

4.5 Hantzschia

The establishment of Hantzschia by Grunow, and various other matters, are discussed in Mann (1977), a copy of which is appended to this dissertation.

4.5.1 Frustule

The symmetry relationships of Hantzschia frustules were described by Hustedt (1930) in the following manner: 'Apikalachse gebogen, isopol; Pervalvarachse gerade, ebenfalls isopol; Transapikalachse gerade, aber heteropol. Zellkörper zur Valvarebene spiegelconsimil, zur Transapikalebene spiegelsymmetrisch, zur Apikalebene asymmetrisch. Apikalebene gewölbt, die beiden anderen Schnitte ebene Flächen.' While Hustedt's meaning is quite apparent, unless the German 'Achse' and 'Ebene' are rather differently applied than 'axis' and 'plane', his use of these terms is loose. He states that the apical axis is bent, but if so, what is the apical axis, where is it to be drawn? Hustedt seems to mean by it the 'midline', where the valve or frustule is seen in valve view. The classic diagrams of axes and planes of symmetry (e.g. Hustedt 1930, f.2, 3; Anon. 1975, f.6) are almost always based on a Navicula-like diatom, which invariably leads to trouble when this 'formula' is then applied indiscriminately to diatoms with more complex symmetry relationships. In order to prevent confusion, axes are taken here to be straight lines: thus, the apical axis is the straight line which joins the two apices of the valve. 'Plane' is taken in its strict meaning of a 'surface such that the straight line joining any two points in it lies wholly in it; imaginary surface of this kind in which points or lines in material bodies lie' (Concise Oxford Dictionary, 4th Edition 1956). It is not possible, therefore, to have a curved or bent plane, or axis.

The Hantzschia cell is always 'spiegelsymmetrisch' about the

median valvar plane; thus, both raphes lie on the same side of the frustule (Text F.2A, E). The constancy of this feature is important taxonomically and will be referred to later ('Nitzschia - frustule'; see also Mann 1977).

Hantzschia frustules are asymmetrical about the apical plane (Text F.2D, E), and because of this each may be said to have a dorsal and a ventral side, just as may those of Cymbella, Amphora, Epithemia, Rhopalodia, Eunotia, etc. (see also Mann 1977). In all these genera the ventral side is to be distinguished by its lesser convexity (relative to the dorsal side); it may even be straight or concave (e.g. in Eunotia robusta; Hustedt 1930, f.203). This 'dorsi-ventral' terminology in no way replaces the 'proximo-distal' proposed by Mann (1977; see also Text F.1 top), but is a useful complement to it, especially in Hantzschia and Rhopalodia. Certain cells of H. amphioxys are raphid on the dorsal side of the frustule: the distal margins of the valves are the less convex (F.39, 656), this situation contrasting with that in most Hantzschiae. A similar situation obtains in Rhopalodia gibberula (q.v.).

Hantzschia species are 'spiegelsymmetrisch' about the median transapical plane (Text F.2A, D): there is no heteropolarity as in Gomphonitzschia or Nitzschia sect. Fragilariopsis. Most are straight in girdle aspect, and only slightly curved in valve view (giving the asymmetry about the apical plane), but a few species have a sigmoid twist to the frustule and are therefore diagonally symmetrical about the median transapical plane. In H. spectabilis (unpubl. obs.), H. mirabilis and H. herrmannii (Hustedt 1938, T.40 f.2, 3; T.41 f.37, 38) this twist is obvious only in girdle view, and these taxa are therefore analogous to N. sigmoidea, N. vermicularis and N. flexa (sect. Nitzschia). The other sigmoid Hantzschia, H. sigma, shows a greater resemblance in its symmetry to the Nitzschia species bearing the same epithet; it is sigmoid in both valve and girdle views (Hustedt 1938, T.40 f.5-7

and text, p.463).

The valve margins are sometimes further apart on the ventral side of the frustule than on the dorsal side (F.40), or vice versa, and the dorsal margins may in some cases overlap; this has been observed in recently divided cells of H. virgata and H. amphioxys. In some cases this is owing to a greater degree of overlap of the cincture elements on the two sides, but each cincture element may itself exhibit dorsiventrality (Mann 1977), leading to an asymmetry of the cincture about the median valvar plane (e.g. see F.7). There is nothing, however, of the marked asymmetry of the cincture found in many Amphora species (Peragallo & Peragallo 1897-1908, Pl.50 f.20), Epithemia sorex (q.v.) or Rhopalodia gibberula (q.v.); the planes in which the valve margins lie in a Hantzschia frustule are almost parallel.

4.5.2 Valve morphology and anatomy

Whereas the dorsi-ventral terminology is useful for the description of frustules, only 'proximal' and 'distal' will be used with regard to valve features for the reasons given in Mann (1977).

