PROTOPERIDINIUM BERGH (DINOPHYCEAE) OF THE NATIONAL PARK SISTEMA ARRECIFAL VERACRUZANO, GULF OF MEXICO, WITH A KEY FOR IDENTIFICATION

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ABSTRACT

The morphology of 46 species of Protoperidinium was studied based on 510 phytoplankton net samples taken from May 2005 through February 2007 at 7 stations in the northwestern part of the National Park Sistema Arrecifal Veracruzano, southern Gulf of Mexico. Forty-three species are represented by vegetative cells and three species only by cysts (P. oblongum, P. cf. stellatum and P. subinerme). Descriptions with an emphasis on the first apical and the second intercalary plates and synonymy are given for each species. Cell size variation, the mean and the standard deviation of three or four measurements are given for most species. The hypothecal pore in the first postcingular plate, a stable taxonomic feature, was observed only in P. solidicorne, P. pellucidum, P. ovum, P. sp. E meta-hexa and P. cf. hirobis; the position of the pore is also a conservative characteristic. Twenty-five species are provided with affinities and taxonomic, nomenclatural or biogeographic comments. A dichotomous key for identification of all the species found is presented, and species are illustrated with light microscope photographs. A new combination is proposed: Protoperidinium persicum (J. Schill.) Okolodkov comb. nov. Fifteen species are new records for the Gulf of Mexico, and about 25 species for the state of Veracruz.

Key words: dinoflagellates, Gulf of Mexico, key for identification, Protoperidinium, taxonomy.

RESUMEN

Se estudió la morfológía de 46 especies de Protoperidinium con base en 510 muestras de fitoplancton de red tomadas desde mayo de 2005 hasta febrero de 2007 en siete sitios
georeferenciados en la parte noroeste del Parque Nacional Sistema Arrecifal Veracruzano, en el sur del Golfo de México. Cuarenta y tres especies están representadas por células vegetativas y tres sólo por quistes (\textit{P. oblongum}, \textit{P. cf. stellatum} y \textit{P. subinerme}). Para cada especie se dan las descripciones con énfasis en la primera placa apical y la segunda placa intercalar, así como la sinonimia. La variación de tamaño de células, el promedio y la desviación estándar se presentan para la mayoría de especies. El poro hipotecal en la primera placa postcingular, un rasgo taxonómico constante, fue observado sólo en \textit{P. solidicorne}, \textit{P. pellucidum}, \textit{P. ovum}, \textit{P. sp. E meta-hexa} y \textit{P. cf. hirobis}; la posición del poro es también una característica estable. Para 25 especies se proporcionan notas sobre sus afinidades, al igual que comentarios taxonómicos, nomenclaturales y biogeográficos. Se presenta una clave dicotómica para la identificación, así como ilustraciones de todas las especies encontradas. De éstas, 15 representan nuevos registros para el Golfo de México, y cerca de 25 especies lo son para el estado de Veracruz.

Palabras clave: dinoflagelados, Golfo de México, clave para identificación, \textit{Protoperidinium}, taxonomía.

INTRODUCTION

The coastline of the state of Veracruz extends approximately 745 km along the southwestern Gulf of Mexico, between 22°15'36" N, 97°47'25" W and 18°12'36" N, 94°08'48" W. The coastal zone of the state is influenced by the Loop Current from which anticyclonic gyres separate and drift westward (Monreal-Gómez & Salas de León, 1990; Vidal et al., 1992). Occasional strong northern winds are characteristic of this region. In the Gulf of Mexico, the predominant winds and currents influence the position of the meso-scale gyres and the intensity of upwellings. In its southern part, the intensification of the Yucatan Current, which occurs mainly in summer and autumn, results in a more intensive upwelling above the shelf and in the character of the horizontal circulation in the Bay of Campeche (Bessonov et al., 1971). In summer, the current increases, and in winter it diminishes. The coastal ecosystems of the state of Veracruz and those of the National Park Sistema Arrecifal Veracruzano (NPSAV), which occupies 52,238 ha and includes 23 coral reefs, seem to be influenced by the predominant winds and local factors such as the shallowness of the zone and the proximity to the big city and to the islands.

Information on the species composition of dinoflagellates, and particularly on the genus \textit{Protoperidinium} Bergh, is scarce and scattered mainly throughout unpublished theses (Avendaño-Sánchez & Sotomayor-Navarro, 1982; Echeverría-
Okolodkov.: Protoperidinium (Dinophyceae) near Veracruz, Gulf of Mexico

Valencia, 1983; Suchil-Vilchis, 1990; Zamudio-Reséndiz, 1998; Figueroa-Torres & Weiss-Martínez, 1999; Aquino-Cruz, 2002; García-Reséndiz, 2003; Legaria-Moreno, 2003; Estradas-Romero, 2004; Tejeda-Hernández, 2005). A total of 39 Protoperidinium species have been reported from the state of Veracruz, and only a few of them have been illustrated with line drawings or light photomicrographs of poor quality. The atlas of dinoflagellates of the Caribbean Sea and adjacent areas published by Wood (1968) includes 47 Protoperidinium species. The names of 22 taxa of this genus are given in the list of Rouchiyainen et al. (1971), based on the materials of the Gulf of Mexico, the Florida Straits and the Caribbean Sea. López-Baluja et al. (1992) include 30 Protoperidinium species in their list of phytoplankton of the Gulf of Mexico and Cuban waters. Steidinger et al. (1967) and Steidinger & Williams (1970) report about 40 from the West Florida shelf waters. Balech (1967) lists 23 from the northeastern Gulf of Mexico. Earlier studies include only two representatives of this genus (Graham, 1954; Curl, 1959; Dragovich, 1961, 1963). Based on the samples collected during the period of 1979-2002 in the southern Gulf of Mexico, Licea et al. (2004a) report 28 Protoperidinium species, 8 of them are new records for the Gulf, although the list does not separate those found in different coastal states of Mexico (Tamaulipas, Veracruz, Tabasco, Campeche, Yucatan and Quintana Roo). In general, about 63 representatives of this genus which have been found in the Gulf of Mexico and the Caribbean Sea are known from the literature. Taking into account new taxa described after the publication of Sournia (1986), the genus Protoperidinium includes more than 260 species.

The purpose of the present work was to show the diversity of Protoperidinium species in the waters of the NPSAV, to document records with photomicrographs and to provide data on cell size variation and a key for species identification.

MATERIAL AND METHODS

Phytoplankton samples were taken weekly with a hand net, 20 µm mesh and 30 cm mouth, from seven sites (stations) around the Aquarium of Veracruz, in the northwestern part of the National Park Sistema Arrecifal Veracruzano. Collections were made during the period from May 2005 through February 2007 as part of the monitoring program of the Aquarium of Veracruz “Monitoreo de florecimientos algales nocivos en el área del Acuario de Veracruz en mayo del 2005 - mayo del 2006” and its extension (Fig. 1, Table 1). At each station, the net was towed hori-
horizontally for 5 min. at the velocity of the boat of ca. 2.5 knots to sample a superficial 30-cm layer. Some physical-chemical characteristics, such as temperature, salinity, pH, dissolved oxygen, and some macronutrients were measured in the field and in the laboratory after sampling. The samples taken by net were fixed with a stock formaldehyde solution to a final concentration of 4% and stored in 100-ml dark plastic bottles. To examine the thecal morphology and to identify species, a 0.2% Trypan Blue water solution was added to water mounts (Lebour, 1925; Taylor, 1978). In general, 510 samples were analyzed using an inverted Nikon TS100 microscope; of these, 160 were examined in greater detail using an Olympus BX51 compound microscope equipped with a UPlanApo 60x/0.90 dry objective with a correction ring iris diaphragm.

Table 1. Sampling sites (stations) in the National Park Sistema Arrecifal Veracruzano, Veracruz, Gulf of Mexico, May 2005 - February 2007.

<table>
<thead>
<tr>
<th>Station</th>
<th>Location</th>
<th>Geographic coordinates</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Playa Norte - Planta de residuos</td>
<td>19°13'06.0&quot; N, 96°09'34.5&quot; W</td>
</tr>
<tr>
<td>2</td>
<td>Arrecife Anegada de Adentro</td>
<td>19°13'41.1&quot; N, 96°03'44.4&quot; W</td>
</tr>
<tr>
<td>3</td>
<td>Arrecife Isla de Sacrificios</td>
<td>19°10'32.7&quot; N, 96°05'40.9&quot; W</td>
</tr>
<tr>
<td>4</td>
<td>Hotel “Lois”</td>
<td>19°10'27.1&quot; N, 96°06'51.3&quot; W</td>
</tr>
<tr>
<td>5</td>
<td>Asta Bandera</td>
<td>19°10'37.4&quot; N, 96°07'10.9&quot; W</td>
</tr>
<tr>
<td>6</td>
<td>Hotel “Villa del Mar”</td>
<td>19°11'04.6&quot; N, 96°07'20.6&quot; W</td>
</tr>
<tr>
<td>7</td>
<td>Acuario - Escuela Náutica</td>
<td>19°11'15.2&quot; N, 96°07'19.4&quot; W</td>
</tr>
</tbody>
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About 80 publications, abstracts and theses on the phytoplankton and dinoflagellates of the Gulf of Mexico were examined, with special emphasis on the state of Veracruz. Species are presented alphabetically. Latin names of the taxa are updated, and the names of the synonyms given in the original publications on the Gulf of Mexico are also presented. The works where the species are illustrated are marked with asterisks, one asterisk (*) meaning line drawings, and two asterisks (**) meaning light photomicrographs. The words “also as” before a taxonomic name mean that the taxon was reported under more than one name in the same publication.
The names of the thecal plates are abbreviated according to the Kofoid tabulation system as follows: 1' - first apical plate, 1a - first intercalary plate, 2a - second intercalary plate, 3a - third intercalary plate, 1'' - first postcingular plate, S.a. - anterior sulcal plate, S.s. - left sulcal plate, S.d. - right sulcal plate, S.m. - medium sulcal plate (see also Fig. 2). Length means the length of the cell body without antapical spines, and total length means the length including antapical spines when present. Width of the cell was measured directly in front of the cingulum or behind it, not considering the cingular membranes. Height (or depth in some literature) of the cell was measured in apical or lateral view as the minimum projection of the cell along its longitudinal axis. Mean values with standard deviation are given for each species when more than one cell was measured. Short descriptions of cyst morphology are given for the species for which they are known. Taxonomic, nomenclatural and/or biogeographic notes are given for some species where it was appropriate (original comments and important information taken from the literature).
Fig. 2. Main morphological features of the *Protoperidinium* theca used for species identifications. 1-3. Kofoid tabulation system: 1 - sulcal view, 2 - apical (anterior) view, 3 - antapical (posterior) view; 1'-4' apical plates, 1a-3a intercalary plates, 1''-7'' precingular plates, 1'''-5''' postcingular plates, 1'''' and 2'''' - antapical plates, Po - pore plate, x - canal plate (the Po and x plates constitute the apical pore complex), c1-c3 cingular plates, t - transitional plate; S.a., S.s., S.m., S.d. and S.p. - sulcal plates (anterior, left, median, right and posterior, respectively). 4-7. Cingulum: 4 - circular (no offset), 5 - ascending, 6 - descending, 7 - ascending with overhang. 8-11. Type of the 1' plate: 8 - ortho, 9 - meta, 10 - inverted meta (or right meta), 11 - para. 12-15. Type of the 2a plate: 12 - quadra, 13 - penta, 14 - hexa, 15 - neutra.
Conventional language is used in descriptions. When referring to the sides of the epitheca or hypotheca, ventral view is considered. Much attention has been paid to the morphology of the 1' and 2a plates. The morphological characteristics “ortho-quadra”, “meta-penta”, “para-hexa” and others mean the type of the 1' plate together with the type of the second intercalary plate observed in the same cell (Fig. 2). The presence and the position of the hypotheecal pore in the 1'' plate, which is an extremely conservative morphological feature (Dodge, 1987; Okolodkov, 2003), was checked in all cells of the examined species. Obviously, the presence of the hypotheecal pore in a number of species not previously observed by other authors made it more difficult to compare the results of the present study with data from the literature. Similarly, it was also difficult to make comparisons between more detailed observations and frequently very schematic figures provided by earlier authors who originally described many taxa. Three species of which only cysts were found are not included in the key for identification. The absence of data on the morphology of the sulcal plates did not permit me to make a more complete comparison between the material from Veracruz and the data from the literature, principally from works by Balech.

