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Comparative Morphology and Molecular Phylogeny of *Apicoporus* n. Gen.: A New Genus of Marine Benthic Dinoflagellates Formerly Classified within *Amphidinium*

Sarah F. Sparmann, Brian S. Leander, and Mona Hoppenrath¹

Departments of Botany and Zoology, University of British Columbia, Vancouver, BC, Canada V6T 1Z4

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The composition of the dinoflagellate genus Amphidinium is currently polyphyletic and includes several species in need of re-evaluation using modern morphological and phylogenetic methods. We investigated a broad range of uncultured morphotypes extracted from marine sediments in the Eastern Pacific Ocean that were similar in morphology to Amphidinium glabrum Hoppenrath and Okolodkov. To determine the number of distinct species associated with this phenotypic diversity, we collected LM, SEM, TEM and small subunit ribosomal DNA sequence information from different morphotypes, including the previously described A. glabrum. Both comparative morphological and molecular phylogenetic data supported the establishment of a new genus, Apicoporus n. gen., including at least two species, A. glaber n. comb., and A. parvidiaboli n. sp. Apicoporus is characterized by having amphiesmal pores and an apical pore covered by a hook-like protrusion: neither of these characters has been observed in other athecate dinoflagellates. The posterior end of Apicoporus parvidiaboli possessed varying degrees of "horn formation", ranging from slight to prominent. By contrast, the posterior end of Apicoporus glaber was distinctively rounded and lacked evidence of horn formation. Although these species were previously interpreted to be obligate heterotrophs, TEM and epifluorescence microscopy demonstrated that some cells of both species had unusually small but otherwise typical dinoflagellate plastids. The number and density of plastids in any particular cell varied significantly in the genus, but the plastids were almost always concentrated at the posterior end of the cells or around the nucleus. The presence of cryptic photosynthetic plastids in these benthic species suggests that photosynthesis might be much more widespread in dinoflagellates than is currently assumed. © 2007 Elsevier GmbH. All rights reserved.

Key words: *Amphidinium glabrum*; apical pore; *Apicoporus glaber*; *Apicoporus parvidiaboli*; dinoflagellate; pellicle; heterotrophic; plastid; SSU rDNA.

²Corresponding author; fax +1 604 822 6089. e-mail hoppen@interchange.ubc.ca (M. Hoppenrath).

Introduction

The genus *Amphidinium* Claparède and Lachmann is among the largest and most diverse of all marine benthic dinoflagellates and has long been recognized as being polyphyletic (Dodge 1982;

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Hoppenrath 2000a: Larsen 1985: Larsen and Patterson 1990: Murray and Patterson 2002). One reason for this is the overly generalized criteria used for distinguishing Amphidinium from other athecate genera, such as episome dimensions (shorter than 1/3 of the cell length) and the displacement of the cingulum (Steidinger and Tangen 1997). Over the last 10 years, modern methods have been used to re-investigate the type species of different athecate genera, such as Gvmnodinium Stein and Gvrodinium Kofoid and Swezy (Daugbjerg et al. 2000; Hansen et al. 2000; Hansen and Daugbjerg 2004; Takano and Horiguchi 2004). More precise re-definitions of these genera have caused many of the species formerly assigned to them to be considered "sensu lato taxa"; accordingly, several new genera have been described, such as Akashiwo Hansen and Moestrup, Karenia Hansen and Moestrup, Karlodinium Larsen, and Takayama de Salas, Bolch, Botes and Hallegraeff (Daugbjerg et al. 2000; De Salas et al. 2003). Amphidinium has also been redefined in recent years after reinvestigations of A. operculatum Claparède and Lachmann, the type species, and putative relatives (Flø Jørgensen et al. 2004a: Murray et al. 2004). The genus was subsequently split into Amphidinium sensu stricto and Amphidinium sensu lato. Amphidinium sensu stricto are dorso-ventrally flattened, athecate dinoflagellates with a minute epicone that overlays the anterior ventral part of the hypocone and deflects to the left (Flø Jørgensen et al. 2004a). The epicones can be irregular, triangularshaped or crescent-shaped. Cells may or may not be photosynthetic. Some of the former Amphidinium species that do not fit the above description have been classified into new genera, such as the marine benthic Togula Flø Jørgensen, Murray and Daugbjerg (Flø Jørgensen et al. 2004b) and the freshwater Prosoaulax Calado and Moestrup (Calado and Moestrup 2005).

In an effort to improve our understanding of marine athecate dinoflagellates and the composition of *Amphidinium* sensu stricto, we reinvestigated *Amphidinium* glabrum Hoppenrath and Okolodkov (Hoppenrath and Okolodkov 2000) and several similar morphotypes. These uncultured morphotypes were isolated form marine sand collected near Vancouver and Bamfield, British Columbia, Canada. All of the morphotypes, including the type species, shared many morphological characteristics. However, we observed a great deal of morphological variability at the posterior end of the cells. We evaluated the number of distinct species associated with this phenotypic diversity and whether these species belonged to the *Amphidinium* sensu stricto, or a different genus altogether, using light and electron microscopy and molecular phylogenetic methods based on small subunit ribosomal DNA (SSU rDNA) sequences. Moreover, our ultrastructural studies led to some unexpected discoveries, such as the presence of cryptic photosynthetic plastids in these benthic marine dinoflagellates.

Results

Taxonomic Descriptions

Alveolata Cavalier-Smith 1991 Dinozoa Cavalier-Smith 1981 emend. Cavalier-Smith and Chao 2004 Dinoflagellata Bütschli 1885 emend. Fensome et al. 1993 *Apicoporus* Sparmann, Leander and Hoppenrath n. gen.

Description: Athecate, dorso-ventrally flattened cells with a small, low and wide, beak-shaped, asymmetrical episome with an apical pore beneath a hook-shaped apical protrusion. Descending cingulum with its distal end not connected to the sulcus. Narrow and shallow sulcus on the hyposome, extending as deeper furrow onto the episome and running down to the posterior cell end where it terminates into a semicircular posterior cell indentation (notch). Posterior ventral 'flap' partly covering the notch. With or without cryptic photosynthetic plastids. Vegetative cells with internal dinoflagellatepellicle.

Type species: Apicoporus glaber (Hoppenrath and Okolodkov) Sparmann, Leander and Hoppenrath n. comb. (designated here)

Etymology: Latin *apic*, from apex = top end; Latin *porus* = opening/pore; due to the presence of an apical pore which has so far only been reported in thecate dinoflagellates.

Apicoporus glaber (Hoppenrath and Okolodkov) Sparmann, Leander and Hoppenrath n. comb.

Basionym: *Amphidinium glabrum* Hoppenrath and Okolodkov 2000, Eur J Phycol 35, p. 62

Lectotypification of *Apicoporus glaber*: Hoppenrath and Okolodkov 2000, Eur J Phycol 35, p. 63, Figure 4, here first designated

Paratype: present study Figures 3C, 4A (same specimen)

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