

Symmetry and structure re-visited: is symmetry still over-emphasised as a taxonomic character for naviculoid diatoms?

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Abstract

Background and aims – Over 40 years ago, I explored the use of symmetry and structure as taxonomic criteria for naviculoid diatoms, arguing that structure was the more informative character. This paper examines subsequent progress in the understanding and systematics of naviculoid diatoms with particular reference to the treatment of symmetry as a taxonomic criterion.

Methods and key results – The diatom literature since 1979 has been reviewed showing how SEM studies and data on wall morphogenesis have improved our knowledge of diatom wall structure and ontogenetic pathways. Understanding the inherent asymmetry in raphid diatom valves led to the recognition of two types of dorsiventrality within the Cymbellales and underpins the separation of cymbelloid taxa in different families. Hypotheses of character homology in the Naviculaceae have been supported by more recent molecular phylogenetic analyses, also revealing how shape and symmetry can vary within this family. Over-emphasising the significance of a particular character (out of familiarity or a priori preference?) can lead to relevant discriminative characteristics being ignored. The validity of some new genera is questioned and generic descriptions should be revised.

Conclusion – Whereas valve shape and symmetry remain useful features when identifying taxa, systematic relationships are revealed through wall structure and should be the basis for diatom systematics. Nevertheless, it is important to discriminate between homologous and homoplasious characters and to apply terminology accurately.

Keywords

Bacillariophyceae, characters, classification, diatoms, phylogeny, sigmoidality, structure, symmetry, taxonomic criteria, taxonomy

INTRODUCTION

Just over 40 years ago, I (Cox 1979) wrote a paper exploring symmetry and valve structure as taxonomic criteria for naviculoid diatoms, arguing that structure is more informative of relationships than valve shape and symmetry. As I pointed out then, the use of symmetry as a basis for diatom classification has historical origins and “worked tolerably well with the light microscope ... it has been a useful character for species identification” (Cox 1979: 28). Although details of live structure were included

in some early works (Kützing 1833, 1844; Ehrenberg 1843; Cleve 1894; Smith 1853, 1856), by the late 19th century Schutt (1896) had adopted Smith’s (1872) work as a basis for diatom classification, which was followed by Hustedt (1927–1966, 1930) and subsequent workers (Hendey 1964; Patrick and Reimer 1966; Krammer and Lange-Bertalot 1986–1991). Yet, Smith (1872: 23) had clearly indicated that his classification was “an artificial key to facilitate diatom identification” rather than an attempt to reflect relationships.

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The development of electron microscopy, particularly SEM in the latter 20th century, revealed unsuspected diversity in diatom wall structure and facilitated the recognition of many new genera, or provided evidence for reviving some abandoned ones, particularly among naviculoid taxa, e.g. *Berkeleya* Grev., *Brachysira* Kütz., *Climaconeis* Grunow, *Craticula* Grunow, *Diadesmis* Kütz., *Dickieia* Berk. ex Grev., *Encyonema* Kütz., *Placoneis* Mereschk., *Sellaphora* Mereschk. (Round et al. 1990). Fourtanier and Kociolek (1999) documented the increase in new (validly published) diatom genera over time, showing the strongest increase occurring with the expansion of SEM studies (from 750 to 907 between 1979 and 1999) (Henderson and Reimer 2003). That increase has continued (Guiry and Guiry 2025; Kociolek et al. 2025) although the differences in actual numbers show that many of the validly published names (Fourtanier and Kociolek 1999) do not represent accepted genera (Guiry and Guiry 2025; Kociolek et al. 2025).

Thus, closer attention has been given to the significance of ultrastructural differences, particularly variation in raphe and areola structure, for generic delimitation, e.g. *Aneumastus* D.G.Mann & A.J.Stickle, *Biremis* D.G.Mann & E.J.Cox, *Cavinula* D.G.Mann & A.J.Stickle, *Cosmioneis* D.G.Mann & A.J.Stickle, *Fallacia* A.J.Stickle & D.G.Mann, *Luticola* D.G.Mann, *Petroneis* A.J.Stickle & D.G.Mann, *Seminavis* D.G.Mann in Round et al. (1990), *Chamaepinnularia* Lange-Bert. & Metzeltin in Lange-Bertalot and Metzeltin (1996), *Humidophila* Lowe et al. in Lowe et al. (2014). However, even with greater understanding of diatom structure, symmetry has still exerted a strong influence on how individuals have grouped taxa, particularly at generic level and above (e.g. Kulikovskiy et al. 2023; Guiry and Guiry 2025; Kociolek et al. 2025). Nevertheless, whilst advocating closer consideration of morphological characters, Kociolek et al. (2019) describe symmetry as a “feature of convenience” pointing out that “gomphonemoidness” is an example of homoplasy rather than homology, having evolved on at least six occasions.

Only more recently, with the development of molecular studies exploring phylogenetic relationships, have some conflicts in diatom classifications (Round et al. 1990), particularly at suprageneric levels (families and above) become more apparent (Medlin and Kaczmarek 2004; Kermarrec et al. 2011; Nakov et al. 2014). This paper explores how continuing SEM studies, better understanding of frustule ontogeny, and the results of molecular phylogenies have shown where reliance on shape and symmetry have misled interpretations of taxonomic relationships, with a focus on naviculoid diatoms. But it also shows that shape and symmetry are still being used to separate structurally similar taxa.

FACTORS AFFECTING VALVE SHAPE IN RAPID DIATOMS

Inherent dorsiventrality of raphid diatoms

Although most naviculoid diatoms are ostensibly isopolar and bilaterally symmetrical, Mann (1981, 1983, 1984a) highlighted the inherent asymmetry in all raphid diatoms, which is a result of the way in which the raphe, and thus the valve, is formed. A primary and a secondary side of a raphid valve can often be identified by the presence of an irregularity on the secondary side, the so-called Voigt discontinuity (Voigt 1943), where the silica ribs defining the raphe fissure fuse (Mann 1981, 1983; Cox 2012), as well as the fact that the external polar raphe fissures usually deflect towards the secondary side. The nucleus always lies beneath the primary side of the forming valve, but in many raphid taxa, the nucleus moves from side to side of the frustule for consecutive mitoses (oscillates), meaning that the products of mitosis may have cis or trans configuration of their frustules (Mann 1981, 1983). However, if the nucleus does not oscillate with subsequent mitoses, all frustules show the cis configuration, i.e. the primary sides of the two valves lie on the same side of the frustule. This also allows either the primary or the secondary side to become wider than the other side, i.e. the valve can develop dorsiventrality. Thus, as seen in cymbelloid diatoms, either the primary or the secondary side can be wider (i.e. “dorsal”), *Encyonema* having a wider primary side, whereas in *Cymbella* C.Agardh. the secondary side is wider. This also means that in those cases where dorsiventral cells contain single chloroplasts, the central portion of the chloroplast always lies on the secondary side, away from the nucleus under the primary side (Mann 1981).

