



Research paper

Two new species formally attributed to *Protoperidinium oblongum* (Aurivillius) Parke et Dodge (Peridinales, Dinophyceae): Evidence from cyst incubation experimentsChihiro Sarai^{a,1}, Aika Yamaguchi^b, Hisae Kawami^c, Kazumi Matsuoka^{d,*}^a Faculty of Fisheries, Nagasaki University, 1-14, Bunkyo-machi, Nagasaki 852-8521, Japan^b Microbiology and Biochemistry of Secondary Metabolites Unit, Okinawa Institution of Science and Technology, 1919-1 Tancha, Onnna-son, Kunigami, Okinawa, 904-0412, Japan^c Koshigaya City, Saitama 343-0026, Japan^d Institute for East China Sea Research, Nagasaki University, 1551-7, Taira-machi, Nagasaki 851-2213, Japan

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ABSTRACT

Cyst–theca relationships of the common armored dinoflagellate *Protoperidinium oblongum* were re-investigated by incubation experiments and molecular phylogenetic analysis. Living cysts provided for incubation experiments were collected from several places in Japan, including Omura Bay, West Japan and Lake Saroma in Hokkaido, North Japan. One hundred and four cysts were incubated and 18 motile cells were germinated from these cysts. To clarify their morphological characteristics both cysts and germinated thecate cells were observed, especially the archeopyle type, the number and shape of anterior intercalary plates, and the shape and development of apical and antapical horns. In order to provide molecular phylogenetic analysis, germinated cells from incubated cysts were examined for their LSU rDNA sequences. Results reveal that three morphologically different cysts produced three morphologically different thecate cells, which were previously known as *Protoperidinium oblongum* var. *latidorsale*, *Protoperidinium oblongum* var. *inaequale*, and *Protoperidinium oblongum* var. *symmetricum*. The molecular phylogenetic analysis demonstrated that the *Oceania* group in the genus *Protoperidinium* includes these three varieties as well as *Protoperidinium divergens*, *Protoperidinium claudicans*, and *Protoperidinium steigingeriae*. This group is separated from *Protoperidinium sensu stricto*, and the three plankton forms are phylogenetically separate and independent species. Based on these facts, two new species, *Protoperidinium quadrioblongum* Sarai, Kawami et Matsuoka, the new name for *Protoperidinium oblongum* var. *symmetricum* and *Protoperidinium paraoblongum* Sarai, Kawami et Matsuoka for *Protoperidinium oblongum* var. *inaequale* are described.

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1. Introduction

Since the pioneering studies of Wall and Dale (1968), many more studies have been conducted to establish cyst–motile form relationships. Now more than 60 species of modern marine protoperidiniacean dinoflagellates are known to produce resting cysts (Table 1). A fundamental technique to establish a cyst–motile form relationship is cyst incubation. This technique has its limitations in that sometimes form relationships cannot be confirmed because abnormally shaped thecal plates and topology are observed on cells after germination (Kobayashi and Matsuoka, 1984; Matsuoka et al., 2006). Thus, incubation experiments alone may be insufficient for confirming cyst–motile form relationships. Now since molecular phylogenetic analysis for single cell phytoplankton has been extensively developed (Bolch, 2001; Takano and Horiguchi, 2004) this is regarded as the second technique available to establish cyst–motile form relationships. Cyst incubation and molecular techniques were used to confirm the cyst–theca relationship of *Protoperidinium thulesense* Balech, a heterotrophic species characterized by a unique thecal morphology

(Matsuoka et al., 2006). Gribble and Anderson (2006) conducted a phylogenetic analysis of heterotrophic thecate species of *Protoperidinium* and diplopsalids. Ribeiro et al. (2010) examined the phylogenetic position of *Protoperidinium minutum* (Kofoid) using cyst incubation experiments and the molecular technique. Yamaguchi et al. (2011) also studied *P. minutum* phylogenetically and re-attributed this species to the genus *Archaeoperidinium* Jörgensen. In particular, Gribble et al. (2009) described the cyst of *Protoperidinium steidingeriae* Balech which is identical to a horned cyst of *Protoperidinium oblongum sensu* Wall and Dale (1968). Thus, careful morphological observations and molecular phylogenetic analysis can be used without incubation work to establish cyst–motile form relationships. This approach is helpful in the examination of morphologically cryptic species of modern dinoflagellates.

