Sergio Escobar-Morales and David U. Hernández-Becerril*

Free-living marine planktonic unarmoured dinoflagellates from the Gulf of Mexico and the Mexican Pacific

Abstract: The so-called unarmoured dinoflagellates are not a "natural" (phylogenetic) group but they lack thecal plates, share fragility and possess relatively few morphological characters that can be positively identified. This study depicts the species composition of unarmoured dinoflagellates collected from sites along the coasts of the Gulf of Mexico and the Mexican Pacific and includes their descriptions and illustrations. We identified a total of 25 species belonging to 13 genera and six families that were studied through various techniques using light and scanning electron microscopy. Seven new records for the Mexican Pacific are annotated here that include *Amphidinium flagelans* Schiller, *Gyrodinium cochlea* Lebour, *G. glaebum* Hulburt, *G. metum* Hulburt, *Karenia selliformis* Haywood, Steidinger *et* MacKenzie, *Karlodinium ballantinum* de Salas, and *K. veneficum* (Ballantine) Larsen. The genera *Karenia* and *Karlodinium* belong to the family Kareniaceae, characterised for encompassing the largest number of toxic species among the unarmoured dinoflagellates, and many species produce algal blooms around the world. *Ceratoperidinium falcatum* and *Levanderina fissa* are names recently proposed elsewhere as new taxonomic combinations and are also included here. The diversity of unarmoured dinoflagellates has been strongly underestimated in the past and the new records reported here confirm this. Further studies, including traditional and modern concepts and protocols (including molecular tools), should be undertaken in the near future to understand their real diversity.

Keywords: Gulf of Mexico; Mexican Pacific; new records; phytoplankton; unarmoured dinoflagellates.

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Introduction

Planktonic dinoflagellates are important components in the marine pelagic realm. There are two main groups of dinoflagellates: the thecate (or armoured) forms that have a series of relative rigid thecal plates of different sizes and shapes and the so-called unarmoured (or naked) forms that lack these structures and are in general more fragile. More recently, an intermediate group, the "thin-walled" dinoflagellates, has been recognised (Moestrup and Daugbjerg 2007). Nowadays, it is clear that although several orders of thecate dinoflagellates are considered monophyletic (Dinophysiales, Gonyaulacales, Prorocentrales, Suessiales and Syndiniales; Orr et al. 2012), the unarmoured species are not a "natural" group as they include species of different clades in a phylogenetic tree and belong to more than a single order (Gymnodiniales, Noctilucales, etc.; Daugbjerg et al. 2000) and for that reason they are considered a polyphyletic group (Orr et al. 2012).

Under certain circumstances unarmoured dinoflagellates, especially members of the Kareniaceae family (Bergholtz et al. 2005), may form important blooms (either toxic or harmful) in the coastal zones [as red tides or harmful algal blooms (HAB)] leading to disastrous consequences for the marine ecosystem, public health and economic activities (Zingone and Enevoldsen 2000). The species producing red tides have recently received more attention because their small sizes and delicate forms make it difficult to identify positive species (Siano et al. 2009). Systematic studies on unarmoured dinoflagellates mostly require living samples and particular techniques and protocols [use of scanning/transmission electron microscopy (SEM), molecular sequencing, etc.] due to their delicate forms and that is, in part, the main reason for the limited knowledge about them.

Identification of unarmoured dinoflagellates is based on a combination of various morphological features such

as size and shape of the cells, possible cingulum displacement, size, shape and position of nucleus, number, shape and colour of chloroplasts, presence of pyrenoids, presence of apical groove, ventral pore and possible surface structures (Larsen 2002, Bergholtz et al. 2005).

Unarmoured dinoflagellates in Mexican coasts have been cited in different papers: 8 genera with 19 species have been listed from the southern Gulf of Mexico (Licea et al. 2004), whereas 12 genera with 72 species were listed from the Mexican Pacific (Okolodkov and Gárate-Lizárraga 2006) and more recently Maciel-Baltazar and Hernández-Becerril (2013) provided descriptions and illustrations of 27 unarmoured dinoflagellate species from the southern Mexican Pacific. In the present study, the species composition and the characterisation of the unarmoured planktonic dinoflagellates from the locations in the southern Gulf of Mexico and the tropical Mexican Pacific are presented, especially the species forming blooms or/and red tides in certain locations.

Materials and methods

Study area

The Gulf of Mexico (Figure 1) is located in the subtropical region between 18° to 30°N and 82° to 98°W. It is a relatively large semienclosed basin which connects with the Atlantic Ocean and the Caribbean Sea by the Straits of Florida and the Yucatan Channel, respectively (Monreal-Gómez and Salas de León 1997). The Mexican
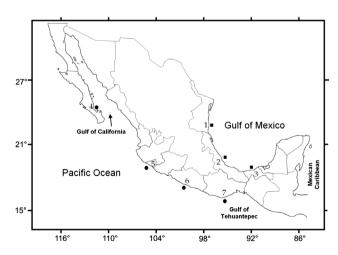
Pacific (Figure 1) is located between 15° to 32°N and 92° to 117°W, covering a coastline 4188 km in length. The study area is divided in seven subregions (Figure 1): (i) coasts of southern Tamaulipas (22°15′–25°52′N and 96°15′–97°47′W), (ii) coasts of middle Veracruz (18°45′–20°58′N and 95°40′–97°18′W), (iii) coasts of Tabasco (18°12′–18°26′N and 94°07′–93°05′W), (iv) southern Gulf of California (25°30′–21°30′N and 112°27′–109°25′W), (v) coasts of Colima (19°01′–19°07′N and 104°18′–104°27′W), (vi) coasts of Guerrero (20°30′–16°40′N and 108°20′–97°20′W) and (vii) coasts of Oaxaca (20°30′–16°40′N and 108°20′–97°20′W). All of these subregions and sites are important for the production of red tides where unarmoured dinoflagellates play a key role (Hernández-Becerril et al. 2007).