Cis-symmetry allows for the development of dorsiventrality, but the latter does not inevitably occur. Mann (1981, 1983) reported the occurrence of cis, or cis and trans-symmetry across several raphid diatom genera, indicating the presence of cis (rather than cis and trans) symmetry in *Seminavis*, *Placoneis*, *Encyonema*, *Cymbella*, *Gomphonema* Ehrenb., *Anomoeoneis* Pfitzer, *Dickieia*, *Lyrella* Karayeva, and *Petroneis* (Mann and Stickle 1988; Jones et al. 2005). Whereas *Seminavis*, *Encyonema*, and *Cymbella* are recognised by their dorsiventrality, the other naviculoid genera are usually bilaterally symmetrical although dorsiventrality may occur, e.g. *Lyrella* (Mann and Stickle 1997). Sporadic dorsiventrality was also noted in *Diploneis* Ehrenb. and *Biremis* (Mann and Stickle 1997).

Auxospore and initial cell structure and constraints on wall development

Auxosporulation and initial cell formation set the maximum size of a diatom cell after sexual reproduction, with the “normal” vegetative valve shape and symmetry essentially being established with the first mitosis of the initial cell (Mann 1984b; Cohn et al. 1989b; Round

et al. 1990; Passy-Tolar and Lowe 1995). Whereas the initial cell is often round in cross-section and somewhat inflated at the centre, following the first vegetative mitotic division, valves of subsequent generations have more flattened surfaces, being formed closely appressed to each other, so-called interactive division (Mann 1994b). The development of frustule heteropolarity or dorsiventrality, as well as more regular valve features also emerge as “normal” mitoses follow (Mann 1984b, 1989; Passy-Tolar and Lowe 1995), presumably as the typical cell cytoskeleton, with its connection points to the frustule, is established (Schmid 1980; Tesson and Hildebrand 2010). Thereafter the rigidity of the frustule largely constrains the shape of subsequent generations, although usually accompanied by gradual size reduction (Mann 1984b; Round et al. 1990; Rose and Cox 2014; Mohamad et al. 2022). However, it should be noted that flexibility in the girdle bands can allow cell size to be maintained (Geitler 1932), or even slightly increased (Rose and Cox 2013).

In the case of pennate diatoms (both raphid and araphid taxa) allometric size reduction results in decreasing length:breadth ratios (Cox 1985, 1993; Round et al. 1990; Mohamad et al. 2022), often with shifts in outline, such that the largest and smallest cells of a species may appear somewhat different. In extreme cases this may result in the ends of a series being recognised as different species (Cox 1985, 2014; Rose and Cox 2014). This is particularly likely if relatively few specimens of a taxon are present in the sample and extremes of size diminution series have been designated as forms (or varieties) of the species in question. Thus, while it is generally recognised that the average cell size of a population decreases during the life history of a taxon, less attention has been paid to establishing how shape changes and which valve features remain constant or which vary with size and may therefore affect the overall appearance of the valve. Some araphid taxa may even become slightly wider as their length decreases, e.g. *Fragilariforma marylandica* Edlund, B.Laub, Siver, P.B.Ham. & E.Morales (Siver and Hamilton 2011).

Perceptions of shape changes with variation in cell size

The most obvious allometric effect of decreasing cell size in pennate diatoms is that cells at the lower end of the size range appear fatter than those at the upper end because valve length decreases while valve width remains more or less the same (Cox 1993; Edlund and Soninkhishig 2009; Windler et al 2014; Mohamad et al. 2022) and the eye perceives shape independent of scale. But there may also be concomitant shifts in apical shape. Thus, longer specimens of *Navicula reinhardtii* (Grunow) Grunow in Van Heurck (1880) were designated *N. reinhardtii* var. *gracilior* Grunow in Van Heurck (1885) and shorter ones, *N. reinhardtii* var. *elliptica* Hérib. but all lie along a single size reduction series (Cox 1986: figs 1, 2a–h). The most striking shape changes are often noted when clones have

been cultured over extended periods (Cox 1983a; Rose and Cox 2014; Mohamad et al. 2022), although field samples can also provide a range of cell sizes of individual taxa (Geitler 1932; Mann 1982a; Steinman and Sheath 1984; Edlund and Soninkhishig 2009; Peng et al. 2017).

Size reduction in a *Pinnularia* sp. (identified as *Pinnularia braunii* var. *amphicephala* (Ant.Mayer) Hust.) is accompanied by a change in apical shape from “weakly capitate to rostrate” (Suzuki and Mayama 1995) and from parallel sided to more rounded. Change in the central portion of valves is also seen in *Neidium dubium* (Ehrenb.) Cleve, from undulate in *N. dubium* f. *constricta* (Hust.) Hust. to straight-sided as the cells diminish in size (Cox 1986: fig. 2v–z). But, whereas in many pennate taxa, outlines become simpler and more elliptical, in some *Eunotia* species marginal undulations become more pronounced (Hustedt 1955) whilst apices do not invariably become more rounded, e.g. *Placoneis clementioides* (Ehrenb.) Kütz. (Cox 1986), *Placoneis nanoclementis* Lange-Bert. & Wojtal (Lange-Bertalot and Wojtal 2014), *Nitzschia fonticola* (Grunow) Grunow in Van Heurck (1881) (Trobajo et al. 2006). Working with cultures of *Eunotia pectinalis* (Kütz.) Rabenh., Steinman and Sheath (1984) suggested that relative inflexibility of girdle bands around the apices maintained their shape, whilst greater flexibility at the centre of the frustule allowed valve breadth to increase as cells decreased in length. Interestingly, the elongated apices of *Gyrosigma fasciola* (Ehrenb.) J.W.Griff. & Henfr. are retained even when cells become very small in culture (Cox 1993), below the sizes that would be observed in nature.

