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Phylogenetic Relationships of the Ceramiales (Rhodophyta) Based on Anatomical and Nuclear SSU rDNA Sequence Data

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The largest red-algal order, the Ceramiales, presently contains the five families Ceramiaceae, Dasyaceae, Delesseriaceae, Rhodomelaceae and Sarcomeniaceae, more than 325 genera and over 1500 species. Members of all four families display uniaxial growth, bipolar spore germination and triphasic Polysiphonia-type life histories with the auxiliary cell in most cases cut-off from the supporting cell of the carpogonial branch after fertilization. The first aim of the current investigation has been to test the general convention that the Dasyaceae, Delesseriaceae and Rhodomelaceae are all monophyletic families of the red-algal order Ceramiales. Phylogenetic relationships among 45 ceramialian taxa, including eight ceramiacean, 18 dasyacean, nine delesseriacean, eight rhodomelacean species and two of uncertain affiliation, based on 34 anatomical characters and nuclear SSU rDNA sequences were determined. Results from our total-evidence approach were consistent with the notion that the Dasyaceae, Delesseriaceae and Rhodomelaceae have evolved from a common ancestor within a paraphyletic Ceramiaceae. Our data indicate, however, that the Rhodomelaceae alone was monophyletic with the Dasyaceae unequivocally polyphyletic and the Delesseriaceae either polyphyletic, or paraphyletic in excluding the Dasya-group. Based on our results, the Heterosiphonioideae subfam. nov. H.-G. Choi, Kraft, I.K. Lee et G.W. Saunders was proposed for Heterosiphonia and five closely related genera, and the Dasyoideae Schmitz et Falkenberg is emended for the remaining taxa. Although the Dasyoideae is a natural group, it is in need of a thorough systematic reinvestigation at the generic level. Our analyses indicate that the genus Dasya is polyphyletic or paraphyletic in excluding Dasyisiphonia, Eupogodon and Rhodoptilum and that Heterosiphonia japonica also has affinities to this group, taxonomic issues that will be addressed in detail elsewhere. The second aim of the current investigation has been to test the general convention that the Ceramiaceae is paraphyletic and the hypotheses regarding subfamilial taxonomy of the family. Phylogenetic relationships among 85 ceramialian (including 67 ceramiacean, six dasyacean, seven delesseriacean, five rhodomelacean algae) and 15 outgroup taxa (including eight related orders of the florideophycean algae) based on nuclear SSU rDNA sequence data were determined. Our results were consistent with the notion that the Ceramiaceae is paraphyletic excluding the Dasyaceae, Delesseriaceae and Rhodomelaceae. Our data indicate, however, that the Ceramiales was monophyletic without bootstrap support in excluding Inkyuleea ballioides and I. mariana, previously placed in the family Ceramiaceae. The genus Inkyuleea differs from the remaining Ceramiales by developing adaxial carpogonial branches on periaxial cells and forming three-celled auxiliary cell branches after fertilization. To date the phylogenetic relationships of Inkyuleea spp. among the membrane-only orders are equivocal and they are in need of thorough systematic investigations at the ordinal level. Spyrida spp. and Warrenia are placed at the root of the Ceramiaceae within the Ceramiales. Although our analyses partially support the subfamilies Callithamnioideae, Ceramioideae and Compsothamnioideae, they present a far more complex scenario in comparison with the previous proposals (Hommersand 1963; Itono 1977; Athanasiadis 1996, 2002). The subfamilies and tribes within the Ceramiaceae are in need of a through systematic reinvestigation at the proper taxonomic levels. This work was supported by Korea Research Foundation grant (KRF-2002-075-C00025). Key words: Ceramiaceae, Ceramiales, Dasyaceae, Delesseriaceae, nuclear small-subunit rDNA, phylogeny, Rhodomelaceae, Rhodophyta, systematics.