Sampling

The study was conducted during 2008–2010. Bottle samples (2 l) were taken at surface or subsurface (maximum 2 m) and then divided in two: one portion was preserved either with 1% Lugol's solution or 1% glutaraldehyde solution, whereas the other was kept alive and L1 culture medium (Guillard and Hargraves 1993) was added to it. Physicochemical features (temperature and salinity) were measured with a CTD (Seabird Co., Bellevue, Washington, USA). Some samples were taken under red tide conditions (especially in Manzanillo, Colima, Mexican Pacific and Tabasco, Gulf of Mexico).

Analysis

Living phytoplankton material was primarily observed *in vivo* with light microscopy [LM; Axiolab Zeiss (Jena, Germany) or Olympus BX40 (Mexico city, Mexico)] to observe general characteristics such as shape, size, swimming of cells, colour of chloroplasts and relative abundances. Preserved samples were also studied to search for certain details and for comparison with living material. Measurements of the specimens were based on our own observations. The number of organisms measured varied as it depended on the population densities of each species; however, the number is given for each species.

Studies by SEM (JEOL JMS 6360 LV, Tokio, Japan) required concentration of samples (1 l) by gravity filtration in a 0.45-µm pore filter and fixation with glutaraldehyde and osmium tetroxide (GTA–OsO$_4$) at final concentrations of 1.5% and 0.7%, respectively for 1 h (Truby 1997). After washing with distilled water, samples were dehydrated through a graduated ethanol series (30%, 40%, 50%, 70%, 90%, 95% and 100%) for 10 min. Thereafter, samples

Figure 1 Study area and sampling sites: (1) coast of south Tamaulipas, (2) coast of middle Veracruz, (3) coast of Tabasco, (4) southern Gulf of California, (5) coast of Colima, (6) coast of Guerrero, (7) coast of Oaxaca.

Table 1 List of unarmoured dinoflagellates found in the present study with their distribution in the seven sites (St1–St7) from both the Gulf of Mexico and the Mexican Pacific.

Species	Gulf of Mexico			Mexican Pacific			
	St1	St2	St3	St4	St5	St6	St7
Akashiwo sanguinea	X	X	X		X	X	X
Amphidinium flagelans[a]							X
Amphidinium globosum					X		
Cochlodinium polykrikoides					X	X	
Cochlodinium pulchellum						X	X
Gymnodinium catenatum				X	X		
Gymnodinium gracile				X			
Gyrodinium cochlea[a]					X		
Gyrodinium glaebum[a]					X		
Gyrodinium glaucum (= *Katodinium glaucum*)					X		
Gyrodinium metum[a]					X		
Gyrodinium spirale	X	X	X		X		
Levanderina fissa (= *Gyrodinium instriatum*)				X	X		
Polykrikos hartmannii				X			
Balechina coerulea (= *Gymnodinium coerulum*)					X	X	
Ceratoperidinium falcatum (= *Gyrodinium falcatum*)					X		
Karenia bicuneiformis					X		
Karenia brevis			X				
Karenia mikimotoi			X		X	X	X
Karenia selliformis[a]					X		
Karlodinium ballantinum[a]						X	
Karlodinium veneficum[a]						X	
Noctiluca scintillans	X	X		X	X		
Pronoctiluca pelagica					X		
Pronoctiluca spinifera					X		

[a]New species records for this region.

were critical point dried with ethanol-CO_2, and gold coated (Truby 1997, Botes et al. 2002) for observation in SEM.

Results

A total of 25 species have been identified for both the Gulf of Mexico and the Mexican Pacific areas. The geographical distribution of the species is given in Table 1. The classification follows Fensome et al. (1993) in general, also new additions proposed more recently elsewhere. Conspicuous synonyms, selected references, a short description and illustrations for each species are given below.

Class: Dinophyceae Pascher
Order: Gymnodiniales Apstein
Family: Gymnodiniaceae Lankester

Genus: *Akashiwo* Hansen *et* Moestrup
***Akashiwo sanguinea* (Hirasaka) Hansen *et* Moestrup (Figures 2 and 3)**
Basionym: *Gymnodinium sanguineum* Hirasaka
Synonyms: *Gymnodinium splendens* Lebour, *Gymnodinium nelsonii* Martin
References: Schiller (1933, p. 418, fig. 438), Steidinger and Tangen (1997, p. 451, pl. 19), Daugbjerg et al. (2000, p. 308), Faust and Gulledge (2002, p. 42, pl. 26, figs. 1–4), Hallegraeff et al. (2010, p. 146, fig. 4.2 A).
Medium-sized cell, pentagonal in shape and dorsoventrally flattened. Both epicone and hypocone are about the same length, cingulum is nearly equatorial. A ventral ridge is also present. Epicone is subconical and hypocone is truncated by the sulcus, forming two prominent lobes, and the apex shows a spiral apical groove in a clockwise direction. The nucleus is centrally located and there are several chloroplasts radiating from the centre. The size is variable, usually 45–65 μm in length and 35–40 μm in width. Ten specimens were measured.

Genus: *Amphidinium* Claparède *et* Lachmann
***Amphidinium flagelans* Schiller (Figure 4)**
Reference: Schiller (1933, p. 291, figs. 283a–b).
Solitary and elongate cell, 20 μm long and 10 μm wide. The reduced epicone has a subconical shape, which is approximately 1/5 of the total cell length and a conical hypocone with a prominent antapex, and surface striations are evident. Only one cell found and measured.

