



FIELD OBSERVATIONS ON RARE OR OVERLOOKED DINOFLAGELLATES FROM THE ARGENTINE SEA

OBSERVACIONES DE CAMPO SOBRE DINOFLAGELADOS RAROS O DESCONOCIDOS EN EL MAR ARGENTINO

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SUMMARY

Background and aims: Planktonic dinoflagellates have a great ecological significance in marine environments. While some dinoflagellate species commonly reach bloom concentrations and are thus conspicuous components of marine phytoplankton, others occur in very low abundances which make them difficult to detect in field studies. Here we analyzed dinoflagellate composition and abundance in five oceanographic expeditions carried out in continental shelf and slope waters of the Argentine Sea.

M&M: Plankton abundance was estimated by the Utermöhl method, using inverted microscopy, whereas further optical and scanning electron microscopy was applied for the identification of dinoflagellate species.

Results: We focused on the occurrence of seven dinoflagellates that have been previously poorly documented or overlooked in marine environments worldwide: *Dinophysis microstrigiliformis*; *Gyrodinium* sp.; *Karlodinium elegans*; *Oxytoxum laticeps*; *Peridiniella danica*; *Peridiniella globosa* and *Prorocentrum nux*. The latest and *K. elegans* are observed for the first time in field conditions after their original descriptions based on cell cultures. While most species were detected in low or moderate abundances, *P. nux*, which is the smallest *Prorocentrum* species, reached 82,000 cells L⁻¹ in slope waters. Very small *Gyrodinium* cells (11.5 µm long; 8.7 µm wide) with a distribution restricted to slope waters during spring, were not possible to be accurately assigned to a species.

Conclusions: This study contributes to the understanding of dinoflagellate diversity in the Argentine Sea and the worldwide distribution of little known species.

KEY WORDS

Biogeography, dinoflagellates, diversity, *Karlodinium elegans*, *Prorocentrum nux*, South Atlantic Ocean.

RESUMEN

Introducción y objetivos: Los dinoflagelados planctónicos son de gran relevancia en los ecosistemas marinos. Mientras que algunas especies suelen formar floraciones y ser componentes conspicuos del fitoplancton, otras se encuentran en abundancias muy bajas, lo cual hace difícil su detección. Aquí analizamos la composición y abundancia de dinoflagelados en cinco expediciones oceanográficas realizadas en aguas de la plataforma continental y del talud del Mar Argentino.

M&M: La abundancia se estimó con microscopio invertido (método Utermöhl) y se utilizó microscopía óptica y electrónica de barrido para la identificación específica.

Resultados: Nos enfocamos en la ocurrencia de siete dinoflagelados que previamente han sido poco documentados en ambientes marinos de todo el mundo: *Dinophysis microstrigiliformis*; *Gyrodinium* sp.; *Karlodinium elegans*; *Oxytoxum laticeps*; *Peridiniella danica*; *Peridiniella globosa* y *Prorocentrum nux*. Esta última especie y *K. elegans* se observan por primera vez en el campo desde su descripción basada en cultivos celulares. Si bien la mayoría de las especies se detectaron en abundancias bajas o moderadas, *P. nux*, el *Prorocentrum* más pequeño, alcanzó 82.000 células L⁻¹ en aguas del talud. Células pequeñas de *Gyrodinium* sp. (11,5 µm de largo y 8,7 µm de ancho), con una distribución restringida a las aguas del talud durante la primavera, no pudieron ser asignadas con precisión a nivel específico.

Conclusiones: Este estudio contribuye al conocimiento de la diversidad de dinoflagelados en el Mar Argentino y la distribución mundial de especies poco conocidas.


PALABRAS CLAVE

Biogeografía, dinoflagelados, diversidad, *Karlodinium elegans*, Océano Atlántico Sur, *Prorocentrum nux*.

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INTRODUCTION

Planktonic microalgae comprise an essential biotic component of the world oceans. Among microalgae, dinoflagellates are of great ecological significance as they contribute to primary production and are determinant in trophic webs, representing a strong influence in biogeochemical cycles and biotic interactions (Graham & Wilcox, 2000). Moreover, dinoflagellates include the largest number of toxigenic species among marine phytoplankton, which can produce harmful blooms with negative impacts to human health and marine life and generate economic losses to fisheries, aquaculture and exploitation of natural mussel's beds (Lassus *et al.*, 2016).

Dinoflagellates are ubiquitous in marine environments; comprising heterotrophic, autotrophic and mixotrophic species and also ecto- and endoparasitic species and symbionts (Hackett *et al.*, 2004). According to the presence or absence of cellulose inside the amphiesmal vesicles they are divided in two big groups: thecate and unarmored dinoflagellates. Within the thecate group taxonomical classification is based on the number, position and shape of the thecal plates, while in the unarmored group cellular shape, ultra-structural characters of the flagellar apparatus and shape of the apical groove are usually used to differentiate genera (Daugbjerg *et al.*, 2000). With the advent of molecular technics in the last decades, phylogeny and morphological traits for classification of some unarmored dinoflagellates were reconsidered (Daugbjerg *et al.*, 2000).

An important contribution to knowledge about the diversity and distribution of dinoflagellates, not only in the South Atlantic Ocean but also worldwide, comes from the copious work done by E. Balech (e.g. Balech, 1976, 1988, 1995, 2002). More recent studies have continued this line of research in the Argentine Sea, mainly covering coastal areas or toxigenic species (e.g. Akselman 1985, 1986, 1987; Akselman & Negri, 2012; Akselman *et al.*, 2015; Fabro *et al.*, 2015; Antacli *et al.*, 2018; Tillmann *et al.*, 2019; Sunesen *et al.*, 2020a). However, the recent description of new dinoflagellate species (Tillmann & Akselman, 2016; Boutrup *et al.*, 2017; Tillmann, 2018; Tillmann *et al.* 2018; Sunesen *et al.*, 2020b) and the finding of new records (e.g. Fabro *et al.*, 2016, 2017, 2019; Tillmann *et al.*,

2016) suggest that dinoflagellate diversity in the Argentine Sea is higher than previously known.

While some dinoflagellate species commonly reach bloom concentrations and are thus conspicuous components of marine phytoplankton, others occur in very low abundances which make them difficult to detect in field studies (Steidinger & Tangen, 1997). Within this low-abundance species, small thecate and unarmored dinoflagellates are less studied in field conditions, as most of the research is directed to bigger armoured species with easily preserved morphological features (De Salas *et al.*, 2008). In order to increase knowledge on dinoflagellate diversity in the Argentine Sea, we focused on the occurrence of small and rare dinoflagellates previously overlooked or poorly documented, by the analysis of plankton samples obtained in five oceanographic expeditions in different seasons. Based on detailed light and electron microscopy observations, we found cells of seven dinoflagellates that are poorly documented or found for the first time in the Southeast Atlantic Ocean and have also been rarely mentioned from marine environments worldwide. For each taxa we provide a detailed morphological characterization and describe their distribution patterns, compared with previous observations.

