

# Spines and homologues in ‘araphid’ diatoms

David M. Williams

Department of Life Sciences, the Natural History Museum, Cromwell Road, London, SW7 5BD, UK  
Email: d.m.williams@nhm.ac.uk

**Background and aims** – Many diatoms have spines on the surface of their valves. These structures differ from one taxon to another. Are all these spines the same? Are they homologues of one another? This paper sets out to explore some of the issues surrounding the determination of homologues with reference to members of Fragilariaceae.

**Methods** – A variety of spines from species in Fragilariaceae are examined (in the SEM) and position on the valve documented relative to those already recorded in the literature.

**Key results** – Spines that occur on the valves of some ‘araphid’ diatoms in Fragilariaceae can be interpreted in the light of where they are found. Spines that occur on the virgae can be thought of as modifications of that structure; spines that occur on the vimines can be thought of as modifications of that structure – the two kinds of spines are not homologues of each other. The term ‘spine’, on its own, is not useful for understanding taxon relationships; the term ‘spine’ is not even a character in the comparative biology sense but a descriptive catch-all for something that simply ‘sticks out from a surface’.

**Conclusions** – Systematic characters, those applicable to comparative biology, are modifications of other characters and so are, in one sense, like taxonomies: hierarchical. A consequence of this is that plotting morphological characters on molecular trees of relationships is a futile endeavour – treating characters and their modifications, as if they are static (unit) features of a non-changing entity, is book-keeping not science.

**Key words** – ‘araphid’ diatoms, diatoms, Fragilariaceae, homologues, spines.

## INTRODUCTION

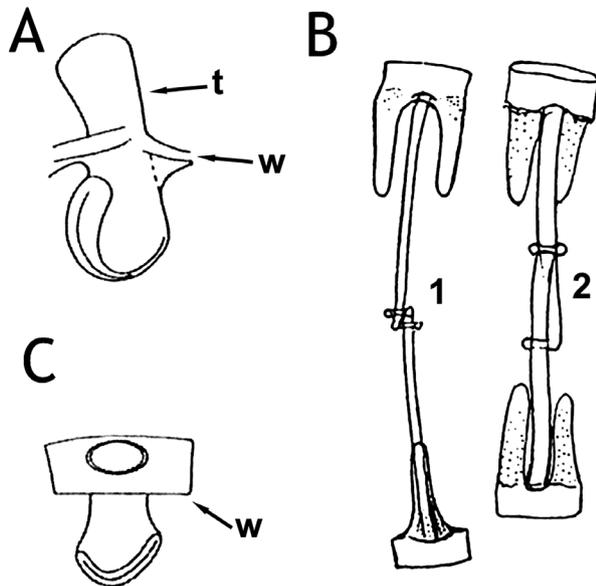
All organisms have parts. Organisms that belong to different species share parts with some species, differing in others. This makes systematics possible. The parts of organisms that are shared are usually referred to as characters but, in the framework of comparative biology, they are equivalent to homologues. Systematics is based on determining or discovering homologues, the parts of organisms that are equivalent rather than just similar, and thereby determining homology, their relationships. Homologues and homology are different (Williams & Ebach 2012).

Influential in the early literature on homology is Richard Owen (1804–1892), vertebrate palaeontologist and first

superintendent of the Natural History Museum in London (Rupke 1994, 2009). Owen (1847: 173) noted that “The corresponding parts in different animals being thus made namesakes are called technically ‘homologues’ ” suggesting that homologues usually (but not always) share the same name (‘namesakes’). Giving names to the parts of organisms provides a common language via terminology. The direct equivalence between terminological names and homologues is, of course, not always exact – but this is what makes systematics interesting. The general question addressed by comparative biology (and hence systematics) is: what are the parts of organisms and how do they relate one to another? The specific question addressed in this paper is: What are spines on diatom valves?

THE INTERPLAY BETWEEN TERMINOLOGY,  
HOMOLOGUES, HOMOLOGY AND TAXA

Most parts of organisms are abstracted from the whole, some being more obvious than others with respect to whatever current terminology is available. For example, the structure now called a rimoportula (previously called the ‘jelly pore’, ‘mucilage pore’, and referred to here as the labiate process) was defined in the first diatom terminology paper as “[...] a tube or an opening through the valve wall with an internal flattened tube or longitudinal slit often surrounded by two lips” (Anonymous 1975: 327), with illustrations (drawings) given from two ‘centric’ diatoms: *Lauderia* Cleve and *Thalassiosira bioculata* (Grunow) Ostenfeld (= *Shionodiscus bioculatus* (Grunow) Alverson, Kang & Theriot). (the two drawings in Anonymous 1975, figs 30 and 31, are reproduced here as fig. 1A & B; for details see figure legends; both drawings are after Hasle 1973). Two ‘special types’ of rimoportula were noted: the periplekton, given without a definition (and said to be found only in the genus *Rutilaria* Greville), and curiously, the raphe systems, with no further explanation (Anonymous 1975: 327).



**Figure 1** – Reproduction of drawings in Anonymous (1975). A, rimoportula of a specimen of *Lauderia* (t = tube; w = valve wall, Anonymous 1975, fig. 30, after Hasle 1974); B, periplekton (after Jurilj 1965: 76, figs 1 and 2; C, rimoportula of a specimen of *Thalassiosira bioculata* (w = valve wall, Anonymous 1975, fig. 31, after Hasle 1974; reproduced with permission from Schweizerbart science publishers [www.schweizerbart.de/journals/nova\\_hedwigia](http://www.schweizerbart.de/journals/nova_hedwigia)). A & C reproduced with permission from Schweizerbart Science Publishers. These images are not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder ([https://www.schweizerbart.de/journals/nova\\_hedwigia](https://www.schweizerbart.de/journals/nova_hedwigia)). B reproduced with permission of the publisher (journal *Acta Botanica Croatica*, University of Zagreb). This image is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the publisher (<http://www.abc.botanic.hr>).

The revised terminology paper, which appeared a few years later, expanded on these earlier definitions by including an additional special type of labiate process, called the bilabiate process, which had “[...] two internal slit-like openings placed end to end” (as in *Streptothecha tamesis* Shrubsole, see Hasle & Syvertsen 1996: 22, part of their fig. 8); by providing a definition for the periplekton (“in which the external part is forked above, the two arms clasping the stem of the similar process on the adjacent valve”, see fig. 1C, after Jurilj, 1965: 76) and a species given as the example (*Rutilaria radiata* Grove & Sturt); and modifying the text on the raphe system (“It also appears that the raphe [...] is an evolutionary development of the labiate process”, Ross et al. 1979: 521).

Here, then, is a series of terms all relating in one way or another to what is understood as the rimoportula such that one might interpret the special terms – the bilabiate process, the periplekton and the ‘raphe system’ – as modified (or derived) rimoportulae (I will return briefly to the ‘raphe system’ below). In this sense we have a hierarchy of characters and character-types:

Rimoportulae  
Bilabiate process  
Periplekton  
Raphe

Each may (or may not) associate (or define) a particular taxon. In this example, each of the characters does pick out a taxon:

Diatoms: rimoportulae  
Order Lithodesmiales: bilabiate process  
Genus *Rutilaria*: periplekton  
‘Raphid’ diatoms: raphe

Each of the derived (or modified) forms of the rimoportula is a synapomorphy for their respective group and each has gained, with time, an enhanced definition outlining, or capturing, so to speak, its uniqueness from the assumed primitive form, the rimoportula. The bilabiate process, for example, was more clearly defined by Hasle & Syvertsen as “a process consisting of an external shorter or longer tube, sometimes reduced to a low ring (LM), and an internal part with a longer or shorter stalk and a trapezoid end piece closed at the tip but open at each of the two slanting side by a longitudinal slit (EM)[...]” (Hasle & Syvertsen 1996: 226). This is evidence for the taxon it defines, the order Lithodesmiales (Kaczmarek et al. 2005: 132):

“All of the non-fultoportulate extant diatoms of this lineage possess an unusual bilabiate process [...]. Such a process is not known outside Lithodesmiaceae and Bellerophyceae [...] supporting the molecular grouping of these diatoms as a natural clade, even though they are currently placed in separate orders [...]” (Kaczmarek et al. 2005: 132)

Hasle & Syvertsen included in their Lithodesmiaceae the following genera: *Lithodesmium*, *Ditylum*, *Bellerophcea*, *Streptothecha* [= *Helicothecha*], *Lithodesmioides* and *Neostreptothecha*; Kaczmarek et al. (2005) have the same composition with the addition of *Mediopyxis*, which was described after 1996 (Kühn et al. 2006: 321).

Kaczmarek et al. go on to suggest that:

“Here, the external tube of the bilabiate process in modern Lithodesmiales may be derived from the central tube of the fossil genus *Archeptyrgus*” (Kaczmarek et al. 2005: 134)

It should be noted that direct comparisons between particular structures that resemble one another can be instructive. For example, Sato et al. (2008: 377) use the term bilabiate process for a structure in *Pseudostriatella*, but comment that “Processes with two entire labiate slits [...] were also commonly seen. This bilabiate process is not the same as the bilabiate process in the Lithodesmiales”. The structure in *Pseudostriatella* should probably, then, have a new name but could be considered yet another modification of the rimoportula. Vishnyakov et al. (2015: 223) refer to ‘bilabiate rimoportulae’ in some species of *Hannaea*, by which they mean the usual kind of rimoportula with paired internal lips (M. Kulikovskiy, Timiryazev Institute of Plant Physiology of RAS, Moscow, Russia, pers. comm.).

