Phytotaxa 217 (3): 249–264
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.217.3.2

Towards a phylogenetic classification of species belonging to the diatom genus *Cyclotella* (Bacillariophyceae): Transfer of species formerly placed in *Puncticulata*, *Handmannia*, *Pliocaenicus* and *Cyclotella* to the genus *Lindavia*

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Abstract

Cyclotella is a commonly encountered name in the diatom literature. The name is attached, however, to a historically vaguely defined and polyphyletic genus whose taxonomy and systematics remain muddled despite numerous taxonomic treatments. One recent chapter in this history concerns species informally known as the "*Cyclotella comta*" group, which have one or more rimoportulae on the valve face. These species were grouped into a new genus, *Puncticulata*, a name that has been applied inconsistently since its introduction. The name *Puncticulata* eventually was shown to be illegitimate, as some species had once been classified within *Handmannia*, which had nomenclatural priority. An inventory of names within *Cyclotella sensu lato* revealed that both *Puncticulata* and *Handmannia* are later synonyms of *Lindavia*. We identify a rimoportula positioned on the valve face as a synapomorphy for a group of taxa with the *Cyclotella comta* and *C. ocellata* bauplans (including *Pliocaenicus*), and accordingly, we transfer taxa with this synapomorphy into the genus *Lindavia*.

Key words: *Cyclotella*, *Handmannia*, *Lindavia*, Thalassiosirales, diatom, *Puncticulata*, rimoportula

Introduction

As traditionally conceived, *Cyclotella* (Kützing 1834: 535) de Brébisson (1838: 19) is the most taxonomically, ecologically, and morphologically diverse genus of freshwater planktonic diatoms (Fourtanier & Kociolek 2011). This reflects, in part, that *Cyclotella* exemplifies a "catch all" genus of diatoms—vaguely defined to include species of Thalassiosirales with a central area distinct from the valve margin (Round 1970, Round & Håkansson 1992, Håkansson 2002, Burić *et al*. 2007). This definition encompasses a broad range of morphological variation in other characters, e.g. arrangement and ultrastructure of the fultoportulae and rimoportulae. Theriot *et al*. (1987) interpreted these and other characters in a phylogenetic framework and concluded that the "defining" features of *Cyclotella* were plesiomorphic and, further, that there appeared to be no morphological characters supporting monophyly of *Cyclotella*.

This suggestion was later corroborated by molecular phylogenetic analyses (Alverson *et al*. 2007), which showed that *Cyclotella* is polyphyletic, with species split among three distinct clades corresponding to three morphological subgroups originally recognized by Lowe (1975). One clade corresponded to Lowe's (1975) *meneghiniana* group and included *C. meneghiniana* Kützing (1844: 50), the model species, *C. nana* Hustedt (1957: 212) [formerly *T. pseudonana* (Hustedt) Hasle & Heimdal (1970: 565)], and the type species, *C. distinguenda* Hustedt (1927: 320) (Håkansson 1989, Alverson *et al*. 2007, Alverson *et al*. 2011). Some classifications have placed a few of these species in the genus *Stephanocyclus* Skabitschevsky (1975: 205; Stoermer & Julius 2003). A second clade included species in Lowe's (1975) *stelligera* group, which are now classified in the genus *Discostella* Houk and Klee (2004: 204–205). The third clade included members of Lowe's (1975) *comta* group, which is the focus of this article.

Lowe's (1975) *comta* group included *Cyclotella* species with one or more "submarginal" rimoportulae, *i.e.*

Accepted by Saúl Blanco Lanza: 4 Jun. 2015; published: 26 Jun. 2015