***Amphidinium globosum* Schröder (Figure 5)**
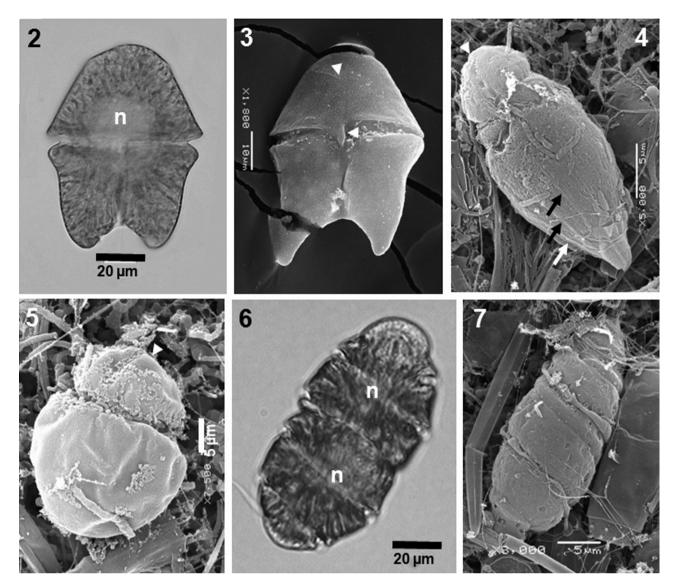References: Schiller (1933, p. 294, fig. 287a–b).
Solitary cell with a subspherical shape, 10 μm long and 9.5 μm wide. The epicone is reduced and semispherical, the cingulum is deeply excavated and the hypocone is globular. No ornaments are apparent in the thecal surface. One specimen encountered and measured.

Genus: *Cochlodinium* Schütt
***Cochlodinium polykrikoides* Margalef (Figure 6)**
Synonym: *Cochlodinium heterolobatum* Silva
References: Margalef (1961, p. 76, fig. 27m), Faust and Gulledge (2002, p. 21, pl. 9, figs. 1–7), Taylor et al. (2003, p. 394, fig. 15.4), Larsen and Nguyen (2004, p. 121, pl. 22, fig. 3), Matsuoka et al. (2008, p. 262, fig. 1).
Cells forming short- to medium-length chains, ellipsoidal in shape. Epicone is round to conical, the cingulum runs around the cell almost two times, the nucleus in some cells was located in the epicone, close to the apex, whereas in other cells it was centrally placed, and

Figures 2–7 Unarmoured dinoflagellates of the family Gymnodiniaceae, LM and SEM images. (2, 3) *Akashiwo sanguinea*, complete cell showing the central nucleus (n) and radiating peripheral chloroplasts, LM, and another cell with spiral-curved apical groove and ventral ridge (arrowheads), SEM. (4) *Amphidinium flagelans*, cell showing apical groove (arrowhead) and surface striae (arrows), SEM. (5) *Amphidinium globosum*, complete cell with reduced epicone and apical groove (arrowhead), SEM. (6) *Cochlodinium polykrikoides*, short chain of two cells, with the central nuclei (n) and elongated rod-like chloroplasts, LM. (7) *Cochlodinium pulchellum*, cell in dorsal view showing the cingulum turning and its flagellum, SEM.

numerous "rod-like" chloroplasts are present. Cells are 30–36 μm in length, 25–30 μm in width. Fifteen cells were measured.

Cochlodinium pulchellum Lebour (Figure 7)
References: Kofoid and Swezy (1921, p. 376, fig. HH-13), Schiller (1933, p. 534, figs. 564a–b), Maciel-Baltazar and Hernández-Becerril (2013, p. 249, fig. 2E).
Cells small and elongate, apparently solitary. The cingulum runs around the cell almost 2.5 times. Cells are 25 μm in length and 10 μm in width. One specimen found and measured.

Genus: *Gymnodinium* Stein *emend*. Hansen *et* Moestrup
Gymnodinium catenatum Graham (Figures 8 and 9)
References: Graham (1943, p. 259), Steidinger and Tangen (1997, p. 447, pl. 18), Faust and Gulledge (2002, p. 39, pl. 23, figs. 1–7), Larsen (2002, p. 150), Taylor et al. (2003, p. 394, fig. 15.5), Larsen and Nguyen (2004, p. 122, pl. 22, fig. 4).
Cells may form short to long chains and are irregular in shape from ellipsoidal to elongate, 45–50 μm in length and 25–35 μm in width. The rounded epicone has an apical groove in the shape of a horseshoe, the hypocone is straight towards the antapex and has a deeply excavated sulcus with intrusion into the epicone, the cingulum is

descending and deeply excavated with a displacement lower than 1/5 of the total cell length. A central nucleus and numerous brown chloroplasts are present. A total of 20 cells were measured.

Gymnodinium gracile Bergh (Figure 10)
Synonym: *Gymnodinium abbreviatum* Kofoid *et* Swezy
References: Kofoid and Swezy (1921, p. 165, fig. Z-3), Schiller (1933, p. 365, fig. 371), Hansen and Larsen (1992, p. 85, figs. 4.41 a–d, 4.43b), Steidinger and Tangen (1997, p. 446, pl. 19).
Solitary cells with an elongate to ovoid shape, 80–90 μm long and 30–36 μm wide. The epicone is rounded with
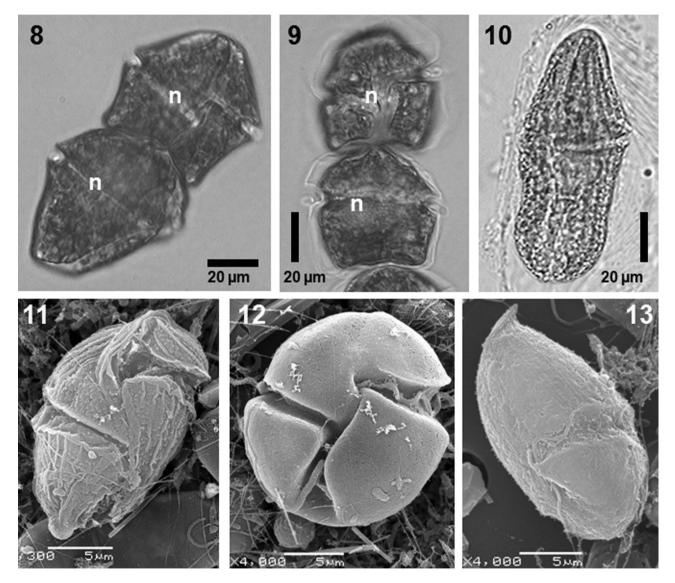
numerous longitudinal striae and the hypocone is somewhat irregular. The cingulum is moderately excavated and slightly displaced. Three specimens were measured.

