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What's in a name? – Diatom classification should reflect systematic relationships.

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Large numbers of diatom taxa are currently being described each year and molecular data sets are providing phylogenetic evidence that challenges the traditional systematic arrangement of diatoms, but is such information being integrated into the classification? The traditional diatom classification originated as an aid to identification rather than as an arrangement expressing perceived relationships, and characters for identification continue to bias taxonomic descriptions. Reference to types for nomenclatural purposes has resulted in overly narrow taxon descriptions; i.e. types have been considered representative specimens (typical) of taxa, whereas they may not lie at the centre of the range of variation of a taxon. This paper discusses how taxonomic concepts are subject to change in the light of new data and that such changes should be reflected in the systematic arrangement. It presents some thoughts on character choice and the need to make appropriate comparisons before new taxa are erected. The importance of the suprageneric classification is also discussed.

Keywords: Identification, classification, diatom, type specimens, terminology

Introduction

In the introduction to their catalogue of diatom genera, FOURTANIER and KOCIOLEK (1999), showed how the rate of publication of new diatom genera had varied over the preceding two centuries, but was, at the time of writing, in an exponential growth phase. A high rate has been maintained (95 new genera since 1999), while more than 2,000 new species have been described over the same period (FOURTANIER and KOCIOLEK, 2007). However the integration of such new taxa into a meaningful systematic framework is much rarer. Even if an author refers a new genus to a family, e.g. Naviculaceae Kützing, it is unclear whether such an allocation refers to the family as originally defined (KÜTZING 1844), or in the sense of a particular publication, e.g. ROUND et al. (1990). Whereas the description of species and genera has proceeded apace, consideration of generic and suprageneric relationships has been largely neglected. Some attempts have been made to revise higher groups in the light of molecular phylogenetic analyses, cytological and reproductive characters (MEDLIN and KACZMARSKA 2004, MANN in ADL et al. 2005), but these efforts appear

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to have had little impact on those investigating previously unexplored or understudied areas and habitats. Most interest seems to have been directed to recording new taxa (using traditional criteria) rather than understanding how they relate to each other (using a variety of approaches).

While recording and describing new taxa is important, and correct identification underpins all other research (e.g. ecological, life history, phylogenetic, stratigraphical) into those taxa, the description of new taxa cannot occur in a vacuum, but must take account of what is already recognised and described. With the apparent dichotomy between traditional approaches to describing new species (e.g. LANGE-BERTALOT and colleagues, see METZELTIN and KUSBER 2001) and phylogenetic analyses based on molecular biology (MEDLIN and KACZMARSKA 2004, BRUDER and MEDLIN 2007, KOOISTRA et al. 2007, MEDLIN et al. 2008, RAMPEN et al. 2009), it is appropriate to evaluate whether the current paradigms of diatom classification are helping or hindering diatom taxonomy and systematics.

Paradigms

WILLIAMS (2007) provided an overview of the development of diatom classification, showing how, with its emphasis on valve morphology and particular wall features, it has been dominated by a desire to aid identification (explicitly or implicitly) rather than reflect relationships. 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. It may be argued that the latter simply reflects the evolution of the groups, but on the other hand it may indicate that even when molecular studies underlie an analysis, diatomists interpret the data in terms of superficial (shape, symmetry) rather than structural (type of pores, presence of raphe, fultoportulae, rimoportulae) features. Alternatively, perhaps we still know too little about some of our specimens to compare and discuss the structural features adequately.

