

### 3: TERMINOLOGY

Our various contemporary languages, because they evolved over a period during which diatoms were unknown and unsuspected, are frequently unable to provide a sufficient range of words to describe the structures which have now become apparent in this group of organisms. Therefore, it has become necessary either to employ words from extant languages, redefining them for use within the confines of 'diatomology', or to borrow words from extinct tongues, usually classical Greek or Latin, again with redefinition, in order to communicate concisely and accurately this newly discovered information.

At first, diatom terminology evolved slowly, workers adding piecemeal to the stock of descriptive words and phrases. Thus, by the time W. Smith published his 'Synopsis of the British Diatomaceae' (1853, 1856), the individual diatom cell had come to be called a 'frustule' and was known to have a siliceous epiderm consisting of two 'valves' (1853, pp. xiii, xiv). Since this time, the meaning of 'frustule' has changed somewhat, coming to refer only to the exoskeleton of a diatom cell, (e.g. Patrick & Reimer 1966, p.1; 'the cell wall or frustule of a diatom': also, Hendey 1964, p.4, Anonymous 1975, p.325, etc.).

Some of the early terminology has not lost its worth, but the usage of 'punctum', where sometimes solid structures (e.g. the 'keel punctum' of Hasle 1964), but more often what are now known to be areolae (sensu Anon. 1975) (e.g. in Boyer 1927) are meant, illustrates the case of a term becoming worthless through imprecise application.

The sudden and rapid increase in the knowledge of diatom structure made possible by the electron microscope led to a correspondingly urgent need of new terms, a need soon recognised and provided for superabundantly by diatomists! (vide the discussion of terminology in Hasle 1972a). The resultant chaos prompted the publication in 1975 of a set of proposals for a standardisation of diatom terminology

(Anon. 1975), based partly on an earlier contribution by Ross & Sims (1972). A companion paper on the terminology of the diatom girdle was also published (Von Stosch 1975) and it is these three papers which will be used as the framework for the present discussion.

Firstly, the philosophical bases of these terminologies must be examined; what are their objectives and how are they to be understood? Ross & Sims considered it important that just as 'a specific name should be applied to one species only, and ... each individual species should have only one correct name, so it should be the case that each morphological term refers to only one homologous kind of structure, which in its turn has only one morphological term corresponding to it.' But they qualified this by noting the need for 'single terms to cover groups of structures that cannot always be separated under the light microscope.' Thus, 'areola' was suggested as a general term for 'the regularly repeated passage through the valve wall occluded by a velum that is a single element of the general pattern of structure': it therefore covers both poroids and loculi (sensu Ross & Sims 1972, Anon. 1975). Further, they suggested the application of the type method to terminology, so that each term should be typified by a diatom taxon in which it is exemplified; 'the use of the term will then imply that the structure referred to is homologous with that found in the species so designated.'

There is no discussion of underlying theory in the Anon. proposals and neither is there any reference to previously published terminologies. The intended method of application of their terms is therefore unknowable. However, from the format it seems as though Ross & Sims' (1972) type method has been adopted since after each definition, excepting those terms of a more general nature, one or more diatom taxa are mentioned (and usually illustrated) in which the particular structure occurs. Thus, it is implied, for instance, that the

stigmata of Didymosphenia (the 'type' mentioned in Anon. 1975) are homologous with those in Cymbella spp., or in Navicula mutica (which structures agree with the written definition of stigma). But these stigmata are very different, one from another, (Dr. E. J. Cox pers. comm., and author's unpubl. obs.), and it would be better to assume non-homology until proved otherwise than vice versa. Again, are the ocelli of Auliscus to be regarded as homologous with those of Striatella? Anon. do not follow Ross & Sims exactly since more than one 'type' is often given per term: the underlying assumptions, however, seem to be similar.

Perhaps the worst case of implied homology is in the different kinds of vela. Thus, 'cribrum' is to be applied to the coarse structures found in centric diatoms, e.g. in the type of the term, Triceratium antediluvianum (Ross & Sims 1972, Anon. 1975) and to the fine 'sieve plates' found, for example, in Hantzschia (see Mann 1977). The finer type, however, with 5 nm. diameter perforations, is widely distributed in many genera of raphid pennate diatoms (Helmcke & Krieger 1953- ) and must be regarded as different from the Triceratium structure.