MATERIALS AND METHODS

Field Sampling

The continental shelf and slope waters of the Argentine Sea were sampled during five oceanographic expeditions (Fig. 1). Expedition 1 (E1) was conducted in austral autumn on board the *R/V Puerto Deseado* from March 30th to April 14th, 2012. A total of 47 stations were sampled between ≈ 38 and 56 °S. The second expedition (E2) was carried out in late austral summer on the *R/V Bernardo Houssay* from March 11th to March 22nd, 2013, with 24 sampling stations located between ≈ 39 and 43 °S. This cruise was divided in two legs K1 and K2, which comprise 8 and 16 sampling stations, respectively. The third expedition (E3) was conducted in austral spring aboard the *R/V Puerto Deseado*, from October 26th to November 9th, 2013, with 47 sampling stations located between ≈ 40 and 47 °S. The fourth expedition (E4) was conducted on board the

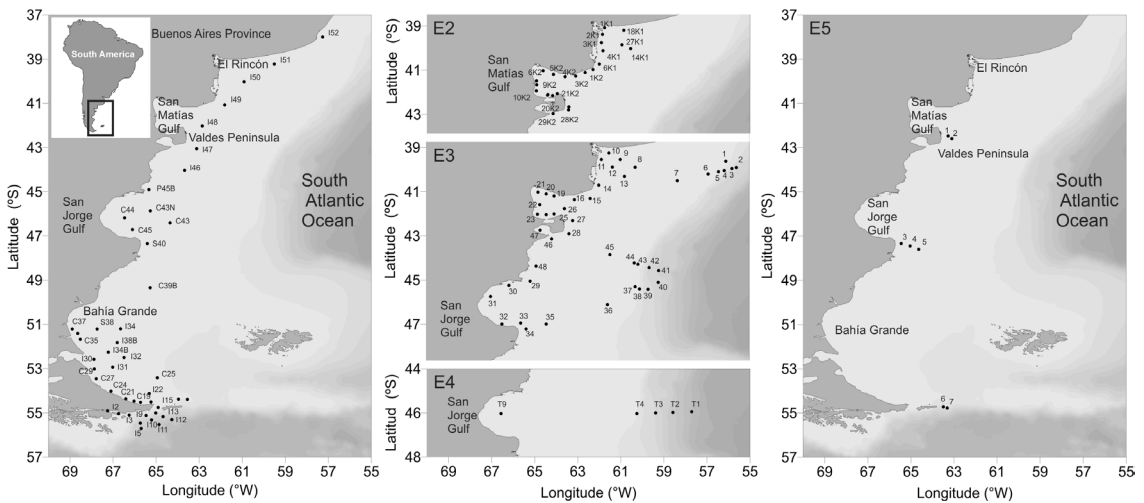


Fig. 1. Letters and numbers on maps indicate various sampling sites. Expeditions across the Argentine Sea. E1: autumn; E2: late summer; E3: spring; E4 and E5: summer.

Canadian *R/V Coriolis II* in austral summer from 30th January to 15th February 2014, in a transect consisting of 5 sampling stations from internal shelf waters of San Jorge Gulf to slope waters in front of the gulf. The last expedition (E5) was carried out in austral summer from January 6th to January 12th, 2016, with seven sampling stations located between ≈ 38 and 55°S . The conductivity (salinity)/temperature/depth (CTD) data were available throughout all expeditions, except from leg K2 of expedition E2, during which no CTD measurements were performed. During this leg, only surface water temperature was measured with a multiparameter probe TOA-DKK Model WQC.

During all expeditions, Niskin bottle samples were taken from surface water (~ 4 m depth). Aliquots of 250 mL were fixed with acidic Lugol's iodine solution for quantitative analyses. Plankton net samples were additionally collected for qualitative morphological analysis by vertical net tows through the upper 20 m of the water column with a 20 μm -mesh Nitex net and fixed with acidic Lugol's iodine solution.

Plankton analysis

Nano- (≈ 5 -20 μm) and microplankton (20-200 μm) abundance was estimated using the Utermöhl (1958) inverted microscope method. Subsamples (50 mL) from the mixed water obtained by Niskin bottles were left to settle for 24 h in a composite

sedimentation chamber prior to cell counting under an inverted microscope (Leica DMIL LED). The organisms were counted in two stages; at least 400 cells of the dominant taxa were counted in random fields or in transects of the chamber to estimate general plankton composition, whereas the whole chamber bottom was scanned to count sparse species.

Further morphological examination of selected samples was conducted with a phase contrast/differential interference contrast optical microscope (LM) Leica DM2500 equipped with a DFC420C camera, and with scanning electron microscopy (SEM): Jeol JSM-6360 LV SEM (JEOL, Tokyo, Japan), Carl Zeiss NTS SUPRA 40 (Zeiss, Oberkochen, Germany) and FEI Quanta FEG 200 (FEI, Eindhoven, the Netherlands). Bottle and net sample aliquots were filtered through 0.2 μm polyamide filters and 3 μm polycarbonate filters for SEM analyses. The material on the filters was dehydrated by serial ethanol treatment and final critical point dehydration (BAL-TEC CPD-30, Balzers, Liechtenstein). Specimens were sputter-coated with Au with a sputter fine coat Jeol JFC 1.100 (Jeol, Tokyo, Japan) for samples observed with Jeol JSM-6360 LV SEM or with gold-palladium (Cressington Scientific Instruments, Watford, UK and Emscope SC500; Ashford, UK) for samples observed with Carl Zeiss NTS SUPRA 40 and FEI Quanta FEG 200.

RESULTS AND DISCUSSION

Dinophysis microstrigiliformis Abé, *Publ. Seto Mar. Biol. Lab.* 15. 1967, Fig. 2.

Balech 1988, p. 230, lám. 8. Figs. 12-13.

Cells with elongated shape, longer than wide. The left sulcal list (LSL) is long, extending until the posterior end of the cell. The three ribs from the LSL are thin, R3 is shorter than R2 and the distance between R2 and R3 is larger than between R1 and R2 (Fig. 2A). The anterior cingular list (ACL) is smooth and conic (Fig. 2B). *Dinophysis* species are mixotrophic with cryptophycean-like plastids (Schnepf & Elbrächter, 1988). Dimensions: length average $36.4 \mu\text{m} \pm 3.5$, width average $21.3 \mu\text{m} \pm 2.5$ ($n = 8$).

Distribution and habitat. *D. microstrigiliformis* is a very rare species, which has been mentioned only a few times worldwide and always in very low abundances. According to Ivin *et al.* (2014) is probably a neritic and boreal species recorded near the coast of northern Japan and in Avacha Bay, Russia.

But the species has been found in the Southern Atlantic in some occasions. Haraguchi & Odebrecht (2010) found one cell in internal shelf waters from Southern Brazil ($\approx 34^\circ\text{S}$, 51°W) during winter. In the Argentine Sea, records of the species correspond to one cell found in external shelf waters in front of Buenos Aires Province (37°S) and a few more thecae at 41°S (Balech *et al.*, 1984; Balech, 1988). In our study, *D. microstrigiliformis* was only detected in net tow samples and it was confined to the southern Argentine Sea ($\approx 55^\circ\text{S}$) during autumn (Table 1), which supports its distribution in polar and sub-polar waters.

