

## **Morphology of two bloom-forming or potentially toxic marine dinoflagellates from the Mexican Pacific, *Heterocapsa pygmaea* and *Protoceratium reticulatum* (Dinophyceae)**

David U. HERNÁNDEZ-BECERRIL<sup>a\*</sup>, Mónica C. RODRÍGUEZ-PALACIO<sup>b</sup>  
& Cruz LOZANO-RAMÍREZ<sup>b</sup>

<sup>a</sup>*Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM), Apartado Postal 70-305, México D. F. 04510, México*

<sup>b</sup>*Laboratorio de Ficología Aplicada, Departamento de Hidrobiología, Universidad Autónoma Metropolitana-Iztapalapa, Apartado Postal 55-535, C. P. 09340, México, D. F.*

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**Abstract** – The morphology of the bloom-forming or potentially toxic marine planktonic dinoflagellates *Heterocapsa pygmaea* (recorded here for the first time in Mexico) and *Protoceratium reticulatum* was studied based on clonal, non-axenic, “semicontinuous” cultures isolated from Mexican Pacific samples, using light-, scanning- and transmission electron microscopy. Emphasis was placed on morphological variability, including cell size, cell shape, and tabulation. *Heterocapsa pygmaea* has minute external scales useful for accurate taxonomic identification.

**Cultures / dinoflagellates / Dinophyceae / *Heterocapsa pygmaea* / Mexican Pacific / morphology / phytoplankton / *Protoceratium reticulatum***

**Résumé** – La morphologie de deux dinoflagellés planctoniques marins responsables d’effloraisons phytoplanctoniques ou potentiellement toxiques, *Heterocapsa pygmaea* (signalé au Mexique pour la première fois dans ce travail) et *Protoceratium reticulatum*, a été étudiée à partir de cultures cloniques, non-axéniques et « semi-continues » isolées d’échantillons du Pacifique mexicain, en microscopies photonique, électronique à balayage et électronique à transmission. Les observations sont centrées sur la variabilité morphologique, surtout les dimensions, la forme et la tabulation des cellules. *Heterocapsa pygmaea* possède des écailles externes très délicates, très utiles pour une identification taxinomique précise.

**Cultures / dinoflagellés / Dinophyceae / *Heterocapsa pygmaea* / morphologie / Pacifique mexicain / phytoplankton / *Protoceratium reticulatum***

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\* Correspondence and reprints: dhernand@cmarl.unam.mx  
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## INTRODUCTION

Earlier studies of planktonic dinoflagellates from the Mexican Pacific have shown a diverse flora, with an important content of tropical and subtropical species (Kofoid, 1907; Graham, 1943; Hernández-Becerril, 1988a, 1988b; Gómez-Aguirre, 1998). Since then, few new records have been found in this area (Hernández-Becerril & Bravo-Sierra, 2004).

Here we describe the morphology of two little-known thecate dinoflagellates, *Heterocapsa pygmaea* Loeblich, Schmidt *et* Sherley and *Protoceratium reticulatum* (Claparède *et* Lachmann) Bütschli, based on cultures isolated from Mexican Pacific samples freshly collected by us. *Heterocapsa circularisquama* Horiguchi, which is closely related to *H. pygmaea*, may form red tides and is known to be toxic. It may cause serious damage to bivalve molluscs such as oysters and clams (Horiguchi, 1995; Uchida *et al.*, 1995); it has also been associated with mortality in fish mass cultures (Iwataki *et al.*, 2002a). However, toxicity in *Heterocapsa pygmaea* has not been confirmed (Uysal *et al.*, 2003). *Protoceratium reticulatum*, which is able to produce cysts which may favour its permanency in the water column (Reinecke, 1967; Montresor *et al.* 1998), has been shown to produce yessotoxin, a secondary metabolite which may be toxic for marine life and human populations (Satake *et al.*, 1997, 1999; Boni *et al.*, 2001; Paz *et al.* 2004; Samdal *et al.*, 2004).