Speculation to one side, the naming of parts can imply (and can provide) support (evidence) for taxa at whatever taxonomic level – in this case, potentially tracing a structure (and its homologues) back into the Cretaceous (Gersonde & Harwood 1990). It should be noted that the bilabiate process is a homologue. What, then, is homology? The bilabiate process is evidence for the taxon Lithodesmiales, which is short-hand for ‘all organisms with the bilabiate process are more closely related amongst themselves than to any other taxon’. Homology is a relationship. If the proposition offered by Kaczmarek et al. (2005) is deemed reasonable then the taxon Lithodesmiales would need to include *Archeptyrgus*, a more inclusive relationship.

The same development can be noted for the periplekton. A more precise definition was provided by Witkowski et al. (2011) as:

“[...] a rimoportula modified to function as a linking structure; it consists of an elongate stem (caulis), at its summit bearing two arms (brachia) that form a loop around the stem of the periplekton of the sibling [...]” (Witkowski et al. 2011: 380).

And that, too, serves, to define a taxon, in this case the genus *Rutilaria*:

“The most important feature of *Rutilaria* is the periplekton, which in our opinion has no counterpart in any diatom lineage” (Witkowski et al. 2011: 380).

Although they suggest the periplekton has “no counterpart”, it is clearly understood to be a modified rimoportula (Witkowski et al. 2011: 379, table 2, and as noted above in the definition: “a rimoportula *modified* to function as a linking structure”, my emphasis). Once again, the taxon *Rutilaria* is equivalent to a homology statement, the statement of a relationship concerning all species of *Rutilaria* relative to all other diatoms.

Finally, for the ‘raphe system’, there is such a wealth of literature on the apparent relationship between it and the rimoportula that there is no need of further discussion (a review of the various relationships can be found in Williams & Kociolek 2011). Suffice to say that if one considered the rimoportula to be the precursor to the raphe (its unmodified

form), then the latter, more accurately, should also be considered a modified rimoportula. This, and other related propositions, are still, or should be, attractive research problems but if this version concerning the raphe and its homologues is correct (and I am not supporting or promoting it here), then the specified homology statement (relationship) would be:

Diatoms: rimoportulae

‘Raphid’ diatoms: raphe

Another interesting (and puzzling) aspect of the two terminology papers is that the section entitled “Processes”, with processes defined as “projections with homogeneously silicified walls” (Anonymous et al. 1975: 327; Ross et al. 1979: 521), includes not only the rimoportula but occluded processes, strutted processes (now known by its Latin name *fultoportulae*) and, rather surprisingly, spines. I doubt very much whether the intention was to understand rimoportulae, occluded processes, strutted processes and spines as modified versions of some general kind of process, but the implication lingers when terminology (the names of parts) is mixed in with homologues (the parts themselves). That to one side, it is the latter, the spines, I am interested in below.

#### WHAT IS A SPINE? SPINES AS PROCESSES

When describing *Hemiaulus amplexans* for the first time, Grove & Sturt wrote that “The most remarkable feature in this little form is the presence of a very long, stout central spine, terminating in a bent claw” (Grove & Sturt 1887: 76, emphasis mine). It is the ‘stout central spine’ that is now known as the periplekton discussed briefly above (first named by Jurlij, 1965, using only light microscopy; for further illustrations of Grove & Sturt’s specimens of *Hemiaulus amplexans* see Ross 1995: figs 8–10 and pl. 1d–f and Witkowski et al. 2017: 23, figs 99, 100, the latter two publications using the revised name of *Rutilaria amplexans* (Grove & Sturt) Ross). That Grove & Sturt referred to this structure as a spine is entirely understandable as a general definition of the term ‘spine’ refers to something that simply ‘sticks out from a surface’. Diatomists encounter and refer to spines frequently, so it might seem a reasonable question to ask: what exactly is it, this spine?

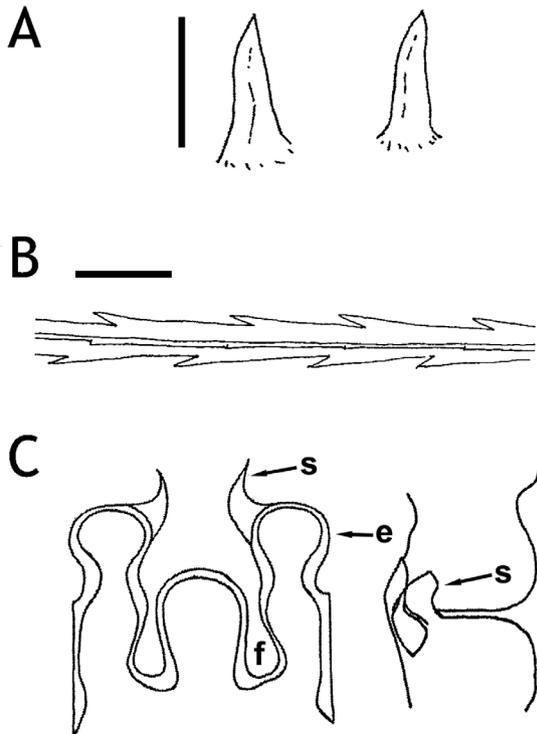
In the first terminology paper, the term spine was defined like so: “a closed or solid structure projecting out from the wall” (Anonymous 1975: 328). Three different ‘kinds’ of spines were discussed: a spinule, defined as a “very small spine”; a granule, defined as a “small, rounded projection on surface of the valve”; and a linking spine, defined as an “interdigitating spine that connects frustules in chains”. Note that two of these kinds are more or less concerned with size, the third with function. Three examples were given: *Thalassiosira eccentrica* (Ehrenb.) Cleve (for a spine, fig. 2A), *Corethron* Castracane (for a spine, fig. 2B) and for the ‘linking spine’, an example from the Hemiaulaceae (all three drawings are reproduced here in fig. 2A–C, respectively). Even a glance at these three drawings, it is clear that their spines share very little in common – with the sole exception that they do indeed protrude from the valve surface. No changes were made in the revised terminology paper (Ross et al. 1979: 522, except for a few cosmetic additions: *Corethron*

was given an authority (“Castr.”) and the species in Hemiaulaceae was specified as *Hemiaulus polycistinorum* Ehrenb.).

For the purposes of species identification, these definitions and distinctions might work perfectly fine; for understanding the structure of diatom valves, how they are put together – what are their homologues – they are almost useless (see Cox 2009).

#### WHAT IS A SPINE? SPINES AS STRUCTURES

Before addressing this question from the structural point of view (comparative morphology), I need to briefly discuss the terminology of some basic diatom valve parts. Again, I use as my starting point the first terminology paper (Anonymous 1975). Here the phrase ‘basal siliceous layer’ occurs, defined as “the layer that forms the basic structure of the various components of the frustule” – in short, the siliceous surface of any particular valve. This is followed by definitions of



**Figure 2** – Reproduction of the drawings of spines from Anonymous (1975): A, drawing of spine from *Thalassiosira eccentrica* (Anonymous 1975, fig. 35, after Fryxell); B, drawing of spine from *Corethron* (Anonymous 1975, fig. 36, after Fryxell); C, drawing of linking spine from *Hemiaulus capitatus* (Anonymous 1975, fig. 20, “fold f, elevation e, linking spines s, left optical section of valve[...] from Ross”). Scale bars: A = 2  $\mu\text{m}$ ; B = 10  $\mu\text{m}$ . All three drawings reproduced with permission from Schweizerbart Science Publishers. These three images are not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder ([https://www.schweizerbart.de/journals/nova\\_hedwigia](https://www.schweizerbart.de/journals/nova_hedwigia)).

striae, with a stria being “a row of areolae or puncta or an alveolus”; punctate stria is defined as “a stria consisting of a row of elements [...] of unknown structure” and alveolate stria as “a stria consisting of an alveolus” (Anonymous 1975: 327).

