

Review paper

## How to define a diatom genus? Notes on the creation and recognition of taxa, and a call for revisionary studies of diatoms

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**Abstract** – We highlight the increase in the number of diatom genera being described, and suggest that their description be based on the concept of monophyly. That is, a new genus will contain the ancestor and all its descendants. Past criteria or guidance on how to circumscribe genera are reviewed and discussed, with conceptual and actual exemplars presented. While there is an increase in the rate of genus descriptions in diatoms, and there are many journal and series dedicated to facilitating this important activity, we call for revisionary works on diatom groups, to assess and establish monophyletic groups at all levels of hierarchy in the diatom system.

**Keywords:** Bacillariophyta, cladistics, genera, monophyly, phylogeny, revisionary studies, systematics

### Introduction

During the last 15 years of studies in diatom taxonomy, over 80 new genera have been described (FOURTANIER and KOCIOLEK 2011). Exploring the period from 1930–1969, it took some 40 years to describe a comparable number of genera in the 20<sup>th</sup> century (FOURTANIER and KOCIOLEK 2011). In a previous review, we noted that over a much longer period, 1805–1975 (documented in 5 year periods), there was an average of between 3 and 4 new generic descriptions per year (WILLIAMS and KOCIOLEK 2011: Table 14). The number of diatom genera being described is increasing. In 2013 alone the journal »Phytotaxa«, dedicated to publishing descriptions of new botanical taxa, accounted for seven new diatom genera. As editors of the diatom section of »Phytotaxa«, as well as being working diatom taxonomists

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ourselves, we have been frequently asked by authors whether the specimens encountered in any study constitute a new genus, and if so, on what characters could (should) they base the description? Ultimately, the reviewer community has helped with those decisions – but when pressed for an answer by those who ask whether they should propose a new genus of diatoms, our reactions have not necessarily been satisfying to them. The question has been addressed a number of times in the diatom community (e.g. ROUND 1997a, b, KOCIOLEK 1997, 1998, WILLIAMS 2009, WILLIAMS and KOCIOLEK 2011) but we return to it here in an attempt at clarification.

In short, genera should be monophyletic; indeed, ideally all taxonomic categories should be monophyletic. The study and discovery of monophyly is often associated with a theory of systematics called cladistics. When cladistics was first mooted as a way of understanding the living world, its primary focus was on phylogenetic relationships and how to discover them. Ushered in as a reasoned critique of the old palaeontological approach to phylogeny (»... if only I had enough fossil evidence then all would become clear ...«), its baggage was a rather copious supply of new words and terms, most, but not all, coming directly from Willi Hennig (1913–1976), often considered to be the founder of cladistics (Schmitt 2013). With time, cladistics was understood to apply more generally to problems of taxonomy rather than simply being a refined version of phylogenetics. In a previous series of papers we attempted to show how many of the early diatomists followed what would amount to a cladistic understanding of their data and the taxa so discovered: AGARDH (1824), PFITZER (1871), PETIT (1877), and MERESCHKOWSKY (1902, 1903a) would be among those to whom this approach might be applied. The approach is quite simple: how do data relate to conclusions? Put another, more specific way, how do characters relate to taxa? What do we mean by character?

Cladistics offered a solution to the problem of ‘characters’ by subdividing them into different ‘kinds’: synapomorphies, symplesiomorphies and convergences. The latter term might be viewed as straightforward, an old term, perhaps differently used in a modern sense, but nonetheless an old term (HAAS and SIMPSON 1946). But the first two words, synapomorphies and symplesiomorphies, both from Hennig, are of some significance – and while some systematists still consider them new (and their occurrence in the pages of journal »Diatom Research« still relatively rare), they are over 60 years old (HENNIG 1953: 14).