However, what might be considered more structural aspects of the valve, the “building-blocks” such as striae and areolae, remain more consistent within a species. Stria densities vary little with decreasing valve length (Cox 1983a) and, if measured, areola spacing along the striae does not change (Edlund and Soninkhishig 2009) and it has been suggested (F.R. Schoeman pers. comm.) that different areola spacing along a stria could discriminate similar taxa. Landmark-based morphometrics confirm that the orientation of the striae and shapes of central areas vary little within a taxon (Novais et al. 2009; Veselá et al. 2009; Pouličková et al. 2016). Similarly, the shape of apices with apical pore fields can remain the same despite cell size reduction (Lange-Bertalot et al. 2017: plates 79–84, 95–101). Interestingly, another feature that remains constant over a size reduction series is the length of the widely separated raphe fissures in *Berkeleya rutilans* (Trentep. ex Roth) Grunow and *B. obtusa* (Grev.) Grunow (Mizuno 1977, 1979; Lobban 1984). To compensate for reduction in valve length in these species, the central area becomes shorter as cell length decreases while raphe slit length is maintained. Stability of these components is presumably necessary both for the structural integrity of the valves and to maintain their function.

Where valve shapes diverge from having bilateral and apical symmetry shifts along a size gradient can be more striking, shown well by size reduction series in cymbelloid,

amphoroid, epithemoid, and gomphonemoid diatoms (Krammer 2002, 2003; Levkov 2009: plates 1–120; Levkov et al. 2016; Lange-Bertalot et al. 2017: plates 79–102; Kamakura et al. 2024). Liu et al. (2020) discuss the potential problems if only part of the size range is present in a sample. And where the raphe path curves, again this may accentuate perceived differences between larger and smaller valves, e.g. in *Donkinia* Ralfs, in which the path of its sigmoid raphe traverses the more or less straight valve more sharply in shorter specimens (Cox 1983a: figs 43, 44, 1993: fig. 2).

STRUCTURE RATHER THAN SYMMETRY REVEALS RELATIONSHIPS

Historically, frustule symmetry has been used as one of the diagnostic characters for allocation both to genus and higher taxonomic groups, and within the naviculoid diatoms, valve shape and symmetry were easy guides to the discrimination of several genera, e.g. *Gyrosigma* Hassall, *Pleurosigma* W.Sm., *Amphora* Ehrenb. ex Kütz., *Cymbella*, *Gomphonema* (Hustedt 1930; Patrick and Reimer 1966; Barber and Haworth 1981). Although classifications have differed in the ranks accorded to groups of these genera, if naviculoid genera were grouped at family level, heteropolar taxa (*Gomphonema*, *Gomphoneis* Cleve, and *Didymosphenia* Mart.Schmidt) were placed in the Gomphonemataceae, while dorsiventral ones (*Cymbella*, *Encyonema*, and sometimes *Amphora*) were placed in the Cymbellaceae (Patrick and Reimer 1975). Interestingly within his Naviculaceae, Hustedt (1930) created a subfamily, the Gomphocymbelloideae, for the heteropolar and dorsiventral taxa but only with Round et al. (1990) was the order Cymbellales created, containing the Cymbellaceae, Gomphonemataceae, Mastogloiaaceae, and Rhoicospheniaceae. The rationale for their new order rested on the shared chloroplast structure (Round et al. 1990), although by this time SEM had also provided new evidence of shared wall features within these families. There are, however, significant differences in some characters between the families, particularly with respect to areola and raphe structure.

Structural variation within the Cymbellales

Considering some members of the Cymbellales (Cymbellaceae and Gomphonemataceae) in relation to their raphe structure rather than symmetry, I (Cox 2002) suggested that *Cymbella*, *Didymosphenia*, and *Gomphocymbella ancyli* (Cleve) Hust. (now *Gomphocymbellopsis* Krammer) formed a separate group from *Brebissonia* Grunow, *Encyonema*, *Gomphocymbella beccarii* (Grunow) Forti (now *Afrocymbella* Krammer), *Gomphoneis*, *Gomphonema*, *Placoneis*, and *Reimeria* Kociolek & Stoermer. Taxa in the former group (= Cymbellaceae) have hidden internal central raphe fissures and stigmata (Cox and Van de Vijver 2024), while the latter (= Gomphonemataceae) have visible

internal central raphe fissures and stigmoids (Cox and Van de Vijver 2024). Subsequently recognised genera, *Cymbopleura* (Krammer) Krammer, *Delicata* Krammer, *Encyonopsis* Krammer, *Karthickia* Kociolek, Glushch. & Kulikovskiy, and *Oricymba* Krammer, E.J.Cox, Van de Vijver & Tuji, also have hidden internal central raphe endings and belong with the Cymbellaceae, while genera recently separated from *Gomphonema* (*Gomphodelpha*, *Gomphonella*) (Jahn et al. 2019; Abarca et al. 2023) and *Cymbellopsis* Krammer (with visible internal central raphe endings) belong with the Gomphonemataceae. However, treating *Didymosphenia* as a member of the Cymbellaceae (dorsiventral), and *Encyonema*, *Placoneis*, and *Reimeria* as members of the Gomphonemataceae (heteropolar) shows that symmetry is not invariably a good guide to relationships and the family descriptions need revising. The original criterion of symmetry for recognising these families is inappropriate, but the use of the raphe feature as a discriminating criterion is supported by molecular studies (Kermarrec et al. 2011; Nakov et al. 2018; Jahn et al. 2019), which clearly separate the Cymbellaceae, including *Cymbella* and *Didymosphenia*, from members of the Gomphonemataceae, although the latter may warrant subdivision (Mironov et al. 2024).

