe-sternum is very strongly silicified, whereas even in the largest Nitzschia species the raphe-sternum is not well developed and the interraphe distance is small (Nitzschia sp.B Eilat) or 0 (N. sigmoidea). I suggest, therefore, that one of the primary functions of the fibulae is to prevent the movement of one side of the valve relative to the other, and that in this they obviate the need for central raphe endings. This is probably not the only function of the fibulae, however, since they also have the effect of separating the cytoplasm immediately under the raphe from the remainder of the cell, thus allowing the chromatophore to occupy a greater portion of the peripheral cytoplasm than would otherwise be possible, and probably also facilitating motility.

One other observation may be relevant here. Pleurosigma angulatum, which has a sigmoid raphe system, interrupted centrally, moves in

sigmoid paths, reversing frequently (unpubl. obs.). As it begins movement again after a stationary period or a reverse, the front half of the diatom is in contact with the substratum and the cell follows a path corresponding to the curvature of the raphe on that half; as the diatom proceeds, however, it rocks back onto the posterior half of the cell and the path becomes straight, and then exhibits a curvature opposite to that followed at first. Nitzschia sigmoidea and N. sigma, however, do not follow sigmoid paths, in spite of the fact that their raphe systems are sigmoid, but move in simple curves or straight lines, as do other Nitzschia species. It is impossible to say whether these differences are owing to the presence/absence of central raphe endings, but clearly there is some difference between Pleurosigma and Nitzschia in raphe function, even though the courses of the raphe system are similar.

Another interesting point about Nitzschia is that the raphe often (always?) 'makes no distinction' terminally between the proximal and distal sides: the terminal fissures may be directed toward either side (see N. mollis var. africana, N. sinuata, N. communis, etc., and also Denticula tenuis). In Amphora or Cymbella, whose valves are also asymmetrical about the apical plane, the terminal fissures always point in the same direction within a species, and in most Hantzschia species, but apparently not in H. fenestrata which is like Nitzschia (unpubl. obs.), only distal curvatures are to be found.

With regard to the taxonomy of the Nitzschiaceae, the present study indicates the need for several changes in classification. It was mentioned in section 4.1 that the traditional description of the Nitzschiaceae is inadequate. The family itself, however, seems to be a valid, natural grouping, and so it would be useful to have a description or definition of the group which might be used in identification. Fortunately, there is no need so far of a disjunctive definition of

the Nitzschiaceae since just a few characters have been found which appear to be common to the family as a whole, and which, taken together, distinguish it from any other. Thus, the possession of hymena in which the pores are circular, and a fibulate raphe system of a length which is less than ½ of the valve circumference, serves to refer an organism to this group. This characterization should be regarded, however, not as an inviolable 'rule' by which the Nitzschiaceae stands or falls, but as the first alternative of an indefinitely long, disjunctive definition of which the other alternatives are as yet unknown. Who can tell if some exceptional organism may not yet be found which clearly belongs to the Nitzschiaceae (judging by the whole gamut of characters), yet, for instance, lacks hymena.

The definition given is not the basis for the family, but a consequence of its recognition. The Nitzschiaceae has been reckoned valid on the basis of many characters, and it is possible to make the following additional statements about it:

Cells active and solitary, or planktonic/sedentary and colonial, the first alternative predominating. Cells usually linear or linear-lanceolate, isopolar and 'spiegelsymmetrisch' or 'diagonalsymmetrisch' about the median valvar plane: valves usually asymmetrical about the apical plane since raphe system is usually eccentric. Most often, valve constructed of transapical costae alternating with single rows of round/oval poroids in which there are hymena. Valve face rarely corrugated. Fenestrae (sensu Paddock & Sims 1977) hardly ever present. Raphe system usually lying ± in one plane, fibulate; fibulae not often extended across the whole width of the valve, usually discrete, and all ± alike within a valve. Central raphe endings often absent; when present, usually coaxial-symmetrical and without central fissures. Internal raphe fissures not bordered by prominent ridges, external fissures often bordered. Internal polar raphe ending, a simple helictoglossa; terminal fissures usually present, unbranched. Cincture ± the same width on both sides of the frustule, although bands may show dorsiventrality. Chromatophores usually 2 in number, arranged ± symmetrically about the median transapical plane. Nucleus central.

The more important conclusions about taxonomy reached as a result of this study are the following:

a. Denticula elegans, D. tenuis and D. thermalis, and probably D. linearis, D. bacillum and D. parva, should be transferred from the Epithemiaceae to the Nitzschiaceae, and placed near Nitzschia sect. Grunowia.

b. The marine planktonic Denticula group (including D. seminae etc.) should also be transferred into the Nitzschiaceae, but placed near Fragilariopsis. Since D. elegans is the type species of Denticula, a new genus is probably required.

c. The 'Sumatran' Denticula species (including D. vanheurckii etc.) should be left in the Epithemiaceae and either united with Epithemia or included in a new genus.

d. The Epithemiaceae, modified as above, is a natural grouping.

e. Amphiprora should be included in a new family, probably with Auricula.

