



Attributing *Ceratocorys*, *Pentaplagodinium* and *Protoceratium* to Protoceratiaceae (Dinophyceae), with descriptions of *Ceratocorys malayensis* sp. nov. and *Pentaplagodinium usupianum* sp. nov

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ABSTRACT

The gonyaulaclean family Protoceratiaceae is characterised by five precingular plates. It currently encompasses the type genus *Ceratocorys* and the fossil genus *Atopodinium*. Fourteen strains of *Ceratocorys*, *Pentaplagodinium*, and *Protoceratium* were established from Malaysian and Hawaiian waters, and their morphologies were examined using light and scanning electron microscopy. Two new species, *Ceratocorys malayensis* sp. nov. and *Pentaplagodinium usupianum* sp. nov., were described from Malaysian waters. They share a Kofoidian plate formula of Po, Pt, 3', 1a, 6'', 6C, 6S, 5''', 1p, 1'''''. *Ceratocorys malayensis* has a short first apical plate (1') with no direct contact with the anterior sulcal plate (Sa) whereas *Pentaplagodinium usupianum* had a parallelogram-shaped 1' plate which often contacted the Sa plate. The genera *Ceratocorys* and *Pentaplagodinium* were emended accordingly to incorporate species bearing five or six precingular plates. The *Protoceratium* strain from Hawaii was morphologically similar to *P. reticulatum*, but differed in the lack of a ventral pore in plate 1' and slight or lack of contact between plates 1' and Sa, and is here designated as *P. cf. reticulatum*. The maximum-likelihood and Bayesian inference analyses based on SSU, LSU and ITS ribosomal DNA sequences revealed that these three genera are monophyletic and form a well-resolved group. Our results support *Protoceratium* and *Pentaplagodinium* as members of the family Protoceratiaceae, characterised by the presence of one anterior intercalary plate. Seven strains of *Protoceratium cf. reticulatum*, *Ceratocorys malayensis* and *Pentaplagodinium usupianum* were examined for yessotoxin production by LC-MS/MS but none produced a detectable amount of toxin.

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INTRODUCTION

The Gonyaulacales is a major order of dinophytes that is subdivided into five suborders based only on morpho-anatomy (Fensome *et al.* 1993). One of these, Gonyaulacineae, encompasses two extant families, Gonyaulacaceae and Ceratocorythaceae, and one fossil family, Areoligeraceae. Ceratocorythaceae have five precingular plates, L-type ventral organisation and strong dextral torsion, whereas Gonyaulacaceae have six precingular plates, L- to S-type ventral organisation and sinistral to dextral torsion (Fensome *et al.* 1993). Thus, the key difference between Gonyaulacaceae and Ceratocorythaceae is the number of precingular plates (six versus five). The Gonyaulacaceae was subdivided further into three subfamilies by Fensome *et al.* (1993): Cribroperidinioideae (with L-type ventral organisation and dextral torsion), Leptodinioideae (with L-type ventral organisation and sinistral or neutral torsion), and Gonyaulacoideae (with S-type ventral organisation and neutral torsion). The criteria used to distinguish subfamilies of Gonyaulacaceae, however, were

sometimes inconsistent (Helenes 2000) or gradational in nature, and, in some instances, tentative (Fensome *et al.* 1993).

Currently, the Ceratocorythaceae include only the extant genus *Ceratocorys* F.Stein and the fossil genus *Atopodinium* Drugg (Fensome *et al.* 1993). *Ceratocorys* is characterised by three apical plates, one small anterior intercalary plate and five precingular plates (3', 1a, 5''). The third Kofoidian precingular plate in *Ceratocorys* is considered homologous to both the third and fourth precingular plates in other gonyaulacoid dinoflagellate genera (Mertens *et al.* 2018b). Additionally, cells of *Ceratocorys* are often characterised by an angular body, shorter epitheca relative to hypotheca, small to large spines on the hypotheca, and heavily ornamented theca (Carbonell-Moore 1996). Twelve *Ceratocorys* species have been described, e.g. *Ceratocorys anacantha* M.C. Carbonell-Moore, *C. armata* (Schütt) Kofoid, *C. bipes* (Cleve) Kofoid, *C. horrida* Stein; all are exclusively marine and found only in tropical and subtropical waters (Carbonell-

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