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Three Dinophyceae from Clipperton Island lagoon (eastern Pacific Ocean), including a description of Peridiniopsis cristata var. tubulifera var. nov.

Alain Couté[1] , Catherine Perrette[2] , Nicolas Chomérat[3, *]

[1] Département Régulations, Développement et Diversité Moléculaire (RDDM), Muséum National d'Histoire Naturelle, UMR 7245, 57 Rue Cuvier – Case 39, 75005 Paris, France
[2] Eau-Céans, 1 Rue de la Prairie, 94440 Santeny, France
[3] Ifremer, Laboratoire Environnement et Ressources Finistère Bretagne Nord – Station de Concarneau, Place de la Croix, 29900 Concarneau, France

*: Corresponding author : Nicolas Chomérat, email address : nicolas.chomerat@ifremer.fr

Abstract :

Clipperton Island is a small French coral atoll in the eastern Pacific Ocean, which has been rarely investigated because of its remote location and difficult access. There is little scientific information on this ecosystem and only a few microalgae have been reported from the lagoon. To date, only one dinoflagellate taxon, *Peridiniopsis cristata*, is known to inhabit the lagoon. During an expedition in 2005 to study the lagoon and the surrounding oceanic waters of Clipperton Island, a further investigation of the lagoon phytoplankton was undertaken. In addition to *P. cristata,* which was still abundant in the upper water layer, two other thecate dinoflagellates were recorded. One dinoflagellate was identified as *Durinskia baltica*, while the other had the same thecal plate arrangement as *P. cristata* but was slightly smaller, (27) 30–40 µm long, 26–32 µm wide, and its plates were unornamented and devoid of prominent lists. Hence, the latter taxon is described as *P. cristata* var. *tubulifera* since it represents an extreme variation in the ornamentation of the nominate variety. This study provides a description and detailed illustrations of the three taxa found in this peculiar tropical marine ecosystem

Keywords : dinoflagellates ; lagoon ; morphology ; phytoplankton ; taxonomy

Introduction

Clipperton Island is a deserted small coral atoll located southeast of Socorro Island, as part of the Revillagigedo Archipelago in Eastern Pacific Ocean. This island has been first registered in 1711 by the captains of two French vessels, and is now an overseas possession of France (Sachet 1960). This small island has had a chaotic history (Sachet 1962a, Reyes Bonilla et al. 1999) and has got the reputation of being one of the most obscure, isolated and unpleasant places on earth (Jean-Baptiste et al. 2009). The island has been inhabited on some occasions and an exhaustive historical sketch is given by Sachet (1960, 1962a). Phosphate guano was mined on the island until 1917, and there are signs that human impacts have affected the inland ecosystem already naturally damaged (Jost 2003).

Owing to its situation on the way of the North Equatorial Current, and its frequent exposure to the Countercurrent, this is a place where swells meet, and in addition with the fringing reef of about one hundred meters wide, the access and landing from the Ocean is very difficult and only possible during calm weather (Jost 2003). Therefore, it has been the subject of relatively little scientific investigation (Charpy et al. 2010), and most studies in the past decade concern coral reefs and invertebrate fauna (Carricart Ganivet and Reyes Bonilla 1999, Monniot 2007, Salvat et al. 2008, Sanvicente-Añorve et al. 2010).

Clipperton atoll is the only coral one in the east equatorial Pacific Ocean, and contrary to most Indo-Pacific atolls, which can exchange water with the surrounding ocean through 'passes' in the atoll rim, the lagoon has been locked form the ocean for about 150 years (Sachet 1962a). Consequently, it possesses very peculiar biogeochemical characteristics with slightly brackish surface waters resulting from its

isolation and heavy rainfall, and a deeper layer of salty and anoxic water with hydrogen sulphide, and deeper, methane (Charpy et al. 2009).

There were very scarce investigations on microalgae from the Clipperton lagoon and only a handful of data exists, as a result of rare sampling conducted during scientific or military expeditions. Only one species of dinoflagellates has been documented to date from this lagoon, first described as *Glenodinium cristatum* by Balech (1961) and later transferred to the genus *Peridiniopsis* Lemmermann by Bourrelly (1968). The morphological characteristics of this apparently endemic taxon have later been further studied with scanning electron microscopy (SEM) by Ricard and Bourrelly (1982), with only a few available photomicrographs.

During the recent Clipperton expedition (Étienne 2005), sampling of the lagoon allowed to further investigate the phytoplankton of this closed atoll environment. It revealed a higher diversity than previously recorded, with 16 taxa of Cyanophyta, 21 Chlorophyta, 3 Dinophyta, 2 Euglenophyta and only 1 taxon of Heterokontophyta (Charpy et al. 2010). Among dinoflagellates, two unidentified taxa were reported in addition to the endemic *P. cristata* (Balech) Bourrelly (Couté et al. 2009, Charpy et al. 2010). The examination of the thecal morphology of these two taxa revealed that one species belongs to *Durinskia baltica* (Levander) Carty *et* Cox, while the other possesses all the characters of the genus *Peridiniopsis* without, however, be assigned to any known species. Thus, the aim of this taxonomic study is to provide a description and detailed SEM illustrations of the three thecate dinoflagellates found in Clipperton lagoon, including a new variety of *P. cristata.*

Material and methods

Sampling area

Clipperton Island is the only coral atoll lost in the eastern equatorial Pacific Ocean (10°18′N and 109°13′W) at ca. 945 km southeast from the Socorro Island in the Revillagigedo Archipelago and 1300 km southwest from the western Mexican coasts (Figure 1). The surface area of the island is 8.9 km^2, with only 1.7 km^2 emerged. The ring-shaped atoll is elliptical with a circumference of 11.8 km (Figure 1C), enclosing a lagoon of 7.2 km^2 (Jost 2003) with a marked stratification at about 10 m. The surface water lagoon is brackish, with the deep waters up to 30 m showing a salinity close to that of the surrounding ocean and high concentration of hydrogen sulphide, while in the deepest parts (>40 m), this gas is replaced by methane. Historical descriptions of Clipperton Island indicate that the lagoon became isolated from the ocean between 1839 and 1858 (Jost 2003, Jean-Baptiste et al. 2009). When no connexion exists between the ocean and the lagoon, a freshwater or slightly brackish lens formed at the surface of the saline oceanic waters due mainly to the high precipitation rate largely exceeding the evaporation one (Niaussat 1986).

The lagoon is highly eutrophic (Carsin et al. 1985) and the nutrient input by seabird droppings is high but dissolved nitrogen and phosphorus concentrations in water remain low owing to the high nutrient uptake by autotrophic phytoplankton cells (Charpy et al. 2010). Obvious events of hypoxia and anoxia are responsible for the disappearance of biological communities that formerly prospered, thus only remain abundant cyanobacteria and unicellular organisms which can cope with such extreme conditions (Reyes Bonilla et al. 1999). The main part of the lagoon is 2–5 m deep (Jost 2005) and is colonized by dense macrophyte beds (*Najas marina* var. *latifolia* A. Braun, *Potamogeton pectinatus* L. and *Ruppia maritima* L.) covered by epiphytic filamentous

cyanobacteria (Couté and Garrouste 2009). The lagoon has three deep basins (>20 m), including a spot known as Trou-Sans-Fond with acidic waters at its base (Charpy et al. 2010). This hole corresponds to a former volcanic pipe of 200 m in diameter, with a depth believed to exceed 90 m but actually measured at 37 m during the Clipperton expedition (Charpy et al. 2009). However, the deepest spot of this basin may have been overlooked or could have been filled with organic matter (Charpy et al. 2009). The maximum depth (45 m) has been found in the basin located at the east of the atoll.