The valve is elongate, although there is a wide range in shape from small, compact forms of H. amphioxys (F.94; Hustedt in A.Schmidt Atl., T.329 f.18) to the very long, slender valves of certain taxa, e.g. H. elongata (Hustedt op. cit., T.329 f.1), H. virgata var. gracilis (F.53-4; Hustedt op. cit., T.345 f.8), H. spectabilis (Hustedt 1930, f.809a), etc. There is a corresponding range in the actual size of the diatoms, the smallest specimens of H. amphioxys being a mere 20 μm . long (teste Hustedt 1930; the smallest observed in this study were 23 μm . in length - F.94), while Hustedt (1938) gives 340 μm . as the upper limit for H. mirabilis, (1930) 430 μm . for H. elongata, and (1930) 450 μm . for H. spectabilis. Nevertheless, even in the two last-

mentioned taxa, the breadth of the valve is still remarkably small (maximally 13 and 15 μm . respectively, see Hustedt 1930).

The proximal margin is usually to some extent concave, though there are several exceptions worth note. In the H. weyprechtii group (H. weyprechtii, H. baltica, 'Nitzschia petitiana' - see Cleve & Grunow 1880, p.104) the proximal margin is straight or slightly convex (F.134; Simonsen 1960, T.2 f.16-18), as it is also in H. herrmannii (Hustedt 1938, T.40 f.2, 3) and H. vivax (F. 129). The proximal and distal margins in H. spectabilis (unpubl. obs.) and H. mirabilis (Hustedt 1938, T.41 f.37) are more or less straight, and are parallel to one another, while in H. sigma (ibid., T.40 f.5) they are both sigmoid. With the exception of the last three species, almost all Hantzschia species have a convex distal margin.

H. amphioxys is extraordinarily variable in outline (F.80-81, 86-95, 97-98): some forms are all but symmetrical about the apical plane (excluding the asymmetry inevitably present because the raphe is eccentric), whereas others are very strongly bent (compare F.92-93 with F.87-88). The reversed forms of H. amphioxys (noted above, and see F.89), where the distal margins are concave and the proximal convex, are probably chance variants of the normal type. Frenguelli (1942) noted a solitary example of such a form and gave it varietal status, but this is hardly justifiable; the basic valve construction and the course and structure of the raphe are very similar to those of more typical H. amphioxys (compare F. 656, 658 with 657, 661). Indeed, in one sample reversed and normal forms were found together, but with the former occurring as only a small minority of the total H. amphioxys complement (less than 5%, 164 valves counted). At most this variant deserves recognition at the level of a forma.

In face view the valve is frequently narrower at the centre than it is somewhat nearer the poles; often it is widest approximately

halfway between centre and pole (F.36, 53, 97 etc.).

Turning now to considerations of the structure of the valve rather than of its outline, by the use of the SEM it may be observed that well-defined distal mantles occur in H. amphioxys (F.643) and H. spectabilis (unpubl. obs.). Indeed, some valves of the former possess 'marginal ridges' sensu Anon. (1975)(F.647). In H. marina, H. virgata, Hantzschia sp.A (Mann 1977, and see 'The identity of Hantzschia sp.A, Chapter 4.5.8), and H. weyprechtii, however, the valve distal to the raphe is more or less evenly curved and thus no mantle is distinguishable (e.g. H. marina, F.581, 592).

Mann (1977) distinguished three types of valve construction, which may be exemplified by H. amphioxys, H. marina, and H. weyprechtii respectively.

1. H. amphioxys type

Here 'the valve is composed of transapically orientated costae, circular or ovoid in section, each separated from the next by a single row of poroids' (Mann 1977). The poroids are each delimited by the two adjacent transapical costae and the two adjacent linking frets (F.638, 671, 676-7). The depth of the frets and their positions relative to the costae are variable within the genus. In H. amphioxys the frets are much shallower than the costae and lie towards the outside of the cell (F.671), so that they are often not at all obvious in SEM pictures of valve interiors (F.650, 662, 667, 670, 683). The external surface of the fret, however, lies only a little below the maximum elevation of the costae, making the latter less conspicuous than they are internally (compare F.663 with 662). The other Hantzschia species of this group which have been studied with the EM show the following variations on the above pattern:

- a. H. virgata; costae slightly deeper than frets, external surfaces of both at exactly the same level. Internally the costae

project further than the frets (F.612, 617, 621, 631-2, 634).

- b. Hantzschia sp.A; costae deeper than frets, costae very obvious externally but hardly projecting beyond frets internally (F.695-7).
- c. H. spectabilis; costae deeper than frets, but frets placed such that the costae project above them approximately equally on either side (Mann 1977, f.53, 55-57, 59).

In H. virgata the costae and frets are so positioned that when the hymena are in position there appears to be a smooth external 'skin' of silica over the whole valve (Round 1970a, Mann 1977; F.617, 631-2).

Each poroid in Hantzschia valves is closed by a hymen, the position of which is variable - at the outside of the valve in H. virgata (F.631-3), slightly lower in Hantzschia sp.A (F.696-7, 699), and at this position or even lower in H. amphioxys (F.658, 661). The hymen pores are arranged randomly in the two species (H. virgata and H. amphioxys) where TEM observations have been made (Mann 1977 and F.526-31). The boundaries of the hymena are well-defined - there is a marked difference in thickness between the hymen and the immediately surrounding silica of the frets or costae.