Observations. This species was described based on one cell from Japan (Abé, 1967). The author stated that it may be an aberrant form of *D. lapidistrigiliformis*, with smaller and more elongated theca, and longer LSL. Balech (1988) found also one cell from the northern Argentinean Sea (37°S) and remarked that *D. microstrigiliformis* is very similar to *D. sacculus*, but with a longer LSL and a regular and convex dorsal edge. *Dinophysis*

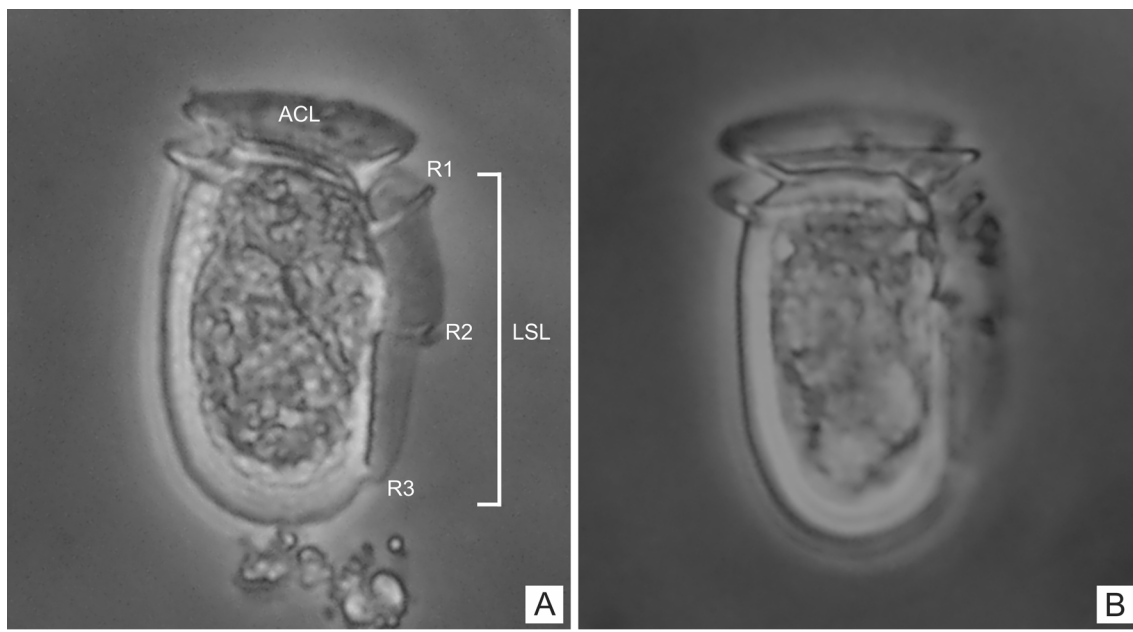


Fig. 2. LM images of *Dinophysis microstrigiliformis*. **A-B:** lateral views; note that the LSL is large (ends almost at the hypothecal antapex), R3 is shorter than R2 and the distance between R2 and R3 is larger than between R1 and R2. Abbreviations= LSL: left sulcal list. ACL: anterior cingular list. R: sulcal list rib. Scale bars: $10 \mu\text{m}$.

Table 1. Summary of the occurrence, abundance, and physical conditions in which the reported dinoflagellate taxa were found. n/d: not detected. M_e : median. Relative contribution: abundance percentage of the analyzed taxa with respect to the total abundance of phytoplankton.

Taxon	Expedition and station	Abundance (cells L ⁻¹)	Temperature (°C)	Salinity (psu)	Total Phytoplankton (cells L ⁻¹)	Relative contribution (%)
<i>Dinophysis microstrigiliformis</i>	E1: C20, I9, I22	n/d	8.5	32.8; 33.3	113,500; 1,946,500; 969,400	-
<i>Gyrodinium</i> sp.	E3: 5, 42	4,900; 6,500	8.0; 8.3	33.7; 33.8	2,750,900; 3,253,300	0.2; 0.1
<i>Karlodinium elegans</i>	E3: 5, 43	1,600; 14,600	8.0; 9.4	33.7	2,750,900; 3,427,590	0.05; 0.4
<i>Oxytoxum laticeps</i>	E1: I46, C16, I11, I13, I14, I15	40-440 ($M_e=100$)	5.4-17.2 ($M_e=8.5$)	32.6-34.2 ($M_e=33.7$)	48,880-4,139,105 ($M_e=541,990$)	0.001-0.4 ($M_e=0.03$)
	E2: 3K2					
	E3: 15, 43					
	E4: T1, T2, T3					
	E5: 7					
<i>Peridiniella</i> spp.	E1: C16, C21, I12, I13, I14, I15, I48, I49	20-9,000 ($M_e=220$)	7.9-16.3 ($M_e=13.8$)	33.2-33.8 ($M_e=33.4$)	74,760-24,050,740 ($M_e=1,442,938$)	0.00007-0.54 ($M_e=0.02$)
	E2: 18K1, 21K2					
	E3: 1, 2, 3, 5, 6, 7, 8, 10-16, 20, 27, 30, 31, 37, 38, 41-44, 47, 48					
	E4: T2, T3					
	E5: 2, 4					
<i>Prorocentrum nux</i>	E2: 10K2	82	16.2	-	342,900	27

microstrigiliformis is considered as a currently accepted taxonomic entity (Guiry & Guiry, 2019). However, the morphological similarity with *D. lapidistrigiliformis* and *D. sacculus* might justify a taxonomic revision. In this sense, Reguera and González-Gil (2001) suggested that small and dimorphic cells of *D. sacculus* mentioned by Bardouil *et al.* (1991) probably corresponds to *D. microstrigiliformis*. Likewise, Haraguchi & Odebrecht (2010) stated that *D. lapidistrigiliformis* may be a stage in the life cycle of *D. fortii*.

Gyrodinium sp. Kofoid & Swezy, 1921. Fig. 3.

Ovoid to spindle cell shape, slightly dorsoventrally compressed. The epi- and hypocone are similar in size (Fig. 3A-C). The apex is rounded whereas the antapex can be rounded (Fig. 3B) or

conical (Fig. 3C). The apical groove is elliptical and bisected into two equal parts by a central line (Fig. 3C). Cells are ornamented with longitudinal striations, with the same number of striae in the epi- and hypocone, about 12 in ventral view. The sulcus is straight, narrow, well defined, and extends into the epicone. On the hypocone, the sulcus is well defined and deep, broadening toward the antapex. The cingulum is not superposed and only slightly displaced, about 1/10 of the total cell length. The genus *Gyrodinium* contains only heterotrophic species (Daugbjerg *et al.* 2000). Dimensions: length average $11.5 \mu\text{m} \pm 2.0$, width average $8.7 \mu\text{m} \pm 1.9$ ($n = 20$).

Distribution and habitat. In the Argentine Sea, the genus *Gyrodinium* is mainly represented by *G. fusus*, a big species ($\approx 80 \mu\text{m}$ long) frequently

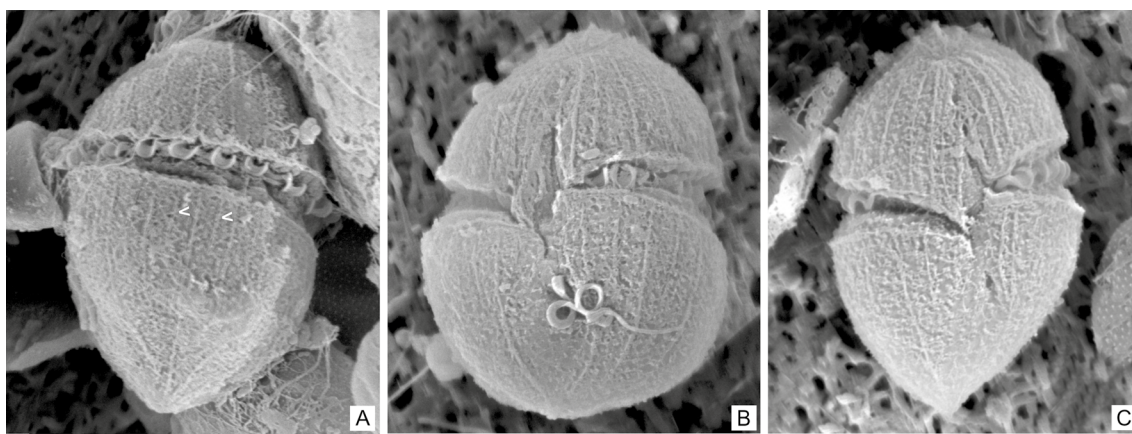


Fig. 3. SEM images of *Gyrodinium* sp. **A:** lateral view; note the faint stria in the hyposome among pairs of prominent striae (arrowheads). **B-C:** ventral views. Scale bars: 5 μ m.

