

The cytoplasm is restricted to a thin peripheral layer except at the centre (see above), and near the apices of the diatom (F.136-7), the rest of the cell interior not occupied by chromatophores or nucleus being filled by a large vacuole.

4.5.7 Intraspecific variation in Hantzschia

Most recent taxonomic work on diatoms has been concerned with the delimitation of genera and the higher categories, or with the re-allocation of misplaced species (e.g. see Cox 1975a, b, Dawson 1973a, b, 1974, Evensen & Hasle 1975, Hasle 1972b, 1973a, b, 1975, Round 1970a, b, 1972a, b, 1973, etc.). There have been few studies where intraspecific variation has been considered, although a certain amount of information is to be found within papers such as those listed above and in two papers by Geissler (1970a, b). Yet obviously it is necessary to have a clear idea of the type and magnitude of variation present within species before an accurate assessment can be made of the significance of interspecific or intergeneric differences. During preparation of a paper presented at the Fourth Symposium on Recent and Fossil Marine Diatoms (Mann 1977), it was noted that several characters of the frustule show variation within H. marina, as this taxon is presently circumscribed. This was subsequently investigated in greater detail, and companion studies made of H. virgata and H. amphioxys.

4.5.7.1 H. marina

This species was first described by Donkin (1858) from intertidal sand in Northumberland, and on the basis of his observations, limited by the microscope lenses in current use, he assigned it to Epithemia, an assessment which was doubted by Roper (pers. comm. to Donkin 1858), who considered it to belong in Nitzschia. Walker-Arnott (1858) claimed that the taxon had already been named E. radula by De Brébisson, but in a reply Donkin (1859) asserted that De Brébisson, on his own admis-

ion, had published no description and that 'he had adopted all my names for those particular species, with which he was previously acquainted.'

Grunow (in Cleve & Grunow 1880) transferred the taxon to Hantzschia and placed it in the monotypic 'Gruppe: Pseudoepithemia', believing like many subsequent authors that the pronounced transapical thickenings of the valve are inwardly directed extensions of the fibulae. The falsity of this (see above, and Mann 1977), in conjunction with certain other inaccuracies of the original and subsequent descriptions (e.g. Donkin's belief that the girdle is hyaline on the ventral side, a belief probably engendered by the collapse of the girdle during slide preparation), requires the development of a new description which will truly define the species.

Intensive studies have been made of two samples, one obtained from marine intertidal sand at Aberdeen, the other from a similar habitat in Cornwall (see Appendix 1). Also examined were samples from Borth, Sandbay, Montrose, Newgale and Portland, all again from marine intertidal sand.

During SEM examination of the Aberdeen material, it was noted that certain H. marina cells differed from the majority in the construction of their areolae; subsequent examination showed this to be correlated with various other differences, making it possible to separate the total H. marina complement into two distinct populations. Later, examination of the sample from Cornwall revealed a similar division, but the Cornish populations both differed from either of the Aberdeen types. These four will be referred to as the A₁, A₂, C₁ and C₂ populations respectively.

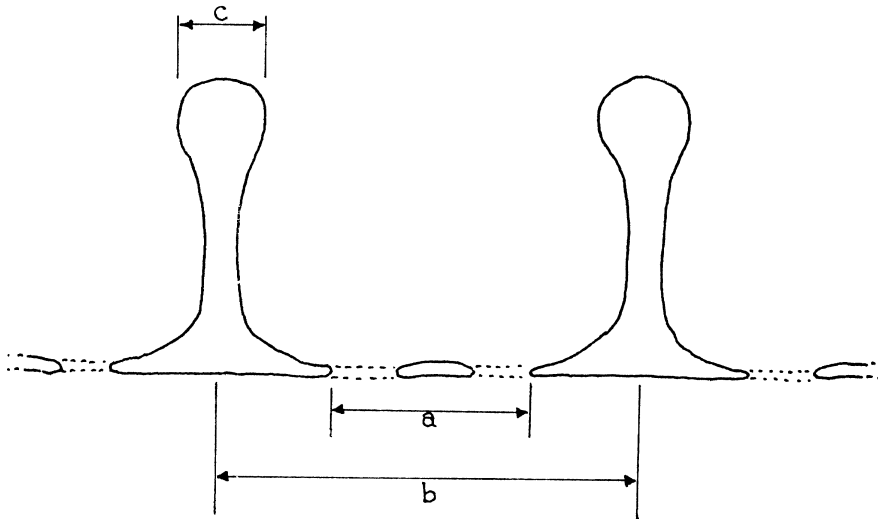
Valve structure and size

All the populations possess the same basic construction described above in section 4.5.2, but they differ in the dimensions of the

TABLE 1

Hantzschia marina - variation between the A & C populations
in valve dimensions, etc.

Character:	Population: A1	A2	C1	C2
Valve length ($\mu\text{m.}$) N.B. this may not represent the total length variation exhibited during the life-cycle.	45-95	100-130	65-80	75-115
Valve width ($\mu\text{m.}$) (at centre)	7-8	10-12	6.5-7.5	10-13
Valve depth ($\mu\text{m.}$) (at centre)	3.8-4.4	6.8-7.0	4.4-5.4	6.6-7.6
Hoops - no. in 10 $\mu\text{m.}$	7.2-7.6	6.0-6.6	7.6-8.0	4.4-5.0
Ratio A*	0.55-0.70	0.45-0.55	0.55-0.65	0.55-0.75
Ratio B**	0.23-0.25	0.38-0.44	0.33-0.40	0.19-0.24
Size of poroids	++	+	++++	+



* Ratio A = $\frac{a}{c}$

** Ratio B = $\frac{c}{b}$

various components. C_1 cells have 7.6-8.0 hoops in 10 μm . (F.4) while at the other extreme C_2 cells have 4.4-5.0 (F.3); the A_1 and A_2 populations are intermediate, having 7.2-7.6 (F.2) and 6.0-6.6 (F.1) respectively. There are also differences in the ratios of maximum hoop width and 'strial strip' width to interhoop distance, etc. (F.575-578).

Similarly, the populations differ with respect to the valve length, width and depth. This is of particular help in distinguishing between the A populations, where the difference in hoop spacing, although diagnostic, is not obvious; the difference in valve depth, however, is very marked (F.21, 25). The variation in the dimensions of the fundamental 'building blocks' of the valve, and of the valve itself, is summarized in Table 1; it can be seen from this that it would be quite possible to separate the populations on the basis of these characters alone.

Areolae

The poroids of A_1 thecae are reniform or oval in outline, and are closed by hymena, the pores of which are in hexagonal array (F.521, 578). In the valve poroids the hymena appear to be composite, since, within a single hymen, it is possible to distinguish several sectors which differ in the orientation of the lattice (F.521, and see Mann 1977, f.26, 27). The hymena in the poroids of the first two bands are not composite (F.523), but again the hexagonal array is present. By contrast, the hymen pores of C_1 or C_2 valves are not regularly, but randomly arranged (F.522, 525) and, as in H. virgata (Mann 1977, f.29), it is not possible to distinguish different sectors within the hymena. The hymena of bands and valves are again similar (compare F.524 with 525): in the populations studied, therefore, the hymena of a single theca are either all of the hexagonal type, or all of the random type.

There is also variation in the outline of the areola. A_1 cells vary from those where the overwhelming majority of the areolae are reniform (F.611) to those where there is a high proportion of oval areolae (F.578). Sometimes, in the reniform type, there are two projections into the lumen of the areola instead of the usual one. The poroids of A_2 cells, however, possess cribra (F.577, 608-10); these are occasionally incomplete and then they take a form reminiscent of the occlusions of C_2 poroids (see below). C_1 cells have the simplest poroids - oval in outline with no other occlusion save the hymen (F.522, 576, 602-3) - whereas the reniform poroids of C_2 valves (F.3, 5-6, 9, 10) are partially occluded by one or two prominent projections which usually branch two or three times dichotomously (F.525, 575, 588, 589), although variations on this are quite common.

Raphe and associated structures

Internally the central raphe endings of cells from all populations are remarkably similar and are of the type also present in H. virgata var. intermedia and H. amphioxys: they are noncoaxial-asymmetrical (see elsewhere, and Mann 1977). The ends of the internal fissures are frequently both slightly bent towards the distal margin (F.593). The knob described before (near end of section 4.5.4.5), which lies near the central raphe endings, is present throughout, though variously developed - very prominent in A_2 cells (F.609), less so in C_2 (F.593).

Externally the central raphe endings are more variable, deflected towards the proximal margin in some cells, straight in others. Within the A_1 population some cells have very simple endings (Mann 1977, f.49), but a small ridge may also be present just distal to the raphe (F.607); A_2 and C_2 cells, however, have strongly deflected raphe endings (F.606, 587).

At the poles, the external fissure is in all cases abruptly bent above the presumed position of the helictoglossa (F.586), but populations

differ with regard to the course of the terminal fissure. In the C₂ population it is ± straight (F.584-5), whereas in the others the terminal fissure is again bent, abruptly, at the edge of the marginal strip, so that it comes to run more or less parallel to the distal margin (F.605, 610, and see Mann 1977, f.47).