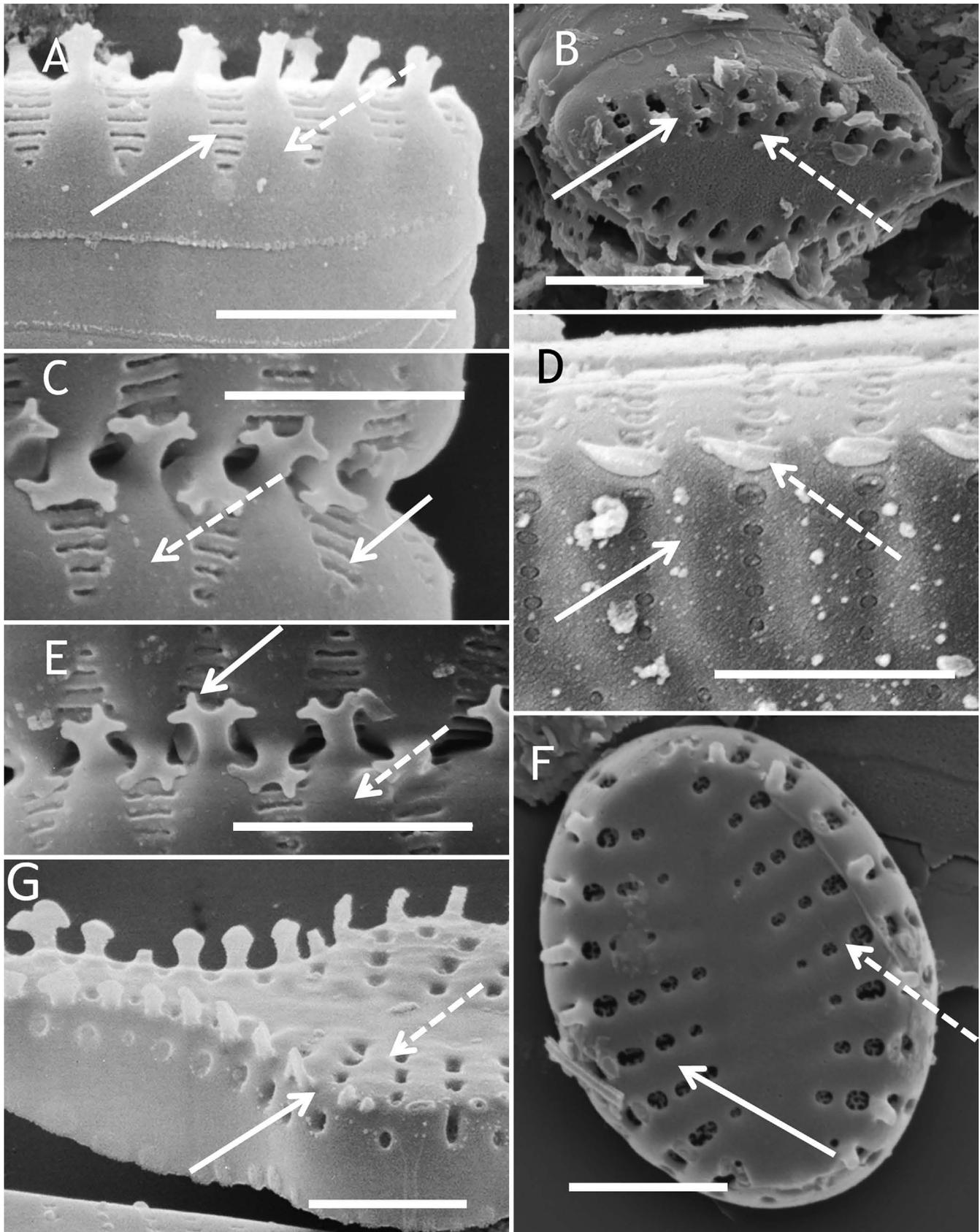
The revised version expanded on these definitions, dealing with the striae found in centric diatoms separately from those found in pennate diatoms. For the latter, which is the focus of interest in this paper, three ‘types’ were given: parallel, “when they are perpendicular to the median line of the valve or to the raphe; radiate, “when they are inclined from the valve margin towards the centre of the valve; and convergent, “when they are inclined from the valve margin towards the apex” (Ross et al. 1979: 525 et seq.). Each ‘type’ describes the orientation of the striae rather than its structure, again, possibly helpful in species identification. After these descriptions, a new term was introduced: the interstria, described as “the non-perforate strip of basal siliceous layer between two striae. In many pennate diatoms the striae are depressed into the basal siliceous layer on the inner side of the valve, and occasionally on the outer side of the valve, and in such cases the interstriae have often been called costae [...], but only those interstriae where the basal siliceous layer is thickened should be termed costae” (Ross et al. 1979: 526). It is to this set of terms that Cox & Ross (1981) provided a revised terminology that clarified much relating to the basic morphology of diatom valves.

After discussing certain aspects of pennate diatom valve terminology, Cox & Ross noted that “the term ‘interstria’ was [...] a rather unsatisfactory term, being negative rather than positive in meaning. In addition, there is a need for a term for the bars that separate the areolae within a stria” (Cox & Ross 1981: 272). Here I need to quote the whole of their next paragraph:

“The structure of pennate diatoms with a single row of areolae in their striae bears some resemblance to basket-work. There are two latin words for the materials from which baskets were made, ‘virga’ and ‘vimen’. These may have been synonyms but the other ways in which they were used suggests that ‘virga’ applied to stiffer rods than ‘vimen’ did, and hence we suggest that the bars between the striae be called ‘virgae’ rather than ‘interstriae’, and the crossbars between these be called ‘vimines’.” (Cox & Ross 1981: 272).

This, then, was not only a way of describing the parts of the valves, rather than the ‘holes’ formed by the parts, but a way of discussing what exactly spines are in relation to the virgae and vimines in pennate diatoms, and therefore in relation to the entire valve structure itself. I will demonstrate this with a few examples from an array of images from some ‘Staurosirid’ specimens (‘Staurosirid’ *sensu* Williams 2011 and Li et al. 2018).

For the first set of images (fig. 3A, C, E & G), in fig. 3A the virgae are the thicker bars (indicated by a dashed arrow in fig. 3A, E & G) and the vimines are the cross-members (indicated by a solid arrow in fig. 3A, E & G). As the virgae descend towards the valve edge away from the margin, they broaden and coalesce to form the valve edge (fig. 3A & G). The specimen in fig. 3G has fewer mantle vimines than the



**Figure 3** – Various specimens that probably belong to the ‘Stausosirid’ group of ‘araphid’ diatoms *sensu* Williams (2011) and Li et al. (2018). The specimens are labelled so as to just illustrate the virgae (dashed line), the vimines (solid line) and the spine that emerges from one or the other structure. Scale bars: A = 3  $\mu\text{m}$ ; B & F = 5  $\mu\text{m}$ ; C–E = 1.5  $\mu\text{m}$ ; G = 2.0  $\mu\text{m}$ .

specimen in fig. 3A so the valve edge occupies a greater area. The vimines extend between adjacent virgae as thin strips of silica (fig. 3A, C, E & G). The specimen in fig. 3G has shorter mantle vimines than that in figure 3A. At the valve margins, spines extend from the surface, jutting out at an angle and then, towards the tips, branch out into a pair of two minor spines for the specimen in fig. 3A, C, E & G. For the specimen in fig. 3G, the spine has a broader, flatter tip with no bifurcations. Much as these details are of interest, it is the fact that in both sets of specimens the spine extends from the virgae (fig. 3A, C, E & G): rather than a spine, it might be better thought of as a modified virga. The characters can be expressed like so:

#### Virgae

modified virgae {= ‘spine’#1}

The specimens in fig. 3B, D & F have a similar arrangement of virgae and vimines (the virgae indicated by a dashed arrow, vimines by a solid arrow in fig. 3B, D & F). In these cases the spines emerge instead from the vimines (e.g., fig. 3D): rather than a spine, it might be better thought of as a modified vimen. In these terms the characters here are:

#### Vimines

modified vimines {= ‘spine’#2}

That is, the spines are not homologues, ‘spine’#1  $\neq$  ‘spine’#2 – they are modification of different structures: in one case, there are virgae, modified virgae and unmodified vimines, in

the second case, there are vimines, modified vimines and unmodified virgae.