Because H.L Smith's classification was developed to help identify specimens (and most other morphologically-based classifications are essentially variants on this), diagnoses and artificial keys are inextricably linked. Species and generic descriptions focus on the characters that allow discrimination of taxa (at whatever level), rather than shared characters that group specimens into species, species into genera, and so on. Thus they tend to rely on frustule morphology at the LM level, particularly shape, symmetry and the presence or absence of distinctive features. For example, the traditional separation of the freshwater araphid genera, *Asterionella*, *Diatoma*, *Fragilaria*, *Hannaea*, *Martyana*, *Meridion*, *Synedra, Tabellaria*, and *Tetracyclus* rests on the particular combinations of valve symmetry, the presence or absence of septa, presence or absence of costae, mode of colony formation or its absence in each genus (Tab. 1). However, more detailed studies of valve structure and the use of cladistic analysis revealed the heterogeneity of some of these genera, and the likelihood that generic boundaries were incorrectly drawn for others (WILLIAMS 1985; WILLIAMS and ROUND 1986, 1987). A recent molecular analysis (MEDLIN et al. 2008) indicates that there may also be problems with the genera as defined by WILLIAMS and ROUND (1986, 1987), highlighting the need for more studies on these taxa.

Tab. 1. Distribution, as presence (+) or absence (–), of characters traditionally used to distinguish freshwater araphid diatom genera.

	valve symmetry				septa	costae	habit			
	isopolar	heteropolar	Bilaterally symmetrical	dorsiventral	present / absent	present / absent	solitary cells	attached substratum at one end	attached by pads of mucilage, zig-zag or stellate colonies	attached valve face to valve face
Asterionella	+	+	+	–	–	–	–	–	+	–
Diatoma	+	–	+	–	–	+	–	–	+	+
Fragilaria	+	–	+	–	–	–	–	–	–	+
Hannaea	+	–	–	+	–	–	+	–	–	–
Martyana	–	+	+	–	–	–	+	+	–	–
Meridion	–	+	+	–	–	+	–	–	–	+
Synedra	+	–	+	–	–	–	+	+	–	–
Tabellaria	+	–	+	–	+	–	–	–	+	–
Tetracyclus	+	–	+	–	+	+	–	–	–	+

Identification v. classification

Thirty years ago, I pointed out that there has been confusion between the use of characters for diatom identification and their use for systematics (COX 1979). Whereas shared characters are fundamental to recognising relationships expressed by systematics (cladistic theory demands that these are shared derived characters), distinctive differences (that may or may not have systematic significance) are required for identification. Thus the presence of a raphe system defines the monophyletic raphid diatoms, but it may be subtle differences in details of the raphe system, e.g. its external path including details of the polar fissures, presence or absence and type of internal ribs beside the raphe slits, that are needed to discriminate between raphid diatoms. Thus, oppositely deflected central raphe fissures combined with forked external polar raphe fissures aid identification of *Neidium* spp., while the presence of strong internal ribs beside the raphe slits are characteristic of *Frustulia* spp.

Valve outline and symmetry were critical characters in H.L. Smith's artificial system. Both are relatively easy to define and to observe, but particular shape and symmetry characters can be shared by structurally diverse taxa. 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. Nor are all members of a genus necessarily the same shape, e.g. *Climaconeis* includes both straight and lunate-valved species (COX 1982) and slight dorsiventrality is seen in some members of otherwise 'bilaterally symmetrical' genera, e.g. *Lyrella* (MANN and STICKLE 1997), *Placoneis* (COX 2003).

Over the last thirty years there have been major developments in systematic methods, with a shift from phenetics to cladistics and the development of molecular biology. However, discovering shared (derived) homologous characters remains critical to the delimitation of 'natural' groups. In this search for informative characters it is necessary to understand diatom structure and development rather than simply relying on LM morphology. The subdivision of *Navicula* sensu lato reflects the discovery that similarly shaped, bilaterally symmetrical raphid diatoms have different underlying frustule structures (raphe, areolae, cingulum), as well as types and numbers of chloroplast, modes of sexual reproduction, etc. As more functional characteristics linked to the survival of the organism, these are potentially more accurate guides to relationships than shape, symmetry and stria arrangement.

Typological method

Accompanying the process of systematics as it seeks to reflect the relationships between organisms, the codes of nomenclature provide rules that govern how taxa (of any rank) are named. The rules are concerned with the validity and legitimacy of names, their application and the choice of the correct name (ROSS 1993). Names are fixed to specimens, the oldest name has priority, and the rules govern how to decide what should be the correct name of a taxon when several names have been applied to it. The rules do not address the definition of the taxon concerned, but only apply to the name. As ROSS (1993) stated, »it is names, not the taxa to which they apply that have types and, although such expressions as »the type of the species« are often used, these are shorthand for »the type of the specific name«.