The fibulae are of virtually identical form throughout, being of the same size relative to the valve and with adjacent, distal fibula bases always 'enclosing' the first two poroids of an interhoop series (F.589, 603, 608, 611). Nowhere are the fibulae extended into trans-apical costae. The spatial relationship between the fibulae and the 'hoops' and poroids of the proximal mantle is rather variable (F.6, 20, 609, 611).

There appears to be little difference between the populations in the degree by which the raphe canal is elevated externally above the general level of the valve: the canal is no more developed, relative to the rest of the valve, in the largest cells of the C₂ and A₂ populations than it is in the smallest of the A₁ population. In no case have perforations been observed in the canal wall: the raphe-sternum always reaches to the fibulae.

The features noted above, which have proved (so far) to be constant within H. marina, are worthy of note because of their inconsistency within other taxa, e.g. H. amphioxys and H. virgata.

Cincture

The girdle of A₁ cells was described in part by Mann (1977), but recent observations require a revision of certain conclusions then made. It has been found that, whereas the 'valvocopulae' (i.e. first bands) of A₁, A₂ and C₁ cells are open (F.22 and Mann 1977, f.47; F.27-28; F.33, 604), those of C₂ cells are not (F.590-1). This last phenomenon is observable using the light microscope (F.9, 11), and

appears to be quite constant throughout the C_2 population. Furthermore, it is now clear that the girdle of H. marina can be more complex than was thought earlier. Five bands, not three, may be distinguished, at least in C_2 cells: the first two are similar to those described for A_1 cells (Mann 1977), the third and fourth are more or less like the third of A_1 , while the fifth is unlike any of the others. Thus, it is possible to distinguish three groups of band morphologies in C_2 cinctures, although each of the five bands differs in some way from any of the others and may be identified even when isolated from its context; these groups are:

Group 1. (comprising bands 1 and 2)

The first two bands correspond to the 'valvocopula' and 'copula' described by Mann (1977). Both bear two transversely aligned rows of round poroids, these being more closely spaced transversely on the second band than on the first (F.7-8, 10). The first band, moreover, is wider than the second in both distal and proximal halves. The partes exteriores of both thin only gradually towards their abvalvar margins and are only a little thicker than the corresponding partes interiores. The second band bears no ligula, correlated with the fact that the first band is closed (F.596, 599). The proximal and distal halves of either band often differ in width and in poroid spacing (F.7, 10, 12).

Group 2. (comprising bands 3 and 4)

These each bear but a single transversely aligned row of poroids (see the 'pleura' of Mann 1977), which are usually elongated longitudinally, often triangular (F.598), and of very varied size (F.7, 10, 15-19). The distal half of the third band bears much larger poroids than, and is a third as wide again as, the proximal half (F.7, 15-17). The fourth band is more finely marked than the third (compare F.19 with 15, and see F.598). Both possess a prominent ridge which runs internally along the junction of the pars exterior and the pars interior, although

the ridge is present on only the distal half of band 4 (F.7, 15-19, 597). The ridge diminishes abruptly in depth towards either margin of the band and thus appears in the light microscope as a dark line, tangential to the advalvar boundaries of the poroids.

Both bands bear ligulae centrally where they underlap the open ends of the adjacent cincture element (F.16, 595-6, 599). In the case of the third band the ligula is so long that in vivo it must project well beneath the first band.

Group 3. (comprising band 5)

The fifth band is narrow (F.7, 598-9) and without the internal ridge of Group 2 bands. It is delicate and apparently structureless, and is thus difficult to observe with the light microscope. Again, it bears a ligula centrally (F.595, 599).

In other populations all five bands cannot always be distinguished even in what appear to be complete frustules (e.g. Mann 1977, f.45), but, though it is possible that this is because of infraspecific variation, it is more likely to be the result of the fairly vigorous acid-cleaning methods used. The first three bands of A_1 , A_2 and C_1 cells would seem to be quite similar to those of C_2 cells, except that their first bands are open (F.22-24, 26-29, 33-35).

Certain other features of the cincture are worth note. The proximal end of the second band (at least in A_1 , C_1 and C_2 cells) is somewhat expanded, whereas the distal end is of more or less the same width as the rest of the distal half (F.14, 24, 33, 35, 599). In C_2 cells, and perhaps in other populations, the first band narrows at each pole (F.9), while the second is no wider centrally than elsewhere (F.596). Hence 'gaps' are left to be filled both at the pole where the open ends of band 2 are situated and at the other pole. The open ends of band 2 are underlain by the prominent ligula of band 3 (see above

TABLE 2

Some measurements of the bands of Hantzschia marina frustules.

1. Variation in poroid spacing (all figures being nos. in 10 $\mu\text{m}.$).

	population: A1	A2	C1	C2
<u>1st band: distal half</u>				
advalvar row	10.6	9.0	10.2	7.2
abvalvar row	11.6	9.1	10.0	7.0
: <u>proximal half</u>				
advalvar row	11.0	10.0	9.9	6.4
abvalvar row	11.1	9.0	10.4	6.4
<u>2nd band: distal half</u>				
advalvar row	13.6	-	15.4	8.5
abvalvar row	14.3	-	16.0	8.7
: <u>proximal half</u>				
advalvar row	15.5	-	15.4	8.5
abvalvar row	15.5	-	17.0	8.3
<u>3rd band: distal half</u>	-	7.5	14.3	5.0

2. Width of first band (in $\mu\text{m}.$)

	population: A1	A2	C1	C2
distal half	4.0	6.2	3.4	7.0
proximal half	3.1	5.3	2.3	5.7

and F.599); at the other end, the 'gap' is filled, partly by the ligula of band 4, but also by the curiously extended proximal end of band 3 (F.17-18, 596).

Just as the dimensions of the valve, linear density of the hoops, etc., vary between the populations, so also do the dimensions etc. of the bands (see Table 2). The poroids of the distal half of the third band are especially variable, in size and spacing (even within the same population); in the A_2 and C_2 populations these poroids are large, often larger than those of the corresponding group 1. bands, and usually very broadly triangular (F.15-17, 29); those of the distal halves of A_1 and C_1 cells are rather narrower (Mann 1977, f.45; also F.34), while those of the proximal halves of the third bands in all populations are elongate-ovate.

Discussion

It would be possible on the basis of the foregoing to give each of the four populations formal taxonomic recognition. A_2 cells, for example, could be separated as a taxon diagnosed by the presence of complete cribra, the particular linear density of the hoops, the dimensions of the valves and girdle bands, etc. In fact, each population is quite distinct and no cell of any one population could be confused with a cell of any other.

Were one to adopt the species concept outlined by Petersen (1950) in which 'a difference in the number of stripes between two types...' (constitutes) '..a strong argument in favour of considering the two types as two independent species', then the four populations might each be given specific status! (Petersen drew his conclusions from a consideration of Geitler's 1932 work, where it was established that the structure of the valve does not change greatly during the course of size reduction according to the MacDonald-Pfitzer rule; see also

section 4.3). The narrowness of Petersen's species concept, were it to be applied rigorously, would lead to the recognition within the Bacillariophyta of a bewildering array of microspecies; such a classification would be totally unwieldy and undesirable.