#### Virgae

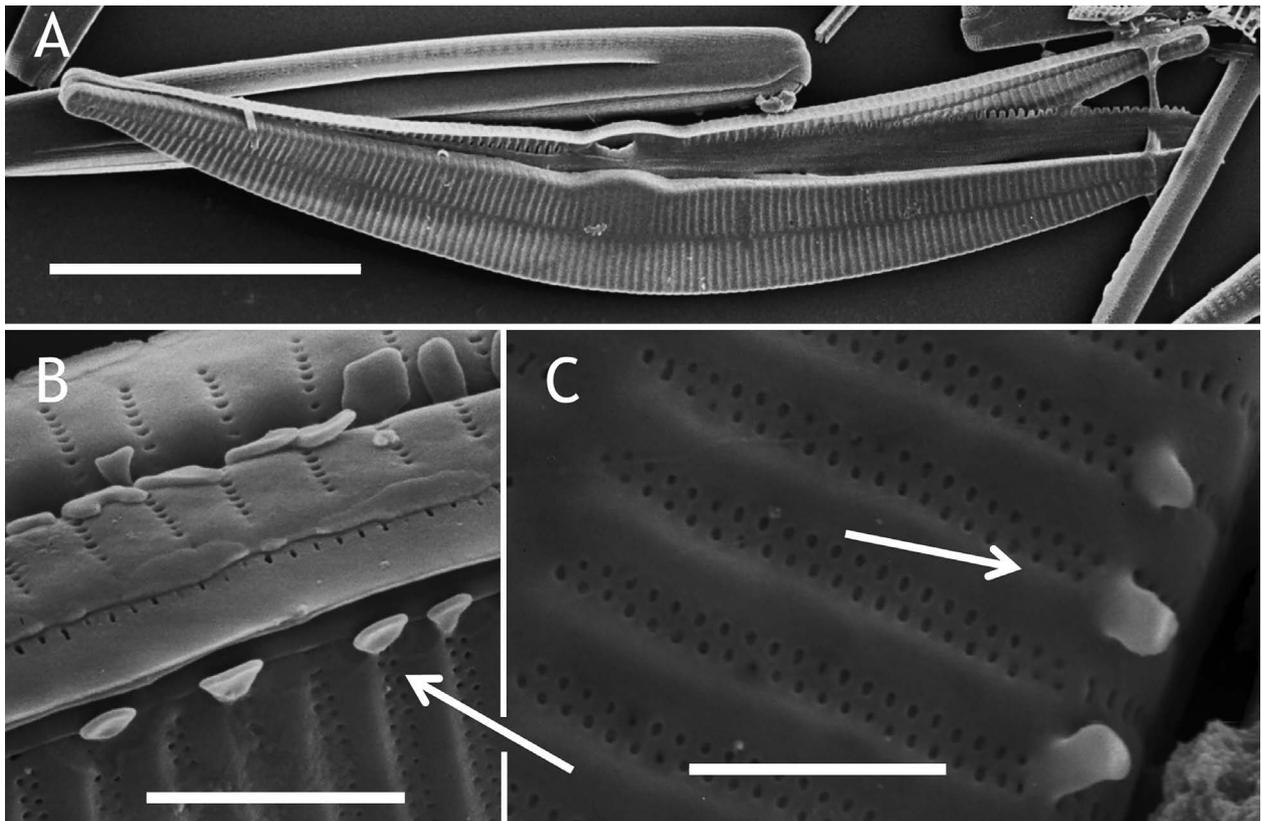
modified virgae {‘spine’}

#### Vimines

modified vimines {‘spine’}

For me, this is an improved way of understanding and documenting the spines and, as a consequence, the structure of the valves. Of course, both projections are spines with respect to the classical definition above. They are also marginal spines, as discussed by many others (e.g. Li et al. 2018), and some are also linking spines, helping form colonies (fig. 3C & E). Yet, as noted above, these are either descriptive (‘spine’) or express a function (‘linking’) rather than relate to the structure, which is the source of all homologues.

Morales et al. (2010) recognised some while ago the usefulness of this distinction by noting that for *Pseudostaurosira* Williams & Round the spines were “Interrupting striae [vimines], less common on costae [virgae] or even absent, solid and sometimes serrate” and for *Staurosira* Ehrenb. the spines were “On costae [virgae], never along striae, sometimes absent, hollow, never serrate” (Morales et al. 2010: 99, table 2, but see Morales et al. 2015 and Grana et al. 2018). One might interpret the description of *Pseudostaurosira* above as having species with variation in the derivation of their spines relative to their virgae and vimines, the basic valve structure.



**Figure 4** – *Hammaea* cf. *baicalensis*, a few images to illustrate its spines (These specimens, from Lake Baikal, are probably of a new species that will be described in due course). A, external view of whole valve; B & C, illustrating the spines emerging from (biseriate) vimines, straddling a pair of adjacent virgae (arrows). Scale bars: A = 20  $\mu$ m; B & C = 2  $\mu$ m.

A final example is *Hannaea baicalensis* Genkal, Popovskaya & Kulikovskiy (fig. 4A–C, see also Genkal et al. 2008 and Vishnyakov et al. 2015; for the time being, these specimens should probably be referred to as *Hannaea* cf. *baicalensis* as there are a number of features that distinguish them from those described as *Hannaea baicalensis* by Genkal et al. 2008. This will be undertaken in due course). The spines on these valves appear to emerge from (biseriate) vimines and straddle a pair of adjacent virgae (fig. 4B & C, arrows; Genkal et al. 2008: pl. II, fig. 7; Vishnyakov et al. 2015, their fig. 5c, and more clearly on their fig. 6b). Here, then, is a modification of the vimines and what appears to be a structure fused across two adjacent virgae that forms the spine (fig. 4B & C, especially fig. 4C, arrow). Thus, the characters here might be better thought of as:

#### Vimines

modified vimines fused with virgae {'spine'#3}

If we compare variations in spines to the situation found with rimoportulae and their modified parts, it is more than possible that different modifications can be found with respect to the virgae and vimines. It is more than possible that many of the spines found in these permutations are not homologues of one another.

Consider further the case of *Hannaea*. The spines in *Hannaea baicalensis* might be thought of as another unique modification, neither emerging directly from the virgae nor the vimines but a kind of fusion of both, perhaps a putative synapomorphy (unique character) for the genus. Other species in the genus *Hannaea* also have spines situated on the margin and also appear to be neither derived from nor direct modifications of the virgae or vimines, such *Hannaea linearis* (Holmboe) Álvarez-Blanco & Blanco (Álvarez-Blanco & Blanco 2013: figs 38, 42) and *Hannaea superioensis* Bixby & Edlund (Bixby et al. 2005: fig. 11). Conversely, other species lack spines altogether, such as *Hannaea hovsgolensis* Vishnyakov, Kulikovskiy & Genkal (Vishnyakov et al. 2015) and *Hannaea arcus* (Ehrenb.) R.M.Patrick (although there are an enormous number of different specimens included under the name *Hannaea arcus*), or have spines normally associated with *Fragilaria* s. str. (see below). But *Hannaea* remains an interesting case as it is clearly in need of revision as it is yet another genus based, in part, on valve symmetry (see also Cox 2009): that is, the lunate shape of its valves – but it includes exceptions, such as *Hannaea inaequidentata* (Lagerst.) Genkal & Kharitonov (Genkal & Kharitonov 2008), *Hannaea arcus* var. *kamtchatica* (Boye-Petersen) Bao & Reimer (Bao & Reimer 1992), *Hannaea arcus* f. *recta* (Cleve) Foged (Foged 1981) and *Ceratoneis jogensis* H.P.Gandhi (Gandhi 1966).

It might be that *Hannaea* includes species rightly placed in *Fragilaria*, given that genus can be sufficiently characterised, which at the moment it cannot, but a short discussion on its spines is relevant to the thrust of this paper.

#### WHAT IS A SPINE?

##### A BRIEF RETURN TO 'FRAGILARIA'

It is clear, regardless of the evidence used (molecular or morphological), that the genus *Fragilaria* is, at present, an al-

most impossible concept to articulate – it is doubtful that any two definitions of the characters of the genus in common use today would agree; and even more doubtful that any single synapomorphy has been identified. Thus, its status is indeterminate, or in terms of comparative biology, it is aphyletic, without -phyly (see Ebach & Williams 2010, Williams & Ebach 2018). By this, I mean it cannot be judged monophyletic but nor can it be thought of as either para- or polyphyletic. The purpose of this paper is not to explore the monophyly of *Fragilaria* (or other any genus discussed herein) but to explore the nature of the spines that have played such a big part in previous (and current) definitions of the genus. In spite of it being clearly established for some time that spines are not a crucial part of that definition (e.g. Williams & Round 1987), descriptions of the genus still include reference to the presence of spines of some kind or another. For example, compare two online diatom identification resources for the character combinations needed to identify species of *Fragilaria* that both include among their character lists reference to spines and yet both document species of *Fragilaria* that lack them! (Spaulding & Edlund 2008, Mann et al. 2018).

Rather than writing another definition of the genus, I take a different approach here, one that is not entirely satisfactory but serves the purpose of this paper. Two tables have been assembled. The first is a list of all species of *Fragilaria* that have been described since 1986 (table 1; the date was chosen with reference to the two revisions concerned with *Fragilaria* and their spines, Williams & Round 1986, 1987). The list omits new combinations as well as some recently restudied species – there are 73 entries from 1986 to 2017. These names have been omitted simply because in many cases the nomenclature is impenetrable making the relevant taxa almost impossible to understand. For example, Tuji presented a detailed and useful study on Ehrenberg's *Fragilaria sepes*, which he (Tuji) considered to be a synonym of *Fragilaria nana*. Because of priority considerations, the name *Fragilaria nana* had been changed to *F. nanana* but some now consider the correct name for this taxon to be *Fragilaria tenera* var. *nanana*. In addition, some specimens of *Fragilaria nana* (*sensu* Lange-Bertalot 1993) are now thought to be *Fragilaria saxoplanctonica* – as far as can be established, none of these names seem to correspond to what I have called 'classical' species of *Fragilaria* (see Tuji 2004 for *Fragilaria sepes* and Cantonati et al. 2017 for *Fragilaria saxoplanctonica*).

For each name in the table, a judgement has been made on what is (either certain, probably or maybe) a more accurate generic assignment for that species based on what might be thought of as a 'classical' species of *Fragilaria*, which have been picked out in bold. While this might appear to be as subjective as every other definition of the genus, 'classical' is here taken to mean species that share characters with *Fragilaria capucina* Desm., as documented in Tuji & Williams, with the exception of linking spines, which are indeed conspicuous in *Fragilaria capucina* (Tuji & Williams 2006). Of the 73 names, 24 (about 33%) might be considered 'classical' species of *Fragilaria*.