Sampling

Samples were only collected at surface with a plankton net (20 µm mesh) at several locations in the lagoon covering almost all the area during the J.-L. Étienne's expedition in February 2005 (Figure 1C, small arrows). The average surface water salinity (0–10 m) measured during the expedition was 5.7 psu (Charpy et al. 2009).

Living subsamples were observed at the base camp immediately after collecting and later fixed using neutral formaldehyde (4–5% final concentration) for further morphological studies.

Microscopical examination

Live phytoplankton samples were examined on the atoll using a Zeiss Axioscop 2+ (Carl Zeiss, Oberkochen, Germany) microscope but micrographs of fixed cells were taken when back in the laboratory (in Paris) using an Axioscop microscope fitted with a digital camera. For SEM, cells were isolated individually using a micropipette and prepared according to Couté (2002). They were dehydrated in a graded series of ethanol solutions (15%, 30%, 50%, 70%, 90%, 95%, and absolute) and then critical-point dried with a EMS 850 (EMS, Fort Washington, USA). Then they were prepared according to

Chomérat and Couté (2008). Observations were made with a JSM–840A (Jeol Ltd, Tokyo, Japan) microscope at the Muséum National d'Histoire Naturelle (NMNH) in Paris, France.

Measurements were taken on the SEM micrographs. Line drawings were made from SEM micrographs.

Results

Only three dinoflagellate taxa belonging to the order Peridiniales were recorded in the lagoon during the 2005 Clipperton expedition.

Durinskia baltica (Levander) Carty *et* Cox (Figures 2, 5–11, 34–40)

Basionym   *Glenodinium balticum* Levander 1894, p. 52.

Reference   Carty and Cox 1986, p. 200, figs. 11–14.

Synonyms   *Glenodinium cinctum* sensu Levander 1892, p. 407, figs. 1–4; *Peridinium balticum* (Levander) Lemmermann 1910, p. 657.

Description   Cells are almost spherical, 21–22 µm long and 21–24 µm wide, and slightly flattened with the dorsiventral length varying from 19 to 22 µm. The cingulum is median and slightly descending (Figure 5). Epitheca and hypotheca are smooth and roughly equal in size (Figures 2, 5, 6, 34, 35).

The thecal surface is smooth with numerous and dispersed circular pores, with a thecal plate formula being: Po, X, 4′, 2a, 6″, 5c, 4s, 5‴, 2⁗ (Table 1). The epitheca is

composed of the apical pore complex (APC) and 12 plates. Two plates form the APC, a small and elongated quadrangular X plate and a Po plate (Figures 9, 39). The apical series comprises four plates unequal in size. The ventral 1′ plate is five-sided, because of the large contact with the sulcal area (Figures 5, 34). Plates 2′ and 4′ are six-sided, the latter being the largest of the apical series, while plate 3′ is four-sided, almost rectangular in shape (Figures 7, 36). The two intercalary plates are unequal in size. Plate 1a is rather small and pentagonal, located on the left lateral side of the cell, while plate 2a is hexagonal and extends on almost all the dorsal part of the cell (Figures 6, 7, 36). Precingular plates 1″, 4″ and 6″ are four-sided while plates 2″, 3″ and 5″ are five-sided (Figures 5–7, 11).

The cingulum comprises five plates among which C_1 is the smallest of the series (Figures 10, 34, 38). The sulcus is short and comprises four visible plates (Figures 5, 10, 38). Plate Sd forms a short sulcal list (Figure 10). Plate Ss, in contact with the first cingular plate C_1, is elongated and partially hidden by the list. Plate Sm is the smallest while Sp is the largest of the series (Figures 10, 38).

The hypotheca is composed of five postcingular and two antapical plates almost equal in size (Figures 8, 37). The postcingular plate 3‴ is the smaller of the series and quadrangular as the others, except plate 2‴ which is pentagonal (Figure 37).

A variation in the epithecal pattern has been observed in some cells. In most specimens, the plates 1a and 2a are contiguous (Figures 6, 7) but on others, they are found to be shortly separated by an extra edge of the apical 3′ plate (Figures 11, arrow, 40, arrowhead). In the latter, the 1a plate is usually four-sided (Figures 11, 40) rather than five-sided (Figures 7, 39). In addition, plates 2a and 3′ are five-sided, excluding the small indentation by the APC (Figure 11), whereas in the most common epithecal pattern, the former is hexagonal (Figure 6) and the latter four-sided (Figure 7).

This species is photosynthetic and brownish in colour (Figure 2).

It is illustrated and referred as to Dinophyceae Peridiniales sp. "Dino1" in Couté et al. (2009) and Charpy et al. (2010).

***Peridiniopsis cristata* (Balech) Bourrelly var. *cristata* (Figures 3, 12–17, 25, 26, 28, 29, 32, 33, 41–45)**

Basionym   *Glenodinium cristatum* Balech 1961, p. 47, fig. 1.

As a nomenclatural note, *Peridiniopsis* being of a feminine gender (Sournia 1986), the combination *P. cristatum* proposed by Bourrelly (1968) is incorrect. Therefore, we make the correction here to *cristata* without any modification of the authority (McNeill et al. 2006).

Description   Cells are (37)43–57 µm long, including the antapical "crest", and (31)33–41 µm wide. They are slightly compressed dorsiventrally with a depth of 31–37 µm. The epitheca is conical to pyriform while the hypotheca is hemispherical (Figures 3, 12, 13, 16, 17, 25, 26, 41–43). The epitheca is higher than the hypotheca (Figures 12, 13), but the latter possesses an antapical membranous extension resembling a crest (Figures 12, 13, 16, 17, 25, 26, 41–43).

The thecal plate formula is Po, X?, 3′, 1a, 6″, 6c, 5s(?), 5‴, 2⁗ (Table 1). The epitheca is symmetrical in respect to the sagittal plane and is composed of an apical pore complex and 10 plates, three apical, one intercalary and six precingular plates. Due to the strong ornamentation and the presence of a dorsal membranous crest near the apical pore, only the Po plate of the APC can be observed (Figure 32) and the

occurrence of an X plate cannot be confirmed. These crests are formed by a thin extension of the plates on both sides of the suture (Figure 32, arrows). The apical plate 1′ is four-sided and rhombic (Figures 12, 14, 25, 41), and its contact with the anterior sulcal plate Sa is short (Figures 12, 25, 28, 41). The dorsal suture of plates 2′ and 3′ is bordered by membranous extensions of the plates on both sides of the suture, forming a prominent dorsal crest of about 5 μm wide (Figures 13, 14, 16, 17, 26, 32, 33, 43). The intercalary plate 1a is located dorsally and is hexagonal (Figures 13, 14, 42, 44). Among the plates of the precingular series, 1″, 3″, 4″ and 6″ are four-sided, while 2″ and 5″ are five-sided (Figures 12, 13, 16, 17, 41–43).

The cingulum is deeply excavated (cavizone) and slightly descending. It is composed by six plates of approximately the same size (Figures 12, 13, 16, 17, 41–43).

The sulcus area is large and bordered by prominent membranous lists, formed like the "crests" (Figures 12, 15–17, 28, 29, 41, 45). It is composed of four major plates but some smaller could be hidden by the lists. The anterior sulcal plate (Sa) slightly indents the epitheca (Figures 25, 28). The right sulcal plate (Sd) is relatively high and forms a sulcal list which overlaps the furrow (Figures 25, 28, 29, 41). The left sulcal plate (Ss) is small, located just below the Sa plate (Figure 28), while the Sp plate is the largest of the series (Figures 28, 29). A fifth small plate Sm seems to be present below the list of Sd of a weakly ornamented cell (Figure 28), but its suture with Ss is difficult to observe and its presence has not been confirmed in other specimens.

