

# Rampant homoplasy and adaptive radiation in pennate diatoms

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**Background and aims** – We examine the possibility of the independent evolution of the same features multiple times across the pennate diatom tree of life.

**Methods and key results** – Features we have studied include symmetry, raphe number and amphoroid symmetry. Phylogenetic analysis, with both morphological and molecular data suggest in each of these cases that the features evolved from 5 to 6 times independently. We also look at the possibility of certain features having evolved once and diagnosing large genera of diatoms, suggestive of an adaptive radiation in genera such as *Mastogloia*, *Diploneis* and *Stauroneis*.

**Conclusion** – Formal phylogenetic analyses and recognition of monophyletic groups allow for the recognition of homoplasious or homologous features.

**Key words** – Diatoms, homoplasy, phylogeny, characters, monophyly, molecular data, morphological data, species flocks.

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## INTRODUCTION

For some time now we have advocated basing diatom taxa, and by extension, the discovery of a natural system of classification, on monophyly alone (Kociolek & Williams 2015, Williams & Kociolek 2010). It is heartening to see that now some who raised issues in opposition to this criterion (Mann 1997, Medlin 2010, 2016, Medlin & Kaczmarek 2004) have adopted this approach (Medlin 2018, Vanormelingen et al. 2007, 2008). In both morphological and (especially) molecular studies there has been a tremendous amount of work

characterizing monophyletic groups and placing them within a natural classification (Lundholm et al. 2002a, 2002b).

For some results, under some circumstances, there are inconsistencies between the evidence from morphology and the evidence from molecules. The reasons for inconsistencies, or incongruence, are many but in this paper, we will discuss a few examples relating to the discrimination of homology from homoplasy, discriminating signal from noise. We have focused on this aspect of inconsistency because it is best rectified by reconsideration of the morphological characters involved.

## HOMOPLASIES AND HOMOLOGUES

Diagnosing monophyletic groups with morphological features that are synapomorphic for a lineage is an important part, if not the most important part, of systematic studies. This involves recognizing characters that might be understood as homologues in different taxa. Whereas there have been methods (or tests) for determining whether features are homologous (Patterson 1982), formal phylogenetic analyses and the determination of most parsimonious hypotheses will identify which character states are homologous and which are not; those that are not are usually called homoplasies. For example, the valve process first called a strutted process but now better known by its Latin name, *fultoportula*, was defined as: “[...] a tube through the valve surrounded by 2–5 chambers or pores [...] through the valve wall separated internally by arched supports, often with threads extruded from the exterior part” (Anonymous 1975: 328, Ross et al. 1979: 522). Thalassiosiraceae Lebour was given as an example, where it was later noted of that family that the “[...] *fultoportulae* [...] are confined to the centric order Thalassiosirales” (Round et al. 1990: 35) and, later, “all having strutted process [*fultoportula*] as the main morphological, taxonomic character” (Hasle & Syvertsen 1996: 29 – they go on to define the *fultoportula* more precisely than in the two terminology papers). The processes were first formally recognised by Hasle (1972), who used the term ‘strutted tubuli’, and Ross & Sims (1972: 160), who used the term *fultoportula* – that is, the structure, and its limited distribution in diatoms, was recognized by morphologists once the structure was examined using the scanning electron microscope (“Under the light microscope it is often impossible to distinguish between spines, rimoportules and *fultoportules*”, Ross & Sims 1972: 160). Hasle used the feature to diagnose the Thalassiosiraceae (1973) and Hasle & Syvertsen refer to the “main morphological, taxonomic character” of the family (Hasle & Syvertsen 1996: 29), which, adopting a more modern terminology, means *fultoportulae* are recognized as homologous and as a synapomorphy for Thalassiosiraceae (-ales). Further, recent summaries of molecular data and their results, support the view that *fultoportulae* evolved only once, that they are synapomorphic for Thalassiosiraceae (-ales) (Sims et al. 2006, Theriot et al. 2015). *Fultoportulae* are homologous for all taxa that possess it; it diagnoses a monophyletic group and we recognize this group in our classification system.

Similarly, it appears that the raphe system evolved once and it is homologous for all taxa that have it (or used to have it, because some taxa do not have a raphe caused by secondary loss). The presence of a raphe system diagnoses a monophyletic group that we recognize in our classification system as raphid diatoms (Bacillariophyceae Haeckel). As noted above for *fultoportulae*, these homologous features have been recognized for some time (Mereschkowsky’s 1901 “Mobiles” and H.L. Smith’s 1872 Raphidae, Hasle’s 1972 description of the strutted process).