Although it had historically been placed within the cymbelloid diatoms, I (Cox 1979) previously pointed out that *Cymbella pusilla* Grunow showed the structural characters of *Navicula* Bory. Recognising the structural differences from *Cymbella* sensu stricto, Krammer (1979) created a new genus, *Navicella* Krammer, for it but retained it as a cymbelloid taxon. He (Krammer 2003) subsequently replaced that generic name with *Navicymbula* Krammer because *Navicella* was a later homonym but continued to treat it as a member of the Cymbellaceae. Reid and Cox (2004) transferred *Navicymbula pusilla* (Grunow) Krammer to *Seminavis* (as *Seminavis pusilla* (Grunow) E.J.Cox & G.Reid), a genus of taxa with dorsiventral valves but structural features of *Navicula*, which Round et al. (1990) placed in the Naviculaceae, alongside *Navicula*, *Trachyneis* Cleve, *Pseudogomphonema* Medlin, *Rhoikoneis* Grunow, *Haslea* Simonsen, and *Cymatoneis* Cleve. A position within the Naviculaceae is supported by phylogenetic analyses that show *Seminavis* and *Pseudogomphonema* falling with *Navicula* (Nakov et al. 2018; Lobban et al. 2020). It is unclear why Diatoms of North America (Spaulding et al. 2021) retain the use of *Navicymbula* or that DiatomBase (Kociolek et al. 2025) keeps it in the Cymbellaceae.

Amphora – another example of structural variation but shared symmetry

The large genus *Amphora* sensu lato was primarily defined by a distinct asymmetry in the valve mantle and girdle bands alongside strongly dorsiventral valves. The valve and frustule asymmetry, in which both valves lie in the same plane, has been the criterion on which the genus is defined (Round et al. 1990; Levkov 2009; Cantonati et al.

2017) although the structural diversity within *Amphora* s.l. has long been recognised (Cleve 1895). Cleve (1895) not only noted the structural diversity within *Amphora*, but also the variation in live structure, dividing it into several subgenera, some of which are now recognised at the genus level (Stepanek and Kociolek 2014, 2016, 2019). Phylogenetic analysis based on concatenated molecular markers also shows that the amphoroid clades are distributed across the phylogeny of raphid diatoms rather than all together (Stepanek and Kociolek 2014). Thus, Cleve's subgenera *Diplamphora* Cleve and *Oxyamphora* Cleve form subclades within *Amphora*, but can be discriminated on the presence or absence of a marginal ridge and differences in their chloroplast arrangement. *Tetramphora* Mereschk. falls near *Mastogloia* Thwaites ex W.Sm. in the molecular trees (Stepanek and Kociolek 2019) with a distinctive chloroplast arrangement showing similarities to that of *Mastogloia*. *Halamphora* Cleve forms a separate clade with another chloroplast arrangement (Stepanek and Kociolek 2016). Again, symmetry and structure (including chloroplast arrangement) tell different stories.

Shared structure but differing symmetry

Earlier, considering structural features to be more taxonomically informative than symmetry, the lunate *Okedenia inflexa* (Bréb. ex Kütz.) Eulens. ex De Toni was transferred into *Climaconeis* (Cox 1982), a transfer that is also supported by the chloroplast arrangement. *Climaconeis* is now generally accepted as a genus comprising both straight and arcuate cells, and the number of species within it has increased, alongside more geographic data (John 1991; Takano 1992; Prasad et al. 2000; Reid and Williams 2002; Prasad 2003; Lobban et al. 2010; Park et al. 2016). Similarly arguing that valve structure is more informative than symmetry, Witkowski et al. (2014) transferred *Amphora scabriuscula* Peragallo & Peragallo (= *Navicula scabriuscula* (Cleve & Grove in Cleve 1893) Meresch.) to *Navicula* (as *Navicula petrovii* Nevarova, Witkowski, Kociolek & Lange-Bert.), based on similarities of valve structure to both *Trachyneis* and some large marine species of *Navicula*, such as *Navicula cancellata* Donkin. Witkowski et al. (2014) infer that the secondary side of the valve is the ventral one, meaning that in this case the primary margin of the valve has retained its convex curvature whilst the secondary side has lost this and the ventral girdle view is narrower than the dorsal one (Witkowski et al. 2014: figs 4, 5).

Medlin (1991) explored the significance of frustule shape in some heteropolar flexed diatoms, *Rhoicosphenia* Grunow, *Campylopyxis* Medlin, and *Rhoikoneis* (group 1), compared with similar, but isovalvar genera, *Cuneolus* Giffen, *Pseudogomphonema*, and *Trachyneis* (group 2). She pointed out that features of the raphe system, areolae and cingulum are probably more stable and potentially more informative of higher-level taxonomic relationships. She also indicated that her group 2 taxa belong to the

Naviculaceae, group 1 taxa to the Rhoicospheniaceae. Mann (1990) discussed the live structure and reproduction of *Campylopyxis* and compared it with *Dickieia* (also placed in the Cymbellales by Mann [1994a]), with the same chloroplast type and reproductive behaviour. Thus, while flexed frustules might define the genus, they do not determine its higher-level taxonomic position. While *Campylopyxis* is usually placed in the Rhoicospheniaceae, *Dickieia*'s position is currently uncertain (Kociolek et al. 2025) although Bruder and Medlin's (2007, 2008) phylogenetic analyses show it falling outside the Cymbellales.

Similar structural characteristics are seen between *Dickieia* (Cox 1985; Mann 1994a), symmetrical about three axes, and the slightly dorsiventral *Krsticiella* Levkov (Levkov et al. 2007). Although Levkov commented on similarities between *Krsticiella* and *Campylopyxis*, he did not pick up on Mann's (1990) paper on the latter genus, with its comparison to *Dickieia*, or include any reference to *Dickieia* in his taxonomic remarks. Yet it is only the slight dorsiventrality of *Krsticiella* and the freshwater (rather than marine) habitat that separate it from *Dickieia*.

