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Phalacroma gibbosum sp. nov. (Dinophyceae) from the southern Gulf of Mexico

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With 42 figures and 1 table

Abstract: Within the marine dinoflagellates, the order Dinophysales includes members with very distinctive morphology and ecology. During a survey of the phytoplankton from the southern Gulf of Mexico, three specimens of an unknown dinophysoid species were found in formalin-fixed net samples, and were studied by light and scanning electron microscopy. A new species is proposed and formally described: *Phalacroma gibbosum* sp. nov. Its most characteristic features are as follows: (1) a distinctive trapezoid shape , (2) epitheca low with an elevation in the dorsal part of the epitheca (hump) , (3) cingular lists fairly developed, with strong but discontinuous ribs, (4) an elongation of the posterior end of the hypotheca, (5) a mamilliform structure in the ventral margin of the hypotheca, and (6) theca covered by deep, circular areolae, with small pores, one per 3–5 areolae. This new species is morphologically similar and presumably closely related to *Phalacroma favus* and *P. rapa*. Molecular phylogenetic studies grouped these two species together with true *Phalacroma* species (including the type species), and this is regarded as an indication that *Phalacroma gibbosum* is also a member of that genus.

Key words: Dinoflagellates, Dinophysales, Gulf of Mexico, New species, Phytoplankton.

Introduction

Dinoflagellates constitute a heterogeneous taxonomic group of eukaryotic and unicellular microorganisms, measuring between 5–250 µm (and until 2 mm, in some cases), the free-living fraction consists of motile cells having usually two unequal flagella, one of which is transversal (located in the cingulum) and the other is longitudinal (arising from the sulcus), and generally with an episome (epitheca) and a hyposome (hypotheca) separated by a cingulum (Fensome et al. 1993, Steidinger

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& Tangen 1997). The dinoflagellates are the second most species-rich group of the marine phytoplankton (Simon et al. 2009).

Within the marine dinoflagellates, the order Dinophysales includes members with very distinctive morphology that distinguishes them from other dinoflagellates groups, such as the sagittal serrate suture extended throughout the body, usually laterally depressed, with reduced epitheca, generally elongate hypotheca, cingular and sulcal lists of variable development, and a fairly constant number of plates (Sournia 1986, Fensome et al. 1993, Hernández-Becerril et al. 2008).

For the Gulf of Mexico several studies dealt with the planktonic dinoflagellates (Graham 1954, Balech 1967a, b, c, Licea et al. 2003, 2004), or more specifically with the Dinophysales (Norris 1969, Norris & Berner 1970, Hernández-Becerril et al. 2003, Parra-Toriz et al. 2012). A list of 644 dinoflagellates taxa in the gulf includes 174 species of Dinophysales (Steidinger et al. 2009), and a record specifically for the southern gulf, lists 252 species of dinoflagellates including 53 species of the Dinophysales (Licea et al. 2004).

During a survey of phytoplankton from the southern Gulf of Mexico, three specimens of a new dinoflagellate species, belonging to the Dinophysales, were found and studied by light and scanning electron microscopy. In this study the material is described and discussed in the context of its similarities and possible relationships with other species, and it is proposed as a new species, *Phalacroma gibossum* sp. nov.

Material and methods

The southern Gulf of Mexico is a subsystem of the greater gulf, a region almost restricted to the coastal and oceanic waters surrounding the Mexican states of Veracruz, Tabasco, and Campeche with an extended shelf at the extreme south-eastern part, and a very deep area in the Canyon of Campeche (Fig. 1). It is a highly productive area with coastal lagoons, estuaries and rivers (particularly the Coatzacoalcos and the Grijalva-Usumacinta) contributing nutrients and organic matter to the coast, whereas oceanographic processes (eddies, circulation and transport of water masses) affect the more oceanic areas. Climatic seasonality includes the "dry" (February to May), "rainy" (June to October) and "windy" (October to February) seasons (Salas-de-León & Monreal-Gómez 1997, Day et al. 2004).

This study is based on net (54 µm mesh) samples, collected from 20 to 200 m depth, obtained during the oceanographic cruises "PROMEBIO I" (August, 1999) and "PROMEBIO III" (April, 2000), from the southern Gulf of Mexico. In total, 17 phytoplankton samples were obtained, and all of them were immediately fixed with 4% formalin. Only two samples: "A" (21°00'N, 93°05'W, PROMEBIO I) and "B" (20°40'N, 93 00'W, PROMEBIO III) (Fig. 1) contained specimens of the new species. These were isolated by the micropipette and analyzed by light microscopy (LM, Olympus BX40, with attached camera Hitachi KP-D50 Color Digital), for identification, measurement and dissection of thecal plates, using sodium hypochlorite (Taylor 1978, Taylor et al. 2003). Some specimens were rinsed in several small drops of Mili-Q water and then mounted on a glass coverslip, air-dried and covered with gold for observation by scanning electron microscopy (SEM, JEOL JSM6360LV). The general terminology follows classical and recent works on dinoflagellates (Taylor 1971, Balech 1980, Fensome et al. 1993, Steidinger & Tangen 1997, Taylor et al. 2003). Terminology more specific to the Dinophysales followed Tai & Skogsberg (1934), Balech (1980) and Sournia (1986), and for thecal ornamentation recommendations of Hallegraeff & Lucas (1988) were followed. This means that the areolae are the depressions spread all over the theca, and pores are the tiny circular perforations scattered in the theca. We use the term depth to refer to the distance from the dorsal to the ventral margin.