Identification of homoplasies, the noise, is also a natural outcome of any formal phylogenetic study, from both morphological and molecular data sets. In recent molecular studies, one surprising outcome was, contrary to over a century of various classification systems erected for many, and some-

times contradictory, reasons (Schütt 1898, Karsten 1928, Patrick & Reimer 1975, Krammer & Lange-Bertalot 1986), that the canal raphe system, used to suggest close relationships between Bacillariales Hende, Rhopalodiales D.G.Mann and Surirellales D.G.Mann, evolved twice: once in Bacillariales, positioned in the more basal part of the raphid diatom tree of life, and a second time in a clade uniting Rhopalodiales and Surirellales (first shown in Medlin & Kaczmarska 2004). Whereas the feature canal raphe can separately diagnose Bacillariales and Rhopalodiales + Surirellales, a single group (taxon) uniting all three is not recognized using molecular data (Medlin & Kaczmarska 2004, Ruck & Theriot 2011). Similarly, Witkowski et al. (2015) elegantly demonstrated that the systematic position of the enigmatic genus *Simonsenia* Lange-Bert., and the homoplastic nature of some of its features. When the genus was first proposed (Lange-Bertalot 1979), prior to the arrival of large-scale (in terms of taxa and/or genes) molecular studies, *Simonsenia* was thought to be an intermediate between groups that possess canals and keels on only the side of the valve (Bacillariales) and the Surirellales, which have canals, keels and fenestrae and portulae around the periphery. *Simonsenia* has keels, fenestrae and portulae on one side of the valve. Witkowski et al. (2015) showed that keels, fenestrae and portulae are homoplastic between the Bacillariales and Surirellales. As Witkowski et al. (2015: 1) noted “Lack of homology between the surirelloid and simonsenioid keels is reflected in subtle differences in the morphology and ontogeny of the portulae and fenestrae”, thus, there is no single group (taxon) of that has all of these features.

Recognition of homology and homoplasy is a natural outcome of any formal phylogenetic study. Our attention in this paper focuses on situations where features that have been used to support classification schemes have not only turned out to be homoplasious, but also the degree of homoplasy is substantial, which we term here, “rampant” homoplasy, because the apparent same features is identified in several lineages. We suggest these features have been used to classify diatoms for a number of reasons: their ease of recognition (features that are “Convenient”); those thought to be fundamental because of their function and importance (“Conservative” features); and those features that are, because of their structural organization, so complex that it could have evolved once (“Complex” features).

Identifying rampant homoplasy in morphology for pennate diatoms is based on the recent accumulation of molecular studies that facilitate the interpretation (or re-interpretation) of character state evolution. It is quite possible that similar outcomes will be elsewhere in other groups of diatoms as well. For each example, we cite one or more analysis that supports the notion of rampant homoplasy within pennate diatoms. Our examples are mostly drawn from the raphid pennate diatoms.

## FEATURES OF CONVENIENCE

Various aspects of diatom valve symmetry have been recognized for a long time, with O. Müller (1895) documenting the first understanding of the various aspects of both valve and frustule symmetry. Symmetry has been applied many times in the development of classification schemes, both in

**Table 1 – Freshwater ‘araphid’ diatoms and features related to symmetry.**  
Data after Cox (2009).

Taxa	Valve symmetry			
	isopolar	heteropolar	bilaterally symmetrical	dorsiventral
<i>Asterionella</i>	+	+	+	–
<i>Diatoma</i>	+	–	+	–
<i>Fragilaria</i>	+	–	+	–
<i>Hannaea</i>	+	–	–	+
<i>Martyana</i>	–	+	+	–
<i>Meridion</i>	–	+	+	–
<i>Synedra</i>	+	–	+	–
<i>Tabellaria</i>	+	–	+	–
<i>Tetracyclus</i>	+	–	+	–

pre-Darwinian (Agardh 1824, 1830–1832) and post-Darwinian classifications (Williams 2007). Symmetry has been used at various levels of the taxonomic hierarchy within raphid diatoms, at the levels of order (Cymbellales D.G.Mann in Round et al. 1990), families (Rhoicospheniaceae Chen & Zhu, Gomphonemataceae Kütz. in Round et al. 1990) and groups of genera (*Gyrosigma* Hassall and *Pleurosigma* W.Sm. within the Naviculaceae, in Patrick & Reimer 1966). Mann (1986) argued for the use of symmetry to distinguish between members of the Diatomaceae, calling such symmetry features “complex”. That symmetry may not be a useful character for natural classifications (as opposed to artificial classifications – identification schemes) was commented on several times by Cox (Cox 1979, 2009). In the 2009 paper Cox wrote:

“H.L. Smith’s explicitly artificial classification (SMITH 1872) modified by SCHÜTT (1896), formed the basis of the modern diatom classifications (HUSTEDT 1930, 1927–1966; PATRICK and REIMER 1966; HENDEY 1937, 1964; SIMONSEN 1979; ROUND et al. 1990), and although MEDLIN and KACZMARSKA (2004) and MANN in ADL et al. (2005) presented new classifications, their groups are still described largely in terms of their shape and symmetry.”

