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The Taxonomic Position of *Phaeodactylum tricornutum*

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SUMMARY: A revised taxonomic description of *Phaeodactylum tricornutum* Bohlin is presented, with special emphasis on the details of the silica valve, a structure hitherto unobserved. The features distinguishing *P. tricornutum* from *Nitzschia closterium* (Ehr.) W. Sm., with which it has frequently been confused, are summarized. In view of the unique characters of *P. tricornutum*, it is proposed to establish within the Bacillariales a new suborder, the Phaeodactylinae, to which *Phaeodactylum* is assigned as the only known genus.

In 1897 Bohlin described a new genus of unicellular algae, *Phaeodactylum*, with a single species, *P. tricornutum*. The organism was stellate with three narrow arms, possessed yellow-brown chromatophores and was weakly silicified. On the basis of the chemical nature of the cells and their characteristic plane of division, parallel with that of the arms, Bohlin considered that *P. tricornutum* was closely related to the diatoms. Wilson (1946), in a study of the various cell forms of '*Nitzschia closterium* W. Sm. forma *minutissima*', recognized the triradiate form of this organism as identical with *P. tricornutum* Bohlin. Since Hendey (1954) found no evidence for siliceous structures in the cell walls of this organism, he felt that it could not be classed as a diatom, and the presence of leucosin, as shown by Parke (recorded by Hendey, 1954), suggested to him a possible relationship to the Chrysophyceae. On the basis of the absence of movement, the absence of a raphe, and the absence of siliceous structure, Bourrelly & Dragesco (1955) also concluded that *P. tricornutum* could not be regarded as a diatom, but was a 'primitive Chrysococcalian'. Since the oval cells of *P. tricornutum* have now been shown to possess a silica valve (Lewin, Lewin & Philpott, 1958), it seems necessary to describe the organism more precisely on this basis, and to assign it to an appropriate taxonomic position. Though the specific epithet *tricornutum* might appear inappropriate, having been based on an atypical form, it has to be retained according to the rules of the International Code of Botanical Nomenclature (Lanjouw *et al.* 1956).

NEW DESCRIPTION

The emended description of the species is as follows:

***Phaeodactylum tricornutum* Bohlin emend.**

Unicellular, normally with one parietal brown chromatophore in central region. Two typical forms of cells. (a) Ovate, 8μ . long $\times$ 3μ . wide, one silica valve per cell. Cells may be slowly motile, or immobile in mucilaginous clumps. (b) Fusiform, up to $25\text{--}35\mu$. long, with two more or less blunt, slightly bent arms.

Silica wall absent. Non-motile. Rarely variants occur (triradiate, cruciform, lunate, etc.) which tend to persist in clones.

Valve weakly silicified, with a thin ragged margin; 6.2μ . long by 1.6μ . wide. Girdle bands absent. Valve flat, linear lanceolate, slightly curved, symmetrical about the transapical plane (as in *Cymbella* spp.); one edge convex, the other more or less straight with a median bulge. Ends broadly rounded but not capitate. Raphe slightly curved. Central area small, frequently with a pore on the side of the bulge. Striae approximately 60 (equivalent to 95 in 10μ .), mostly transverse but radiating in region of bulge. Puncta 2–6 per stria. (These details are revealed by electron microscopy. Under the light microscope it is just possible to detect the axial area, but no other features of the valve can be distinguished.)

CLASSIFICATION

Phaeodactylum tricornutum should undoubtedly be assigned to the Chrysophyta, since the cells possess golden-brown chromatophores, store leucosin and oil, and develop a silica wall at certain stages. The genus exhibits sufficient diatom characteristics to justify its inclusion within the class Bacillariophyceae. Among these features are the following: vegetative division longitudinal (usually not by formation of endospores), silica valve of a pennate diatom type, gliding movement of the oval cells, and auxospore formation.

The taxonomic position of *Phaeodactylum tricornutum* within the Bacillariophyceae is not readily apparent. Since the valve structure so closely resembles that of *Cymbella* spp. it might seem desirable to place the genus within the family Cymbellaceae. On the other hand, each oval cell possesses only one valve, and this feature distinguishes *P. tricornutum* from diatoms of all existing suborders. It is felt that this character, and the total absence of a siliceous wall from cells of the fusiform phase, provide sufficient justification for the formation of a new suborder. In the same way, various members of the Achnanthaceae, although their raphidate valves indicate close affinities to certain genera of the Biraphidineae, have been set apart as a separate suborder, the Monoraphidineae, on the basis of possessing dissimilar valves. It is therefore proposed that a new suborder, the Phaeodactylinae, be established. The taxonomic position of *P. tricornutum* would then be as follows:

Phylum	Chrysophyta
Class	Bacillariophyceae
Order	Bacillariales (Hendey, 1937)
Suborder	Phaeodactylinae (nov.subord.). Unlike all other diatoms hitherto described, the cells do not possess more than one silicified valve, which, when present, only partially covers the cell. Cellulae valva unica, cellulam partim tegenti, instructae, vel nudaе.
Family	Phaeodactylaceae (nov.fam.). Characteribus subordinis Phaeodactylinae. The only family of the suborder.

