

Some commentary on molecules and morphology, species and higher taxa in diatoms, with a note on the relationships of the genus *Cistula* Cleve

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INTRODUCTION

This paper formed part of the “Diatoms are going molecular: implications for identification, taxonomy and phylogeny” session, contributed as a commentary on the significance of morphology to modern systematics as the molecular age develops. Molecular sequence data for diatoms have been available since the late 1980s (Medlin et al. 1988) but only recently made easy enough to acquire in sufficient quantities that their relevance is seen as self evident, relating to problems posed by “identification, taxonomy and phylogeny”. Seen from a general perspective, a recent summary suggests the following: “Revision of species taxonomy in diatoms increasingly requires a rigorous, multidisciplinary approach incorporating crossing experiments and molecular genetic analysis, as well as careful morphological analysis” (Vanormelingen et al. 2007).

One might imagine that this prescription suggests what is required to discover species taxa. Yet, surprisingly, it contains no such thing. It simply suggests: Revision of species taxonomy requires lots of data. Is that true? Whatever the answer to that question might be (and it is an empirical one), data sources are not equivalent to a method(s) of discovery no matter how self-evident it might appear.

Now fashionable, ‘cryptic species’ – those hidden from view – are being discovered everywhere, largely as a result of molecular data. ‘Cryptic clades’ (higher taxa) are also becoming fashionable: “Several major molecular clades are cryptic, with no or few morphological or life history traits that can be convincingly argued to be synapomorphies” (Mann in Adl et al. 2005: 431, note 18).

Rather than examine the notion in detail, we first present some basic ideas, hidden by the passage of time, concerning ‘cryptic species’ and their meaning. That “revision of species taxonomy” is understood (mistakenly in our view) as resolved (or possibly resolved) by gaining many varied datasets, it leaves the question of higher taxa (‘Cryptic clades’) unanswered, a topic we briefly discuss using the genus *Cistula* Cleve as an example.

Species (Taxa)

With respect to species and their differentiation, molecular data are increasingly used to solve the apparent problem of “cryptic species” (Evans 2007). Sixty years ago Ernst Mayr wrote of “cryptic species”, referring to them as “sibling species”: “Many of the cases of so-called ‘ecological or physiological’ races of the literature are nothing but sibling or cryptic species” (Mayr 1947: 282; Mayr never let go of this view, see Mayr 1996). “Sibling species” were discussed even earlier “...pairs or larger groups of related species are so similar that they are generally considered as one species, or at least have in the past for a long time been mistaken for one another” (Mayr 1940: 258).

The idea relates not to the efficacy of data in resolving the question of species discovery but to a particular species concept: “Species in sexual cross-fertilizing organisms are reproductively isolated populations. Such populations may or may not be distinguishable

in morphological characters. Mayr (1940) has proposed the designation 'sibling species' for species that are morphologically similar or identical ...The theoretical interest of sibling species lies in that their existence shows that reproductive isolation may arise without divergence in morphological traits, and that physiological differences are not necessarily accompanied by morphological ones" (Burla et al. 1949: 300). Whatever truth there may be in that final sentence, the original notion of 'cryptic species' was tied to a particular theory that *explains* species existence ("Species ...are reproductively isolated populations") rather than any particular observation or proposition of how to species taxa are *discovered*. As Mayr embraced the populational view of species 'origin', he created a species concept that reflected an integrated, but heterogeneous, breeding population continuously moulded by the forces of natural selection. Species, as populations (biological entities), were promoted to replace the idea that species were taxa (diagnosable units) with "The primary criterion of species rank as a natural population is reproductive isolation" (Mayr 1963: 31). Thus his *concept* was designed to *explain* what might be *discovered*. In any case, the discussion of 'cryptic species' in the 1940s concerned evidence other than molecular, hence these data were not required to find solution to the problem – if it was a problem at all.

Rather than state the problem, perhaps illumination is possible by considering the solution: Where once one species was recognised, now there are many. That solution is the everyday experience of working taxonomists. The appropriate question for systematists is: How might such units (taxa, species) be discovered?