Rather than the terms synapomorphy and symplesiomorphy, the most often encountered words are ‘similar’ or ‘similarity’, which are applied to both characters and taxa. One might, then, re-phrase the above concerning characters: cladistics offered a solution to the problem of ‘similarity’ by subdividing it into different ‘kinds’. Interestingly enough, one might also find scattered in the same diatom literature reference to taxa (or characters) being ‘related’ or ‘closely related’ and sometimes one gets the impression that ‘similar’ and ‘related’ or ‘closely related’ (even ‘closely similar’) are all meant to mean much the same thing. Yet they are not: synapomorphies, symplesiomorphies and convergences might all be construed as kinds of similarity – but only synapomorphies depict, or characterize, monophyletic groups.

### **The importance of monophyly**

It is almost universally accepted today that the only groups of species that should be recognized (named) are monophyletic groups (e.g. DONOGHUE 1985, MISHLER and BRANDON 1987, MISHLER and THERIOT 1997). Why monophyly? It might be said that, given the rela-

tionship between monophyly and synapomorphy, the only groups that can be recognized are monophyletic groups; these groups can be discovered – they have characters of their own (KOCIOLEK et al. 1989, WILLIAMS and KOCIOLEK 2011, but see below). Monophyletic groups represent a specific part of evolutionary history: they are collections of species that are more closely related amongst themselves rather than to anything else. For example, all species recognized as belonging in a genus are (presumed) most closely related amongst themselves and (presumed to) share a common ancestor. The same holds for any other generic group. That proposition reveals another useful parameter of monophyletic groups: they are predictive. That is, one expects to find more characters (synapomorphies) congruent with those already known; they will specify the same group or, at the very least, will not contradict it. Monophyletic groups, then, are the basis for any natural classification. They are the groups that should receive formal identity and a name. Of course, some of these groups, with further study, may turn out not to be monophyletic. But this reflects the process of systematics, its scientific aspect, if you will: sampling characters and testing them against known (named) groups.

### **Other types of classification systems**

A classification of monophyletic groups is not the only way to represent organisms. There are many ways to classify. One might choose a functional approach and group, say, all organisms that are autotrophs, contrasting them with heterotrophs, or all organisms that fly, contrasted with all those that do not. This is not uninteresting but, by definition, reflects only one property and constitutes a very special kind of classification, one that is based on a specifically defined character or characters rather than characters that are discovered as properties of the taxa.

Alternatively, one might choose to classify organisms on the basis of some defined organizational criteria. Diatoms, like other organisms, have many groups like this, often referred to as grades, evolutionary grades (HUXLEY 1959). Examples of grades are ‘centric’ diatoms, defined by their symmetry (HUSTEDT 1927); ‘araphid’ diatoms, also defined by their symmetry along with their lack of a raphe (ROUND et al. 1990); ‘monoraphid’ diatoms, defined by their possession of one valve per frustule having a raphe, the other lacking it (PATRICK and REIMER 1966). These groups reflect a kind of organization rather than any specified relationships.

These two kinds of classifications, functional groups and grades, may collectively be referred to as examples of artificial classifications. This does not imply they are necessarily wrong – just that they reflect something imposed rather than discovered.

### **What does it take to describe a genus? Some traditional responses**

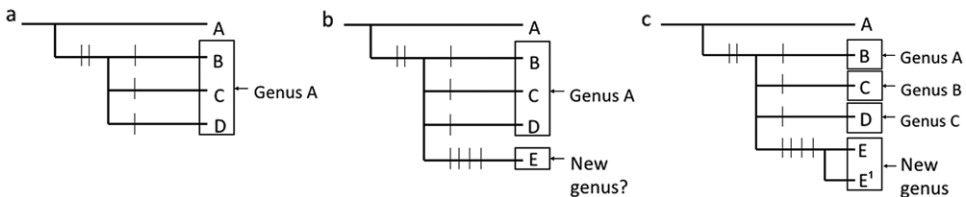
The diatom literature speaks to the idea that in some way creating a genus of diatoms is a task that should be done with care, and that a substantive body of evidence must be demonstrated to support its creation (e.g. VAN HEURCK 1896). It may be, however, that diatomists have been – and still are – too cautious in their readiness to erect genera. For example, »The Catalog of Fishes« (ESCHMEYER 1988a, b, online version 2014, see also ESCHMEYER et al. 2010) treats just over 64,000 names ascribed to extant fish species, which is about the