The hypotheca comprises five postcingular and two antapical plates of a nearly equal size (Figures 15, 45). A prominent antapical crest (6–7 μm long) is present and results from the membranous extension of the borders of the antapical plates 1‴′ and 2‴′ (Figures 12, 13, 15–17, 25, 26, 45). Except for the postcingular plate 3‴ which is five-sided, all the other plates are four-sided (Figures 15, 45).

The thecal ornamentation is quite variable, probably in relation with the age of the cells. On newly divided cells with a thin theca, the plates are verrucose with numerous small warts lying between thecal pores (Figures 25, 28). On older cells, the warts are thicker (Figure 26) and merge to form reticulations and areolae surrounding the thecal pores (Figure 29). The crests are smooth or ornamented by small warts but never have reticulations (Figures 16, 17, 26, 33, 43).

This species is photosynthetic and brownish in colour (Figure 3).

Peridiniopsis cristata var. *tubulifera* Couté, Perrette *et* Chomérat var. nov. (Figures 4, 18–24, 27, 30, 31, 46–51)

Diagnosis   Organismus unicellularis, photosyntheticus, cum stigmate et theca. Cellulae pyriformes leviter compressae dorso-ventraliter in laterale visu. Longitudo: (27)30–40 μm; latitudo: 26–32 μm. Formula thecae laminarum: Po, X, 3′, 1a, 6″, 6c, 5s, 5‴, 2⁗. Epitheca late conica, ad apicem colliformis. Lamina X minima et apicalis porus cum parva propria tubuliformi apicali fauce sublatus. Hypotheca rotundata et brevior quam epitheca. Cingulum paulo excavatum et leviter descendens. Sulcus brevus et ad antapicem latior. Thecae laminae laeves et cum circularibus poris ornatae.

Description   Unicellular photosynthetic organism with a theca and a stigma. Cells pyriform, slightly compressed dorsiventrally in lateral view. Length: (27)30–40 μm; width: 26–32 μm. Thecal plate formula: Po, X, 3′, 1a, 6″, 6c, 5s, 5‴, 2⁗. Epitheca widely conical, forming a neck at the apex. Plate X small and apical pore with a prominent rim, forming a characteristic apical tubular structure. Hypotheca hemispherical and shorter than epitheca. Cingulum moderately excavated and slightly

descending. Sulcus short widening at the antapex. Thecal plates smooth and with circular pores dispersed.

Holotype SEM stub no. 124.2005.AC deposited at the RDDM Department (Cryptogamy building) of the Muséum National d'Histoire Naturelle (MNHN) of Paris, France. Holotype specimen illustrated in Fig. 18.

Type locality Brackish surface water (0.5 m), lagoon of Clipperton Island (10°18'N 109°13'W), Eastern Pacific Ocean. Collected with a plankton net by A. Couté in February 2005.

Etymology The specific epithet comes from *tubulus* and adjectival suffix –*fer*, meaning bearing a small tube.

Morphology Cells are roughly pyriform, (27)30–40 μm long, 26–32 μm wide and 22–26 μm thick. The epitheca is broadly conical, forming a well defined neck at the apex (apical horn) and the hypotheca is hemispherical. The outline of the cells reminds a fig-fruit shape and is very similar to the shape of the nominate variety excluding the crests (Figures 18, 19, 46, 47). Some more rounded cells are found (Figures 4, 24) and may correspond to cyst-forming cells.

The thecal plate formula is Po, X, 3′, 1a, 6″, 6c, 5s, 5‴, 2⁗ (Table 1). The epitheca is nearly symmetrical in respect to the sagittal plane and is composed of 12 plates, including the pore plate Po, the canal plate X, three apical, one intercalary and six precingular plates. The plates of the apical pore complex are located on the

prominent neck formed by the apical plates (Figure 30). The X plate is very small (0.8 µm long by 0.4 µm wide) and four-sided while Po is rounded (Figure 30). The tubular rim bordering the apical pore is high and prominent (Figures 31, 50). The apical plate 1′ is four-sided and rhombic (Figures 18, 22, 24, 46), sometimes five-sided, depending on the length of the suture with the anterior sulcal plate Sa. The intercalary plate 1a is located dorsally and is six-sided (Figures 19, 22, 47, 48). Among the plates of the precingular series, 1″, 3″ and 4″ are quadrangular while 2″, 5″ and 6″ are pentagonal (Figures 22, 48).

The cingulum is slightly excavated and descending about half its width (Figures 18, 24, 46). It is composed by six plates nearly equal in size (Figures 18–21, 46, 47). The sutures of cingular plates are not facing those of the pre- and postcingular plates and are shifted (Figures 19–21).

The sulcus is short and broad towards the antapex. It is composed of five plates. The anterior sulcal plate (Sa) slightly indents the epitheca (Figures 18, 24, 27, 46, 51). At its posterior end, Sa forms a small incurved list (Figures 24, 27, 46). The right sulcal plate (Sd) is relatively high and forms a developed sulcal list which borders the furrow (Figures 18, 27, 46, 51). The left sulcal plate (Ss) is small, contacts shortly the first cingular plate C_1 and is located just above the small plate Sm (Figures 27, 51). The Sm plate borders the flagellar pore that is partially obscured from the view by the right sulcal list. Both of these plates are deeply excavated in the sulcus. The posterior sulcal plate (Sp) is the largest of the sulcal plates (Figures 18, 23, 24, 27, 46, 49, 51). It is broad and nearly reaches the antapex of the cell (Figure 24, 46).

The hypotheca comprises five postcingular and two antapical plates (Figures 23, 49). Except for the plate 3‴ which is five-sided, all other postcingular plates are four-sided. The two antapical plates have almost the same size (Figures 23, 49)

The plates are smooth with circular thecal pores, including those of the sulcal series. A row of pores borders the cingulum on the epitheca and hypotheca and on each side of the cingulum (Figures 19, 21).

This species is photosynthetic and brownish in colour (Fig. 4).

It is illustrated and referred as to Dinophyceae Peridiniales sp. "Dino 2" in Couté et al. (2009) and Charpy et al. (2010).

Discussion

Phytoplankton studies of the Clipperton lagoon are very scarce (Charpy et al. 2010). The first mention of microalgae in the lagoon was made by Taylor (1939) who reported only 13 taxa of microalgae belonging to Cyanophyceae and Chlorophyceae. Later, Sachet (1962b) reported a total of 24 species of Cyanophyceae, 10 species of Chlorophyceae and one unidentified species of Dinophyceae (*Glenodinium* sp.), which was later described by Balech (1961) as *Glenodinium cristatum*. Since the inconsistencies regarding the accurate circumscription of the genus *Glenodinium* Ehrenberg, Bourrelly (1968) transferred *G. cristatum* to the genus *Peridiniopsis* mainly based on its thecal characteristics. *Peridiniopsis cristata* has been again recorded in March 1980 and studied by Ricard and Bourrelly (1982) who first used SEM to further investigate the morphology of this dinoflagellate. It is remarkable that this species, still present in recent samples, has never been reported elsewhere in any other tropical regions, and appears as endemic to Clipperton lagoon (Ricard and Bourrelly 1982), which is very unusual for a planktonic dinoflagellate. Surprisingly, Popovský and Pfiester (1990) mentioned its occurrence in saline ponds of France but this statement without any reference is inconsistent with the mention by Ricard and Bourrelly (1982), and actually very doubtful. Interestingly, Iltis and Couté (1984) found a resembling

taxon in the Lake Poopó at an altitude of 3686 m in Bolivia, but with some morphological differences and they described it as *P. cristata* var. *boliviensis* (incorrectly named *P. cristatum* var. *boliviense*). Cells of this variety are more rounded and the apical crest (i.e. the list between plates 2′ and 3′) is absent or hardly developed which contrasts with the type of the nominate variety from Clipperton lagoon. In the description of *P. cristata* var. *boliviensis*, the photomicrograph (Iltis and Couté 1984, pl. 3, fig. 8) probably does not correspond to the same taxon since the biconical shape and the acuminate antapex do not remind the outline observed in SEM (Iltis and Couté 1984, pl. 3, figs 1–7). The thecal arrangement and ornamentation in the nominate variety and *P. cristata* var. *boliviensis* are rather similar.