As opposed to explanation, species appear to be "diagnosable by a unique combination of character states". After all, if diatom diversity is not known, what is there to explain?

Species, like any other taxon, can be regarded as testable hypotheses. That is, further study revealing further characters may suggest alternative character distributions. Each character set (data source) requires evaluation when conflict occurs, rather than simply giving primacy to breeding (a primitive trait) – or, as is now being suggested, molecular data. No data source has or can have primacy. Species discovery – like taxon discovery in general – is not an issue of data sources.

Higher Taxa

Taxon discovery relates to all levels in the systematic hierarchy: species, genus, family, order, etc. Consider what is known of the genus *Cistula* (*Cistula* currently has one species and a variety; a fuller account is in preparation):

Cistula (Fig. 1, 2) currently resides in the family Amphipleuraceae Grunow alongside three other genera: *Frickea* Heiden, *Amphipleura* Kütz. and *Frustulia* C.Agardh. Round et al. noted that "the structure of *Frickea*, in particular the raphe system, the fineness of the valve structure and the elongate helictoglossa, suggests a relationship with *Frustulia*" (Round et al. 1990: 534). It is not clear what sort of relationship that implies. Nevertheless, they somewhat more directly note that "*Frustulia* is most closely related to *Amphipleura*" (Round et al. 1990: 538). These notions may be represented as a branching diagram (Fig. 3a), which captures the two aspects of relationship: that *Frickea*, *Amphipleura* and *Frustulia* together form a monophyletic group, named as the family Amphipleuraceae (Fig. 3a, node 2) and that *Amphipleura* and *Frustulia* form a monophyletic group (unnamed) nested within that larger group (Fig. 3a, node 1). Other than its inclusion in the Amphipleuraceae, the relationships of *Cistula* was not considered.

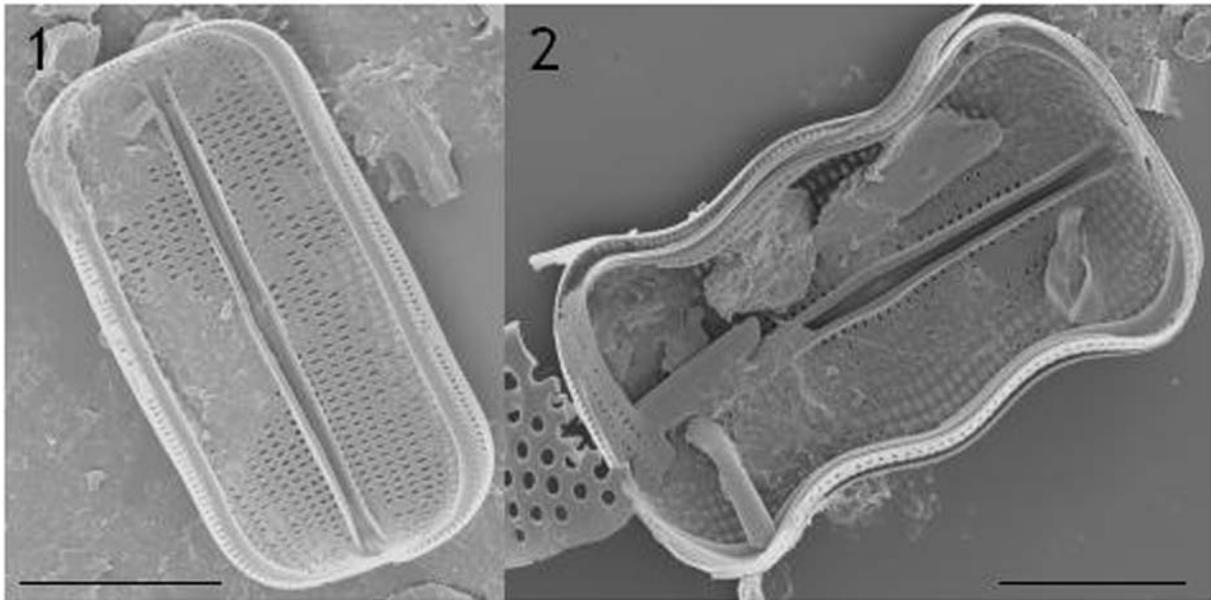


Fig. 1-2. SEM of *Cistula*. Fig. 1 *Cistula lorenziana* Grunow. Fig. 2. SEM of new species of *Cistula*. Bar = 10µm, specimens from Palawan, the Philippines.