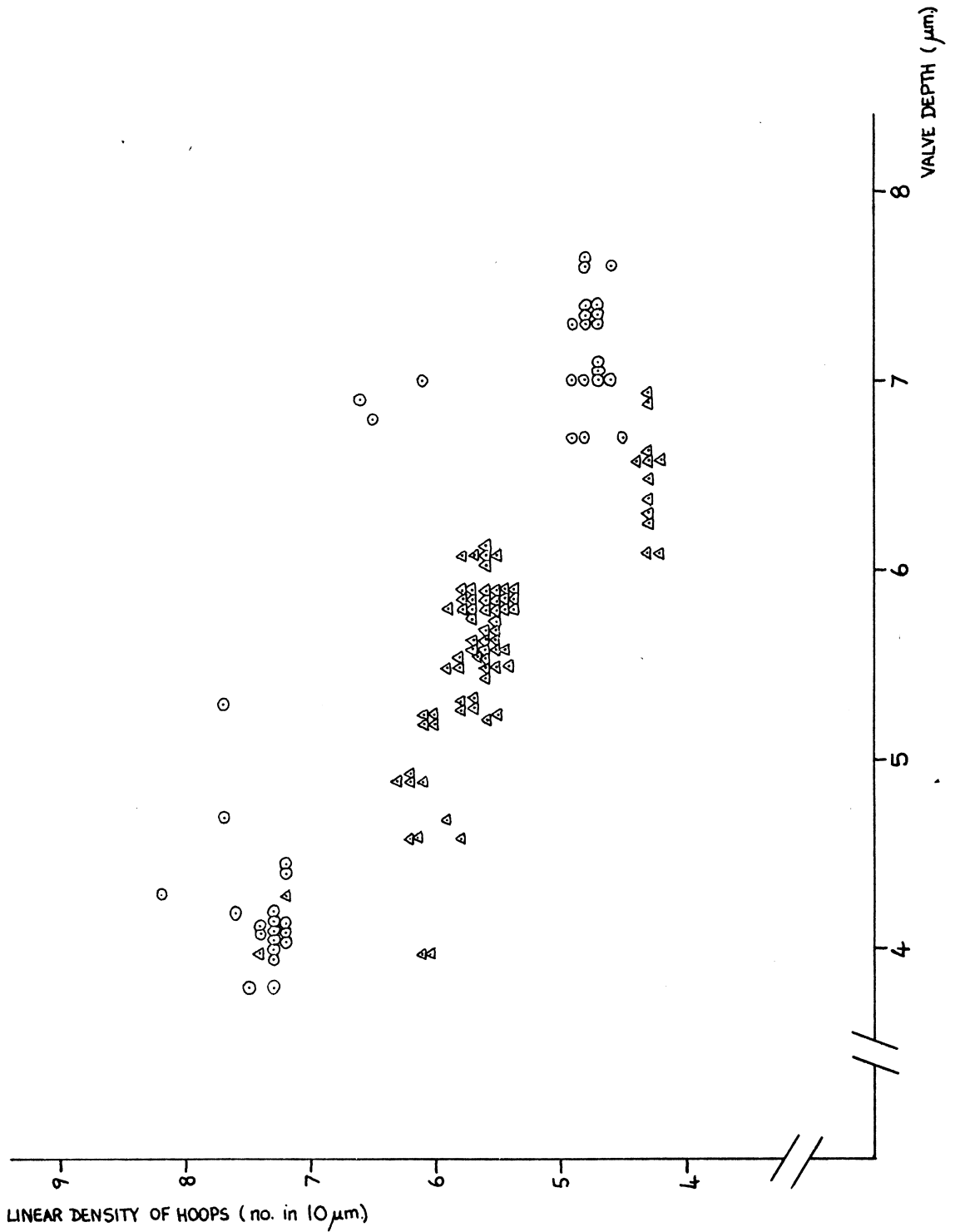
Rather, it must be recognised that within a species a degree of genotypic variation is to be expected. Geissler (1970a, b), after a study of several diatom species, drew some conclusions about the variability of different features of the diatom frustule. She distinguished between qualitative and quantitative characters, examples of the first being 'die Grundform der Frusteln und der Schalenmuster, das Vorkommen einer Rhaphe oder Pseudorhaphe, die Bautype von Rhaphe und Durchbrüchen sowie die Ausbildung von Buckeln, Fortsätzen, Gallertporen, isolierten Punkte' etc. She claimed that most of the qualitative characters 'haben sich als konstant erwiesen', and considered that these, in conjunction with quantitative characters (e.g. 'Form und Grösse der Schalen sowie die Anzahl der Bauelemente in einer Längeneinheit') of low variability, were the most useful taxonomically. As can be seen, however, there is variation within H. marina in both qualitative and quantitative characters.

In order for it to be possible to recognise any taxon as distinct from another, there must be clear discontinuities between them in one or more characters. In the case of a qualitative character the discontinuity will show itself in that 'the frequency of the character is very low in some populations and very high in others, and that intermediate frequencies do not exist' (Stebbins 1950), while 'in quantitative characters, a discontinuity between two groups of populations will consist of the absence of certain intermediate values between the contrasting series of mean or modal values found in the two groups' (ibid.).

In the present case the populations were clearly separable in

Hantzschia marina: graph plotting valve depth (measured at centre) against hoop linear density.

Aberdeen & Cornish populations represented by circles, Donkin material (B.M. slide 388) by triangles.



both qualitative and quantitative characters (sensu Geissler 1970a, b) (see Tables 1 & 2, and above), but the possibility remained that this was merely a sampling artefact, and that the populations represented groups isolated from a \pm continuous spread of variation. Therefore, other material of H. marina was studied, particularly Donkin's type material (B.M. slide 388), and compared with the A and C populations. It was found that, if the Donkin data is pooled with the data from the A and C populations, there appears to be fairly continuous variation in certain features, e.g. valve depth and linear density of hoops (see graph); moreover, these two characters are significantly negatively correlated. Among other quantitative characters, the length ranges differ, but, owing to the particular mode of vegetative reproduction in diatoms, this matter must be left out of consideration until the total length range is known for each population, especially since the ranges do overlap to an extent. The spacings of the poroids in the girdle bands differ between the A and C populations, but if these spacings are calculated relative to the spacing of the hoops the differences virtually disappear. The A and C populations may be separated according to the exact course of the terminal fissure or the degree of deflection of the central raphe endings, but the second at least seems to be subject to continuous variation - not or slightly deflected in A₁ cells, more so in C₂ and A₂. In H. amphioxys it has been found that the terminal fissure may vary from epi- to hypo-theca of the same frustule, and thus perhaps not too much emphasis should be placed upon the variation found in H. marina.

Two qualitative characters require more detailed examination. Firstly, the hymena, in which the perforations are arranged either randomly or in a hexagonal array; within a theca all the poroids are of the same type. Here there is a clear discontinuity, but it is quite possible that the ability to organize a hexagonal lattice might be

lost by mutation at a single locus. Certainly this difference is insufficient in itself to warrant division of the species, especially in view of the marked differences in other characters between, for instance, the C_1 and C_2 populations, which both have randomly arranged hymen pores, and the presence of characters (e.g. course of terminal fissure, outline of areola) which link C_1 cells with those of other populations.

Secondly, the areolae, where a tentative 'explanation' may be offered for the morphological variation encountered. It is noticeable that in diatoms with large areolae there is a tendency for a cribrum, or another such structure, to be present, adpressed to one or other surface of the hymen. This is exemplified in the coarse forms of Nitzschia sigma, and in N. sinuata, N. amphibia as well as in H. marina. There seems to be an ill-defined upper limit for the width of unsupported hymen allowable, which may be related to the mechanical strength of amorphous silica. Thus, in a taxon where the poroid size varies considerably about a mean corresponding to this upper limit, one might predict that there would be a corresponding variation in the degree of occlusion of the poroid by coarser structural elements, e.g. cribra. One difficulty with this hypothesis, however, is that although the poroids of A_2 and C_1 valves are of approximately the same size, A_2 poroids are closed by cribra, whereas C_1 poroids are not. As noted before, there is variation within each of the populations with regard to poroid outline and occlusion, which supports the idea of continuous variation within the species.

It is suggested, therefore, that the discreteness of the populations is fortuitous. Cleve-Euler (1952) lists three varieties of H. marina besides the type (her 'var. genuina'): of these, var. lata almost certainly does not belong in H. marina (it resembles more the members of Nitzschia sect. Fragilariopsis), while the vars. obtusa

and leptocephala (= H. pseudomarina), which are distinguished principally by the linear densities of the hoops (9-10 and 10-13 in 10 μm ., respectively), probably represent the upper end of a continuum of variation. That they are separate entities is highly questionable.

Donkin's original description (1858) gives the number of hoops in 10 μm . as 4.3 (his measurements were in fractions of an inch, and have been converted to their metric equivalents), but this is true of only some of the specimens on B.M. 388. Moreover, the length range given (100-180 μm .) excludes a large number of smaller valves present on this slide, and it may be that it was prepared from more than one sample; there is no more specific location given on the slide than 'Northumberland'.

The species itself is well defined with respect to other taxa: it could not be confused with, and shows no continuity with, any other species of Hantzschia, nor with species of any other genus. There are some internal discontinuities (e.g. in the type of hymen and in the nature of the first band - whether it is closed or open), but these do not seem to justify separation at specific or even varietal level: indeed, all judgment about infraspecific categories in H. marina must be suspended until a much more complete review can be made of the variation pattern and its origins.

4.5.7.2 H. virgata

Round (1970a) described various aspects of frustule structure in H. virgata var. intermedia, and gave a general account of the taxonomy of Hantzschia. He also remarked that 'the distinction between H. virgata v. intermedia and H. virgata requires reinvestigation when material of the latter is refound and scanning electron microscope studies can be undertaken.' Such material has now been obtained and the opportunity taken of studying both this and other varieties of the species.

Van Landingham (1971) lists six varieties, namely borealis, capitellata, gracilis, kariana, leptocephala and wittii, in addition to the type. Of these, var. capitellata is synonymous with var. leptocephala (see Cleve-Euler 1952) and therefore superfluous, while the list omits var. intermedia.

Material of vars. virgata and leptocephala was obtained from Sandbay, var. intermedia from Llandudno, var. gracilis from Borth and from Cornwall. In addition, B.M. slides 26, 12955, 20246, 20247, 20250, 66978 and 77766 were studied.

var. virgata

The valve was well described by Roper (1858) in his original description of the species - 'linear-lanceolate, slightly arcuate, with produced and rather obtuse extremities; striae distinct, dilated at intervals into prominent ridges on the inner margin. Length .00405" to .0053"; striae 26 in .001"' (equivalent to 103-5 μm ., 10 in 10 μm . respectively). The 'prominent ridges' noted by Roper are now known to be fibulae, while 'stria' has changed its meaning since his time (Roper's striae are my transapical costae).

