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The dinoflagellate genus *Prorocentrum* along the coasts of the Mexican Pacific

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Abstract

We surveyed the dinoflagellate genus *Prorocentrum* Ehrenberg in Mexican Pacific waters, where it is rather common and sometimes causes red tides in coastal areas or shrimp farms. Material collected from Baja California and the Gulf of California was analyzed. Thirteen species were identified, all of them planktonic (although *P. mexicanum* is also epiphytic). All species are described by light microscopy, and most are also described by scanning electron microscopy; comments on morphology, taxonomy and distribution are made. Red tides were caused by *P. dentatum*, *P. minimum* and *P. triestinum*. *Prorocentrum mexicanum* and *P. minimum* were suspected of being toxic. Four species, previously reported in the Gulf of California, were not found. A total of 18 species, including the new records *P. dactylum* and *P. lebourae* have been to date reported from the Mexican Pacific.

Introduction

The genus *Prorocentrum* Ehrenberg belongs to the Desmokont dinoflagellates, which have two dissimilar flagella emerging from the anterior part of the cell, but no typical cingulum nor sulcus. The cell is composed of two large lateral thecae (Fensome et al., 1993; Steidinger & Tangen, 1997). The genus forms a homogeneous group of armored dinoflagellates of small to medium size, varying from circular or subcircular to elliptical or pyriform in shape, and having chloroplasts. There are two opposing thecae: left and right, united by lines or bands-shaped sutures. Some species may develop spines or anterior projections. The surface is ornamented with poroids, pores, areolae and minute spines. The genus has been merged with (Abé, 1967, and additions by Dodge, 1975), *Exuviaella* Cienkowski, although a recent paper (McLachlan et al., 1997) has proposed the reinstatement of the latter.

The position of the genus and of the family Prorocentraceae (which also includes *Haplodinium* Klebs and *Mesoporos* Lillick, following Fensome et al., 1993) is controversial. Some authors (e.g. Dodge, 1983; Fensome et al., 1993) consider it as evolutionarily advanced, showing plate reduction (e.g. the periflagellar plates), as primitive and ancestral, based on the position of the flagella and lower chromosome numbers (Taylor, 1980; Steidinger & Tangen, 1997). Molecular data by Zardoya et al. (1995) partially supports the primitive condition of the Prorocentrales.

The main specific morphological characters of *Prorocentrum* are the shape and size of cells, presence of apical processes, indentation of the right theca, pore pattern on the thecal surface, and number and pattern of periflagellar plates (Steidinger & Tangen, 1997).

Species of *Prorocentrum* are planktonic, benthic or epiphytic, and are distributed world-wide, reaching their highest diversity in tropical and subtropical areas; some benthic species have recently been described from tropical areas (e.g. Fukuyo; 1981; Faust, 1990, 1993, 1994).

Some species may produce 'red tides' in coastal areas and coastal lagoons; others are toxic, producioning Okadaic Acid, a powerful toxin that causes diarrhetic Shellfish Poisoning in humans (e.g. *Prorocentrum lima* (Ehr.) Dodge, Lee et al., 1989) or other