While the above description of structure is true in general for the species mentioned, there is a modification in H. virgata var. virgata which is noteworthy since it is in some ways similar to the H. weyprechtii type construction (see below). The structure of the major part of the valve in this variety is as described above for H. amphioxys, with the modifications noted for H. virgata. Within the interspace, however, and distal to the raphe, there are often two rows of poroids between adjacent transapical costae, these poroids being placed alternately (F.62-65).

Sterna (excepting the raphe-sternum) are not present, unless the thin ridge of silica running between the proximal fibula bases in H.

virgata vars. virgata, gracilis and leptocephala (e.g. F.623) is to be so categorized. The raphe-sternum may be fairly broad, reaching bilaterally to the fibulae, in which case the subraphe canal wall (where a canal may be distinguished) is unperforate, as in H. spectabilis (Mann 1977, f.53, 55), some H. amphioxys (F.676, 678), H. virgata var. intermedia (F.634, 637), Hantzschia sp.A (F.696-7), or it may extend only to the distal fibulae, one or more rows of poroids intervening proximally between sternum and fibulae, as in H. virgata var. gracilis (F.621-3), or again the raphe-sternum may fail bilaterally to reach the fibulae, as in some H. amphioxys (F.646, 658).

At the poles the raphe-sternum is wider and is fused to the valve margin. In this expanded, polar region the sternum is often pierced by a few pores, usually smaller than the valve poroids and not associated with any costae (F.651-2, 663, 672). It is not clear whether they are occluded by hymena.

The raphe-sternum may also be expanded centrally if central raphe endings are present (F.646-7, 658, 667).

Various other Hantzschia species appear to be similarly constructed to H. amphioxys, though without EM observations the structural details remain unknown. H. segmentalis plainly belongs to this group: here the poroids are very regularly arranged near the raphe, but distally, while they remain in transapical rows, they are irregularly and widely spaced (suggested in Brun's 1895 Pl.17 f.109, 110: see also F.122, 125, 127). Hustedt's illustrations of H. elongata (in A.Schmidt Atlas, T.329 f.2), H. distinctepunctata (ibid., f.21, 22, and 1938, T.40 f.4), and his (1938) remarks about H. mirabilis show that these too belong here. H. faba, H. limi (see illustrations in Frenguelli 1926), H. directa (Pantocsek 1902, T.9 f.242), H. vivax (F.130), H. borivliana (Gandhi 1962, p.474), are also of this type^{of} construction, and so too, probably, are several species which resemble H. amphioxys in other respects,

e.g. H. sigma, H. exilis, H. subandina, etc.

2. H. marina type

The main features of this type were described by Mann (1977), who noted that previous authors had assumed that the transapical bars visible in the light microscope are on the inside of the cell, whereas careful observation with the aid of this instrument demonstrates clearly that they are external. SEM observations confirm this and show that the valve consists of transapically directed 'hoops' which run around the exterior of the valve, each separated from the next by a strip of silica perforated by two rows of poroids: these rows are offset transapically such that the poroids are arranged alternately (F.1-6, 8, 581-3, 602). Each hoop is of maximum width (measured in the apical direction) near its top, so that in section it is somewhat pyriform (F.582, 586, 594, 603). The poroids, reniform or oval in outline (F.575-578), sometimes with cribra (for more detailed information, see 'Intra-specific variation'), are closed by hymena which are elevated slightly above the general level of the valve (F.582, 589, 602-3), and in which the pores are arranged randomly (F.522, 524-5) or in hexagonal array (F.521, 523). The hoops do not project at all into the lumen of the cell (F.588-9, 603, 608), and it has been questioned (Mann 1977) whether they can be regarded as homologous with the transapical costae of H. amphioxys, etc.

The basic structure of the valve is uninterrupted by sterna, except by the raphe-sternum which reaches bilaterally to the fibulae (F.589, 592, 594, 608): the canal wall is thus unperforate. At the poles the raphe-sternum is much expanded, especially distally, and is fused to the margins (F.585, 605). As in the first group, in this polar region the raphe-sternum is often perforated by a few circular pores (F.31, 33, 610) which are much smaller than the normal valve poroids. Each appears to be occluded by a thin silica plate (F.586),

but it is unknown whether this is a hymen.

H. marina is the only species possessing this type of structure; the only other species of this type that has been described, H. pseudo-marina, is considered here not to be separate from H. marina (see later).

3. H. weyprechtii type

Mann (1977) remarked that this type is 'in some ways intermediate between the first two.' Transapical costae are present (F.700) and are very similar in form to those of, for example, H. amphioxys or Hantzschia sp.A, but in H. weyprechtii they are generally separated by a double row of poroids, placed alternately like those of H. marina (Mann 1977, f.32, 69, 71, 73). But, in view of the presence of double rows of poroids in parts of the H. virgata var. virgata valve and the presence of single rows in some H. weyprechtii valves (unpubl. obs.), and in view of the form of the transapical costae, it would seem that this type is much more similar to H. amphioxys, H. virgata, etc., than it is to H. marina, which, with its peculiar construction, stands alone among the members of the Nitzschiaceae.