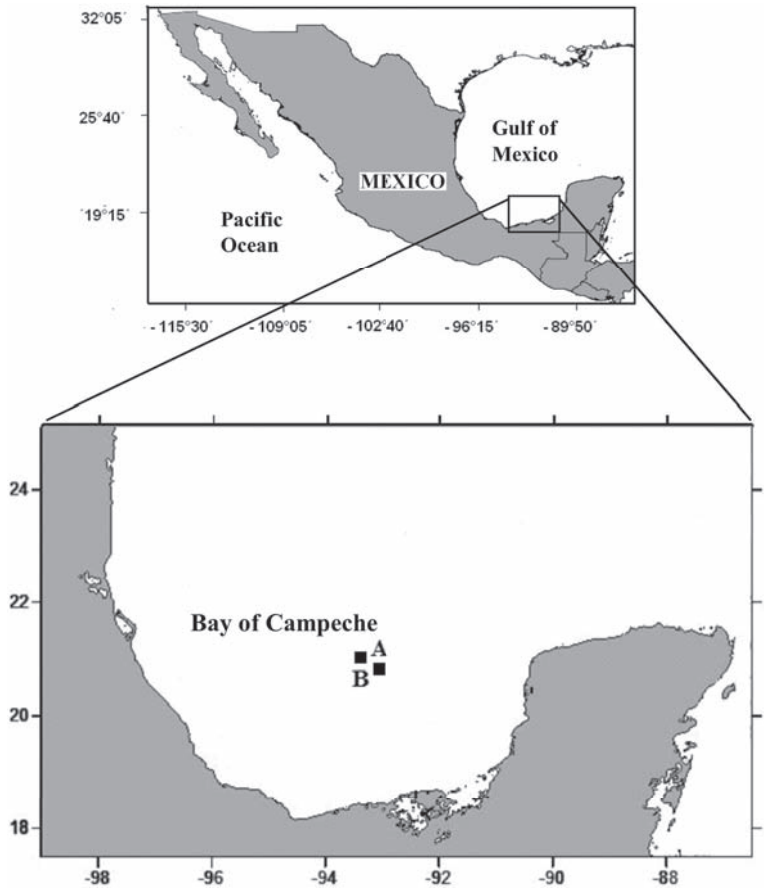


Fig. 1. Study area and location of stations A and B where *Phalacroma gibbosum* was found.

Results

Order Dinophysales Graham 1951

Family Dinophysaceae Bütschli 1885

Genus *Phalacroma* Stein 1883

***Phalacroma gibbosum* sp. nov.**

Formal description: Solitary cells, from medium-sized to relatively large, with trapezoid shape in lateral view, and obovate in dorsal or ventral views (Figs 2–6). The epitheca is low, larger and deeper than hypotheca (Figs 2–4), irregularly triangular (equilateral triangle) in apical view (Fig. 7). The epitheca shows a distinct hump located at the dorsal part of this (Figs 4–5). The hypotheca is asymmetric in right and left

lateral views, irregularly triangular (isosceles triangle) in dorsal or ventral views, with a posterior elongation (Figs 2–6); the dorsal margin is gently sinuous, slightly convex in the middle, and the ventral margin is concave, with a conspicuous mamilliform structure at the R3 level of the left sulcal list (Figs 2–4, 9, 10, arrows). Cingular lists developed, both are wide and supported by strong ribs, which are discontinuous along the lists, since close to the dorsal margin these ribs become shorter (Figs 3–7). Cingulum excavated, with two rows of pores at the edges. Left sulcal list developed, with wavy margin, more extended between R2 and R3, with all ribs (R1–R3) nearly equidistant, R3 very strong and longer than the others, with some ornaments (weaker ribs) present (Figs 3, 4), this list extends from the R3 until the mamilliform structure. Right sulcal list reduced. Theca covered by deep, circular areolae (Figs 2–4, 8–12), with small pores, one per 3–5 areolae. Measurements: total length 80–97 µm, total depth (including lists) 60–77 µm, cell depth (excluding lists) 45–67 µm.