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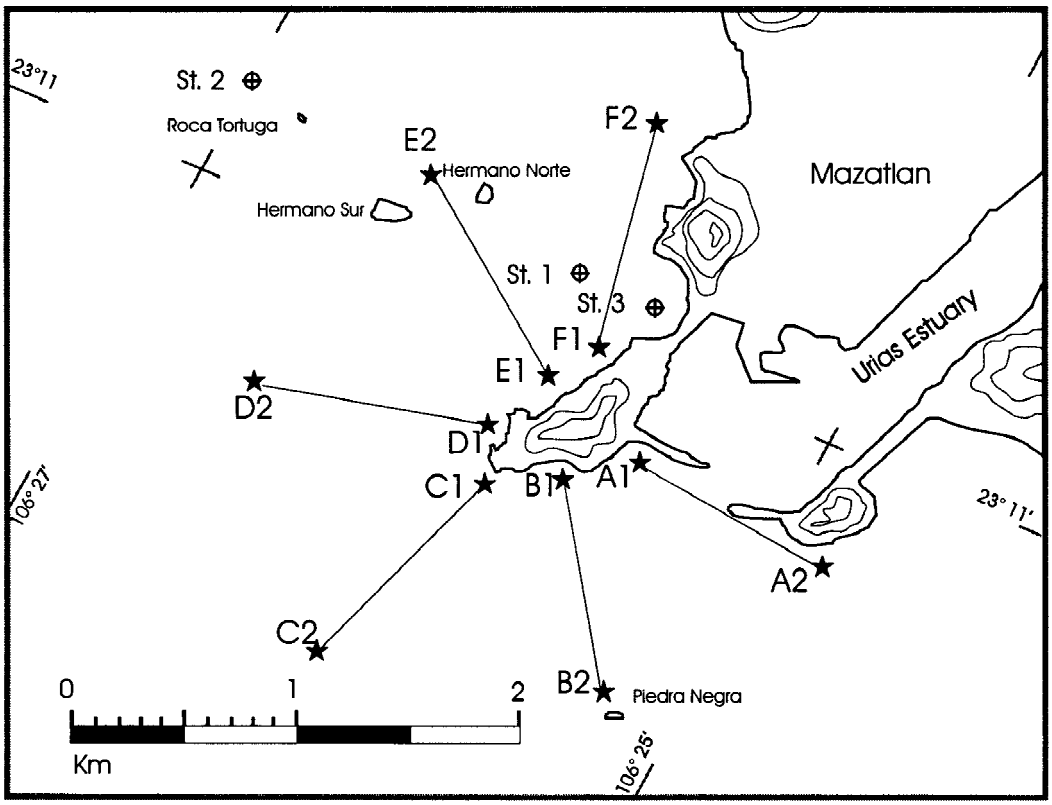


Figure 1. Map of the bay of Mazatlan, in the Mexican Pacific, exhibiting sampling points for this study.

toxins in coral reef areas (e.g. *P. mexicanum* Osorio-Tafall and *P. concavum* Fukuyo, Carlson & Tindall, 1985).

In this paper, we study the species found along the coasts of the Mexican Pacific.

Material and methods

Samples were obtained from 'red tides' formed by *Prorocentrum* species in the bay of Mazatlán, México (23° 15′ and 23° 11′ N, 106° 29′ and 106° 25′ W), Pacific Coast of Mexico (Figure 1); 200 ml were collected with a bottle or a bucket and fixed with lugol solution. Collections of 'red tides' were made on April 1992, April 1994 and December 1996. Other blooms formed by *Prorocentrum minimum* were collected from shrimp farms, close to the bay of Mazatlán, following the same protocol (Cortés & Agraz, 1994). In addition, net (64 μm mesh) haulings were made in the Gulf of California during three cruises (CORTES I, II and III, on May 1982, March 1985 and July–August 1985, respectively), preserved in 4% formalin. Sampling stations are given in Figure 2.

Analysis was carried out using an inverted photomicroscope Zeiss ICM 405, under phase contrast (specially for cell counting). Observations were also made by SEM (JEOL JSM-35), using dehydrated and critical point treated material, coated with gold. Measurements were taken on the light microscopy.

Results

Thirteen species identified are described in alphabetical order. Some data cell abundance are available on species forming red tides (*P. dentatum*, *P. minimum* and *P. triestinum*). Taylor (1976) provided a list of references after Schiller's (1933) treatise of dinoflagellates. In this paper, we annotate, important references after 1976.