At present it is a matter of conjecture as to whether the raphe-sternum reaches to the fibulae in H. weyprechtii; Mann's (1977) f.34 suggests that it does not, but little sign can be seen of poroids in the subraphe canal wall in SEM pictures (F.700), although this may be because the hymena lie flush with the outer surface of the valve. Hymena have not yet been observed with the TEM, but SEM observations indicate their presence.

In all three groups the costae (or hoops) are more feebly developed on the proximal side of the raphe than they are distally (F.690, 696; 587, 607; 700).

4.5.3 Irregularities in structure

For the most part, the transapical costae or hoops run unbranched,

each one more or less parallel to the next, from margin to raphe-sternum. But there are certain exceptions to this which have a degree of constancy in position or form and are thus worthy of record. Some forms of H. amphioxys are strongly bent (as noted above), and in these the central striae are distinctly radiate and more widely spaced than the remainder (F.87-8). In general the striae are orientated at right angles to the midline of the valve.

Discontinuities in the structure of the valve often occur in a region something over halfway between centre and pole (F.3, 36, 76, 80, 81, 86-95, 98, 581, 638, 644, 656, 669, 675, 680). These are particularly common in H. amphioxys (Mann 1977), where they occur also at the centre and occasionally elsewhere (F.86, 97). The disturbance of the normal pattern may be slight - a mere narrowing of one costa - or very marked (e.g. Mann 1977, f.3). While these discontinuities are not fixed in their form (there can be great variety within a single population), they have certain features in common. Firstly, they tend to occur more frequently in particular positions on the valve than elsewhere (as noted above). Secondly, no new structural elements are introduced, i.e. the disturbance contains only costae (hoops), poroids, frets, etc., although these may be distorted. Thirdly, the disturbances are semi-conservative in form: by this is meant that, for example, though costae may be changed in orientation, they often remain of the same width; if a costa is narrowed then usually it is unchanged in orientation; poroids tend to occur in rows even if these are very short and not at all transapical; etc.

These discontinuities have been observed in H. amphioxys and H. virgata, and also in H. marina. In the last species hoops may be abnormally spaced (F.30), sometimes so that only one row of poroids intervenes between adjacent hoops (F.3), in which case the poroids may lose their normal orientation, or one or two hoops may be incomplete etc.

These discontinuities are probably equivalent to those found by Voigt (1942, 1943, 1956, 1962) in various naviculoid diatoms. So far as is known, they have not previously been reported in the Nitzschiaceae although some authors' illustrations show them (e.g. Lund 1946, f.13A). The discontinuities may well owe their existence to a cause common to both groups of diatoms, but it must be noted that there are differences between the naviculoids and the Nitzschiaceae, the chief of which being that, whereas in the former Voigt established that discontinuities occur in every valve of a species, occupying exactly the same relative position on the valve, in Hantzschia only a proportion of the valves possess discontinuities; moreover, these are not exactly positioned. As for their cause, this is discussed elsewhere, in the chapter on cell division and auxospore formation.

4.5.4 Raphe and associated structures

Some Hantzschia species have a biarcuate raphe system, the raphe 'being more or less equidistant from both margins at the poles, while the central endings lie very close to the proximal margin' (Mann 1977). Round's (1970a) f.2A illustrates this for H. virgata var. intermedia (and see F.41, 42) and such an arrangement is also to be found in H. marina (F.8, 32, 583) and Hantzschia sp.A (F.113-5, 695). The raphe in H. amphioxys (F.656), H. spectabilis (unpubl. obs.), H. weyprechtii (F.133), and H. virgata vars. gracilis (F.56), leptocephala and virgata follows a course more or less parallel to and close to the proximal margin, or at least maintains a constant position on the valve (Mann 1977). This is almost certainly true also of H. vivax, H. herrmannii, H. sigma, H. mirabilis, H. distinctepunctata (vide Hustedt's 1930, 1938 illustrations) and most other Hantzschia species.

Within Hantzschia there are forms in which the raphe-slit is continuous from pole to pole (e.g. H. spectabilis, Mann 1977; probably also H. vivax, F.129, and H. segmentalis, F.122-3, in both of which

no 'central nodules' are visible in the light microscope), but the majority of taxa possess two raphe-slits per valve. Fractures suggest that in this genus the raphe-slit is < shaped in cross section for most of its length (F.594, 677), as it is in many other diatoms, e.g. Pinnularia (Lauterborn 1896), Gomphonema (Dawson 1972), etc.