Genus: *Gyrodinium* Kofoid *et* Swezy *emend*. Hansen *et* Moestrup
Gyrodinium cochlea Lebour (Figure 11)
References: Schiller (1933, p. 452, fig. 481).
Solitary, subspherical shaped, about 30 μm long and 15 μm wide. Epicone is slightly acute in the apex; hypocone has a subspherical shape with a lobed antapex process. The cingulum is deeply excavated, displaced more than 1/4 of the

Figures 8–13　Unarmoured dinoflagellates of the family Gymnodiniaceae, LM and SEM. (8, 9) *Gymnodiniun catenatum*, two cells in a short chain and details of a longer chain with the central nuclei (n) and the cingulum displaced, LM. (10) *Gymnodinium gracile*, complete cell with surface striations, LM. (11) *Gyrodinium cochlea*, cell in ventral view showing the great cingular displacement and surface striations, SEM. (12) *Gyrodinium glaebum*, cell in ventral view, with a descending cingulum and an open intrusion of the sulcus into the epicone, SEM. (13) *Gyrodinium glaucum*, complete cell in partial ventral view, showing pointed apex of the epicone and displaced cingulum, SEM.

total length of the cell; sulcus is deeply excavated, and it has an open intrusion into the epicone. Numerous surface striations are present. One complete cell was encountered and measured.

Gyrodinium glaebum Hulburt (Figure 12)

Reference: Hulburt (1957, p. 211, pl. 1, figs. 17–18).

Solitary cell, irregularly shaped, nearly circular, 18 µm long and 16 µm wide. The epicone is slightly hemispherical with the right side of the cell straight, the cingulum is downward, very excavated with a displacement around 1/5 of the total length of the cell. The hypocone is slightly wider and also has a deeply excavated and sigmoid sulcus with an open intrusion into the epicone. Only one specimen found and measured.

Gyrodinium glaucum (Lebour) Kofoid *et* Swezy (Figure 13)

Synonyms: *Spirodinium glaucum* Lebour, *Massartia glauca* (Lebour) Schiller, *Katodinium glaucum* (Lebour) Loeblich III
References: Kofoid and Swezy (1921, p. 556, pl. 9, fig. 94), Ojeda (2005, p. 80, pl. 14, fig. 3).

Cell solitary, fusiform and small, 21–25 µm in length and 10–13 µm in width. Epicone is larger than the hypocone, and has a pointed and slightly twisted apex. Wide cingulum, displaced about three times its width. Longitudinal striae are present in the cell surface. Three specimens were measured.

Gyrodinium metum Hulburt (Figure 14)

Reference: Hulburt (1957, p. 211, pl. 1, figs. 11, 12).

Solitary cell, 17.9 µm long and 14.8 µm wide with the hypocone larger than the epicone and the cingulum slightly excavated displaced about 1/4 or less of the total cell length of the cell. Epicone is conical and has one slit on the top and hypocone is more rounded. One cell was found and measured.

Gyrodinium spirale (Bergh) Kofoid *et* Swezy (Figure 15)

Basionym: *Gymnodinium spirale* Bergh
Synonym: *Spirodinium spirale* Entz
References: Kofoid and Swezy (1921, p. 275, fig. DD-14), Schiller (1933, p. 498, figs. 530a–e), Hansen and Larsen (1992, p. 82, figs. 4.38a–c, 4.43c), Steidinger and Tangen (1997, p. 453, pl. 20).

Solitary, fusiform cell, 100–120 µm in length and 25–35 µm in width. A descending cingulum, very displaced, about 1/4 of the total cell length is characteristic of the species. The nucleus is adjacent to the intercingular region and there are numerous food vacuoles and evident surface striations in the amphiesma. Five specimens were measured.

Genus: *Levanderina* Moestrup, Hakanen, Hansen, Daugbjerg *et* Ellegaard

Levanderina fissa (Levander) Moestrup, Hakanen, Hansen, Daugbjerg *et* Ellegaard (Figures 16 and 17)

Basionym: *Gymnodinium fissum* Levander
Synonyms: *Gyrodinium pavillardii* Biecheler, *Gyrodinium uncatenum* Hulburt, *G. uncatenum* (Hulburt) Hallegraeff, *Gyrodinium instriatum* Freudenthal *et* Lee, *G. instriatum* (Freudenthal *et* Lee) Coats
References: Steidinger and Tangen (1997, p. 452, pls. 1, 19), Moestrup et al. (2014, p. 272, figs. 1–25).

Solitary cells with a nearly rounded to hexagonal shape, 47–50 µm in length, 30–38 µm in width. The epicone is trapezoidal, the cingulum is considerably displaced (with an inverted "Z" shape) and is deeply excavated, and the hypocone is more rounded with two short lobes. There is a central nucleus and numerous disc-shaped brown chloroplasts. Fifteen specimens were measured.

Genus: *Polykrikos* Bütschli

Polykrikos hartmannii Zimmermann (Figure 18)

Synonym: *Pheopolykrikos hartmannii* (Zimmermann) Matsuoka *et* Fukuyo
References: Hulburt (1957, p. 215, pl. 4, fig. 7), Matsuoka and Fukuyo (1986, p. 812, figs. 8–10), Steidinger and Tangen (1997, p. 457, pl. 21), Tang et al. (2013, p. 1086, figs. 1 A–B, 2 A–F).