In the key for identification, numbers without parentheses mean the number of a pair of statements, and numbers in parentheses mean the successive number of species according to the order in which they appear in the text following the key.

RESULTS AND DISCUSSION

Key for identification of species of the genus *Protoperidinium*

1a One intercalary plate, the apical pore complex (APC) is absent .........................
                          .................................................. Subgenus *Testeria* Faust, (1) *Protoperidinium concinnum*
1b More than one intercalary plate, the APC is present .................................. 2
2a Two intercalary plates .............................. 3 (subgenus *Archaeperidinium*)
2b Three intercalary plates ............................ 8 (subgenus *Protoperidinium*)

Subgenus *Archaeperidinium* (Jörg.) Balech

3a Cells strongly compressed dorsoventrally .................................................
                            .................................................................... (2) *Protoperidinium compressum*
3b Cells slightly or not compressed dorsoventrally ......................................... 4
4a Cells fusiform ................................................................. (3) *Protoperidinium abei*
4b Cells not fusiform ........................................................................................................ 5
5a Cells globular .............................................................. (4) *Protoperidinium* sp. A ortho-2a
5b Cells pentagonal or discoid ......................................................................................... 6
6a Cells not compressed anteroposteriorly, with coarsely sculptured theca ..............
......................................................................................................................... (5) *Protoperidinium thorianum*
6b Cells strongly compressed anteroposteriorly ...................................................... 7
7a Cells discoid, with a circular Po plate and the apex strongly displaced to the ventral side ........................................................................................................... (6) *Protoperidinium excentricum*
7b Cells irregularly pentagonal, with a very long Po plate slightly displaced to the ventral side .................................................................................................................. (7) *Protoperidinium denticulatum*

Subgenus *Protoperidinium* (Gran) Balech
8a Plate 1' inverted meta ........................................... (8) *Protoperidinium thulesense*
8b Plate 1' ortho, meta or para ............................................................... 9
9a Plate 1' para, plate 2a hexa ........................................................................... 11
9b Plate 1' ortho or meta, plate 2a quadra, penta or hexa .................................. 10
10a Plate 1' ortho ......................................................................................... 16
10b Plate 1' meta ............................................................................................. 28

Species *Para*
11a One (left) antapical spine ....................... (9) *Protoperidinium norpacense*
11b Two antapical spines ...................................................................................... 12
12a Two low conical antapical horns ........ (10) *Protoperidinium latissimum*
12b No antapical horns ......................................................................................... 13
13a Cells with antapical horns ending in spines .................................................... (11) *Protoperidinium solidicorne*
13b Cells without antapical horns, only spines are present .................................. 14
14a Cells pyriform or quadrangular, apical horn not well-separated, two sulcal lists, antapical spines divergent, hypothecal pore closer to cingulum .................................................. (12) *Protoperidinium pellucidum*
14b Cells globular or ovoid, apical horn well-separated, one (left) sulcal list, antapical spines parallel, hypothecal pore closer to sulcus.................................................. 15
15a Cells globular, antapical spines <1/6 of the body length, plate 2a less than twice as large as plate 4", hypothecal pore in the proximal part of plate 1"............................. (13) *Protoperidinium cf. subsphaericum*
15b Cells ovoid or subpyriform, antapical spines ca. 1/5 of the body length, plate 2a more than twice as large as plate 4", hypothecal pore in the distal part of plate 1" ........... (14) *Protoperidinium ovum*

Species *Ortho*

16a Cells with high conical antapical horns ......................................................... 17
16b Cells with low conical horns or without horns ................................................. 20
17a Cells strongly compressed dorsoventrally ...................................................... 18
17b Cells slightly compressed dorsoventrally ...................................................... 21
18a No apical horn ......................... (15) *Protoperidinium* sp. B ortho-quadra
18b Apical horn present ................................................................. (19)
19a Apical and antapical horns relatively short, sides of epitheca convex, plate 2a penta (sometimes quadra) ................................................................. (16) *Protoperidinium claudicans*
19b Apical and antapical horns relatively long, sides of epitheca straight or slightly concave, plate 2a quadra .................... (17) *Protoperidinium venustum*
20a Apical horn short, cell length/width ratio <1.4 ........................................... (18) *Protoperidinium depressum*
20b Apical horn long, cell length/width ratio >1.6 ............................................... (19) *Protoperidinium oceanicum*
21a Antapical horns low conical ending with spines ........................................ 22
21b No antapical horns or spines ........................................................................... 25
22a Epithecal plates with longitudinal ribs, proximal sides of plate 1' much shorter than distal ones ...................................... (20) *Protoperidinium obtusum*
22b Epithecal plates have no longitudinal ribs, all four sides of plate 1' subequal in length or proximal sides are longer than distal ones ...................... (23)
23a Hypotheca with two large antapical horns and deeply incised antapex ........ (21) *Protoperidinium conicum*
23b Hypotheca with very low antapical horns ............................................. 24
24a Antapical spines short, central part of the ventral side of the cell concave ... (22) *Protoperidinium pentagonum*
24b Antapical spines strong and relatively long, central part of the ventral side of the cell slightly concave ................. (23) *Protoperidinium divaricatum*
25a Plate 1' not rhomboid, with very short proximal sides, and its distal sides are well separated near cingulum ........... (24) *Protoperidinium* cf. *argentinense*
25b Plate 1' rhomboid, with all four sides subequal in length ......................... (26)
26a Theca punctate or pimpled, cells $>70$ µm long, hypotheca is asymmetrical, left antapical horn is larger .................................. (25) *Protoperidinium persicum*

26b Theca smooth or faintly reticulated, cells $<50$ µm long, hypotheca is symmetrical ................................................................. 27

27a Hypotheca almost equal to epitheca in length or slightly shorter .................. ....................................................................................................... 27

27b Hypotheca longer than epitheca .............................................................................................................................. (27) *Protoperidinium* sp. C ortho-hexa

Species *Meta*

28a Cingulum with ends overhanging by 1-2 times its width ......................... 29

28b Cingulum with ends not overhanging ................................................................. 32

29a Two antapical spines .................................................................................... (28) *Protoperidinium quarnerense*

29b No antapical spines ..................................................................................... 30

30a Cells with two short wings at antapex, plate 2a hexa (sometimes penta) ... ........................................................................................................ (29) *Protoperidinium sphaeroides*

30b Cells without wings at antapex .................................................................. 31

31a Cell compressed anteroposteriorly, plate 2a quadra (sometimes penta) ....... ................................................................................................. (30) *Protoperidinium simulum*

31b Cells not compressed anteroposteriorly, plate 2a penta ................................ ........................................................................................................ (31) *Protoperidinium* cf. *cristatum*

32a Two antapical horns ..................................................................................... 33

32b No antapical horns ......................................................................................... 35

33a Cells shorter than wide or cell length/width ratio is about $<1.1$ .................. ........................................................................................................ (32) *Protoperidinium crassipes*

33b Cells longer than wide, cell length/width ratio $>1.1$ ................................. 34

34a Cells stout, with relatively longer antapical horns, epitheca and hypotheca are subequal in length .............................. (33) *Protoperidinium divergens*

34b Cells robust, often irregularly outlined, with relatively shorter antapical horns, epitheca longer than hypotheca .................. (34) *Protoperidinium brochii*

35a No antapical spines ....................................................................................... 36

35b One or two antapical spines ........................................................................ 37

36a Cells with two short wings at antapex, 2a penta ........................................ (35) *Protoperidinium cristatum*

36b Cells without wings at antapex, plate 2a hexa ........................................... (36) *Protoperidinium* sp. D meta-hexa
37a One (right) antapical spine and prominent left sulcal list .............................................................. (37) Protoperidinium curvipes
37b Two antapical spines .................................................................................................................. 38
38a Hypothecal pore in plate 1” not present .................................................................................. 39
38b Hypothecal pore in plate 1” present ...................................................................................... 40
39a Cell not pyriform, without apical horn, plate 2a quadra .......................................................... (38) Protoperidinium pacificum
39b Cells pyriform, with apical horn, plate 2a penta ........................................................................ (39) Protoperidinium pyriforme var. pyriforme
40a Apical horn relatively shorter, hypotheca shorter than epitheca, with prominent left sulcal list .................................................................................................................. (40) Protoperidinium oviforme
40b Apical horn relatively longer, hypotheca and epitheca subequal in length, no prominent sulcal lists .................................................................................................................. (41) Protoperidinium cassum
41a Apical horn relatively long, with a spine emerging from its left margin, sides of epitheca and hypotheca almost straight, two long antapical spines .......................................................... (42) Protoperidinium sp. E meta-hexa
41b Apical horn relatively short, without spine, sides of epitheca and hypotheca convex, two relatively short antapical spines .................................................................................................................. (43) Protoperidinium cf. hirobis

Taxonomic descriptions

(1) Protoperidinium concinnum ("concinna") Faust, 2006 (Pl. 1, Fig. 1-6)

Cells elongated, with rounded or quadrangular body with slightly convex or almost straight margins of both epitheca and hypotheca, noticeably dorsoventrally compressed. Plate 1' ortho, the only intercalary plate is hexa. The APC is absent. Cingulum planozone, descending, with 0.5-1.3 cingulum width offset. Plates 2' and 4' are connected along a long suture that lies between the apex and the 1' plate and is almost as long as the latter. The 1a plate is hexa, and it is about twice as long as plate 4'. The apical horn is long, slender and pointed. The hypothecal pore is absent. Antapical conical horns are long and slender, strongly diverged. A teratological cell found once has both apical and antapical horns broadly rounded and shorter. Length 90-132 µm (117.6±9.8 µm), width 43-77.5 µm (64.8±8.6 µm), height 27.5-48.0 µm (39.5±6.4 µm); n=16.
Taxonomic note: The studied cells in general correspond well to the original descriptions and figures of *P. concinnum* and *P. novellum* (“novella”) Faust (Faust, 2006). These species share the same unusual plate pattern (the absence of the APC, wide connection between the 2' and 4' plates, and the presence of only one intercalary plate), cingulum morphology and cell shape, although the cells from Veracruz have a more rounded body on both sides of the cingulum. The size characteristics of the cells were also somewhat different, so that I conventionally ascribe them to *P. concinnum* because at present I cannot give a preference to any of Faust’s species or discriminate between them.

Biogeographic note: The finding of this species in Veracruz waters is a new record for the Gulf of Mexico and the second published record of *P. concinnum* originally described from the Gulf Stream offshore of Point Lookout, North Carolina, USA, and also known from the waters outside mangrove cays of Belize in the Caribbean and Gulf Stream offshore of Fort Pierce Inlet, Florida, USA (Faust, 2006).

(2) *Protoperidinium compressum* (T. H. Abé) Balech, 1974 (Pl. 1, Fig. 7 and 8)  
**Bas.:** *Congruentidium compressum* T. H. Abé, 1927: 420, fig. 36A-E.