From the original description of *Peridiniopsis cristata* var. *cristata* (Balech 1961) and its reinvestigation by Ricard and Bourrelly (1982), this study revealed that the Clipperton lagoon specimens are unambiguously the same taxon. In contrast with Balech (1961) who identified four sulcal plates, Bourrelly (1985) found a fifth small sulcal plate Sm located below Ss. In our study, Sm has been putatively identified on a young cell and was probably hidden by the sulcal list in most well-developed specimens. In addition, Ricard and Bourrelly (1982) reported a pore on the upper right corner of the C_2 plate of the nominate variety which has not been previously mentioned by Balech (1961) in his detailed description. During our investigations of *P. cristata* var. *cristata* from the type locality, no specimen was found to possess this peculiar feature. For this reason, and since no other dinoflagellate is known to possess a pore on the C_2 plate, we consider that this pore or hole may result from an artefact or the activity of a parasitic organism. Thus, in our opinion, this criterion is probably of no taxonomical value and should not be further considered.

In spite of a very different ornamentation, it is striking that the thecal arrangement of the new variety *Peridiniopsis cristata* var. *tubulifera* is very similar to that of the nominate variety and they have the same plate formula. The cells of the new variety *tubulifera* are smaller than the ones of the nominate variety but their size ranges overlap when the length of the latter is considered without the lists. The major difference between these two taxa is the total absence of ornamentation and lists on the theca of *P. cristata* var. *tubulifera* while the nominate variety is usually ornamented. In addition, the apex of this new variety is peculiar, because of the presence of the tubular rim structure, not seen in *P. cristata* var. *cristata*. This structure may be present in the latter but hidden by the prominent apical crest surrounding the apical pore. This tubular rim is typical of the Peridiniaceae (Toriumi and Dodge 1993) but it is generally less developed and not as high as in *P. cristata* var. *tubulifera* where it is particularly prominent. In some other genera, the plates of the apical series can form a rather similar tubular neck or horn, as in *Protoperidinium tuba* (Schiller) Balech (Schiller 1931–1937) or in the fossil dinoflagellates *Gonyaulax jurassica* Deflandre and *Rhynchodiniopsis aptiana* Deflandre (Grassé 1952).

Since no other major morphological difference than the ornamentation was found to distinguish *P. cristata* var. *tubulifera* from the nominate variety, we consider that they very likely belong to the same species but correspond to different varieties with an extreme variation in the ornamentation. For several species in cultures, it has been demonstrated that ornamentation is highly variable and cannot be a taxonomic criterion for identification (e.g. Craveiro et al. 2009). A variable ornamentation has been reported in cells of *P. cristata* var. *cristata*, ranging from verrucose to strongly reticulate, but all cells possessed apical and antapical lists (= "crests"), whereas these lists were always absent in *P. cristata* var. *tubulifera*. No specimen with a transitional

ornamentation and rudimentary lists has been found in the samples. For *P. cristata* var. *boliviensis*, Iltis and Couté (1984) observed only specimens with developed crests and there is no mention of cells with a different ornamentation.

Bourrelly (1968, 1985) and Popovský and Pfiester (1990) placed *P. cristata* var. *cristata* in the group *borgei* of *Peridiniopsis*, which is defined by an epithecal plate pattern of 3′, 1a and 6″. This definition encompasses widely different and unrelated species, some being now transferred to another genus (Boltovskoy 1999), but the resemblance of *P. cristata* var. *cristata* and *P. cristata* var. *tubulifera* with *P. borgei* Lemmermann is conspicuous. They are in the same size range and are similarly shaped but *P. borgei* possesses a large central vacuole and a dorsal starch-envelopped pyrenoid (Calado and Moestrup 2002), which have not been observed in living specimens of the taxa from Clipperton lagoon.

From an ecological point of view, species in the genus *Peridiniopsis* are generally found in freshwater environments and it is a common genus in freshwater plankton (Bourrelly 1985, Popovský and Pfiester 1990, Lewis and Dodge 2002), but some taxa are described from brackish waters such as *P. salina* Trigueros (Trigueros 2000) and *P. cristata* var. *cristata* (Balech 1961). The new variety *P. cristata* var. *tubulifera* can also be placed in the group of brackish species as it is co-occurring with *P. cristata* var. *cristata* in Clipperton lagoon. In addition, although the bolivian variety *P. cristata* var. *boliviensis* was described from an inland mountain lake that does not receive seawater, it can be considered as a brackish form since the salinity in Lake Poopó was 7.5 psu (Iltis and Couté 1984) and thus slightly higher than the salinity observed in the upper water layer of Clipperton lagoon.

Durinskia baltica has not been previously recorded from Clipperton lagoon and this is the first report of this species to date. This taxon has had a long and complex

taxonomical history before Carty and Cox (1986) erected the genus *Durinskia* for dinoflagellates with the plate formula Po, X, 4′, 2a, 6″, 5c, 4s, 5‴, 2⁗ to accommodate *Peridinium balticum* (Levander) Lemmermann. Although it has been described with thecal plates with numerous transversally oriented pores, *P. dybowskii* Woloszyńska has been considered to be conspecific with *D. baltica* which does not have this feature (Schiller 1931–1937, Popovský and Pfiester 1990). However, this is questionable since these species seem to have very different habitats, *P. dybowskii* being reported from humus rich habitats with low pH (Hansen and Flaim 2007) while *D. baltica* occurs generally in brackish waters. The recent combination, *Durinskia occulata* (Stein) Hansen *et* Flaim, proposed by Hansen and Flaim (2007) for a species described from the Moldau River by Stein (1883) and found again in an Italian lake, corresponds to a morphologically close taxon with the same thecal plate arrangement than *D. baltica*. *Durinskia occulata* has a more globular shape compared to the more pronounced dorso-ventral flattening of both *P. dybowskii* and *D. baltica* (Hansen and Flaim 2007). The present material is somewhat smaller than the dimensions given for *D. occulata* from Ampola Lake, i.e. 28–34 μm in length and width (Hansen and Flaim 2007) but it presents similarities in the ornamentation and thecal plate arrangement. Since *D. occulata* has only been recorded in freshwater habitats and its tolerance to brackish waters has not yet been demonstrated, we consider it as a freshwater species separate from *D. baltica* which is commonly found in brackish waters, and even in some marine environments (Carty and Cox 1986). Moreover, the present material was in the same size range than given by Levander (1894) for *Glenodinium balticum*, i.e. 22–30 μm. Consequently, we consider that this material fits morphologically and ecologically more with *D. baltica* than with *D. occulata*. Nevertheless, further investigations using

molecular data are necessary to conclude about these taxa with the same thecal plate pattern which may be synonyms.

In a clonal culture of this species, Chesnick and Cox (1985) observed some variations in the plate pattern and the number of plates in some thecal series can differ from the typical organization. However, the thecal variation of the 3′ and 2a plates that we observed, and the resulting disconnection of plates 1a and 2a was not reported by these authors and appears as a new type of variation for this species. Interestingly, variations of the thecal plate pattern are not rare in dinoflagellates from brackish waters, as reported also for *Protoperidinium bolmonense* Chomérat *et* Couté (Chomérat and Couté 2008).

