

Systematic Palaeontology (Palaeobotany)

# Diatom phylogeny: Fossils, molecules and the extinction of evidence

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## Abstract

Diatom phylogeny is progressing, thanks largely to the use of molecular data in determining relationships. Although these data are now accumulating at great speed and quantity, relationships among diatom higher taxa have become anything but clear. While progress in molecular systematics is still possible, significant taxa for determining higher-level relationships reside among groups with high levels of extinction. It is therefore a priority to examine fossil taxa and determine morphological synapomorphies as a test (or point of focus) for any further molecular studies. *To cite this article: D.M. Williams, C. R. Palevol 6 (2007).*

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## Résumé

**Phylogénie des diatomées : les fossiles, les molécules et l'extinction d'évidence.** La phylogénie des diatomées progresse, grâce notamment à l'utilisation des données moléculaires, en établissant des relations. Bien que ces données s'accumulent maintenant à grande vitesse et en quantité, les relations parmi les taxa de diatomées les plus élevés sont devenues tout sauf claires. Tandis que le progrès en systématique moléculaire est encore possible, les taxa significatifs pour déterminer des relations de plus haut niveau se trouvent parmi des groupes à niveaux élevés d'extinction. C'est donc une priorité que d'examiner des taxa fossiles et de déterminer les synapomorphies morphologiques en tant que test (ou point de focalisation) pour toute étude moléculaire ultérieure. *Pour citer cet article : D.M. Williams, C. R. Palevol 6 (2007).*

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*Mots clés :* Diatomées ; Phylogénie ; Molécules ; Fossiles

## 1. Introduction

Diatom phylogeny is a subject that has once again becoming interesting [22]. There is no doubt that interest has been re-kindled by the accumulation of molecular sequences and the production of phylogenetic

trees from those data. Efforts began in 1992 [3] with the acquisition of 18S rRNA sequence data for six diatom species (although the first 18S rRNA sequence was available as early as 1988 [14]). The phylogenetic trees derived from these data supported the monophyly of diatoms as a whole but conflicted with a higher taxon, the 'centric' diatoms, the Coscinodiscophyceae, defined by the bilateral symmetry of their paired valves: they are usually circular (Fig. 1, re-drawn from ([3] (Fig. 2B));

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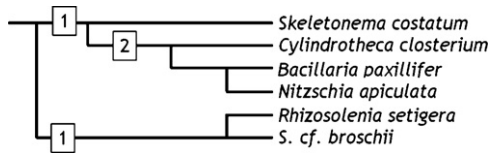


Fig. 1. Summary diagram of diatom relationships, after [3]; node 1, on two separate branches, represents the (non-monophyletic) Coscinodiscophyceae (*sensu* Round et al.), node 2 – on one branch – represents the monophyletic Bacillariophyceae (*sensu* Round et al.).

Fig. 1. Diagramme récapitulatif des relations entre diatomées, d'après [3]; le nœud 1, sur deux branches séparées, représente les Coscinodiscophyceae (non monophylétiques) (*sensu* Round et al.); le nœud 2 – sur une branche – représente les Bacillariophyceae monophylétiques (*sensu* Round et al.).

node 1, on two separate branches, node 2 – on one branch – is the monophyletic Bacillariophyceae (*sensu* Round et al.); in [3] six trees were produced, using differing numbers of sequences and different programs). The same conflict was noted a year later, along with conflict in a second higher taxon, the Fragilariophyceae (Fig. 2, re-drawn from [16]; the results were not unequivocal). Both conflicts have persisted through to the most recent molecular phylogenetic trees (see, for example, [2,15,23,28,29]). Thus, of the three generally recognised, and accepted, higher taxa in diatoms – Coscinodiscophyceae, Bacillariophyceae and Fragilariophyceae – two were non-monophyletic. The conflict between classification and phylogeny could easily be resolved by simply modifying the classification: that is, the conflict was derived from an older classification that reflected a poorly articulated notion of similarity, rather

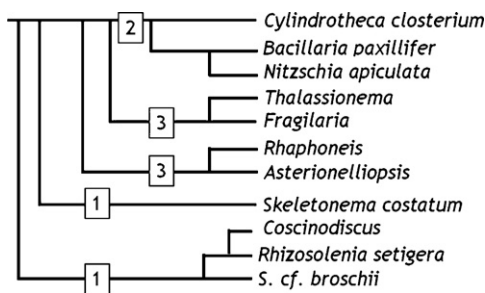


Fig. 2. Summary diagram of diatom relationships, after [15]; node 1, on two separate branches, represents the (non-monophyletic) Coscinodiscophyceae (*sensu* Round et al.), node 2 – on one branch – represents the monophyletic Bacillariophyceae (*sensu* Round et al.) and node 3 represents the (non-monophyletic) Fragilariophyceae (*sensu* Round et al.).