## MATERIAL AND METHODS

Bottle surface water samples were collected in May 2004 (25A) and April 2006 (46A and 76A) from 5 miles off-shore Acapulco Bay, Guerrero, Mexico, in the tropical Mexican Pacific (16°48' 49.6" N, 99° 54' 21.7" W). Samples were concentrated by inverse filtration. Single cells were isolated by micropipetting and placed in multiwell chambers with 200 µl of f/2 medium (Guillard & Ryther, 1962; Guillard, 1975) and/or L1 and L1SE (enriched with soil extract) media (Guillard & Hargraves, 1993). Culture media were prepared with prefiltered and sterilized sea-water from the original collecting localities. Three culture strains were obtained (*Heterocapsa pygmaea*: 25A and 46A; and *Protoceratium reticulatum*: 76A). All cultures were clonal, non-axenic, "semicontinuous", and maintained at irradiances of 90.5 mmol m<sup>-2</sup> s<sup>-1</sup> and 166.8 µmol m<sup>-2</sup> s<sup>-1</sup>, 12:12 photoperiod, and t = 18 and 20° C ± 1° C. Living specimens were observed and measured using an Olympus light microscope (LM). Glutaraldehyde-fixed (1%) material was rinsed with distilled water, dehydrated in ethanol, critical-point dried, sputter-coated with Au, and examined using a JEOL JSM-6360LV scanning electron microscope (SEM). Cell whole-mounts of *Heterocapsa pygmaea* in 2% aqueous uranyl acetate (Iwataki *et al.* 2002b) were examined using a JEOL TEM1200 EXII transmission electron microscope (TEM). Terminology follows Steidinger & Tangen (1997) and Iwataki *et al.* (2004).

## RESULTS AND DISCUSSION

### *Heterocapsa pygmaea* Loeblich, Schmidt *et* Sherley

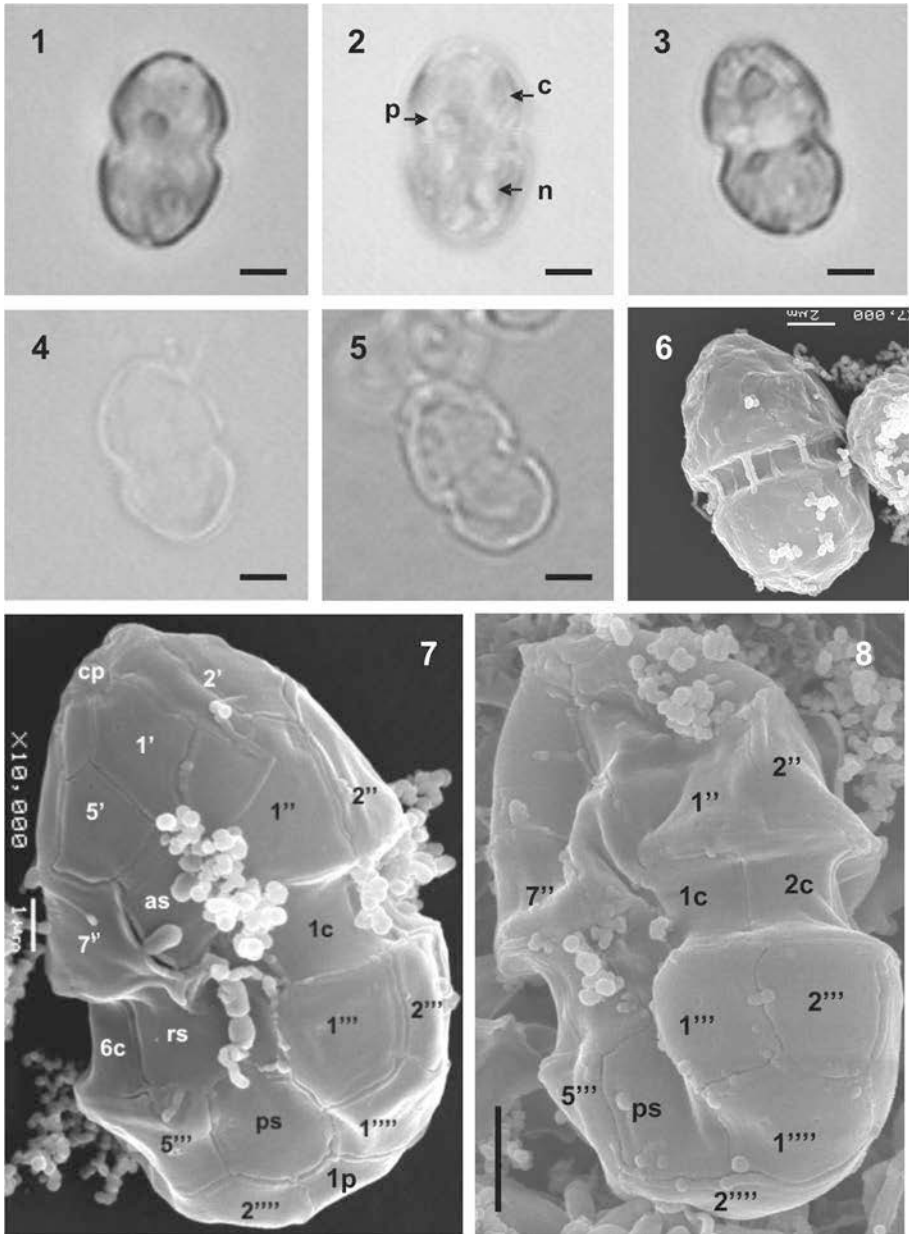
**Figs 1-14**Loeblich *et al.*, *J. Plankton Research* 3: 73, figs 1-14 (1981).