Pseudocolonial species, cells of 90–100 µm in length and 35–40 µm in width. Two cells (zooids), the posterior zooid is slightly rounded in the antapex, whereas the anterior zooid is straight in the apex. The cingulum is extremely displaced. There are two nuclei, each located in the intercingular region, and numerous small chloroplasts of brown-greenish, yellow colour. Four cells were measured.
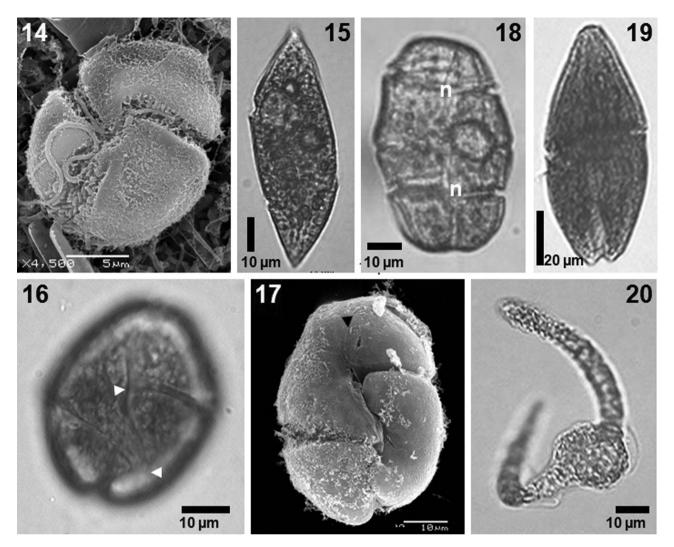
Family: Ptychodiscaceae (Schütt) Lemmermann
Genus: *Balechina* Loeblich Jr. *et* Loeblich III
Balechina coerulea (Dogiel) Taylor (Figure 19)

Basionym: *Gymnodinium coerulum* Dogiel
References: Kofoid and Swezy (1921, p. 165, fig. Z-4), Schiller (1933, p. 344, figs. 349 a, b), Taylor (1976, pl. 37, fig. 443, pl. 40, fig. 481), Steidinger and Tangen (1997, p. 461, pl. 22).

Solitary cells with an oval shape, 80–90 µm long and 35–40 µm wide. The conical epicone is slightly shorter than the hypocone that ends in two short lobes; the cingulum is descending, moderately excavated. There are numerous food vacuoles distributed irregularly in the whole cell, surface striations and blue granules. Ten specimens were measured.

Figures 14–20 Unarmoured dinoflagellates, LM and SEM. (14) *Gyrodinium metum*, cell in ventral view showing its conical epicone, SEM. (15) *Gyrodinium spirale*, typical Lugol-fixed cell, LM. (16, 17) *Levanderina fissa*, cell showing cingular displacement (arrowheads), LM, and another cell with horseshoe-shaped apical groove (arrowhead), SEM. (18) *Polykrikos hartmanii*, two-zooid pseudocolony with two nuclei (n), LM. (19) *Balechina coerulea*, cell in dorsal view, LM. (20) *Ceratoperidinium falcatum*, one-cell stage of the life cycle, LM.

Family: Ceratoperidiniaceae Loeblich III *emend*. Reñé *et* de Salas
Genus: *Ceratoperidinium* Loeblich III *emend*. Reñé *et* de Salas
***Ceratoperidinium falcatum* (Kofoid *et* Swezy) Reñé *et* de Salas (Figure 20)**
Basionym: *Gyrodinium falcatum* Kofoid *et* Swezy
Synonym: *Pseliodinium vaubanii* Sournia
References: Kofoid and Swezy (1921, p. 229, fig. CC-11), Schiller (1933, p. 460, figs. 490a–b), Gómez (2007, p. 176, figs. 16–19), Reñé et al. (2013, p. 678, figs. 4 D–E).
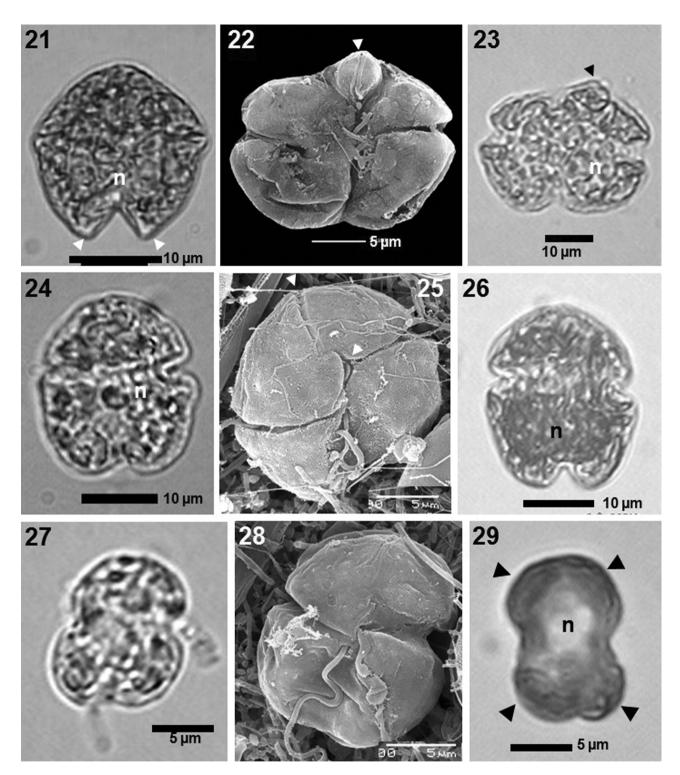Solitary, fusiform to acute cells, 40–60 μm long and 17–25 μm wide. Epicone and hypocone are about the same proportion with a very displaced, descending cingulum (more than 1/5 of the total cell length). Longitudinal surface striations occur in the cells (in some stages of the life cycle). Twelve cells were measured.