recorded in shelf waters from 36 to 39 °S, including estuarine areas (Akselman, 1985; Barria de Cao & Piccolo, 2008). By contrast, the small *Gyrodinium* sp. cells found in this study were mainly observed in high salinity slope waters (St. 5 and 42 from E3, Table 1). In those samples, *Gyrodinium* sp.-like cells densities were 6.5×10^3 and 4.9×10^3 cells L^{-1} , respectively (Table 1). At both stations, total plankton abundance was around 3×10^6 cells L^{-1} but species composition varied considerably: at station 5 diatoms were the dominant group, while at station 42 a bloom of the dinoflagellate *Prorocentrum cordatum* was observed.

Observations. The genus *Gyrodinium* was described by Kofoed & Swezy (1921) to comprise unarmored dinoflagellates with a descent cingulum displaced by more than one-fifth of the total body length, in contrast to *Gymnodinium* which was defined by a cingulum displacement less than one-fifth of the cell length. More recently, Daugbjerg *et al.* (2000) proposed the apical groove system as a more useful character to distinguish these genera, as cingular displacement varies even within clonal species (e.g., Takano & Horiguchi, 2004). Consequently, the authors redefined *Gyrodinium* to contain exclusively heterotrophic species with an elliptical apical groove and longitudinal striations in the amphiesma surface, while *Gymnodinium* species have a horseshoe-shaped apical groove and no striations. From the about 100 species originally

described as *Gyrodinium*, only *G. helveticum*, *G. rubrum*, *G. spirale*, *G. fusiforme*, *G. moestrupii* and *G. jinhaense* (Takano & Horiguchi, 2004; Yoo *et al.*, 2012; Jang *et al.*, 2019), were assigned to *Gyrodinium* sensu Daugbjerg *et al.* (2000). The cells analyzed in this study showed an elliptical apical groove and longitudinal striations, which agrees with the above mentioned *Gyrodinium* definition, which has also been supported by phylogenetic analysis (Takano & Horiguchi, 2004). *Gyrodinium* sp. cells found in this study resemble, in general shape and size (17 μ m length, 12 μ m wide), the species *G. carteretensis* described by Campbell (1973). However, no striation is mentioned in the original description of *G. carteretensis* and the cingular displacement is bigger than in our specimens (1/3 vs. 1/10 of the total cell length). Moreover, in the original description is established that cells present chloroplast, so this species does not agreed with the *Gyrodinium* definition by Daugbjerg *et al.* (2000). The recently described *Gyrodinium jinhaense* (Jang *et al.*, 2019) is similar in size to the cells found in our study, especially considering *G. jinhaense* cells starved for 2 days (13-26 μ m long, and 7-12 μ m wide). However, *G. jinhaense* contour is more slender, the cingulum is displaced about one quarter of the cell length and the posterior sulcal area is widened toward the antapex, forming a slightly S-shaped line. Moreover, the cell surface in *G. jinhaense* is ornamented with 16 longitudinal striations in ventral view; while

in *Gyrodinium* sp. there are no more than 12. In one of our pictures (lateral view) one faint stria is present in the hyposome among pairs of prominent striae (Fig. 3A, arrowheads), thus resembling the species *G. heterostriatum* (*sensu* Gómez *et al.*, 2020). However, cells in this study are considerably smaller than cells from *G. heterostriatum*; despite this species has a very wide size range (30–70 μm long; 25–60 μm wide). Moreover *Gyrodinium* sp. cells have a lower number of striae in the hypocone in ventral view (12 or less vs. about 25) and finally in *G. heterostriatum* the episome is smaller than the hyposome while in our species both are almost equal in size. Considering the above mentioned morphological and size differences compared to other similar *Gyrodinium* species, the cells observed in our study could not be assigned to species level. Additional molecular and morphological analyses are needed for a reliable identification.

Karlodinium elegans Cen, Lu & Huang. *J. Oceanol. Limnol.* 39: 245. 2021. Fig. 4.

Ovoid cells with pointy apex, the epicone is conical and displays rows of parallel furrows that are twisted to the left side in relation to the cell longitudinal axis. Each epicone furrow carries rows of rounded structures ending in small pores (micro-processes *sensu* Paulmier *et al.*, 1995; knobs *sensu* Cen *et al.*, 2021) (Fig. 4A, B). The hypocone is rounded and its surface is ornamented with quadrilateral pits formed by longitudinal and horizontal stripes (Fig. 4C). The cingulum is displaced; its anterior side is delineated from the epicone by a list; below the cingulum the surface displays two parallel rows of knobs (Fig. 4C, arrows). The sulcus invades slightly the epicone as a finger-like protrusion (Fig. 4A, arrowhead). The apical groove begins ventrally, above the sulcus, is directed obliquely to the apex and extends to the middle region of the dorsal epicone (Fig. 4B, double arrowhead). The ventral pore is a thin and long slit located far from the apical groove at the left side of the sulcal region (Fig. 4D, triangle; Fig. 4E). This is an autotrophic species with several yellowish-brown chloroplasts distributed in the cell periphery (Cen *et al.*, 2021). Dimensions: length average $14.9 \mu\text{m} \pm 2.7$, width average $11.1 \mu\text{m} \pm 2.0$ ($n = 24$).

Distribution and habitat. *Karlodinium elegans* was recently described based on two clonal cultures (PTB601 and PTB602) obtained from samples collected during a dinoflagellate bloom in Pingtan coastal area, Fujian, SE China. Our SEM analyses revealed the presence of *K. elegans* in bottle samples at stations 5 and 43 from E3, which correspond to relatively cold (8–9.4 °C) slope waters at ≈ 40 and 45 °S. In these samples, *Karlodinium*-like cells densities were 1.6×10^3 and 14.6×10^3 cells L^{-1} respectively (Table 1); total plankton abundances were 2.7×10^6 and 3.4×10^6 cells L^{-1} . Both samples were dominated by diatoms, mainly *Hemiaulus* sp. and also *Thalassiosira* sp. at station 5.

Little is known about the occurrence of *Karlodinium* species, or the family Kareniaceae in general (De Salas *et al.*, 2008 and references therein). Even though Kareniaceae representatives and other unarmored dinoflagellates may be a dominant component of the dinoflagellate flora in Antarctic (Gast *et al.*, 2006, 2007; Mascioni *et al.*, 2019) and Arctic waters (Luo *et al.*, 2011), they are widely unrecognized in field surveys due to the potential for misidentification when applying only routine morphological analysis. For this reason, it is important to perform more deep morphological or molecular studies of this group, especially considering that several species in the lineage are known to be ichthyotoxic (Bergholtz *et al.*, 2005).