4.5.4.1 Internal polar raphe endings

Simple helictoglossae have proved to be present in all species where SEM examination of the internal endings has been possible. The helictoglossae of H. spectabilis are large, those of H. amphioxys and H. virgata smaller (Mann 1977, and see F.613, 625, 650, 662, 674). In H. marina and Hantzschia sp.A the internal polar raphe endings have so far been impossible to observe because of the narrowness of the valve relative to its depth at this point. Mann (1977) was of the opinion that in these species the inner thickening visible at the pole in girdle view (using the light microscope, F.9, 117) represents the helictoglossa, since it is at this point that the external fissure bends abruptly, a feature usually correlated with the beginning of the blind terminal fissure.

4.5.4.2 External polar raphe endings

The raphe continues past the helictoglossa 'as an unbranched blind groove which curves away towards the distal margin' (Mann 1977); as noted in the preceding section, it is often bent slightly, but abruptly, above the helictoglossa, the direction of the bend being towards the distal margin (F.586, 624, 651, 663). Thus, in H. amphioxys (in part)(F.651, 672, 691-4), H. marina (in part)(F.605, 610) and H. virgata var. intermedia (F.633) this terminal fissure comes finally to run parallel to the distal margin and away from the pole. The curvature of the fissure is less in Hantzschia sp.A (F.699), H. marina (in part)(F.585), H. virgata vars. virgata and gracilis (F.626) and

H. weyprechtii, and least in H. spectabilis, where it continues to the very edge of the valve (Mann 1977). In all species examined, except the last, the end of the terminal fissure is usually somewhat expanded and shallower than the remainder (e.g. F.584, 641).

4.5.4.3 External central raphe endings

These are simple and undeflected in some taxa, e.g. H. weyprechtii (F.700), Hantzschia sp.A (F.696), H. virgata var. intermedia (F.632), H. marina (in part)(Mann 1977, f.49), but in others there is a deflection of the endings towards the proximal margin. In H. virgata vars. gracilis (F.631) and virgata (F.617) the deflection takes the form of a gentle double bend, but in H. marina (in part)(F.587, 606) and H. amphioxys (in part)(F.639, 689) it can be quite abrupt, with the effect in the latter that the central endings come to lie on the proximal mantle. Such deflections were noted by Hustedt (1928b) in his excellent light microscope study of Hantzschia. The internal endings are not so deflected and thus centrally either there must be a change in the slit's cross section, or short terminal parts of the external and internal fissures must be blind. The end of the external fissure is often slightly expanded. In all cases the endings are symmetrical, whether coaxial (H. weyprechtii) or noncoaxial (Hantzschia sp.A, H. virgata var. intermedia, H. marina).

4.5.4.4 Internal central raphe endings

These are of two types, both described by Mann (1977). Those of the first type are noncoaxial-asymmetrical (H. amphioxys, F.642; H. marina, F.593; Hantzschia sp.A, Mann 1977, f.79; H. virgata var. intermedia, F.637), while in the second they are coaxial-symmetrical (H. weyprechtii, Mann 1977, f.34, 69). In H. virgata vars. virgata (F.619) and gracilis (F. 622-3) the internal fissures are continuous from pole to pole much as in H. spectabilis, which species does not, however,

have external central endings, unlike the first two (Mann 1977).

Sometimes the endings lie in a flat-topped platform of silica which is an expansion of the narrow ridges which in these species, viz. H. marina (F.593) and H. virgata (F.637) border the internal fissures. The raphe-sternum is thus thicker in the immediate vicinity of the raphe-slit and thins bilaterally before becoming thicker again opposite the fibula bases (F.594). Similar narrow ridges border the external fissure in H. spectabilis (Mann 1977, f.53).

4.5.4.5 Fibulae and subraphe canal

The raphe is subtended by numerous fibulae which take various forms depending on the species. The confusion arising from differing interpretations and representations of subraphe structure, as it is observed using the light microscope, has been commented upon by Round (1970a) and Mann (1977): thus, 'Kielpunkte' has come to refer in some cases to the fibulae, in others to the interspaces (Mann 1977). The lack of consistency in the representation of subraphe structure is particularly marked in H. amphioxys, where the interspaces are much smaller than the fibulae (F.650, 664, 670) and may appear in the light microscope to be 'solid' if the wrong focus is chosen. Authors describing new species of Hantzschia or Nitzschia always note the numbers of striae and fibulae/interspaces in a given distance (usually 10 μm .), but it is usually left for the illustration to convey any information about the form and size of the fibulae and their spatial relationship to the transapical costae. Thus, for instance, from Hustedt's (1938) written description of H. mirabilis it is not possible to deduce that the fibulae are broad structures consisting of several subraphe costae much as in H. amphioxys, which is the reasonable inference from his figures (T.41 f.37-8). Clearly this would not matter if all illustrations were as unambiguous as in the particular instance cited, but they are not and the form of the fibulae in H. limi, for example, is

quite unguessable, even though Frenguelli's figures (1926, Lam.7 f.8-13) may be entirely accurate, judged by the rules of his method of representation.