This is a new record for the Mexican Pacific, where only two other *Heterocapsa* species have been reported so far: *H. niei* (Loeblich) Morrill *et* Loeblich and *H. triquetra* (Ehrenberg) Stein (Okolodkov & Gárate-Lizárraga, 2006). It is mainly a coastal species distributed in the Pacific Ocean (California, Japan), eastern coast of USA, northern Atlantic Ocean and the Mediterranean Sea. Abundant populations (up to  $9.7 \times 10^4$  cells  $l^{-1}$ ) have been recorded in northern Spain (Trigueros *et al.*, 2000).

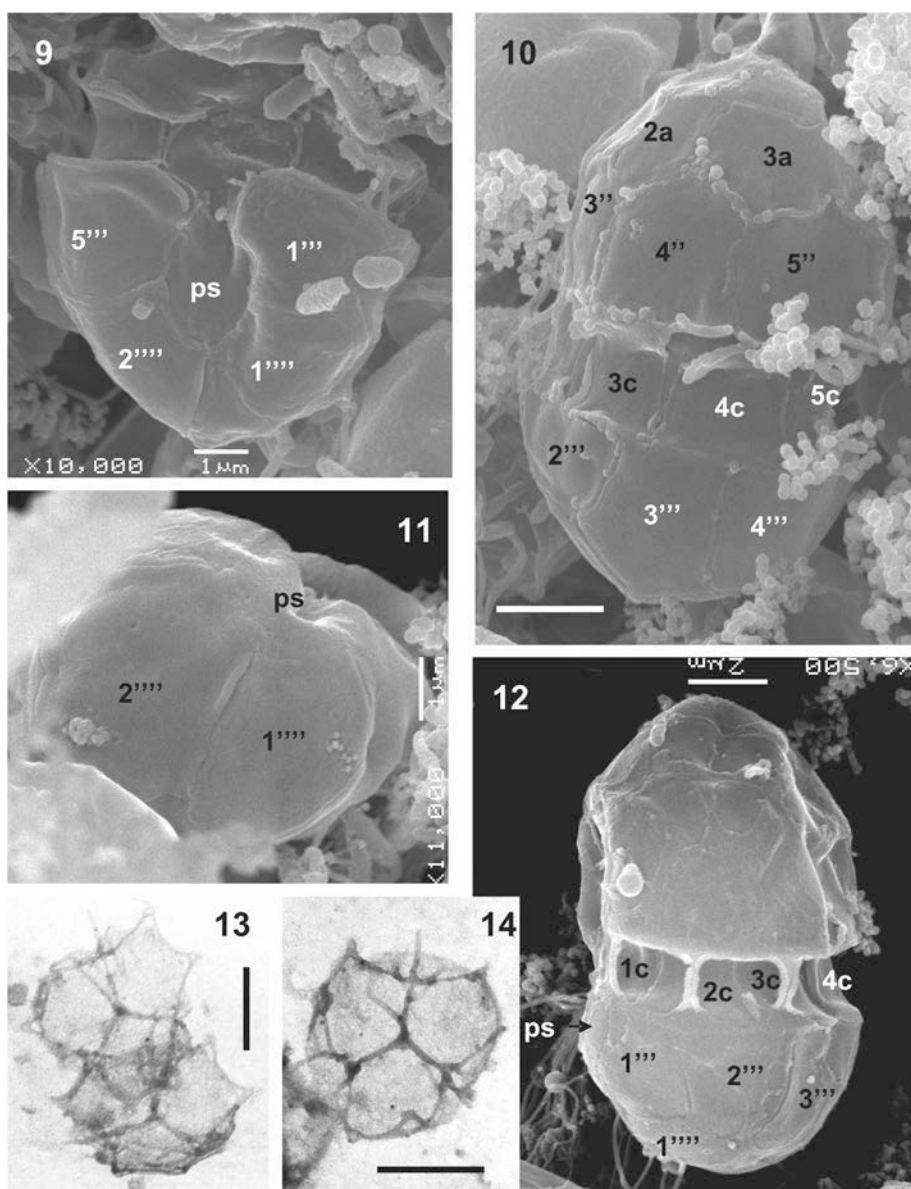
Cells from the Mexican Pacific are free-living, solitary, small-sized (12.5-13.7  $\mu m$  long and 7.5-8.7  $\mu m$  wide) and thecate. By LM cells are slightly flattened dorsiventrally, biconical with epicone and hypocone approximately equal in length or the epicone is slightly larger than the hypocone (Figs 1-5). The epicone is more acute than the hypocone, which is more rounded (Figs 1, 3, 5). The cingulum is almost imperceptibly displaced (descendent), wide and well excavated, whereas the sulcus is very conspicuous and fairly deep, especially towards the posterior end (Figs 1-3). Thecal plates are difficult to observe in living specimens (Figs 4, 5). The nucleus is displaced towards the hypotheca (Fig. 2). There are multiple yellow-brown chloroplasts scattered in the cell, and a large pyrenoid in the epitheca close to the cingulum (Fig. 2).

By SEM the cingulum sometimes shows a few vertical bridge-like structures which are probably artefactual (Figs 6, 12). There are no lists either in the cingulum or the sulcus. The plate formula is: Po, cp, 5', 3a, 7'', 6c, 5s, 5''', (1p ?) and 2'''. All thecal plates appear very thin, and the sutures are inconspicuous (Figs 7-12). A few scattered fine pores are present (Figs 7-9, 11). Sulcal plates are relatively large and easily observed in SEM (Figs 7-9). One specimen showed what can be interpreted as an intercalary antapical plate (1p) (Fig. 7). By TEM the external body scales become visible. They are about 400 nm in diameter and have a finely reticulated triangular to irregularly circular basal part, and a complex three-dimensional structure consisting of a central spine and six peripheral uprights, some of which form minute triangular to circular arches, and interconnecting bars and smaller spines (Figs 13, 14). These features coincide with previous descriptions (Morrill & Loeblich III, 1981; Uysal *et al.*, 2003; Iwataki *et al.*, 2004).