f. Hantzschia is a 'good' genus and should be retained.

g. Within Hantzschia the distinctness of H. marina should be recognized by the erection of subgenera.

h. The groups Panduriformes, Dubiae (sensu Hustedt 1956), Grunowia, Epithemioideae, Pseudonitzschia and Fragilariopsis (sensu Hasle 1972b), all at present classified as sections of Nitzschia, are probably all natural groupings.

i. Nitzschia sect. Tryblionella (sensu Hustedt 1930) is a heterogeneous group. The 'Pseudotryblionella' group (including N. jelineckii, N. graeffei, N. rabenhorstii and N. salvadorina) should be separated from it, as should the 'Apiculatae' and the N. navicularis group. New sections/genera will be necessary.

j. Nitzschia sect. Tryblionella should be understood to refer only to the N. tryblionella group of species.

k. Nitzschia sects. Panduriformes, Tryblionella (sensu j.) and 'Apiculatae' should be investigated thoroughly and perhaps placed in a separate genus.

l. N. angustata is misplaced and should be transferred out of the sect. Tryblionella to a position near the sect. Lanceolatae.

m. N. amphiprora and N. ocellata do not belong together, and thus the

sect. Pseudoamphiprora is heterogeneous. N. ocellata should be placed near the sect. Perrya, and N. amphiprora in the sect. Dubiae.

n. Sect. Perrya is probably a genus in its own right.

o. The sects. Insignes and Scalares should be combined.

p. The close relationship between the sect. Spathulatae, the 'Sigmoideae', N. recta and N. dissipata should be recognized taxonomically.

q. Nitzschia sect. Nitzschia should be split into four groups corresponding to Grunow's sects. Sigmoideae (which should be called 'Nitzschia'), Sigmata and Obtusae, and an unnamed group including N.?clausii and Nitzschia sp.B (Eilat). Each group should be given sectional status.

r. The sects. Lineares and Dissipatae are unnatural groupings requiring further detailed study.

s. N. dissipata and N. recta should be placed in the same section.

t. N. lorenziana should be transferred from the sect. Nitzschiella to the Sigmata.

u. The sect. Nitzschiella should be retained, but a group of species including N. acicularis removed and transferred to the sect. Lanceolatae.

v. The sect. Lanceolatae, as modified above, is probably natural. It should be tackled using numerical taxonomic methods.

w. The genera Cymbellonitzschia and Gomphonitzschia are probably not natural groupings: cell symmetry has been overstressed at the expense of other characters.

x. The sect. Fragilariopsis is probably worthy of generic status.

An attempt has been made to represent the major groupings in a 2-dimensional display (see chart); the separation of the groups was done subjectively, but was based upon as many characters as possible. While a 2-D diagram cannot hope to do justice to the complex interrelationships indicated by the variation pattern and thus cannot help but be misleading on occasion, it is hoped that the diagram will be useful.

As a check on the conclusions offered above, consider some of their effects on the distribution of ecological characters.

The sect. Panduriformes are marine, and usually occur in the benthos of the littoral region (unpubl. obs., Peragallo & Peragallo 1897-1908, Cholnoky 1963a, Giffen 1975, 1976, etc.).

The 'Pseudotryblionella' group (N. jelineckii, N. graeffei, etc.) are also all marine (Cleve & Grunow 1880, Hustedt 1952), while the N. tryblionella and N. apiculata groups contain both freshwater (N. debilis, N. tryblionella, N. hungarica, etc.) and marine forms (N. circumsuta, N. nicobarica, etc.), but it should be added that the freshwater forms are restricted to more eutrophic situations, and often 'stray' into brackish localities (e.g. N. apiculata in the salt-marsh at Sandbay). By contrast, N. angustata occurs only in freshwater: Kolbe (1927) classified it as an 'Oligohalob', and it is often to be found in conjunction with such species as Denticula tenuis, D. elegans, N. amphibia and Epithemia spp., which tend to indicate calcareous conditions (unpubl. obs., Round 1957, 1958a, 1959, 1960). Ecological considerations, therefore, support the reclassification of this species. Note also that N. angustata is ecologically and morphologically similar to N. amphibia.

The sect. Grunowia consists entirely of freshwater species; the resemblance between N. sinuata, N. solgensis and N. denticula, and Denticula tenuis and D. elegans in morphology is reflected in ecological similarities, since all are indicators of base-rich conditions (unpubl. obs. and Round 1959). Thus, ecological considerations permit the transfer of Denticula (sensu stricto) to a position near the sect. Grunowia, although they would also support a classification near Epithemia.

The sect. Nitzschia sensu Hustedt (1956) contains species with a great variety of different ecological preferences. The morphological distinctness of the 'Sigmoideae' is reflected in the fact that this is

a mostly freshwater group, whereas the other three sigmoid groups reach their maximum developments in brackish/marine waters. The '*Sigmoideae*' are similar to *N. dissipata* and *N. recta* in ecological requirements, but the other group with external flaps, etc., the sect. *Spathulatae*, is exclusively marine.