The second table lists those species of *Fragilaria* that have information published that includes data on their spines. It is not intended to be exhaustive. Four groups can be recognised (these groups do not necessarily imply monophyletic taxa):

**Table 1 – Species of *Fragilaria* described from 1986 to 2018.**Species in bold are (probably) ‘classical’ species of *Fragilaria*.

<b>Name</b>	<b>Author</b>	<b>Year</b>	<b>Alternative name</b>
<i>Fragilaria acidobiontica</i>	Charles	1986	<i>Fragilariforma</i>
<i>Fragilaria construens</i> var. <i>lunata</i>	Stone in McLaughlin & Stone	1986	<i>Staurosira?</i>
<i>Fragilaria lapponica</i> var. <i>inflata</i>	Stone in McLaughlin & Stone	1986	<i>Staurosira?</i>
<i>Fragilaria flavovirens</i>	Takano	1986	<i>Gedaniella flavovirens</i>
<i>Fragilaria telum</i>	Carter & Denny	1987	<i>Fragilariforma</i>
<i>Fragilaria incognita</i>	Reichardt	1988	<i>Distrionella</i>
<i>Fragilaria opephoroides</i>	Takano	1988	<i>Serratifera opephoroides</i>
<i>Fragilaria germainii</i>	Reichardt & Lange-Bertalot	1990	<i>Distrionella</i>
<i>Fragilaria oblonga</i>	Drebes & Schulz	1990	??
<i>Fragilaria canariensis</i>	Lange-Bertalot	1993	<i>Staurosira</i>
<i>Fragilaria cassubica</i>	Witkowski & Lange-Bertalot	1993	??
<i>Fragilaria eichhornii</i>	Witkowski & Lange-Bertalot	1993 [1995]	??
<i>Fragilaria eichhornii</i>	Witkowski & Lange-Bertalot	1993 [1995]	<i>Opephora</i> ??
<i>Fragilaria exiguiformis</i>	Lange-Bertalot	1993	<i>Fragilariforma</i>
<i>Fragilaria gedanensis</i>	Witkowski	1993	??
<i>Fragilaria guenter-grassii</i>	Witkowski & Lange-Bertalot	1993	<i>Gedaniella guenter-grassii</i>
<i>Fragilaria neoproducta</i>	Lange-Bertalot	1993	Staurosirid
<i>Fragilaria sopotensis</i>	Witkowski & Lange-Bertalot	1993	??
<i>Fragilaria synegrotesca</i>	Lange-Bertalot	1993	??
<i>Fragilaria constricta</i> var. <i>elliptica</i>	Tynni	1994	??
<i>Fragilaria crotonensis</i> f. <i>curvata</i>	Tynni	1994	??
<i>Fragilaria neoelliptica</i>	Witkowski	1994	??
<i>Fragilaria geocollegarum</i>	Witkowski & Lange-Bertalot	1995	<i>Pseudostaurosiropsis geocollegarum</i>
<i>Fragilaria improbula</i>	Witkowski & Lange-Bertalot	1995	??
<i>Fragilaria polonica</i>	Witkowski & Lange-Bertalot	1995	<i>Pseudostaurosira polonica</i>
<i>Fragilaria barbararum</i>	Witkowski et al.	1996	??
<i>Fragilaria labei</i>	Witkowski & Metzeltin	1996	??
<b><i>Fragilaria nanoides</i></b>	<b>Lange-Bertalot</b>	<b>1996</b>	
<i>Fragilaria oldenburgioides</i>	Lange-Bertalot	1996	Staurosirid
<i>Fragilaria opacolineata</i>	Lange-Bertalot	1996	<i>Staurosira opacolineata</i>
<i>Fragilaria spinarum</i>	Lange-Bertalot & Metzeltin	1996	??
<i>Fragilaria acutirostrata</i>	Metzeltin & Lange-Bertalot	1998	Staurosirid
<i>Fragilaria construens</i> var. <i>fossilis</i>	Gandhi	1998	Staurosirid
<i>Fragilaria construens</i> var. <i>indica</i>	Gandhi	1998	Staurosirid
<i>Fragilaria crassa</i>	Metzeltin & Lange-Bertalot	1998	Staurosirid
<i>Fragilaria leptostauron</i> var. <i>trigona</i>	Gandhi	1998	Staurosirid
<i>Fragilaria rolandschmidtii</i>	Metzeltin & Lange-Bertalot	1998	<i>Fragilariforma</i>
<i>Fragilaria santaremensis</i>	Metzeltin & Lange-Bertalot	1998	Staurosirid
<i>Fragilaria henryi</i>	Lange-Bertalot	1999	??
<i>Fragilaria viereckiana</i>	Moser	1999	Staurosirid
<i>Fragilaria bronkei</i>	Witkowski et al.	2000	Staurosirid
<i>Fragilaria germainii</i> f. <i>acostata</i>	Lange-Bertalot	2000	<i>Distrionella</i>
<i>Fragilaria husvikensis</i>	Van de Vijver, Denys & Beyens	2000	<i>Distrionella</i>

Table 1 (continued) – Species of *Fragilaria* described from 1986 to 2018.

Name	Author	Year	Alternative name
<i>Fragilaria suboldenburgiana</i>	Camburn & Charles	2000	??
<i>Fragilaria capucina</i> f. <i>lanceolata-baikali</i>	Flower & Williams	2004	
<i>Fragilaria capucina</i> f. <i>sublanceolata-baikali</i>	Flower & Williams	2004	
<i>Fragilaria longifusiformis</i>	Siver et al.	2006	
<i>Fragilaria dzonoticola</i>	Novelo, Tavera & Ibarra	2007	
<i>Fragilaria nevadensis</i>	Linares-Cuesta & Sánchez-Castillo	2007	
<i>Fragilaria pennsylvanica</i>	Morales	2007	??
<i>Fragilaria acutirhombica</i>	Metzeltin, Lange-Bertalot & Nergui	2009	
<i>Fragilaria crassirhombica</i>	Metzeltin, Lange-Bertalot & Nergui	2009	
<i>Fragilaria recapitellata</i>	Metzeltin & Lange-Bertalot	2009	
<i>Fragilaria boreomongolica</i>	Kulikovskiy et al.	2010	
<i>Fragilaria uliginosa</i>	Kulikovskiy et al.	2010	
<i>Fragilaria cochabambina</i>	Morales	2009	<i>Ulnaria</i>
<i>Fragilaria flexura</i>	Hoff & Lange-Bertalot	2011	??
<i>Fragilaria amphicephaloides</i>	Lange-Bertalot	2013	
<i>Fragilaria neointermedia</i>	Tuji & Williams	2013	
<i>Fragilaria crenophila</i>	Graeff et al.	2013	<i>Williamsella</i>
<i>Fragilaria perdelicatissima</i>	Lange-Bertalot & Van de Vijver	2014	
<i>Fragilaria aquaplus</i>	Lange-Bertalot & Ulrich	2014	
<i>Fragilaria saxoplanctonica</i>	Lange-Bertalot & Ulrich	2014	??
<i>Fragilaria tenera</i> var. <i>nanana</i>	Lange-Bertalot & Ulrich	2014	
<i>Fragilaria tenuissima</i>	Lange-Bertalot & Ulrich	2014	
<i>Fragilaria candidagilae</i>	Delgado et al.	2015	
<i>Fragilaria microvaucheriae</i>	Wetzel & Ector	2015	
<i>Fragilaria neotropica</i>	Almeida et al.	2016	
<i>Fragilaria spectra</i>	Almeida et al.	2016	
<i>Fragilaria rinoi</i>	Delgado et al.	2016	
<i>Fragilaria iraqiensis</i>	Al-Handel et al.	2016	<i>Williamsella</i>
<i>Fragilaria billingsii</i>	Wengrat et al.	2016	
<i>Fragilaria asterionelloides</i>	Tuji & Williams	2017	
<i>Fragilaria misarelensis</i>	Almeida, C.Delgado, Novais & S.Blanco	2019	

Group 1, ‘classical’ species of *Fragilaria* but without spines; Group 2, a distinct group of *Fragilaria*-like species but also without spines; Group 3, ‘classical’ species of *Fragilaria* with spines that emerge from the vimines; Group 4, ‘classical’ species of *Fragilaria* with spines that are not associated directly with either the vimines or the virgae; Group 5, a mixture of species with different kinds of spines and possibly none belonging to the ‘classical’ species of *Fragilaria* (compare with table 2). The Groups without spines cannot speak to any issue on relationships relative to that character, however determined. The groups with spines, either emanating from the virgae or vimines, can only be evaluated with reference to

other characters, to establish whether Groups 1–4 do indeed form monophyletic groups and how they might be related amongst themselves. Regardless of the outcome, it seems incontrovertible that some spines are the homologues of the virgae, others homologues of the vimines – and that neither can be homologues of each other.