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Genus	<i>Phaeodactylum</i> (Bohlin, 1897). The only genus. Cells existing in two typical forms: motile oval cells which possess a silica valve, and non-motile fusiform cells lacking a silica valve.
Species	<i>P. tricornutum</i> . The only known species. (Description p. 427.)

Clarification of the distinctions between

Phaeodactylum tricornutum Bohlin and *Nitzschia closterium* (Ehr.) W. Sm.

Over the past fifty years the organism known as '*Nitzschia closterium* forma *minutissima*' has been widely used in investigations of various aspects of physiology and biochemistry of diatoms and for studies of marine plankton. It is obvious now that a most atypical diatom was selected. *Phaeodactylum tricornutum* is apparently not even a normal component of marine phyto-

Table 1. *Comparative features of Nitzschia closterium* (Ehr.) W. Sm.
and *Phaeodactylum tricornutum* Bohlin

	<i>N. closterium</i>	<i>P. tricornutum</i>	
		Fusiform cells	Oval cells
Length	25–100 μ . (Cupp, 1943)	Up to 25–35 μ .	8 μ .
Motility	Actively motile	Non-motile	Slowly motile
Silica wall	Two valves with irregular markings. Multiple, fraying intercalary bands (see Pl. 1, figs. 2 & 4)	None (see Pl. 1, fig. 1).	Single valve of <i>Cymbella</i> type. No girdles or intercalary bands (see Pl. 1, fig. 3)
Form of colonies	Spreading rapidly over surface in reticulate pattern with fimbriate margin	Rounded, margin entire	Spreading for short distances, margin irregular
Growth in liquid media	Cells settle and grow in mucilaginous masses	Cells separate, tend to remain suspended	Cells settle and grow in small mucilaginous clumps
Heterotrophic growth (in darkness on 0.5 % w/v, glucose)	Yes (3 isolates tested) (Lewin, unpublished)	No (3 isolates tested)	

plankton, since it has usually been reported from intertidal rock-pools or seawater tanks. It therefore seems unjustifiable to extend conclusions drawn from studies with this alga to diatoms in general or to phytoplankton. As a further complication, physiologists using the Plymouth strain often dropped the designation '*forma minutissima*', and referred to it in publications simply as '*N. closterium*'. Since a true *N. closterium* exists, which is very different from *P. tricornutum* (see Table 1), it is often difficult to be sure which of the two organisms was being studied. As far as can be determined, the Plymouth strain of '*N. closterium* f. *minutissima*' was the subject of investigation in the following papers: Ahmad (1930); Barker (1935); Bidwell, Krotkov & Reed (1952); Chu (1946*a, b*); Clarke & Mazur (1941); Dutton &

Manning (1941); Dutton, Manning & Duggar (1943); French (1955); Harvey (1933, 1937, 1953*a, b*); Hutner (1948); Jameson, Drummond & Coward (1922); Ketchum (1939*a, b*); Ketchum, Lillick & Redfield (1949); Ketchum & Redfield (1938, 1949); King & Davidson (1933); Leigh-Clare (1927); Levring (1945); Lovern (1936); Lucas (1936); Pace (1941); Peach & Drummond (1924); Spencer (1952, 1954); Stanbury (1931); Strain & Manning (1942); Waksman, Stokes & Butler (1937); Villeret (1955); von Brand, Rakestraw & Renn (1937, 1939); von Brand & Rakestraw (1940); ZoBell (1935). In 1954, Ryther isolated another strain of *P. tricornutum* from the Great South Bay, Long Island, N.Y., which likewise was referred to as '*N. closterium*' in the following papers: Ryther (1954, 1956*a, b*); Ryther & Vaccaro (1954). Riley (1943) obtained a crude culture of '*N. closterium*' from a tank containing sea water from Long Island Sound enriched with commercial fertilizer. The cells had the same dimensions as *P. tricornutum* and, as in *P. tricornutum*, dense cultures could be grown without added silicate. Unfortunately, since the culture has been lost, it is no longer possible to determine its identity. The information contained in all of the papers listed above, with the possible exception of Riley (1943), should in the future be considered as relating to *P. tricornutum*.

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EXPLANATION OF PLATE

Electron micrographs. Each scale line represents 2 μ .

- Fig. 1. Fusiform cells of *Phaeodactylum tricornutum* Bohlin.
 Fig. 2. Silica wall of *Nitzschia closterium* (Ehr.) W. Sm.
 Fig. 3. Silica walls of oval cells of *P. tricornutum*.
 Fig. 4. Enlarged portion of silica wall of *N. closterium*.

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J. C. LEWIN—THE TAXONOMY OF *PHAEODACTYLUM TRICORNUTUM*. PLATE 1
(Facing p. 432)