Morphological Evidence

The diagram in Fig. 3a implies that there is evidence (characters, homologies) supporting both nodes 1 and 2.

The following morphological characters were used in the analyses: internal central and polar endings similar or dissimilar; presence or absence of accessory rib; form of external central raphe and polar endings; form of helictoglossa; relationship of helictoglossa with rib; positioning of raphe; relationship of raphe sternum and rib; presence or absence of cibra, hymens and volae; morphology of areola; form of external areola openings and internal central fissure morphology.

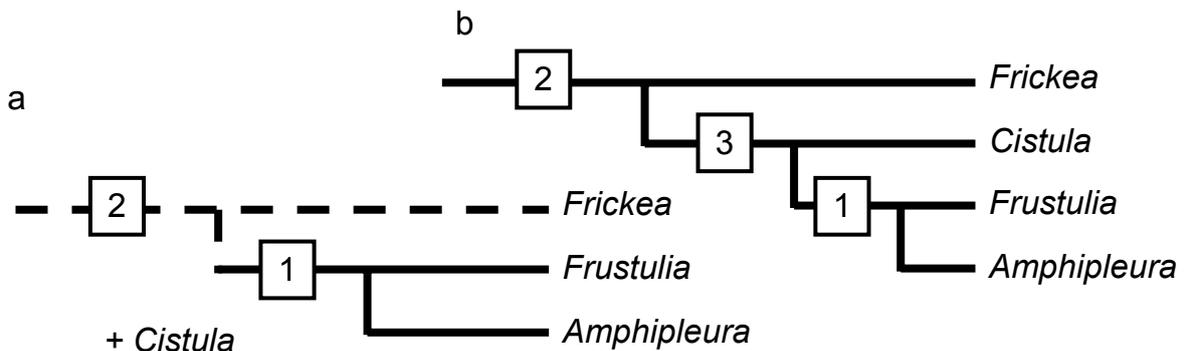


Fig. 3. Relationships of the Amphipleuraceae. 3a: Relationships as implied by Round et al. (1990); 3b: Most parsimonious tree from 14 characters.

Morphological Analysis

Our preliminary dataset consists of 10 binary and four multi-state characters. *Petroneis* Stickle & D.G.Mann was used as outgroup, as it is one of the earliest biraphid diatoms (Kociolek & Stoermer 1986). Parsimony analysis of these data yielded one most parsimonious tree (length 19, ci 100, ri 100, using Hennig86 (Farris 1988), with *ie** [implicit enumeration], all characters were unordered), (Fig. 3b).

RESULTS & DISCUSSION

The diagram in Fig. 3b suggests two monophyletic groups: *Frustulia* and *Amphipleura* are most closely related, as suggested by Round et al. (1990), based on the synapomorphy of the helictoglossa being fused with the accessory rib, (Fig. 3b, node 1); *Cistula* is most closely related to the group *Frustulia* and *Amphipleura* based on the relationship of raphe sternum and rib and the elongate external areola openings (Fig. 3b, node 3).

Further data (molecules or morphology) may contribute to our understanding of these relationships, as applied to nodes (1-3) discovered through analysis. Nevertheless, evidence may be based on prepared specimens in established collections. Of course, it may well be advantageous, even appropriate, to find new specimens, still living, isolate them, extract DNA sequences, analyse them, compare the results to what is already known. Yet, in many instances, all that remains are museum specimens. These often provide sufficient data for determining relationships, species or otherwise, even if that is in the form of preliminary hypotheses of relationships among species, genera, families, and so on – even among the parts that were once considered species.

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