Family: Kareniaceae Bergholtz et al.
Genus: *Karenia* G. Hansen *et* Moestrup
***Karenia bicuneiformis* Botes, Sym *et* Pitcher (Figure 21)**
Synonym: *Karenia bidigitata* Haywood *et* Steidinger
References: Botes et al. (2003, p. 566, figs. 10–19), Haywood et al. (2004, p. 172, figs. 5 a–e), Hallegraeff et al. (2010, p. 158, figs. 4.4 C–D).
Solitary cells of rhomboid shape, strongly flattened dorsoventrally, 20–22 μm in length, 18–19 μm in width. The epicone has a triangular shape, the cingulum is deeply excavated and the hypocone is truncated with two prominent conical lobes. A central nucleus and several

Figures 21–29 Unarmoured dinoflagellates of the family Kareniaceae, LM and SEM. (21) *Karenia bicuneiformis*, cell in ventral view with the characteristic two lobes on the hypocone (arrowheads) and the nucleus (n), LM. (22, 23) *Karenia brevis*, cell in ventral view, shows the characteristic apical carina with a straight apical groove (arrowhead), SEM and another cell with the carina (arrowhead) and position of nucleus (n), LM. (24, 25) *Karenia mikimotoi*, complete cell, showing position of nucleus (n), LM, and another cell in ventral view, with straight apical groove and right-deflected sulcal insertion into the epicone (arrowheads), SEM. (26) *Karenia selliformis*, Lugol-fixed cell, showing a reniform nucleus (n), horizontally located in the hypocone, LM. (27, 28) *Karlodinium ballantinum*, cell with several small chloroplasts, LM, and another cell in ventral view, SEM. (29) *Karlodinium veneficum*, living cell with four chloroplasts (arrowheads) and the nucleus (n), LM.

greenish chloroplasts are present in the cell. Four cells were measured.

Karenia brevis (Davis) Hansen *et* Moestrup (Figures 22 and 23)

Basionym: *Gymnodinium breve* Davis

Synonym: *Ptycodischus brevis* (Davis) Steidinger

References: Steidinger and Tangen (1997, p. 447, pl. 18), Faust and Gulledge (2002, p. 37, pl. 22, figs. 1–4), Taylor et al. (2003, p. 395, fig. 15.7), Haywood et al. (2004, p. 172, figs. 1a–b).

Solitary cells of ellipsoidal form and flattened dorsoventrally, 16–25 µm in length and 18–36 µm in width. The epicone is subconical with a prominent apical process (carina) showing a straight apical groove which continues towards the dorsal part; the descending cingulum is moderately excavated and is slightly displaced. The sulcus is moderately excavated with an open insertion into the epicone. The hypocone has a bilobed form as a consequence of the sulcus excavation. The rounded nucleus is located in the left margin of the hypocone. There are numerous greenish chloroplasts of irregular form distributed all over the cell. Twenty cells were measured.

Karenia mikimotoi (Miyake *et* Kominami *ex* Oda) Hansen *et* Moestrup (Figures 24 and 25)

Basionym: *Gymnodinium mikimotoi* Miyake *et* Kominami *ex* Oda

Synonym: *Gymnodinium nagasakiense* Takayama *et* Adachi.

References: Steidinger and Tangen (1997, p. 449, pls. 1, 18), Faust and Gulledge (2002, p. 40, pl. 24, figs. 1–7), Taylor et al. (2003, p. 396, fig. 15.8), Larsen and Nguyen (2004, p. 123, pl. 22, fig. 5), Hallegraeff et al. (2010, p. 159, figs. 4.3 D–F).

Solitary cells, pentagonal to rounded, flattened dorsoventrally, 18–25 µm long and 22–30 µm wide. The epicone is rounded with a straight apical groove in the apex and the hypocone is bilobed. The cingulum is displaced about two times its width. Numerous greenish chloroplasts are present in the cell. Five specimens were measured.

Karenia selliformis Haywood, Steidinger *et* MacKenzie (Figure 26)

References: Haywood et al. (2004, p. 170, figs. 4a–j), Hallegraeff et al. (2010, p. 159, figs. 4.4 A–B).

Solitary and rounded cells, dorsoventrally flattened (moderately), 22–24 µm long and 18–19 µm wide. The epicone is subspherical with a straight apical groove in the apex; the cingulum is moderately excavated as well as the sulcus. The hypocone is slightly asymmetrical due to the discontinuity of truncated lobes by the sulcus. The nucleus is elongated and nearly reniform, and is horizontally located in the hypocone, and numerous lobed green-yellow chloroplasts are present in the cell. Three specimens were measured.

Genus: *Karlodinium* Larsen
Karlodinium ballantinum de Salas (Figures 27 and 28)

References: de Salas et al. (2008, p. 247, figs. 5 E–G, 11 C), Siano et al. (2009, p. 49, figs. 14–18), Hallegraeff et al. (2010, p. 160, figs. 4.5 A–C).

Cells are of minute size, usually 12–15 µm in length. The cells are oval in shape and rather asymmetrical in the hypocone. They show a straight oblique apical groove and absence of ventral pore. The nucleus is centrally located and there are more than eight chloroplasts. Three cells were measured.

Karlodinium veneficum (Ballantine) Larsen (Figure 29)

Basionym: *Gymnodinium veneficum* Ballantine

Synonym: *Gymnodinium galatheanum* Braarud

References: Bergholtz et al. (2005, p. 184, fig. 13), de Salas (2008, p. 253, fig. 11e), Siano et al. (2009, p. 50, figs. 19–23), Hallegraeff et al. (2010, p. 161, figs. 4.5 D–F).