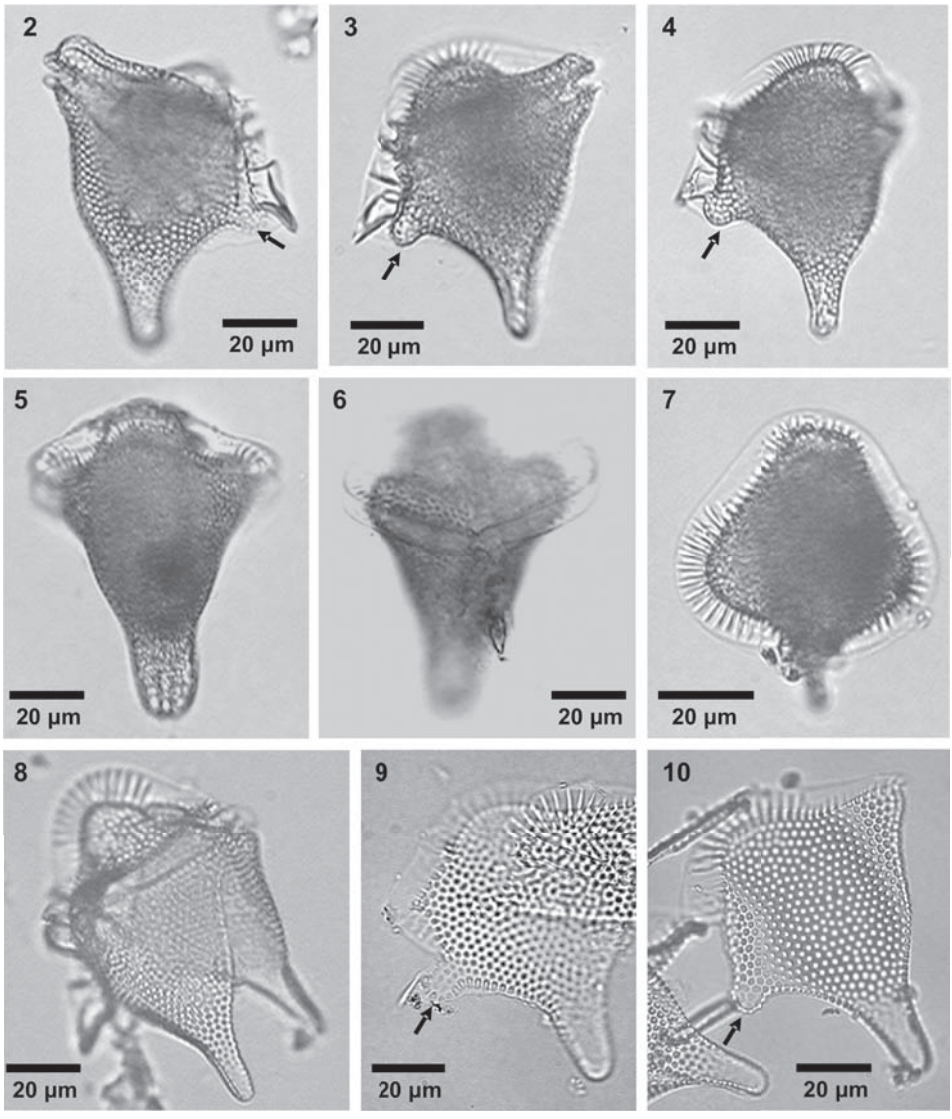
TYPE LOCATION: This species was found in the oceanic zone of the southwest of the Gulf of Mexico, specifically it was first encountered at Station A (oceanographic cruise PROMEBIO I), at 21°00'N, 93°05'W (Fig. 1).

HOLOTYPE: Slide 2281, deposited at Phycological Collection (Colección Ficología), Herbario Nacional, Instituto de Biología, Universidad Nacional Autónoma de México (MEXU).

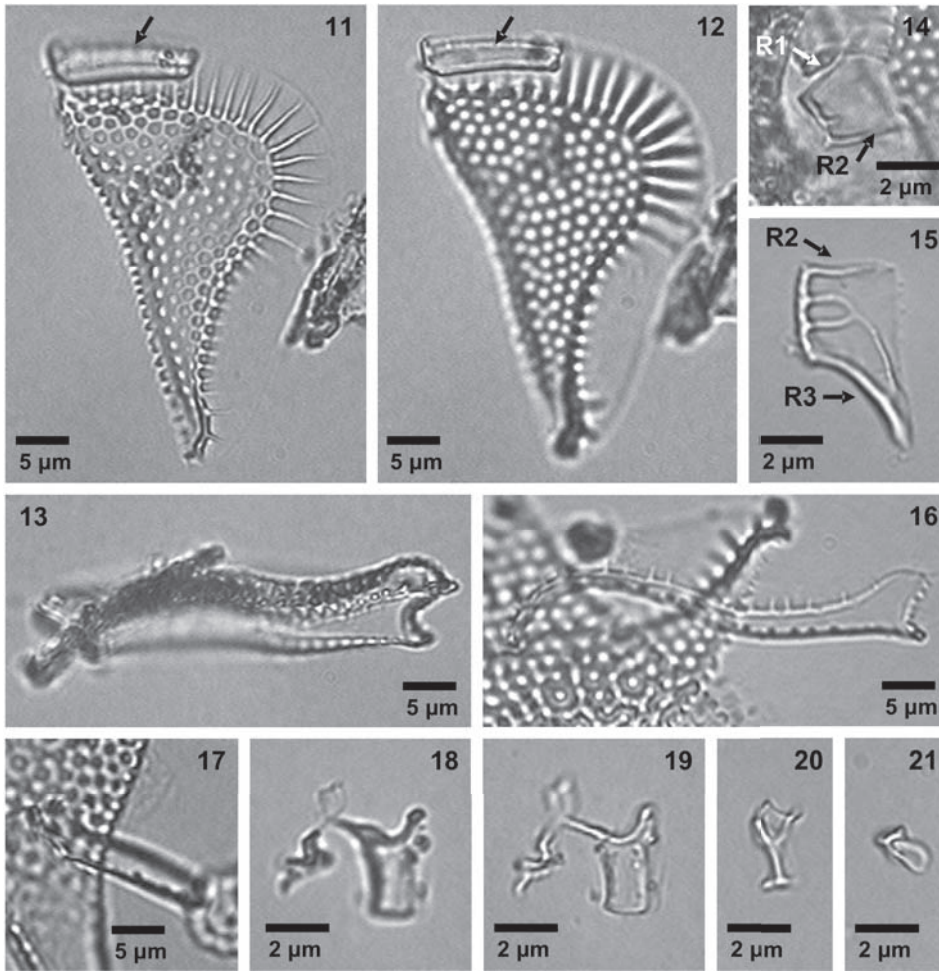
ETYMOLOGY: The Latin epitethon *gibbosum* refers to the most characteristic feature, the hump of the epitheca.