The *Insignes-Scalares* are all brackish or marine forms (see Peragallo & Peragallo 1897-1908, etc.).

The separation of the *N. acicularis* and *N. longissima* groups of the sect. *Nitzschiella* is supported by the fact that the first is predominantly freshwater, the second exclusively marine. The suggestion that *N. lorenziana* belongs near *N. sigma* is allowed by their ecologies: both are brackish-water forms (Hustedt 1930).

Pseudonitzschia and *Fragilariopsis* are marine.

The Nitzschiaceae is a difficult group, full of problems for the taxonomist but full of interest. The family is so large that it could not be expected that a few years would be sufficient to 'clear up' its taxonomy. This has meant, for instance, that perhaps the most important group within it - *Nitzschia* sect. *Lanceolatae* - has been dealt with only cursorily in this dissertation. Nevertheless, it is hoped that this preliminary study has distinguished some of the most critical gaps in our knowledge, posed relevant questions, and provided some useful suggestions as to how the gaps may be filled and the questions answered.

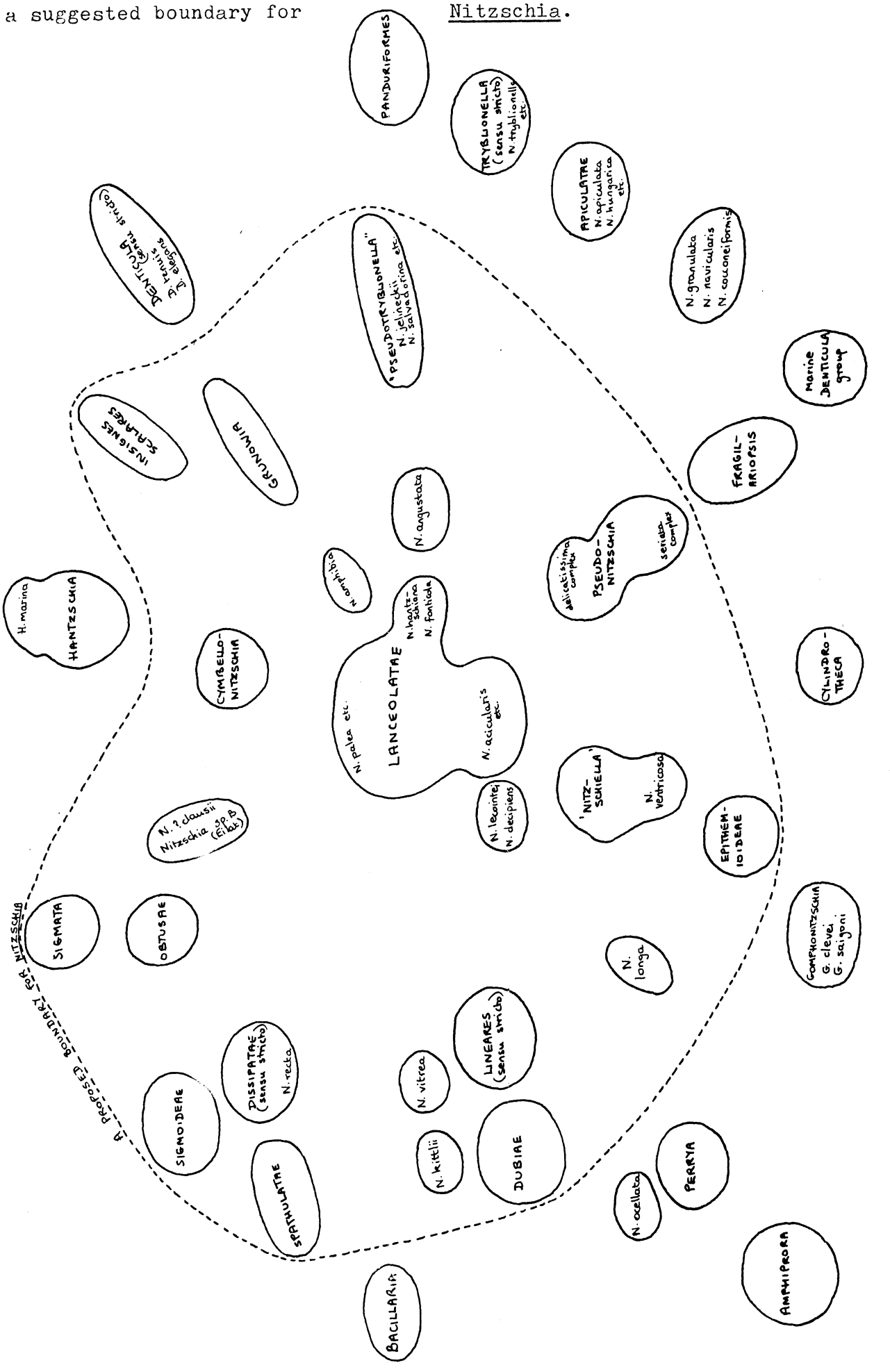



Chart: an attempt to show some of the suggested relationships within the Nitzschiaceae by means of a 2-dimensional display, and a suggested boundary for Nitzschia.