same number of names treated by the »Catalogue of Diatom Species« (FOURTANIER and KOCIOLEK 2011). But ichthyologists have sorted those ca. 64,000 taxon names into 12,000 genera, while diatomists have recognized only ca. 1,200 diatom genus names (FOURTANIER and KOCIOLEK 2011). This situation is likely to become worse if we assume that there still remains a significantly higher proportion of diatom species diversity yet to describe versus that already known in fishes.

Other examples that might suggest our descriptions of diatom genera may be too conservative. For example, very few freshwater diatom genera have narrow (specific) biogeographic circumscriptions. Most that come to mind have only recently been described: *Gomphocymbella* O. F. MÜLLER (1905, c. 15 species, mostly in Africa, excluding fossils); *Tibetiana* LI et al. (2010, 1 species, so far, from China); *Eunophora* VYVERMAN et al. (1998, 5 species from New Zealand and Tasmania); *Perinotia* METZELTIN and LANGE-BERTALOT (2007, 1 species from South America) and *Tetralunata* HAMSHER et al. (Accepted, 19 taxa from Indonesia). Also, the Hawaiian Islands, which occupies ca. 6,400 square miles, comparable in area to Los Angeles County in California, has nearly 80% of the diatom genera found in the entire North American Flora (KINGSTON 2003, KOCIOLEK and SPAULDING 2003a, b, LOWE 2003, STOERMER and JULIUS 2003) even though the number of species present are less than 1% of the flora of North America (KOCIOLEK 1997, personal observations).

Below we address some of the commonly understood criteria:

1. A genus requires many features: Suppose we have a genus A diagnosed by two characters (two synapomorphies). That genus consists of three species (B, C, D), each diagnosed by a single character (Fig. 1a). Study of more specimens yields a further species (E) with the same two characters (two synapomorphies), suggesting it too belong to genus A. It is recognized as an additional species as it has four unique characters of its own. It would be tempting to promote species E to a genus as it has many (four) characters of its own, relative to the single character for each of the other included species, making E readily distinguishable. The consequences of that action, however, are profound. If E is recognized as a genus (Fig. 1b) then it will render genus A undiagnosable as it cannot now be diagnosed by the two generic synapomorphies as species E (now genus E), also has them also; it also renders genus A a collection of species where only some of the most closely related species are included (E is now excluded). Thus, under these circumstances, species E is best included in genus A, albeit an unusual – in the sense of having four distinctive characters – member of it.



**Fig. 1.** A) Conceptual model of relationship between taxa as part of a genus (Genus A). B) Results of relationships with the addition of a highly derived taxon (E) recognized as a separate genus, making Genus A, with taxa B, C and D, non-monophyletic. C) Conceptual model of relationships, with taxa A, B, and C as new genera, required by identifying taxon E as a separate (new) genus.

Further, imagine that as our investigations proceed we discover yet another species, E, with the four characters that diagnose species E thus making them most closely related relative to all the other species in genus A (Fig. 1c). This presents a problem of representation. Species E and E<sup>1</sup> now share a number of characters amongst themselves only. It could be named a genus. As a consequence, B, C and D have unclear relationships and could now be considered three monotypic genera. The meaning being that these three have no specified relationships outside the immediate group of A—E<sup>1</sup>. While this example may be unusual, the point here is that classification at the genus level may have consequences elsewhere. Many of these consequences can be seen in the sub-divisions made of larger diatom genera, such as *Eunotia*.