Here the cyst–motile form relationship in *Protoperidinium oblongum* (Aurivillius) Parke and Dodge, 1976 is examined by studying the morphology and conducting molecular phylogenetic analysis.

2. Taxonomic history of *Protoperidinium oblongum*

Protoperidinium oblongum is a common protoperidinoid dinoflagellate in coastal waters and surface sediments mainly in temperate regions

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Table 1
Modern protoperidiniacean dinoflagellate cysts and their biological affinities including the *Protoperidinium oblongum* complex. References before 1995 were cited in Head (1996).

Species	Author	Remarks
Diplopsalid		
<i>Diplopelta symmetrica</i>	Dale et al. (1993)	Cysts may not fossilize
<i>Diplopsalis lebouriae</i>	Matsuoka (1988)	? Cysts of <i>Diplopsalis lenticula</i> sensu (Wall and Dale 1968)
<i>Diplopsalis lenticula</i>	Wall and Dale (1968), Matsuoka (1988)	Unlike cysts of <i>D. lenticula</i> sensu Wall and Dale (Matsuoka 1988)
<i>Diplopsalopsis latipeltata</i>	Dale et al. (1993)	Cysts may not fossilize
<i>Diplopsalopsis orbicularis</i>	Wall and Dale (1968), Matsuoka (1988)	? <i>Dubridinium cavatum</i> (Reid)
<i>Dissodium parvum</i> (= <i>Diplopelta parva</i>)	Matsuoka (1988), Bolch and Hallegraeff (1990)	
<i>Gotoius abei</i>	Matsuoka (1988)	
<i>Lebouraia pusilla</i>	Kawami (2009MS)	Not preserved in sediment?
<i>Oblea acanthocysta</i>	Kawami et al. (2006)	<i>Diplopelta parva</i> sensu Matsuoka (1986)
<i>Oblea rotunda</i>	Lewis (1990)	
<i>Preperidinium meunieri</i> (= <i>Diplopeltopsis minor</i>) (= <i>Zygabikodinium lenticulatum</i>)	Wall and Dale (1968)	<i>Dubridinium caperatum</i>
Clade I (<i>Protoperidinium</i> sensu strict)		
<i>Protoperidinium achromaticum</i> ?	Bolch and Hallegraeff (1990, as <i>Protoperidinium</i> sp. 2)	
<i>Protoperidinium avellanum</i>	Wall and Dale (1968)	<i>Brigantedinium cariacense</i>
<i>Protoperidinium brochii</i>	Blanco (1989)	
<i>Protoperidinium claudicans</i>	Wall and Dale (1968), Reid (1977)	<i>Votadinium spinosum</i>
<i>Protoperidinium compressum</i> (= <i>Stelladinium stellatum</i>)	Wall and Dale (1968 as <i>Peridinium stellatum</i>)	<i>Stelladinium reidii</i>
<i>Protoperidinium conicoides</i>	Granand Braarud (1935), Wall and Dale (1968)	<i>Brigantedinium simplex</i>
<i>Protoperidinium conicum</i>	Wall and Dale (1968)	<i>Selenopemphix quanta</i> (= <i>Multispinula quanta</i>)
<i>Protoperidinium denticulatum</i>	Wall and Dale (1968)	? <i>Brigantedinium cariacense</i>
<i>Protoperidinium divaricatum</i>	Matsuoka et al. (1982)	<i>Xandarodinium</i> sp. of Matsuoka et al. (1982)
<i>Protoperidinium</i> sp. cf. <i>P. divergens</i>	Dale (1993)	
<i>Protoperidinium excentricum</i>	Wall and Dale (1968)	
<i>Protoperidinium</i> sp. cf. <i>P. expansum</i>	Hallegraeff and Bolch (1992)	
<i>Protoperidinium granii</i>	Nordli (1951a)	
<i>Protoperidinium latissimum</i>	Wall and Dale (1968)	
<i>Protoperidinium leonis</i>	Evitt and Davidson (1964), Wall and Dale (1968)	
<i>Protoperidinium nudum</i>	Wall and Dale (1968)	
<i>Protoperidinium pentagonum</i>	Wall and Dale (1968)	
<i>Protoperidinium pentagonum</i> s.l.	Lewis et al. (1984)	<i>Trinovantedinium applanatum</i> (as <i>T. capitatum</i>) and other morphotypes
<i>Protoperidinium punctulatum</i>	Wall and Dale (1968)	? <i>Brigantedinium cariacense</i>
" <i>Protoperidinium sinuosum</i> "	Matsuoka (1992a)	<i>Brigantedinium majusculum</i>
<i>Protoperidinium subinermis</i>	Wall and Dale (1968)	
<i>Protoperidinium thorianum</i>	Lewis et al. (1984)	
<i>Protoperidinium thulesense</i>	Dodge (1985), Matsuoka et al. (2006)	
Clade II (<i>Oceanica</i> group)		
<i>Protoperidinium oblongum</i>	Wall and Dale (1968)	<i>Votadinium calvum</i> (Wall and Dale 1968, Pl. 1, fig. 25–28 only)
<i>Protoperidinium</i> sp. cf. <i>P. oblongum</i>	Evitt (1967)	
<i>Protoperidinium steidingeriae</i>	Gribble et al. (2009)	
Clade III (<i>Monovela</i> group)		
<i>Archaeperidinium saanichi</i>	Mertens et al. (2012)	
<i>Protoperidinium americanum</i> (= <i>Peridinium americanum</i>)	Lewis and Dodge (1987)	
<i>Protoperidinium minutum</i> (<i>Archaeperidinium minutum</i>)	Wall and Dale (1968), Fukuyo et al. (1977), Ribeiro et al. (2010), Yamaguchi et al. (2011)	Yamaguchi et al. (2011) re-established the genus <i>Archaeperidinium</i> based on morphological features and molecular analysis.
	Zonneveld and Dale (1994)	
<i>Protoperidinium monospinum</i>	Kawami et al. (2009)	
<i>Protoperidinium tricingulatum</i>	Kawami et al. (2009)	
<i>Protoperidinium parthenopes</i>	Kawami and Matsuoka (2009)	