Dissection of specimens shows details of the epithecal plate E3 with the sagittal serrate suture, the development of the anterior cingular list with discontinuous ribs along it, the ornamentation of the theca, and one cingular plate (possibly C4) (Figs 11, 12). The epitheca in side view exhibits its hump at the end next to the dorsal margin and the cingulum (Fig. 13). The left sulcal list divides into two parts, the upper one is part of the hypothecal plate H1 and is limited by R1 and R2, also it is shorter than the other part, less developed and with few or no additional ornaments (Fig. 14), and the lower part between R2 and R3, is part of the hypothecal plate H4, and is more extended and with ornaments consisting of thinner forked ribs (Fig. 15). Some cingular plates were observed, a very elongate C2 and possibly C1, (Figs 16, 17, respectively). Finally, sulcal plates, the tongue-shaped posterior one (Sp) with two longitudinal rows of pores close to the edges, and other plates (Figs 18, 19), as well as the right sulcal plate (Sd) (Fig. 20) and the left sulcal plate (Ss) (Fig. 21).

Observations by SEM confirm the shapes of the cell in left lateral and ventral views, respectively (Figs 22, 23), the characteristic mamilliform structure close to the ventral margin, at the R3 level of the left sulcal list (Fig. 22) , and the noticeable hump in the epitheca (Figs 23, 24, 27). The two cingular lists have strong ribs, which are discontinuous, being shorter and disappearing at about 3/4 of its length from the ventral to the dorsal margins (Figs 22–24). The ribs are elevated and some do not reach the edge of the lists (Figs 25, 28). In the ventral area, the slight displacement of the cingulum is evident (Fig. 26), and the ribs (R1–R3) and ornaments (weaker ribs) of the left sulcal list (Figs 26, 27) are also apparent; there is an extension of the left sulcal list running from R3 until just down the mamilliform structure (Fig. 22, 27, arrows). Some teeth were found in the posterior elongation in the right half of a cell, the large plate H3, the