Cells pentagonal, very compressed dorsoventrally, with no or a very short, non-separated apical horn. Plate 1' ortho, two intercalary plates. Cingulum cavozone, ascending, with 0.5 cingulum width offset. Plate 1' rhomboid, symmetrical, with proximal sides about 1.5 times longer than distal ones. Plate 1a is about 1.5 times smaller than plate 2a. Epitheca has slightly convex sides. The hypothecal pore is absent. Hypotheca has slightly concave sides drawn into two compressed low conical horns terminated with spines widely separated and diverged. Length 42.5-80 μm (56.1±7.9 μm), width 30-75 μm (46.8±8.7 μm), height 15-23.5 μm (19.1±3.1 μm); n=17.

Cysts are stellate, dorsoventrally compressed, smooth-walled, with one apical, two lateral and two antapical needle-shaped horns. Hypotheca is slightly longer than epitheca. The archeopyle is intercalary, two-paraplate. Length 34 μm excluding horns, horns up to 20 μm, total length 54-63 μm (Bolch & Hallegraeff, 1990: 182, fig. 22; Lewis & Dodge, 1990: fig. 6.35; Nehring, 1994: fig. 1J).

Taxonomic note: The studied cells ascribed to *P. compressum* have much in common with the original description and drawings by Abé (1927). However, there are some important differences: 1) the cells from Veracruz have two intercalary plates vs. one in Abé (both of them are easily seen in dorsal view); 2) the 1' plate is at least two times broader in its widest part than the cingulum, while Abé illustrated the 1' plate slightly wider than the cingulum; 3) the cells from Veracruz have antapi-
cal spines not separated from the horns, while in Abé they are well separated; 4) the cingulum in the studied cells is ascending to a greater extent, and in Abé’s cells the displacement is less pronounced (0.25 between the proximal ends of the cingulum and 0-0.5 between its distal ends). Also, the specimens from Veracruz differ from those of Matzenauer (1933: 481, fig. 75a, b), who pictured them with only one intercalary plate in dorsal view and the cingulum without displacement of its ends. Rochon et al. (1999) described in detail the differences in the thecae of vegetative cells between *P. compressum* and the closely related *P. stellatum*. The studied specimens are in good correspondence with the description of *P. compressum*, having the 2'' and 6'' plates folded around the longitudinal margins of the epitheca and the 2a plate which does not contact the right longitudinal margin.

Gulf of Mexico: Estradas-Romero, 2004; Tejeda-Hernández, 2005** (as *Protoperidinium sp.* 3).

(3) *Protoperidinium abei* (Paulsen) Balech, 1974 (Pl. 1, Fig. 9-12)
Bas.: *Peridinium abei* Paulsen, 1931: 73.
Nom. syn.: *Peridinium biconicum* T. H. Abé, 1927: 416, fig. 34.

Cells fusiform, with a tapered, non-separated apical horn. Ortho 1' plate, two intercalary plates. Cingulum strongly cavozone, descending, with 1.25-1.5 cingulum width offset, with numerous noticeable longitudinal ribs. The right part of the hypotheca forms a strong horn with a noticeable sulcal list, and it is larger than the left one. Plate 1' has equally short proximal margins and long distal margins that are almost parallel in the middle part of the plate and strongly convex in its distal part; plate 1' is widest in its distal quarter. Plates 1a and 2a are hexagonal, almost equal in size. The hypothecal pore is absent. Length 57-77 µm (65.0±6.6 µm), width 37-48 µm (44.4±3.4 µm), height 37-50 µm (44.8±4.2 µm), L/W ratio 1.37-1.61; n=8.

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967; Steidinger & Williams, 1970**; Avendaño-Sánchez & Sotomayor-Navarro, 1982; Aquino-Cruz, 2002** (as *Protoperidinium sp.* 5); Licea et al., 2004a; Tejeda-Hernández, 2005** (as *Gonyaulax Jolliffei*).

(4) *Protoperidinium sp.* A ortho-2a (Pl. 1, Fig. 13-15)

Cell ovoid, without apical horn. Ortho, with two intercalary plates. Cingulum slightly cavozone, descending, with 0.2 cingulum width offset. Plate 1’ is trapezoid, with a longer left proximal margin compared to the right one. Plate 1a is heptagonal and 2a is hexagonal, the former being the largest epithecal plate and about twice as large as the latter. The S.a. plate inserts deeply onto the epitheca. Sulcus is very sha-
Plate 1. Fig. 1-6. *Protoperidinium concinnum* (Fig. 5 and 6, a teratological cell). Fig. 7 and 8. *P. compressum*. Fig. 9-12. *P. abei*. Fig. 13-15. *P. sp. A ortho-2a*. In Plates 1-15, scale bar = 10 µm.
llow. The S.s. plate is well noticeable, as long as the 1" plate. The hypothecal pore is absent. No antapical spines. Length 29-30 µm (29.7±0.6 µm), width 26.5-27 µm (26.8±0.3 µm), height 23-26 µm (24.7±1.5 µm); n=3.

Affinities: I could not find any species with the same combination of morphological features in the literature. From the ventral view it superficially resembles *P. gibbosum* (Matzen.) Balech and *P. joubini* (P. A. Dang.) Balech; however, these two species have three intercalary plates with the 2a plate of penta type (see Dangeard, 1927: 361, fig. 27a, b; Balech, 1988: 93, pl. 31, fig. 11-15; 97, pl. 34, fig. 3-6). Furthermore, the examined specimens resemble *P. asymmetricum* Balech (=*Sphaeridinium asymmetrica* T. H. Abé, 1927: 391, fig. 11-13) in cell shape and the morphology of the sulcal area. The studied cells probably represent an undescribed species.

Locality: st. 1, 6 July 2005, in a plankton haul.

(5) *Protoperidinium thorianum* (Paulsen) Balech, 1973 (Pl. 2, Fig. 1-4)
Bas.: *Peridinium thorianum* Paulsen, 1905: 3, fig. 1a, b.

Cells subpentagonal, with straight or slightly convex sides, without apical or antapical horns. Plate 1' ortho, two intercalary plates. Cingulum deeply cavozone, with numerous longitudinal ribs, descending, with 0.8-1.0 cingulum width offset. Plate 1' with the distal margins 2.3-2.5 times longer than the proximal ones and convex near the cingulum. A comparatively long canal stretches from the pore complex into the 3' plate. The hypothecal pore is absent. Hypotheca has no apical horns or spines. Length 43-62.5 µm (53.0±7.3 µm), width 40-52 µm (45.9±4.6 µm), height 35-50 µm (42.2±5.4 µm); n=12.

Cysts spherical, smooth-walled, dark-brown. The archeopyle is hexagonal, symmetrical, probably formed by the loss of the 2a paraplate. Diameter 50-55 µm (Lewis et al., 1984: 31, fig. 2d).

A new record for the Gulf of Mexico.

(6) *Protoperidinium excentricum* (Paulsen) Balech, 1974 (Pl. 2, Fig. 5-7)
Bas.: *Peridinium excentricum* Paulsen, 1907: 14, fig. 17a-f.

Cells discoid, strongly compressed anteroposteriorly, with the apical horn situated very close to the ventral side of the cell. Plate 1' ortho, two intercalary plates. Cingulum deeply cavozone, ascending, with about 0.5 cingulum width offset, with numerous longitudinal ribs. Plate 1' is rhomboid, symmetrical, narrow, as wide as the cingulum. Plate 2a is about four times larger than plate 1a. Hypotheca is slightly
Plate 2. Fig. 1-4. *Protoperidinium thorianum*. Fig. 5-7. *P. excentricum*. Fig. 8-10. *P. denticulatum* (two connected cells).
Okolodkov. *Protoperidinium* (Dinophyceae) near Veracruz, Gulf of Mexico

longer in its left part, sometimes bearing a small spine at the antapex. Length 17.5-37 µm (24.9±6.0 µm), width 37.5-66.3 µm (48.1±9.0 µm), height 33.8-55 µm (41.4±6.2 µm); n=14.

Cysts ovoid, compressed anteroposteriorly (to a greater extent, antapically) and slightly dorsoventrally, without any appendage, smooth-walled, pale-brown or dark-brown, with an indented parasulcus. The archeopyle is an indistinctive zig-zag split. Width about 50 µm (Wall & Dale, 1968: 278, pl. 4, fig. 8; Lewis et al., 1984: 26, fig. 2h).

Gulf of Mexico: Steidinger et al., 1967; Steidinger & Williams, 1970**. A new record for the southern Gulf of Mexico and the state of Veracruz.

(7) *Protoperidinium denticulatum* (Gran et Braarud) Balech, 1974 (Pl. 2, Fig 8-10)

Bas.: *Peridinium denticulatum* Gran et Braarud, 1935: 381, fig. 58.

Cells irregularly pentagonal, compressed anteroposteriorly. Ortho 1' plate, two intercalary plates. Cingulum strongly cavozone, descending, with 1.0-1.2 cingulum width offset, with numerous noticeable longitudinal ribs. A chain of two cells was examined. The hypotheca of the first (apical) cell is connected to the hypotheca of the second (terminal) cell, which is in correspondence with Balech’s (1988: pl. 22, fig. 6) and opposite to Dodge’s (1982: 174, fig. 19B) and Hermosilla’s (1973: 54, pl. 29, fig. 1) observations. The epitheca of the apical cell and the hypotheca of the terminal cells are rounded and similar in shape, while the hypotheca of the latter and the epitheca are trapezoid and similar to each other. The epitheca of the apical cell has an apical elevation situated closer to the ventral side. Both cells have a very long Po plate displaced to the ventral side of the cell. The 1' plate lies almost entirely in the right half of the epitheca and has unequal proximal margins (the left one is twice as long) and convex distal margins. Other plates could not be distinguished. Length 24-29 µm (27.0±2.6 µm), width 35-40 µm (38.3±2.9 µm), height 30-33 µm (32.0±1.7 µm); n=3.

Cysts spherical, without any appendages, smooth-walled, dark-brown. The archeopyle is hexagonal, laterally elongated, formed by the loss of the 2a intercalary paraplate. Diameter 40-56 µm (Wall & Dale, 1968: 277, pl. 3, fig. 30; Bolch & Hallegraeff, 1990: 184, fig. 23, as *P. cf. denticulatum*).

Morphological note: A cell with unusual epitheca tabulation was found at st. 6: 6'2a"5"2". The cell has the appearance of the terminal cell of *P. denticulatum* described above, including the cingulum offset and the morphology of the 1' plate. The apical plates 2' to 6' occupy almost all the anterior surface of the cell, and the in-
tercalary plates are barely seen in the apical view. Intercalary plates are almost equal in shape (hexagonal) and size, being very short and very wide. We consider the examined cell a teratological form of *P. denticulatum* until more cells are examined.

A new record for the Gulf of Mexico.

(8) *Protoperidinium thulesense* (Balech) Balech, 1973 (Pl. 3, Fig. 1-4)
Bas.: *Peridinium thulesense* Balech, 1958: 92, pl. 6, fig. 152-160.

Cell pentagonal, without apical horn. Inverted meta (or right meta)-quadra. Cingulum strongly cavozone, ascending, with 0.3 cingulum offset, with numerous longitudinal ribs. There are only 3 apical plates. Plate 1' is widest in the distal quarter, contacts the APC only along its proximal left margin and contacts plates 2' and 3', 3a, 1", 6" and 7". Plate 2a is trapezoid, about 1.6 times shorter than plate 4". Plate 3a is as long as plates 2a and 4" together. Length 55 µm, width 66 µm, height 53 µm; n=1.

Cysts spherical, brown. The archeopyle is slit-like (Dodge, 1985: 68).

Taxonomic note: The cell from Veracruz is in good correspondence with the descriptions and illustrations of Balech (1958: 92, fig. 152-154; 1988: 105, pl. 39, fig. 1-3, 5) and especially with those of Hermosilla and Balech (1969: 11, fig. 1, 3, 5-7). However, it is larger compared to cells reported from elsewhere. It is different from the cell illustrated by Braarud (1935: 108, fig. 27), that has an ascending cingulum with ca. 0.75 offset, value seemingly within the variation range of this feature in this species (Hermosilla, 1973: 43, pl. 19, fig. 19-25).