She provided an example:

“Thus, the possession of lunate valves allows *Hannaea* to be discriminated from other non-raphid, fragilarioid diatoms, but lunate valves are also found in a diverse range of raphid diatoms, e.g. *Amphora*, *Climaconeis*, *Cymbella*, *Encyonema*, *Epithemia*, *Rhopalodia*, *Seminavis*. Valve outline may aid the identification of a number of genera, but is not a systematically reliable, defining character” (Cox 2009: 444–445).

We return to *Hannaea* below.

Valve asymmetry has been used to identify what appear to be monophyletic groups amongst the freshwater biraphid diatoms, including those asymmetrical to the apical

axis (“cymbelloid” diatoms) and those asymmetrical to the transapical axis and cuneate in girdle view (“gomphonemoid diatoms”). Diatoms assigned to these “cymbelloid” lineages together form a monophyletic group, by virtue of the arrangement of their chloroplasts, pyrenoids and nucleus (Mereschkowsky 1902, Cox 1996) but also include diatoms who do not have asymmetry in the outline of their valves (Nakov et al. 2014, Kulikovskiy et al. 2014).

The “gomphonemoid diatoms” have been recorded from both marine and freshwater environments. Phylogenetic studies on gomphonemoid diatoms have shown that a group of freshwater diatoms with septa and pseudosepta are monophyletic (Bruder & Medlin 2008), which include *Gomphonema* Ehrenb., *Gomphoneis* Cleve, *Gomphocymbella* O.Müll. (a gomphonemoid diatom that has secondarily become cymbelloid and is not closely related to *Cymbella* C.Agardh and its allies, see Kociolek & Stoermer 1990), and *Gomphosinica* Kociolek et al. (Kociolek & Stoermer 1990, 1993, Kociolek et al. 2015). There are other freshwater diatoms, such as *Didymosphenia geminata* (Lyngb.) Mart.Schmidt, which were once included in *Gomphonema* (by C.A. Agardh) that have been shown, using a formal analysis of both morphological and molecular data, to belong with the “cymbelloid” diatoms (Kociolek & Stoermer 1990, Nakov et al. 2014a). A second “cymbelloid” genus with gomphonemoid symmetry is *Gomphocymbellopsis* Krammer, but it, too, is part of the cymbelloid diatom lineage (Krammer 2003). It is a second example of a genus that has become secondarily “gomphonemoid” – it is not closely related to *Didymosphenia* Mart. Schmidt and represents a second case of homoplasy relating to gomphonemoid symmetry within the cymbelloid diatoms. A third group of freshwater diatoms that has “gomphonemoid” symmetry is the family Rhoicospheniaceae, which includes *Rhoicosphenia* Grunow and *Gomphosphenia* Lange-Bert.

In addition to these two examples of homoplasy in the feature of “gomphonemoidness” in the cymbelloid diatoms, Majewska et al. (2015) examined another aspect of “gom-

phonemoid” diatom evolution that includes marine taxa, such as the free-living genera *Gomphoseptatum* Medlin and *Gomphonemopsis* Medlin, as well as epizooic taxa, such as *Chelnicola* Majewska et al., *Poulinea* Majewska et al., *Cuneolus* Giffen and *Tripterion* R.W.Holmes et al., along with other and freshwater groups. Results of their character analysis yielded at least three distinct instances of gomphonemoid symmetry evolution (fig. 1). Medlin (1985) described the situation of convergence in the features of “gomphonemoid” symmetry between *Rhoiconeis* Grunow and other gomphonemoid diatoms. Thus, it appears that within raphid diatoms, asymmetry about the transapical axis, and a cuneate shape in girdle view, has evolved on at least six different occasions. In Medlin (1991) possible reasons for parallel evolution among genera with these shapes were given, such as becoming colonial as an adaptation to an attached habitat, and conforming to fluid dynamics to minimise drag. Nakov et al. (2014) modelled the transition between solitary and colonial forms and found that gains in coloniality were generally faster than losses across the diatom phylogenetic tree.