## DISCUSSION

It has been noted before that spines on the valve surface or margin of species in Fragilariaceae can occur on different parts of the valve (e.g. Morales et al. 2010: 99, table 2;

**Table 2 – Species recently described as *Fragilaria* (partly derived from table 1) documented for the occurrence and placement of marginal spines.**

Abbreviations and symbols: + = presence of spines; Vg = spines on virgae; Vm = spines on vimines; NA = not applicable; \* = Possibly not a ‘classical’ *Fragilaria*. <sup>1</sup> Although their figure 81 suggests a few very small spines on the vimines. <sup>2</sup> The original description in Drouat et al. (2007) lacks any details of the valve. <sup>3</sup> The spines on these specimens are scattered on the surface. <sup>4</sup> The spines on these specimens are few and very small. <sup>5</sup> These appear to be in pairs either side of the virgae.

	Spines	Vg	Vm	Reference
<b>Group 1</b>				
<i>Fragilaria spectra</i>	–	NA	NA	Almeida et al. 2016
<i>Fragilaria rinoi</i>	–	NA	NA	Delgado et al. 2016 <sup>1</sup>
<i>Fragilaria gracilis</i>	–	NA	NA	Tuji 2007
<i>Fragilaria asiatica</i>	–	NA	NA	Rioual et al. 2017
<i>Fragilaria candidagilae</i>	–	NA	NA	Delgado et al. 2015
<i>Fragilaria perdelicatissima</i>	–	NA	NA	Lange-Bertalot & Ulrich 2014
<i>Fragilaria aquaplus</i>	–	NA	NA	Lange-Bertalot & Ulrich 2014
<i>Fragilaria pectinalis</i>	–	NA	NA	Wetzel & Ector 2015
<i>Fragilaria boreomongolica</i>	–	NA	NA	Kulikovskiy et al. 2010
<i>Fragilaria misarelensis</i>	–	NA	NA	Novais et al. 2019
<b>Group 2</b>				
* <i>Fragilaria saxoplanctonica</i>	–	NA	NA	Lange-Bertalot & Ulrich 2014
* <i>Fragilaria crenophila</i> var. <i>sinensis</i>	–	NA	NA	Rioual et al. 2017
* <i>Fragilaria iraqiensis</i> (= <i>Williamsella iraqiensis</i> )	–	NA	NA	Al-Handal et al. 2016
* <i>Fragilaria crenophila</i> (= <i>Williamsella angusta</i> )	–	NA	NA	Graeff et al. 2013
<b>Group 3</b>				
<i>Fragilaria tenera</i>	+	–	+	Almeida et al. 2016 Lange-Bertalot & Ulrich 2014
<i>Fragilaria neotropica</i>	+	–	+	Almeida et al. 2016
<i>Fragilaria rhabdosoma</i>	+	–	+	Tuji 2004
<i>Fragilaria neointermedia</i>	+	–	+	Tuji & Williams 2014
<i>Fragilaria tenera</i> var. <i>lemanensis</i>	+	–	+	Lange-Bertalot & Ulrich 2014 <sup>2</sup>
<i>Fragilaria tenera</i> var. <i>nanana</i>	+	–	+	Lange-Bertalot & Ulrich 2014
<i>Fragilaria tenuissima</i>	+	–	+	Lange-Bertalot & Ulrich 2014
<i>Fragilaria vaucheriae</i>	+	–	+	Wetzel & Ector 2015 <sup>3</sup> Delgado et al. 2016 <sup>4</sup>
<i>Fragilaria capucina</i>	+	–	+	Tuji & Williams 2006
<i>Fragilaria capucina</i> var. <i>mesogongyla</i>	+	–	+	Rivera & Cruces 2008
<i>Fragilaria fusa</i>	+	–	+	Wengrat et al. 2016
<i>Fragilaria billingsii</i>	+	–	+	Wengrat et al. 2016
<i>Fragilaria uliginosa</i>	+	–	+	Kulikovskiy et al. 2010 Wetzel & Ector 2015
<i>Fragilaria nevadensis</i>	+	–	+	Linares-Cuesta & Sanchez-Castillo 2007
<i>Fragilaria longifusiformis</i>	+	–	+	Siver et al. 2006 Ludwig et al. 2015
<b>Group 4</b>				
<i>Fragilaria microvaucheriae</i>	+	+	+	Wetzel & Ector 2015 <sup>5</sup>
<i>Fragilaria asterionelloides</i>	+	+	+	Tuji & Williams 2017
<b>Group 5</b>				
* <i>Fragilaria pennsylvanica</i>	–	NA	NA	Morales 2007
* <i>Fragilaria flexura</i>	–	NA	NA	Hoff et al. 2011
* <i>Fragilaria sepes</i>	+	–	+	Tuji 2004
* <i>Fragilaria bronkei</i>	+	–	+	Witkowski et al. 2000
* <i>Fragilaria oldenburgioides</i>	+	+	–	Lange-Bertalot & Metzeltin 1996
* <i>Fragilaria spinarum</i>	+	+	–	Lange-Bertalot & Metzeltin 1996
* <i>Fragilaria viereckiana</i>	+	+	–	Moser 1999

Wegrat et al. 2016: 198, table 2; Li et al. 2018: 23, table 4; and most recently Grana et al. 2018: 65, table 2). These commentaries have, more or less, echoed the early view of Morales et al. that for members in the ‘staurosirid’ diatoms, the position of the spine, relative to the virgae or vimines, is, in some cases, unique to a particular genus – it can define it. As has been recently summarised by Grana et al.

“Morales *et al.* (2010a) also include the presence of flaps covering the areolae, *the position of spines generally interrupting the striae*, the serrate nature of spines in some species, and the point of insertion of the volae parallel to the valve axis in *Pseudostaurosira*. In contrast, *Staurosira* does not possess flaps, *the spines are on the vimines*, such spines are never serrate, and the volae are inserted perpendicularly with respect to the apical axis. Our observations expand the morphological diversity in *Pseudostaurosira* and *Staurosira*, revealing that as detailed examination of material collected in previously unexplored regions is done, additional features can be used to better define the current taxonomic boundaries” (Grana et al. 2018: 69, my italics).

My efforts here, such as they are, have not been to clarify or otherwise the monophyly of any particular group of diatoms. What I wanted to examine was the implications behind the position of the spines relative to the valve structure, a task enhanced by adopting Cox & Ross’s ‘virga–vimen’ terminology, and to offer some reasons why noting just the presence or absence of spines (or even the complexity of their variation) is insufficient for determining the relationships amongst these groups of ‘araphid’ species. My main point is: across all pennate diatoms virgae and vimines are homologues of each other. Within some ‘araphid’ diatoms the spines on the valve margin are either homologues of the virgae (modified virgae) or homologues of the vimines (modified vimines), but the spines are not homologues of each other. This is important. Three things emerge from this observation:

1. The term ‘spine’, on its own, is not useful for understanding taxon relationships. As Eileen Cox recently wrote, reflecting on her own past experience,

“Thirty years ago, I pointed out that there has been confusion between the use of characters for diatom identification and their use for systematics (Cox 1979). Whereas shared characters are fundamental to recognising relationships expressed by systematics (cladistics theory demands that these are shared derived characters), distinctive differences (that may or may not have systematic significance) are required for identification” (Cox 2009: 445)

If I could be presumptuous enough to modify some of Cox’s words, I would offer the following minor change: “Whereas shared *homologues* are fundamental to recognising relationships expressed by systematics [...]” (my italics). In most studies up to now, ‘spine’ has been used, quite legitimately, as a feature for identification and, occasionally, illegitimately in my view, used for determining, or suggesting relationships.

2. The term ‘spine’ is not even a character in the comparative biology sense but a descriptive catch-all for something that simply ‘sticks out from a surface’, occasionally with func-

tional implications (e.g. a linking spine), often with its appearance well documented.

3. Finally, systematic characters, those applicable to comparative biology, are modifications of other characters and so are, in one sense, like taxonomies, hierarchical, as noted above for rimoportulae as well as spines. As such, taxonomists are faced with discovering where in the taxonomic hierarchy each character fits, when those characters, and their modifications, are homologues. In the world of comparative biology this has been known for some time by the rather clumsy name heterobathmy literally meaning ‘different steps on a stair’, from the Greek *bathmos*, a step or stair (originally coined by the botanist Takhtajan 1959: 11, 13 as ‘heterobathmie’, for an English translation see Takhtajan 1991: 227 et seq.). When applied to taxonomy, it means finding the correct level (‘step’) in the taxonomic hierarchy (‘stair’) for each character (homologue). Alongside synapomorphy, heterobathmy is perhaps the next most important concept of comparative biology – maybe these two concepts are all we need. A consequence of this, homologues as hierarchical, as ‘steps on a stair’, is that plotting morphological characters on a molecular tree of relationships is a futile endeavour – treating characters and their modifications as if they are static (unit) features of a non-changing entity is a book-keeping exercise rather than a science.

#### ACKNOWLEDGEMENTS

Eduardo Morales and Maxim Kulikovskiy provided useful information and comment. I would also like to thank David Mann and two referees for numerous helpful comments on an earlier version of this manuscript.