Fig. 2. Diagramme récapitulatif des relations entre diatomées, d'après [16]; le nœud 1, sur deux branches séparées, représente les Coscinodiscophyceae (non monophylétiques) (*sensu* Round et al.); le nœud 2 – sur une branche – représente les Bacillariophyceae monophylétiques (*sensu* Round et al.) et le nœud 3 représente les Fragilariophyceae (non monophylétiques) (*sensu* Round et al.).

than some understanding of relationship. Nevertheless, a revised classification, based on a 9000-sequence analysis, is not without its own problems and progress in determining evolutionary relationships among diatoms rendered problematic once again [32,33].

Below I treat the problem from the perspective of diatom phylogeny, rather than classification (although the two are – and should be – linked) by first providing a brief account of the development of diatom phylogeny prior to DNA trees, second I offer comments on the post-genomic phylogenies, and third I close by highlighting the role fossil diatoms will play in achieving knowledge of diatom relationships.

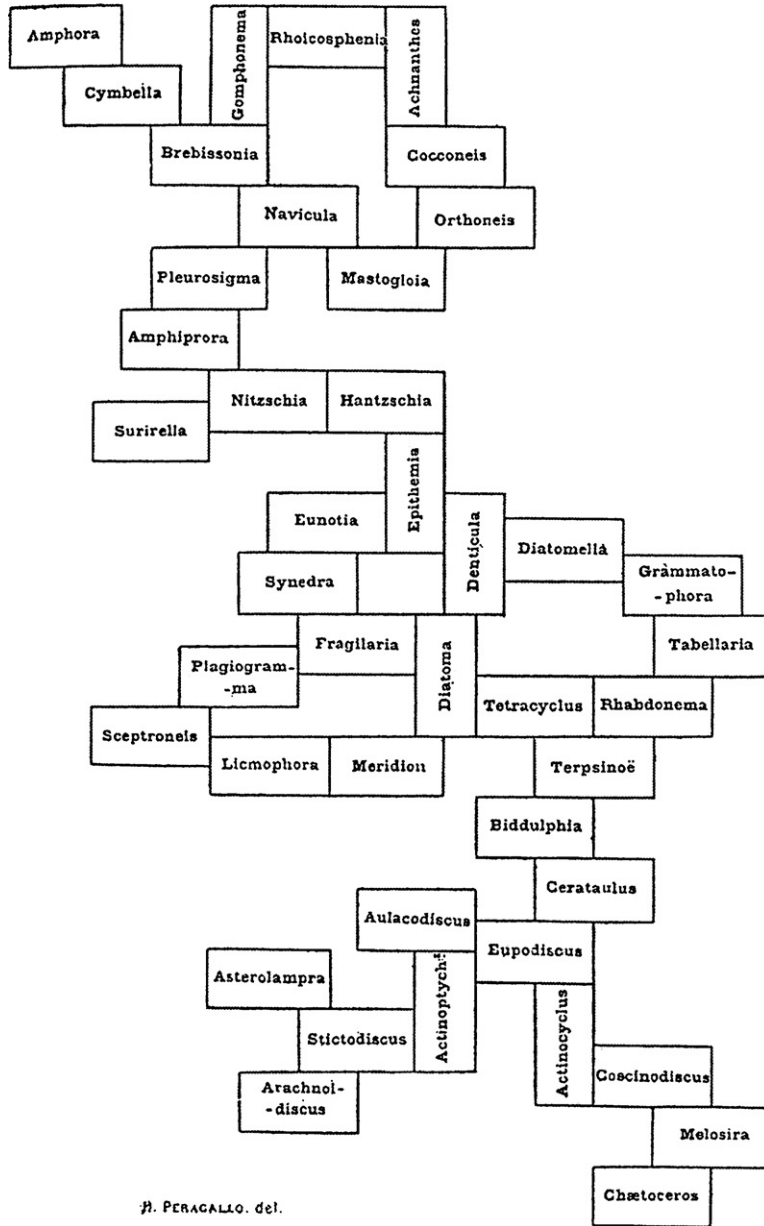
## 2. Diatom phylogeny: a brief note on pre-genomic efforts