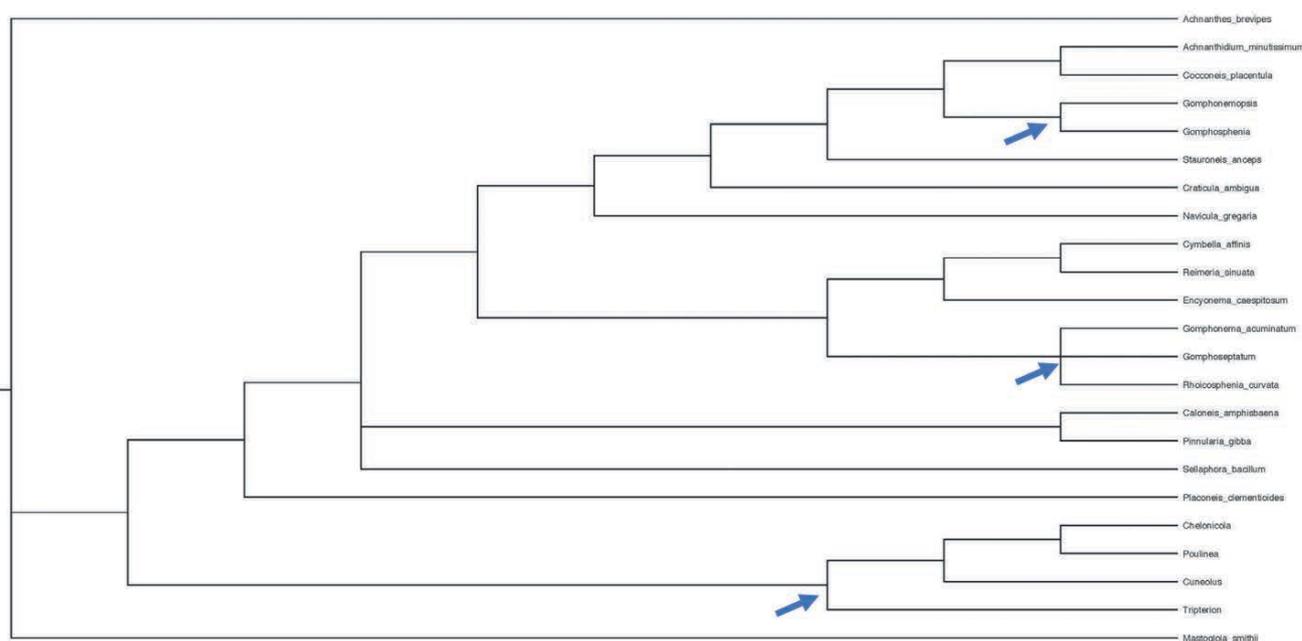
We noted above the ‘araphid’ genus *Hannaea* R.M.Patrick, which is a genus hard to define if its lunate symmetry is ignored. Cox tabulated some features that relate several freshwater ‘araphid’ genera to *Hannaea*: *Asterionella* Hassall, *Diatoma* Bory, *Fragilaria* Lyngb., *Martyana* Round, *Meridion* C.Agardh, *Synedra* Ehrenb., *Tabellaria* Ehrenb. and *Tetracyclus* Ralfs (Cox 2009: table 1, the first four characters are aspects of ‘valve symmetry’ features re-drawn here as our table 1).

Although a relatively simple dataset, and perhaps almost meaningless in its simplicity, analysis of the four symmetry characters yields ambiguous solutions, yielding multiple most

parsimonious trees that collapse into a bush with the application of any consensus method. Regardless of this analysis and its result, species in the genera *Hannaea* and *Meridion* have, now and on occasions in the past (Williams 1985), included types with alternative symmetries, suggesting that other characters determine species’ inclusion and testifying to the un-informativeness of considerations of symmetry regardless of levels of homoplasy (Williams, 1985).

### CONSERVATIVE FEATURES: RAPHE NUMBER

Among the raphid diatoms, the raphe system itself, in many variations, has been considered a very conservative feature. Using molecular data, evolution of a canal raphe system is homoplasious relative to Bacillariales and Rhopalodiales + Surirellales (Medlin & Kaczmarksa 2004, Ruck & Theriot 2011). At finer levels of taxonomic hierarchy, the position or the presence or absence of a raphe system has been used to diagnose major groups (Karsten 1928, Hustedt 1930, Round et al. 1990). The Eunotiales Silva, for instance, as a monophyletic group is diagnosed as not only having a rimoportula (which appears to be a shared but primitive feature found also in those pennate diatoms lacking a raphe system), but by having its raphe system not on the valve face but shifted primarily onto the valve mantle (Round et al. 1990). Within groups, such as genera, details of the raphe have been used to recognize them or, species or species groups. Higher level groupings within the Eunotiales, for example, are based on the position of the raphe system (Burliga et al. 2013), and groups of species, such as in the genus *Neidium* Pfutzer (Reimer in Patrick & Reimer 1966) and within *Achnanthis* Kütz. are organized, in part, by raphe features (Jüttner et al. 2011, Peres et al. 2012, Karthick et al. 2017).



**Figure 1** – Cladogram showing phylogenetic relationships between different groups of gomphonemoid diatoms. ‘Gomphonemoid” symmetry evolved at those points in the tree indicated by arrows. Figure after Majewska et al. (2015), reproduced with permission of the publisher (Magnolia Press). This figure is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder (<https://www.mapress.com/j/>).

