

ORIGINAL PAPER

Aurearenophyceae *classis nova*, a New Class of Heterokontophyta Based on a New Marine Unicellular Alga *Aurearena cruciata* gen. et sp. nov. Inhabiting Sandy Beaches

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A new heterokontophyte alga, *Aurearena cruciata* gen. et sp. nov., was isolated from sandy beaches in Japan. Isolates were characterized by light and electron microscopy, spectroscopy of pigment composition, and molecular phylogenetic analyses using 18S rDNA and *rbcL*. The alga usually possessed a cell wall but also retained two heterokont flagella beneath the cell wall. Each walled cell first produced only a single flagellate cell that subsequently divided into two flagellate cells. Electron-opaque vesicles, possibly associated with cell wall formation, were observed beneath the cell membrane. The chloroplast consisted of two compartments, each enclosed by a chloroplast envelope and the inner membrane of the chloroplast endoplasmic reticulum; these two compartments were surrounded by a common outer membrane of chloroplast endoplasmic reticulum. Molecular phylogenetic trees suggested that this alga was a new and independent member of the clade that included the Phaeophyceae and Xanthophyceae (PX clade). A new class, Aurearenophyceae *classis nova* was proposed for *A. cruciata*.

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Introduction

The heterokontophytes, which include brown algae and diatoms, are major primary producers in the present-day hydrosphere (Falkowski et al. 2004). The brown algae (Phaeophyceae) form large marine forests in coastal regions and provide

diverse habitats for a variety of animals to grow and reproduce. In addition, they may play a significant role in the global carbon cycle by fixing carbon dioxide and releasing dissolved organic carbon for export to deep water (Itoh et al. 2007; Wada et al. 2007). Brown algae are also economically important as food and as a source of alginic acid and fucoidan (McLachlan 1985; Smit 2004).

Ultrastructural observations, biochemical analyses, and molecular phylogenetic approaches have revealed that the greatest phylogenetic

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diversity among photosynthetic organisms lies in the heterokontophyte algae (e.g., Andersen 2004a, b). These algae are classified as the Heterokontophyta and, at present, comprise 15 distinct classes. Of these, eight classes (Bolidophyceae, Chrysomerothryceae, Pelagophyceae, Phaeothamniophyceae, Pinguiphyceae, Schizocladophyceae, Synchromophyceae, and Synurophyceae) have been recognized in the past two decades (Andersen 1987; Andersen et al. 1993; Bailey et al. 1998; Cavalier-Smith et al. 1995; Guillou et al. 1999; Horn et al. 2007; Kawachi et al. 2002; Kawai et al. 2003). These recent taxonomic developments suggest that our understanding of the true diversity of the heterokont algae is still incomplete.

The members of the Heterokontophyta are characterized by formation of flagellate cells that have two unequal heterokont flagella — an anterior flagellum bearing tripartite tubular hairs and a smooth posterior flagellum — and a chloroplast bounded by four membranes (e.g., Andersen 2004a). They are believed to have arisen via so-called secondary endosymbiosis of a red alga (Cavalier-Smith 1993, 1995). Molecular phylogenetic studies, calibrated for evolutionary rates of gene sequences as a molecular clock, suggest that these algae evolved 170–270 Ma (Medlin et al. 1997). They should have evolved much later than the green algae, which acquired a cyanobacterium and converted it to a plastid by primary endosymbiosis. The Heterokontophyta have radiated out rapidly in relatively recent geological periods — the Mesozoic and Cenozoic eras. On the basis of the fossil record, it is well accepted that diatoms appeared 190 Ma in the Jurassic period of the Mesozoic era (Sims et al. 2006). This could be why, despite the morphological distinctness of the classes, it is difficult to elucidate their phylogenetic relationships and branching order based on morphological and biochemical data. Molecular phylogenetic studies of the Heterokontophyta have been based mainly on the sequences of *rbcL*, a chloroplast-encoded gene for the large subunit of ribulose biphosphate carboxylase/oxygenase (RuBisCO), and the nuclear-encoded small subunit ribosomal RNA gene (18S rDNA) (e.g., Andersen et al. 1993; Bailey et al. 1998; Cavalier-Smith and Chao 2006; Kawai et al. 2003; Van de Peer et al. 1996). These phylogenetic analyses support the monophyly of each class of the Heterokontophyta with confidence, but have failed to determine the relationships among the classes. At present, the global phylogeny of the Heterokontophyta is far

from clear. Despite these undetermined relationships, several higher phylogenetic groups have been recognized. One of these large groups is the clade including the Phaeophyceae and Xanthophyceae (Ariztia et al. 1991; Cavalier-Smith et al. 1995; Van de Peer et al. 1996). O'Kelly and Floyd (1985) suggested that the Chrysomerothryceae and Phaeothamniophyceae be added to this large clade based on ultrastructural studies. Cavalier-Smith et al. (1995) proposed the super-class Fucistia for this large clade. Molecular phylogenetic studies supported the addition of the Chrysomerothryceae, Phaeothamniophyceae, and, subsequently, the Schizocladophyceae to this clade (Andersen et al. 1998; Bailey et al. 1998; Cavalier-Smith and Chao 2006; Kawai et al. 2003; Saunders et al. 1997). However, the monophyly of this assemblage and the relationship among its members have not been well resolved at the molecular phylogenetic level.

The assemblage that includes the Chrysomerothryceae, Phaeophyceae, Phaeothamniophyceae, Schizocladophyceae, and Xanthophyceae is referred to here as the PX clade, P and X referring to the two major taxa of the clade, the Phaeophyceae and Xanthophyceae. The life forms in the PX clade are very diverse, e.g., unicells, colonies, filaments, coenocytes, or macroscopic thalli. Their habitats are also very diverse, encompassing freshwater, soil, or marine environments. In our opinion, one of the most important evolutionary events to have occurred in the PX clade was the emergence of true multicellularity in the Phaeophyceae. In conjunction with multicellularity, a complex organization of the thallus comparable to the land plants evolved in the Phaeophyceae, including the development of an epidermis and cortex, transfer tissue including sieve plates, sexual organs, and receptacles. The diversification and evolution of brown algal seaweeds have given rise to marine forests that are essential components of present-day coastal ecosystems. All the members of the PX clade possess a cell wall, and one of the characteristic features of this clade is the absence of flagellate cells in the vegetative phase; this is in distinct contrast to the other classes of Heterokontophyta. Approximately 100 years ago, some species in the Xanthophyceae were described as naked forms. However, these species were described based solely on light microscopic features, and there has been no ultrastructural or molecular evidence in support of their presumed taxonomic status. For example, *Chlorarachnion reptans*, presently recognized as the type species of the Chlorarachniophyta, was

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