(Fig. 1). The species was first recorded as a variety of *Peridinium divergens* Ehrenberg by Bergh in 1882. Later, Aurivillius (1898) named this dinoflagellate as *Peridinium divergens* var. *oblongum* Ehrenberg, by Bergh (1882; figs. 39 and 40). The plate topology and shapes, especially the first apical and the anterior intercalary plate(s) are important morphological criteria for identification of species in the genus *Protoperidinium*. The schematic illustration of these characters was introduced by Lebour in 1925 (Fig. 2). According to this, Bergh's drawings clearly showed an ortho first apical plate (Berg, 1882; fig. 39; ortho-hexa type, Fig. 3A) and a large, and probably, hexagonal anterior intercalary plate (Berg, 1882; fig. 40) (Fig. 3A). The figures suggest that there were no other anterior intercalary plates, because the single plate occupied a large portion of the dorsal anterior area. Interestingly, Berg's figure 40 also suggested the presence of a cordate cyst within the theca containing protoplasm.

Several dinoflagellate specimens, described as *Peridinium oceanicum* Vanhöffen by Cleve (1900a, pl. VII, figs. 17, 18), may include *Protoperidinium oblongum* because organisms smaller than the typical *Peridinium oceanicum* were observed. Cleve (1900b) named this species *Peridinium oblongum* Aurivillius. However, the articles written by Cleve (1900a,b) suggest some confusion as to whether the dinoflagellate was a new species or a new variety. The name *Peridinium oblongum*

(Aurivillius) Cleve was first used by Paulsen (1907, fig. 20) and the organism was considered different from *Peridinium oceanicum* because of its small size. However, the name used by Paulsen (1908) to explain his drawings of *Peridinium oceanicum* Vanhöffen var. *oblongum* Aurivillius suggests that he was also unsure about the organism's status (fig. 70a–e of Paulsen, 1908).

The confusion, regarding the classification of the *Peridinium oceanicum*, probably came about because only the external outline of the thecate cell, cell size, and the development of apical and antapical spines or horns were taken into consideration as to whether the organism was a new species or variety. Recent knowledge suggests that these morphological criteria are inadequate for the differentiation of similar species of *Protoperidinium oblongum*. Several examples can be cited including Meunier (1919) who classified this organism as *Peridinium oceanicum* Vanhöffen. However, some of the cells were believed to be identical to *Peridinium oblongum* var. *latidorsale* (pl. 1, fig. 18–20 of Meunier, 1919), because this dinoflagellate has only a single anterior intercalary plate and a cordate cyst in the thecate cell. A taxonomic confusion of *Peridinium oblongum* (Aurivillius) occurs in Lebour (1925) where an illustration (1925, p. 121, pl. 24, figs. 1a, b, and c) shows an orthogonal 1' plate and

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