At this stage it is opportune to remind ourselves of the ultimate purpose of any terminology: this is to render communication more simple and effective. Two types of term may be distinguished. Those in the first group are adjectival, describing the form, position, function, etc., of a structure; here there can be no question of implied homology. The structure qualified by an adjectival term is itself referred to by a substantival term of the second group. The narrower the definition of a term, the more information that term can convey, but the fewer the number of instances in which it may be applied, and the more likely it is (substantival terms only) that all the structures referred to are homologous. There is no need, however, for an 'absolute

rule of homology' as seems to be suggested by Ross & Sims. For instance, few would question the usefulness of the word 'leaf', this referring to the 'lateral appendage, or lateral organ, borne by the stem' (Esau 1965): 'leaf' also implies certain details of growth and construction, (determinate apical growth etc.), yet many have questioned whether all leaves are equivalent, or homologous. Thus, Eames (quoted by Esau 1965) divided leaves into two types, microphylls and megaphylls, the first presumed to be derived by enation from the stem, the second from a branch system which became limited in growth (and was, therefore, overtopped by the main branch), and assumed a leaf-like form. It is non-proven, then, whether all leaves are homologous, but this would not seem an adequate reason for the rejection of 'leaf' in botanical descriptions.

Extreme care must be taken that terminology does not imply homology when this is not established. Also, it must not presuppose hypotheses; this is not its function. Thus, Von Stosch's (1975) arbitrary division (following O.Müller 1886, 1895) of girdle elements into three groups - 'valvocopulae', 'copulae' and 'pleurae' - is unfortunate in view of our almost total ignorance of the bands of pennate diatoms. Von Stosch himself notes the presence of more than three types of band in Rhabdonema arcuatum and in the oogonial hypovalve of Rh. adriaticum and this is true also in Hantzschia (see later). Moreover, the proposal to designate the open (i.e. abvalvar, sensu Von Stosch 1975) end of a complete theca as the reference point in the classification of girdle elements (Von Stosch 1975, p.14) is also arbitrary, neither justified nor explained by its proposer, yet the categories of elements recognised seem to be regarded as valid groupings of homologous structures, a contention which is impossible to prove.

The terms used in this dissertation are those of Anon. (1975), but without any implication of homology, and with the emendations and

additions given below; (see also Text F.1-6). Unless stated otherwise, all passages quoted are from Anon. (1975).

### Axes and Planes of Symmetry

It is not true to say that 'where the symmetry is not bilateral, only the perivalvar axis and the valvar plane can be recognised.' The apical plane, and consequently the transapical plane, may be recognised in any bipolar diatom, as long as the frustule is not twisted as in Amphiprora or Cylindrotheca (Text F.3C-E), though it may not be useful descriptively, (as in Eunotia elegans, vide Hustedt 1930, f.248). Thus, in Hantzschia amphioxys the valve is asymmetrical about the apical plane, but symmetrical about the median transapical plane, (i.e. that plane halfway between the poles of the diatom and at right angles to the apical plane; vide Text F.2).

'Proximal' and 'distal' are defined as in Mann (1977: see also Text F.1).

### Frustule

This consists, according to Anon. (1975), of epitheca + hypotheca, or, otherwise stated, epivalve + girdle + hypovalve (Text F.2B & E).

A theca is thus a valve with its associated girdle elements -

epitheca = epivalve + epicingulum,

hypotheca = hypovalve + hypocingulum,

epicingulum + hypocingulum = cincture.

It is worth note, however, that this definition is inapplicable to Phaeodactylum tricornutum, which has, in its ovate form, only one silica valve per cell, with no girdle or intercalary bands (Lewin 1958).

### Marginal ridge

'A ridge between the valve face and the valve mantle, continuous or interrupted, perforated or solid.' So far, this term, unfortunate in its implication that the ridge lies on the margin of the valve, has

not been applied to structures in raphid pennate genera, but it is used here for the wall-like developments of silica found between valve face and valve mantle in certain Nitzschiaceae (Text F.1, top): Schoemann & Archibald (1976- ) used 'ridge' for such structures in Nitzschia apiculata and N. hungarica.