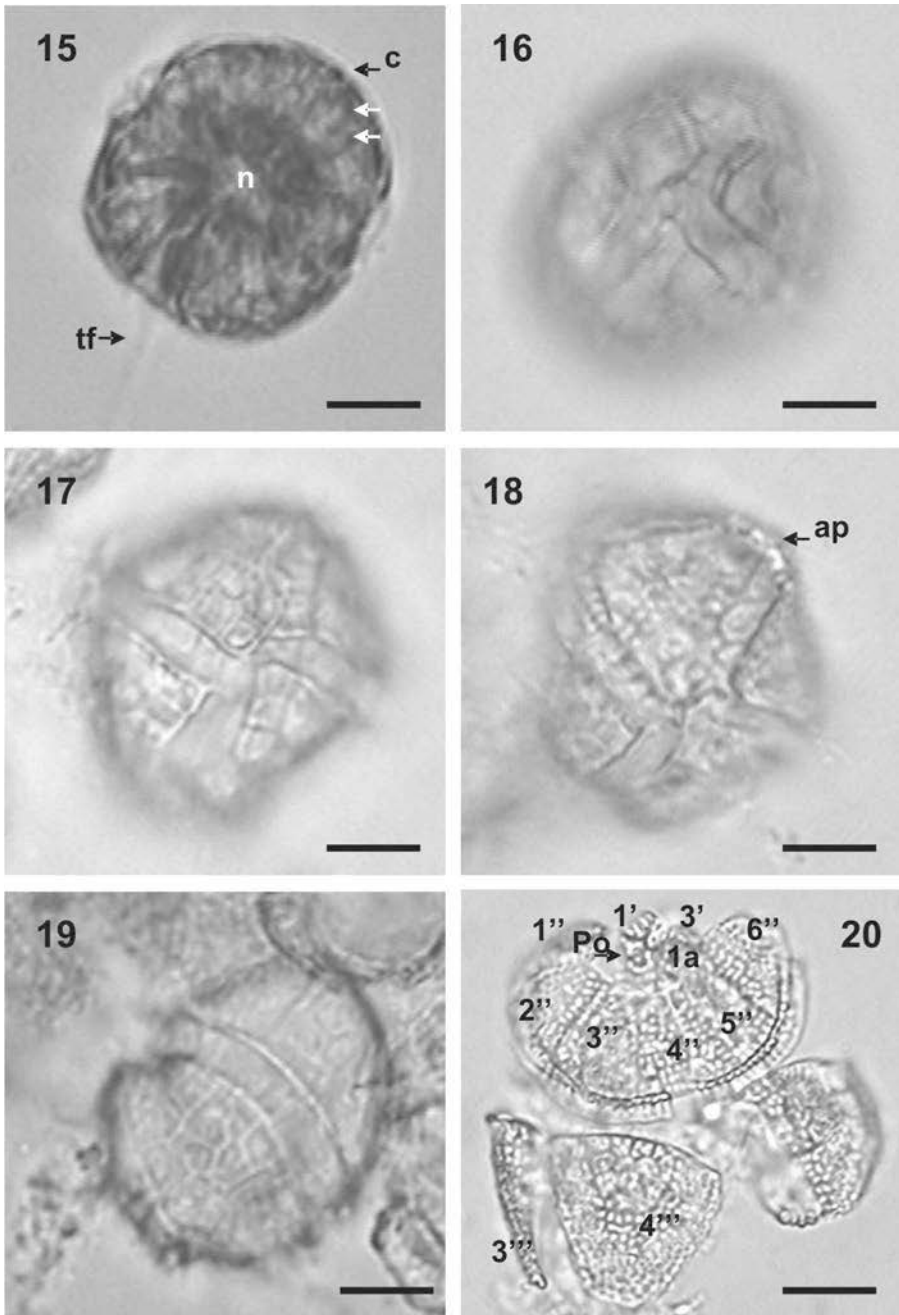
*Heterocapsa* forms a relatively homogeneous genus comprising free-living species with small to medium-sized cells. Apart from the cell size and the general biconical shape (with the epicone at times larger than the hypocone), the characteristic plate formula is: Po, cp, 5', 3a, 7'', 6c, 5-8s, 5''', 0-1 p, 2'''' (Horiguchi, 1995; Steidinger & Tangen, 1997; Iwataki, 2008). Von Stosch (1969) and Balech (1977) proposed 8 precingular plates (8'') instead of seven (7'') for *Heterocapsa* (*Cachonina*) *niei* (Loeblich) Morrill *et* Loeblich, interpreting the anterior sulcal plate (as) as the eighth precingular plate (8'') (von Stosch, 1969), or the first precingular plate (1'') (Balech, 1977). In addition, at least 12 of the 14 recognized species (Iwataki *et al.*, 2004), possess body scales on the external surface of the plasma membrane (Iwataki *et al.*, 2002a, 2002 b, 2004; Iwataki, 2008) which have been shown to be taxonomically significant at the species level (Morrill & Loeblich III, 1981; Hansen, 1996; Horiguchi, 1995; Iwataki *et al.*, 2002a, 2002b, 2004; Iwataki, 2008).