It is therefore possible that the »type specimen« of a species is not the most typical (representative) example of that species; the author may not have been aware of the full morphological range of that species when describing it. This is particularly likely if a species is described from only one or a few specimens in a single sample. If on the other hand, large populations from several sites are available for study before describing a new species, it is possible (and advisable) to choose a representative specimen as the nomenclatural type.

A generic name is similarly linked to a specimen via the generitype, the species on which it was based. With respect to early generic names, this often creates a problem because the author may have included a number of unrelated species in the genus, which would now be separated into two or more different genera. It then becomes necessary to distinguish and name the newly recognised taxa. The concept of the genus has changed, and this must be expressed via its systematic treatment, but the original names remain linked to the same specimens (Fig. 1). With closer examination it may become apparent that the generitype too is not the most representative species within the genus, but because of the rules its status cannot be changed.

Changing taxonomic concepts

Because taxonomic descriptions are based on the information available at the time of writing and may be heavily influenced by prevailing paradigms (such as the previously held 'live characters are uninformative or misleading'), they should be considered open to amendment in the light of new information and new analyses. However, it seems that some prefer to describe new genera rather than to amend existing ones. For example, if the interpretation of a genus is too tightly limited to the characters seen in the generitype, closely re-

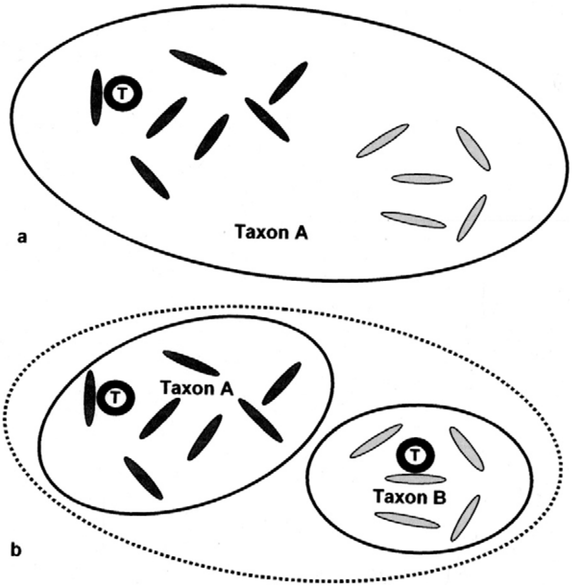

Fig. 1. Relevance of type specimens to changing taxon concepts. a – Distribution of specimens of a variable taxon A in morphological space, with the historical type (T) at the edge of the morphological spectrum. b – Taxon A has been subdivided, but is still defined by its historical type. In defining taxon B, a type is chosen at the centre of its morphological space.

lated species may be unnecessarily separated into new genera. Was it assumed that the generitype is typical of the genus and is not just one member of a group defined by particular characters? The extreme case is of course the creation of tightly defined monotypic genera.

In the case of *Navicula*, *Navicula tripunctata* shows a suite of characters that helped to define *Navicula* section *lineolatae* (HUSTEDT 1930, 1927–1966) and *Navicula* subgenus *Navicula* (PATRICK 1959). However, if we compare it with other species that have generally been accepted as members of the same group, it is possible to recognise a range of variation in a number of characters, including raphe fissures, accessory ribs, stria arrangement and pores around the valve apices (COX 1999b). Does this mean that we should restrict *Navicula* to those species that share all aspects of their characters with *N. tripunctata*, or do we look for the group that contains the latter and describe the genus for the group? If we circumscribe the group before seeking to describe its salient characters, some of the features of the generitype may not appear in the description. But the generic description should be wider than the generitype description.