In conclusion, this study brings new data on the diversity of planktonic dinoflagellates in Clipperton lagoon. The presence of *Peridiniopsis cristata* var. *cristata* described in 1961 from this lagoon and endemic of this area is remarkable. The knowledge of this ecosystem is still to be improved and, as sampling is only made from time to time during expeditions, the plankton dynamics is not understood yet. For several years, *P. cristata* var. *cristata* was considered as the unique dinoflagellate living in this lagoon but this study revealed that other taxa are present. Whether *P. cristata* var. *tubulifera* constitutes a particular morph in the life cycle of *P. cristata* var. *cristata* or belongs to a different species has not been demonstrated and remains to be verified. In addition, further studies should manage to better understand their population dynamics and their seasonality. In addition, in order to better understand their evolution in this isolated ecosystem, their molecular phylogenetic relationships with other dinoflagellates from distant locations should be investigated. In particular, it is necessary to clarify the relationships between *P. cristata* var. *cristata* and its two varieties *boliviensis* and *tubulifera*.

Acknowledgements

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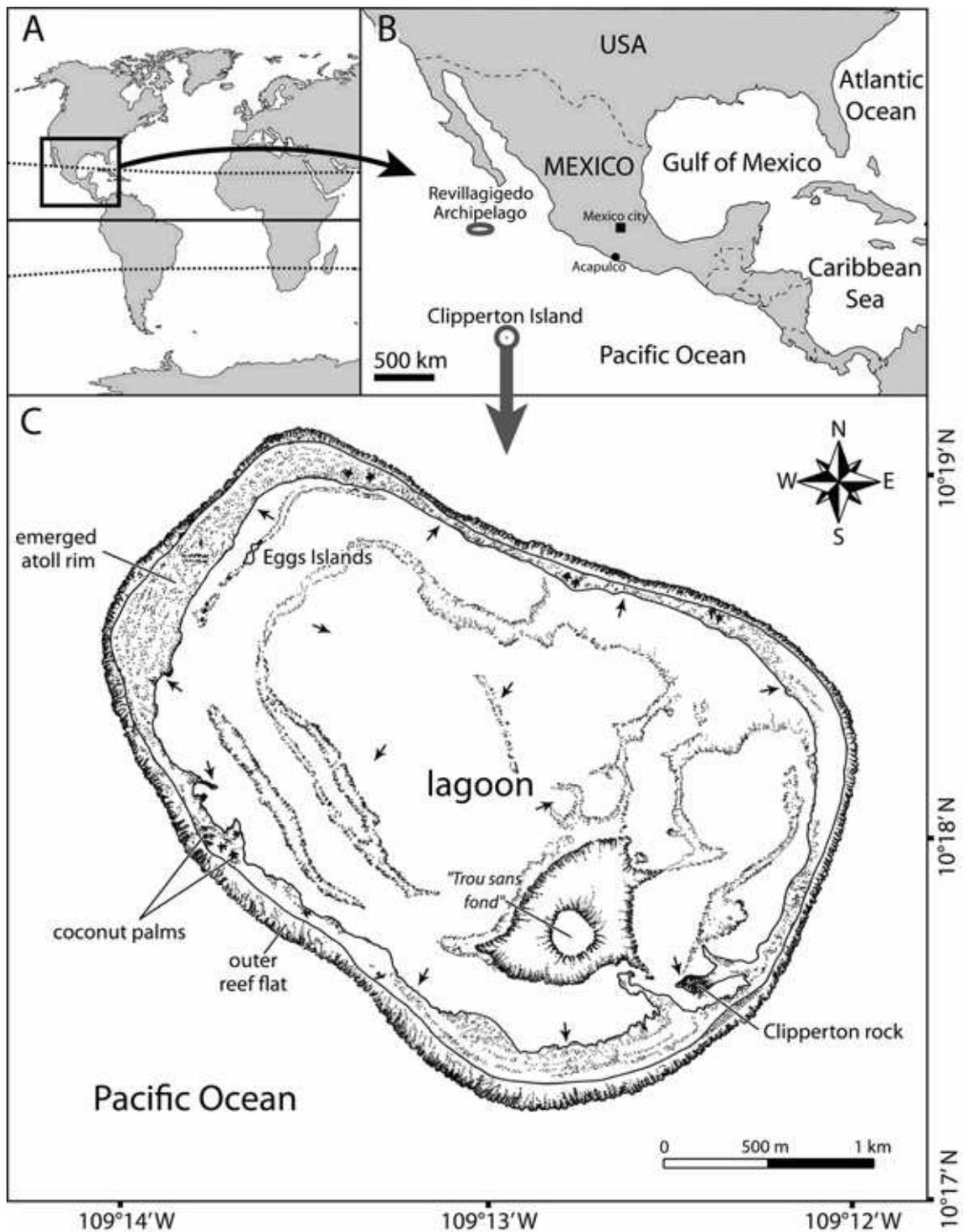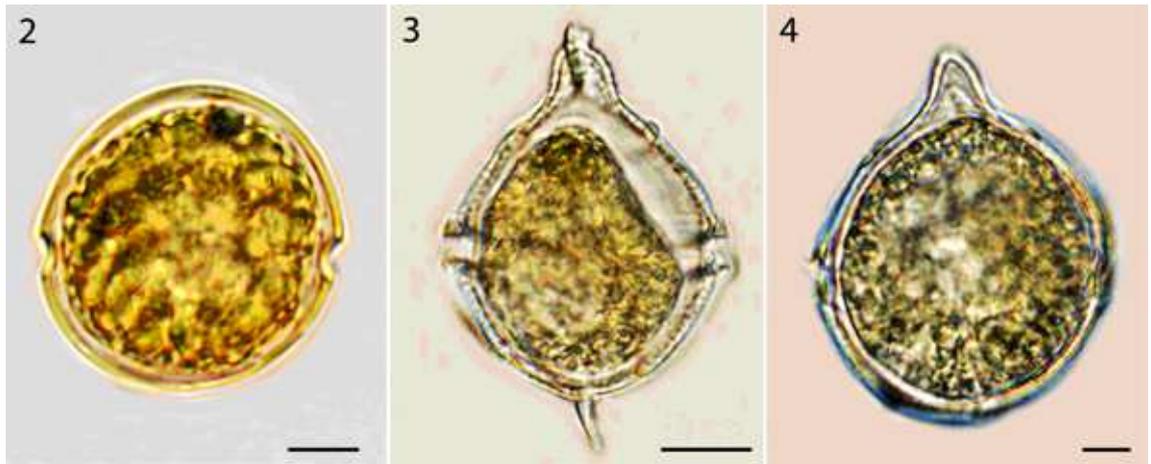
Figure legends:

Figure 1   Location of Clipperton Island (A) off Central America, and (B) more precisely in the eastern equatorial part of Pacific Ocean, (C) Clipperton Island and lagoon. Small arrows indicate net sampling collection.

Figures 2–4   Thecate dinoflagellates from Clipperton Island lagoon fixed in formaldehyde, LM.

(2) *Durinskia baltica*. (3) *Peridiniopsis cristata* var. *cristata*. (4) *Peridiniopsis cristata* var. *tubulifera* var. nov.