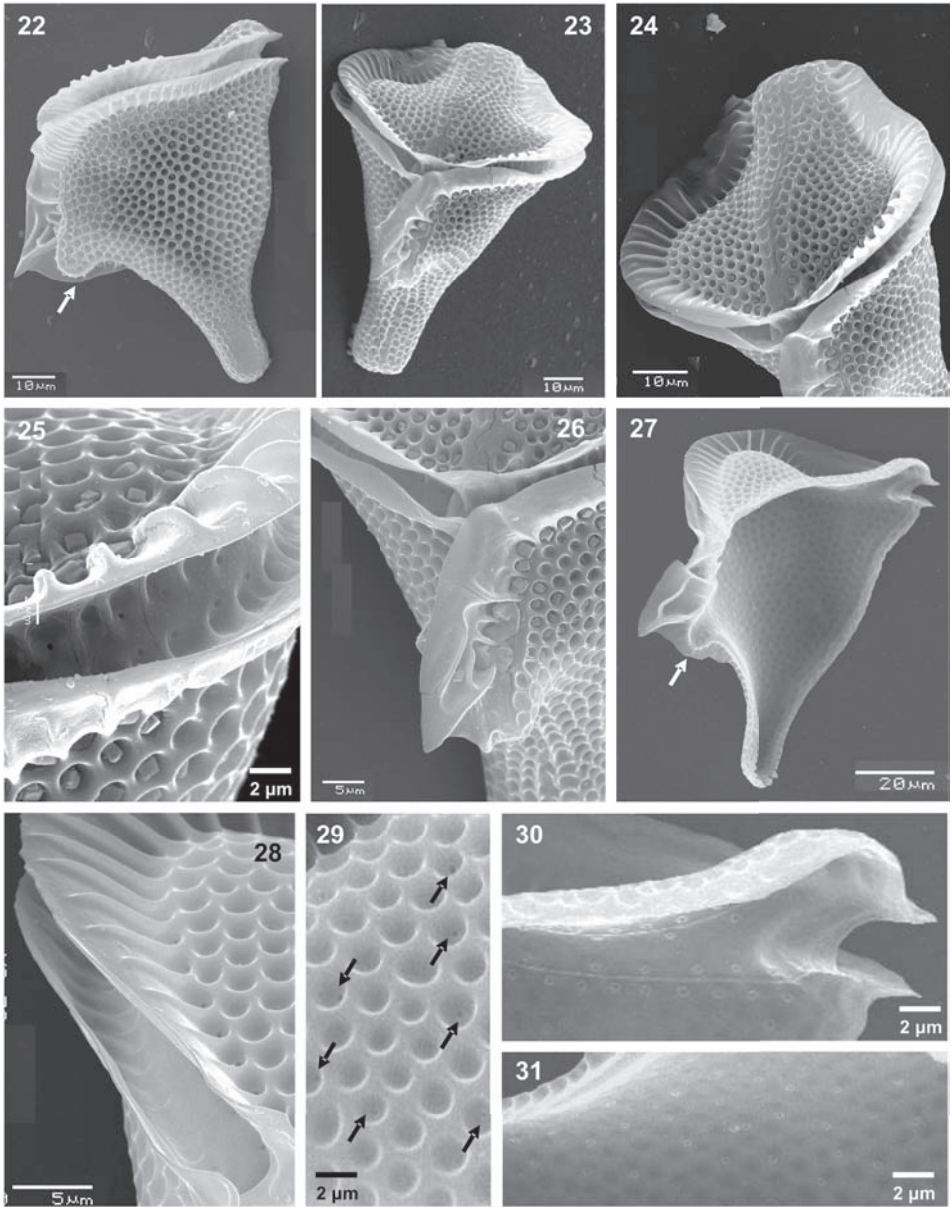


Figs 2–10. *Phalacroma gibbosum*, LM. Fig. 2. A complete cell in right lateral view; an arrow points to the mamilliform structure of the ventral margin. Figs 3, 4. One cell in two different positions: left lateral view and left latero-dorsal view, respectively; the arrows point to the mamilliform structure. Figs 5, 6. Dorsal and ventral views of a cell, respectively. Fig. 7. Apical view of the epitheca, showing the anterior cingular list. Fig. 8. Two halves of a dissected cell. Figs 9, 10. Right and left halves of the theca, respectively; the arrows point to the mamilliform structure.



Figs 11–21. *Phalacroma gibbosum*, LM. Figs 11, 12. Two different focuses of the left half of the epitheca (the large plate E3), showing one cingular plate (possibly C4, arrowed) and part of the anterior cingular list. Fig. 13. Epitheca and cingulum in lateral view, showing a hump in the dorsal side. Fig. 14. Upper part of the left sulcal list with R1 and R2. Fig. 15. Lower part of the left sulcal list, between R2 and R3. Fig. 16. The elongate cingular plate C2. Fig. 17. Another cingular plate, C1. Figs 18, 19. Three sulcal plates: the tongue-shaped posterior one (Sp) with other two unidentified plates. Fig. 20. The right sulcal plate (Sd). Fig. 21. The left sulcal plate (Ss).

Figs 22–31. *Phalacroma gibbosum*, SEM. Fig. 22. A complete cell in left lateral view; an arrow points to the mamilliform structure of the ventral margin. Fig. 23. Same cell in ventral view, showing the epitheca, cingular lists and left sulcal list. Fig. 24. View of the epitheca and the two cingular



lists. Fig. 25. Detail of the cingulum with two rows of pores and the anterior and posterior cingular lists. Fig. 26. Detail of the left sulcal list and the slight displaced cingulum. Fig. 27. Internal view of the right half of a cell, with a part of humps in the epitheca and the mamilliform structure of the ventral margin (arrow). Fig. 28. View of the cingulum, the two cingular lists, and the ornamentation of the epitheca. Fig. 29. Detail of the theca ornamentation, with the scattered pores arrowed. Fig. 30. Internal view of the cingulum showing a hump of the epitheca, the cingulum (plate C3) and upper part of the hypotheca, with some pores. Fig. 31. Internal view of the hypotheca with scattered pores.