When a new species with a unique combination of characters is discovered, establishing its closest relatives requires careful comparison with potentially a large number of different taxa, a process that should be undertaken with as open a mind as possible. It is also important to avoid a priori judgements on the relative importance of particular characters until all the evidence has been assembled, as well as ensuring that morphological characters are carefully evaluated from specimens to ensure that previous ways of describing characters do not mislead. Thus, as in the case of *Climaconeis*, the inclusion of both dorsiventral and bilaterally symmetrical taxa in the genus (COX 1982) was based on the shared structural and chloroplast characters, rather than allowing valve symmetry to be an over-riding character that would split the genus. But if the original generic description of *Okedenia* had been tightly adhered to, *Okedenia inflexa* would not have been transferred to *Climaconeis*, but have remained in its own monotypic genus.

In an elegant morphological study of *Attheya,* CRAWFORD et al. (1994) investigated four new species, and two taxa previously placed in *Chaetoceros*, one of which had been transferred to *Gonioceros*. The study revealed the characteristic structure of the horns at the corners of the cells, one of the diagnostic characters of *Attheya*, providing a link among these taxa that is supported by reproductive and ecological evidence. However *Attheya* species differ variously from each other on characters that are often considered genus specific. Nevertheless, relying on such character differences would generate several monotypic or very small generic groupings. CRAWFORD et al. (1994) argued against this, treating them all as members of one genus. Subsequent investigations of the phylogenetic position of *Attheya* using molecular techniques (KOOISTRA et al. 2007, RAMPEN et al. 2009) confirm that its species form a distinct group, although its phylogenetic position varies between different analyses.

Characters and character states

Whatever the group of organisms the choice of characters on which they are compared is critical to the outcome of that comparison. Comparative biology relies on the evaluation of homologous characters, those shared as a result of common ancestry, rather than analogous characters, which may be functionally similar, but derived independently. And homologous features can be expected to display detailed similarities, for example in position, structure and development. Molecular biology similarly relies on the comparison of presumed homologous sites along sequences.

Whereas there are only four possible character states for any one site along a sequence, and these can be unequivocally identified as either A, T, C or G (although secondary structure and codon motifs are also considered when aligning), defining morphological characters and character states is ostensibly a more subjective exercise. But, even for diatoms, it is possible to utilise positional, structural and developmental information to interpret cytological phenomena and wall features. However, the way in which such features are described can have a significant impact on their interpretation. The terms used to describe particular features across a number of taxa will affect the comparisons between those taxa and hypotheses of relationships.

For example, MANN (1981) used the term vola (originally for hand-like occluding structures in centric diatoms [ROSS and SIMS 1972]) to describe any flap-like pore occlusion, whereas COX (2004) found that there are two types of flap-like occlusion in the Cymbellales that differ from volae in centric diatoms and are better discriminated by the use of two terms, foricula and tectulum. Following MANN (1981), volate areolae would be recorded for a wide range of diverse diatoms, whereas COX'S (2004) terminology facilitates differentiation between the different types of occlusion. Similarly, discrimination between a stauros and a fascia reflects underlying differences in the way the solid transverse areas are formed, a stauros being a solid structure ab initio, while a fascia is formed by silica infilling between virgae later in valve development (COX 2001). Whether solid areas of silica interrupting transverse striae are similarly the product of silica infilling has not been investigated, but could be relevant to determining the affiliations of genera such as *Fogedia* and *Stenoneis*.

As mentioned above (paradigms) superficial morphological appearance (LM) rather than structural information (as revealed by SEM) has often been used to define taxa, but even when structural features have been incorporated, their evaluation has usually ignored underlying developmental processes and the possibility of phenotypic plasticity. The occurrence of Janus cells, in which the valves of a single cell (genotype) differ significantly, reveals the potential phenotypic response (STOERMER 1967, MCBRIDE and EDGAR 1998), but the findings have not been incorporated into species descriptions. Similarly, size reduction may have such a marked effect on valve outline that the extremes would be identified as different taxa (COX 1985).