Scale bars=5 μm (Figures 2, 4); 10 μm (Figure 3).
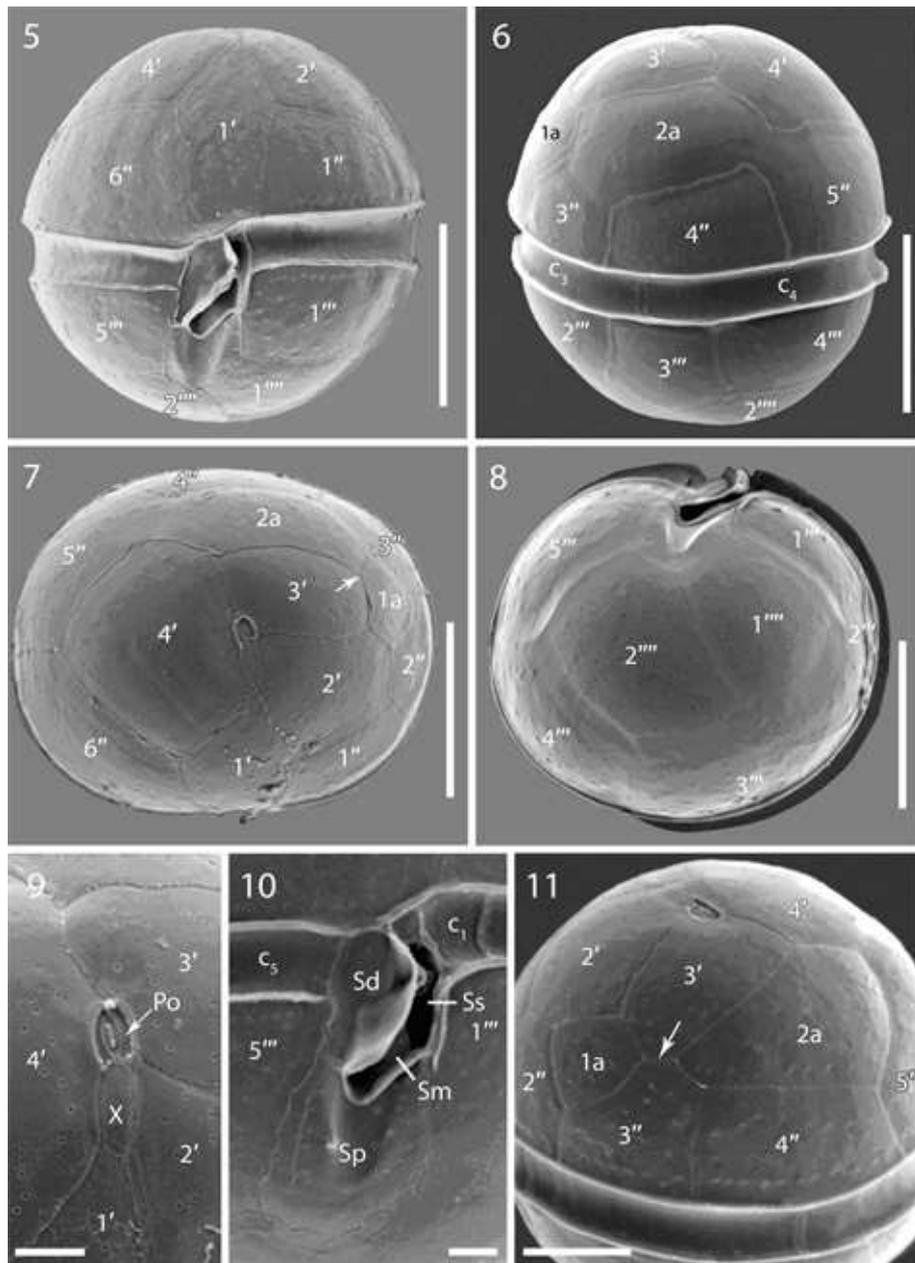
Figures 5–11 *Durinskia baltica*, SEM.

(5) Ventral view. (6) Dorsal view. (7) Apical view showing the arrangement of thecal plates. Note that the two anterior intercalary plates 1a and 2a are contiguous (arrow). (8) Antapical view. (9) Detail of the apical pore complex (APC). (10) Detail of the sulcal area. (11) Variation of the epithecal plate pattern on a specimen with the two anterior intercalary plates 1a and 2a disconnected (arrow).
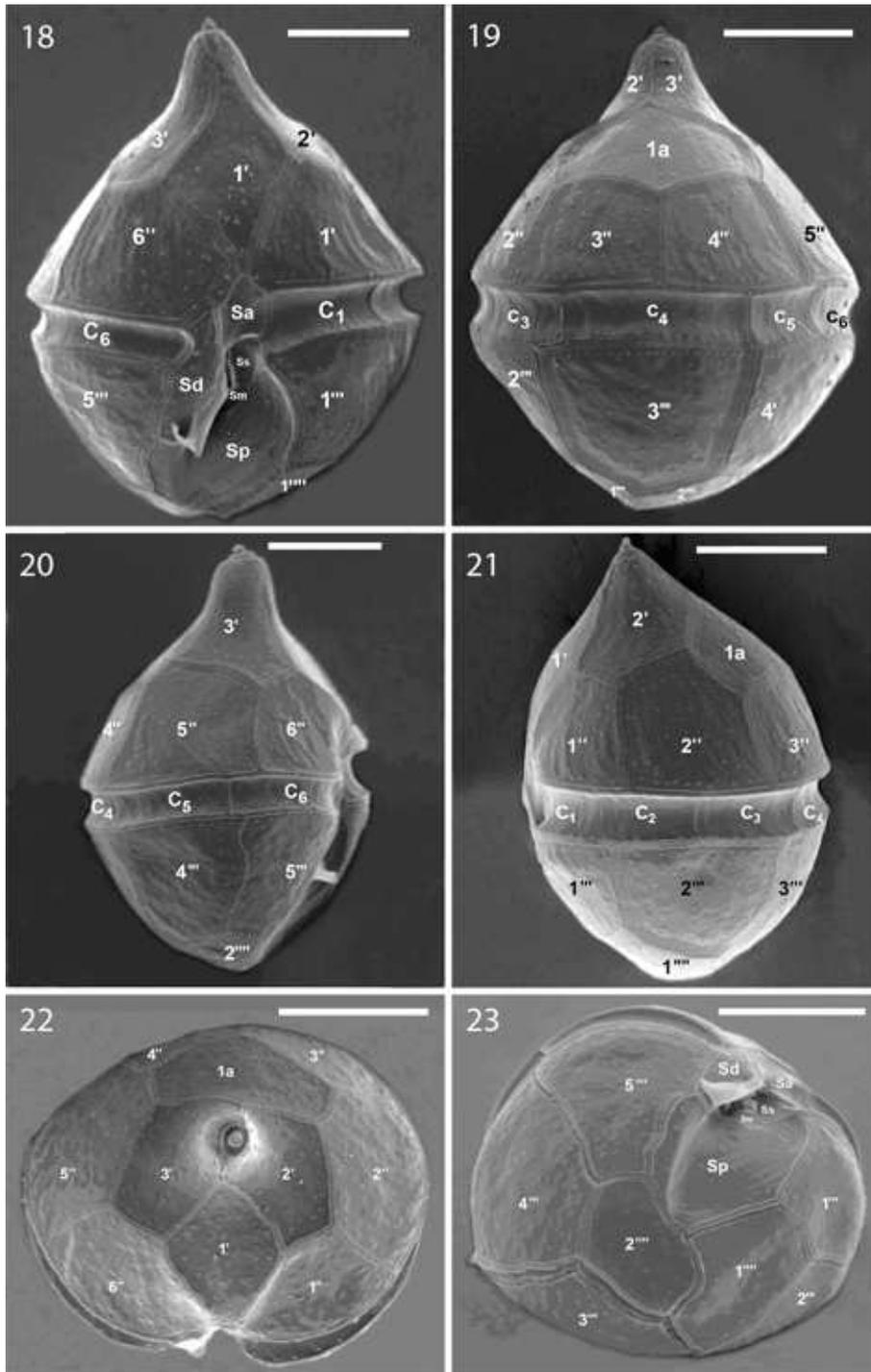
Scale bars=10 μm (Figures 5–8); 5 μm (Figure 11); 2 μm (Figures 9–10).
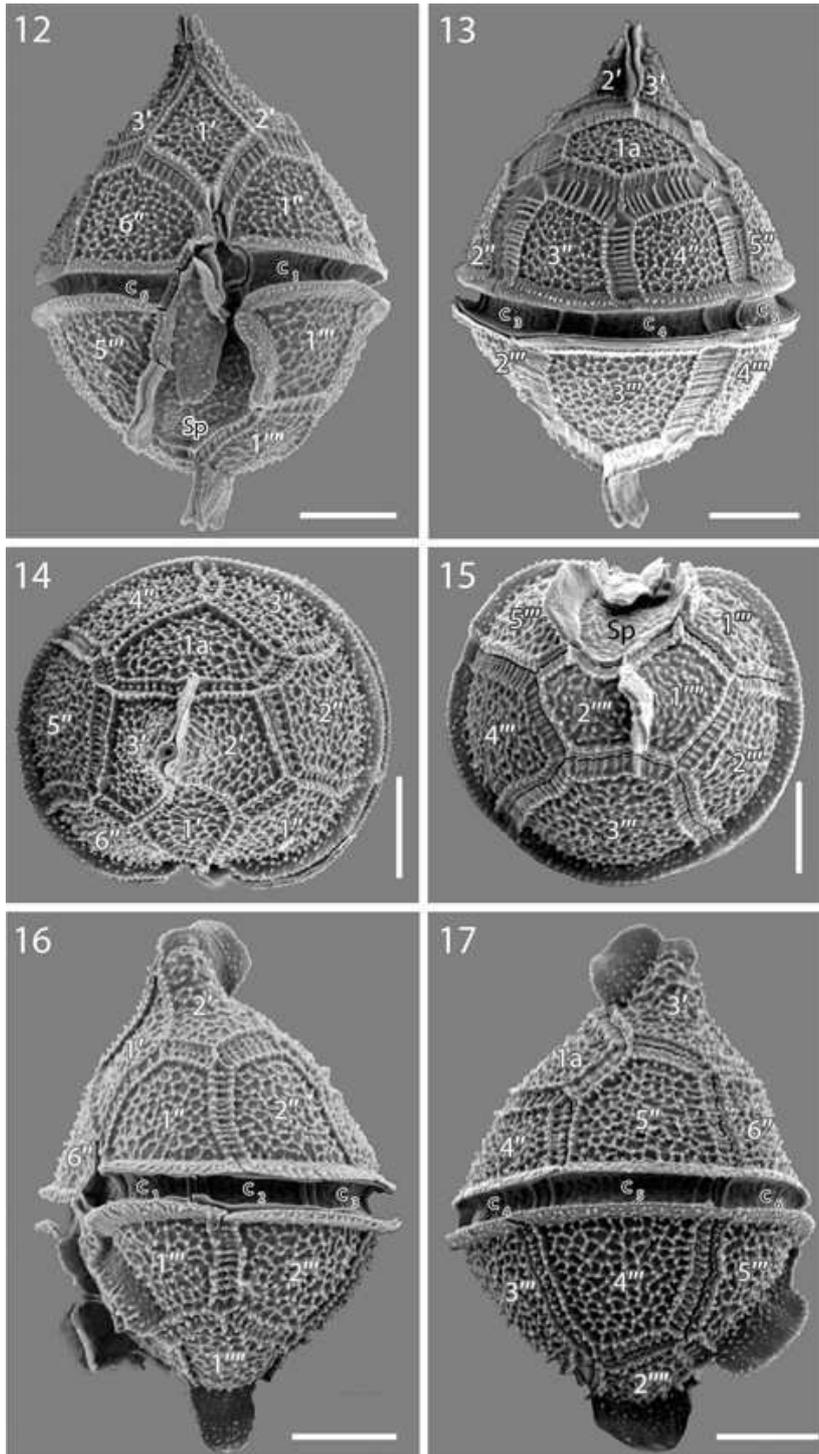
Figures 12–17   *Peridiniopsis cristata* var. *cristata*, SEM.