Solitary cells, small in size, 8–12 µm in length. The cell has a bilobed shape with an epicone slightly longer than the hypocone. Four elongate, yellow-brownish chloroplasts are present often with an orange stigma and also a pyrenoid. Nucleus is central or located in the left side of the hypocone. Ten specimens were measured.
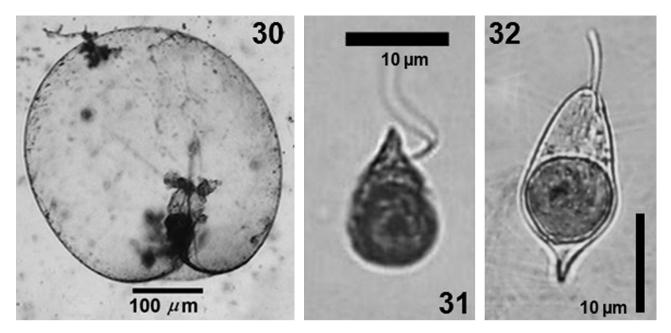
Class: Noctiluciphyceae Fensome et al.
Order: Noctilucales Haeckel
Family: Noctilucaceae Saville-Kent
Genus: *Noctiluca* Suriray *in* Lamarck
Noctiluca scintillans (Macartney) Kofoid (Figure 30)

Basionym: *Medusa scintillans* Macartney

Synonym: *Noctiluca miliaris* Suriray *ex* Lamarck

References: Kofoid and Swezy (1921, p. 406, figs. KK1-6), Schiller (1933, p. 553, figs. 582a, b), Taylor (1976, pl. 39, figs. 478, 479), Steidinger and Tangen (1997, p. 466, pl. 23), Faust and Gulledge (2002, p. 46, pl. 30, figs. 1–4), Taylor et al. (2003, p. 398, fig. 15.11), Larsen and Nguyen (2004, p. 124, pl. 23, figs. 1–3).

Solitary cells of spherical to subspherical shape, variable in size but generally large (usually larger than 300 µm and up to 2000 µm in diameter), inflated with a ventral groove, deep and wide, and having a tentacle in the posterior region. As it is a heterotrophic and phagotrophic form, sometimes food vacuoles are found distributed in the whole cell. Ten cells were measured.

Figures 30–32 Noctilucoid unarmoured dinoflagellates, LM. (30) *Noctiluca scintillans*, typical globular cell. (31) *Pronoctiluca pelagica*, cell showing the large nucleus and one anteriorly inserted flagellum. (32) *Pronoctiluca spinifera*, cell with anterior tentacle and spine-like structure at the antapex.

Class: *Insertae sedis*
Family: Protodiniferaceae Kofoid *et* Swezy
Genus: *Pronoctiluca* Fabre-Domergue
***Pronoctiluca pelagica* Fabre-Domergue (Figure 31)**
Synonym: *Rhynchomonas marina* Lohmann
References: Schiller (1933, p. 268, figs. 258a–i), Taylor (1976, pl. 37, figs. 426–428), Gómez (2013, p. 72, figs. 2 s–y). Cells found solitary, rather small, with a tear shape, 12–14 μm in length and 9–10 μm in width. Cells are acute in the apex and rounded in the antapex. A nucleus of considerable size is at the bottom of the cell, and there are two flagella inserted in the apex. Two cells were measured.

***Pronoctiluca spinifera* (Lohmann) Schiller (Figure 32)**
Synonym: *Protodinifer tentaculata* Kofoid *et* Swezy
References: Schiller (1933, p. 270, figs. 259a–d), Taylor (1976, pl. 37, fig. 429), Gómez (2013, p. 72, figs. 2 a–j).
Solitary cells with a subconical shape, 20–22 μm in length and 10–12 μm in width. The apex is narrow and acute with a tentacle and the flagella are inserted in this area. Close to the antapex, the cell becomes wider and develops a spine-like structure. The nucleus is large and round. Several vacuoles are present. Two cells were measured.

Discussion

Morphology and taxonomy

Unarmoured dinoflagellates have become an important research subject because they are one of the main sources of HAB. They encompass the more delicate, fragile and evasive portion, and one of the least-studied components of the marine phytoplankton. Very often their study includes observation of living specimens with an increasing use of cultures as fixatives that destroy or deform some structures, such as the apical grooves, that may be diagnostic characters (Takayama 1985, Bergholtz et al. 2005). The use of specialised modern methods of collection and study has yielded a better knowledge of their morphology, taxonomy and phylogeny (Daugbjerg et al. 2000, Bergholtz et al. 2005, Garcés et al. 2006, Moestrup et al. 2014).

Many of the unarmoured forms were described in the late 1800s and early 1900s, considering a basic and traditional taxonomy; however, recently many changes and proposals have been made concerning these groups including the genera *Gymnodinium* and *Gyrodinium* and the description of about 18 new species of the genera *Karenia*, *Karlodinium* and *Takayama* de Salas, Bolch,

Botes *et* Hallegraeff (Botes et al. 2003, de Salas et al. 2003, 2004a,b, Chang and Ryan 2004, Haywood et al. 2004, Bergholtz et al. 2005), six of them very recently (de Salas et al. 2008), and several reported as ichthyotoxic. In addition, new genera (e.g., *Levanderina*) or new species allocations (e.g., *C. falcatum*) have been proposed (Reñé et al. 2013, Moestrup et al. 2014).

Several authors agree on the use of a set of morphological characters for identifying unarmoured dinoflagellates to the specific level; among these are the shape, the size, the possible presence, flattening or twisting of the cell surface structures (apical grooves, ventral pores), the shape and relative location of the nucleus, and the presence, location, shape and colour of the chloroplasts (Daugbjerg et al. 2000, Larsen 2002, Flø Jørgensen et al. 2004).

Morphological characters such as the cingulum displacement had been traditionally considered important to separate species of the genera *Gymnodinium* and *Gyrodinium*, proposed to be 1/5 of total cell length for *Gymnodinium* and exceeding this proportion for *Gyrodinium* (Steidinger and Tangen 1997); however, this feature has been more recently recognised as a character which is not suitable for generic separation (Bolch et al. 1999). Members of the genus *Gymnodinium sensu stricto* possess a horseshoe-shaped apical groove, although this character is not always visible with LM (Daugbjerg et al. 2000).