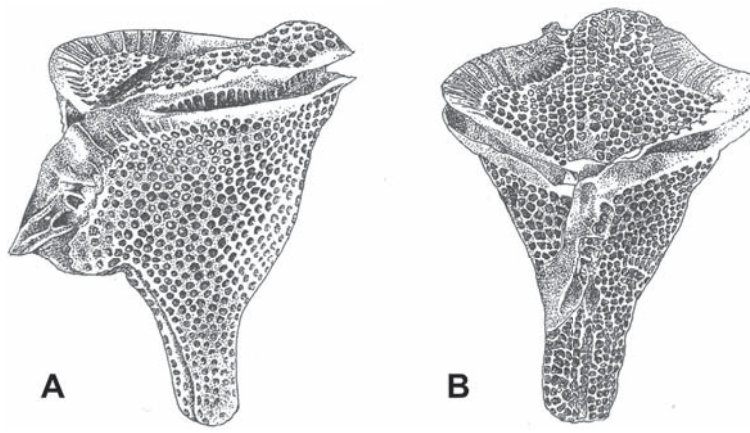


Fig. 32. A diagram of *Phalacroma gibbosum*, in left lateral view (A) and ventral view (B).

cingular plates C3 and C4, the plates E3 and most possibly E4, and the right sulcal list and lower part of the left sulcal list (bearing H4) (Fig. 27). The cingulum has two rows of pores at the edges (Figs 25, 30). The theca is covered by regularly spaced deep and nearly circular areolae, with small pores, one per 3–5 areolae (Fig. 28, arrows Fig. 29), although there is a continuous row of pores along the suture of the dorsal margin (Fig. 27) and also along the suture next to the cingulum (Fig. 30). An internal view of the theca shows again the arrangement of one pore surrounded by 3–5 areolae (Fig. 31).

Fig. 32 shows diagrams of *Phalacroma gibbosum* in left lateral view (Fig. 32 A) and ventral view (Fig. 32 B), which can be considered the iconotypes of this new species.

Environmental conditions and associated flora

At the sites where *P. gibbosum* was found the surface temperature ranged between 25°C and 29.5°C, and surface salinity ranged between 35.2 and 36.5.

The associated flora found in the samples, in which *P. gibbosum* was encountered included, for Station A, dinoflagellates such as *Amphisolenia palaeotheroides* Kofoid, *Centrodinium eminens* Böhm, various species of the genus *Tripos* Bory (*Ceratium*) (*Tripos brevis* (Ostenfeld et Schmidt) Gómez, *T. candelabrus* (Ehrenberg) Gómez, *T. fusus* (Ehrenberg) Gómez, *T. kofoidii* (Jörgensen) Gómez, *T. macroceros* (Ehrenberg) Gómez, *T. pentagonus* (Gourret) Gómez), *Ceratocorys horrida* Stein, *Ornithocercus magnificus* Stein, *O. thumii* (Schmidt) Kofoid & Skogsberg, *Phalacroma argus* Stein, *P. doryphorum* Stein, *P. rapa* Jörgensen, *Podolampas palmipes* Stein, *Protoperidinium depressum* (Bailey) Balech, *P. divergens* (Ehrenberg) Balech, *Pyrocystis elegans* Pavillard, and *Scrippsiella trochoidea* (Stein) Balech ex Loeblich III, and diatoms such as *Planktoniella sol* (Wallich) Schütt, *Coscinodiscus* sp. and *Skeletonema* sp. A high concentration of the filamentous cyanobacterial genus *Trichodesmium* Ehrenberg ex Gomont was also noticeable.

At Station B, the diversity was lower, and the dinoflagellates were only represented by *Tripos candelabrus*, *T. vultur* (Cleve) Gómez and *Gonyaulax kofoidii* Pavillard, whereas the diatoms observed were *Chaetoceros affinis* Lauder, *C. angulatus* Schütt, *Hemiaulus membranaceus* Cleve, *Planktoniella sol*, and *Pseudosolenia calcar-avis* (Schultze) Sundström, and there was a much lower concentration of *Trichodesmium* filaments.