Since Roper's description the size range has been somewhat extended, so that, for example, Van der Werff & Huls (1957-) give dimensions of 50-150 μm . x 6-12 μm ., with 4-6 fibulae and 9-15 striae in 10 μm . The Sandbay material can be slightly wider than this (up to 13 μm .), measurement being made at the centre of the valve; this is not, however, the widest point, (which is approximately halfway from centre to apex), but certainly the most easily determinable. Otherwise, cells from Sandbay have dimensions which fall within the above limits, having lengths of 70-130 μm ., with 10.5-11.5 striae in 10 μm . The depth of the valve is 7-9 μm .

It was noted by Geissler (1970b) that, whereas during the course of vegetative multiplication the width of the valve usually reduces

as does the length, in some cases it can increase. The latter condition seems to apply in H. virgata var. virgata; an analysis of 15 pairs of measurements showed a highly significant (near 99%) negative correlation between length and width, although it might be argued that this is the result of genotypic variation, or of phenotypic variation other than that caused by processes operating during vegetative division.

The poles are usually rostrate (F.62-63), but sometimes slightly capitate, though this is not as pronounced as in var. leptocephala. If the frustule is observed in girdle view it can be seen that the raphe system is slightly biarcuate (F.61): in this view, however, the frustule is unstricted centrally - contrast var. intermedia.

The basic construction of the valve has already been described (section 4.5.2, and see Mann 1977). Certain disturbances of the normal pattern may occur in a sector of the valve approximately halfway from centre to apex, which are probably to be regarded as Voigt discontinuities, although they are not present in more than 20% of the valves studied.

Some of the transapical costae bear fibulae and if so they widen towards the fibula bases (F.62-64, 618, 620). Beyond the fibula base the transapical costa narrows again (F.615), and within the interspace the striae frequently become double, so that instead of one row of poroids there are now two between each adjacent pair of costae. This may be seen in original Roper material (B.M. slides 20246, 66978) and in the Sandbay specimens (F.63, 65; 62, 64). The doubling is present only on the distal side of the raphe, and apparently only within the interspace (F.615, 620).

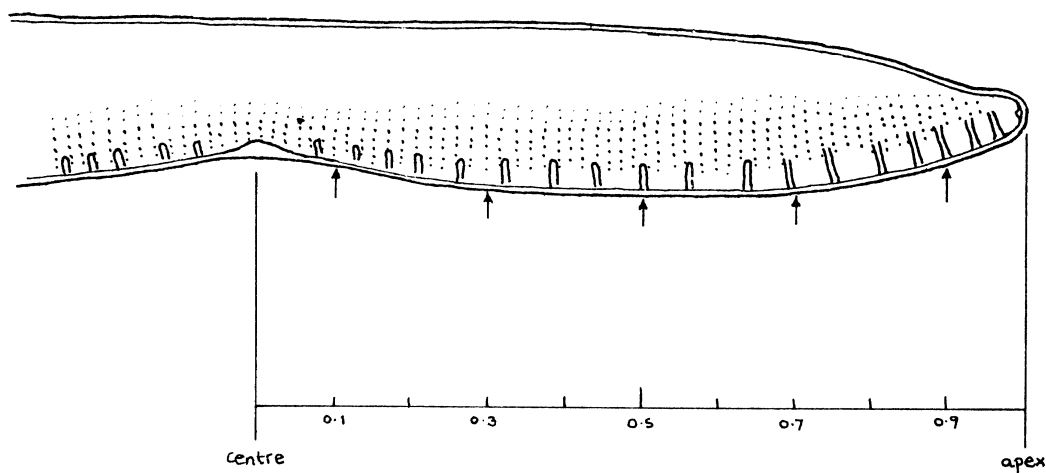
Proximally the fibulae spring from a well-developed ridge (see before): this has the effect that each proximal transapical stria is separated into a larger part lying outside the interspace and a smaller part, of only one or two poroids, lying within the interspace (F.65, 66, 620). This break in the proximal striae was noted by Round (1970a)

and drawn by Hustedt (in A.Schmidt Atlas, T.345 f.24).

The morphology of the fibula, as revealed by light microscopy, was one of the major features used by Round (1970a) to separate the var. intermedia from the type. SEM observations greatly aid an understanding of this morphology. The fibulae of var. virgata are massive plates, almost triangular if viewed in an apical direction (Mann 1977, f.64), slightly thicker towards the inside of the cell and flaring also near the raphe so as to delimit oval portulae (F.69, 612, 615, 618, 620). The interspace is constricted, then, at two levels - at the opening into the main cell body, and at the opening into the 'subraphe canal' (although a canal as such cannot be distinguished, as noted above). The plate-like fibulae extend some distance across the valve (F.62-64) and it is this fact, coupled with the hardly biarcuate disposition of the raphe, which gives the typical appearance of the var. virgata in girdle view, where the fibulae extend to the 'edge' (not the margin) even at the centre of the valve (see Round 1970a; and F.61, 65-66: contrast the var. intermedia, F.41-42).

In descriptions of the Nitzschiaceae it is almost mandatory to give the numbers of fibulae and costae/striae in 10 μm . This, however, gives a very poor impression of the actual spatial relationship between these two features of the valve. Of course, in some species, e.g. H. marina, there is an exact correspondence between the numbers of fibulae and hoops/costae - all that need be said about H. marina is that "Number (fibulae) = Number (hoops) - 1" - but in H. virgata and many others it is possible to obtain much more useful measures of fibula spacing than the customary 'numbers in 10 μm '. In this study the spacing of adjacent pairs of fibulae has been measured relative to the spacing of the transapical costae/striae. A mean value of the fibula spacing in a single valve, or in a population, may then be derived, which value will be independent of any variations there may

be in the absolute value of the stria linear density. This mean, together with the variance, may be used as a basis for the analysis of interpopulation differences. Thus, an analysis of 15 valves of the var. virgata from Sandbay gave a mean fibula spacing of 2.366 units, variance 0.325, where a 'unit' is the apical distance between the centres of adjacent transapical costae: in the calculation of these figures, the data from all the valves were pooled and treated as if they came from the same distribution - any variation in spacing with valve length (which was absent in var. virgata) will cause distortion in the results. The central interspaces were excluded from consideration for reasons which will become obvious later.



Furthermore, the variation in the mean spacing of the fibulae along the length of the diatom may also be studied. For this, the interspaces nearest to each of the points 0.1, 0.3, 0.5, 0.7 and 0.9 of the distance from centre to apex (see above) were taken as representative of these points for each half-valve of the 15 valves and the spacings of the fibulae at these points found, so that a total of 30 measurements of spacing was available for each point. Again, spacings were measured in terms of costae/striae rather than $\mu\text{m.}$, this having

TABLE 3

Hantzschia virgata - analysis of the variation in fibula spacing: pooled data from a number of valves; central interspaces excluded from the analysis.

(See text for explanation of 'unit')

variety:	No. of units intervening between fibulae						Mean spacing	Variance
	1	2	3	4	5	6		
<u>virgata</u> (15)*	16 2.5%	378 60.4%	219 35.0%	13 2.1%	0 0%	0 0%	2.366	0.325
<u>gracilis</u> (15)*	20 2.4%	502 60.9%	292 35.5%	10 1.2%	0 0%	0 0%	2.354	0.302
<u>intermedia</u> (25)* (Llandudno)	8 1.0%	237 27.6%	402 46.8%	192 22.4%	17 2.0%	2 0.2%	2.976	0.638
<u>intermedia</u> (15)* (Barnstable)	12 3.2%	231 61.4%	121 32.2%	12 3.2%	0 0%	0 0%	2.354	0.357
<u>leptocephala</u> (25)*	52 7.0%	418 56.0%	238 31.9%	39 5.1%	0 0%	0 0%	2.353	0.473

* the number given in brackets is the number of valves analysed.

Result: the significance of the differences between the mean spacings is summarized below (where S.D. = significantly different
0 = not different
judging by 't' at 5%).

	<u>virgata</u>	<u>gracilis</u>	<u>inter-</u> <u>media</u> (L)	<u>inter-</u> <u>media</u> (B)	<u>lepto-</u> <u>cephala</u>
<u>virgata</u>	-				
<u>gracilis</u>	0	-			
<u>intermedia</u> (L)	S.D.	S.D.	-		
<u>intermedia</u> (B)	0	0	S.D.	-	
<u>leptocephala</u>	0	0	S.D.	0	-

TABLE 4

Hantzschia virgata var. virgata - analysis of the variation
in fibula spacing along the valve.

15 valves studied: 30 measurements for each point.
(See text for explanation of 'unit', '0.1', '0.3', etc.).