Taxa have been grouped by the number of raphe systems present, with frustules either having one (monoraphid) or two (biraphid) raphe systems. The classical order Achnanthes Silva, raphe diatoms with a raphe on one valve only, has been recognized in floras and other treatments as a single group (Karsten 1928, Hustedt 1930, Patrick & Reimer 1966, Round et al. 1990, Krammer & Lange-Bertalot 1986, Kociolek et al. 2015a), even though the idea that some may not be closely related dates back to Cleve (1895). Cleve suggested that many of the physically smaller monoraphid diatoms might be quite different from one another, based on chloroplast and organelle features. Others made similar observations: Geitler (1981), for example, offered data on patterns of reduction division and sexual reproduction that suggested monoraphid diatoms were diverse in these attributes. Studies recognizing vestigial raphe branches on the rapheless valves of certain species (Andrews 1981) aligned with a separate study on valve ontogeny, which demonstrated monoraphid diatoms are, early in their valve ontogenies, actually biraphid, and only later is one of the two raphes filled in (Boyle et al. 1984, Mayama & Kobayasi 1989). Kociolek & Williams (1987) used these data to suggest that the biraphid condition is primitive and the monoraphid condition derived within the raphid diatoms, which has been substantiated by molecular data (see below).

A substantial challenge to the concept of Achnanthes being non-monophyletic, however, came with the molecular work of Medlin & Kazmarska (2004, summarized in Sims et al. 2006), and since gained further support in subsequent studies (Thomas et al. 2016). These studies proposed that the genus *Achnanthes* Bory (used here in the strict sense: those relatively large diatoms with complex areolae found in marine and brackish waters, and sometimes in areophilous freshwater habitats; see Kociolek et al. 2015b), are part of the Bacillariales lineage and *not* closely related to other monoraphid diatoms. Earlier, Cox (2009) associated *Achnanthes* with *Mastogloia* Thwaites on the basis of their shared complex areolae but reported that this has not found further support with either molecular (see above) or morphological data (Stephens & Gibson 1980, Yohn & Gibson 1981, 1982).

After this initial insight into the systematic position of the genus *Achnanthes* (s. str.), other observations on the phylogenetic position of monoraphid diatoms also concluded that the condition evolved independently on several occasions. Thomas et al. (2016), for example, focused on the phylogenetic position of *Rhoicosphenia* relative to other monoraphid diatoms and the gomphonemoid diatoms. Their results showed that complete raphe loss on valves happened at least twice in the Cymbellales alone. Kulikovskiy et al. (2019) have shown the independent loss of the raphe system on five separate occasions: twice in a lineage of naviculoid diatoms containing *Stauroneis* Ehrenb. and its relatives (in *Schizostauron* Grunow and in *Madinithidium* Desrosiers et al. + *Karayevia* Round & Bukht.), once in the Bacillariales (*Achnanthes*), once in the Cymbellales (*Achnanthidium* + *Pauliella* Round & Basson + *Lemnicola* Round & Basson + *Cocconeis placentula* Ehrenb.) and once in *Cocconeis stauroneiformis* H.Okuno which, in the tree by Kulikovskiy et al., is the sister taxon to the Surirellales + Rhopalodiales.

Thus, the monoraphid condition may have evolved independently at least five or six times.

Other cases of raphe loss in raphid diatoms, aside from forming the monoraphid conditions, can be found in genera and species where the raphe system has been entirely lost. For example, Cox (2006) documented this loss in *Diadsmis gallica* W.Sm (= *Humidophila gallica* (W.Sm.) Lowe et al.; Lowe et al. 2017), part of the family Diadesmidae D.G.Mann (in Round et al. 1990), where during chain formation the species can have valves or frustules that do not produce a raphe system (Cox 2006). The diatom can, apparently, produce a raphe system or rapheless valves interchangeably with subsequent cell divisions.

The genus *Diprora* Main (2003), an endemic monotypic genus first described from caves in Hawaii, produces no raphe system at all during any stage of its life cycle. Yet, molecular data placed it as most closely related to *Fallacia* Stickle & D.G.Mann (in Round et al. 1990) (Kociolek et al. 2013: fig. 2).

Finally, in the Eunotiales, there are at least four genera (*Burliganiella* C.E.Wetzel & Kociolek, *Bicudoa* C.E.Wetzel et al., *Sinoperonia* Kociolek et al. and *Actinella* F.W.Lewis) that in total or in part have species that produce no raphe system (Wetzel & Kociolek 2018, Wetzel et al. 2012, Liu et al. 2018, Kociolek & Rhode 1998, respectively). *Sinoperonia* is unusual: its lone species, *Sinoperonia polyraphiamorpha* Kociolek et al., endemic to SE Asia, produces frustules with either 2, 1 or 0 raphe systems (Liu et al. 2018). In summary, loss of the entire raphe system may have occurred at least six times, although verification awaits formal analysis of the available data.