Systematic account

Prorocentrum dactylum (Stein) Dodge, Figure 6

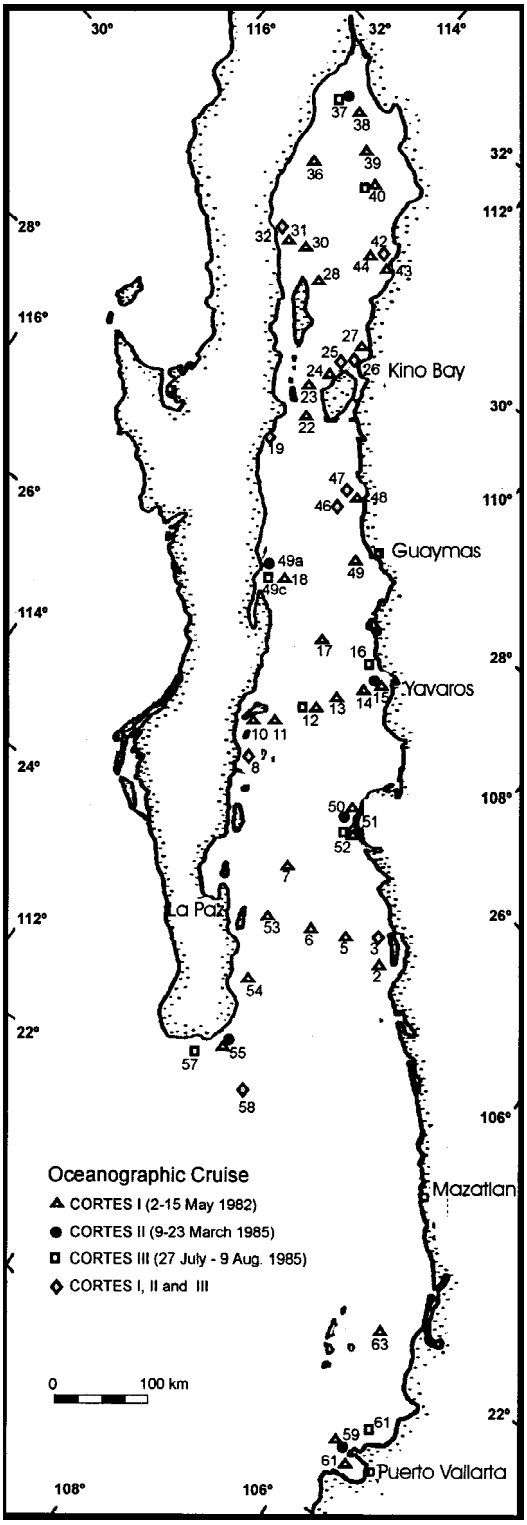


Figure 2. Sampling points in the Gulf of California and further south used for this study, obtained during three different oceanographic cruises (CORTES I, II and III).

Dodge, 1975, 109 pp., Figure 1 G.

Basyonym: Dinopyxis dactylus Stein

Stein, 1883, pl. 1, Figures 20–23.

Cells elongate, with anterior end rounded and posterior end slightly acute. No spine present at anterior end. Poroid pattern on thecae inconspicuous. Length: 35 μm, width: 10 μm.

Distribution: rare in the bay of Mazatlán, at water surface and at temperatures higher than 25 ° C. A new record for the Mexican Pacific.

Remarks: This species was scarce and no material was available for study by SEM. Measurements are considerable lower than those provided by Dodge (1975).

Prorocentrum dentatum Stein, Figures 7–10

Stein, 1883, pl. 1, Figures 14 and 15; Dodge, 1975, 116 pp., Figure 4 K (non L), pl. 4 A, B; Steidinger & Tangen, 1997, 423 pp., pl. 8.

Synonyms: Prorocentrum obtusidens Schiller

Schiller, 1928, 57 pp., Figure 15.

Prorocentrum veloi Osorio-Tafall

Osorio-Tafall, 1942, 437 pp., pl. 34, Figures 4–6.

Cells small, rather elongate and lanceolate. Anterior end with small central depression and protuberance on one side. Posterior end acute.Margins nearly parallel. No spine on anterior end. Minute spines evenly spread over thecae. Some pores (30–35) arranged on periphery of thecae. Suture bands present in most specimens; ornamented with small granule-like structures in perpendicular rows to main axis of cell. Length: 17–20 μm, width: 7–11 μm.