Observations. The family Kareniaceae comprises three genera, i.e. *Karlodinium*, *Karenia* and *Takayama*, which share plastids with fucoxanthin and its derivatives as the major accessory pigments (De Salas *et al.*, 2003; Benico *et al.*, 2019). The genus *Takayama* possess a sigmoid apical groove (De Salas *et al.*, 2003), while in *Karlodinium* and *Karenia* the groove is straight; although *Karlodinium* differs from *Karenia* by the presence of a ventral pore at the left side of the apical groove (Daugbjerg *et al.*, 2000). The general appearance and main morphological features (e.g. long slit-like “ventral pore”, longitudinal striations curving to the left side on the epicone, the apical groove extending to the middle region of the dorsal epicone, and a very special and unusual surface ornamentation on the hypocone) of *Karlodinium* cells analyzed in this work were identical to that reported in the original description of *K. elegans*. Regarding cells size, our specimens were a little smaller than

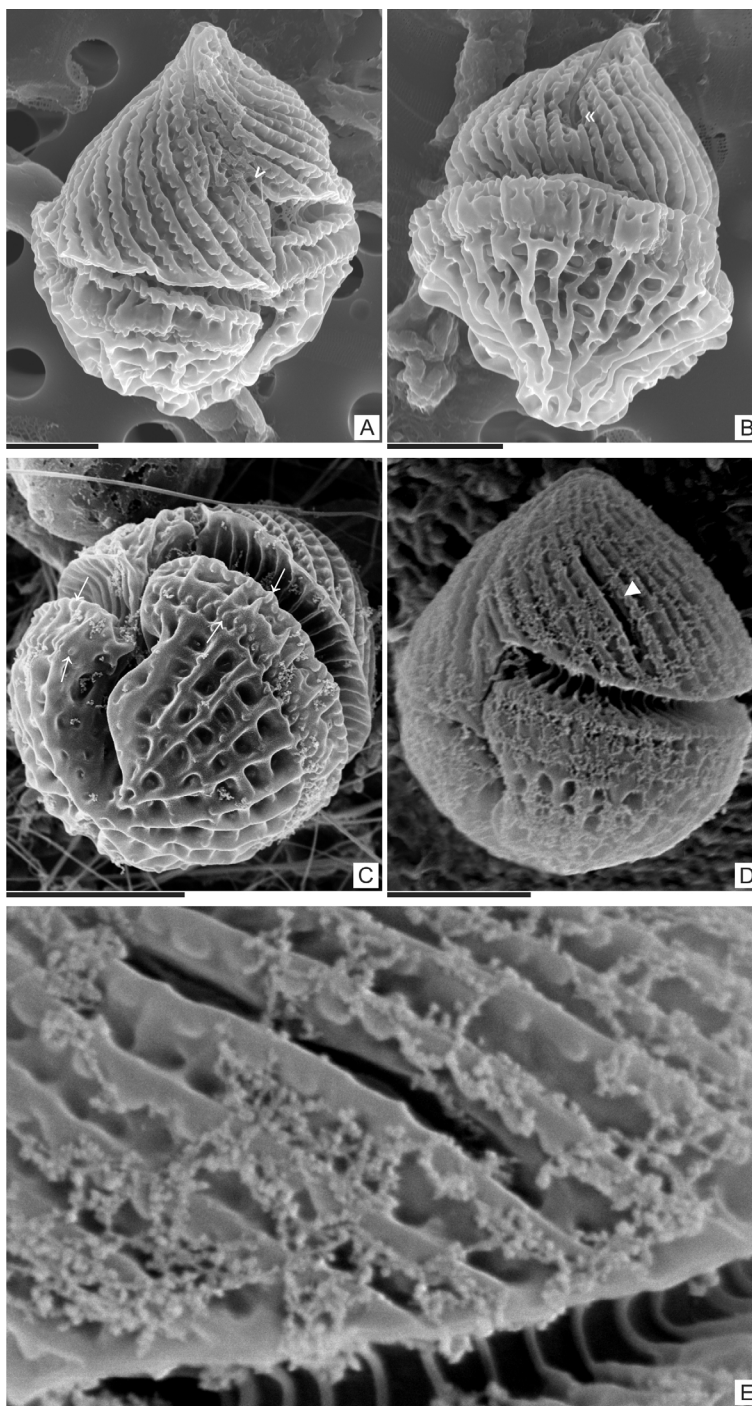


Fig. 4. SEM images of *Karlodinium elegans*. **A:** ventral view, note how the sulcus invades the epicone as a finger-like protrusion (arrowhead). **B:** dorsal view, note the apical groove ending in the dorsal region of the epicone (double arrowhead). **C:** antapical view, note the list in the anterior side of the cingulum, the ornamentation of longitudinal and horizontal stripes forming quadrilateral pits in the hypocone and the two rows of knobs in the upper hypocone and in the epicone striation (arrows). **D:** latero-ventral view, note that the ventral pore is a thin and long slit (triangle). **E:** detail of D showing the ventral slit. Scale bars: 5 μ m.

those described by Cen *et al.* (2021), i.e. 19-27 μm long, 15-23 μm wide. Morphologically two species of *Karlodinium* are similar to *K. elegans*: *K. corrugatum* and *K. gentenii*. All of them show parallel micro-processes rows below the cingulum. Particularly, *K. corrugatum* differs from *K. elegans* by presenting parallel and not twisted furrows in the epicone and *K. gentenii* has a ventral pore next to the apical groove instead of a long slit (De Salas *et al.* 2008; Nézan *et al.*, 2014). According to Nézan *et al.* (2014) a mixed fixation with Lugol's solution and glutaraldehyde allows to see fine details of the cell surface by removing the membranous material or mucilage that covers the cell. Likewise, Cen *et al.* (2021) established that the double fixation revealed a much clearer cell surface. Although cells analyzed in our study were fixed only with Lugol's solution, the main morphological features mentioned above could be observed. Unfortunately, the lack of samples preserved with other fixatives such as glutaraldehyde or osmium tetroxide did not allow performing a more detail examination of other key morphological features as the position and shape of the cell organelles.

Oxytoxum laticeps Schiller 1937, Fig. 5.

Burns & Mitchell 1982, pp. 72-73, figs. 5-11;
Gómez *et al.* 2008, p. 28, fig. 35.

The epitheca represents 20-26 % of the total cell length, shows a domed shape, without apical spine, and it is smooth with occasional small pores arranged in random orientation (Fig. 5A-D). The hypotheca is cone-shaped, it is larger and wider than the epitheca, with convex sides which taper down to the antapex, ending in a pointy extension (Fig. 5A-D). The cingulum is wide, deep, slightly displaced and presents well developed lists (Fig. 5C). The sulcal plate extends slightly into the hypotheca and a small sulcal wing covers the flagellar pores. (Fig. 5D). There is also a small ribbed list on the ventral and dorsal antapical end of the hypotheca (Fig. 5C, D). The hypothecal surface is covered with microtubular rods (*sensu* Burns & Mitchell, 1982) arranged in rows from the antapex to the cingulum. The apical end of the tube is projected beyond the thecal plane and ends in a pore (Fig. 5C, D). It is an autotrophic species (Gómez *et al.*, 2016). Dimensions: length average 16.7 $\mu\text{m} \pm 1.4$, width average 12.4 $\mu\text{m} \pm 1.8$ ($n = 20$).