#### Hyaline fields/ sterna

Hyaline fields are defined as 'areas where the basal siliceous layer is not penetrated by areolae or puncta.' This is objectionable on several counts. Firstly, the use of 'hyaline' is inappropriate since diatom frustules can only be described as hyaline (i.e. of a glassy appearance) when they are viewed with visible light, and then the whole frustule is hyaline, not merely the parts without areolae. In the electron microscope, frustules appear to be anything but hyaline, yet it is only by using this instrument that it may be determined conclusively that a given part is without perforation. Furthermore, 'area' in present usage denotes superficial extent and is a 2-dimensional concept: it is, therefore, not strictly applicable to solid structures. 'Area', however, has been used in diatom descriptions for a long time, (although this may be because of the need to produce representations of diatoms in 2-D), and it is unlikely that change is possible. Nevertheless, in this study a different term, 'sternum', will be used, this denoting an elongate part of the valve where areolae are sparse (relative to the rest of the valve) or missing, and which is often thickened perivalvarly (Text F.1, top). By the use of qualifying adjectives (e.g. axial, lateral, etc.) its position may be indicated. 'Sternum' has been chosen because of the resemblance between the construction of many pennate diatoms and that of the human rib-cage.

The 'raphe-sternum' is the usually unperforate strip of silica, again often thickened perivalvarly, which contains the raphe (Text F.1,

top, centre right). The introduction of this term avoids the difficulties encountered when one attempts to apply 'axial area' (one of Anon.'s terms) to such species as Nitzschia acuminata or N. debilis, where in strict accord with Anon.'s definition, the amorphous band of silica along the mid-line of the valve would have to be called the 'axial area', whereas in raphid diatoms this term is usually applied to the area alongside the raphe (Cox 1975a). 'Raphe-sternum' and 'axial sternum' can coexist, however, without confusion!

'Central area' (sensu Anon. 1975) is replaced by 'raphe-sternum centrally expanded' (Text F.1, top) or some such descriptive phrase, 'lateral area' by 'lateral sternum'. With regard to the latter, the Anon. definition excludes its application to the lateral interruptions of the striae in Pinnularia trevelyana (Peragallo & Peragallo 1897-1908, Pl.11 f.1-3). The definition is therefore emended so as to refer to an apically orientated sternum lateral to an axial sternum, (whether or not this includes the raphe), or lateral to the apical plane.

### Keel

Traditionally, this term was applied to taxa where the raphe runs at the apex of a more or less sharply angled elevation of the valve; the elevation was then called a 'keel' (e.g. in Van Heurck 1896), or if it was particularly well developed, an 'ala'. Thus, Hustedt (1930) noted that the valves of Amphiprora possess 'S-förmig gebogenen Kiel, der dem basalen Schalenteil mit breiter Basis aufsitzt'; the keel was the whole of the elevated, sharply angled portion of the valve. But Anon. use the term to describe the 'summit of the ridge bearing the raphe in those members of the Pennales whose valve is sharply angled at the raphe', (apparently also the usage of Deby 1880): it is hard to see why the term 'keel', so-defined, should ever be necessary. Paddock & Sims (1977) use 'keel' ambiguously; here, it describes a sharply angled outward fold of the valve which bears a raphe at its

apex (Text F.1, bottom).

### Costa

'An elongated, solid thickening of the valve.' This definition presupposes a certain view of diatom structure in which it is assumed that the valve is basically a layer of silica (the 'basal siliceous layer'), variously thickened and perforated, (R.Simonsen, pers. comm.). The costa, then, is not a structure in its own right, but only a modification of the basal layer. There is, however, at least one other view of diatom structure and this may be explained by reference again to the human thorax; in this, each rib (costa) is a structure in its own right, joined to a vertebra at one end and to the sternum at the other. If one now imagines a row of frets linking adjacent ribs together (and, therefore, also delimiting a row of pores), then one has a good model of the construction of many pennate diatom valves. It would be ridiculous to suggest that each rib in the human is an elongated solid thickening of a basal bony layer and, similarly, in this view of diatom structure the concept of a basal siliceous layer is redundant. In this dissertation, 'costa' should be understood to refer to a bar of silica, usually somewhat thicker pervalvarly than the mean valve thickness and running ± transapically from margin to sternum, or sternum to sternum (Text F.1, top & 4C, C').

### Raphe

Considerable discussion of raphe terminology occurred at the 4th Symposium on Recent and Fossil Marine Diatoms (see Cox 1977, Paddock & Sims 1977, Mann 1977, and endpage of *Nova Hedwigia*, Beih. 54, 1977). Several changes to the Anon. terminology were proposed and the following is a synthesis of these, with additions.

