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Molecular and Morphological Investigations of the Stauros-bearing, Raphid Pennate Diatoms (Bacillariophyceae): *Craspedostauros* E.J. Cox, and *Staurotropis* T.B.B. Paddock, and their Relationship to the Rest of the Mastogloiales



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Several lineages of raphe-bearing diatoms possess a “stauros,” which is a transverse, usually thickened area free of pores across the center of the valve. It has been suggested that this structure has evolved several times across the raphid diatoms, but we have noticed similarities beyond the stauros between two marine genera—*Craspedostauros* and *Staurotropis*—in the structure of their pore occlusions. We have isolated, cultured and extracted DNA from several strains of both genera to infer the phylogenetic relationship between these taxa, as well as test the suggested relationship of *Craspedostauros* to *Achnanthes* and *Mastogloia* based on plastid morphology. DNA sequence data (nuclear-encoded rRNA SSU, plastid-encoded *rbcl* and *psbC*) suggest that, except for *Mastogloia*, these genera are

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closely-related, though not sister taxa. The DNA phylogeny also suggests that the Mastogloiales are not monophyletic, with clades containing *Achnanthes* and *Craspedostauros* sister to clades containing taxa in the Bacillariales. Using evidence from molecular and morphological data, we describe the following new taxa: *Craspedostauros alyoubii* and *C. paradoxa* from the Red Sea and Guam, respectively; *Staurotropis khiyamii* and *S. americana* from the Red Sea and the Gulf of Mexico, respectively; and *Dreuhlagia cuneata* n. gen., n. sp. from Guam.

Key words: Diatoms; phylogeny; *Craspedostauros*; *Staurotropis*; *Dreuhlagia*; Mastogloiales.
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Introduction

The distinctive silica cell wall (“frustule,” comprised of two shells=“valves,” joined by parallel overlapping strips of silica=“copulae”) of the photosynthetic microeukaryotes of the Bacillariophyta (“diatoms”) serves as a morphological synapomorphy to define the clade. Complexity in the ultrastructure of the valves continues to be used in the classification of groups within the diatoms. One such complex character is the raphe, a putative synapomorphy for the Bacillariophyceae (commonly called the “raphid pennates”). Several genera of raphid pennate diatoms bear an internal transverse rib of silica at the center of the valve, termed a “stauros.” In recent decades, these genera have been placed in several disparate families based on morphology other than the stauros (Round et al. 1990), and there are also genera, such as *Haslea* Simonsen and *Achnanthes* Bory, in which only some species have a stauros. Cox and Williams (2000) estimated the phylogeny of several stauros-bearing diatom genera by frustule and protoplast characters, and suggested multiple origins of the stauros across the raphe-bearing diatoms. Of particular interest here are the genera *Craspedostauros* E.J. Cox and *Staurotropis* Paddock.

Cox (1999) distinguished *Craspedostauros* from *Stauroneis* Ehrenberg by (1) the presence of cribrate areolae, (2) plate-like plastids with central pyrenoids, H-shaped as seen in valve view and located “fore-and-aft” of the central area, and (3) a central fascia (a transverse hyaline area of the valve) wider than the associated stauros. *Craspedostauros* is a relatively small genus; Cox (1999) gave ultrastructural details for six species, with *C. neoconstrictus* E.J. Cox as the type species, and she transferred *Stauronella indubitabilis* Lange-Bertalot and Genkal to *Craspedostauros* on the basis of illustrations in Lange-Bertalot and Genkal (1999). Sabbe et al. (2003) added *C. laevisissimus* from the Antarctic. In discussing the possible relationship of *Craspe-*

dostauros to other taxa, Cox (1999) noted that a few diatoms have the same plastid arrangement as *Craspedostauros* (in particular, species of *Mastogloia* Thwaites and *Aneumastus* Mann & Stickle). Cox (1999) also pointed out that *Aneumastus* and several *Mastogloia* and *Achnanthes* species have similar cribrate areolae to *Craspedostauros*; there are also several *Achnanthes* spp. that have a stauros on the raphe-bearing valve. In Cox and Williams’ (2000) analysis, *Craspedostauros* was in a clade with *Mastogloia* and *Aneumastus*, supporting Cox’s placement of *Craspedostauros* in the Mastogloiaceae. However, alternative interpretations of homology were also explored (Cox 1999, 2006; Cox and Williams 2000, 2006). Those authors noted that the H-shaped plastid arrangement of *Mastogloia* was very similar to that of *Climaconeis* (Cox 2006) and that *Nitzschia* and *Hantzschia* also had fore and aft plastid arrangements, although they argued that the resemblance was based on homoplasy. Cox (2006) suggested that *Achnanthes sensu stricto* also belongs in the Mastogloiales based on plastid morphology and positioning, as well as areolae with cribrate occlusions like those of *Craspedostauros*.

Staurotropis seychellensis (Giffen) Paddock is a marine pennate diatom with a central raphe raised on a prominent keel, but with a stauros and cribrate areolae similar to *Craspedostauros*. Giffen (1980) originally assigned *Staurotropis seychellensis* to *Tropidoneis* Cleve, but he noted that the presence of the stauros distinguished it from all other species in the genus. In addition to the stauros, Paddock (1988) noted a number of other differences between this taxon and *Tropidoneis*, including the cribrate areolae (described as “quadrate rota” by Paddock), striate girdle bands, the lack of silica swellings at the distal ends of the raphe (“helicotoglossae”) and the presence of small projections on the valve interior (“apodemes”). Based on these characters, Paddock erected the monotypic *Staurotropis* Paddock for the taxon. He noted the similarity of the areolae between *S.*

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