Point:	No. of 'units' intervening between fibulae.				Mean spacing	Variance
	1	2	3	4		
0.1	2	15	13	0	2.367	0.378
0.3	0	17	11	2	2.500	0.397
0.5	0	15	12	3	2.600	0.455
0.7	0	16	12	2	2.533	0.395
0.9	1	10	19	0	2.600	0.317

Result: spacing means and their variances insignificantly different
('t' at 5%, 'F' at 2½%).

Central interspace:

mean spacing (15 measurements) = 2.667 (variance
2.524)

All other interspaces:

mean spacing (pooled data, 626 measurements)
= 2.366 (variance
0.325)

Result: the mean spacing of the median pair of fibulae is insignificantly different from the mean spacing of other pairs, although the variances differ ('F' at 2½%); N.B. in view of the difference between the variances, an appropriate modification of the 't' test was employed.

certain advantages where the valve is curved or where the linear density of the transapical costae changes along the valve. An analysis of the data thus obtained revealed that the mean spacing and the variance do not vary from one part of the valve to another (judged insignificant by *t* at 5%, and *F* at 2½% respectively)(Table 4).

In members of the Nitzschiaceae with central raphe endings (which grouping includes H. virgata) there is often a wider separation of the central pair of fibulae; this is sometimes used as a diagnostic character, e.g. by Archibald (1972a, b) in his key to the freshwater Nitzschiae of South Africa. In some specimens of the var. virgata the central interspace is indeed obviously wider than are the neighbouring interspaces, the criterion of 'obviousness' being that the central interspace must exceed either neighbouring interspace by the width of at least two transapical costae, but if the population is considered as a whole, then the central interspace does not appear to be significantly wider than the others (Table 4). However, SEM investigations reveal that in certain cells, opposite the central raphe endings, there is an almost complete fibula (probably equivalent to the nodule/knob found just distal to the raphe endings in var. intermedia - see Round 1970a, Mann 1977), which just fails to meet the proximal mantle (F.618, 619). Now, since it is usually impossible to see with the light microscope whether the structure opposite the central raphe endings is a complete bridge or only a horn-like projection, it may be that the absence of any significant size difference between the central and other interspaces is only apparent, not real. Nevertheless, in some cells all the fibulae are complete yet the central interspace is no wider than the rest (unpubl. obs.).

Centrally, the internal raphe fissures are continuous (F.619), unlike the external fissures which are deflected towards the proximal margin (F.617). At the pole, the raphe ends internally in a simple

helictoglossa (F.613), while externally the terminal fissure continues to near the distal margin, ending simply (Mann 1977, f.62).

The cincture consists of five bands, which, as in H. marina, may be classified into three groups on the basis of their morphologies. The first group comprises the first two bands, which are open and possess large round poroids (F.67-68, 614, 616). The first band has four transverse rows of poroids, with 9-11 poroids in 10 μ m. transversely, and is about twice the width of the second, which has only two transverse rows, with 11-12 poroids in 10 μ m. (F.67-68). The pars interior of each bears a 'fringe' (F.614), which so fits beneath the adjacent element, be it valve or first band, that in vivo no poroid of that element would be obscured. Indeed, the interlocking between these elements is very close and exact, and in complete thecae it is often impossible to detect the junctions between them, when they are viewed from the inside (Mann 1977, f.68).

The second group comprises the third band only. It is open (F.616), and is about half the width of band 2. Externally it has a ridged appearance, with approx. 28-30 ridges in 10 μ m. (F.614). Between each pair of ridges I believe there to be a line of small poroids, but this needs confirmation.

The fourth and fifth bands make up the third group. They are similar to one another in size, and bear one or two transverse rows of tiny poroids, about 40 in 10 μ m. (F.614, 616). Neither is as wide as band 3, and one at least may be closed (F.616).

var. gracilis

This is a much more slender variety than the type (compare Hustedt in A.Schmidt Atlas, T.345 f.8 & 9 with T.329 f.24-26), and Hendey (1964) gives its dimensions as 70-90 x 6-7 μ m., with 4-5 fibulae and 14-15 striae in 10 μ m. Van der Werff & Huls (1957-), on the other

hand, give linear densities of 5-6 in 10 μm . for the fibulae and 16 in 10 μm . for the striae. Valves from intertidal sand in Cornwall were considerably longer than Hendey allows, being 90-150 μm . long, with only 11.5-12.0 striae in 10 μm . However, the specimen illustrated by Hustedt (op. cit.) in T.345 f.8 is well over 100 μm . long and so, in view of the existence (in material from Borth) of forms with around 13 striae in 10 μm ., and in view of the similarities between my specimens and those figured by previous authors, I feel justified in referring them to this taxon.

The valve is slightly arcuate (F.53-54), with a raphe which remains parallel to the proximal margin for most of its length. The trans-apical costae are less robust than those of var. virgata, and the costae which bear fibulae are hardly, if at all, thickened near the fibula base (F.621). Voigt discontinuities may be distinguished in a minority of valves. Within the interspace the striae do not become double.

The fibulae are slender structures resembling those of Cylindrotheca (see Reimann & Lewin 1964), except for the fibula nearest the pole, which is a much more massive thing (F.56-57, 621-3, 625). The fibulae spring proximally from a ridge, as in the type, which separates the proximal transapical striae into major and minor parts, but there is usually only one poroid in the minor part (F.57, 60, 621, 623).

An analysis of the spacing of the fibulae in 15 valves (again, excluding the central interspace in each) gave a mean spacing within the population of 2.354, variance 0.3020 (Table 3). These values are not significantly different from those of the type. Again there is no variation of the spacing along the valve, except that in var. gracilis the central interspace is consistently and significantly wider than the others (Table 5): it may always be distinguished, the median fibulae being separated by 5-6 striae (F.53-55, 57).

TABLE 5

Hantzschia virgata var. gracilis - analysis of the variation
in fibula spacing along the valve.

15 valves studied: 30 measurements for each point.
(See text for explanation of 'unit', '0.1', '0.3', etc.).

Point:	No. of 'units' intervening between fibulae.				Mean spacing	Variance
	1	2	3	4		
0.1	0	17	12	1	2.467	0.326
0.3	0	13	17	0	2.567	0.254
0.5	0	13	15	2	2.633	0.378
0.7	0	17	11	2	2.500	0.397
0.9	0	14	14	2	2.600	0.386

Result: spacing means and their variances insignificantly different
(*'t'* at 5%, *'F'* at 2½%).

Central interspace:

mean spacing (15 measurements) = 5.533 (variance 0.267)

All other interspaces:

mean spacing (pooled data, 824 measurements)
= 2.354 (variance 0.302)

Result: although the variances for these two 'populations' of inter-
spaces are similar, the mean spacings are highly significantly
different (*'F'* and *'t'* as above).

TABLE 6

Hantzschia virgata var. intermedia (Llandudno material) -
analysis of the variation in fibula spacing along the valve.

25 valves studied: 50 measurements for each point.
(See text for explanation of 'unit', '0.1', '0.3', etc.).

Point:	No. of 'units' intervening between fibulae.					Mean spacing	Variance
	1	2	3	4	5		
0.1	1	24	22	3	0	2.540	0.417
0.3	0	7	30	12	1	3.140	0.449
0.5	1	5	20	20	4	3.420	0.738
0.7	0	1	22	25	2	3.560	0.374
0.9	0	12	26	12	0	3.000	0.490

Result: the significance of the differences between the spacings is
summarized below (S.D. = significantly different,
0 = not different,
judging by 't' at 5%, 'F' at 2½%).

	<u>Means</u>					<u>Variances</u>				
	0.1	0.3	0.5	0.7	0.9	0.1	0.3	0.5	0.7	0.9
C.1	-				0.1	-				
0.3	S.D.	-			0.3	0	-			
C.5	S.D.	0	-		0.5	S.D.	0	-		
0.7	S.D.	0	0	-	0.7	0	0	S.D.	-	
C.9	S.D.	S.D.	S.D.	S.D.	-	0.9	0	0	0	0

Distribution for central interspace:

C.I.	No. of 'units' intervening between fibulae					Mean spacing	Variance
	5	6	7	8	9		
C.I.	0	2	6	10	7	7.880	?

The mean for all other interspaces (pooled data, 858 measurements) is 2.976, which proves to be highly significantly different from the value given above for the central interspace (25 measurements).

Opposite the central raphe endings there is a small nodule like that found in the var. intermedia (F.57, 622), but the inner fissure is continuous from pole to pole, as in the type (F.622-3). Externally, the central endings are virtually identical in form to those of the var. virgata (F.631); so also are the polar raphe endings, both internally and externally (F.625, 626).

As far as it is known, the cincture is very similar to that of the type. The first two bands are very similar to one another, with large round poroids. The first has four transverse rows (F.57-59, 628), the second two (near the poles) to three (at the centre)(F.57-59, 630); the first, and probably the second also, bears a fringe-like development of the pars interior like that noted in the var. virgata (F.59, 623, 627-8, 630). As in the type, the first has slightly fewer poroids transversely than the second. The third band appears to be similar to that of the type, being much thinner and narrower than the first two bands, and having a much finer ornamentation (F.58, 623). Any other bands are at present unknown.

var. intermedia

Many aspects of the frustule structure in this taxon have already been noted and described (Round 1970a, Mann 1977). The dimensions given by Round (1970a) are 50-75 x approx. 10 μm ., with about 5 fibulae and 9 transapical striae in 10 μm . The Llandudno specimens are somewhat larger - 70-100 μm . long, with about 13 striae in 10 μm .; nevertheless, the disposition of the raphe, the form of the fibulae, cincture structure, etc., all confirm their affinity with Round's specimens (compare F.36 & 41 with 37, 38, 42).