Affinities: The only species that resembles *P. thulesense* is *P. deficiens* (Meunier) Balech (see Schiller, 1937: 266, fig. 267a-e). Their similarity is so strong that I suspect that these two names are synonyms. The original drawings of Meunier (1919: 44, pl. 20, fig. 5-8) demonstrate the 2a plate in the form of a quadrant rather than a trapezoid, which might be a discriminative feature. Recent molecular phylogenetic studies have shown a great infraspecific variation in *P. conicum* from the same water mass within the same harbor, which can be indicative of the presence of cryptic species, whereas morphological differences were not observed (Yamaguchi & Horiguchi, 2005; Yamaguchi et al., 2006). Thus, molecular information can help distinguish between very closely related species.

Plate 3. Fig. 1-4. Protoperidinium thulesense. Fig. 5-7. P. norpacense (in Fig. 6 arrowheads indicate two sulcal lists). Fig. 8-10. P. latissimum.
A new record for the Gulf of Mexico.

(9) *Protoperidinium norpacense* (Balech) Balech, 1974 (Pl. 3, Fig. 5-7)

Bas.: *Peridinium norpacense* Balech, 1962: 149, pl. 20, fig. 302-306.

Cell ovoid, with a button-like apical horn. Para-hexa. Cingulum planozone, ascending, with 1.0 cingulum width offset. Plate 1' is almost symmetrical. Plates 1a and 3a are pentagonal and are about half the size of plate 2a. Plate 2a has four lateral margins equal in length, and it is about 1.5 times longer than the 4'' plate. The hypothecal pore is absent. Only a left, slightly curved antapical spine is present, and two sulcal lists are noticeable. Length 57.5 µm, total length 67.5 µm, width 53.0 µm, height 52.0 µm; n=1.

Locality: st. 4, 10 January 2006, in a plankton haul.

A new record for the Gulf of Mexico.

(10) *Protoperidinium latissimum* (Kof.) Balech, 1974 (Pl. 3, Fig. 8-10)

Bas.: *Peridinium latissimum* Kof., 1907: 175, pl. 5, fig. 31, 32.

Tax. syn.: *P. pentagonum* var. *depressum* T. H. Abé, 1927: 409, fig. 29; *P. pentagonum* var. *latissimum* (Kof.) J. Schill., 1937: 242, fig. 243a-j; *P. pentagonoides* Balech, 1949: 403, pl. 5, fig. 111-113, pl. 6, fig. 114-130.

Cells pentagonal, without apical horn, with the slightly convex epitheca invaginated ventrally and the hypotheeca with concave sides. Para-hexa. Cingulum strongly cavozone, circular, without offset. Plate 1' is widely rhomboid, with the right distal margin longest. Plate 2a is trapezoidal, equal to plate 4'' in length, with much longer proximal lateral margins compared to the distal ones. Hypotheeca is drawn out into two low conical horns ending in strong spines. Length 77.0±0.0 µm, width 82.8±0.4 µm, height 40.0±0.0 µm; n=2.

Cysts pentagonal, dorsoventrally compressed, concavo-convex to hemispherical in apical view (with dorsal surface strongly convex) smooth-walled, The cingulum is reflected by two broad lateral, weakly excavated lobes. The archeopyle is intercalary, subtriangular, with briefly truncated angles, formed by the loss of the 2a paraplate. Length 65-100 µm, width 56-85 µm, height 32-43 µm (Wall & Dale, 1968: 274, pl. 2, fig. 7).

Localities: st. 6 and 7, 20 September 2005, in plankton hauls.

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967 (as *Peridinium pentagonum* var. *latissimum*); Steidinger & Williams, 1970** (as *Peridinium pentagonum* var. *latissimum*); Aquino-Cruz, 2002**; Tejeda-Hernández, 2005**.
(11) *Protoperidinium solidicorne* (L. Mangin) Balech, 1974 (Pl. 4, Fig. 1-3)

Cell subpentagonal, with the epitheca drawn into a non-separated apical horn. Para-hexa. Cingulum planozone, ascending, with 0.9 cingulum width offset. Plate 1' is asymmetrical, with the right distal margin longest. Plate 2a is about equal to plate 4” in length, with the proximal lateral margins about 2.3 times longer than the distal ones. The hypothecal pore is present, situated near the median longitudinal line of the 1” plate, closer to its posterior margin than to the sulcus. Hypotheca has two high conical horns ending in two strong, strongly divergent spines emerging from their inner side. Length 68.0 µm, width 48.0 µm, height 37.5 µm; n=1.

Morphological note: The studied cell is 1.5 times smaller than those described by Balech (1971a: 25, pl. 6, fig. 105-111). Furthermore, the *P. solidicorne* described by Balech (1971a, 1988) lacks a hypothecal pore whereas the cell from Veracruz possesses one. The rest of the morphological characteristics are very similar.

Affinities: The examined specimen is rather similar to *P. diabolus* (Cleve) Balech in many morphological features including the presence of the hypothecal pore and in its location closer to the sulcus than to the cingulum (Balech, 1976: 43, fig. 7a-n). However, the latter has no antapical horns. *P. pallidum* (Ostenf.) Balech subsp. *daedalum* Balech also has some features in common with the specimen from Veracruz; however, the former is considerably larger, has shorter antapical horns, a longer epitheca and a less pronounced cingulum (Balech, 1978: 184, pl. 7, fig. 200-205, pl. 7, fig. 206; 1988: 117, pl. 48, fig. 16-21).

Locality: st. 3, 18 October 2005, in a plankton haul.
Gulf of Mexico: Steidinger & Williams, 1970 (identification is incomplete). A new record for the southern Gulf of Mexico and the state of Veracruz.

(12) *Protoperidinium pellucidum* Bergh, 1881 (Pl. 4, Fig. 4-7)
Nom. syn.: *Peridinium pellucidum* (Bergh) Schütt, 1895: pl. 14, fig. 45.

Cells pyriform or quadrangular, with a short, not well-separated apex. Para-hexa. Cingulum planozone, ascending, with 0.5-0.9 cingulum width offset. Plate 1' with slightly concave proximal and distal margins; its suture contacting the 2” plate is about twice as long as that contacting the 6” plate. Plates 1a and 3a are pentagonal and are about half the size of plate 2a. Plate 2a is trapezoid, has long proximal and short distal lateral margins, and is 1.2-1.5 times longer than plate 4”. The hypothecal pore is present, and it is situated closer to the cingulum. Two antapical spines are slightly divergent, and two sulcal lists are noticeable between spines. Length 35-50
Plate 4. Fig. 1-3. *Protoperidinium solidicorne*. Fig. 4-7. *P. pellucidum* (in Fig. 4 arrowhead indicates the hypothecal pore, in Fig. 5 arrowheads indicate two sulcal lists). Fig. 8-13. *P. cf. subsphaericum* (in Fig. 8 and 13 arrowhead indicates the hypothecal pore, in Fig. 11 arrowhead indicates a pseudospine).
µm (41.0±4.5 µm), total length 40-59 µm (49.1±5.2 µm), width 35-46 µm (40.4±3.2 µm), height 35-42.5 µm (34.6±3.6 µm); n=10.

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967; Steidinger & Williams, 1970**; Aquino-Cruz, 2002**; Tejeda-Hernández, 2005**.

(13) Protoperidinium cf. subsphaericum (Balech) Balech, 1974 (Pl. 4, Fig. 8-13)


Cells spherical, with a short, well-separated apical horn. Para-hexa. Cingulum planozone, ascending, with 0.7-0.8 cingulum width offset. Plate 1' is slightly asymmetrical, and it contacts the 2' plate more than the 6' plate. The 2a plate is large, with the proximal lateral margins longest. Plates 1a and 3a are small. The hypothecal pore in the 1'' plate is situated closer to the sulcus than to the cingulum, and it is about one-third of the distance from the cingulum to the distal margin of the 1'' plate. Antapical spines are almost parallel to each other, the left spine supporting a prominent sulcal list. Length 32.5-40 µm (36.4±2.9 µm), total length 37.5-45 µm (41.0±2.9 µm), width 30-34 µm (32.4±1.5 µm), height 30-33 µm (31.4±1.6 µm); n=5.

Taxonomic note: The studied cells are about 1.7 times shorter than those described in Balech (1959; 1971b: 157, pl. 33, fig. 650-651, pl. 34, fig. 652-657; 1988: 119, pl. 50, fig. 9-13). All the specimens from Veracruz are spherical, whereas Balech (1971b) reported the variation in cell shape from ellipsoid and ovoid to spherical in P. subsphaericum. The specimens from PNSAV have even more similarity with Protoperidinium sp. J described and illustrated by Balech (1988: 122, pl. 52, fig. 10-12), including size and the presence of a pseudospine of the same length near the left antapical spine, and differing from Balech’s figures only in a more pronounced cingulum offset and the presence of the hypothecal pore. They are somewhat similar to P. aequatoriale Balech; however, the latter has only one (right) antapical spine and a prominent left sulcal list (1971a: 26, pl. 6, fig. 112-116, pl. 7, fig. 117 and 118). The cell from Veracruz is also somewhat similar to P. capurroi (Balech) Balech subsp. subpellucidum Balech (in epithecal plate pattern and in size), also described from the SW Atlantic; however, the latter has the cingulum offset less than 0.5 cingulum width and a smaller 2a plate.

Locality: st. 4, 10 May 2005, in a plankton haul.

Gulf of Mexico: Licea et al., 2004a. Most likely a new record for the state of Veracruz.
(14) *Protoperidinium ovum* (J. Schill) Balech, 1974 (Pl. 5, Fig. 1-4)
Bas.: *Peridinium ovum* J. Schill., 1911: 332, fig. 1A-D.
Tax. syn.: *Peridinium nipponicum* T. H. Abé, 1927: 396, fig. 16.

Cells ovoid, with a short, well-separated apical horn. Para-hexa. Cingulum planozone, ascending, with 0.6-1.0 cingulum width offset. The hypothecal pore is present (larger cells have the pore situated closer to the distal end of plate 1''). Two antapical spines are slightly curved and parallel to each other; the left sulcal list is noticeable. Length 31-38.9 µm (39.2±6.7 µm), total length 37.5-60 µm (47.5±7.9 µm), width 24.3-42 µm (33.2±6.3 µm), height 22.5-38.8 µm (31.8±5.5 µm); n=10.

Gulf of Mexico: Steidinger et al., 1967; Steidinger & Williams, 1970**; Rouchiyainen et al., 1971; Aquino-Cruz, 2002**; Licea et al., 2004a; Tejeda-Hernández, 2005**.

(15) *Protoperidinium* sp. B *ortho-quadra* (Pl. 5, Fig. 5-8)

Cell elongated, with slightly concave sides of the epitheca and hypotheca, without apical horn and with two long antapical horns. Ortho-quadra. Cingulum planozone (clearly excavated), descending, with 1.0 cingulum width offset. Plate 1' symmetrical, with the proximal sides longest. Plate 2a trapezoidal, small, slightly shorter than plate 4''. Sulcus extends far onto the epitheca. Length 50 µm, width 32.5 µm, height 22.5 µm; n=1.

Affinities: The species has a very particular outline. It is similar in a number of features to *P. venustum* (strong dorsoventral compression, cingulum offset, extension of the sulcus); however, the latter has a different cell shape, a distinguishable apical horn and planozone cingulum. Probably an undescribed species.

Locality: st. 1, 20 February 2007, in a plankton haul.

(16) *Protoperidinium claudicans* (Paulsen) Balech, 1974 (Pl. 5, Fig. 9-12)
Bas.: *Peridinium claudicans* Paulsen, 1907: 16, fig. 22a-d.