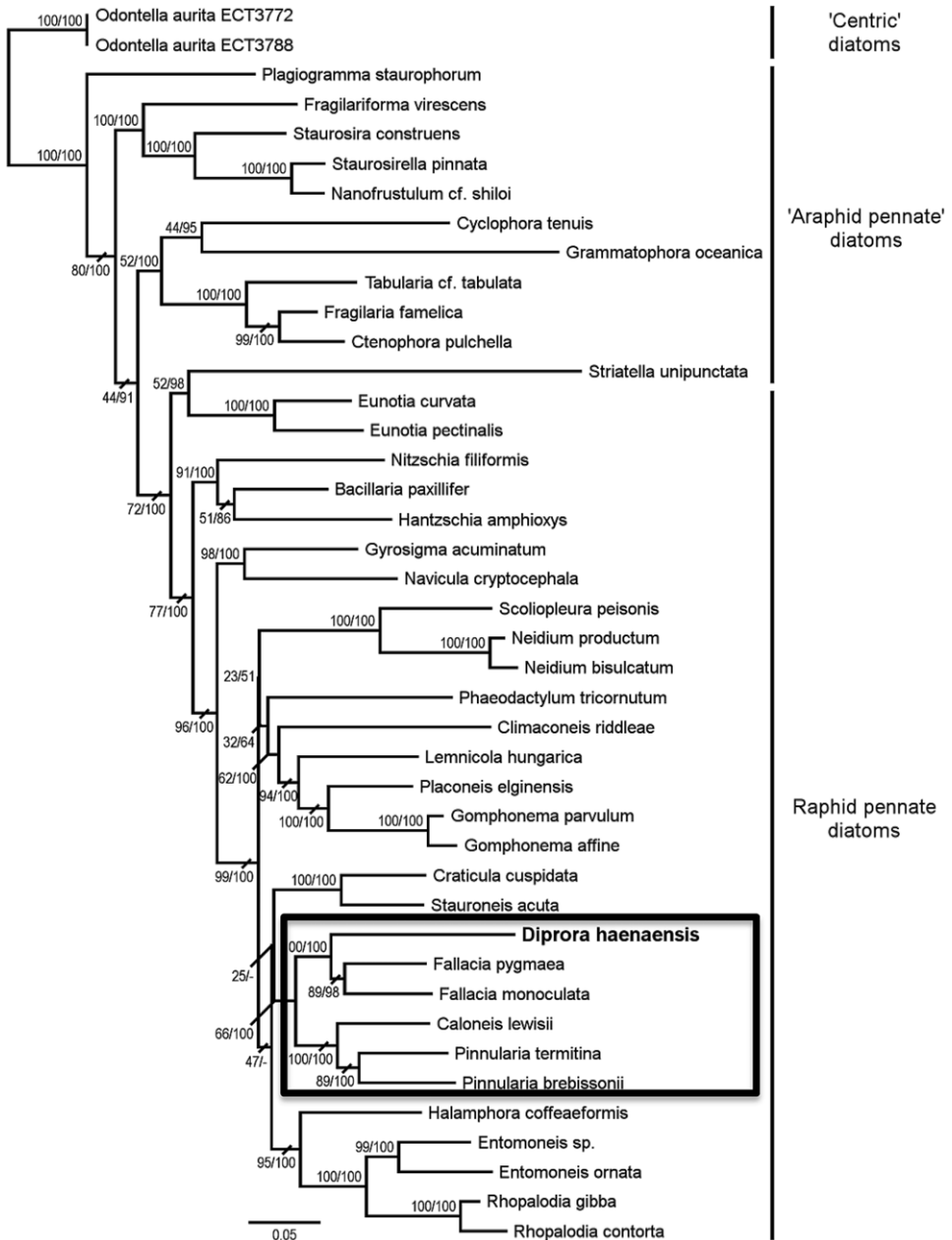
2. Homogeneity of features: ROUND (1996) called for very narrow circumscriptions of diatom genera, suggesting that with this approach there would be homogeneity within a genus, which would yield a more natural classification. Initially this would seem to make sense. Except, as KOCIOLEK (1998) demonstrated, there are occasions where two things might look very similar but may actually be more closely related to other taxa that, due to many derived features, look unlike their closest allies. Even in this case, we would still argue for the recognition of monophyletic groups rather than groups based on »overall similarity«, a concept that was discredited some time ago because it lacks the properties of monophyletic groups outlined above.
3. Good characters: CLEVE (1895) summarized his thoughts on a wide variety of features, indicating his experience in the use of different features at different levels of taxonomic hierarchy, and which ones are ‘useful’ for classification. HUSTEDT (1928) suggested that the raphe is a good guide to genera (and that other attributes could be used to diagnose species). COX (1890) also reviewed features he thought were helpful at the level of genus. Throughout the years a wide range of features have been thought of as ‘good’ characters, including symmetry, sigmoid shape, and possession of specialised structures (costae, for example KÜTZING 1833, SCHÜTT 1896, KARSTEN 1928, HUSTEDT 1928, among many others). Of course, over the years, and based on the experience of individual researchers, there have been differing ideas about the efficacy of certain features and their ability to explain or support placement of taxa within groups. And, as COX (2010) and others have indicated, ideas about whether symmetry or special features have changed over time, and what was thought to be ‘good characters’ in the past have been shown to not reflect evolutionary descent.