VALVE MORPHOGENESIS INFORMS INTERPRETATION OF STRUCTURE

In my earlier paper (Cox 1979), I also discussed both the similarities between areola structure in *Gyrosigma*, *Haslea*, and *Navicula* and the variation in internal raphe structure in *Gyrosigma* and *Pleurosigma*, later discussing the value of morphogenetic information for taxonomy (Cox 2010). Areola structure with hymenate internal occlusions, internal raphe fissures flanked by one or two longitudinal ridges and non-porous girdle bands are all shared across *Navicula* sensu stricto, *Gyrosigma*, *Haslea*, and *Pleurosigma*, although *Gyrosigma* and *Pleurosigma* were recognised primarily by their sigmoid shape and the angle of intersection of the striae. However, the valves of some *Gyrosigma* and *Pleurosigma* species are almost straight (Sterrenburg et al. 2015) and Du et al. (2023) argue that, based on their phylogenetic analysis, sigmoidality cannot be used as a criterion to define *Pleurosigma*. Similarly, Poulin et al. (2004) argued that, despite its sigmoid valve, *Gyrosigma nipkowii* F.Meister belongs in *Haslea*, sharing both structural and biochemical features with the latter.

Gradations in areola structure and in raphe features are seen across *Navicula*, *Haslea*, and *Gyrosigma* such that allocation of individual taxa to one or other of these genera has been somewhat contentious (Sterrenburg et al. 2015). In summarizing the taxonomic history of *Haslea*, Sterrenburg et al. (2015) emphasised the continuous longitudinal fissures (external areola openings) as a distinctive characteristic of the genus, while questioning that all members should be lanceolate in outline. They (Sterrenburg et al. 2015) emended the generic description but also provided morphological comparisons with *Gyrosigma* and *Pleurosigma*, emphasising the similarities in the wall construction, with the formation of a basal

network of ribs over which silica strips are deposited and gradually widen, leaving narrow external fissures over the areolae. But whereas the external siliceous strips in *Gyrosigma* (and *Haslea*) are longitudinally oriented and build up from the vimines, in *Pleurosigma* the oblique orientation of the areolae means that the external layer builds up over vertical “pillars” on the basal layer, as a mesh or in a stellate manner (Sterrenburg et al. 2005) and, unlike in most pennate diatoms, a clear virga-vimen system is not found. Unfortunately, Sterrenburg et al. (2005) do not show any very early stages of basal layer formation, which might reveal how the oblique striation is initiated.

A transition from the presence of continuous slits over the areolae in *Haslea*, to external slits extending over several areolae in *Gyrosigma* and over single areolae in *Navicula* was postulated (Cox 1979: figs 10–12) and supported by observations (Cox 1999a: figs 40–42). It was also suggested that the formation of additional cross connections would explain the formation of double pores in some *Navicula* spp. (Cox 1999a: figs 44, 45, 52) and in *Hippodonta* Lange-Bert., Witkowski & Metzeltin (Cox 1999a: figs 12, 47, 48, 2002: figs 24.9, 24.10), which could be interpreted as the end of that developmental trajectory. Thus, the contrasting final external appearance of the areolae in these genera should not be interpreted as representing fundamentally different (non-homologous) characters, but as different stages along the same ontogenetic trajectory forming the areola system (Cox 2010). It is of course possible that double pores could be initiated in a different way, which would constitute another character.

Similarly, the variation in internal rib development beside the raphe sternum within the Naviculales can be considered variants on the same basic pattern. In considering the morphological variation in and between *Navicula*, *Haslea*, and *Gyrosigma*, possible developmental pathways for both raphe and accessory rib formation in these genera have been presented (Cox 2002: figs 24.5, 24.7, 24.8). However, although when evaluating *Haslea* valve morphology in relation to that of *Gyrosigma* and *Pleurosigma*, Sterrenburg et al. (2015) mentioned the structure of the accessory rib in *Haslea*, they did not discuss internal raphe structure in detail, simply noting the presence of a similar rib in *Gyrosigma*. Rather they (Sterrenburg et al. 2015) focussed on the sandwich-like structure of the valve as seen in *Gyrosigma* and *Pleurosigma* discussed above. However, if the rib system beside the raphe sternum is considered (Cox 2002: fig. 24.5), degrees of development of single and double accessory ribs can be seen across *Navicula*, *Haslea*, *Gyrosigma*, and *Pleurosigma*. But, whereas the first three genera show greater accessory rib development on the primary side of their valves, in *Pleurosigma* there is more or less equal development of ribs on either side of the central nodule, restricted to the central part of the valve.

Cardinal et al. (1989) compared the degree of development of central bars in *Donkinia*, *Gyrosigma*, and

Pleurosigma and discussed its taxonomic value at the species level for *Gyrosigma* and *Pleurosigma*. *Donkinia* has a relatively small central nodule flanked by short, very thick bars (Cox 1983a: figs 40–42; Cardinal et al. 1989: fig. 1). In *Gyrosigma* and *Pleurosigma*, the central nodule is usually somewhat more elliptical and the flanking bars are usually narrower (Cardinal et al. 1989: figs 1–38). In *Pleurosigma*, the central bars are more or less the same length, in *Gyrosigma*, the bar on one side is often longer or more strongly developed than on the other (Cox 1977: figs 26–29, 1979: figs 6, 7, 9; Cardinal et al. 1989: figs 4, 7–9, 11–13, 16–18). Similar asymmetry is seen in *Haslea* and *Navicula* (Cox 1999a: figs 59, 63–76, 2002: fig. 24.5) suggesting a closer relationship between these genera and *Gyrosigma*, less so with *Pleurosigma* and *Donkinia* (see Lobban et al. 2020 below).

Taxonomic treatment of sigmoid genera and non-sigmoid relatives

Based on her cladistic analysis of the relationships of sigmoid diatom genera using morphological characters, Reid (2012: figs 7, 14) concluded that *Haslea* and *Gyrosigma* should be placed in the Naviculaceae, whereas *Pleurosigma* belongs in a separate family (Pleurosigmataceae), with *Toxonidea* Donkin, *Donkinia*, *Plagiotropis* Reimer, *Rhoicosigma* Grunow, and her new genera, *Costasigma* G.Reid, *Arcuatasigma* G.Reid, *Carinasigma* G.Reid, and *Cochlearisigma* G.Reid, all based on taxa she separated from the former genera. However, it should be noted that some of the characters used in her analysis relate to frustule shape or symmetry, e.g. valve vaulting, rather than structure alone. A recent 3-gene DNA sequence phylogeny (Lobban et al. 2020) showed *Pleurosigma* separate from *Rhoicosigma* + *Gyrosigma*, *Carinasigma*, and *Donkinia*, with *Plagiotropis* outside this group and *Haslea* sister to the *Navicula* clade (including *Cymatoneis*, *Hippodonta*, *Seminavis*, *Pseudogomphonema*, *Trachyneis*, *Rhoikoneis*).