(12) Ventral view. (13) Dorsal view. (14) Apical view. (15) Antapical view. (16) Left lateral view. (17) Right lateral view.
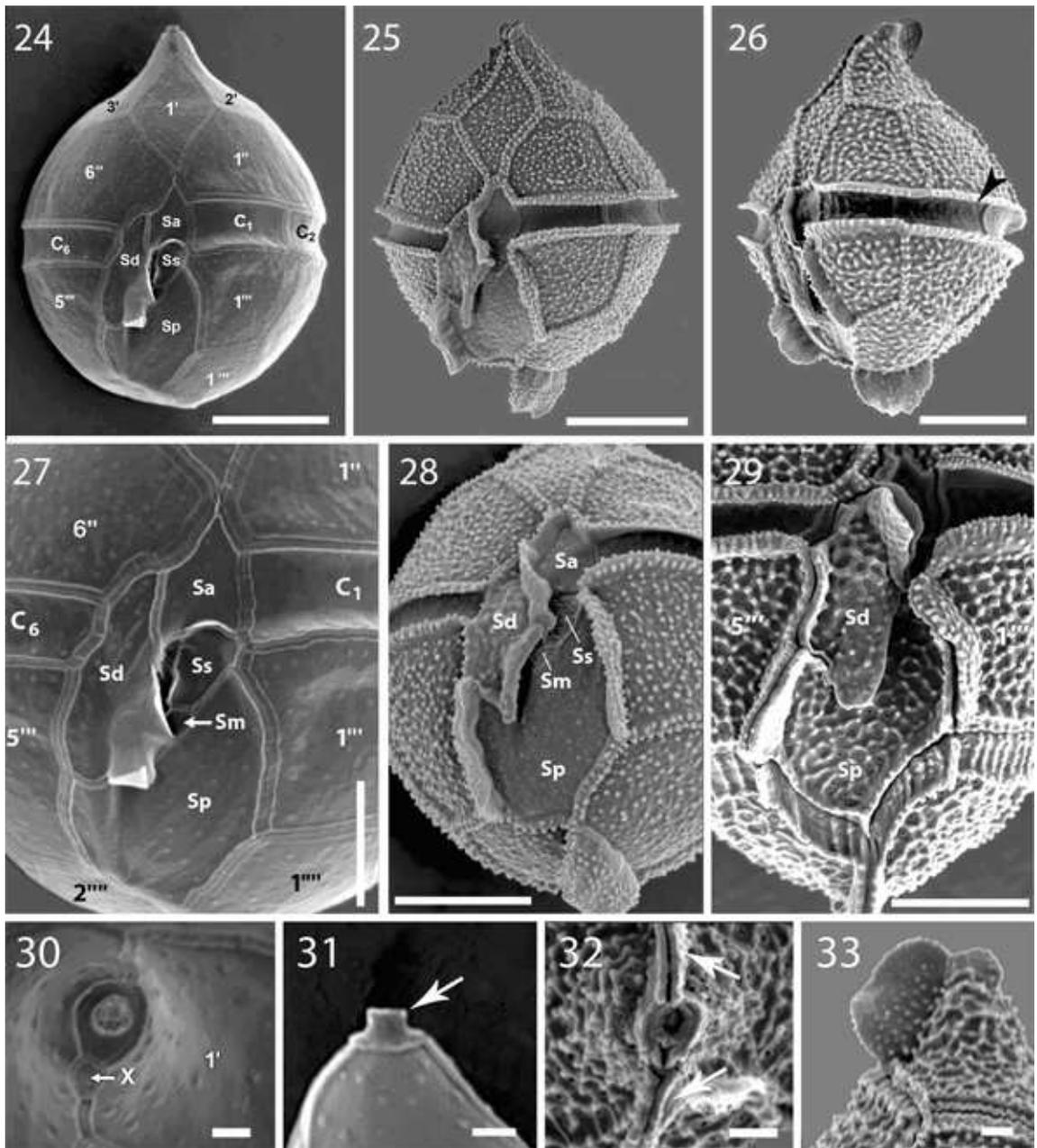
Scale bars=10 µm.