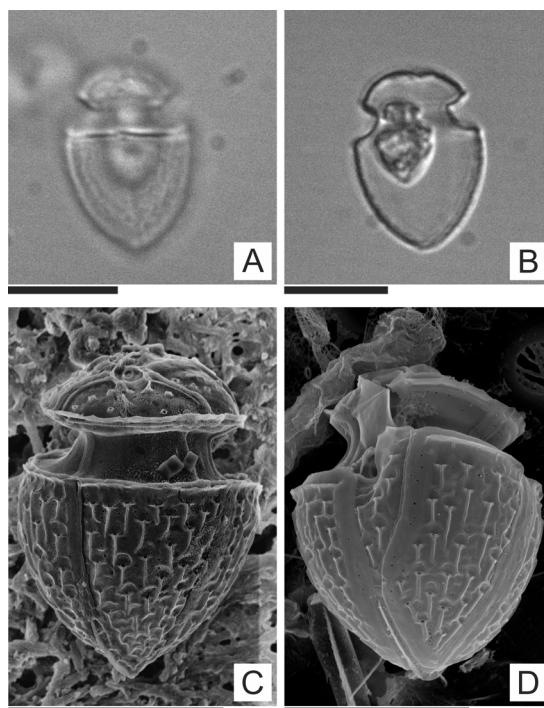


Fig. 5. LM (A-B) and SEM (C-D) images of *Oxytoxum laticeps*. **C:** dorsal view. Note the longitudinal ridges on the plates. **D:** ventral view. Note the small sulcal wing covering the flagellar pores. Scale bars: 10 μm .

Distribution and habitat. The species of the family Oxytoxaceae usually occur in low densities in the open ocean, and the smaller ones are rarely retained in net samples (Gómez, 2018). However, *O. laticeps* is commonly found in New Zealand coastal waters (Burns & Mitchell, 1982), and densities up to 2.6×10^5 cells L^{-1} have been observed in Crozet Basin (Indian Ocean) (Kopczyńska & Fiala, 2003). *O. laticeps* was described from the Mediterranean Sea and it was listed in the north, central equatorial, tropical and southeast Pacific (Hasle 1960; Venrick, 1982; Iriarte & Fryxell, 1995; Gómez *et al.*, 2008), in Canary Islands (northeast Atlantic) (Ojeda, 1996) and in the Caribbean Sea (Pérez-Castresana *et al.*, 2014). Our finding represents the first record of *O. laticeps* for the southwest Atlantic Ocean, although Balech (1988) found one cell of the similar species *O. mediterraneum* at northeast Argentine Sea. *O. laticeps* was found in bottle samples during

all expeditions but in low abundances and in a few stations (Table 1). Maximum cell densities (around 400 cells L⁻¹) were detected during both summer expeditions in slope waters at the southern sampling area (≈46-55 °S), where total planktonic abundances of ≈1.3 x10⁶ cells L⁻¹ were primarily represented by blooms of the diatom genus *Pseudonitzschia* (St 7 from E5) and small (<5 μm) unidentified phytoflagellates (St. T2 from E4).

Observations. *Oxytoxum* and *Corythodinium* are the only two genera within the family Oxytoxaceae, which form their own clade within the dinokaryotic dinoflagellates according to molecular data (Gómez *et al.*, 2016). Both genera are morphologically similar but can be distinguished by the position of the cingulum, always anterior in *Oxytoxum* and median or anterior in *Corythodinium*, and by the larger and broader epitheca in *Corythodinium* (Taylor, 1976). Although some species possess intermediate characteristics between both genera; molecular data support the generic separation (Gómez *et al.*, 2016). Within the genus *Oxytoxum*, Dodge and Saunders (1985) designated *O. laticeps* as the type species of Section Excavatum (II), which comprises species with a reduced and domed epitheca and sulcus deeply excavated and partly covered by a large list composed of extensions of Sd and 6'' plates and by a list which is an extension of 1'''. The closest species to *O. laticeps* is *O. mediterraneum*, which was also described by Schiller (1937). The presence of rows of hexagonal pores on the hypotheca of *O. mediterraneum*, differentiate it from *O. laticeps*. Additionally, a spine process in the antapex is found only in *O. laticeps* and the epitheca of *O. mediterraneum* is more flattened (Schiller, 1937). Burns & Mitchell (1982) analyzed New Zealand field material and found that these features that differentiate both species were found in the same specimen due to a multilayered structure of the theca, and consequently considered *O. mediterraneum* as a synonym of *O. laticeps*. More recently, Gómez (2018) reviewed the synonymy of the dinoflagellate genera *Oxytoxum* and *Corythodinium* and placed *O. laticeps* in a group composed by *O. sphaeroideum* and allied species that present a small size, rounded cell shape and absence of spines. The author remarked that there were lots of species misidentifications within *Oxytoxum* and *Corythodinium* in the past, and that

the identity of *O. laticeps* remains unclear, but both *O. mediterraneum* and *O. laticeps* are considered as accepted names. Cell length measurements from our specimens were in the range mentioned by Burns & Mitchell (1982) (15-25 μm) and by Dodge & Saunders (1985) (15-20 μm), but were smaller than those mentioned in Gómez *et al.* (2008) (30 μm). The surface morphological characteristics of the hypotheca agreed with that mentioned by Burns and Mitchell (1982) for cells with persistent outer wall, characterized by a system of microtubular rods arranged in slanting rows from the antapex to the girdle with a microtubule that ends in a small pore. Another morphologically similar species is *Oxytoxum stropholatum* (Dodge & Saunders, 1995) which was placed into *Corythodinium* by Gomez (2018). Our specimens share with *C. stropholatum* the presence of a sulcal wing covering the flagellar pores, but differed in general cell size (24-25 μm long; 14-17 μm wide according to Dodge & Saunders, 1995) and in the shape of the epitheca, which is flattened and only slightly narrower than the hypotheca in *C. stropholatum*, while the cells analyzed in this study present a domed shaped epitheca which is sharply narrower than the hypotheca.

Peridiniella danica (Paulsen) Okolodkov & Dodge. *Eur. J. Phycol* 30. 1995. Fig. 6A-C

Glenodinium danicum Paulsen (Basionym) Okolodkov & Dodge 1995, pp. 301-302, 304, figs. 1-11.

Plate formula is: Po, X, 4', 3a, 7'', 6c, 4s, 6''', 2'''. Cells are almost rounded. The thecal surface is slightly or deeply rough. Cingulum is deeply excavated, displaced one girdle width, and presents lists at both sides. Sulcus is concave with two lists, the left one more prominent than the right one (Fig. 6A). The apical pore plates are surrounded by a collar that extends ventrally to the sulcus, covering partially plate 1' (Figs. 6A-C). The apical pore complex consists of a central structure surrounded by a horseshoe-shaped plate (Po) and another small plate (x) located in the ventral left region of the apical pore complex (Fig. 6B). Both epitheca and hypotheca show pores in the plates which can be arranged in straight rows that run through the edges of the plate or forming concentric rows (Fig. 6A, arrowhead). Intercalary plate 2a can be six-sided