One example of the use of apparent ‘good’ or, what is sometimes referred to as, ‘conservative’ characters for the recognition of diatom genera is amphoroid symmetry. The combination of different valve mantle heights between the dorsal and ventral margins, combined with the number and structure of the girdle elements, provide an easily recognizable symmetry. Possession of those features was used to unite a diversity of forms, with differing valve morphologies, ecologies, biogeographies and cytoplasmic features (CLEVE 1895, MERESCHKOWSKY 1903b). Cleve stated »The asymmetrical form is not a sufficient characteristic for a natural family, but is merely a facies, which may occur in groups of very different types and seem to depend on the method of growth, Amphorae occurring attached to algae and other objects« (CLEVE 1895: 99). *Amphora* was retained because »If the above named large groups of Amphorae were admitted as distinct genera, which I believe they ought to be, the synonymy would be still more intricate than it is at present. I propose for this reason, that the species of the different groups should retain their generic name *Amphora*, which in

all cases signifies that they are asymmetrical Naviculae. This will also afford an opportunity of testing my views, which are entirely new, before admitting the proposed new genera« (CLEVE 1895: 100) But regardless of his point of view, the group of species remained within *Amphora* for over a century (see HUSTEDT 1930, SCHOEMAN and ARCHIBALD 1986). LEVKOV (2009) separated out one group from *Amphora*, recognizing the subgenus *Halamphora* (Cleve) Levkov at the level of genus, due to its possession of a dorsal raphe ledge, finely biseriate striae on the dorsal portion of the valve and uniseriate striae on the ventral section of the valve. A phylogenetic analysis of 30 species of the diatom genus *Amphora sensu lato* using 3 genes (SSU rDNA, *rbcL* and *psbC*) within the context of the raphid diatoms showed the origin of ‘amphoroid’ symmetry in six different lineages (STEPANEK and KOCIOLEK 2014). Amphoroid species were retained in *Biremis* (Round et al. 1990) and *Lyrella* (MANN and STICKLE 1997), and analysis of the morphology of *Amphora scabriuscula* Cleve & Grove in Cleve and a new species, *Navicula petrovii* Nevrova et al. in WITKOWSKI et al. (2014) suggests they, too, have amphoroid symmetry as a homoplasy (independently derived), and that this species is better placed within *Navicula* Bory (WITKOWSKI et al. 2014). This is just one example, of many, related to a feature that was deemed a »good« or »conservative« that has been shown to be homoplasious across several lineages of diatoms. COX (2010) also has examples where this concept can be applied, and suggests that we do not know *a priori* which features should be used to diagnose lineages, but rather those will be identified through formal analyses.