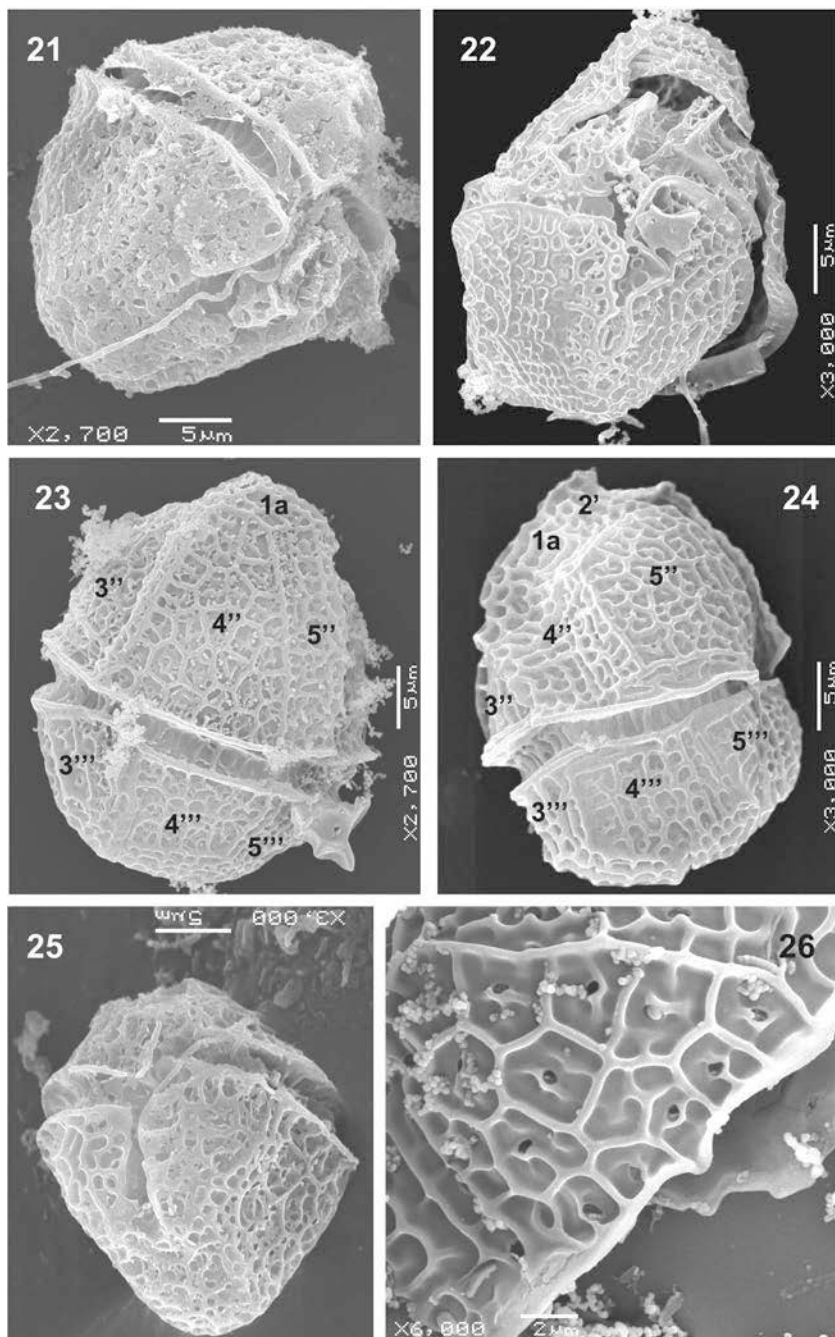
Figs 1-8. *Heterocapsa pygmaea*, LM and SEM. **1-3.** Living cells showing chloroplasts (c), nucleus (n) and pyrenoid (p), LM. **4, 5.** Empty thecae of cells, LM. **6.** Complete cell in lateral view, SEM. **7, 8.** Two other cells in ventral view, showing some plates of the apical, precingular, cingular, sulcal, postcingular and antapical series, SEM. Scale bars (unless stated otherwise): 2  $\mu$ m.