Raphe: an elongated slit or pair of slits through the valve. Each raphe-slit is frequently in the shape of a V on its side ( < ) in



cross-section, for part or all of its length; the two halves of the V are termed the inner and outer fissures.

When a pair of slits is present in a valve, each raphe-slit has a polar ending and a central (or at least centripetal) ending, except in the *Surirelloid* genera, where it is not possible to say which ending is which since the raphe occupies the whole perimeter of the valve face. The distance between the central endings is here termed the 'interraphe distance': in *Surirella*, *Campylodiscus* etc., there are two such per valve. Where two fissures approach each other centrally in the same plane, (the two external fissures or the two internal), the central raphe endings are said to be coaxial; if, however, they approach each other such that, if extrapolated centripetally, they would intersect at a point equidistant from both endings (as in *Epi-themia*), they are noncoaxial-symmetrical, while if they satisfy neither of the above conditions, they are noncoaxial-asymmetrical (Text F.4B).

Cox (1975a) commented on the unapt use of 'nodule' by diatomists to refer to the structures terminating raphe-slits and she noted that 'nodule' suggests 'a structure which is circular or oval in valve view, and which is obviously thicker than the rest of the valve.' Anon.'s statement that 'when a pair of fissures is present, they are separated by a central nodule' shows that the term is one of convenience only, and cannot be understood to have any descriptive value beyond communication of the fact that two raphe-slits are present per valve. As Cox noted, 'nodule' is misleading - consider the application of Anon.'s definition to *Amphipleura pellucida*, where 'central nodule' would refer to the entire thickened elongate rib which runs for more than 0.6 of the valve length between the centripetal raphe endings (vide Cox 1975a, f.1, 24). Anon. also claim that the 'terminal pore is inside a terminal nodule' (at the poles) but frequently no pore is visible

and no nodular thickening (unpubl. obs., and Cox 1977). 'Nodule' should be applied only to nodular thickenings of the valve, sensu Cox.

Internally at the pole, a raphe-slit usually (always?) ends in a small structure resembling a rolled tongue (Text F.4A; F.662, 674), for which Anon. suggested the term 'infundibulum'. But this word had already been applied to a different structure, in Surirella (see Cox 1977), and so 'helictoglossa' was proposed instead (Mann 1977 and Cox 1977). Cox (1977) rightly criticized Anon.'s use of 'central-' and 'terminal-pore' ('pores in a slit is a contradiction in terms!'), and these will not be used. Further, Cox criticized Anon.'s distinction of raphe, terminal and central fissures, but this was probably unjust since the last two terms can be useful in concise description and diagnosis, referring to the blind external fissures which continue past the helictoglossa (Text F.4A), or past the internal central raphe ending: thus, in Hantzschia spectabilis one may say 'terminal fissure reaching to the valve margin' instead of 'outer fissure continuing past the helictoglossa to the valve margin as a blind groove.' It makes little difference that it is often impossible to tell from the exterior exactly where the outer fissure becomes blind.

So far, only the raphe itself has been considered, but in many genera, belonging to the Surirellaceae, Epithemiaceae or Nitzschiaceae, associated with the raphe are various other siliceous structures. (Here it is relevant to note that the raphe with its associated structures, if any, together constitute a 'raphe system'). In the above taxa, the raphe is subtended by silica bars and/or plates (Text F.5A-E), which have previously been called 'carinal puncta/dots/pores', 'Kielpunkte', etc., (for discussion, see Round 1970a, Mann 1977). Anon. termed these subtending structures 'fibulae', but involved them as elements of the 'canal raphe system', this being defined as 'a raphe with a tubular

passage running along its inner side, separated from the rest of the interior of the frustule by siliceous elements (the fibulae..)..' Mann (1977) pointed out the anomaly that Cylindrotheca could not be said to possess a canal raphe (and, therefore, no fibulae) although it was for this genus that the term 'fibula' was coined, by Reimann & Lewin (1964). The term was therefore redefined so as to exclude reference to a canal raphe system (Mann 1977). Indeed, the subraphe canal (Text F.5A-C) distinguishable in many species of Nitzschia, Surirella, etc., is probably to be regarded as a consequence of the presence of fibulae, rather than vice versa (Paddock & Sims 1977). Therefore, in place of 'canal raphe system', 'fibulate raphe system' will be employed, this being applicable to Cylindrotheca and to Hantzschia virgata (see Mann 1977) as well as to taxa with well-developed canals.