Despite their contrasting valve shapes and raphe path, *Plagiotropis* and *Donkinia* have vaulted valves and similarly positioned lobed chloroplasts (hence their proximity in Reid’s analysis; Reid 2012: fig. 7) but the internal central bars of *Plagiotropis* (as *Tropidoneis* in Cox 1983b: figs 26, 27) are more similar to those of *Pleurosigma* (Cardinal et al. 1989: figs 20–35) than *Donkinia* (Cox 1983a: figs 40–42; Cardinal et al. 1989: fig.1), although their stria intersection is at right angles rather than oblique as in *Pleurosigma*. The molecular phylogeny (Lobban et al. 2020) would indicate that some frustule shape or symmetry characters used by Reid (2012) may be misleading, whilst also showing shape/symmetry diversity within the *Navicula* clade by the inclusion of *Seminavis*, *Pseudogomphonema*, and *Rhoikoneis* (cf. Medlin 1991).

Stauros vs pseudostauros?

The presence of a thickened central area (stauros) across the valve of raphid diatoms was originally used to define

the freshwater genus *Stauroneis* Ehrenb. (Ehrenberg 1843) but the term *stauros* later covered any transverse thickening (Cox and Williams 2000; Cox 2001; Ashworth et al. 2017), although different ontogenetic pathways can result in similar end-products. Cleve's definition of a *stauros* (Cleve 1894: 6) recognised its origin from the "central nodule", i.e. the initiation centre of a raphid diatom, rather than as subsequent thickening of the *virgae* (pseudostauros). Whether or not taxa possess a true *stauros* or a pseudostauros, their occurrence across the diatom phylogeny (Ashworth et al. 2017) shows that these are features that have arisen on more than one occasion in different groups, examples of homoplasy in raphid diatoms (Kociolek et al. 2019). Thus, a true *stauros* is found not only in *Stauroneis* (even Cleve [1894] recognised that this structure occurred in "widely different forms"), but also in some *Climaconeis*, *Craspedostauros* E.J.Cox, *Druehlago* Lobban & Ashworth, *Staurotropis* species (Paddock and Sims 1981; Paddock 1988; Prasad et al. 2000; Ashworth et al. 2017), while pseudostauri are found in *Haslea*, *Membraneis* Paddock, *Plagiotropis*, and *Ephemeria* Paddock (Paddock 1988; Cox 2001; Massé et al. 2001; Talgatti et al. 2014; Sterrenburg et al. 2015; Ashworth et al. 2017). It should perhaps be noted that the latter group of taxa have central bars or accessory ribs from which the pseudostauros develops over one or a few central *virgae*, whereas taxa with a *stauros* do not have central bars or accessory ribs beside the raphe and the *stauros* is continuous with the central nodule (Cox 2001).

WHICH STRUCTURAL FEATURES ARE TAXONOMICALLY INFORMATIVE?

One answer to this question is that all are potentially taxonomically informative, but care should be taken that their significance is not based on a priori assumptions or personal preference, perhaps influenced by the degree of familiarity with particular groups of taxa. In revising their concept of *Haslea*, Sterrenburg et al. (2015) suggested that earlier descriptions (Round et al. 1990; Massé et al. 2001; Talgatti et al. 2014), which all mentioned the accessory rib along one side of the raphe sternum, did not "accurately describe the essential point of the *Haslea* valve morphology", stressing instead the sandwich-like structure of the valve, like that of *Gyrosigma* and *Pleurosigma*. However, despite suggesting that the valve formation process in *Pleurosigma* has been fully documented (Sterrenburg et al. 2015), the earliest stages in basal layer development were not illustrated (Sterrenburg et al. 2005). Thus, it remains unclear how the oblique striation of *Pleurosigma* is established, whereas the perpendicular intersection seen in *Gyrosigma* and *Haslea* follows from the sequential formation of *virgae* and *vimines* (as in other naviculoid diatoms, Cox 1999b).

In disregarding the significance of the presence of an accessory rib that often partially overlaps the raphe sternum, Sterrenburg et al. (2015) considered areola structure rather than raphe details a diagnostic character

for *Haslea*, placing several taxa in that genus, although their accessory ribs do not overlap the raphe sternum (cf. Cox 1977: figs 26, 38). Two such taxa, *Haslea tsukamotoi* Sterrenburg & F.Hinz and *H. avium* M.A.Tiffany, Herwig & Sterrenburg, were transferred to *Navicula* by Li et al. (2017) who also pointed out that the helictoglossae are elongate and narrow in *Haslea*, shorter and more rounded in *Navicula*. This transfer is supported by phylogenetic analyses (Li et al. 2017: figs 2, 3; Lobban et al. 2020: fig.1), which clearly place these taxa within the *Navicula* clade. On the other hand, despite its sigmoid valve outline, the transfer of *Gyrosigma nipkowii* F.Meister to *Haslea* (Poulin et al. 2004) is supported by the accessory rib overlapping the raphe sternum as well as other morphological, biochemical and molecular evidence.

It is clear that valve shape and stria orientation alone do not allow reliable separation of *Pleurosigma*, *Gyrosigma*, *Haslea*, and *Navicula*, but greater attention must be given to raphe features, particularly accessory and central bars. *Pleurosigma* and *Gyrosigma* species can lack sigmoidality, whereas *Haslea* species may be straight, sigmoid or arcuate. A pseudostauros may or may not be present, while some *Navicula* species have *Haslea*-like striae, with longitudinal strips over the external valve surface (Cox 1999b). There are also differences in the shape of the helictoglossae, elongate in *Haslea* versus short in *Navicula* (Li et al. 2017). Although Sterrenburg et al. (2015) discounted the significance of an accessory rib overlapping the raphe sternum, this would seem to be a generic characteristic of *Haslea*, even if the degree of overlap may vary. On the other hand, its absence, the ribbon-like chloroplasts and more or less symmetrical central bars in *Haslea alexanderi* Lobban & C.O.Perez may indicate that this species, despite its shape and perpendicularly intersecting striae, belongs with *Pleurosigma*. Unfortunately, the authors (Lobban et al. 2020) were unable to obtain molecular data for this species and therefore could not include it in their phylogeny.