Cells pyriform, noticeably dorsoventrally compressed (width/height ratio 1.13-1.85), with epitheca drawn into apical horn. Ortho-penta. Cingulum planozone, descending, with 1.5 cingulum width offset. Plate 1' rhomboid, with nearly equal sides along the right margin and a longer proximal margin that distal one. Plate 2a is about twice as wide as long. The hypothecal pore is absent. Hypotheca is drawn into two high conical horns terminated with two strong spines; frequently the left spine is directed backward and the right one upward-backward. Length 85-102.5 µm (90.8±7.1 µm), width 52.5-67.5 µm (58.7±5.4 µm), height 31-51 µm (41.4±6.5 µm); n=12.
Plate 5. Fig. 1-4. Protoperidinium ovum. Fig. 5-8. P. sp. B ortho-quadra. Fig. 9-12. P. claudicans. Fig. 13-16. P. venustum.
Cysts (*Votadinium spinosum* P. C. Reid) heart-shaped (cordate) to pyriform, dorsoventrally compressed, with surface covered with numerous short-pointed spines. The antapical sulcus separates two broadly rounded asymmetric antapical lobes. The archeopyle is subrectangular or subpentagonal, intercalary, formed by the loss of the 2a paraplate, which is subapical in position. Length 47-76 µm, width 47-76 µm (Wall & Dale, 1968: 273, pl. 2, fig. 1, 2; Dodge, 1982: 182, fig. 20H; 1985: 45; Bolch & Hallegraeff, 1990).

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967; Steidinger & Williams, 1970** (according to these authors, the intergradations between *P. claudicans* and *P. oblongum* appear to be numerous); Zamudio-Reséndiz, 1998 (as *P. cf. claudicans*); Aquino-Cruz, 2002**; Tejeda-Hernández, 2005**.

(17) *Protoperidinium venustum* (Matzen.) Balech, 1974 (Pl. 5, Fig. 13-16)
Bas.: *Peridinium venustum* Matzen., 1933: 464, fig. 45a, b.

Cells elongated, strongly dorsoventrally compressed (width/height ratio 1.37-2.54), with slender apical horn not well-separated. Ortho-quadra. Cingulum planozone, descending, with one cingulum width offset. Plate 1' is symmetrical, with the proximal margins longest. Plate 2a is small, wider than long, about 1.3 times shorter than plate 4'. The hypothecal pore is absent. Hypotheca has two pointed horns. Length 80-95 µm (88.3±6.0 µm), width 48-72.5 µm (60.2±7.7 µm), height 25-53 µm (30.2±9.5 µm), L/W ratio 1.37-2.54; n=8.

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967 (as *Peridinium venustum/oblongum*); Steidinger & Williams, 1970** (furthermore, apparent intergradations between *P. venustum* and *P. oblongum* were observed); Zamudio-Reséndiz, 1998 (as *P. cf. venustum*); Licea et al., 2004a; Tejeda-Hernández, 2005**.

(18) *Protoperidinium depressum* (Bailey) Balech, 1974 (Pl. 6, Fig. 1-3)
Bas.: *Peridinium depressum* Bailey, 1854: 12, fig. 33, 34.

Cells elongated, with rounded or quadrangular body with slightly convex or almost straight margins of both epitheca and hypotheca. Ortho-quadra. Cingulum planozone, descending, with about 1.5-2.0 cingulum width offset (depends much on the angle of view). Plate 1' is rhomboid, symmetrical. Plates 2a and 4" are almost equal in length. Apical horn is conical, not separated. The hypothecal pore is absent. Antapical horns are conical, the right one being slightly larger, ending in short strong divergent spines. Length 132-165 µm (150.3±11.4 µm), width 102-135 µm (119.8±12.4 µm), height 78-102.5 µm (93.9±8.4 µm), L/W ratio 1.18-1.38; n=13.
Protoperidinium oceanicum (Vanhöffen) Balech, 1974 (Pl. 6, Fig. 4-7)
Bas.: Peridinium oceanicum Vanhöffen, 1897: pl. 5, fig. 2.
Nom. syn.: Peridinium divergens var. oceanicum Ostenf., 1899: 60.

Cells elongated, with quadrangular body, with more or less separated, slender apical horn. Ortho-quadra. Cingulum planozone, descending, with about 1.0-2.0 cingulum width offset. Plate 1' is rhomboid, symmetrical. Plate 2a and plate 4'' are nearly equal in length. The hypothecal pore is absent. Hypotheca has two antapical high, conical, slender horns ending in strong spines. Length 100-130 µm (120.2±10.4 µm), width 68-77 µm (72.5±3.3 µm), height 50-60 µm (52.4±4.3 µm), L/W ratio 1.64-1.79; n=6.

Localities: st. 4, 18 April 2006; st. 3, 20 February 2007, in plankton hauls.


Protoperidinium obtusum (G. Karst.) Parke et Dodge in Parke et Dixon, 1976 (Pl. 6, Fig. 8-10)
Bas.: Peridinium divergens var. obtusum G. Karst., 1906: 149, pl. 23, fig. 12-
Nom. syn.: Peridinium obtusum (G. Karst.) Fauré-Fremiet, 1908: 223.
Tax. syn.: Peridinium leonis f. matzenaueri J. Schill., 1937: 239, fig. 238a, b.

Cells quadrangular, with almost straight sides, with no apical horn. Ortho-quadra. Cingulum cavozone, descending, with 0.75-1.0 cingulum width offset, strongly inclined ventrally-antapically in relation to the longitudinal axis of the cell. Plate 1' is rhomboid, with the distal sides 1.5-2.0 longer than the proximal ones; distal sides are slightly or strongly concave toward the 1' plate anteriorly and straight or slightly convex posteriorly. Plate 2a is equal to plate 4'' in length. Precingular plates are characterized by a reticulation pattern tending to form longitudinal ridges. The hypothecal pore is absent. Hypotheca has two antapical low conical horns ending
in strong spines. Length 67.5-86 µm (75.2±5.7 µm), width 68-77 µm (66.4±5.1 µm), height 35-50 µm (42.9±5.9 µm); n=10.

Morphological note: Unlike Karsten (1906: 149, pl. 23, fig. 12; reproduced in Schiller, 1937: 240, fig. 241a, b), Balech (1949: pl. 3, fig. 42; 1988: pl. 28, fig. 4), Hermosilla (1973: pl. 15, fig. 5, 11, 12) and Dodge (1982: 188), who indicate exclusively the hexa-type of the 2a plate for *P. obtusum*, Okolodkov (2005) reported hexa, penta and quadra 2a plates in the specimens from the Mexican Pacific. However, while in the Pacific cells with the hexa 2a plate were the most common, in Veracruz waters only specimens with the quadra 2a plate have been found.

Nomenclatural note: As noted by Sournia (1990: 337), the combination *Protoperidinium obtusum* (G. Karst.) Balech, 1988 is invalid because it was published earlier by Parke & Dodge (1976: 545, 549).

Affinities: Elbrächter (1975) thoroughly compares *P. obtusum* with the closely related *P. marielebourae* (Paulsen) Balech, following Schiller (1937) who considers *Peridinium obtusum* Lebour, 1925 to be synonymous to *Peridinium marielebourae* Paulsen, 1930.

Gulf of Mexico: Legaría-Moreno, 2003 (as *P. aff. obtusum*).

(21) *Protoperidinium conicum* (Gran) Balech, 1974 (Pl. 6, Fig. 11-14)
Bas.: *Peridinium conicum* Gran, 1902: 185, 189, fig. 14.

Cells quadrangular, with no apical horn, noticeably dorsoventrally compressed. Ortho-hexa. Cingulum cavozone, circular, without offset. Plate l’ rhomboid, symmetrical, as wide as long. Plate 2a is trapezoid, with long proximal and very short distal lateral margins. The hypothecal pore is absent. Hypotheca is drawn into two high conical horns ending in very short spines. Length 52-100 µm (75.1±12.4 µm), width 45-83 µm (64.1±10.6 µm), height 30-58 µm (42.3±7.4 µm); n=23.

Cysts (*Multispinula quanta* Bradford ex Harland et P.C. Reid in Harland, P.C. Reid, Dobell et G. Norris, 1980; *Selenopemphix quanta* (Bradford) Matsuoka, 1985) ovoid to kidney-shaped, compressed anteroposteriorly, with a small truncated apical projection, smooth-walled, ornamented by several rows of moderately long needle-shaped spines. The cingulum is outlined by two rows of spines. The archeopyle is intercalary, elongated equatorially, subtrapezoidal with rounded angles, formed by the 2a paraplate, which is often attached. Length 28-52 µm, width 46-71 µm, height 37-49 µm (Wall & Dale, 1968: 273, pl. 2, fig. 4, 5; Dodge, 1982: 186, fig. 21G; 1985: 47; Bolch & Hallegraeff, 1990: 180, fig. 16a-c; Lewis & Dodge, 1990: fig. 6.36; Matthiessen, 1991: 33, pl. 3, fig. 2, 3; Nehring, 1994: fig. 1K).
Plate 6. Fig. 1-3. *Protoperidinium depressum*. Fig. 4-7. *P. oceanicum*. Fig. 8-10. *P. obtusum*. Fig. 11-14. *P. conicum*. 

(22) *Protoperidinium pentagonum* (Gran) Balech, 1974 (Pl. 7, Fig. 1 and 2)

Bas.: *Peridinium pentagonum* Gran, 1902: 185, 190, fig. 15.

Cells pentagonal, without apical horn, with the slightly convex epithea invaginated ventrally and the hypotheca with concave sides. Ortho-hexa. Cingulum strongly cavozone, circular, without offset. Plate 1' is widely rhomboid, with the right distal margin longest. Plate 2a is trapezoidal, equal to plate 4" in length, with much longer proximal sides compared to the distal ones. The hypotheca is drawn out into two short antapical horns ending in strong spines. Length 70-108 µm (91.3±19.4 µm), width 80-130 µm (104.3±25.0 µm), height 50-102 µm (71.5±27.1 µm); n=3.

Cysts (*Trinovantedinium applanatum* (Bradford, 1977) Bujak et Davies, 1983) pentagonal with broadly rounded antapical lobes separated by a shallow antapical sulcus, with a blunt apex, dorsoventrally compressed, covered with numerous spiniules 5-7 µm long which have minutely expanded or acuminate tips, colorless. The cingulum is excavated and fringed by low ridges bearing minute spines. The archeopyle is hexagonal, formed by the loss of the 2a and 4" paraplates. Length 54-96 µm (Wall & Dale, 1968: 274, pl. 2, fig. 9, 10; Dodge, 1982: 188, fig. 21L; 1985: 63; Lewis et al., 1984: 31, pl. 2, fig. 1, 5; Matthiessen, 1991: 41, pl. 3, fig. 1; Nehring, 1994: 144, fig. 3A, B; Rochon et al., 1999).

Localities: st. 4, 10 May 2005; st. 1, 6 July 2005, in plankton hauls.

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967; Steidinger & Williams, 1970**; Avendaño-Sánchez & Sotomayor-Navarro, 1982; Echeverría-Valencia, 1983*; Suchil-Vilchis, 1990 (although *Peridinium pentagonum* is given in the list on p. 70, a line drawing of a *Ceratium* sp. is presented under the name of the former); Zamudio-Reséndiz, 1998; Aquino-Cruz, 2002**; Licea et al., 2004a; Tejeda-Hernández, 2005** (as *Protoperidinium* sp. 4).

(23) *Protoperidinium divaricatum* (Meunier) Parke et J. D. Dodge, 1976 (Pl. 7, Fig. 3-6)

Bas.: *Peridinium divaricatum* Meunier, 1919: 48, pl. 19, fig. 55-58.