Can one feature diagnose a genus? Yes, why not? After all, each character provides evidence for or against a particular grouping of species. At the moment, the only synapomorphy to diagnose *Ulnaria* is their closed bands, at the very least a closed valvocopula; no other synapomorphy (or character) has yet been suggested to contradict that grouping of species. MORALES et al. (2014), following VAN DE VIJVER and COCQUYT (2009), suggested »the absence of spines and lack of ribbon-like colonies holding cells together by spines« also characterise species of *Ulnaria*. Such characters do indeed form part of its description but as they are both absences they hardly constitute additional evidence for the genus *Ulnaria* – but neither do they contradict it.

Does every taxon in the genus (or group) have to possess all the features used to diagnose that genus (group)? Initially this may seem an uninteresting question. By virtue of identifying features and using them to diagnose groups, it would follow that all the taxa to be included in that group should have the diagnostic feature(s). But some recently published papers in diatoms argue against this conclusion. For example, the monotypic diatom genus *Diprora* Main was described as endemic from caves in Hawaii (MAIN 2003). This diatom has valves with typical pennate symmetry, but bears no hint of a raphe system at any stage during the ontogeny of the valve (KOCIOLEK et al. 2013). Because of its symmetry and its lack of a raphe, Main suggested that it must be an ‘araphid’ diatom. It is worth remembering here that ‘araphid’ diatoms are not a natural group, so to place it in such a group is the same as declaring it to be unknown. A phylogenetic analysis of pennate diatoms using three genes (SSU rDNA, *rbcL*, *psbC*) showed *Diprora haenaensis* Main to be nested deep within the raphid pennate diatoms, being closely related to *Sellaphora*, *Fallacia* and *Pinnularia* (Fig. 2, see also KOCIOLEK et al. 2013). Thus, while never exhibiting the feature of a raphe system, we would still assign this genus to the raphid diatoms. Its phylogenetic position within this group is supported by non-morphological (molecular) data, and its lack of a raphe is due to secondary loss.



**Fig. 2.** Phylogenetic position of *Diprora* nested deep within the raphid diatoms. After KOCIOLEK et al. (2013).

A similar situation of secondary loss was described for some of the most derived species within the genus *Gomphoneis* Cleve, where these smaller species have secondarily lost internal laminae of silica (marginal lamina, axial plate), features used to help diagnose the

genus (KOCIOLEK and STOERMER 1989). Therefore, a phylogenetic context can help us understand certain cases where species within a genus (or a genus within a Family or Order) may not possess the features used to diagnose a genus (or group).

## Current state of diatom taxonomy and systematics

### Discovery and description

Estimates suggest that for Life in its entirety roughly 16,000–18,000 new taxon descriptions are added each year (MORA et al. 2011, FONTAINE et al. 2012). Diatom taxonomy adds roughly 200+ to that total, around 1.2% of newly described biodiversity (Table 1).

**Tab. 1.** Numbers of New TAXON records per year (data derived from the online Catalogue of Diatom Names, FOURTANIER and KOCIOLEK 2011). \* indicates numbers for entries up until 19<sup>th</sup> September 2011, a number we suspect is lower than it should be. The average number of descriptions is recorded to include 2011 (225) and to exclude it (252).

Year	Number of records	Number of publications
2005	244	39
2006	195	67
2007	414	42
2008	97 <sup>1</sup>	50
2009	370	61
2010	194	65
2011	62*	26*
Average number	225 [252*]	50 [54*]

Remarkably, there is a working taxonomist – Horst Lange-Bertalot – who has described nearly as many species (> 1,400; 1,145 in DE CLERCK et al. 2013; on Lange-Bertalot's contribution see KUSBER and JAHN (2003)) as the early pioneers in the field, such as Ehrenberg (1795–1876, 2,055 names, this figure includes all microalgae); Kützing (1807–1893, 2,636 names, this figure includes all microalgae), Grunow (1826–1914, 1,251 names), Hustedt (1886–1968, 1,219 names; all figures taken from DE CLERCK et al. 2013: Table 1), the first three all of whom worked a century or more before him.