SUPPORT FROM MOLECULAR STUDIES

Phylogenetic studies using genetic data are providing another perspective on diatom relationships although taxonomic coverage remains patchy and not all taxa are amenable to culturing, which is often required to obtain sufficient material for extraction and analysis. Whereas genetic data have often been used to differentiate taxa (within and between species, genera) (Jahn et al. 2019; Majewska et al. 2022; Abarca et al. 2023), they have also provided support to confirm morphologically inferred relationships (Poulin et al. 2004; Kermarrec et al. 2011; Stepanek and Kociolek 2014; Li et al. 2017). However, some rather unexpected relationships are also being revealed that should stimulate re-examination of the criteria on which taxa have been discriminated, in particular some of the more obvious features, such as frustule and valve shape and symmetry.

In exploring the relationships of raphid taxa with a stauros, Ashworth et al. (2017) created a new genus, *Druehlago*, distinguished from *Craspedostauros* by its stalked habit, cuneate frustules, heteropolar valves, and multiple lenticular chloroplasts. They (Ashworth et al. 2017) discussed the similarities between *Craspedostauros* and *Achnanthes* Bory, which their molecular phylogeny showed as closely related, also pointing out that, whereas *Achnanthes* (like *Craspedostauros*) usually had two fore and aft chloroplasts, it may also have many lenticular chloroplasts as seen in *Druehlago*. Despite their similarities, Majewska et al. (2022) supported the recognition of *Druehlago* as distinct from *Craspedostauros*, but a recent phylogeny from Sugawara et al. (2024) places *Druehlago* within *Craspedostauros*, in a clade with *Craspedostauros* and *Achnanthes* (Sugawara et al. 2024: appendix S2). Sugawara et al. (2024: fig. 4a) also show a mature auxospore of *Druehlago* in which the chloroplast configuration resembles the fore and aft arrangement of *Craspedostauros* and *Achnanthes*, in contrast to the initial and vegetative cells with many chloroplasts (Sugawara et al. 2024: figs 1c, 4b). The position of *Druehlago* within *Craspedostauros* argues against its recognition as a distinct genus and again illustrates the unreliability of symmetry as a basis for generic allocation, although not all workers would agree (Majewska et al. 2022).

This group of taxa also illustrate the potential that frustule shape can be modified while retaining the same structural features, i.e. areola, raphe and cingulum construction. Thus, *Craspedostauros* species are usually symmetrical about three axes, whereas *Druehlago* is heteropolar and *Achnanthes* has flexed frustules and has become functionally monoraphid. *Achnanthes* and *Druehlago* share a stalked habit, whereas *Craspedostauros* is epipellic or epibiontic, albeit without any evidence of stalks (Majewska et al. 2021). One species, *Craspedostauros danayanus* Majewska & Ashworth is reported to attach by one end of the valve, but there is no evidence of specialised apical pore fields (Majewska et al. 2021).

Shifts in frustule shape but retention of areola, raphe and cingulum structure are also shown by the phylogenetic relationships of *Navicula*, *Pseudogomphonema*, *Seminavis*, and *Rhoikoneis* (Nakov et al. 2018; Lobban et al. 2020). Whereas *Navicula* species are isopolar with straight girdle regions, *Pseudogomphonema* is heteropolar with slightly cuneate girdle regions, *Seminavis* has a dorsiventral valve with a slightly asymmetric girdle, and *Rhoikoneis* has isopolar valves with a flexed girdle region. Yet they all share the same areola structure, typical *Navicula*-like raphe systems and plain (non-porous) girdle bands. Structure is a better guide to their relationships than cell shape and symmetry.

A recently described new biraphid genus, *Yuzaoea* Chenhong Li, Honghan Liu, Yahui Gao & Changping Chen, is compared to *Rhoicosphenia* (Liu et al. 2024), from which it differs in being isopolar rather than heteropolar and having fully developed raphe systems on both valves but sharing a flexed girdle view. Based

on *rbcL* and SSU rRNA gene datasets the genera form a clade sister to several monoraphid genera, supporting the hypothesis that progressive reduction in the raphe system, from biraphid to monoraphid has occurred on more than one occasion (Kulikovskiy et al. 2016), ending in the araphid state (Kociolek et al. 2013). To what extent the loss of a raphe system on one valve is also linked to the development of valve flexure seen in many monoraphid genera remains unexplored.

As mentioned above, molecular studies (Poulin et al. 2004; Li et al. 2017; Lobban et al. 2020) are helping to clarify the affinities of taxa within the *Pleurosigma-Gyrosigma-Haslea-Navicula* complex. Lobban et al. (2020) and Li et al. (2017) showed that some taxa (*H. tsukamotoi*, *H. avium*) (accessory rib overlapping raphe sternum and shorter rather than longer helictoglossae) placed in *Haslea* by Sterrenburg et al. (2015) fell within the *Navicula* clade. They are also confirming the suggestion that genera such as *Pseudogomphonema* (Medlin 1991) and *Seminavis* (Round et al. 1990), with different valve and frustule symmetries but shared areola and raphe characters, belong with *Navicula* in the Naviculaceae (Lobban et al. 2020) rather than with dorsiventral or heteropolar taxa in the Cymbellales (Round et al. 1990). Other molecular studies (Kermarrec et al. 2011; Nakov et al. 2018; Jahn et al. 2019) are confirming that dorsiventrality or heteropolarity should not be relied upon to allocate to families in the latter order, confirming my earlier suggestions based on morphological and morphogenetic evidence (Cox 2002). Details of raphe and isolated pore structure (stigmata or stigmoids, Cox and Van de Vijver [2024]) are better guides to relationships within the Cymbellales than simple shape or symmetry.