The history of diatom classification and its relationship to phylogeny is as complex as that of any other taxon [30]. It merits study [32,33]. Some interpretations understand it to harbour a rich history of varied intellectual development (see [32,33]), while others see it of less or even no significance: “History suggests that, in many cases, diatomists might just as well have been classifying scraps of wallpaper as diatoms” because “[D]iatom taxonomy has developed largely without a conceptual basis, using a restricted range of characters drawn from just one part of the phenotype (the valve)” ([13] (p. 482)). The latter idea is at best unfounded ([32], and below). Yet there has been a divorce, so to speak, of representations of phylogeny and its accompanying classification, rather than a lack of any “conceptual basis” to the investigations [32].

To begin, an early explicit phylogenetic diagram for diatoms was offered by Hippolyte Peragallo in 1897 [21] (Fig. 3). He presented a scheme depicting a series of diatom genera, their names enclosed in separate boxes, each abutting and inter-linking with other such boxes. For example, the genus *Fragilaria* was ‘connected’ to *Plagiogramma*, *Synedra* and *Diatoma*. The impression gained (and, perhaps, meant to be conveyed) is that *Fragilaria* ‘gave rise’ to *Synedra*, which in turn ‘gave rise’ to *Eunotia* (Fig. 3). ‘Gave rise’ being interpreted as one taxon being ancestral in some way to another, such that, in the example above, *Fragilaria* is ancestral to *Synedra*.

Another phylogenetic diagram, presented by Merezhkowsky in 1903, included hypothetical ancestral taxa, those based not on specimens but supposition: *Archaideae* is the ancestor of the raphid diatoms (“mobilées”), *Protonées* is the ancestor of the *Archai-deae*, *Copuloneis* is the ancestor of *Protonées* and *Tabellarioideae*, with *Urococcus* as ancestor of all

ARRANGEMENT SYNOPTIQUE:  
des  
DIATOMÉES



J. PERACALLO. del.

Fig. 3. Reproduction of genealogy from [21]; diatom genera have their names enclosed in boxes, abutting and inter-linking with other such boxes, implying descent.

Fig. 3. Reproduction de généalogie d’après [21]; les noms des genres de diatomée figurent dans des boîtes, contiguës et liées à d’autres, impliquant la descente.

diatoms (Fig. 4 after [17]). Merezhkowsky also included some previously described taxa in ancestral positions: Melosireae leading to (ancestral to) the Anaraphideae, Fragilarioideae leading to (ancestral to) *Copuloneis*, *Auricula* leading to (ancestral to) the Carinatae and

*Libellus* leading to (ancestral to) Polyplacatae (Fig. 3; Merezhkowsky revised his classification with the *Archaideae* added to the “mobilées” and the Anaraphideae re-named Centrales, a version of the ‘centric’ diatoms referred to above, ([18] (pp. 203–204)); some