Cells quadrangular, with concave sides, with no apical horn. Ortho-hexa. Cingulum deeply cavozone, descending, with about 0.5-1.0 cingulum width offset. Plate 1' is rhomboid, symmetrical, with the proximal margins about twice as long as...
the distal ones. Plate 2a is trapezoidal, almost as long as plate 4" or up to 1.5 times longer, with very long proximal and very short distal lateral margins, sometimes almost neutra or even neutra in plate 2a. The hypothecal pore is absent. Hypotheca has two low conical horns ending in strong, very divergent spines, the right horn being slightly larger. The left spine is directed downward-backward and the right one upward-backward. Length 63-83 µm (71.6±6.8 µm), width 46-75 µm (64.3±9.9 µm), height 35-52 µm (46.7±6.0 µm); n=7.

Cysts (Xandarodinium xanthum P. C. Reid) ovoid or elliptical, smooth-walled, with hollow tubular processes terminating in simple solid spines or multifurcate solid tips, light-brown. The archeopyle is intercalary, formed by loss of a single paraplate. Diameter 46-63 µm (Bolch & Hallegraeff, 1990: 182, fig. 21; Rochon et al., 1999: 52, pl. 14, fig. 3, 4). Although most authors have reported the cyst-theca relationship between X. xanthum and P. divaricatum (Head, 1996), according to Rochon et al. (1999), the biological affinity of X. xanthum is unknown, but there is some similarity with the cyst of P. divaricatum.

A new record for the Gulf of Mexico.

(24) Protoperidinium cf. argentinense Balech, 1979 (Pl. 7, Fig. 7-11)

Cells almost quadrangular, with slightly convex sides, without apical horn. Ortho-hexa. Cingulum strongly cavozone, circular, without offset. Plate 1' has equally short proximal margins and long distal margins that are almost parallel in the middle part of the plate and strongly convex in its distal part; plate 1' is widest in its distal quarter. Intercalary plates are almost equal in size. Plate 2a is trapezoid, with long proximal and short distal lateral margins. The hypothecal pore is absent. Hypotheca with two noticeable sulcal lists. Length 35-40 µm (36.7±2.9 µm), width 28-37 µm (31.7±2.9 µm), height 25-26.5 µm (25.8±1.5 µm); n=3.

Locality: st. 7, 17 May 2005, in a plankton haul.

Affinities: The cells from PNSA V are strikingly similar to Peridinium achromaticum Levander in Abé (1927: 412, fig. 31A-F), so that I consider them belonging to the same species, but not to Protoperidinium achromaticum (Levander) Balech discussed in detail by Balech (1976). Also, the specimens from Veracruz are similar to P. argentinense in shape, size and cingulum. However, the former has three intercalary plates, which differentiates them from a group of morphologically similar species that includes P. argentinense, P. nux, P. thorianum and P. cf. thorianum from the Southern Hemisphere that have only two intercalaries (Balech, 1971b, 1973, 1979, 1988). The cells from Veracruz and the species of this group in general have a characteristic 1' plate with rounded distal margins on both sides, and the su-
Plate 7. Fig. 1 and 2. *Protoperidinium pentagonum*. Fig. 3-6. *P. divaricatum*. Fig. 7-11. *P. cf. argentinense* (in Fig. 8 arrowheads indicate two sulcal lists).
tures between 1" and 2' and between 7" and 4' are located closer to the apex than to the cingulum. As in *P. argentinense*, in the cells from Veracruz the cingulum is circular, with the ends not displaced. Both *P. thorianum* and *P. cf. thorianum* have the cingulum displaced 1.0-1.3 its width (Paulsen, 1905; Lebour, 1925; Balech, 1971b, 1973, 1988). The 1' plate is pentagonal, has a wide base, and it is widest just near the cingulum, unlike *P. argentinense*, *P. thorianum* and *P. cf. thorianum*. In its width, the sulcus is similar to that in *P. thorianum* but wider than in both *P. argentinense* and *P. cf. thorianum*. The studied cells are considerably smaller than *P. thorianum* or *P. cf. thorianum*. They are very similar in cell shape and size, cingulum and the 1' plate morphology to *Protoperidinium nux* (J. Schill.) Balech (=*Peridinium levanderi* T. H. Abé, 1927: 413, fig. 32); however, the latter has only two intercalary plates. To some extent, the examined cells are similar to *P. nudum* in size, plate pattern and cingulum morphology; however, the 1' plate in *P. nudum* is narrow rhomboid and is continuously tapering towards the cingulum.

A new record for the Gulf of Mexico.

(25) *Protoperidinium persicum* (J. Schill.) Okolodkov comb. nov. (Pl. 8, Fig. 1-4)

Cells quadrangular, without apical horn. Ortho-hexa. Cingulum strongly ca-vozone, circular, without offset. Plate 1' is widely rhomboid, symmetrical or almost symmetrical; its proximal and distal sides are almost equal to each other. Plate 2a is about twice as long as plate 4", with the proximal lateral margins twice as long as the distal ones. The hypothecal pore is absent. Antapical horns are in the form of a low cone or are absent, the left horn being larger so that the cell looks asymmetrical in ventral view. The surface of the theca is characteristically pimpled. Length 75-77 µm (76.0±1.4 µm), width 73-81.5 µm (77.3±6.0 µm), height 57-66 µm (61.5±6.4 µm); n=2.
Affinities: *P. persicum* is similar to *P. punctulatum* in the cell shape, plate pattern, position of the cingulum and ornamentation of theca; however, unlike *P. punctulatum*, in *P. persicum* the left antapical horn is larger and thus the cell in ventral view is asymmetrical.

Nomenclatural note: *Peridinium schilleri* Böhm, 1931 (9 June 1931) is a later homonym to *Peridinium schilleri* Paulsen, 1931 (3 March 1931), and therefore the former cannot be used as basionym; *Peridinium persicum* is the oldest available name. Under the current International Code of Botanical Nomenclature, the combination *Protoperidinium persicum* J. Schill., 1937 in Gómez (2005: 202) was not validly published; no citation of basionym is given (Art. 33.3; Greuter et al., 2000).

Locality: st. 1, 6 July 2005, in a plankton haul.

Gulf of Mexico: A new record for the state of Veracruz.

(26) *Protoperidinium cf. subinerme* (Paulsen) A. R. Loebl., 1969 (Pl. 8, Fig. 5-8)

Cells quadrangular, without apical horn; sometimes the apex is slightly drawn. Ortho-hexa. Cingulum strongly cavozone, circular, without offset. Plate 1' is rhomboid, symmetrical, its distal sides are 1.2-1.8 times longer than the proximal ones. Plate 2a is 1.3-1.6 times longer than plate 4", with the proximal lateral margins 1.4-1.2 times longer than the distal ones. The hypothecal pore is absent. No antapical horns, a low membrane posteriorly surrounding the sulcal area. The surface of the theca is faintly reticulated. Length 31-42.5 μm (37.3±4.2 μm), width 34-47.5 μm (40.8±4.2 μm), height 29-42.5 μm (34.5±4.5 μm); n=10.

Affinities: The cells from Veracruz are in good agreement with the original description and drawings of Balech (1988: 89, pl. 29, fig. 32-36) of *Protoperidinium* sp. aff. *P. subinerme*, which is, according to him, probably a new species. Not all the studied cells have the epitheca longer than the hypotheca, one of the important features of Balech’s species. The specimens from PNSAV satisfactorily correspond with the original description and illustrations by Paulsen (1904: 24, fig. 10a-d), who pictured it with the 2a plate of neutra type (most likely by mistake), but Paulsen’s cells are 1.5-2.0 times longer and have a wider 1’ plate. In addition, they are also similar to another ortho-hexa species, *P. vulgare* Balech. However, the latter has a rhomboid 1’ plate with nearly equal sides, and the cingulum is slightly ascending (Balech, 1988: 89, pl. 29, fig. 4-9). The specimens from Veracruz also resemble *P. parvicollum* (Balech) Balech (Balech, 1988: 91, pl. 29, fig. 17-21), a cold-water Antarctic species; however, the latter is larger and has a stronger reticulation of the thecal plates.

A new record for the Gulf of Mexico.
Plate 8. Fig. 1-4. *Protoperidinium persicum*. Fig. 5-8. *P. cf. subinerme*. 

Okolodkov: *Protoperidinium* (Dinophyceae) near Veracruz, Gulf of Mexico
(27) Protoperidinium sp. C ortho-hexa (Pl. 9, Fig. 1-5)

Cell ovoid, without apical horn, with the rounded hypotheca distinctively larger than the epitheca with slightly convex sides. Ortho-hexa. Cingulum strongly cavozone, descending, with 0.2 cingulum width offset. Plate 1' is regularly rhomboid with equal sides. Plate 2a is trapezoidal, about 1.5 times longer than 4'' plate, with much longer proximal lateral margins compared to distal ones. The hypothecal pore is absent. No antapical spines. The sulcal area is bordered with a continuous membrane from behind and laterally. Length 48 µm, width 40 µm, height 33 µm (n=1).

Locality: st. 6, 20 September 2005, in a plankton haul.

Affinities: No affinities have been found. Probably an undescribed species.

(28) Protoperidinium quarnerense (Schröder) Balech, 1974 (Pl. 9, Fig. 6-10)
Bas.: Peridinium globulus var. Stein, 1883: pl. 9, fig. 8; P. quarnerense Schröder, 1900: 18.

Cells subglobal, slightly compressed anteroposteriorly, with a short, well-separated apical horn. Meta-penta. Cingulum planozone, ascending, with 2.0 cingulum width offset, with their ends overhanging 1.3-1.5 cingulum width. Plate 1' is very asymmetrical, very wide, almost quadrangular, with the right distal and left proximal sides longest. Plate 2a is about 1.5-1.8 wider than long, about 1.5-2.0 times longer than plate 4''. The hypothecal pore is absent. Antapical spines are thin, slightly divergent. Length 27.5-60 µm (44.4±13.3 µm), total length 33-65 µm (49.9±13.2 µm), width 32-58.8 µm (46.1±11.9 µm), height 30-56.5 µm (41.5±12.1 µm); n=8.

Morphological note: The examined cells correspond well to the description and illustrations by Balech (1988: 112, pl. 45, fig. 5-7) and Dangeard (1927: 359, fig. 22), and are different from those of Balech (1976: 33, fig. 3a-d). In the latter, the cingulum offset is 1.0-1.5, and its ends are only slightly overlapping (although in Fig. 3a and b the overlap is not present at all).

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967 (as Peridinium globulus var. quarnerense); Steidinger & Williams, 1970** (as P. globulus var. quarnerense (Schröder). A new record for the southern Gulf of Mexico and the state of Veracruz.

(29) Protoperidinium sphaericum (J. Murray et Whitting) Balech, 1974 (Pl. 10, Fig. 1-8)
Bas.: Peridinium sphaericum J. Murray et Whitting, 1899: 328, pl. 30, fig. 1a, b; non Peridinium sphaericum Meunier, 1910: 36, pl. 1bis, fig. 29-31.
Plate 9. Fig. 1-5. *Protoperidinium* sp. C ortho-hexa (in Fig. 5 arrowheads indicate a continuous membrane). Fig. 6-10. *P. quarnerense*.
Cells globose, with a button-like apex. Meta-hexa. Cingulum planozone, ascending, with 1.5-2.5 cingulum width offset, with their ends overhanging 1.0-1.2 cingulum width. Plate 2a is 2.8-3.5 times longer than plate 4"; it is displaced to the left and contacts the 2' plate. Plate 3' is very small. The hypothecal pore is absent. Hypotheca bears two characteristic broad wings emerging from plates 1''' and 2'''', situated above the S.p. plate and forming an angle of about 50-55° between them. Length 48-70 µm (56.5±11.8 µm), width 46-68 µm (54.7±11.7 µm), height 43-67 µm (52.5±12.8 µm); n=3.

Morphological note: The specimens from Veracruz are very similar to detailed figures by Abé (1940: fig. 8, 10-13).