Supra-generic classification

While many new species and genera are being described, there have been very few recent revisions to the higher level classification since ROUND et al. (1990). The most notable was that by MEDLIN and KACZMARSKA (2004), who delineated two new subdivisions (Coscinodiscophytina and Bacillariophytina) and recognised the Mediophyceae as a new class, based primarily on molecular data, although they integratedcytological and reproductive information where this was available. These major groups were adopted by MANN (ADL et al. 2005), albeit noting that the Coscinodiscophytina and the Mediophyceae are both paraphyletic. MANN also divided the former subdivision into six groups, again based on molecular phylogenetics, the characteristics of the groups being very briefly circumscribed with reference to wall features (ADL et al. 2005).

On the other hand, for one of the relatively few family descriptions of the late 20th century, the Cymatosiraceae, the authors considered reproductive behaviour important for its systematic position (HASLE et al. 1983).This family was erected to include two previously known genera, *Cymatosira* and *Campylosira*, and seven new genera, *Plagiogrammopsis*, *Brockmanniella*, *Minutocellus*, *Leyanella*, *Arcocellulus*, *Papiliocellulus* and *Extubocellulus*, four of them based on previously known species, and three on new species. Despite their elongate valve shape, the previously known species had not been considered pennate diatoms (SIMONSEN 1979), but had been placed in the 'centric' Biddulphiaceae. Interestingly, the primary reasons for placing the new family among the centric diatoms were the possession of flagellate male gametes and auxospore formation, not the more traditional wall structure or valve outline (HASLE et al. 1983).

With respect to the raphid diatoms, the inclusion of chloroplast characters in morphological analyses (COX and WILLIAMS 2000, 2006) can produce interesting differences in supra-generic groupings compared to their treatment by ROUND et al. (1990), often correlated with structural differences, e.g. areola type. Thus, *Craspedostauros,* which would traditionally have been placed within *Stauroneis*, grouped with *Mastogloia* and *Aneumastus* (COX and WILLIAMS 2000), while genera of the Berkeleyaceae were separated in different parts of the tree (COX and WILLIAMS 2006) based on different numbers and arrangements of chloroplasts. The latter study also indicated that *Achnanthes* sensu stricto should be moved to the Mastogloiales. Based on molecular phylogenies (e.g. SIMS et al. 2006, RAMPEN et al. 2009), *Achnanthes* sensu stricto is close to the Bacillariales rather than most naviculoid diatoms, but two »*Stauroneis*« species, *S. constricta* and *S. simulans* are close to *Achnanthes* in one study (RAMPEN et al. 2009). The former has been transferred to *Craspedostauros* (COX 1999a), whereas the generic affinity of the latter is uncertain, but probably not **to** *Stauroneis*.

In discussing the systematic position of *Achnanthes* sensu stricto it was suggested that the other genera of the Achnanthales are probably more closely related to different biraphid genera than to each other (COX 2006). Developmental studies have revealed that the monoraphid condition is derived; monoraphid diatoms initiate raphe slits on both new valves after mitosis, but one is subsequently infilled with silica (BOYLE et al. 1984). The association of the monoraphid condition with a variety of pore types suggests that raphe loss has occurred on more than one occasion, and hence the order Achnanthales should be rejected. This is also supported by the relatively limited molecular data available on monoraphid diatoms (SIMS et al. 2006, BRUDER and MEDLIN 2007).

Higher level classifications are assumed to reflect and interpret perceived relationships between genera and are essential to furthering our understanding of the group because they present hypotheses of relationships that can be tested. The description of new taxa without any reference to their relationship to other taxa is little more than stamp-collecting. We currently have more names and types than ever but unless they are integrated into a higher level classification they do not contribute to our understanding of the interrelationships and evolution of the group. Nor in many cases do we have detailed ultrastructural, let alone cytological, reproductive or molecular, information on them.