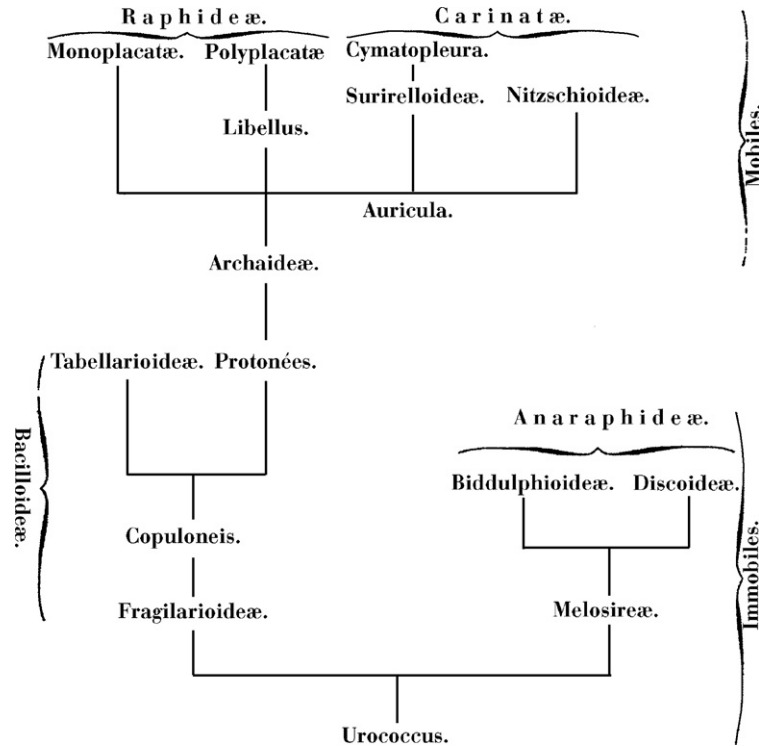


Fig. 4. Reproduction of genealogy from ([17] (p. 260), appears in a slightly different form in [18] (p. 204)).

Fig. 4. Reproduction de généalogie d'après ([17] (p. 260)), apparaissant sous une forme légèrement différente qu'en ([18] (p. 204)).

years later, Peragallo proposed a classification based on a combination of his earlier diagram and that of Merezchkowsky [22], see [32]).

Like Peragallo, the Italian biologist Achille Forti developed Merezchkowsky's ideas. Forti chose to represent genealogical relationships as a series of networks, some with reticulating lines (Fig. 5, from [5]). It might be reasonable to assume that in Forti's diagram if a genus is 'connected' by lines to another genus that is to be interpreted as the one having 'given rise' to the other, as in the above examples of Peragallo and Merezchkowsky. In comparison to Peragallo's diagram, Forti's is upside down. Nevertheless, it still implies that *Fragilaria* 'gave rise' to *Synedra* as well as *Himantidium* and *Eunotia* (Fig. 5; *Himantidium* became a synonym for *Eunotia*).

In more recent times, diatom phylogenetic diagrams continued attempting to represent certain aspects of the notion that some taxa 'give rise' to others, with the ancestral taxon often left unnamed, as in Simonsen's 'pedigree' ([26] ("uncertain - not common - ancestors")) or else diagrams with a mixture of unnamed (and unknown) ancestors and fossil taxa (Fig. 6, after [19]). Of significance is that most of the early schemes (Peragallo, Merezchkowsky, and Forti) are based on a whole suite of data (the valves, the plastids, reproductive behaviour,

etc.) not "just one part of the phenotype (the valve)" ([13] (p. 482)). If anything, the "conceptual basis" was an attempt to 'find' and represent direct ancestry via supposed relationships, a view traceable to Ernst Haeckel, the creator of such phylogenetic trees [34].

Thus, or so it seemed, phylogeny was understood to be complex, requiring the identification of (real or imaginary) ancestors and some taxa could reasonably be assumed to have 'given rise' to other taxa – this is a "conceptual basis" of sorts.

### 3. Diatom phylogeny: post-genomic conundrums

Diatom phylogeny, as revealed by molecular data, is certainly progressing from its humble beginnings. Its most comprehensive 'estimate' can be found in Medlin and Kaczmarska [15] (see also [1]) based on ca. 9000 sequences. While these might be useful places to examine progress (see below), it is worth noting that there are numerous diatom phylogenies (most, if not all, based on 18S RNA) in various papers and book chapters [2,9–11,15,23,28,29]. Still, even with such vast amounts of data depicting relationships precisely, curiously accounts of phylogeny continue to have as its "conceptual basis" the idea that some taxa gave rise to others,

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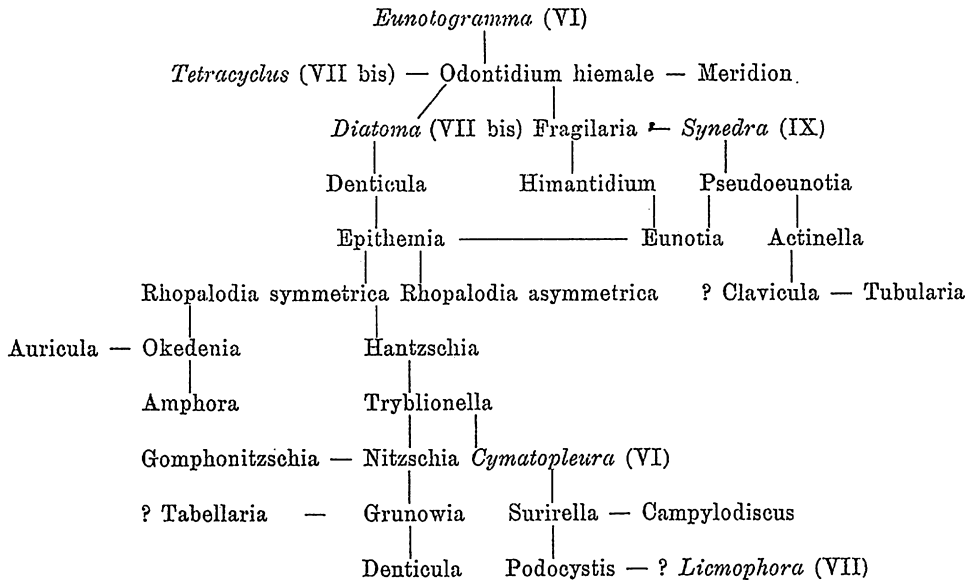