#### REFERENCES

- Al-Handal A., Kociolek J.P., Abdullah D. (2016) *Williamsella iraqiensis* sp. nov., a new diatom (Bacillariophyta, Fragilariophyceae) from Sawa Lake, South Iraq. *Phytotaxa* 244: 289–297. <https://doi.org/10.11646/phytotaxa.244.3.5>
- Almeida P.D., Morales E.A., Wetzel C.E., Ector L., Bicudo, D.C. (2016) Two new diatoms in the genus *Fragilaria* Lyngbye (Fragilariophyceae) from tropical reservoirs in Brazil and comparison with type material of *F. tenera*. *Phytotaxa* 246: 163–183. <https://doi.org/10.11646/phytotaxa.246.3.1>
- Álvarez-Blanco I., Blanco S. (2013) *Nitzschia imae* sp. nov. (Bacillariophyta, Nitzschiaceae) from Iceland, with a redescription of *Hannaea arcus* var. *linearis*. *Anales del Jardín Botánico de Madrid* 70: 144–151. <https://doi.org/10.3989/ajbm.2358>
- Anonymous (1975) Proposals for a standardization of diatom terminology and diagnoses. *Nova Hedwigia*, Beiheft 53: 323–354.
- Bao W.-M., Reimer C.W. (1992) New taxa of the diatoms from Changbaishan Mountain, China. *Bulletin of Botanical Research* 12: 357–361.
- Bixby R.J., Edlund M.B., Stoermer E.F. (2005) – *Hannaea superioris* sp. nov., an endemic diatom from the Laurentian Great Lakes. *Diatom Research* 20: 227–240. <https://doi.org/10.1080/0269249X.2005.9705633>
- Cantonati M., Kelly M.G., Lange-Bertalot H. (2017) Freshwater benthic diatoms of Central Europe: over 800 common species used in ecological assessments. Schmittner-Oberreifenberg, Koeltz Botanical Books.

- Cox E.J., Ross R. (1981) The striae of pennate diatoms. In: Ross R. (ed.) Proceedings of the 6th Symposium on Recent and Fossil Diatoms: 267–278. Koenigstein, Koetz Science Publishers.
- Cox E.J. (1979) Symmetry and valve structure in naviculoid diatoms. *Nova Hedwigia*, Beiheft 64: 193–206.
- Cox E.J. (1979) What's in a name? – Diatom classification should reflect systematic relationships. *Acta Botanica Croatia* 68: 443–454. Available from <https://hrcak.srce.hr/41441> [accessed 4 Mar. 2019].
- Delgado C., Novais M.H., Blanco S., Almeida, S.F.P. (2015) Examination and comparison of *Fragilaria candidagilae* sp. nov. with type material of *Fragilaria recapitellata*, *F. capucina*, *F. perminuta*, *F. intermedia* and *F. neointermedia* (Fragilariales, Bacillariophyceae). *Phytotaxa* 231: 1–18. <https://doi.org/10.11646/phytotaxa.231.1.1>
- Delgado C., Novais M.H., Blanco S., Almeida, S.F.P. (2016) *Fragilaria rinoi* sp. nov. (Fragilariales, Bacillariophyceae) from periphytic river samples in Central Portugal. *European Journal of Taxonomy* 248: 1–16. <https://doi.org/10.5852/ejt.2016.248>
- Druart J.C., Lavigne, S., Robert, M. (2007) *Fragilaria tenera* var. *lemanensis*, une nouvelle variété pour le Léman (France-Suisse). *Cryptogamie Algologie* 28: 283–287.
- Ebach M.C., Williams D.M. (2010) Aphyly: a systematic designation for a taxonomic problem. *Evolutionary Biology* 37: 123–127. <https://doi.org/10.1007/s11692-010-9084-5>
- Foged N. (1981) Diatoms in Alaska. *Bibliotheca Phycologica* 53.
- Gandhi H.P. (1966) The fresh-water diatom flora of the Jog-Falls, Mysore State. *Nova Hedwigia* 11: 89–197.
- Genkal S.I., Kharitonov V.G. (2008) On the morphology and taxonomy of *Hannaea arcus* (Bacillariophyta). *Novosti sistematiki nizshikh rastenii [Novitates Systematicae Plantarum non Vascularium]* 42: 14–23.
- Gersonde R., Harwood D.M. (1990) Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 1: Vegetative cells. In: Barker P.F. et al. (eds) Proceedings of the Ocean Drilling Program, Scientific Results, 113, Ocean Drilling Program, College Station, Texas: 365–402. Available from <http://hdl.handle.net/10013/epic.11541> [accessed 4 Mar. 2019].
- Graeff C.L., Kociolek J.P., Rushforth S.R. (2013) New and interesting diatoms (Bacillariophyta) from Blue Lake Warm Springs, Tooele County, Utah. *Phytotaxa* 153: 1–38. <https://doi.org/10.11646/phytotaxa.153.1.1>
- Grove E., Sturt G. (1887) On a fossil diatomaceous deposit from Oamaru, Otago, New Zealand. Part III. *Journal of the Quekett Microscopical Club*, 2nd Ser., 3: 63–78. Available from <https://www.biodiversitylibrary.org/page/2032105> [accessed 4 Mar. 2019].
- Hasle G.R. (1973) The “mucilage pore” of pennate diatoms. *Nova Hedwigia*, Beiheft 45: 167–186.
- Hasle G.R., Syvertsen E.E. (1996) Marine Diatoms. In: Tomas C.R. (ed.) *Identifying Marine Phytoplankton*: 5–385. USA, Academic Press, Inc. <https://doi.org/10.1016/B978-012693018-4/50004-5>
- Jurilj A. (1965) Neobični i neistraženi uređaji za vezanje u kolonije kod nekih alga [Les appareils curieux et peu connus servant à lier les algues en colonies (Diatomées)]. *Acta Botanica Croatia* 24: 73–78.
- Kaczmarek I., Beaton M., Benoit A.C., Medlin L.K. (2005) Molecular phylogeny of selected members of the order Thalassiosirales (Bacillariophyta) and the evolution of the fuloportula. *Journal of Phycology* 42: 121–138. <https://doi.org/10.1111/j.1529-8817.2006.00161.x>
- Kühn S.F., Klein G., Halliger H., Hargraves P., Medlin L.K. (2006) A new diatom, *Mediopyxis helysia* gen. nov. and sp. nov. (Mediophyceae) from the North Sea and the Gulf of Maine as determined from morphological and phylogenetic characteristics. *Nova Hedwigia* 130: 307–324.
- Kulikovskiy M.S., Lange-Bertalot H., Witkowski A., Dorofeyuk N.I., Genkal S.I. (2010) Diatom assemblages from Sphagnum bogs of the world. I. Nur bog in northern Mongolia. *Bibliotheca Diatomologica* 55: 1–326.
- Lange-Bertalot H., Ulrich S. (2014) Contributions to the taxonomy of needle-shaped *Fragilaria* and *Ulnaria* species. *Lauterbornia* 78: 1–73.
- Lange-Bertalot H., Metzeltin D. (1996) Indicators of oligotrophy. 800 taxa representative of three ecologically distinct lake types, carbonate buffered-oligodystrophic-weakly buffered soft water with 2428 figures on 125 plates. *Oligotrophie-Indikatoren. 800 Taxa repräsentativ für drei diverse Seen-Typen: Kalkreich - Oligodystroph - Schwach gepuffertes Weichwasser mit 2428 Figuren auf 125 Tafeln. Iconographia Diatomologica* 2.
- Li C.L., Witkowski A., Ashworth M.P., Dąbek P., Sato S., Zgłobicka I., Witak M., Khim J.S., Kwon C.-J. (2018) The morphology and molecular phylogenetics of some marine diatom taxa within the Fragilariaceae, including twenty undescribed species and their relationship to *Nanofrustulum*, *Opephora* and *Pseudostaurosira*. *Phytotaxa* 355: 1–104. <https://doi.org/10.11646/phytotaxa.355.1.1>
- Linares-Cuesta J.E., Sánchez-Castillo P.M. (2007) *Fragilaria nevadensis* sp. nov., a new diatom taxon from a high mountain lake in the Sierra Nevada (Granada, Spain). *Diatom Research* 22: 127–134. <https://doi.org/10.1080/0269249X.2007.9705700>
- Mann D.G., Kelly M., Jüttner I. (2018) *Fragilaria Lyngbye*, H.C.; 1819; 182. In: Jüttner I., Bennion H., Carter C., Cox E.J., Ector L., Flower R., Jones V., Kelly M.G., Mann D.G., Sayer C., Turner J.A., Williams D.M. (eds) (2018) *Freshwater Diatom Flora of Britain and Ireland. Amgueddfa Cymru – National Museum Wales*. Available from <https://naturalhistory.museum-wales.ac.uk/diatoms/browsespecies.php?-recid=3714> [accessed 15 Aug. 2018].
- Morales E.A. (2007) *Fragilaria pennsylvanica*, a new diatom (Bacillariophyceae) species from North America, with comments on the taxonomy of the genus *Synedra* Ehrenberg. *Proceedings of the Academy of Natural Sciences of Philadelphia* 156: 155–166. [https://doi.org/10.1635/0097-3157\(2003\)153\[0155:FPAN DB\]2.0.CO;2](https://doi.org/10.1635/0097-3157(2003)153[0155:FPAN DB]2.0.CO;2)
- Morales E.A., Edlund M.B., Spaulding S.A. (2010) Description and ultrastructure of araphid diatom species (Bacillariophyceae) morphologically similar to *Pseudostaurosira elliptica* (Schumann) Edlund et al. *Phycological Research* 58: 97–107. <https://doi.org/10.1111/j.1440-1835.2010.00567.x>
- Morales E.A., Wetzel C.E., Van de Vijver B., Ector L. (2015) Morphological studies on type material of widely cited araphid diatoms (Bacillariophyta). *Phycologia* 54: 455–470. <https://doi.org/10.2216/15-21.1>
- Moser G. (1999) Die Diatomeenflora von Neukaledonien. *Bibliotheca Diatomologica* 43: 1–205.
- Novais M.H., Almeida S.F.P., Blanco S., Delgado C. (2019) Morphology and ecology of *Fragilaria misarelensis* sp. nov. (Bacillariophyta), a new diatom species from southwest of Europe. *Phycologia*. <https://doi.org/10.1080/00318884.2018.1524245>
- Owen R. (1847) Report on the archetype and homologues of the vertebrate skeleton. In: *Report of the British Association of the Advancement of Science for 1846*: 169–340. London, John Murray. Available from <https://www.biodiversitylibrary.org/page/12921332> [accessed 4 Mar. 2019].