The traditional distinction of the genus *Amphidinium*, based on the character of a reduced epicone, has been slightly modified to consider the epicone to be 1/3 or less of the total cell length (Steidinger and Tangen 1997), although more recently the epicone morphology (e.g., minute, triangular or left-deflected) is an additional character for the genus (Flø Jørgensen et al. 2004). In that sense, the species recognised in this work, *A. flagelans* and *A. globosum*, could be considered as *Amphidinium* species *sensu lato*.

Members of the genus *Cochlodinium* differ in shape, size, cingulum rotation, the presence of striations and presence/absence of chloroplasts and eyespots (Steidinger and Tangen 1997). As in long-chain-forming Gymnodiniales species, *C. polykrikoides* cells show variability. The formation of chains implies that the terminal cells are morphologically distinct from the inner cells (Larsen 2002, Matsuoka et al. 2008); these chains usually consist of two to eight cells, and exceptionally up to 16 cells (Margalef 1961, Matsuoka et al. 2008).

The species *G. cochlea* and *G. spirale*, recognised in this study have a cingular displacement exceeding 1/5 of the total length of the cell, and also fine longitudinal striations corresponding to what "traditionally" is recognised as characteristic of *Gyrodinium*. In contrast, the species *G. glaebum* and *G. metum* lack longitudinal stripes or furrows, as well as an elliptical apical groove. Both species (here studied by SEM) were previously described by Hulburt (1957), who depicted only the cingular displacement and a slightly sigmoid sulcus for both species. The species *G. cochlea*, *G. glaebum* and *G. metum* are new records for the Mexican Pacific.

Tang et al. (2013) provided some evidence for using the name *Pheopolykrikos hartmannii*, instead of *Polykrikos hartmannii*, including the presence of chloroplasts and the molecular phylogenies. However, the type species of the genus *Pheopolykrikos* Chatton, *P. beauchampii* Chatton, distantly clade from *P. hartmanii* in molecular phylogenies in Hoppenrath and Leander (2007) and Tang et al. (2013). In addition, Hoppenrath et al. (2010) showed some ultrastructural characters of the species that relate it more with *Polykrikos* species. Therefore, we use the name *Polykrikos hartmanii* instead *Pheopolykrikos hartmanii*. A closely related species, in terms of morphology (including presence of chloroplasts) and molecular phylogeny, is the newly described species *Polykrikos tanit* Reñé, although the latter is smaller and has a characteristic peduncle, absent in *Pheopolykrikos hartmannii* (Reñé et al. 2014).

Karenia species may be morphologically highly variable, but are mostly flattened dorsoventrally (noticeably in the species *K. bicuneiformis*), regularly elliptical or pentagonal in shape, with a straight apical groove, and some possess an apical process called a carina (Botes et al. 2003, de Salas et al. 2004a,b, Haywood et al. 2004, Steidinger et al. 2008); some authors claim that specific features, such as the morphology of the apical carina and the sulcus intrusion in the epicone, help to differentiate some species (Haywood et al. 2004, Steidinger et al. 2008). *K. selliformis* shows a hypocone slightly larger than the epicone, the right lobe of hypocone is slightly larger than the left one, and also the reniform nucleus is horizontally located in the hypocone (Figure 25). Most species of *Karenia* have been described only recently and therefore we are still recognising the diversity and distribution patterns of its species.

Regarding the genus *Karlodinium*, cell shape and size, and the number of chloroplasts are important morphological characters considered to distinguish species. The two species found in this study were recognised on the basis of those characters: *K. ballantinum* has more than eight chloroplasts, whereas *K. veneficum* has only four (Bergholtz et al. 2005, Garcés et al. 2006, de Salas et al. 2008, Siano et al. 2009).

Finally, the two species of *Pronoctiluca* detected in this work, *P. pelagica* and *P. spinifera*, although apparently two separate species, have been found with intermediate forms, suggesting different stages of one species (Gómez 2013). This has to be dealt with in detail, considering molecular sequences.

Diversity

We identified a total of 25 species belonging to 13 genera and 6 families in phytoplanktonic material from seven sites, three in the Gulf of Mexico and four in the Mexican Pacific (Figure 1 and Table 1). New records for the Mexican Pacific are annotated here and include the species *A. flagelans*, *G. cochlea*, *G. glaebum*, *G. metum*, *K. selliformis*, *K. ballantinum* and *K. veneficum* (Table 1). Also, new names recently proposed by other authors (Reñé et al. 2013, Moestrup et al. 2014), *C. falcatum* and *L. fissa*, were incorporated in this study to replace traditional names used historically. *G. glaucum* has been extensively recorded as *K. glaucum* by several authors (Okolodkov and Gárate-Lizárraga 2006).

A recent study of unarmoured dinoflagellates from the southern Mexican Pacific (Maciel-Baltazar and Hernández-Becerril 2013) annotated some new records including species of *Karenia* such as *K. bicuneiformis* and *K. papilionacea* (not found in our study).

From the species studied here, those considered harmful either forming red tides (at least in Mexican waters) or being toxic (in Mexico and elsewhere) are *A. sanguinea*, *C. polykrikoides*, *G. catenatum*, *L. fissa* (= *Gyrodinium instriatum*), *N. scintillans* (Hernández-Becerril et al. 2007). In addition, various *Karenia* species have been observed to cause red tides in Mexican coasts, whereas *Karlodinium* species have been extremely poorly studied.

Because of its characteristic size and shape and the nature of the red tides it forms (colour and extent), especially in the Mexican Pacific (e.g., Gulf of California and Banderas Bay), *N. scintillans* is the best-known unarmoured dinoflagellate in both Mexican littoral regions. The species has been found with numerous complete "food cells", some of which were identified as *G. catenatum*, which suggests that it may regulate some potentially toxic red tides (Alonso-Rodríguez et al. 2005).

The diversity of unarmoured dinoflagellates has been underestimated in the past, and the new records reported here confirm this. More complete studies, using both "traditional" and "modern" concepts and protocols (including cultures and molecular tools), should be undertaken in the near future to understand the "real" diversity and ecological role of unarmoured dinoflagellates in Mexican waters.

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Bionotes

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