Figs 9-14. *Heterocapsa pygmaea*, SEM and TEM. **9.** Hypotheca in ventral view, with some postcingular and sulcal plates, SEM. **10.** Cell in dorsal view, showing apical intercalary, precingular, cingular and postcingular plates, SEM. **11.** Cell in antapical view: the two antapical and the posterior sulcal plates, SEM. **12.** Cell in lateral view with some cingular, postcingular and antapical plates, SEM. **13, 14.** Body scales, TEM. Scale bars: 2  $\mu\text{m}$  (Fig. 10) or 200 nm (Figs 13, 14).



Figs 15-20. *Protoceratium reticulatum*, LM. **15.** Living cell showing chloroplasts (c and white arrows), nucleus (n) and transverse flagellum (tf). **16.** Another living cell showing cingulum displacement, theca, some plates and reticulation. **17-19.** Empty thecae in ventral and dorsal views, showing some details of cingulum, sulcus and apical pore (ap). **20.** Theca with apical pore (Po), apical, apical intercalary (1a), precingular and postcingular plates. Scale bars: 10  $\mu$ m.



Figs 21-26. *Protoceratium reticulatum*, SEM. **21, 22.** Complete cells in ventral view, one still with the transverse flagellum. **23, 24.** Cells in dorsal view, showing some apical, apical intercalary, precingular and postcingular plates. **25.** View of the cingulum, sulcus and hypotheca. **26.** Detail of the areolae and pores in the theca.

Accurate identification of *Heterocapsa* species is important because *H. circularisquama* is toxic (Horiguchi, 1995; Uchida *et al.*, 1995). *Heterocapsa circularisquama* is morphologically very similar to another bloom-forming species, *H. illdefina* (Herman *et Sweeney*) Morrill *et* Loeblich (Hermann & Sweeney, 1976), and “it is almost impossible to distinguish these two species at light microscopical level” (Horiguchi, 1995). Other species also show superficial resemblances, particularly as they are generally small-sized and have thin and transparent thecal plates. Cells of *Heterocapsa pygmaea* are significantly smaller than *H. illdefina* and *H. circularisquama* (both 20-28  $\mu\text{m}$  in length), and their scales are also different (Iwataki *et al.*, 2004). Iwataki (2008) indicated that the presence of two pyrenoids located in the epitheca and the position of the nucleus in the hypotheca are characteristic of *Heterocapsa pygmaea*. We found only one pyrenoid located in the epitheca, suggesting that this character is variable under culture conditions. Variations in tabulation were noted previously (Morrill & Loeblich III, 1981) and all other tabulation details agree well with the original species description (Loeblich III *et al.*, 1981).