Fig. 5. Reproduction of part of the genealogy from [5].  
 Fig. 5. Reproduction d'une partie de la généalogie selon [5].

Система центрических диатомовых водорослей

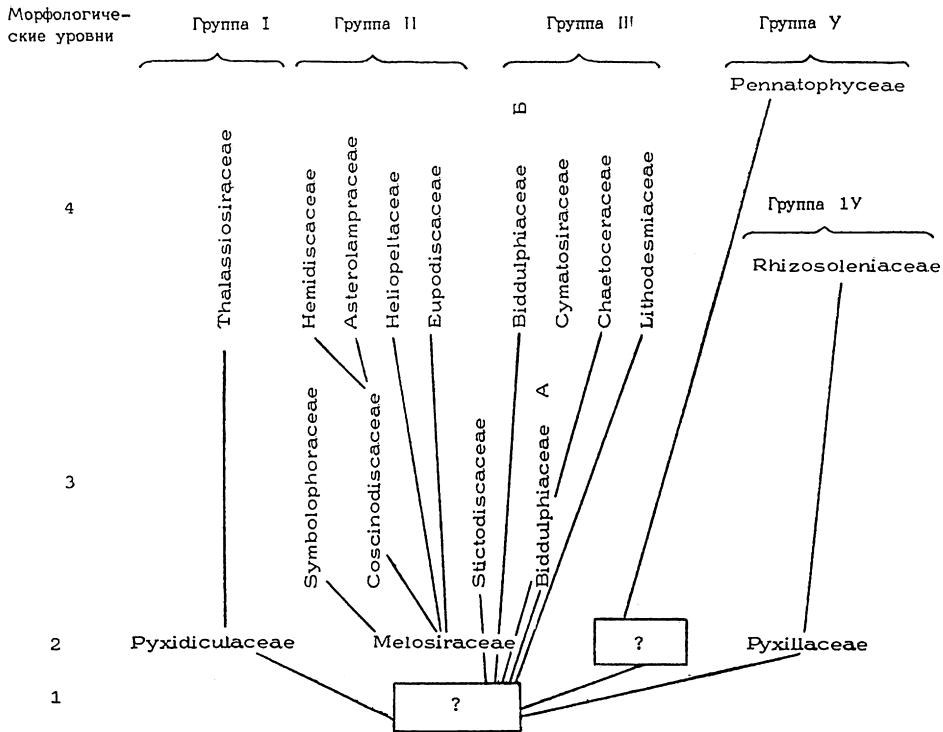


Fig. 6. Reproduction of genealogy from [19].  
 Fig. 6. Reproduction de généalogie selon [19].

even though the phylogenetic diagrams specify only sister-group relationships. Thus such statements appear, derived from representations of diatom phylogeny:

“Radial centric diatoms begot multipolar centrics, multipolar centrics begot pennates and the araphid pennates begot the raphid pennates” ([9] (p. 92)).

However that sentence is supposed to be interpreted, more puzzling is the straight narrative accounts, stories focusing on this or that ancestor, tales of what actually happened:

“It is of interest that the molecular phylogeny of diatoms also favours the centric forms as ancestral ... with some molecular evidence agreeing [data] that the earliest diatoms could have been neritic ... Calibrating the molecular clock of diatoms and other Heterokontophyta from the fossil record, and applying the same nucleotide substitution rate to parts of the molecular phylogeny before the occurrence of fossil diatoms, indicate that diatoms originated close to the Permian–Triassic boundary 250 Mya, some 130 million yr earlier than the first silicified fossil diatoms ... This suggests that silicification evolved late in the evolutionary history of diatoms. It is possible that any earlier silicified diatoms have failed to be preserved for some environmental or taphonomic reasons; however, silicified organisms (sponges) have been found in phosphoritic marine sediments 580 million yr old ... and both radiolarian and sponges were common from the Cambrian onwards ...” ([24] (p. 44)).