In girdle view, the frustule is rounded at the poles since the valve becomes shallower gradually, contrasting with the more abrupt change present in the valves of the foregoing taxa (compare F.41-44 with F.56 or 61).

The raphe system is markedly biarcuate (F.41-42) with fibulae of the type found in var. gracilis (F.634), except that the fibula nearest the pole is not greatly different from any other. The transapical costae do not expand near the distal fibula bases (F.634), nor do the striae become double within the interspace. The ridge which in var. gracilis bears the proximal fibula bases is poorly developed or absent in var. intermedia: hence, the proximal striae are not interrupted as they are in the type or var. gracilis (see also Round 1970a). Voigt discontinuities may be found in about half of the valves.

The central interspace is consistently wider than are the other interspaces, the median fibulae being separated by 6-10 striae in the Llandudno material (F.36-38, 41-42, Table 5). An analysis of the fibula spacing in 25 valves revealed that in this population the fibulae have a significantly (t at 5%) higher mean spacing, 2.976, than in the preceding taxa (Table 3). However, a similar analysis (but of 15 valves) of specimens on B.M. slide 77766 (the Barnstable, U.S.A., material studied by Round 1970a) gave a mean spacing of 2.354, which is not significantly different from the figures obtained for vars. virgata, gracilis or leptocephala. Analysis of the spacings at the 0.1, 0.3, etc. points in the Llandudno material revealed that the fibulae are significantly more closely spaced at the 0.1 and 0.9 positions than at the other points, which are no different from one another as judged by t at 5%.

One of the most surprising differences between this variety and those previously described lies in the nature of the central raphe endings. The inner fissure is not continuous from pole to pole, but takes the noncoaxial-asymmetrical form described earlier, which also occurs in H. amphioxys, etc. (F.637), while externally the slits are not deflected further towards the proximal margin of the valve than the biarcuate nature of the raphe system demands (F.632). Moreover, at the poles the terminal fissure curves off so that it comes to run

parallel to the distal margin and away from the pole (F.633).

The cingulum of var. intermedia is to be distinguished in several ways from those of the other varieties. The most noticeable feature is the lack of a band corresponding to the second of vars. virgata and gracilis (F.46, 636). The first band (F.45-48, 635-6) is fairly similar to the first bands of those two taxa, save that there are usually more transverse rows of poroids (5-6); it is, however, without a 'fringe' and its pars interior has an entire margin (F.635). The second band, which in some ways resembles the third of var. virgata, although it bears well-defined but small poroids, possesses a prominent ligula, closing the gap left by the open ends of band 1 (F.49-52, 635, 636); it is open (F.50). There is some evidence for another, thinner and apparently structureless band abvalvarly (F.46, 636). Details of band structure are difficult to obtain because of the extreme delicacy of the second and subsequent bands: SEM studies of intact frustules reveal virtually nothing about the cincture since the junctions between bands are ± invisible. Whereas the ratio of the linear density of the valve striae to that of the longitudinal rows of poroids on the first band is around 1.0 in vars. virgata and gracilis, in var. intermedia it is approx. 0.8.

var. leptocephala

So far, it has not been possible to examine specimens of this with the electron microscope. Most of the observations noted below were made from B.M. slide 20250.

This is a smaller diatom than any of the preceding: Cleve-Euler (1952) gave dimensions of 55-60 x 7 μm ., with 5.5-6.0 fibulae and 10-13 striae in 10 μm . According to Van der Werff & Huls (1957-), the L.D. of the striae is somewhat higher (15 in 10 μm .), while the specimens on B.M. 20250, a collection made by Roper at St.Meol's,

TABLE 7

Hantzschia virgata var. leptocephala - analysis of the variation in fibula spacing along the valve.

25 valves studied: 50 measurements for each point.
(See text for explanation of 'unit', '0.1', '0.3', etc.).

Point:	No. of 'units' intervening between fibulae.					Mean spacing	Variance
	1	2	3	4	5		
0.1	0	30	19	1	0	2.420	0.289
0.3	1	16	29	4	0	2.720	0.410
0.5	0	18	19	13	0	2.900	0.622
0.7	0	17	30	3	0	2.720	0.328
0.9	8	35	7	0	0	1.980	0.306
centre (25 meas'ts)	0	0	13	9	3	3.600	0.500

Result: the significance of the differences between the spacings is summarized below (where S.D. = significantly different
0 = not different
judging by 't' at 5%, 'F' at 2½%).

	<u>Means</u>					<u>Variances</u>				
	0.1	0.3	0.5	0.7	0.9	0.1	0.3	0.5	0.7	0.9
0.1	-					0.1	-			
0.3	S.D.	-				0.3	0	-		
0.5	S.D.	0	-			0.5	S.D.	0	-	
0.7	S.D.	0	0	-		0.7	0	0	S.D.	-
0.9	S.D.	S.D.	S.D.	S.D.	-	0.9	0	0	S.D.	0

The mean spacing for all except the central interspaces is 2.353, which is significantly lower than that for the central interspaces (see above), although the variances are similar ('t' and 'F' as above).

Cheshire, have 13.5-14.5. The Roper specimens measure 40-70 x 7-8 μm .

The most obvious feature of the valve, and the feature which gives the taxon its name, is the narrowed, capitate end (F.71-72, 76-77). Otherwise this taxon shows many affinities with the type. In girdle view the frustule is fairly sharply angled at the poles (F.73, 75). Voigt discontinuities (F.76) are present in about 40% of the valves, and disturbances of the normal pattern occur also at the centre (F.72).

A transapical costa bearing a fibula widens near the fibula base (F.72, 77-78), and the fibulae themselves are clearly of the same type as in var. virgata. Proximally, the fibulae spring from a longitudinal ridge, which separates the proximal striae into major and minor parts as in the type (F.73-75, 79).

An analysis of the fibula spacing in 25 valves (again, excluding the central interspace) gave a mean spacing of 2.353, which is not significantly different from that in vars. virgata or gracilis, or in the Barnstable var. intermedia (Table 3). There proved, however, to be a significant positive correlation between the length of the valve and the spacing of the fibulae. Moreover, the spacing of the fibulae varies along the valve. The spacing at 0.1 is significantly lower (t at 5%) than at 0.3, 0.5, or 0.7, which three are all similar in their spacings, and it is significantly higher than at the 0.9 spacing (Table 7). Furthermore, if the mean spacing is calculated for the interspace nearest the narrowest point of each half-valve, the value obtained, 1.500, is even lower than that of the 0.9 point, reflecting the fact that near the poles there is a tendency for adjacent fibulae to be separated by only one stria (F.75-77), a spacing which is otherwise of low frequency in H. virgata (Table 3). The central interspace is significantly wider even than the 0.5 interspaces, with a mean spacing of 3.600, yet it is rarely possible to distinguish

it from other interspaces in individual valves except on the grounds of its position; the size distinction is often not obvious.

The raphe is interrupted centrally, but it has not yet been possible to determine any of the details of the raphe structure centrally: a central "nodule" can be seen (F.72-73). At the pole there appears to be a submarginal thickening as well as a helictoglossa (F.75). In this it resembles H. marina and Hantzschia sp.A (see Mann 1977, f.13, 23), and this feature may be related to the deep and narrow nature of the valve at the pole in these taxa.

The cincture is little known, though it seems that the first band bears only two transverse rows of poroids (F.74).

vars. kariana, borealis and wittii

Vars. kariana and borealis have not been observed in the present study. Indeed, they do not seem to have been observed since their original description by Grunow (in Cleve & Grunow 1880): thus, Cleve-Euler (1952) merely repeats the descriptions given by Grunow and reproduces his illustrations. The var. wittii, as H. wittii, was described by Grunow (1880).

Grunow's illustration of var. kariana (in Cleve & Grunow 1880, T.6 f.109) shows a form which clearly belongs close to var. virgata. The fibulae are like those of the latter, and the dimensions of the valve and the linear densities of fibulae and striae fall within the ranges given above for that taxon. Indeed, the only character known at present which separates these two varieties is the outline of the valve at the pole - rostrate or slightly capitate in the type, cuneate in var. kariana (compare Hustedt in A.Schmidt Atlas, T.329 f.24-25 with Cleve & Grunow 1880, T.6 f.109).

The var. borealis comprises smaller forms with a relatively high number of striae (14) in 10 μ m. Again, the fibulae are of the virgata type, with the central pair more widely spaced than the others (Cleve

& Grunow 1880, T.6 f.110). As regards the valve's outline and dimensions, var. borealis seems to be intermediate between vars. virgata and leptocephala.