In H. amphioxys the fibulae are each composed of 1-6 (or more) fused subraphe costae; they range in shape, therefore, from thin ribs to broad plates (F.650, 664, 670, 683). The degree of fusion of the subraphe costae is variable; sometimes a tiny hole may remain between adjacent subraphe costae (F.664) and often a fibula is transapically ridged, the subraphe costae thus remaining to some extent distinct within it (Mann 1977, f.37-38). Adjacent fibulae are usually separated by one or two transapical costae, but the central interspace is wider, containing 3-5 (+) transapical costae (F.80-82, 86-95, 97-99, 664, 666-667, 683).

A wider separation of the central pair of fibulae is present in several other taxa - Hantzschia sp.A (F.108-15, 119, 120), H. weyprechtii (F.133-4), H. virgata var. intermedia (F.36-38, 41-42), H. marina (F.6, 8), H. mirabilis (Hustedt 1938, T.41 f.37, 38), H. sigma (ibid., T.40 f.5, 7), H. distinctepunctata (ibid., f.4), H. elongata (Hustedt in A.Schmidt Atlas, T.329 f.1), etc. In those species where SEM studies have been made, a consistently wider separation of the central fibulae has proved to be correlated with the presence of central raphe endings. Where these are not present, as in H. spectabilis, there is no consistent difference between the central interspace and the remainder. However it must be added that in some varieties of H. virgata the central interspace is not always obviously larger than the others, yet central raphe endings are present (F.63, and see 'Infraspecific variation in H. virgata').

The fibulae of H. amphioxys are joined at their bases by ridges which run parallel to the raphe, one distally, the other proximally (F.99, 664, 667, 670). The effect of this is to further diminish the

size of the interspace and to delimit a canal immediately beneath the raphe. Moreover, the canal walls, and hence also the raphe-sternum, are slightly raised above the general level of the valve (Text F.6D, E, and F.676-7). The ridges are lacking opposite the central raphe endings and so the central interspace is larger not only apically but also transapically (F.664, 666-7). This feature is distinguishable using the light microscope (F.99) and Hustedt's (1938) illustrations show it in H. sigma and H. mirabilis, which also have the same fibula structure as does H. amphioxys. H. elongata is also similar (Hustedt in A.Schmidt Atlas, T.329 f.2).

The fibulae of H. spectabilis, which, like the transapical costae, are massive structures, 'comprise a mixture of more or less fused pairs of, and single, subraphe costae' (Mann 1977). The interspaces are small, the fibulae being separated by only one or two transapical costae, or by none (ibid., f.57, 59). Again a canal may be distinguished, this being set well above the general valve level (ibid., f.53, 55-56; see also Text F.6D).

Each fibula of H. virgata or Hantzschia sp.A represents but a single subraphe costa (F.64, 69, 78, 620-1, 634; 108-12, 697), but the spacing of these serves to set the two species apart (Mann 1977). Adjacent fibulae are separated by 1-6 (+) transapical costae. A ridge joins the proximal fibula bases in Hantzschia sp.A (F.119, 120), and in H. virgata vars. virgata (F.620), gracilis (F.621-3) and leptocephala (F.73, 75, 79), but whereas in the former species a canal is clearly distinguishable, raised above the general level of the valve (F.695-6), in the latter no canal is to be found (Round 1970a, Mann 1977), although the fibulae do flare slightly near the raphe in H. virgata var. virgata thus delimiting a more or less oval portula (F.615). In Hantzschia sp.A (F.697) and H. virgata vars. intermedia (F.634), gracilis (F.621-3), the fibulae are slender and rib-like,

but in H. virgata vars. virgata (F.612, 618), leptocephala (F.71-9), kariana and borealis, and in H. segmentalis (F.122-8) they are extended some way across the valve face and are more massive structures.

Two other variants were noted by Mann (1977) and in these it is not possible to say that the fibulae represent either single or fused subraphe costae. In H. weyprechtii the fibulae are each of approximately the same width as a transapical costa, but the relationship between these two components of the valve is obscure (op. cit., f.69). As in H. amphioxys, there are ridges both proximal and distal to the raphe and a well-defined subraphe-canal is present. The central interspace is slightly wider transapically, as well as apically, than are the other interspaces.

In H. marina transapical costae, as such, cannot be distinguished; hence, neither can subraphe costae. There is a well-developed proximal ridge in this species, and a rather feeble distal ridge (F.589, 594, 608, 611); a canal is present, raised well above the general level of the valve (F.587, 606-7). The fibulae spring from the ridges, each one being opposite a transapical strip of silica which externally bears a hoop (F.1-4, 6, 588-9, 603, 608, 611). None of these strips is without a fibula (except the centremost) and thus the interspaces are very uniform in size. Centrally there is a knob, placed just distal to the internal raphe endings where a fibula base might otherwise be (F.6, 593, 609). No such knob is to be found proximally, however, and the reasons for its existence remain obscure. The ridges mentioned above are no less developed centrally and thus all the interspaces have approximately the same transapical width (F.608-9).