- Rioul P., Flower R.J., Chu G., Lu Y., Zhang Z., Zhu B., Yang X. (2017) Observations on a fragilarioid diatom found in inter-dune lakes of the Badain Jaran Desert (Inner Mongolia, China), with a discussion on the newly erected genus *Williamsella* Graeff, Kociolek & Rushforth. *Phytotaxa* 329: 28–50. <https://doi.org/10.11646/phytotaxa.329.1.2>
- Rivera P., Cruces F. (2008) *Fragilaria capucina* Desm. var. *mesogongyla* Frenguelli, una diatomea presente en la zona norte de la Cordillera de los Andes (Chile), con comentarios sobre la variabilidad del número de procesos labiados en algunos géneros arafidales. *Gayana Botanica* 65: 131–138. <https://doi.org/10.4067/S0717-66432008000200002>
- Ross R., Cox E.J., Karayeva N.I., Mann D.G., Paddock T.B.B., Simonsen R., Sims P.A. (1979) An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia, Beiheft* 64: 513–533.
- Ross R. (1995) A revision of *Rutilaria* Greville (Bacillariophyta). *Bulletin of the Natural History Museum, Botany Series* 25: 1–93. Available from <https://www.biodiversitylibrary.org/page/41132287> [accessed 4 Mar. 2019].
- Rupke N. (1994) Richard Owen: Victorian Naturalist. New Haven, Yale University Press.
- Rupke N. (2009) Richard Owen: Biology without Darwin. Chicago, University of Chicago Press. [Revised edition of Rupke 1994].
- Sato S., Mann D.G., Matsumoto S., Medlin L.K. (2008) *Pseudostriatella* (Bacillariophyta): a description of a new araphid diatom genus based on observations of frustule and auxospore structure and 18S rDNA phylogeny. *Phycologia* 47: 371–391. <https://doi.org/10.2216/PH08-02.1>
- Siver P.A., Morales E.A., Van de Vijver B., Smits M., Hamilton P.B., Lange-Bertalot H., Hains J.J. (2006) Observations on *Fragilaria longifusiformis* comb. nov. et nom. nov. (Bacillariophyceae), a widespread planktic diatom documented from North America and Europe. *Phycological Research* 54: 183–192. <https://doi.org/10.1111/j.1440-1835.2006.00425.x>
- Spaulding S., Edlund M. (2008) *Fragilaria*. In: *Diatoms of North America*. Available from <https://diatoms.org/genera/fragilaria> [accessed 15 Aug. 2018].
- Takhtajan A. (1959) *Die Evolution der Angiospermen*. Jena, VEB Gustav Fischer.
- Takhtajan A. (1991) *Evolutionary Trends in Flowering Plants*. New York, Columbia University Press.
- Talgatti D., Wetzel C.E., Morales E.A., Ector L., Torgan L.C. (2014) Transfer of *Fragilaria atomus* Hust. to the genus *Stauroforma* (Bacillariophyta) based on observation of type and newly collected material. *Phytotaxa* 158: 43–56. <https://doi.org/10.11646/phytotaxa.158.1.3>
- Tuji A. (2004) Type examination of the ribbon-forming *Fragilaria capucina* complex described by Christian Gottfried Ehrenberg. In: Poulin, M. (ed.) *Proceedings of the Seventeenth International Diatom Symposium*. Ottawa, Canada, 25th–31st August 2002: 411–422. Bristol, Biopress Limited.
- Tuji A. (2007) Type examination of *Fragilaria gracilis* Østrup (Bacillariophyceae). *Bulletin of the National Museum of Nature and Science, Series B, Botany* 33: 9–12.
- Tuji A., Williams D.M. (2006) Typification of *Conferva pectinalis* O.F. Müll. (Bacillariophyceae) and the identity of the type of an alleged synonym, *Fragilaria capucina* Desm. *Taxon* 55: 193–199. <https://doi.org/10.2307/25065542>
- Tuji A., Williams D.M. (2013) Examination of types in the *Fragilaria vaucheriae*–*intermedia* species complex. *Bulletin of the National Museum of Nature and Science, Series B, Botany* 39: 1–9.
- Tuji A., Williams D.M. (2017) *Fragilaria asterionelloides*, a new planktonic species of *Fragilaria* from Japanese reservoirs that forms star-shaped colonies. *Bulletin of the National Museum of Natural Science, series B* 43: 45–50.
- Vishnyakov V.S., Kulikovskiy M.S., Genkal S.I., Kuznetsova I.V. (2015) Comparative morphological characteristic of diatoms of genus *Hannaea* Patrick of the two largest lakes of the Baikal Rift Zone with a description of the new species. *Inland Water Biology* 8(3): 222–231. <https://doi.org/10.1134/S1995082915030165>
- Wengrat S., Morales E.A., Wetzel C.E., Almeida P.D., Ector L., Bicudo D.C. (2016) Taxonomy and ecology of *Fragilaria billingsii* sp. nov. and analysis of type material of *Synedra rumpens* var. *fusa* (Fragilariaceae, Bacillariophyta) from Brazil. *Phytotaxa* 270: 191–202. <https://doi.org/10.11646/phytotaxa.270.3.3>
- Wetzel C.E., Ector L. (2015) Taxonomy and ecology of *Fragilaria microvaucheriae* sp. nov. and comparison with the type materials of *F. uliginosa* and *F. vaucheriae*. *Cryptogamie Algologie* 36: 271–289. <https://doi.org/10.7872/crya/v36.iss3.2015.271>
- Williams D.M. (2006) Some notes on the classification of *Fragilaria*, *Synedra* and their sub-groups. *Nova Hedwigia, Beiheft* 130: 17–34.
- Williams D.M. (2011) *Synedra*, *Ulnaria*: definitions and descriptions – a partial resolution. *Diatom Research* 26: 149–153. <https://doi.org/10.1080/0269249X.2011.587646>
- Williams D.M., Ebach M.C. (2012) Confusing homologs as homologies: a reply to “On homology”. *Cladistics* 28: 223–224. <https://doi.org/10.1111/j.1096-0031.2011.00387.x>
- Williams D.M., Ebach M.C. (2018) Aphyly: identifying the flotsam and jetsam of systematics. *Cladistics* 34: 459–466. <https://doi.org/10.1111/cla.12207>
- Williams D.M., Kociolek J.P. (2011) An overview of diatom classification with some prospects for the future. In: Seckbach J., Kociolek J.P. (eds.) *The Diatom World*: 47–91. Dordrecht, Springer. [https://doi.org/10.1007/978-94-007-1327-7\\_3](https://doi.org/10.1007/978-94-007-1327-7_3)
- Williams D.M., Round F.E. (1986) [1987] Revision of the genus *Synedra* Ehrenb. *Diatom Research* 1: 313–339. <https://doi.org/10.1080/0269249X.1986.9704976>
- Williams D.M., Round F.E. (1987) Revision of the genus *Fragilaria*. *Diatom Research* 2: 267–288. <https://doi.org/10.1080/0269249X.1987.9705004>
- Witkowski A., Lange-Bertalot H., Metzeltin D. (2000) *Diatom Flora of Marine Coasts I. Iconographia Diatomologica* 7.
- Witkowski J., Sims P.A., Harwood D. (2011) *Rutilariaceae* redefined: a review of fossil bipolar diatom genera with centrally positioned linking structures, with implications for the origin of pennate diatoms. *European Journal of Phycology* 46: 378–398. <https://doi.org/10.1080/09670262.2011.629685>
- Witkowski J., Sims P.A., Williams D.M. (2017) Typification of Eocene–Oligocene diatom taxa proposed by Grove & Sturt (1886–1887) from the Oamaru Diatomite. *Diatom Research* 32: 363–408. <https://doi.org/10.1080/0269249X.2017.1395366>

Managing Editor: David G. Mann

Submission date: 17 Aug. 2018

Acceptance date: 28 Dec. 2018