Making appropriate comparisons

The history of diatom studies reveals how the acquisition of new data (SEM, TEM, cytological, ontogenetic, reproductive, molecular) can challenge established assumptions, but there have been relatively few, recent, significant changes to the systematic arrangement of diatoms to reflect that knowledge. ROUND et al. (1990) introduced many new orders and families and included monoraphid diatoms within the sub-class Bacillariophycidae, rather than according them the same rank alongside the Eunotiophycidae, but the old, centric, araphid pennate, raphid pennate groupings remained. MEDLIN and KACZMARSKA (2004) made more radical changes by splitting the traditional centric group into two classes and combining all the pennate diatoms in another class. But while a number of research groups and individuals consider how to reflect perceived phylogenetic relationships in formal classifications, there is a steady stream of publications that seem to be directed simply to recording and describing taxa, (particularly non-centric diatoms) without integrating them into a systematic framework (e.g many issues within the Iconographia Diatomologica series). Furthermore there often seems to be a reliance on the generitype as the guide to the characters (as representative) of a genus, rather than referring to the spectrum of variation within the genus.

Comparisons between species and/or genera are also often restricted to examples occurring in the same type of habitat, e.g. all freshwater or all marine, rather than considering that the closest living relatives might be found in another habitat, or that the environmental stresses experienced by inland subaerial or terrestrial diatoms might be closer to those experienced in the marine littoral than in freshwater. The effects of environment should also be considered, including whether particular types of variation are linked to particular environmental variables. For example, changing conductivity may be responsible for the phenotypic plasticity exhibited by Janus cells. The valves within *Mastogloia* Janus cells were identified as *M. grevillei* (biseriate striae) and *M. elliptica* var *dansei* (uniseriate striae) (STOERMER 1967). The former is considered a freshwater and the latter a brackish water diatom. Other types of heterovalvy, particularly in monoraphid and filamentous diatoms have less frequently been allocated to different taxa, probably because heterovalvy is not a function of environment, or valves and frustules of filamentous diatoms remain linked together.

Comparisons of new material against published descriptions and illustrations can provide clues to identity and relationships, but any published description is that author's interpretation of their material, and illustrations may not provide all the relevant information on morphology and structure. It must also be remembered that the author wrote at a particular time and will have interpreted the material in the light of prevailing paradigms, may have used terminology in a different way, and may not have investigated characters that were considered uninformative at that time. In other words, there is no substitute for looking at specimens, and evaluating them character by character.

For example, two *Skeletonema* taxa were present in the material from which *Skeletonema costatum* was originally described but, although he illustrated both morphs, GREVILLE (1866) did not describe them as different species. *Skeletonema costatum* thus became a catch-all for many slightly different taxa, all with the characters described by Greville. Molecular studies highlighted the existence of more than one taxon (SARNO et al. 2005), and because it was possible to link one of them to his drawings and hence to an individual specimen, that name could be fixed to one morph (designated as the lectotype of *S. costatum*) while the other could be described as a new species (ZINGONE et al. 2005).

Conclusions

While recording and describing new taxa constitute an important contribution to evaluating diatom diversity, they should not be regarded as an end in itself, but part of the process of discovering how organisms have evolved and are adapted to the habitats they occupy. To that end, we should consider not only the entities we discover, but how they relate to each other, their ancestors and the rest of the biosphere.

I therefore suggest that, in describing new taxa (at whatever taxonomic level) as many as possible of the following points should be addressed:

- Obtain as much morphological information as possible, such as live structure, LM and SEM of frustules (valves + cingulum), including exterior and interior details, TEM of pore substructure.
- Assess the morphological variability within the taxon, comparing within and between sites if multiple samples are available.
- Compare all the above features with as wide a range of taxa as possible (from specimens, not just illustrations or published descriptions), across a range of habitats, without assuming (a priori) that any one character is more significant than any other.
- Ensure that the patterns of variation in different characters have been documented (LM and EM).
- Determine what groups of specimens can be delimited (Use appropriate morphometric and molecular phylogenetic analyses) and how those groupings are supported.
- Give a full description of all features of the new taxon (taxa) and their range of variation (not just those typically given in differential diagnoses).
- Place new taxa in relation to existing ones, and give reasons for the placement.
- If new taxa group with members of an existing higher taxon, but exhibit characters not previously recorded for the higher taxon, be prepared to modify the diagnosis of the latter.

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