Two other species, Hantzschia sp.A and H. virgata also possess knobs similar to those in H. marina (Mann 1977, f.60, 75). 'Central nodule' would be apt for these structures, were it not that this term is employed traditionally to describe a central interruption of the

raphe; indeed, the absence of any truly nodular thickening intervening between or including the central raphe endings in Hantzschia (except, perhaps, in H. weyprechtii - Mann 1977, f.34, 69), coupled with the presence in several taxa of the knob described above, constitutes a strong argument against the continuance of the use of this term.

4.5.5 Cincture

Mann (1977) stated that in Hantzschia 'the bands are always open and, inside a cingulum, they alternate in orientation such that the split of the first band overlies the central portion of the next formed.' The former conclusion was premature and incorrect, based as it was on the unjustified assumption that within a species the cingulum elements would show a degree of constancy, in type and form, which has since proved to be lacking. Where open bands are present, however, they do indeed alternate in orientation as described above (F.659-60, 693-4). Closed bands are to be found in some cells of H. marina and H. amphioxys (see later), but so far at least, no cingulum has been noted in which all the elements are closed bands.

'Each girdle element tapers somewhat to the abvalvar margin, this overlying the advalvar margin of the adjacent, next-formed element' (Mann 1977). All the cincture elements have a more or less well-defined pars interior. The number of elements per mature cingulum varies within the genus (and even within species), from 3 (4) in H. virgata var. intermedia to 7 in H. amphioxys.

Few general remarks about the cincture may be made. The first band seems always to have at least two transverse (sensu Von Stosch 1975) rows of poroids, of which the advalvar row is often more regular than the other(s) and in vivo lies adjacent to the edge of the mantle. The girdle band poroids are generally simpler in form than those of the valve; they are closed by hymena (F.523-4, 527-8, 532) in which the

pores are arranged as in the valve hymena. Thus, in some H. marina cells the girdle band poroids are circular or somewhat triangular in outline whereas the valve poroids are reniform, but both have hymena in which the pores are in hexagonal array (compare F.524 with 525). Another general feature is the dorsiventrality of the cincture noted by Mann (1977), which is expressed in different ways, depending on the species.

The girdles of H. amphioxys, H. marina and H. marina will be dealt with more thoroughly under the heading of 'Infraspecific variation' (see later). Available information about other species is given below:

H. spectabilis

Some features of the girdle in this species have been described previously (Mann 1977). The proximal half of the first band has three transverse rows of small poroids, which are smaller than those of the valve, whereas the distal half has only two rows (op. cit., f.18). The poroids are more irregularly arranged in the proximal half and are slightly more widely spaced: distally there are 18-21 longitudinal rows (sensu Von Stosch 1975) in 10 μm ., the two poroids in one such row being separated longitudinally by approx. 0.5 μm ., whereas proximally there are 17-18 rows in 10 μm ., each poroid being separated from its neighbour in the same row by approx. 0.7 μm . Moreover, the pars exterior of the first band is much wider proximally than it is distally (4 μm . as against 2 μm .). There is a well-developed fringe on the pars interior of the first band (op. cit., f.18) which is not present on the second and subsequent bands (unpubl. obs.). Otherwise, the second band appears to be very similar to the first, while the third and fourth are narrower and have fewer poroids.

Hantzschia sp.A

The first two bands are very similar one to the other in their

proximal halves: each bears two transverse rows of poroids, and the longitudinal rows are of the same linear density in both (Mann 1977, f.24; and F.118, 121, 695). Moreover, the longitudinal rows have the same spacing as the valve transapical striae, so that in one population (from Sandbay, near Weston-super-Mare) the linear density of the valve transapical striae = the linear density of the longitudinal rows on the 1st. or 2nd. band = 15-16 in 10 μm .; in another (from Borth, near Aberystwyth) L.D. transapical striae = L.D. longitudinal rows = 17-18 in 10 μm .

In the frustules studied all the bands have been open, each band (except the first) bearing a ligula which closes the gap left by the open ends of the adjacent band advalvarly (F.698). The pars interior of the first band has an entire margin (Mann 1977, f.76).

The third and subsequent bands are narrower than either of the first two and are more delicately marked (F.698). Their morphology is not exactly known, but some at least are perforated by tiny poroids, of which there are about 45-50 longitudinal rows in 10 μm .

Nothing is known about the differences between the proximal and distal halves of the cincture elements, except that the distal half of the first band seems to have 2-3 irregular transverse rows of poroids, this contrasting with the proximal half (compare F.116 with 118).

H. segmentalis

The first two or three bands bear two or three transverse rows of poroids and are fairly similar to the first two bands of H. virgata var. virgata. The linear density of the longitudinal rows of poroids on any one of these bands is approximately the same as that of the valve striae (F.128). So far, nothing is known concerning asymmetry of the girdle about the median valvar plane.