“However, a scenario could be proposed in which ‘Urdiatoms’, abundant as non-silicifying unicells in coastal waters, became stranded in isolated pools as eustatic seas flooded the continents. When these saline pools began to dry up, the diatom ancestors, if they survived, must have had to adapt to a semiterrestrial habitat” ([27] (p. 363)).

One wonders what – scientifically – might be made of these kinds of statements and what might be made of their “conceptual basis”. Perhaps one should simply be amazed at the precision and move on.

#### 4. Diatom phylogeny: relationships and molecules

Taxon relationships, as expressed in phylogenetic diagrams (regardless of the source of data), are expressed as sister-groups: Taxon A is more closely related to Taxon B than it is to C. This is different to stating that Taxon A

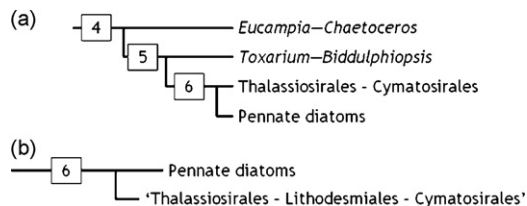


Fig. 7. (a) Representation of phylogenetic tree derived from [29], with pennate diatoms sister to Thalassiosirales (a radially symmetrical group) plus Cymatosirales; (b) Representation of phylogenetic tree derived from [23], with pennate diatoms sister to a modified Thalassiosirales and Cymatosirales (Cymatosirales includes *Hyalosira* sp. – usually part of Fragilariophyceae – and Thalassiosirales are sister to Lithodesmiales) see [7].

Fig. 7. (a) Représentation de l’arbre phylogénétique dérivé de [29], avec les diatomées pennées comme sœurs des Thalassiosirales (un groupe radialement symétrique) et des Cymatosirales; (b) la représentation de l’arbre phylogénétique dérivée de [23], avec les diatomées pennées comme sœurs des Thalassiosirales et des Cymatosirales modifiées (les Cymatosirales incluent *Hyalosira* sp. – faisant habituellement partie des Fragilariophyceae –, tandis que les Thalassiosirales sont « sœurs » des Lithodesmiales), cf. [7].

‘gave rise to’ (begot) Taxon B. The contrast being, the former is a statement of relative ancestry, the latter of direct ancestry.

Given the number of different diatom phylogenies available and the number of differences between the various trees, it is difficult, if not impossible, to summarise relationships with any accuracy, notwithstanding efforts to create a new classification that includes possibly (or possibly not) paraphyletic groups [1,16]; for commentary, see [2] and [33].

Given the significance, in terms of diversity, of pennate diatoms (those with bilaterally symmetrical valves, Bacillariophyceae, as emended in [25] plus Fragilariophyceae), their sister-group relationship is of some import. The results in Sorhannus [29] supported a sister-group relationship of the pennate diatoms with a group that included Thalassiosirales (a radially symmetrical group) plus Cymatosirales (a bilaterally symmetrical ‘centric’ diatom) (Fig. 7a); a similar relationship was discovered recently in [23], although the Thalassiosirales and Cymatosirales were less well defined (Fig. 7b); in that tree the Cymatosirales include *Hyalosira* sp. (usually part of Fragilariophyceae) and the Thalassiosirales are sister to Lithodesmiales (which includes genera such as *Mediopyxis*, *Lithodesmium*, *Ditylum*, *Bellerochea*, *Streptothecha*, *Lithodesmioides* and *Neostreptothecha*; for further discussion see [7]).

Medlin and Kazmarska [15] (and reflected in the classification of Mann in [1]) found only the Cymatosirales as sister to the pennate diatoms (Fig. 8), while Sininghe Damsté et al. [28] had only the genus *Gonioceros*



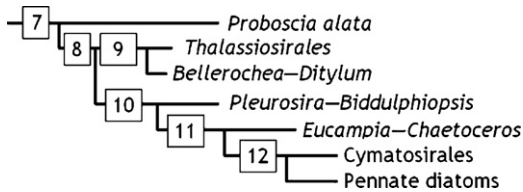


Fig. 8. Representation of phylogenetic tree derived from ([16], reflected in the classification of [1]) with Cymatosirales as sister to the pennate diatoms.