Figures 18–23   *Peridiniopsis cristata* var. *tubulifera*, SEM.

(18) Ventral view. (19) Dorsal view. (20) Right lateral view. (21) Left lateral view. (22)
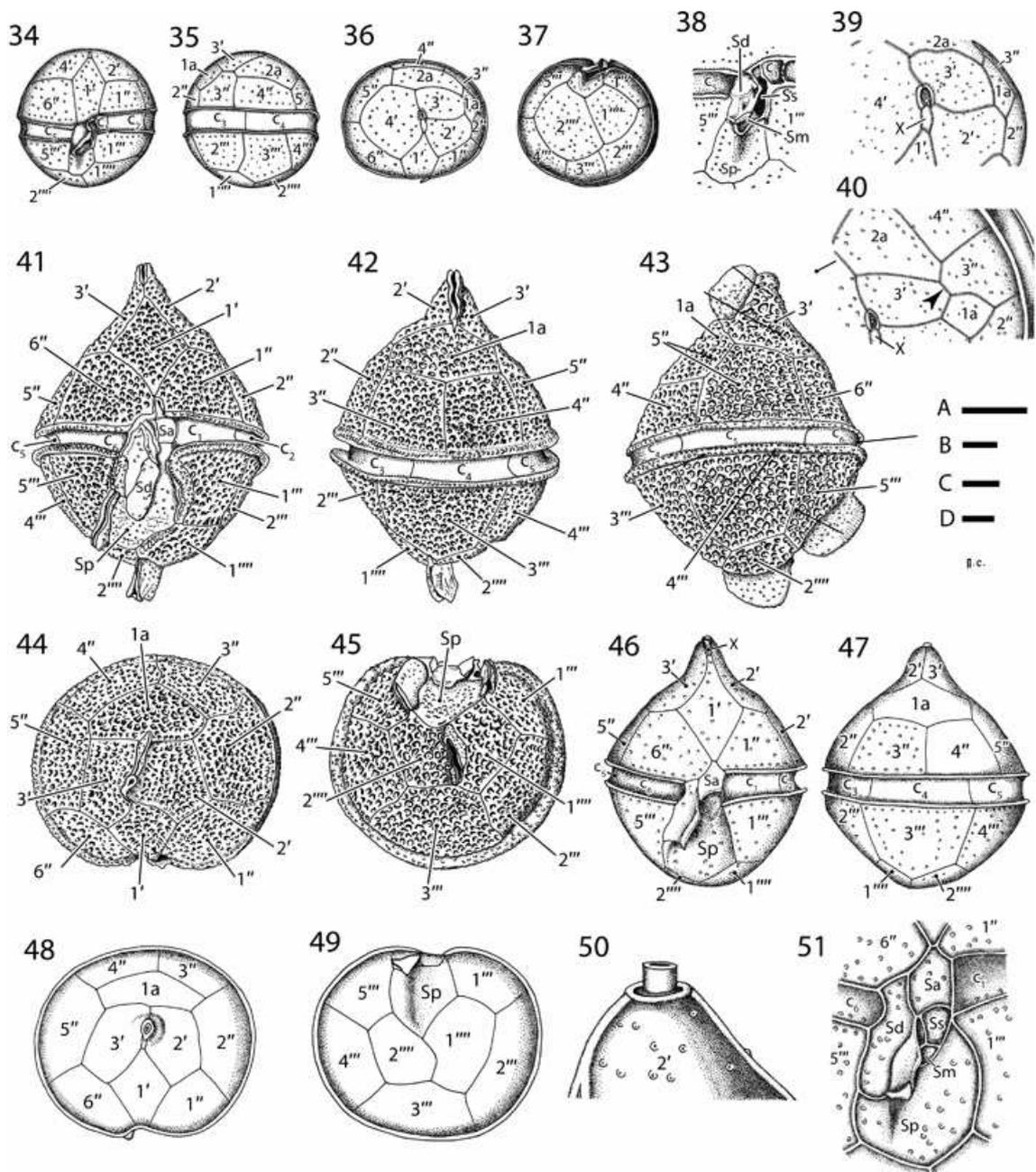
Apical view. (23) Antapical view.

Scale bars=10 μm.

Figures 24–33   Comparison of *Peridiniopsis cristata* var. *tubulifera* with the

nominate variety, SEM.

(24) Ventral view of a rounded cell of var. *tubulifera*, note the absence of

ornamentation. (25) Ventral view of a cell of var. *cristata* with moderate verrucose

ornamentation. (26) Cell of var. *cristata* with strong ornamentation. Note that the C_2

plate is without the pore reported by Ricard and Bourrelly (1982) (arrowhead). (27)

Detail of the sulcal area of var. *tubulifera*. (28) Detail of the sulcal area of a moderately

ornamented cell of var. *cristata* with smooth sulcal plates. (29) Detail of the sulcal area

of a strongly ornamented cell of var. *cristata* with sulcal plates reticulate, some platelets

are hidden by the list of Sd. (30) Apical pore complex of var. *tubulifera*. (31) Lateral

view of the prominent tubular rim (arrow) surrounding the apical pore in var. *tubulifera*.

(32) Apical pore complex of var. *cristata*, with membranous extensions (crests)

surrounding the pore (arrows). (33) Lateral view of the dorsal crest of var. *cristata*.

Scale bars=10 μm (Figures 24–26); 5 μm (Figures 27–29); 2 μm (Figures 32–33); 1 μm

(Figures 30–31).

Figures 34–51   Drawings of the three thecate dinoflagellates from Clipperton Island lagoon.

(34–40) *Durinskia baltica*. (34) Ventral view. (35) Dorsal view. (36) Apical view. (37) Antapical view. (38) Detail of the sulcal area. (39) Detailed part of the epitheca and apical pore complex. (40) Variation of the epithecal plate pattern, with an extra edge of the apical 3′ plate (arrowhead) and resulting in four-sided intercalary 1a plate and five-sided 3′ and 2a plates.

(41–45) *Peridiniopsis cristata* var. *cristata*.

(41) Ventral view. (42) Dorsal view. (43) Right lateral view. (44) Apical view. (45) Antapical view.

(46–51) *Peridiniopsis cristata* var. *tubulifera*. (46) Ventral view. (47) Dorsal view. (48) Apical view. (49) Antapical view. (50) Detail of the apex and tubular rim in lateral view. (51) Detail of the sulcal area.

Scale bars=A/10 µm (Figures 34–37, 41–49); B/5 µm (Figures 38–40); C/1 µm (Figure 50); D/2 µm (Figure 51).

Table 1 Morphometric data, plate formulae and thecal ornamentation of the three dinoflagellate species from Clipperton Island lagoon.

	Durinskia baltica	Peridiniopsis cristata var. cristata	Peridiniopsis cristata var. tubulifera
Length (μm)	21–22	(37) 43–57[a] (33) 39–50	(27) 30–40
Width (μm)	21–24	(31) 32–41	26–32
Depth (μm)	19–22	31–37	22–26
Number of plates in each series			
Apical pore complex	Po, X	Po, X(?)	Po, X
Apical plates (′)	4	3	3
Anterior intercalary plates (a)	2	1	1
Precingular plates (″)	6	6	6
Cingular plates (c)	5	6	6
Sulcal plates (s)	4	5(?)	5
Postcingular plates (‴)	5	5	5
Antapical plates (⁗)	2	2	2
Thecal ornamentation	Smooth	Verrucose to reticulate, with lists (crests)	Smooth, without lists

[a]Including antapical crests. ?, its presence has not been confirmed in other specimens; X(?), the occurrence of an X plate cannot be confirmed.