4.5.6 Chromatophores and cytology

Some details of chromatophore structure may be gleaned from the papers by Kützing (1844), Mereschkowsky (1901, 1903a, b), Heinzerling (1908), Round (1970a) and Mann (1977). H. amphioxys possesses two chromatophores, H-shaped in valve view, placed such that one lies in each polar half-cell; a prominent pyrenoid lies between the two plates of a single plastid (F.103-4). Most of this was illustrated by Kützing (1844, Pl.30 f.1), but it was left to Mereschkowsky and Heinzerling to describe and analyse the chromatophore structure. Mereschkowsky (1901, 1903a) considered that there are four chromatophores per cell; thus, although he noted that for each opposing pair of plates there is a 'pyrénoïde commun qui les réunit en formant un seule système', he compared the chromatophore structure in Hantzschia with that in one group of Nitzschia spp (his 'sixième type', 1903a, p.160) which comprised forms possessing four distinct chromatophores per cell. Heinzerling (1908), however, held that there are but two chromatophores, an opinion shared by Mann (1977).

In H. amphioxys the two distal or the two proximal plates are separated by 'einen im Zentrum kreisförmig erweiterten Spalt' (Heinzerling 1908; see also F.102-4). Usually the distal plates are more widely separated than the two proximal (F.103-4); also, the central widening of the cleft is less marked proximally. As a consequence the distal plates are frequently smaller than the proximal. In some cells lobes of the chromatophores extend under the raphe onto the valve face, thus to some extent obscuring the pyrenoid from view (Mann 1977, f.22). There is also, sometimes, a cleft in the distal plate which reaches to the pyrenoid (F.102); the significance of this is unknown. The pyrenoid is cylindrical, as noted by Heinzerling (1908), and fairly constant in size - approx. 5 μm . (apical diameter) x 2-3 μm . (transapical diameter) x 3 μm . (perivalvar depth)(F.102-4). The cytoplasm sometimes

contains small granular inclusions (F.102), but these are not of constant position.

H. elongata has very similar chromatophores to those of H. amphioxys (Mereschkowsky 1903b, f.33), which is perhaps not surprising in view of their similarity in valve structure and ecology (see Hustedt 1930).

Mereschkowsky (1901, 1903a) also described the chromatophores of H. vivax (under 'Nitzschia vivax') which bear little resemblance to those of H. amphioxys (contra Mann 1977, whose statements were based on the written description supplied by Mereschkowsky 1903a), although it must be added that Mereschkowsky's illustration (1901, T.7 f.4) provides one with little confidence that it does indeed represent H. vivax. The figure shows a cell with two chromatophores, each of which is divided into two halves, joined by a narrow isthmus. The constriction is transverse to the cell (whereas in H. amphioxys it is primarily longitudinal), and is visible in girdle view.

The chromatophores of H. virgata var. intermedia were described by Round (1970a) as 'split cylinders with finger-like extensions' but it is not clear from his illustrations where the pyrenoid is situated. In H. virgata var. virgata the chromatophores each possess a large and conspicuous pyrenoid, and are essentially like those of H. amphioxys but much more elaborately lobed (F.101). H. weyprechtii also has chromatophores similar to these (Mann 1977; and see F.136-7), but they are simpler and occupy a far smaller proportion of the cell length than in H. virgata, H. amphioxys or H. elongata.

H. marina has chromatophores fairly similar to those described by Mereschkowsky (1901) for H. vivax; the pyrenoid is not very prominent. Karsten (1899) seems to have described this species as a new species of Amphora, A. gamma: there are, however, two chromatophores, not one as Karsten thought.

In H. spectabilis, however, there appear to be several pyrenoids per plastid rather than a single large one, and there are probably four chromatophores, not two, disposed like the four plates in H. amphioxys cells (unpubl. obs.). It is unlikely that the H. spectabilis cells observed were undergoing cell division since all the cells possessed four plates; moreover, these were arranged such that the gap between opposing pairs was visible in valve view, whereas during cell division in Nitzschia or Hantzschia (H. amphioxys) the chromatophore division plane is at right angles to this.

There is, then, a certain degree of constancy in chromatophore structure in the species studied. In most cases (leaving a query beside H. vivax and H. marina) there are four plates, representing two chromatophores in H. amphioxys, H. elongata, H. virgata and H. weyprechtii, (also, it seems, in Hantzschia sp.A - preliminary observations), and four in H. spectabilis. From the similarities in valve structure, it is quite likely that several other Hantzschia species (H. sigma, H. mirabilis, etc.) will also prove to have chromatophores like those of H. amphioxys, but since some of these species are rare it may be a long time before it is possible to confirm or deny this speculation.

The nucleus in Hantzschia is central, held between the chromatophores in a bridge of cytoplasm (F.101, 103-4, 136-7): it is often quite large relative to the cell volume. It is spherical in H. weyprechtii (F.136-7) and in many H. amphioxys cells (F.102-4), but in larger specimens of the latter it may be elongated apically (F.106). In H. virgata var. virgata the nucleus is almost as wide as the cell in girdle view, and when seen from this angle is squarish (F.101). The nucleoplasm is uniformly and fairly coarsely granular, and stains easily with aceto-carmin (F.105-7, 135). Nucleoli appear as spherical non-granular, non-staining bodies within the nucleus; a single nucleolus can usually be distinguished in H. amphioxys nuclei (F.105-7).

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 infraspecific 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-