## COMPLEX FRUSTULAR FEATURES

The vast majority of raphid diatom frustules are constructed in such a way as to resemble a petri dish, with a larger epivalve sitting atop a smaller hypovalve, with girdle bands helping to keep the two valves apart and maintain the frustule integrity (Kartsten 1928, Hustedt 1930, Patrick & Reimer 1966, Krammer & Lange-Bertalot 1986, Round et al. 1990). In intact frustules in valve view, it takes optical dissection to observe both valves. One group of raphid diatoms, however, has a complex organization to their valves, where the mantle height of the dorsal margin is higher than the mantle of the ventral margin, and the girdle bands are organized in such a way that the valve faces of both valves occur in the same (or nearly the same) plane. This arrangement of the valves has been thought to be so complex that it could have only evolved once. Species found with this frustule arrangement were assigned to the genus *Amphora* Ehrenb. Cleve (1895) suggested that there were nine subgenera within *Amphora*, but noted that, in his view, some were distantly related. He did not recognize them as distinct genera at the time, worrying about the nomenclatural implications but he essentially offered them as testable hypotheses for the future. Mereschowsky (1903) recognized a considerable variability in the number and organization of the chloroplasts for *Amphora* and attempted to sort this variation at the level of genus: similar observations were made with regard to life history by Mann (1994). Stepanek & Kociolek (2014) examined

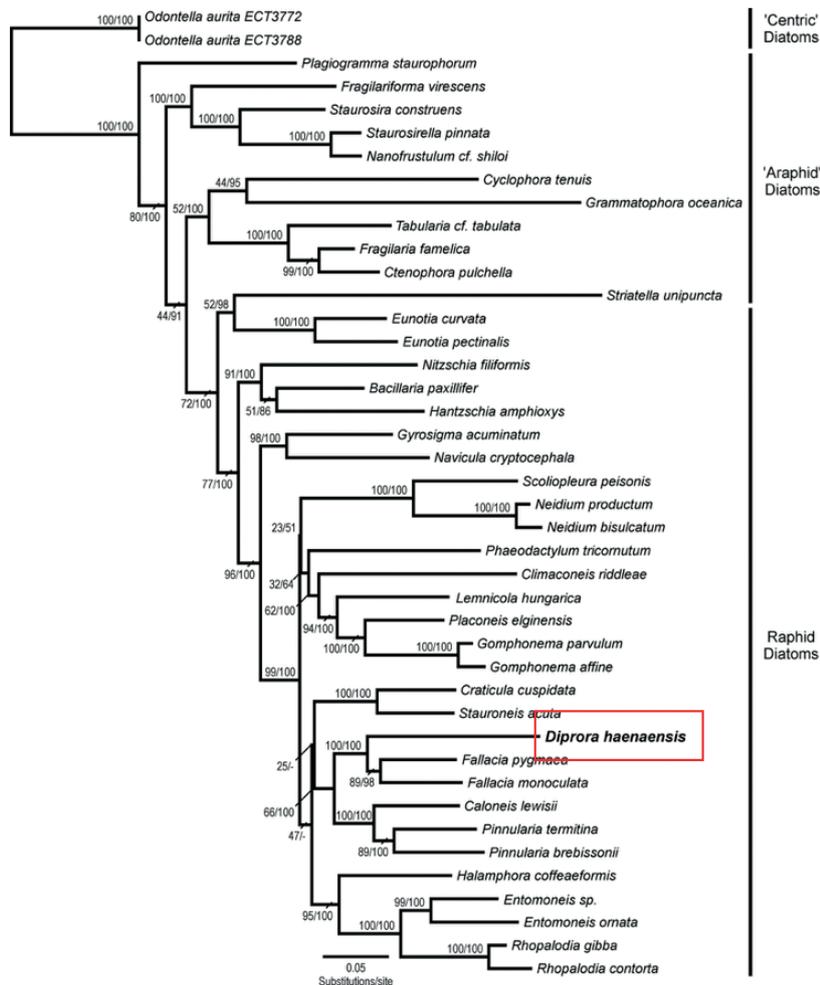
relationships of 24 different amphoroid taxa in a multi-gene study within the context of the raphid diatoms. They found that ‘amphoroidness’, this complex relationship of valve shape and girdle bands, has evolved independently at least four times (fig. 3). It is possible with taxa, such as *Navicula scabriuscula* (Cleve & Grove) Mereschk., a diatom whose valve morphology is typical for *Navicula* Bory s. str. but exhibits amphoroid frustule construction, that the number of times this ‘complex construction’ has evolved may be higher.

### ADAPTIVE RADIATION OR RAMPANT HOMOPLASY IN DIATOMS?

Whereas the features of symmetry, raphe number and amphoroid symmetry have been shown to be homoplastic across the raphid diatom tree of life, possession of these features exclusively does not diagnose groups where all raphid diatoms with those features are a member of that group: there

are some features where this does occur in diatoms. Situations where the evolution of an innovation within a particular ecological context may lead to rapid evolution and extensive number of species, which is known as adaptive radiation (Schluter 2000).

