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Phylogenetic position and systematics of the bryozoan *Tennysonia*: further evidence for convergence and plasticity in skeletal morphology among cyclostome bryozoans

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Abstract

Cyclostomes are an ancient order of marine bryozoans with a fossil record extending back over 450 million years into the Ordovician. The current taxonomy of both fossil and modern cyclostomes is based almost entirely on skeletal characters but newly available sequence data are beginning to reveal rampant convergence of some of them. An unusual combination of skeletal characters in the South African cyclostome *Tennysonia stellata* Busk, 1867 has made this genus difficult to classify. After revising the taxonomy of *Tennysonia*, we use almost complete small and large ribosomal subunits (ssrDNA and lsrDNA) to demonstrate its close phylogenetic affinity with the tubuliporine genus *Idmidronea* (family Tubuliporidae) with which it shares a similar colony form, despite the presence of skeletally open kenozooids between the autozooids, reminiscent of cerioporine cyclostomes such as *Favosipora*. The spaces between the transverse rows of autozooidal apertures, occupied by exterior autozooidal frontal walls in *Idmidronea*, are occupied by kenozooids in *Tennysonia*, thereby maintaining the spacing between lophophores necessary for efficient suspension feeding. Sympatric colonies of *T. stellata* with narrow and broad branches are identical or almost identical on the basis of ssrDNA and lsrDNA sequences, respectively, suggesting within-species ecophenotypic plasticity in this aspect of colony form.

Key words: Bryozoa, Cyclostomata, taxonomy, molecular phylogeny, convergent evolution, suspension feeding

Introduction

The increasing availability of molecular sequence data is making it easier to evaluate the adequacy of traditional morphological characters in bryozoan systematics and taxonomy. In the two living bryozoan orders with mineralized skeletons—Cheilostomata and Cyclostomata—most of these traditional characters are skeletal structures. Indeed, prior to making identifications, it is routine to bleach cheilostome and cyclostome colonies, destroying all of the soft parts and leaving only those characters that would be typically preserved in a fossil. While this has the advantage of allowing for exact concordance in the taxonomy of recent and fossil bryozoans, it raises the question whether this subset of characters is sufficient to distinguish genetic species and to formulate a phylogenetic classification of bryozoans. Skeletally complex cheilostome bryozoans show moderately good to excellent concordance between phenotypic skeletal morphology and genotype (Jackson & Cheetham 1990, 1994; Gómez *et al*. 2007). In contrast, the molecular phylogeny of cyclostome bryozoans by Waeschenbach *et al*. (2009) cuts across traditional taxonomy based on skeletal characters, implying homoplasy, revealing polyphyly at subordinal (Tubuliporina and Cerioporina) and family (Plagioeciidae) level, and showing limited congruence with the only cladistic phylogeny published of the group (Taylor & Weedon 2000).

The South African cyclostome bryozoan *Tennysonia stellata* Busk, 1867, is unusual in sharing skeletal characters with two suborders (Tubuliporina and Cerioporina), each found to be polyphyletic or paraphyletic by Waeschenbach *et al*. (2009). Here we revise the taxonomy of *T. stellata*, based on a redescription of its skeletal morphology utilizing scanning electron microscopy (SEM). Sequencing of ssrDNA and lsrDNA is undertaken to

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