Fig. 8. Représentation d’arbre phylogénétique dérivée de [15], reflétée dans la classification de [1]) avec les Cymatosirales comme « sœurs » des diatomées pennées.

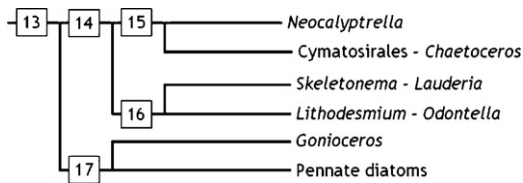


Fig. 9. Representation of phylogenetic tree derived from [28], with *Gonioceros* as sister to the pennate diatoms.

Fig. 9. Représentation de l’arbre phylogénétique dérivée de [28], avec *Gonioceros* comme « sœur » des diatomées pennées.

as sister to the pennate diatoms (Fig. 9). *Gonioceros* is in the order Chaetocerotales, part of the Chaetocerotophycidae, the latter being divided into the Chaetocerotales and Leptocylindrales ([25] (p. 127)). The Chaetocerotales have three families, the Acanthocertaceae (with only one species, *A. magdeburgense* Honigmann), Attheyaceae (with only one genus *Attheya*) and the Chaetocerotaceae with three genera, *Chaetoceros*, *Gonioceros* and *Bacteriastrum*. *Gonioceros* may be more closely related to *Attheya* than any other member of the Chaetocerotaceae and all species recognised in either *Attheya* or *Gonioceros* should be in “one genus in the family Attheyaceae . . .” [4]. Interestingly enough, Sinninghe Damsté et al. [28] found *Chaetoceros* to be most closely related to the Cymatosirales, whereas in Medlin & Kazmarska, *Chaetoceros* is basal to the Cymatosirales [15].

In short, basal pennate relationships remain obscure and uncertain – and the groups so implicated as closest relatives are primarily composed of fossil taxa.

## 5. Relationships and fossils: the way forward

The fact that molecular relationships cannot as yet be succinctly summarised implies that molecular data are either insufficient to yield robust relationships or the samples taken so far have little useful phylogenetic signal. For morphology, there have been no good morphological synapomorphies identified or proposed

for any higher taxon (beyond the presence of a raphe in the raphid diatoms, a group nested within the pennate diatoms). Nevertheless, for relationships within the pennate diatoms, it is possible to reduce options to taxa (Class, sub-class, orders) whose valves are bilaterally symmetrical in a strict sense. Comparison of Orders in the (probably) paraphyletic Fragilariophycidae, Biddulphiopycidae and Mediophyceae is presented in Table 1 (to document overlap in their composition). The table can be understood in two parts: (1) among the first nine orders listed (Fragilariales to Protoraphidales) is the probable sister-taxon to the raphid diatoms; (2) among the remaining 13 orders (Biddulphiales to Triceratiales) is the probable sister-taxon to the pennate diatoms. Of the total, only four Orders lack fossil representatives. Yet, conversely, a glance at the families and genera listed in the Biddulphiopycidae (*sensu* [20]), for example, the vast majority appear extinct. Thus, the Biddulphiales (*sensu* [20]) has three families, Biddulphiaceae, Gryocylindraceae, and Parodontellaceae. Ignoring the Parodontellaceae for the moment (see below on this family [8]), there are 15 genera in the Biddulphiaceae and Gryocylindraceae is monotypic [20]. Of these 16, nearly half are extinct.

Table 1 does not include details of all known extinct groups, whose classification varies, such as artificial monotypic groups harbouring single species, such as *Bilingua rossii* Gersonde et Harwood [6] placed, redundantly, in its own Order (Bilinguales) and family (Bilinguaceae) [20] (there may be other species in the genus, see [31]). There are also larger groups such as the Cymatosirales, its significance noted above. The Cymatosirales presently has two families, the Cymatosiraceae and the Rutilariaceae, the former with 14 genera, of which four are composed entirely of extinct species, the latter with five genera, of which four are composed entirely of extinct species. In terms of numbers of species, around 50% of the Cymatosiraceae are extinct and nearly all (57 of 59) species in the Rutilariaceae are extinct. There is the possible addition of a further family, the Parodontellaceae, of which all of its four genera are composed entirely of extinct species (see [20,32], placing this family in the Biddulphiopycidae; for further comment, see [32]).