Much has been written about adaptive radiations in evolutionary biology, and the examples of the phenomenon are well known to biologists, including Darwin’s finches on the Galapagos Islands (Grant 1981) and silverswords in Hawaii (Robichaux et al. 1990). There are many examples across higher plants (Givnich et al. 2009), free-living animals (Troughton 1959) and parasites (Brooks et al. 1985). There are far fewer examples of adaptive radiation for unicells, because it is difficult to identify the adaptation, the ecological context and/or the resulting species radiations. In microbes, many of the innovations may have been physiological (Anantharaman et al. 2007), or related to life history (Cavalier-Smith 2009).

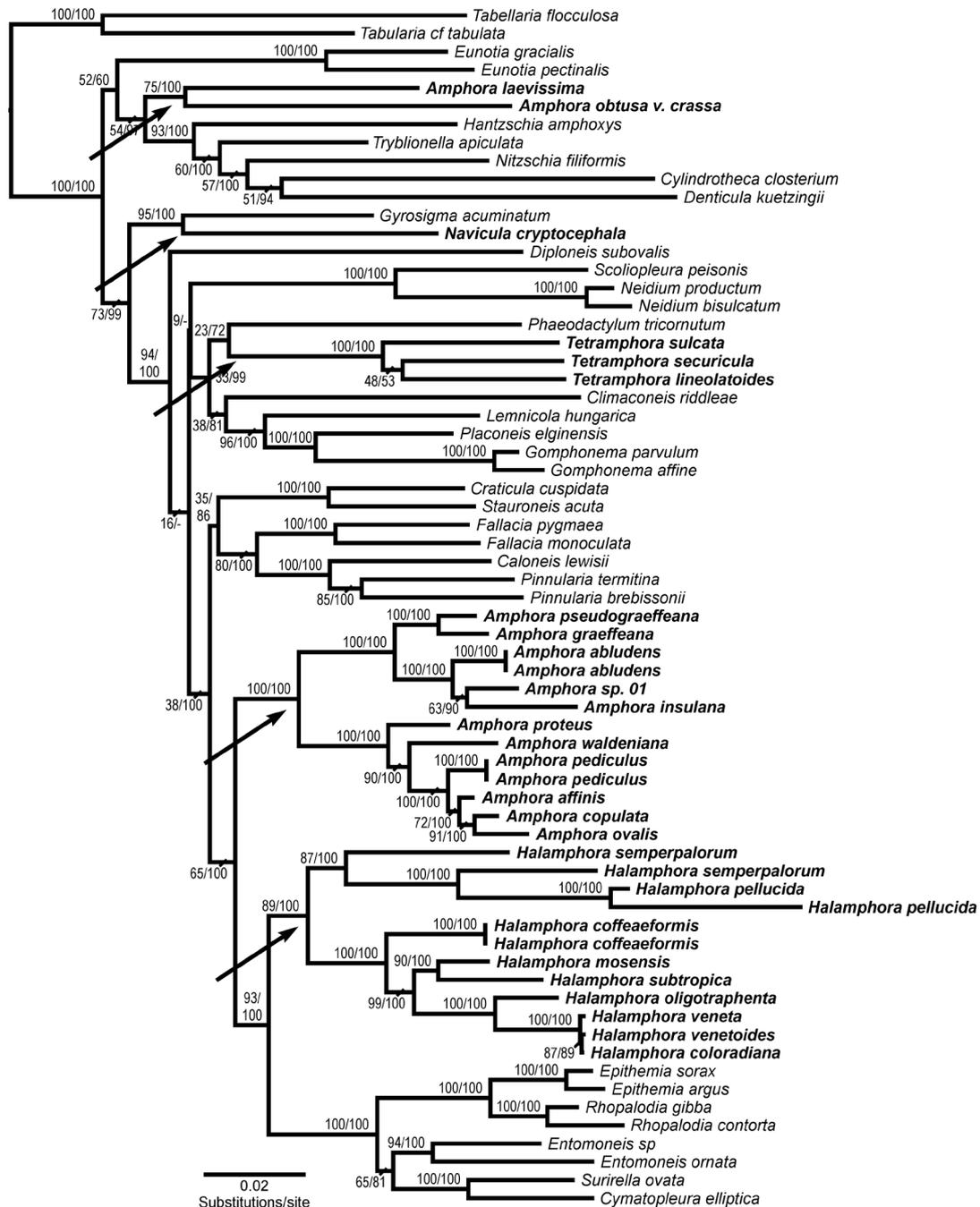


**Figure 2** – Phylogenetic relationships of closely related taxa within certain biraphid symmetrical (naviculoid) diatoms, indicating the position of the *Diprora haenaensis*, a diatom species with no raphe. Figure after Kocielek et al. (2013), copyright © 2013 British Phycological Society, reprinted by permission of Taylor & Francis Ltd, <http://www.tandfonline.com> on behalf of British Phycological Society. This figure is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder (<https://taylorandfrancis.com/contact/rights-and-permissions/>).