Var. wittii is much farther removed from the type than either of the preceding. The fibulae are short and slender, like those of vars. gracilis and intermedia, and in the light microscope appear to be longer near the poles than elsewhere (F.39; Grunow 1880, Pl.13 f.13). From the manner in which the fibulae become almost indistinguishable centrally, it seems likely that the raphe system is biarcuate, as in the var. intermedia: indeed, it is probable that these taxa are identical.

Discussion

The foregoing demonstrates the considerable variation present within the traditionally accepted limits of H. virgata, but what significance has this for the taxonomy of the species? In H. marina it is difficult to see how one could crystallize out distinct taxonomic entities, be they varieties, subspecies or whatever, from the spread of variation, but in H. virgata fairly clearcut groupings emerge. Thus, in most cases it is easy, using the light microscope alone, to classify valves into one of the varieties described above. For example, if a valve of H. virgata has massive fibulae which, in valve view, extend transapically over a half or a third of the valve, then if it has rostrate or slightly capitate ends it may be classified in var. virgata, or, if it is a smaller form with closely spaced striae and capitate ends, in var. leptocephala.

In the course of the present study only a few valves have been observed which could be said to be in any way intermediate between the varieties mentioned above; nor does the literature give much indication of transitional forms, except that the rare var. borealis may be intermediate between vars. virgata and leptocephala. The main question in

H. virgata, therefore, is probably not so much whether it is possible to distinguish 'good' varieties or other infraspecific taxa - a question which is highly pertinent to H. marina - but rather whether the discontinuities in the variation pattern warrant recognition at the species level.

That a valid phenetic grouping^{of} diatoms may be distinguished, corresponding to the presently accepted species H. virgata, is evident from the internal consistency of 'H. virgata' with respect to the basic construction of the valve (the positions of the hymena, the dimensions and positioning of the frets relative to the transapical costae, etc.), the spacing of the fibulae, the lack of a distinct canal beneath the raphe, etc., and from the discontinuities shown in these same matters between this group and any other. Thus, one may distinguish a 'virgata-kind' within Hantzschia, just as one might, using different characters, separate out a 'marina-kind', a 'spectabilis-kind', etc. These 'kinds' are not necessarily equivalent, however, and the problem is how to recognise them formally using the categories authorised by the International Code of Botanical Nomenclature (I.C.B.N.).

One complication is that there is no universally accepted definition of 'species' (see also 'Final Discussion'), although some have sought to standardize the thinking of taxonomists by demanding that a given number of discontinuities be present before specific status is awarded, while others (the proponents of the 'biological species concept') insist upon reproductive isolation as the sole, valid criterion; this problem is well known and widely discussed (see Slobodchikoff 1976).

In diatoms, the 'biological' approach is unworkable, which means that diatom taxa must be delimited on the basis of discontinuities in the variation pattern. Recently, the electron microscope has enabled the study of many new characters, and has provided a better under-

standing of those previously used. Almost inevitably, a given pair of 'species' have been found to differ inter se by a greater amount than was originally recognised. Thus, a 'species' originally distinguishable from another by differences in three characters may now, perhaps, be distinguishable in eight. Yet surely it would be foolish to upgrade most traditionally accepted species to sections or series simply because our overall knowledge has increased. Of course, a general up- or down-grading may be necessary later, if some means can be devised of standardizing the species concept between different plant (and animal) groups, perhaps by the use of DNA hybridization studies. For the present, however, we must concern ourselves with the relative positioning of taxa, the aim of taxonomic revision being to reflect more accurately the phenetic relationships between organisms. To express this in terms of human relationships, we must be more interested in the fact that George is more closely related to Fred than either is to Henry, than we are about the 'level' of their relationship, i.e. whether George is Fred's brother while Henry is their cousin, or George and Fred are cousins but Henry their second cousin, etc. The approach recommended will have a less drastic effect on the current taxonomy than an approach demanding a certain number of correlated character differences for species separation, etc.

By applying the above, essentially conservative, strategy to the case of H. virgata, it may be recommended that, for the present at least, the traditional limits of this species are retained. Within these limits several varieties have already been described, most of which appear to be valid and distinct groupings, but which are not equally separated one from another. Of the four varieties^{described} here in detail the most distinct is the var. intermedia, while of the others vars. virgata and leptocephala are apparently more like each other than either is to var. gracilis. Furthermore, var. gracilis is more

like var. intermedia than are vars. virgata or leptocephala. The distinctness of var. intermedia might best be recognised taxonomically by its separation from the type at the subspecific level. Var. wittii is close to var. intermedia and, if not identical with it, ought to be included within the same subspecies; var. borealis belongs near var. virgata, while var. kariana is scarcely worth separation from the latter except at the level of forma.

4.5.7.3 H. amphioxys

Only a handful of the many described varieties and forms of H. amphioxys (Van Landingham 1971 lists 45 varieties alone) have been studied in the course of this project; consequently, it is possible only to point out the characters in which infraspecific variation has been found, and to compare the list thus obtained with those obtained for H. virgata and H. marina.

Four samples were examined by light and electron microscopy, each sample containing one or more variants of H. amphioxys. The first sample was obtained from a shallow, temporary puddle at Sea Mills, Bristol; the second was a scraping from a 'streak' of diatoms on a wall in Cotham, Bristol, while the third, provided by Dr.P.A.Broady, was an isolate from moss on Signy Island, South Orkneys; the last was from the underside of a subsidiary arch of the bridge over the R. Wye at Bigsweir, Gloucs. Other samples, again from subaerial habitats (soil, moss, etc.) were also examined, but only by light microscopy.

As mentioned previously (section 4.5.2), H. amphioxys is very variable in size and outline. A great variety of forms may be found coexisting in the same habitat. Within the Cotham sample, for instance, there are moderately large forms (30-50 μm . long) with 18-20 striae in 10 μm ., whose valves are variously bent, with rostrate or slightly

TABLE 8

Some features of the Hantzschia amphioxys populations,
observable using the light microscope.

POPULATION	Length range μm .	Striae no. in 10 μm .	Frets no. in 10 μm .	Obvious- ness of poroids	'Capitate- ness of valve poles
Cotham 1	30-50	18-20	28	+	+ / ++
Cotham 2	20-30	20	28	+	0
Cotham 3	25-35	24-26	45*	0	+++
Sea Mills 1	40-50	19-20	28-30(+)	+	+ / ++
Sea Mills 2	60	12.5-13	21-23	+++	+ / ++
Signy	35-45	24	40*	0	+++
Eigsweir	100	13-14	25-27	+	+++

* measured from SEM observations.

capitate ends (F.86-90). Some of these are of the inverse form noted before, where the raphe is on the dorsal (i.e. less convex) side of the valve (F.89). This group will be called the Cotham 1 population. There are also some small (20-30 μm . long), blunt-ended forms (Cotham 2), again with approx. 20 striae in 10 μm . (F.94), and yet a third group (Cotham 3), consisting of shortish, narrower-celled individuals (25-35 μm . long) with 24-26 striae in 10 μm . (F.91-93). The Sea Mills H. amphioxys complement can be split into two parts, the first (Sea Mills 1) containing forms quite similar to the Cotham 1 types, (F.95), the second (Sea Mills 2) containing larger, more robust forms (around 60 μm . long) with 12.5-13.0 striae in 10 μm . (F.80-81). The light microscope reveals a further difference between these two populations in that the striae of the second are conspicuously punctate, whereas it is difficult to resolve any detail in the striae of the first.

The Signy cells (F.98) are very similar to the Cotham 3 cells; both have capitate valve poles and are probably referable to the var. capitata.

The Bigsweir forms are larger than any of the others (approx. 100 μm . long), with 13-14 striae in 10 μm ., although these are not clearly punctate.

Some of the features observable in the light microscope are summarized in Table 8. While it would almost certainly have been possible to fit a published, varietal name to each of the populations described, this name would have signified little and might have been wrong, since many of the varieties are ill-defined and poorly illustrated.

Valve structure

The construction of the valve has already been described (in this thesis and in Mann 1977), but the populations all show slight variations on the basic scheme. Thus, the hymena, which (always?) have randomly arranged pores (F.529-32), lie near the outer ends of the poroids in

the Cotham and Sea Mills 1 populations (F.653-5, 658, 661, 668, 673), but do not lie so in the Sea Mills 2 cells. In these the hymena are rarely visible in scanning electron micrographs (F.646, 651), although TEM observations show that they are present (F.529). It seems, therefore, that in these cells the hymena must be positioned some distance below the external valve surface. Unfortunately, the process of acid cleaning destroyed the hymena in the Signy valves: on other grounds it must be suspected that they would have been found to be positioned as in the Cotham 3 valves, i.e. at the outer ends of the poroids.

In all cases the costae project much further into the cell lumen than do the frets; indeed, the whole internal aspect of the valve is very similar from one population to the next (F.650, 662, 664, 667, 670, 683).