It is more than possible that *Gonioceros*, *Chaetoceros* and the Cymatosirales, referred to above, share putative synapomorphies, such as the possible homology (relationship) between the seta of *Gonioceros* and *Chaetoceros* (seta are long spines, extending from the poles of the valves) and the pili of the Cymatosirales (pili are hair like extensions emerging from the valve surface, at their poles), and in turn these may be homologous to related

Table 1

Comparison of the composition of the (all possibly/probably) paraphyletic Fragilariophycidae, Biddulphiopycidae, and Mediophyceae  
Tableau 1.

Comparaison entre les compositions des Fragilariophycidae, Biddulphiopycidae et Mediophyceae paraphylétiques (toutes possibles/probables)

Round et al. [25]	Round et al. [25]	Nikolaev et al. [20]	Medlin & Kazsmarka [15] Mann in [1]
Class: Fragilariophycidae (P)	Sub-class: Biddulphiopycidae (P)	Sub-class: Biddulphiopycidae (?P)	Class: Mediophyceae (?P)
Fragilariales Tabellariales Licmophorales Rhaphoneidiales Rhabdonematales Striatellales Cyclophorales Climacosphenales Protoraphidales	Biddulphiales Hemiaulales	Biddulphiales Hemiaulales Chaetocerotales Lithodesmiales Cymatosirales Bilinguales Briggerales Stictodiscales Anaulales	Biddulphiales Hemiaulales Chaetocerotales Lithodesmiales Cymatosirales
Thalassionematales Toxariales Ardissonales	Anaulales  Triceratiales <sup>a</sup>		Thalassiosirales Toxariales Ardissonales Triceratiales

<sup>a</sup> In the Triceratiales, Round et al. include two families, one being Plagiogrammaceae, with four genera *Dimerogramma*, *Plagiogramma*, *Glyphodesmis* and *Dimeregrammopsis* nom. nud. ([25] (p. 126)). Kooistra et al. [12] recently provided the new name *Talaroneis* for the invalidly described *Dimerogrammopsis* and presented molecular evidence suggesting it to be most closely related to *Rhaphoneis*, *Asteroplanus* and *Asterionellopsis*. Hence, this family, if monophyletic, is probably more closely related to either the Rhaphoneidiales or Fragilariales rather than other members of the Triceratiales.

structures in the Biddulphiopycidae (*sensu* [20]). These notions require investigation.

## 6. Conclusions

In spite of much (molecular) effort, phylogenetic relationships of diatoms remain poorly understood and poorly represented in classifications [33]. Few, if any, higher taxa have associated, or even hypothesised, morphological synapomorphies. Mann offered the following comment: “Molecular data ... show the centrics as a whole to be paraphyletic, but relationships between the principal groups, and whether particular groups are monophyletic or paraphyletic, is currently unclear. Several major molecular clades are cryptic, with no or few morphological or life history traits that can be convincingly argued to be synapomorphies” ([1] (p. 431, note 18)). For characters to be “convincingly argued as synapomorphies”, analysis is required rather than judgement

– and no relevant morphological data has yet been analysed in such a way to allow any degree of conviction. Such analyses are possible and, in the near future, hopefully, will be published. If the results conflict with current molecular understanding, so be it – that outcome would identify a problem worthy of investigation: why do morphology and molecules differ? However, the central purpose of this contribution is to point out that without consideration of fossil taxa (extinct morphology) much of the diversity that existed between, as it were, the pennate diatoms and all the remaining diatoms, and the diversity that existed between the raphid diatoms and the remaining pennate diatoms is extinct and, of course, inaccessible to direct investigation with molecular methods. Of course, one might entertain the following thoughts:

“Thus, by the end of the Lower Cretaceous, cylindrical, circular, bipolar and possibly triangular forms were present, possessing linking spines and six types



of processes including the rimoportula. Thus, the ancestors of both Clades 1 and 2 almost certainly were present. Sulci, costae, a marginal ridge, a pseudoloculate and perforate valve structure also have been identified, together with signs of vela” ([27] (p. 374)).

Without identifying which characters are derived and which are primitive (discovering synapomorphies), relative to extant forms, the above quotation simply presents a further excursion into the narrative phase of phylogeny, an episode abandoned by systematists (including molecular systematists and palaeontologists) decades ago.

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