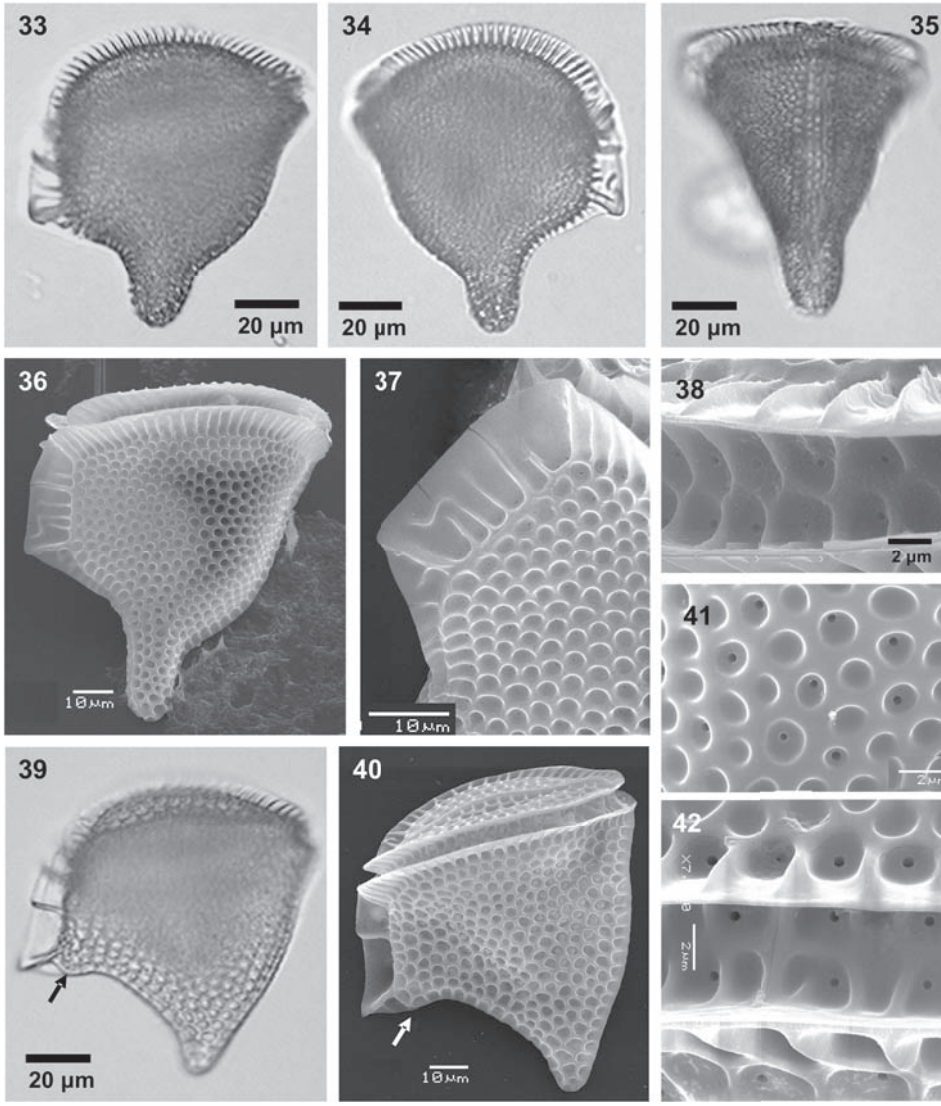
Discussion

General morphology: The investigated specimens bore some superficial resemblances to several related species. However, the morphological characters of the new material did not match any of those already described taxa, and the new species *Phalacroma gibbosum*, is proposed. We consider that *P. gibbosum* presents morphological characters that define it as a new species of the order Dinophysales and the genus *Phalacroma*. The more general characters of dinophysoids are: (1) a strong lateral compression of the theca, (2) the presence of a reduced epitheca and a large hypotheca, and (3) the presence of two prominent sulcal lists (Balech 1988, Hernández-Becerril et al. 2008). The additional characteristic features of *P. gibbosum* are: (1) body with a distinctive trapezoid shape, (2) epitheca low, with a hump, (3) cingular lists moderately developed, with strong but discontinuous ribs, (4) elongation of the posterior end of the hypotheca, (5) a mamilliform process in the ventral margin of the hypotheca, and (6) theca covered by deep, circular areolae, with small pores, one per 3–5 areolae.

The allocation of the new species to a given genus has not been straightforward, especially because most of the genera of the Dinophysales (*Amphisolenia* Stein, *Dinophysis* Ehrenberg, *Phalacroma*, *Pseudophalacroma* Jörgensen, *Sinophysis* Nie et Wang) have recently been subject of several recent studies including molecular phylogenies (Hastrup Jensen & Daugbjerg 2009, Handy et al. 2009, Gómez et al. 2011, Daugbjerg et al. 2013). In addition, multiple new species were described (Hernández-Becerril et al. 2008, Esqueda-Lara et al. 2013). However, according to the possible relationships with other species, we proposed that the species should belong to *Phalacroma*, fitting the recent circumscription provided by Hastrup Jensen & Daugbjerg (2009).

The newly described species *Phalacroma gibbosum*, also shares morphological characters with another genus of the order Dinophysales, *Dinofurcula* Kofoid, especially because of the hump-like elevation of the epitheca, present in *Dinofurcula ultima* Kofoid (Kofoid & Skogsberg 1928, Hernández-Becerril & Bravo-Sierra 2004), although the particular "molar" shape and strong lateral depression of *Dinofurcula* and its species are different.

Some *Phalacroma* species that are similar in morphology to *Phalacroma gibbosum* and therefore might be closely related are *P. favus* Kofoid et Michener and *P. rapa* Stein. All three species share the trapezoidal form in lateral view (Figs 33, 34, 36, 39, 40), some degree of elongation of the posterior end of the hypotheca (Figs 33–36, 39, 40), the arrangement of the cingulum, with two rows of pores at the edges, (Figs 38, 42), and the thecal ornamentation, composed of circular areolae and a proportion of one pore per 3–5 areola (Figs 37, 41). Moreover, *Phalacroma gibbosum* has an



Figs 33–42. *Phalacroma favus* and *P. rapa*, LM and SEM. Figs 33–38. *Phalacroma favus*. Fig. 33. Left lateral view of a specimen, LM. Fig. 34. Righ lateral view of another specimen, LM. Fig. 35. Dorsal view of a cell, LM. Fig. 36. Left lateral view showing the cingular lists, left sulcal list and theca ornamentation, SEM. Fig. 37. Details of the left sulcal list and ornamentation of the theca, SEM. Fig. 38. A detail of the cingulum with its lists and two rows of pores at the edges, SEM. Figs 39–42. *Phalacroma rapa*. Fig. 39. Left lateral view showing a mamilliform structure of the ventral margin (arrow), LM. Fig. 40. Left lateral view of another cell showing the mamilliform structure (arrow), SEM. Fig. 41. Detail of the ornamentation of the theca, SEM. Fig. 42. Detail of the cingulum with its lists and the two rows of pores at the edges, SEM.