Many journals are dedicated, solely or in part, to publishing new species descriptions (Phytotaxa, Nova Hedwigia, Diatom Research, Iconographia Diatomologica, Bibliotheca Diatomologica, Diatom Monographs, Algological Studies, Phytokeys). Species description is important work as it is the baseline for documenting the diversity on, or once inhabiting, the planet. But it is not the only approach to capturing diatom diversity.

### Kinds of description

Certain questions arise concerning the specifics of diatom descriptions (questions that may, indeed, be generalised as applicable to all groups of taxa), such as: How many specimens were used to formulate the description that appears in the protologue (defined as »...



everything associated with a name at its valid publication, i.e. description or diagnosis, illustrations, references, synonymy, geographical data, citation of specimens, discussion, and comments«.)? How were the specimens examined? Where are those specimens now? Were additional data sought, such as breeding behaviour, observations on live material, DNA bar-codes, and so on? Of course, no provisions or guidelines are provided in the Codes of Nomenclature (in the case of diatoms, now the International Code of Nomenclature for algae, fungi, and plants, <http://www.iapt-taxon.org/nomen/main.php>, for the online version; McNEILL et al. 2012 for the printed version). Nor should there be: the quantity of data required to support the description of any new taxon (regardless of rank) is a scientific question, related to the discovery of defining character(s), rather than a question pertaining to nomenclature, the naming of any particular taxon once discovered.

Traditionally, new diatom taxa were illustrated with line drawings, and since the 1970s line drawings have given way to photographs taken with the light microscope. Since the introduction of the scanning electron microscope as a standard in the investigation of diatom morphology, photographs derived from that source have become almost standard. Should new diatom taxa be described in the absence of evidence from scanning electron microscopy? This question requires some consideration.

Before we offer some thoughts on the question above, let us first focus on how diatomists actually behave when they record and present their data (here we ignore the inclusion of ‘additional’ forms of data – breeding behaviour, live material, DNA bar-codes – for the simple reason that the capture of the first two primarily requires light microscopy only, and capture of DNA sequence data involves technology other than a microscope). For simplicity, we focus on just one year, 2008 (as it happens, other years in the five year period documented in Table 1 have more or less the same figures as 2008).

In 2008, 97 new diatom nomenclatural acts were made, appearing in 50 publications, diverse in content, ranging from those dedicated to diatom studies (e.g. *Diatom Research*, *Diatom and the Proceedings of the International Diatom Symposium*), those dedicated to phycology (e.g. *Phycologia*, *Phycological Research*), those dedicated to botany (e.g. *Botany*, *Iheringia*, *Séries Botânica*), through to journals with a much broader scope (e.g. *Мікробіологія і Біотехнологія* = *Microbiology and Biotechnology*). Of the 97 names introduced, 28 were new combinations and one was proposed as a substitute name, leaving 68 new taxa described for that year. It is the last group that is of interest here. Practically all 68 new names published in 2008 were documented with observations gained from both light and electron microscopy (although the numbers of each kind of image varied; on occasion, light micrographs out-numbered electron micrographs) – two names were accompanied with only light micrographs, two with only scanning electron micrographs and one with a combination of light, scanning- and transmission electron microscopy. Thus, if a consensus perspective was to be adopted, one might argue that as a standard for descriptions of new diatom taxa they should have, at the very least, both light- and electron microscope images of relevant structures as supporting evidence. Documenting the exact specimens photographed on a slide or stub (by giving coordinates of the specimens) should be considered by diatomists as a ‘best practice’.