Affinities: *P. sphaericum* is very similar to *P. hamatum* Balech (1979: 43, pl. 8, fig. 174-180; 1988: 113, pl. 45, fig. 9-13) in cell shape, the morphology of cingulum and especially in the epithecal pattern. However, the latter has a right antapical spine (optional) and a prominent right sulcal list.


Gulf of Mexico: Avendaño-Sánchez & Sotomayor-Navarro, 1982 (as *Peridinium spheroides*). The species has been also found near the west African coast between 8°N and 25°N and in Japanese waters in Shimoda Bay (Dangeard, 1927; Abé, 1940).

(30) *Protoperidinium simulum* (Paulsen) Balech, 1974 (Pl. 11, Fig. 1-4)
Bas.: *Peridinium simulum* Paulsen, 1931: 58, fig. 30A, B.

Cells subglobose, significantly compressed anteroposteriorly, with a short, well-separated apical horn. Meta-quadra. Cingulum planozone, ascending, with 2.0 cingulum width offset, with their ends overhanging 1.3-1.4 cingulum width. Plate 1' is very asymmetrical, very wide, almost quadrangular, with the right distal side longest. Plate 2a is about twice as wide as long and about twice as long as plate 4". The hypothecal pore and antapical spines are absent. Length 50-57.5 µm (53.0±4.0 µm), width 61.5-78 µm (67-2±9.4 µm), height 57-68 µm (61.0±6.1 µm); n=3.

Nomenclatural note: *P. simulum* is very similar in shape and plate pattern to *Peridinium majus* P. A. Dang.; however, the latter has plate 2a of penta type. Considering the infraspecific variation in the type of plate 2a in some *Protoperidinium* species such as *P. ovatum* Pouchet, I consider it possible that *P. majus* may be
Plate 10. Fig. 1-8. *Protoperidinium sphaericum* (in Fig. 7 and 8 arrowheads indicate two wings).
synonymous to *P. simulum*. It is questionable if *Peridinium majus* of Abé (1940) is conspecific with *P. majus* of Dangeard (1927), because the latter does not present enough information about the cingulum.


**(31) Protoperidinium cf. cristatum** Balech, 1979 (Pl. 11, Fig. 5-8)

Cells globular, with a button-like apex. Meta-penta. Cingulum planozone, ascending, with 1.5 cingulum width offset and one cingulum width overhang. Plate 1' is asymmetrical, with the right distal margin longest. Plate 2a is equal to 4'' plate in length. The hypothecal pore is absent. No antapical spines. Length 40-41.5 µm (40.8±1.1 µm), width 40.0 µm, height 39-40 µm (39.5±0.7 µm); n=2.

Affinities: The studied species is similar to *P. cristatum* Balech, 1979 (41, pl. 9, fig. 181-187; 1988: 101, pl. 37, fig. 7-10); however, the latter has an optional left right antapical spine, the cell body is wider than long, and the cingulum ends slightly overhanging or not at all. Also, it is similar in the displacement of the cingulum and the cell shape to a number of species, such as *P. hamatum* Balech, *P. sphaeroides* and *P. simulum*.

Locality: st. 2, 10 February 2007, in a plankton haul.

A new record for the Gulf of Mexico.

**(32) Protoperidinium crassipes (Kof.)** Balech, 1974 (Pl. 12, Fig. 1-3)

Bas.: *Peridinium crassipes* Kof., 1907 (Univ. Calif. Publ. Zool. 3, 13): 309, pl. 31, fig. 46, 47.

Cells with quadrangular body, usually shorter than wide (length/width ratio 0.88-1.07), with a conical apical horn not well-separated, slightly or noticeably compressed dorsoventrally. Meta-quadra. Plate 1' is rhomboid, almost symmetrical. Plate 2a is about twice as long as plate 4''. Cingulum strongly cavozone, descending, with 1.0 cingulum width offset. The hypothecal pore is absent. Hypotheca has two low conical horns ending in strong divergent spines. Length 70-97 µm (82.9±8.7 µm), width 70-95 µm (84.6±7.0 µm), height 58-92 µm (72.9±8.3 µm); n=17.

Gulf of Mexico: Steidinger et al., 1967; Steidinger & Williams, 1970**; Zernova, 1974; Zernova & Krylov, 1974; Avendaño-Sánchez & Sotomayor-Navarro, 1982; López-Baluja et al., 1992; Aquino-Cruz, 2002**, Legaria-Moreno, 2003 (as *P. aff. crassipes*); Licea et al., 2004a, b**; Tejeda-Hernández, 2005* ** (also as *Protoperidinium* sp. 2).
Plate 11. Fig. 1-4. *Protoperidinium simulum*. Fig. 5-8. *P. cf. cristatum.*
(33) *Protoperidinium divergens* (Ehrenb.) Balech, 1974 (Pl. 12, Fig. 4-7)
Bas.: *Peridinium divergens* Ehrenb., 1841: 201.

Cell subglobular, with the epitheca drawn into a non-separated apical horn. Meta-quadra. Cingulum slightly cavozone, descending, with about 0.5-0.75 cingulum width offset. Plate 1' is rhomboid, almost symmetrical. Plates 2a and 4'' are almost equal in length. The hypothecal pore is absent. Hypotheca has two high conical horns ending in two short, strong spines. Length 56-75 µm (63.7±5.7 µm), width 43-55 µm (49.1±4.0 µm), height 32-50 µm (37.2±4.5 µm), L/W ratio 1.25-1.41; n=15.


(34) *Protoperidinium brochii* (Kof. et Swezy) Balech, 1974 (Pl. 12, Fig. 8 and 9)
Bas.: *Peridinium brochii* Kof. & Swezy, 1921: 183.

Cells irregularly pentagonal, with a tapered, non-separated apical horn. Meta-quadra. Cingulum planozone, ascending, with 0.5 cingulum width offset. Plate 1' is almost symmetrical. Plate 2a is trapezoid, about 1.5 times longer than plate 4''. Epitheca is larger than hypotheca. The hypothecal pore is absent. Hypotheca has two short conical horns ending in strong spines. Length 70-98 µm (81.9±9.0 µm), width 53.5-87 µm (65.7±8.8 µm), height 40-74 µm (50.8±9.8 µm), L/W ratio 1.13-1.29, in one case 1.41; n=13.

Gulf of Mexico: Balech, 1967; Steidinger et al., 1967 (identification is tentative); Aquino-Cruz, 2002**; Licea et al., 2004a; Tejeda-Hernández, 2005*.

(35) *Protoperidinium cristatum* Balech, 1979 (Pl. 12, Fig. 10-12)

Cells globular, with a button-like apex. Meta-penta. Cingulum planozone, ascending, with 1.75 cingulum width offset. Plate 1' is asymmetrical, with the right distal margin longest. Plate 2a is about 1.3 times longer than plate 4''. The hypothecal pore is absent. No antapical spines. There are two low membranes that form an angle of about 55-60° between them and are situated in plates 1'" and 2'"., on both sides of the S.p. plate. Length 75.0 µm, width 71.0 µm, height 67.5 µm (n=1).

Morphological note: The examined cell is slightly different from those illustrated by Balech, 1979 (41, pl. 9, fig. 181-187; 1988: 101, pl. 37, fig. 7-10) in being 1.5 times longer, in having a more globular cell shape, lacking any apical-antapical com-
Plate 12. Fig. 1-3. *Protoperidinium crassipes*. Fig. 4-7. *P. divergens*. Fig. 8 and 9. *P. brochii*. Fig. 10-12. *P. cristatum*. 
pression, and in having two antapical membranes similar to those in *P. sphaeroides* but lower. Despite that, I consider it as belonging to *P. cristatum*, because it fits the original description by Balech (1979) rather well.

Locality: st. 4, 13 February 2007, in a plankton haul.
A new record for the Gulf of Mexico.

(36) *Protoperidinium* sp. D meta-hexa (Pl. 13, Fig. 1-4)

Cells globular, with a button-like apex. Meta-hexa. Cingulum planozone, ascending, with 0.5 cingulum width offset. Plate 1' is asymmetrical, with the left proximal margin longest. Plate 2a twice as long as plate 4", more than twice as wide as long, with the proximal lateral margins slightly longer than the distal ones. The hypothecal pore is absent. The S.m. plate is well visible so that the species is reminiscent of those of the “Diplopsalis group”. Hypotheca has no spines, the left sulcal list is prominent as in the species of the “Diplopsalis group”. Length 47.5 µm, width 40.6 µm, height 38 µm (n=1).

Affinities. I failed to find morphologically similar taxa. Probably an undescribed species.

A new record for the Gulf of Mexico.

(37) *Protoperidinium curvipes* (Ostenf.) Balech, 1974 (Pl. 13, Fig. 5-8)

Cell globular, slightly pyriform, with a short button-like apical horn. Meta-quadra. Cingulum planozone, ascending, with one cingulum width offset. Plate 1' has the shape of a parallelogram with a cut left distal angle and a longer left proximal margin compared to the right one. Plate 2a is a trapezoid. Plate 4" is slightly longer than plate 2a. Plates 1a and 3a are pentagonal, slightly longer than precingular plates. The hypothecal pore is absent. One (right) antapical spine and a prominent left sulcal list bearing a pseudospine are present. Length 36.3 µm, total length 40 µm, width 35 µm, height 32.5 µm (n=1).

Morphological note: For this species, Balech (1988: 117) indicates plate 1' meta or para and plate 2a neutra, quadra, penta or hexa.

Affinities: Morphologically close to *P. subcurvipes* and *P. sphaeroideum*, but compared with the latter, the studied cell has a larger 2a plate and a slightly pyriform cell shape.

Locality: st. 4, 10 January 2006, in a plankton haul.
Plate 13. Fig. 1-4. *Protothecium* sp. D meta-hexa. Fig. 5-8. *P. curvipes*. Fig. 9-12. *P. pacificum* (in Fig. 10 arrowheads indicate two sulcal lists).
Gulf of Mexico: Steidinger et al., 1967 (identification is tentative); Steidinger & Williams, 1970 (identification is tentative). A new record for the southern Gulf of Mexico and the state of Veracruz.

(38) Protoperidinium pacificum (Kof. et J. R. Michener) Balech, 1974 (Pl. 13, Fig. 9-12)

Cell with slightly rounded sides, with a very short apex. Meta-quadra. Cingulum planozone, ascending, with 1.4 cingulum width offset. Plate 1' slightly asymmetrical, with the right distal side longest. Plate 2a trapezoidal, slightly longer than plate 4''. The hypothecal pore is absent. Two strong, slightly divergent antapical spines situated relatively close to each other, and two prominent sulcal lists, the left one being more pronounced. Length 51 µm, total length 57.5 µm, width 50 µm, height 41 µm (n=1).

Taxonomic note: According to Balech (1988: 107, pl. 40, fig. 13-18), it is not certain that Protoperidinium pacificum sensu Balech, 1974; Peridinium pacificum and Peridinium capdevillei are conspecific.

A new record for the Gulf of Mexico.

(39) Protoperidinium pyriforme (Paulsen) Balech, 1974 subsp. pyriforme (Pl. 14, Fig. 1-4)
Bas.: Peridinium steinii var. pyriformis Paulsen, 1905: 4, fig. 3d, e.
Nom. syn.: P. pyriforme Paulsen, 1907: 13, fig. 15.

Cells pyriform, with a short, well-separated apical horn. Meta-penta. Cingulum planozone, ascending, with 0.8-1.0 cingulum width offset. Plate 1' is asymmetrical, with the right distal side longest. Plate 2a is as long as plate 4'', slightly displaced to the left. The hypothecal pore is absent. Hypotheca has two strong, long, widely winged antapical spines. Length 47.5-52 µm (50.3±1.9 µm), total length 55-60 µm (58.6±2.2 µm), width 37.5-42 µm (39.5±1.8 µm), height 33.8-37.5 µm (36.0±1.6 µm); n=5.