The spaces between fibulae were called 'interspaces' (interspatii) by Anon. Paddock & Sims (1977) emended this to 'interfibular spaces' on the grounds that interspace means between (inter) spaces (spatii), i.e. a solid structure (pers. comm.). This, however, is false (as, in part, is their assertion that the interspaces were formerly called 'keel punctae' (sic!), since, for the most part, it was the fibulae that were so designated), and Anon.'s usage is quite within that allowed by the Oxford English Dictionary.

Paddock & Sims also proposed various other terms which are useful, e.g. 'alar canal' and 'fenestra', but which are inapplicable in the Nitzschiaceae. Their 'portula' will be used here, but, since an interspace is sometimes constricted more than once and at different levels, the term will be used to refer to the hole formed at any abrupt constriction of the interspace, not merely to that nearest the raphe (Text F.5C-E).

'Subraphe costa' (originally introduced by Round 1970a) means the extension under the raphe of a single transapical costa (Text F.5F):

it may itself constitute a single fibula, or it may be fused with one or more adjacent subraphe costae (see Mann 1977).

### Girdle

The terminology given by Von Stosch (1975) is followed, except that no attempt will be made to distinguish copulae, pleurae, etc. Instead, bands will be referred to by numbers, according to the presumed order of their formation, i.e. that element next to the valve margin is the first band, etc.

Mann (1977) used 'arm' to refer to one half of an open band (proximal and distal arms thus being distinguished), but in the case of closed bands this is inappropriate, and 'proximal half' or 'distal half' will be used here instead.

### Vela

Three types of vela were recognised by Anon., following Ross & Sims (1972): these were cribra, rotae, and vela consisting of volae. Cribra are discussed below, while a vola is a projection from the areola wall into the lumen of the areola: rotae do not occur in the Nitzschiaceae. The variation in velum structure is vast (see Helmcke & Krieger 1953- ) and Ross & Sims note that their list of terms 'is not necessarily exhaustive.'

'Cribrum' is defined as 'a velum consisting of a perforated plate' (Ross & Sims 1972), or as 'a velum perforated by regularly arranged pores' (Anon. 1975). The type given in both papers is Triceratium antediluvianum. Mann (1977) hesitated to apply the term to the closing membranes in the poroids of Hantzschia species (F.521-31) on the grounds that the Triceratium structure is 'coarser by an order of magnitude than any of the Hantzschia structures.' In many pennate diatoms (e.g. Helmcke & Krieger 1953- ; T.62, 68, 69, 70, 77, 169, 918, 922 etc.) there is to be found a delicate silica plate perforated by approx. 5 nm.

diameter holes, just as in Hantzschia. In Cocconeis (F.579) and in Anorthoneis, however, elongated perforations occur, but each of these has a width of approx. 5 nm. (Helmcke & Krieger 1953- , T.48, and Dr. R.M.Crawford's unpubl. obs.) and so these are regarded as equivalent to the Hantzschia-type. Clearly, by Anon.'s definition these plates are 'vela' (given as equivalent to the 'Siebmembran' of earlier authors, e.g. Helmcke & Krieger). Only some may be classified as 'cribra', however, since others do not have regularly arranged pores. The constancy and smallness of the perforation size in these pennate diatoms indicates that these plates are probably not equivalent to the cribra of Triceratium antediluvianum, but this in itself would not justify the erection of another term, since, in my view, terminology does not require homology. However, in several diatoms e.g. Nitzschia sigma (F.543) and H. marina (F.525, 575, 577), areolae occur in which there is a coarse cribrum sensu Ross & Sims, each hole of which is closed by a plate of the 5 nm. type described above. Here it would be difficult to describe structure concisely using the one term 'cribrum' ('cribrate cribrum' is cumbersome) and so, in view of the other considerations mentioned above, it would seem helpful to propose that 'hymen' be used to describe the more delicate plate. A formal definition might be: hymen (m., pl. hymena): the delicate silica plate, of almost uniform thickness, closing the areolae of many pennate (and other?) diatoms, perforated by round or elongate pores whose minimum width is approx. 5 nm. (Text F.4C, C').