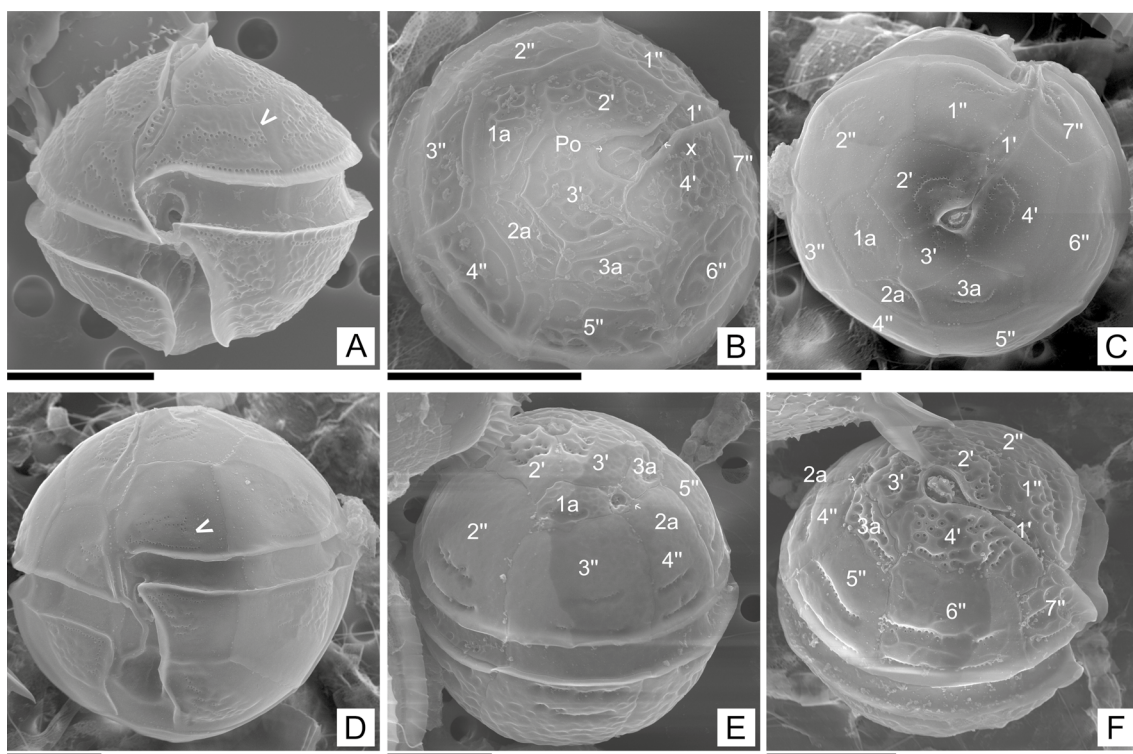


Fig. 6. SEM images of *Peridiniella danica* (A-C) and *Peridiniella globosa* (D-F). **A:** Ventral view, note the collar surrounding the apical pore plates and the arrangement of the pores on the theca surface (arrowhead). **B-C:** antapical views, note the different shape of plate 2a, hexagonal in B and pentagonal in C-D: Ventral view, note the collar surrounding the apical pore plates and the arrangement of the pores on the theca surface (arrowhead). **E:** Dorso-apical view, note the small plate 2a with a depression on the center. **F:** Apical view, note the small 2a plate. Scale bars: 10 μm .

(hexagonal) (Fig. 6B) or five-sided (pentagonal) (Fig. 6C). Autotrophic species. Dimensions: length average $23.9 \mu\text{m} \pm 5.3$ ($n = 6$), width average $22.0 \mu\text{m} \pm 6.1$ ($n = 5$).

Peridiniella globosa (Dangeard) Okolodkov. *Acta Bot. Mex.* 74. 2006. Fig. 6D-F.

Peridinium globosum Dangeard (Basionym). Dangeard 1927 (as *Peridinium globosum*), p. 355, fig. 20.

Plate formula is: Po, X, 4', 3a, 7'', 6c, 4s, 6'', 2'''. Cells are rounded (Fig. 6D). The thecal surface is smooth or slightly rough. The collar surrounding the apical pore plates is not so evident in cells with a smooth theca. Cingulum is deeply excavated, displaced one girdle width and presents lists at both

sides. Both epitheca and hypotheca show pores in the plates which can be arranged in straight rows that run through the edges of the plate or forming concentric rows (Fig. 6D, arrowhead). Intercalary plate 2a is pentagonal, very small and it is depressed with respect to the cell surface or shows a depression on the center (Fig. 6E, F). Autotrophic species. Dimensions: length average $31.3 \mu\text{m} \pm 5.7$ ($n = 5$), width average $32.2 \mu\text{m} \pm 6.1$ ($n = 6$).

Distribution and habitat. *P. danica* seems to be a cosmopolitan species, although it has been found mainly in cold waters, being widely distributed in the northeast Atlantic Ocean (Okolodkov & Dodge, 1995 and references therein). Moreover, *Peridiniella* sp. recently mentioned for the western Antarctic Peninsula by Mascioni et al. (2019)

corresponds to *P. danica* (Mascioni M., pers. com.). By contrast, *P. globosa* is listed in the Mexican Pacific (Okolodkov & Gárate-Lizárraga, 2006) and in the Black Sea (Barinova *et al.*, 2011). In the southwest Atlantic, the only *Peridiniella* species recorded, as far we know, is *P. sphaeroidea* found by Balech (1988) from 36°S to 39°S in temperate waters (15-18 °C). In our study, *Peridiniella* spp. cells were observed during all expeditions, covering a wide area of the Argentine Sea (\approx 39-54 °S). Their abundance was usually low (e.g. from 20 to 1,960 cells L⁻¹) in most expeditions, but peaks of \approx 7 x10³ cells L⁻¹ were recorded during spring at three stations (St. 37, 38 and 42) from southern slope waters. Maximum *Peridiniella* spp. abundances were detected in cold waters (8 °C) (Table 1), which agrees with the background data mentioned above for *P. danica*.

The cell contour and size of *Peridiniella* species are very similar to species of the toxigenic genus *Alexandrium* (Okolodkov & Gárate-Lizárraga, 2006), and therefore, both taxa can be misidentified during routine cell counting with optical microscopy. In this study, *Peridiniella* spp. and *Alexandrium* spp. co-occurred in 19 samples from E3, in which *Alexandrium* sp. cell abundances ranged between 20 and 28,000 cells L⁻¹. This highlights the importance of thecal plate observations during monitoring of harmful algae.

Observations. There are only four described species of *Peridiniella*: *P. danica*, *P. catenata*, *P. sphaeroidea* and *P. globosa*. All these species have a similar almost rounded cell shape and present the median and deep sulcus with lists in both margins, but they can be differentiated by the following characteristics: *P. danica* is slightly dorsoventrally compressed, *P. catenata* is characterized by the presence of antapical spines (Dodge, 1987), *P. sphaeroidea* shows a strong polygonal ornamentation over the surface of the thecal plates (Balech, 1979; Dodge, 1987), and *P. globosa* possess a very small second intercalary plate (2a) and a more globose cell contour than the other species (Dangeard, 1927; as *Peridinium globosum*). Observed cells of *P. danica* were similar in size to materials from the Norwegian Sea presented by Okolodkov & Dodge (1995) (21-25 μ m long, 20-22 μ m wide). In accordance with these authors, we observed two different

shapes of plate 2a (hexagonal or pentagonal) and two different arrangements of the pores (straight rows that run through the edges of the plate or forming concentric rows). By contrast, *P. globosa* showed a very small plate 2a and bigger size than *P. danica*. Plate 1' of our specimens is narrower than that illustrated by Dangeard (1927; as *Peridinium globosum*).