Locality: st. 2, 6 February 2007, in a plankton haul.
Gulf of Mexico: Steidinger & Williams, 1970 (identification is incomplete); Zernova, 1974; López-Baluja et al., 1992. A new record for the southern Gulf of Mexico and the state of Veracruz.
(40) **Protoperidinium oviforme** (P. A. Dang.) Balech, 1974 (Pl. 14, Fig. 5-8)

Cells pyriform, with a rather well-separated, short apical horn. Meta-penta. Cingulum planozone, ascending, with about 0.5-1.0 cingulum width offset. Plate 1' is asymmetrical, with the right proximal side longest. Plate 2a is displaced to the left and is about equal to plate 4" in length. The hypothecal pore is absent. Hypotheca bears two divergent, long antapical spines. The sulcal list (the membrane along the left margin of S.d.) is prominent. Length 37.5-62.5 µm (50.1±6.6 µm), total length 52-80 µm (64.8±7.4 µm), width 29-47 µm (37.7±5.1 µm), height 29-45 µm (37.4±5.1 µm); n=11.

Gulf of Mexico: Balech, 1967; Aquino-Cruz, 2002**; Licea et al., 2004a. Most likely a new record for the state of Veracruz.

(41) **Protoperidinium cassum** (Balech) Balech, 1974 (Pl. 14, Fig. 9-12)

Cell pyriform, with an apical horn not well-separated. Meta-penta. Cingulum planozone, ascending, with 0.5-0.7 cingulum width offset. The 2a plate is small, with almost equal sides, and it is as long as plate 4". The hypothecal pore is absent. Antapical spines are long, slightly divergent and widely winged. Length 23-49 µm (37.5±7.6 µm), total length 31-62 µm (50.7±4.5 µm), width 17.5-41.3 µm (30.5±7.0 µm), height 17-35 µm (27.5±5.4 µm); n=8.

Taxonomic note: The examined cells are smaller than those described by Balech (1971b: 103; 1988: 95). Furthermore, they exhibit a combination of morphological features known for *P. cassum* var. *cassum* (Balech, 1971b: 103, pl. 19, fig. 333-341; 1988: 95, pl. 34, fig. 7-10) and var. *decens* Balech (Balech, 1971b: 105: pl. 20, fig. 342-348; 1988: 96, pl. 34, fig. 11-13), so I prefer not to differentiate between these two varieties.

Gulf of Mexico: Licea et al., 2004a. Most likely a new record for the state of Veracruz.

(42) **Protoperidinium sp. E meta-hexa** (Pl. 14, Fig. 13-16, Pl 15, Fig. 1)

Cells pyriform, with the hypotheca slightly compressed along the longitudinal axis, and a short, not well-separated apex, with a noticeable apical spine on the left side of the Po plate. Meta-hexa. Cingulum planozone or slightly cavozone,
Plate 14. Fig. 1-4. *Protoperidinium pyriforme* subsp. *pyriforme*. Fig. 5-8. *P. oviforme*. Fig. 9-12. *Protoperidinium cassum*. Fig. 13-16. *P. sp. E* meta-hexa (in Fig. 14 arrowheads indicate two sulcal lists).
ascending, with 0.8-0.9 cingulum width offset. Plate 1' is asymmetrical, with the right distal margin longest. Plate 2a is about 1.5 times as long as plate 4", with the proximal lateral margins 2.3-3.0 times longer than the distal ones. The hypothecal pore is present, situated in the median longitudinal line of plate 1"", a little closer to the cingulum than to the sulcus. Hypotheca is half the length of the epitheca, slightly depressed at the antapex, with two long, very divergent, thin spines, and two prominent sulcal lists (the left one being more prominent). The right spine is inclined to the dorsal side, and the left spine is situated noticeably closer to the ventral side of the cell. Length 37-47 µm (39.9±4.8 µm), total length 42.5-57.5 µm (49.3±6.2 µm), width 30-37 µm (32.0±3.4 µm), height 25-31.5 µm (27.7±3.4 µm); n=4.

Affinities: The studied cells are somewhat similar in shape to a number of species, such as *P. diabolus* (Cleve) Balech and *P. pellucidum* subsp. *stellatum* Balech; however, the latter two have the 1' plate of the para type (Balech, 1976: 43, fig. 7a-n; 1978: 188, pl. 9, fig. 227-241). A combination of peculiar features in the specimens from Veracruz (especially the appearance of the apical and antapical spines together with the epithecal tabulation) allows us to suggest that they belong to an undescribed species.

Localities: st. 1, 15 November 2005; st. 6, 25 April 2006, in plankton hauls.

(43) *Protoperidinium cf. hirobis* (T. H. Abé) Balech, 1974 (Pl. 15, Fig. 2-5)

Cells subpyriform-subglobular, with the hypotheca slightly compressed along the longitudinal axis, and a short, not well-separated apex. Meta-hexa. Cingulum planozone or slightly cavozone, ascending, with 0.5-0.75 cingulum width offset. Plate 1' is asymmetrical, with the right distal margin longest. Plate 2a is about 1.5-2 times longer than plate 4", with the proximal lateral margins 1.5-2 times longer than the distal ones. The hypothecal pore is present, situated closer to the proximal right angle of the plate 1"", in about equal distance from the cingulum and sulcus. Hypotheca with two comparatively long, thin spines, and a prominent left sulcal list. Length 25-41 µm (30.7±4.2 µm), total length 30-45 µm (35.4±3.9 µm), width 22.5-37.5 µm (27.6±4.0 µm), height 20-37 µm (24.4±4.5 µm); n=11.

Affinities: The examined cells of this very frequent species share many features with *P. hirobis* (T. H. Abé) Balech in Balech (1988: 103, pl. 38, fig. 12-17); however, they differ significantly from the original description and figures by Abé (1927: 399, fig. 18A-E). The cingulum offset in the specimens from Veracruz is as in Abé’s cells and more pronounced than in Balech’s cells.
Plate 15. Fig. 1. *Protoperidinium* sp. E meta-hexa (arrowhead indicates the hypothecal pore). Fig. 2–5. *P. cf. hirobis* (in Fig. 2 arrowhead indicates the hypothecal pore, in Fig. 3 arrowhead indicates the left sulcal list). Fig. 6. *P. oblongum* (cyst). Fig. 7. *P. cf. stellatum* (cyst). Fig. 8. *P. subinerme* (cyst).
Okolodkov. *Protoperidinium* (Dinophyceae) near Veracruz, Gulf of Mexico

Gulf of Mexico: *P. hirobis* was reported by Avendaño-Sánchez & Sotomayor-Navarro (1982). However, due to the absence of illustrations in their work, it is impossible to conclude if the cells from Veracruz are conspecific with theirs.

**CYSTS**

(44) *Protoperidinium oblongum* (Auriv.) Parke et Dodge in Parke et Dixon, 1976 (Pl. 15, Fig. 6)
Nom. syn.: *P. oblongum* M. Lebour, 1925: 121, pl. 24, fig. 1a-c; *Peridinium oceani-cum* var. *oblongum* (Auriv.) Paulsen, 1908: 55.

- Identified only by a resting cyst. Cyst is cordate, with broadly rounded antapical horns, smooth-walled, browish in color. The archeopyle was not observed. Length 70.0 µm, width 62.5 µm, height 44.0 µm (n=1).
- Taxonomic note: The studied cyst is similar to the third type of cyst of *P. oblongum* described and illustrated by Wall & Dale (1968: 272, pl. 1, fig. 26). Dodge (1985: 58) illustrated a cyst with the archeopyle of subtrapezoidal shape with rounded angles, most probably formed by the loss of the 2a paraplate. He also presented a schematical line drawing of a cyst with an ovoid archeopyle, transversally elongated (Dodge, 1982; Nehring, 1994: fig. 1Q).
- Locality: st. 4, 7 March 2006, in a plankton haul.
- Gulf of Mexico: Aquino-Cruz, 2002** (as cyst).

(45) *Protoperidinium cf. stellatum* (Wall in Wall et Dale) Balech, 1994 (Pl. 15, Fig. 7)
Bas.: *Peridinium stellatum* Wall in Wall et Dale, 1968: 275, pl. 2, fig. 13-15, pl. 3, fig. 16-21; non *Protoperidinium pellucidum* subsp. *stellatum* Balech, 1978: 188, pl. 9, fig. 227-241.

- Identified only by a resting cyst. Cyst stellate in ventral view, strongly dorso-ventrally compressed, with five slender spines, smooth-walled, browish in color. Hypotheca is slightly longer than epitheca. The archeopyle was not observed. Length 36 µm, width 33.5 µm (n=1).
- Morphological and nomenclatural note: The examined cyst is similar to the species designated as *Peridinium* sp. cf. *P. stellatum* (Wall & Dale, 1968: pl. 2, fig. 16). The specimen from Veracruz might belong to *Stelladinium reidii* Bradford,
which is a distinct and separate species from the cyst of *P. stellatum* (Rochon et al., 1999: 50; Martin J. Head, pers. comm., April 2007). Many authors assume *S. reidii* to be the cyst of *P. compressum* (Head, 1996: 1212), although there is no proof of it (Martin J. Head, pers. comm., April 2007). *Protoperidinium stellatum* (Wall in Wall et Dale) Head in Rochon, de Vernal, Turon, Matthiessen et Head, 1999: 48, pl. 11, fig. 11-13, is a later homonym of *Protoperidinium stellatum* (Wall in Wall et Dale) Balech, 1994, and therefore it is illegitimate (M. Head indicated a line drawing of a vegetative cell in ventral view in pl. 3, fig. 16 in Wall & Dale (1968) as holotype).


A new record for the Gulf of Mexico.

(46) *Protoperidinium subinerme* (Paulsen) A. R. Loebl., 1969 (Pl. 15, Fig. 8)
Bas.: *Peridinium subinermis* Paulsen, 1904: 24, fig. 10a-d.

Only a resting cyst was identified. Cyst (*Selenopemphix nephroides* Benedek, 1972, emend. Bujak in Bujak, Downie, Eaton et Williams, 1980) quadrangular in ventral view, smooth-walled, brownish in color. Paracingulum is broad, pre-median, excavated (cavozone), circular, without offset. Epicone is sharply rounded. Hypocone is 1.5 times longer than the epitheca, quadrangular and broadly rounded. The archeopyle was not observed. Length 46 µm, width 50 µm, height 47 µm (n=1). The cysts of *P. subinerme* are illustrated in Wall & Dale (1968), Dodge (1982: 189, fig. 21J; Lewis et al. (1984: 31, fig. 2l; with a hexagonal, trapezoidal archeopyle), Bolch & Hallegraeff (1990: 180, fig. 16a-c) and Rochon et al. (1999: 50, pl. 12, fig. 7-9).


Gulf of Mexico: Balech, 1967; Steidinger et al., 1967 (in both works, as vegetative cells).

ACKNOWLEDGMENTS

The hospitality and generosity of Guadalupe Campos-Bautista, responsible for the red-tide project at the Acuario de Veracruz, A.C., in providing samples and a space in her laboratory is very much appreciated. The Acuario de Veracruz is thanked in general for logistic support and laboratory facilities. Martin J. Head helped me with his advice concerning dinoflagellate cysts. Malte Elbrächter from Deutsches Zentrum für Marine Biodiversitätsforschung, Forschungsinstitut Senckenberg, Ger-
many, kindly revised the synonymy and gave valuable advice. Critical comments of two anonymous referees are very much appreciated. I am thankful to M.M. Gowing from the University of California at Santa Cruz, California, who kindly improved the writing style, and to Boris Okolodkov who prepared illustrations for publication. The financial support of PROMEP (Programa de Mejoramiento del Profesorado de Educación Superior), Mexico, (the project “Dinoflagelados del Parque Nacional Sistema Arrecifal Veracruzano”; UVER-PTC-144) in 2005-2006 is also appreciated.

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Recibido en mayo de 2007.

Aceptado en marzo de 2008.