The counter view relates to two specific viewpoints, one practical, the other philosophical. The practical issue concerns the availability of specimens, their rarity, a problem particularly pertinent when fossil specimens are the primary source of evidence (but the problem does not relate exclusively to fossils, e.g. KULIKOWSKY et al. 2012, THESEN et al. 2012

for relevant discussion with a non-diatom example). In general, when only a few specimens are available (restrictions on collecting, availability of herbarium material, access to regions, and so on) and those specimens have only been found on glass slides, it would appear useful, if not necessary, to still document them using the light microscope rather than delay and err on the side of caution in the expectation that the future will yield further relevant specimens. For example, by the mid-1950s *Synedra berolinensis*, known for nearly half a century, only had a handful of drawings, most copied from one flora to another (WILLIAMS, 2013). Given the ever-changing environmental conditions as well as the disturbing frequency of man-made disasters, further specimens may never be found, as the areas harbouring the original specimens may be altered (or even destroyed) beyond their original condition. Without publication of the original record (details of the original specimens), a part of life on Earth that would have been documented will now disappear forever.

Second, if species names are supposed to represent simple hypotheses about order in nature, then such hypotheses require further examination when more data comes to light, regardless of how well documented any particular taxon was in the first place. To be sure, this may not be generally true for the past where, in some cases, a rather poor line drawing is all that was offered – and all that is left. However, advocating as least light microscopy means that a permanent slide has to be made and it should follow that the preservation of that slide (specimens) is also of significance. Taxonomy, as a science, has an especially close relationship with its past for these two very good reasons.

Given the arguments above concerning rarity, light microscopy alone may be offered but justification for adopting such a procedure would be secured by listing in the protologue all specimens examined (including, of course, the single gathering used for the holotype of a new species) a practice up to now not universally adopted by diatomists (but see ROSS 1995, for an exemplary account) but is by most other botanists.

### **Phylogenetics and revisionary monographs**

Both of these approaches, phylogenetic and revisionary studies, are of significance as this is the process whereby both known and unknown taxa are treated in a specified framework to understand their placement in the »Tree of life« (their phylogenetic placement), yielding a classification system derived from formal analysis of their relationships. Some associate this kind of work exclusively with molecular data (see MANN and EVANS 2007), which have indeed provided dramatic insights and unprecedented contributions to our understanding of diatom phylogeny (SIMS et al. 1996, ALVERSON 2008, RUCK and THERIOT 2011, LUNDHOLM et al. 2002, KEMARREC et al. 2011, RIMET et al. 2011, STEPANEK and KOCIOLEK 2014). But these contributions have come to the fore because they are methodologically set up to provide ready, formal analysis of relationships. These methods are fraught with challenges similar to those that occur in formal studies of phylogeny based on morphology (making of certain assumptions, BAKER and GATESY 2002). There are studies with formal analyses of morphological data (see for example WILLIAMS 1985, 1990, KOCIOLEK and STOERMER 1986, 1988, 1989, 1993, JULIUS and TANIMURA 2001, EDGAR and THERIOT 2004, RUCK and KOCIOLEK 2004). Regardless of the discovery of new sources of data, a purely morphological approach remains necessary for the analysis of fossil diatoms, which at the level of genus and species may include more formally described taxa than all the recent taxa combined.

## A call for revisionary studies and formal phylogenetics

Whatever the approach, molecular, morphological, or both, there is a pressing need for genus- and family-level revisionary studies. Many diatom genus names in everyday use have **never** had a systematic revision; the same is true for many higher levels of classification. For example, barely any of the 11 subclasses, 36 new orders, 4 new suborders 42 new families and 19 genera proposed in ROUND et al. (1990) have never been analyzed in any formal, systematic way. Just as molecular data have turned several assumptions about diatom relationships on their head, to have far-reaching implications for our understanding of diatom evolutionary relationships and requiring a new approach to the way we talk about and teach students about the group (WILLIAMS and KOCIOLEK 2011), we believe that such will be the case once formal analyses of genus- and higher level groups commences in earnest. We are agnostic as to the types of data that should be used in these formal analyses, and in fact, as stated previously, morphology will be necessary for revisionary and phylogenetic analyses for many extinct diatom taxa. It is time for those involved in diatom studies to engage in this important work. Without these formal analyses it will be nearly impossible to advance our knowledge of the many facets of diatom biology and the practical applications of these remarkable organisms.

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