Prorocentrum nux Puigserver & Zingone. *Phycologia* 41. 2002. Fig. 7

Globose cell shape (Fig. 7A) and very convex valve shape (Fig. 7B, C). The periflagellar area is located on the right valve and is not depressed (Fig. 7D, E). The flagellar pore is bi-lobed and surrounded by seven plates (Fig. 7E). The surface of the valves is completely smooth, but shows small and large pores, usually with trichocysts emerging from them (Fig. 7E, F). The intercalary bands are well defined and overgrowth is evident in lateral view (Fig. 7D, G, arrowheads). On the right valve, one small and three large pores are located in the apical zone, close to the periflagellar area (Fig. 7-F), while both valves show a large pore and three small pores at the antapical extreme (Fig. 7G, H, arrows). Additionally, the left valve presents one small and two large pores grouped near the suture halfway between the apical and antapical ends (Fig. 7I, arrow). This is an autotrophic species with two ochre-yellow chloroplasts (Puigserver & Zingone, 2002). Dimensions: length average 7.9 μ m \pm 0.9 (n = 20), width average 7.3 μ m \pm 1.1 (n = 20), depth average 7.8 μ m \pm 1.5 (n = 15).

Distribution and habitat. *P. nux* was described based on a culture (Pronap I) from the Tyrrhenian Sea in the Gulf of Naples (Puigserver & Zingone, 2002). Another strain previously isolated from Plymouth waters (UK) in 1957 was also identified as *P. nux* by Puigserver & Zingone (2002). By contrast, as far as we know, *P. nux* was never detected elsewhere since its original description, probably due to the extremely small size and very thin theca. In our study, very small and globose cells of a thecate dinoflagellate were observed in the San Matías Gulf (station 10K2 from E2, Table 1), and its abundance was estimated as 82,000 cells L⁻¹. Further SEM analyses of bottle

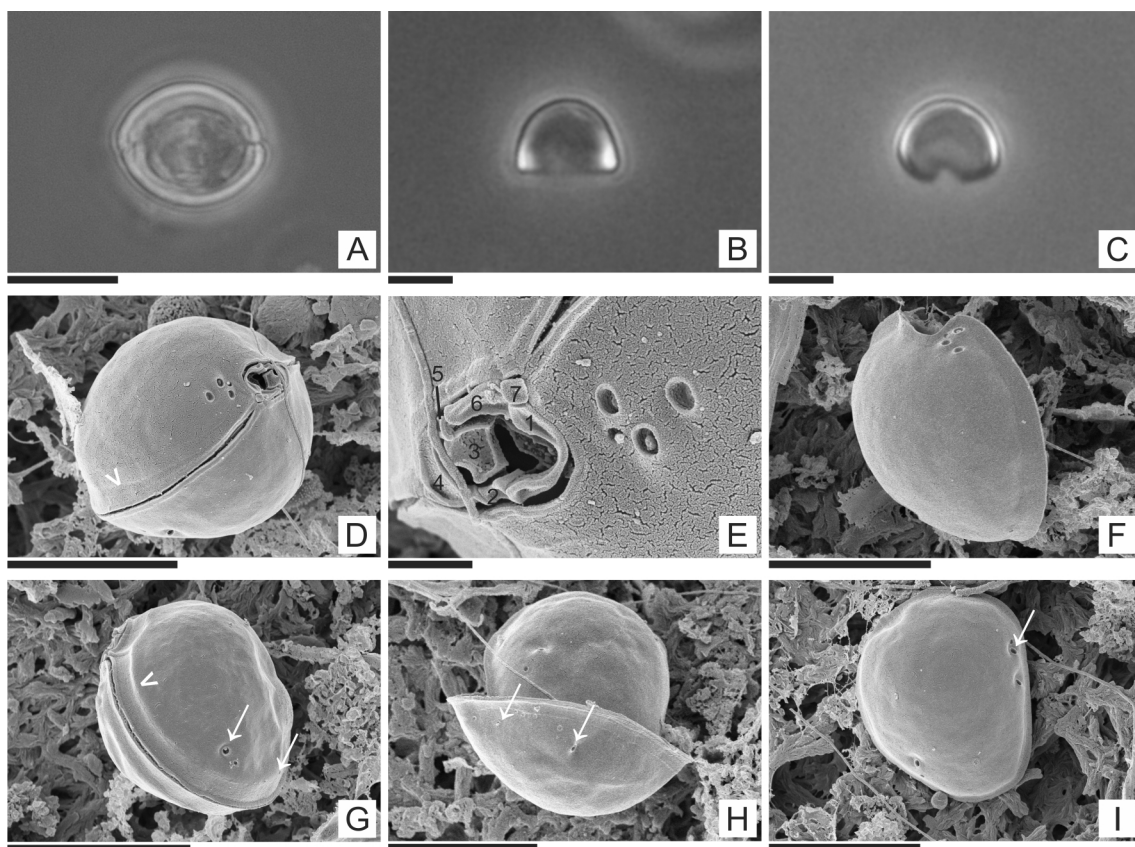


Fig. 7. LM (A-C) and SEM (D-I) images of *Prorocentrum nux*. **A:** Cell in lateral view. **B:** Empty valve in lateral view. **C:** Empty right valve in apical view. **D:** Whole cell, apical view. Note the overgrowth from the intercalary bands (arrowheads). **E:** Detail from 2, note the large pores and the small pore from the periflagellar area and the trichocysts emerging from them. **F:** Empty right valve. **G:** Whole cell, lateral view. Note the overgrowth from the intercalary bands (arrowheads) and the antapical group of pores (arrows). **H:** Whole broken cell, note the antapical group of pores (arrows). **I:** empty left valve, note the pores near the suture in the middle of the cell (arrow). Scale bars A-C, D, F-I: 5 μ m; E: 1 μ m.

sample concentrates revealed that those cells corresponded to *P. nux*, a species that has never been quantified in field samples before. Total plankton abundance at station 10K2 was 3×10^5 cells L^{-1} and was dominated by small (<15 μ m) dinoflagellates, of which *Prorocentrum nux* and *Azadinium*-like cells were the dominant taxa. Until now, there are no reports of harmful events related to *P. nux*, although it is important to consider that small *Prorocentrum* species, such as *P. cordatum*, can produce dense blooms and generate anoxia and harmful effects on marine life (Heil *et al.*, 2005).

Observations. *P. nux* has unique morphological characteristics that differentiate it from other *Prorocentrum* species, such as the globose shape in apical and antapical view, the overgrowth of the intercalary bands and the particular distribution of small and large pores (Puigserver & Zingone, 2002). Cells analyzed in our study were similar in size to those provided in the original description (6.3-9.0 μ m long, 5.3-10.0 μ m wide), which placed *P. nux* as the smallest from all *Prorocentrum* species and even one of the smallest thecate dinoflagellates known until now.

CONCLUSIONS

The detailed examination with optical and electron microscopy of field plankton samples collected in a large latitudinal and seasonal gradient across the Argentine Sea lead to the finding of seven dinoflagellate that are little known from marine waters worldwide. Most of them were rare or scarce; which, together with the requirement of detailed ultrastructural observations for their specific identification, justifies the poor information about their occurrence. However, *Prorocentrum nux*, which can be overlooked during routine microscopy examinations due to its very small size and thin theca, represented an important component of phytoplankton (8.2×10^4 cells L^{-1}). Likewise, small unidentified specimens of *Gyrodinium* with distinctive morphological features were recorded in moderate densities ($4.9 - 6.5 \times 10^3$ cells L^{-1}). The results obtained in this study together with other recent findings from the same area suggest that the Argentine Sea presents high dinoflagellate diversity, and contribute to the understanding of global distribution patterns of small, usually rare and hard to detect dinoflagellate species.

AUTHOR CONTRIBUTIONS

Both authors contributed to article conceptualization, microscopic analysis and writing.

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