The topic of adaptive radiations in diatoms has been touched upon in the past. For example, Round & Crawford (1984) described how the ability to biomineralise silica may have given diatoms a competitive advantage for this unexploited resource in aquatic ecosystems, and Small (1950) described a higher rate of evolution for isogamous (mostly pennate) diatoms. Hobban et al. (1980) and Kitchell et al. (1986) noted that the ability to form spores may have given mem-

bers of the Biddulphiales Krieger the ability to survive and subsequently radiate at and after the K/T boundary. Recently, Nakov et al. (2018) reconfirmed the faster rate of evolution in pennates and described the radiation of raphid pennates after their acquisition of raphe systems.

It would seem that in most of the above-mentioned cases, from the evolution of biomineralization, to isogamy, to the evolution of the raphe system, these were each a single



**Figure 3** – Phylogenetic relationships among the raphid diatoms, with taxon names in bold having ‘amphoroid’ frustule construction. ‘Amphoroidness’ evolved at those points in the tree indicated by arrows. Figure after Stepanek & Kociolek (2014), reproduced with permission of the publisher (Elsevier). This figure is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder (<https://www.elsevier.com/about/policies/copyright/permissions>).

event in the diatom tree of life. The ability to produce resting spores certainly has happened many times within the group, and in fact these features might be deserving of different names for the same outcome.

At finer levels of taxonomic hierarchy, there are several genera or groups of genera within the raphid diatoms that would be interesting to investigate as possible examples of adaptive radiation. This has been documented for groups of species within particular genera, where a monophyletic group of species that are constrained geographically has evolved a number of species within that area or lake (see examples from other groups in Lake Baikal, Sherbakov 1999). Specific examples for these ‘species flocks’ have been shown for *Tetralunata* Hamsher et al. in Lake Toba, Indonesia (Hamsher et al. 2016), *Gomphonema* from Lake Baikal (Kociolek et al. 2018) and *Aneumastus* D.G.Mann & Stickle from ancient lakes in Macedonia (Stelbrink et al. 2018). Kociolek et al. (2017) considered the topic of species flocks in diatoms broadly, and provided other putative examples of the concept in the group.

If entire genera are monophyletic, and we can identify the feature(s) responsible for their success (in terms of numbers of species, ecological niches, etc.), then they may be excellent examples of adaptive radiation. If they are not monophyletic, however, it is possible that they may be other examples of rampant homoplasy.

There are nearly 850 taxa in the genus *Mastogloia* (Kociolek et al. 2018), and many of them are found in tropical waters associated with coral reefs (Hustedt 1933, Hein et al. 2008). They are assigned to the genus based on them having locules, a group of internal chambers located on the first girdle band located next to the valves (valvocopulae). The chambers have external pores, and in many species long mucilage strands are exuded through the pores. Do either locules or the mucilage strands confer some advantage to *Mastogloia* taxa, such as sequestering nutrients in otherwise nutrient-poor waters? Hustedt (1933) identified 11 different groups within the genus, 10 of them based on distinct morphological features (the remaining one recognized for the few *Mastogloia* species that occur in freshwater environments). Paddock & Kemp (1990) among others (e.g. Stevens & Gibson 1980, Yohn & Gibson 1981, 1982) documented the incredible morphological diversity in this genus, with respect to raphe structure, areolar structure and structure of the locules. Did locules evolve once or many times?

The diatom genus *Diploneis* (Ehrenb.) Cleve has canals running internally alongside either side of the raphe system, and these features are also seen in the genera *Lyrella* and *Fallacia*. With nearly 900 taxa in *Diploneis* (and another 200 in *Lyrella* Karayeva + *Fallacia*; Kociolek et al. 2018) it is a large group, but the function of these canals is unknown. Hustedt (1937) recognized 7 groups, one for the (relatively few) freshwater forms, then others based on areolar structure.

Members of the genus *Stauroneis* have the feature of a stauros, a thickened fascia of silica located internally across the central area. Whereas the diagnostic feature of the genus is recognizable even with the light microscope, it is difficult to understand the adaptive significance of a stauros. Cox

(2001) explored the development of this structure. There are over 1200 taxa assigned to the genus (Kociolek et al. 2018).

These three examples of raphid diatoms seem ripe for testing ideas about adaptive radiation in diatom groups. They each offer an opportunity to describe a specific structure and, possibly, relate that structural feature to an ecological context and possible adaptation. However, as we have shown from the examples for symmetry, raphe number and structural complexity, the possibility exists that the diagnostic features for *Mastogloia*, *Diploneis* and *Stauroneis* are homoplastic, and may represent additional examples of rampant homoplasy. Only through formal phylogenetic analyses, of molecular and morphological data, will we be able to know the answers to these interesting questions of evolutionary biology and ecology.

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