Table 1. Comparative morphology of the species *Phalacroma gibbosum* sp. nov., and two closely related species, *P. favus* and *P. rapa*.

	P. gibbosum	***P. favus***	***P. rapa***
Size of cell	Medium-large L= 80–97, D= 60–77	Medium-large L= 54–83, D= 54–63*	Medium-large L= 70–95, D= 58–70*
Shape of cell in lateral view	Trapezoid	Trapezoid	Trapezoid
Shape of cell in dorsal view	Obovate irregular	Obovate irregular	Obovate irregular
Epitheca	Low with a distinct hump in the dorsal part	Low and flat	Low and flat
Hypothecal ventral margin	Concave and with mamilliform structure	Concave	Concave and with mamilliform structure
Hypothecal posterior margin	With a long posterior elongation	With a long posterior elongation	With a short posterior elongation
Width of cingular lists	10.7 µm	7.5 µm	7.5 µm
Ribs in cingular lists	Discontinuous	Continuous	Continuous
Shape of left sulcal list margin	Wavy	Straight	Straight

* Schiller 1933 and own, unpublished observations.

obovate shape in dorsal or ventral views that also occurs in *P. favus* (Fig. 35), and a characteristic mamilliform structure of the hypotheca at the R3 level that is shared with *P. rapa* (Figs 39, 40, arrows). Details of the sulcal plates show additional similarities of *P. gibbosum* to *P. rapa*: the posterior sulcal plate (Sp) in the two species is similar, with a characteristic tongue-shape (as found in many others in the genus *Phalacroma*), but in *P. gibbosum*, this is more reduced in length and slightly wider and two rows of four tiny pores running longitudinally along the edges (Figs 18, 19, and Balech 1988, plate 8, fig. 7).

More similarities and differences of these three species are provided in Table 1, including the details of the epitheca, cingular lists and left sulcal list. Illustrations of the species *P. favus* and *P. rapa* by other authors also confirm the above mentioned morphological characters (Jorgensen 1923, Kofoid & Skogsberg 1928, Balech 1988, Hallegraeff & Lucas 1988, Hernández-Becerril 1992, Hernández-Becerril et al. 2008). Molecular phylogenetic studies revealed that *Phalacroma favus* is closely related to the type species of the genus *Phalacroma*, *P. porodictyum* Stein (Gómez et al. 2011, fig. 6), whereas *P. rapa* is closely related to *P. mitra* Schütt (Gómez et al. 2011, fig. 6),which has been considered to belong into *Phalacroma* (Hastrup Jensen & Daugbjerg 2009). Therefore morphological similarities of *P. gibbosum* with *P. favus* and *P. rapa*, support the allocation of the new species into the genus *Phalacroma*.

Recently, *Phalacroma* s.s. (including *Oxyphysis* Kofoid) and other presumably related genera such as *Dinofurcula*, *Latifascia* Loeblich et A. R. Loeblich and *Proheteroschisma* Tai *et* Skogsberg were grouped together within the Family Oxyphysaceae Sournia

(Gómez, 2012), but this proposal needs to be confirmed with the aid of molecular sequences and detailed morphological studies of the three former genera and their species, and we do not follow it as yet.

Ecological aspects and distribution: The species was found in the area of the Canyon of Campeche (considered a deep area) in samples from two different oceanographic cruises (PROMEBIO I and III), under two presumably different climatic (and perhaps oceanographic) conditions. This suggests that *Phalacroma gibbosum* has no clear preference for any given climatic or oceanographic conditions (e.g. "dry" or "rainy" seasons). The associated flora, however, differed between the two samples. For PROMEBIO I, a strong tropical influence, perhaps caused by intrusion of the water from Caribbean Sea, may be indicated by the presence of relatively high densities of *Trichodesmium* species, and a high diversity of dinoflagellates, including various species (such as *Amphisolenia palaeotheroides*, *Ornithocercus magnificus*, *O. thumi*, *Phalacroma argus*, *P. doryphorum* and *P. rapa*). For PROMEBIO III, different conditions and a less marked tropical influence are indicated by higher number of diatoms species and considerably lower density of *Trichodesmium*.

Phalacroma gibbosum is a very characteristic species that, owing to its shape and size, can not be neglected nor misidentified; at present it may be considered to be distributed in tropical, more oceanic waters in the southern Gulf of Mexico.

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