In their work on “stigmata”, Cox and Van de Vijver (2024) discussed the distribution of different types of isolated pores across raphid diatoms, including the occurrence of fistulae, first described from the small, lightly-silicified cells of *Fistulifera* Lange-Bert. (Lange-Bertalot 1997). Phylogenetic analyses (Gastineau et al. 2018; Majewska et al. 2019; Kim et al. 2020; Tseplik et al. 2022) placed this genus in the same clade as *Proschkinia* Karayeva, a relationship that would not have been expected based on valve morphology, apart from the shared presence of a fistula. The relationships of taxa with a buciniportula (*Olifantiella* Riaux-Gob. & Compère, *Labellicula* Van de Vijver & Lange-Bert., and *Luticola*) have not been investigated using molecular data although, based on partial 18S rRNA sequences, a putative *Olifantiella* species grouped with *Luticola* (Han et al. 2018; Kezlya et al. 2021). However, both cases (fistulae and buciniportulae) would benefit from closer morphological comparisons.

GENERAL DISCUSSION

Whereas shape and symmetry are useful, easily described characters to aid identification, as recognised by Smith (1872), it is clear they are not reliable characters for

revealing systematic relationships, being homoplasious rather than homologous. Closer morphological investigations and molecular phylogenetic studies show that the same underlying structure is found in taxa exhibiting different frustule shapes and symmetries (Poulin et al. 2004; Lobban et al. 2010; Kermarrec et al. 2011; Nakov et al. 2014, 2018; Sugawara et al. 2024). Within the unique diatom reproductive cycle involving gradual size reduction followed by size restitution via auxosporulation, shifts in valve shape can occur and have resulted in different names being applied to larger and smaller representatives of the same taxon (Rose and Cox 2014). On the other hand, the flexibility of the auxospore, perizonium and initial cell provide a potential opportunity to introduce more striking shape changes, which would then persist through vegetative reproduction (Mann 1982b; Cohn et al. 1989b; Toyoda et al. 2006; Idei et al. 2013).

Two examples of species that can produce very different shapes are *Phaeodactylum tricornerutum* Bohlin and *Centronella reicheltii* Max Voigt. Whereas *P. tricornerutum* is unusual in not producing a typical siliceous frustule, *C. reicheltii* has a triradiate frustule that can be reproduced through a series of mitotic divisions (Krieger 1927; Schmid 1997), although it can revert to a fragilarioid form by gradual reduction of one “arm” of the triradiate cell (Schmid 1997). Schmid (1997) suggested that the triradiate morph is a teratological form induced in the auxospore and initial cell, nevertheless it has been recorded from a range of lakes and can produce sizeable populations (Echenique and Guerrero 2004). However, it is unlikely that raphid diatoms could produce tri-radiate frustules because this would require the development of a third raphe fissure from a bi-polar pattern centre (initiating the raphe system), whereas dorsiventrality, heteropolarity or flexure of the apical axis are not precluded. Nevertheless, irregularities in the structure of initial cells (Mann 1989; Nagumo 2003; Toyoda et al. 2006; Levkov 2009; Mann and Pouličková 2010) indicate that establishing the integrity of the cytoskeleton may take one or two mitoses and could offer an opportunity for a shift in shape.

How readily valve and frustule shape can change in natural populations is unclear, but presumably such changes are mediated by cytoplasmic components, nuclear movement, actin and filaments and microtubules of the cytoskeleton (Schmid 1986, 1994). Once a shape change is initiated it can then be perpetuated through subsequent mitoses thanks to the constraints of the siliceous frustule, at least until the next auxosporulation. Work with cytoskeleton inhibitors has shown that disrupting their activity results in abnormal valve morphology, particularly raphe path and stria arrangement, although areola structure seems to be maintained (Blank and Sullivan 1983a, 1983b; Cohn et al. 1989a). Studies on diatom teratologies similarly show that shape, raphe and stria patterns are often disrupted but effects on areola structure have not been reported (Lavoie et al. 2017).

In considering which characteristics are taxonomically informative but not susceptible to change over the life cycle, the following should be considered: areola structure, including the type of occlusion, e.g. hymenate or cribrate; raphe sternum structure and any associated thickenings; type of girdle bands, e.g. with or without rows of pores, type of pore occlusion. Despite still often being ignored, chloroplast structure can be informative, particularly at genus and family level, although the same chloroplast form may occur with different areola, raphe and cingulum characters. For example, within the Cymbellales sensu Round et al. (1990) (all with a single plastid with a central pyrenoid), there is a distinction between the Anomoeoneidaceae + Rhoicospheniaceae and the Gomphonemataceae + Cymbellaceae, the former families having hymenate areola occlusions that are lacking in the latter. On the other hand, variation in chloroplasts has been shown to be indicative of the different clades within *Amphora* sensu lato (Stepanek and Kociolek 2014).

Members of the Naviculaceae share the same type of areola, internally occluded by hymenes with an external slit, simple girdle bands lacking any pores, two chloroplasts lying along each side of the girdle, and the raphe fissure opening laterally in a distinct raphe sternum, often with some form of accessory bar(s) present. But the shape and symmetry of the genera vary from bilaterally symmetrical and isopolar valves with straight girdle regions (*Haslea*, *Navicula*), to bilaterally symmetrical and isopolar valves that are flexed in girdle view (*Rhoikoneis*), to heteropolar valves with slightly cuneate girdles (*Pseudogomphonema*), to dorsiventral valves with biconvex girdles (*Seminavis*), to sigmoid valves with straight girdle regions (*Haslea*, *Gyrosigma*). Yet all could be derived from an ancestor that was symmetrical about all three axes. Similarly, vaulted and keeled frustules could be derived from the same ancestral type.

In using structural characters to explore systematic relationships it is important to distinguish between homologous and homoplastic characters, often requiring a knowledge of their ontogeny rather than relying simply on visual comparison of mature valves. It is also important to describe characters accurately using appropriate terminology (Cox 2010; Cox and Van de Vijver 2024), e.g. the distinction between a stauros and a pseudostauros, which in turn often requires SEM data. LM observations alone may be inadequate.

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