Marginal ridges are present in some, but not all, of the Sea Mills 2 valves (F.647). Sometimes the ridge runs from pole to pole, while in other cases it is of only limited extent, or scarcely distinguishable (F.644). There may be variation in the degree of development of the ridge even between the two valves of a single cell (F.643).

Near the junction of valve face and distal mantle, the frets are deeper than they are elsewhere and their external surfaces are flush with the surfaces of the costae: this is obvious even in those cells without marginal ridges (F.677; 651, 653, 679).

In the Bigsweir cells the valve construction is somewhat more complex, though of the same basic pattern. LM and SEM observations show there to be an external 'reticulum', formed by the outward extension of the transapical costae and certain of the frets (F.682, 684-6, 691). The presence of this reticulum makes observation of the hymena difficult, even though these are placed at the outer ends of the poroids (F.684). In some ways the valve has an appearance reminiscent of Didymosphenia geminata, where again areolae open into deep pits (see

Dawson 1973a, f.31-34). A well-developed marginal ridge is present (F.680-1, 684-6) and may be distinguished using the light microscope: it is not always continuous, but may be interrupted at intervals, apparently randomly (F.680).

Raphe and associated structures

As in H. marina, it is only the external raphe endings which exhibit variation. The external polar endings are all fairly similar, except for a slight variation in the course of the terminal fissure. In some cases this fissure ends parallel to the margin at the very apex of the valve (F.663), or it may continue a little further distally (as is usually the case in Sea Mills 2 valves)(F.651, 672, 691-4), but in other valves the last part of the fissure may be abruptly deflected so that the fissure is not merely bent, but hooked (F.641). This variation should not be accorded much taxonomic emphasis, however, since the valves of a single frustule may differ with regard to this feature, although within each valve the course of the terminal fissure seems to be constant (F.640-1).

The external raphe endings at the centre show the same kind of variation as do those of H. marina. In Sea Mills 2 (F.639, 646) and Bigsweir (F.687, 689) valves the raphe is strongly deflected towards the proximal margin, while there is a lesser deflection in Signy valves (Mann 1977, f.39, 41), and almost none at all in Cotham and Sea Mills 1 valves (F.655, 658, 661, 665, 668; but see Cotham 3 valves, F.673). In the first two the external fissures are to some extent continuous across the centre, so that the endings themselves are only to be seen with difficulty, by viewing obliquely from 'near' the proximal margin.

A subraphe canal is always distinguishable in H. amphioxys, but two features of its construction are variable. Firstly, the canal is more distinct externally in some valves than in others. Thus, in the Cotham, Sea Mills 1 and Signy populations it is not clearly delineated

(F.653-8, 661, 668, 673, 676-8), whereas in Sea Mills 2 valves the transapical costae are often abruptly constricted at the junction of valve face and canal wall (F.646, 651); the Bigsweir valves show a similar differentiation (F.681, 685-6).

Secondly, the canal walls may or may not be porose, though even where they are porose there are only two longitudinal rows of poroids, one on each side of the raphe: each poroid is opposite a transapical stria of either the valve face or the proximal mantle. There is always a gap in the distal row of poroids opposite the central raphe endings (F.646-7, 658, etc.), and the rows are frequently discontinuous at various other places along the valve (F.651). The canal walls of the Signy cells are unperforate (F.676-8; Mann 1977), and few poroids occur in those of the Cotham 3 valves (F.672-3). The other Cotham populations all have perforate canal walls (F.646, 653), as do the Sea Mills populations. The Bigsweir group varies intra se (F.685-6, 689-90).

The fibulae, which together with the longitudinal ridges (see before) form the inner 'wall' of the subraphe canal, separating it from the valve interior, do not appear to differ appreciably in spacing or size (relative to the valve costae) from one population to another, although detailed analysis may prove this to be incorrect.

Cincture

The cincture is fully known for only one of the populations studied, but enough information is available about the others to enable the drawing of certain conclusions concerning infraspecific variation.

The Cotham 1 and 2 frustules each have only one closed band per cingulum; this is the first (F.659-60). In these forms there are at least 6 bands in the epicingulum, while in Sea Mills frustules there are 7, all of which are closed except, it seems, the seventh (F.640-1). Within the Bigsweir population there are forms with cingula like those

of the Cotham cells (F.693-4), and also forms with closed bands (F.691-692). It is quite likely that further analysis will prove that the Bigsweir population can be subdivided.

In all cases the first band is to be distinguished by the presence of a well-developed fringe on the pars interior (F.645, 648-9, 688; Mann 1977, f.35); furthermore, this band always bears two or three transverse rows of poroids (F.83-84, 640-1, 688, 691; Mann 1977, f.41-42). The longitudinal rows of poroids on the first band are more closely spaced than are the valve striae, but the ratio of their linear densities is not constant within the species. Thus, in Bigsweir frustules the ratio of L.D. valve striae to L.D. 1st. band striae is 0.64, but in Sea Mills 2 cells it is 0.79, and in Cotham 1, 0.87. The junction of the pars interior and pars exterior is marked externally in the Bigsweir and Sea Mills 2 populations by a 'wavy line', which in vivo fits exactly against the wavy margin of the valve (F.82-83, 85, 643, 645, 652, 682, 685, 689-90). The wavelength is equal to the distance between adjacent valve costae since each 'projection' of the valve margin lies opposite a valve costa (e.g. F.85, 643).

In the Signy population the second and third bands appear to be very similar to the first, except that the third usually bears only two rows of poroids (Mann 1977). In Sea Mills 2 cells the second and third bands have more longitudinal rows of poroids than the first (20-23 in 10 μ m. as against 16-17); moreover, the third has only one transverse row and even this may be discontinuous (F.83). The Bigsweir cells are similar to the Sea Mills 2 cells (F.84).

Nearer the open end of the cingulum the bands become narrower and more delicate (F.640-1, 659-60, 691-4).

Discussion

Thus, it is clear that H. amphioxys, like H. marina and H. virgata, exhibits much infraspecific variation besides that already well docum-

TABLE 9

List of characters found to vary within species of Hantzschia

a = H. amphioxys

m = H. marina

v = H. virgata

1. Valve shape.	a	v
2. Valve size.	a	m v
3. Position of raphe - on dorsal or ventral side of frustule.	a	
4. 'Biarcuateness' of raphe system.		v
5. Linear density of costae/hoops.	a	m v
6. Linear density of poroids.	a	m v
7. Poroid shape.	a	m
8. Hymen pore arrangement.		m
9. Poroid occlusions other than hymena.		m
10. Position of hymen in poroid.	a	
11. Depth of frets relative to costae.	a	v
12. Marginal ridge - presence/absence, and degree of development.	a	
13. Valve margin - 'wavy'/straight.	a	
14. Form of internal central raphe endings.		v
15. Form of central 'knob' (just distal to central r. endings).		m v
16. Form of external central raphe endings.	a	m v
17. Form of external polar raphe endings.	a	m v
18. Fibula morphology.		v
19. Fibula spacing along the valve.		v
20. Linear density of fibulae.	a(m)	v
21. Longitudinal ridges joining the proximal fibula bases.		v
22. Valve structure within interspace, relative to that of remainder of valve face.		v
23. Poroids in walls of subraphe canal - presence/absence.	a	
24. Open/closed nature of bands.	a	m
25. Margin of pars interior of 1 st band - entire/ + projections.		v
26. Morphology of bands, apart from characters 24 & 25.		v

ented concerning shape, size, striation density, and the 'obviousness' of the poroids (see Cleve-Euler 1952). Whether this hitherto unrecognised variation has much classificatory significance is a question which must remain unanswered until it has been possible to study many more of the vast array of varieties and forms which have been described by previous authors. It is interesting that the larger forms, i.e. the Bigsweir and Sea Mills 2 cells, are also those which possess marginal ridges, the most strongly deflected external central raphe endings, and the most massive transapical costae. The last is elsewhere associated with large size, e.g. in H. spectabilis, Nitzschia sigmoidea.

The characters found to vary within H. amphioxys are listed in Table 9, together with those which vary in H. virgata or H. marina.

4.5.8 The identity of 'Hantzschia sp.A'

Throughout this thesis the epithet 'sp.A' has been used to refer to a species of Hantzschia found at Sandbay in the Severn Estuary, and at Borth (see also Mann 1977). This diatom agrees with none of the Hantzschia or Nitzschia species listed by Hendey (1974) as occurring on British coasts, although both sites given above are more or less marine. It is, for example, quite distinct from H. virgata in the construction of the valve, in the presence of a well-developed subraphe canal raised above the general level of the valve, and in the spacing of the fibulae (1.79 units): the fibulae are frequently separated, one from the next, by only one stria (F.108-9, 697). It appears, therefore, to be a species of Hantzschia new to Britain.

An examination of illustrations of Hantzschia species reveals that there is one diatom which closely resembles Hantzschia sp.A. Hustedt (in A.Schmidt Atlas) figured a new species of Hantzschia, which he named H. distinctepunctata (probably the same as Grunow's H. amphioxys var. amphilepta - see Grunow 1880, Pl.12 f.8). Hustedt's