***Protoceratium reticulatum*** (Claparède *et* Lachmann) Bütschli

**Figs 15-26**

O. Bütschli, *Bronn's Thier-Reich* 1: pl. 52 fig. 2 (1885).

Basionym: *Peridinium reticulatum* Claparede *et* Lachmann, *Mém. Inst. Natl. Genev.* 61 (1): 405, pl. 20 fig. 3 (1859)

By LM cells are solitary, medium-sized (25-42.5  $\mu\text{m}$  long and 17.5-35  $\mu\text{m}$  wide) and irregularly polyhedral (Figs 15-18). The epitheca is broadly conical to slightly rounded and may be nearly equal, shorter or larger than the hypotheca (Figs 17, 18). The hypotheca is more rounded than the epitheca (Fig. 15). The apical pore is not protruding (Fig. 18). A marked reticulate pattern is apparent in the thecae (Figs 16-20). The cingulum is wide and excavated, with incipient lists, and displaced (descending) by about 1-1.5 times its width (Figs 16, 17). The sulcus is wide and deep, and the lists are also poorly-developed (Figs 17, 18). The nucleus is large and located in the posterior part of the hypotheca (Fig. 15). Numerous brownish, rod-like and discoid chloroplasts appear to radiate from the centre of the cell (Fig. 15). A central pyrenoid is present.

By SEM the thecal plates are very thick and the marked reticulation visible by LM (Figs 19-24) appears like a serial pattern of areolae surrounded by 4-6 ridges and bearing a single pore at the centre (Fig. 26). In several specimens this reticulation is less developed (e.g. the ridges are shallow and there are either 0 or 2 pores per areola). Suture lines and suture bands were apparent in the thecae (Figs 23, 24). The plate formula is: Po, cp, 3', 1a, 6'', (6c ?), (6s ?), 6''', (2'''' ?). The first apical plate (1') appeared to lack a ventral pore (Figs 20, 24). No cysts were observed.

The genus *Protoceratium* Bergh has been deemed to contain only four species (Gómez, 2005) in spite of the fact that at least twelve species have been validly described (G. Novarino, personal communication). The best known are *P. areolatum* Kofoid, *P. reticulatum* and *P. spinulosum* (Murray *et* Whitting) Schiller (von Stosch, 1969; Taylor, 1976; Dodge, 1985, 1989; Balech, 1988). The thecal tabulation of the three species has been described, especially that of *Protoceratium reticulatum* (von Stosch 1969; Balech, 1988; Dodge, 1989; Hansen *et al.*, 1996), and also its ultrastructure (Hansen *et al.*, 1996). The plate formula for the genus has been defined as: Po, 3', 0a, 6'', 6c, 6s, 6''', 2'''' (Balech, 1988; Steidinger & Tangen, 1997). However one apical intercalary plate (1a) has been found in *P. reticulatum* (Balech, 1988; Dodge, 1989; Hansen *et al.*, 1996). The cell size and epithecal tabulation



(contact with apical pore, subdivision of plate 1a) of *Protoceratium reticulatum* are known to vary in culture conditions, (Hansen *et al.*, 1996). It is also unclear if this species has 2<sup>'''</sup> or only one 1<sup>'''</sup> and one antapical intercalary plate (1p), as per Reinecke (1967) and von Stosch (1969). (Both authors studied it under the name of *Gonyaulax grindleyi* Reinecke, but following Dodge (1989) we consider *Gonyaulax grindleyi* as a taxonomic synonym of *Protoceratium reticulatum* along with other synonyms, e.g. *Protoceratium aceros* Bergh and others as in Schiller's (1937) work). The cyst produced by this species, which appears in the fossil record, has been named *Operculodinium centrocarpum* (Deflandre *et* Cookson) Wall.

*Protoceratium reticulatum* is cited regularly in the Mexican Pacific and seems to be widely distributed in this area (Hernández-Becerril, 1988a, as *Gonyaulax grindleyi*), but no blooms have been reported nor has toxin production been detected. There are other two *Protoceratium* species of the genus recorded in the Mexican Pacific: *P. globosum* Kofoid *et* Michener and *P. spinulosum* (Murray *et* Whitting) Schiller (Okolodkov & Gárate-Lizárraga, 2006). The species has a wide world distribution in coastal temperate to subtropical waters, but it has not been reported from polar waters.

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