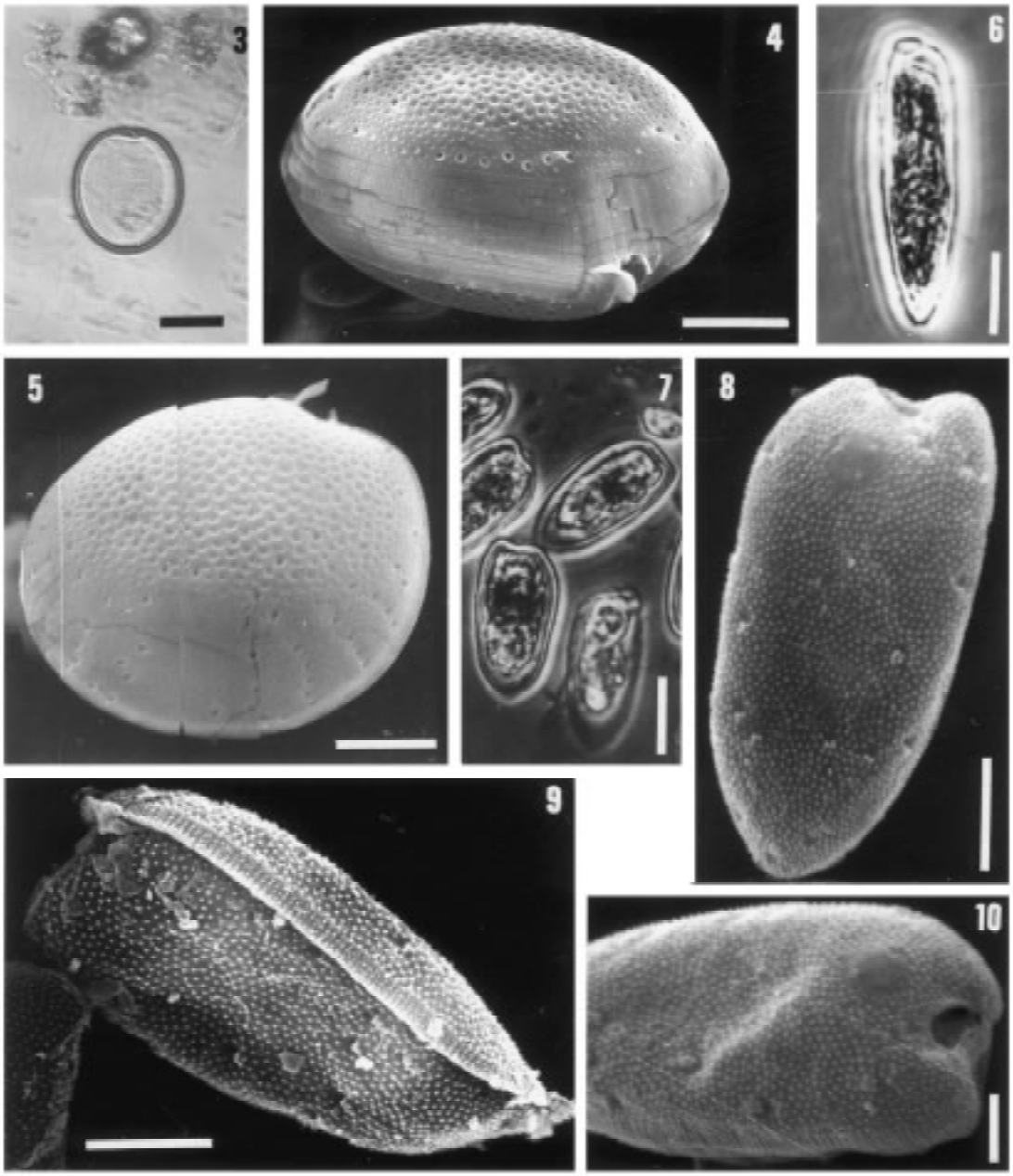
Distribution: Found in the bay of Mazatlán, at surface and at 5 m.

Remarks: This species was part in red tide in the bay of Mazatlán, with densities ranging from 8000 to 32 000 cels ml^{-1}.

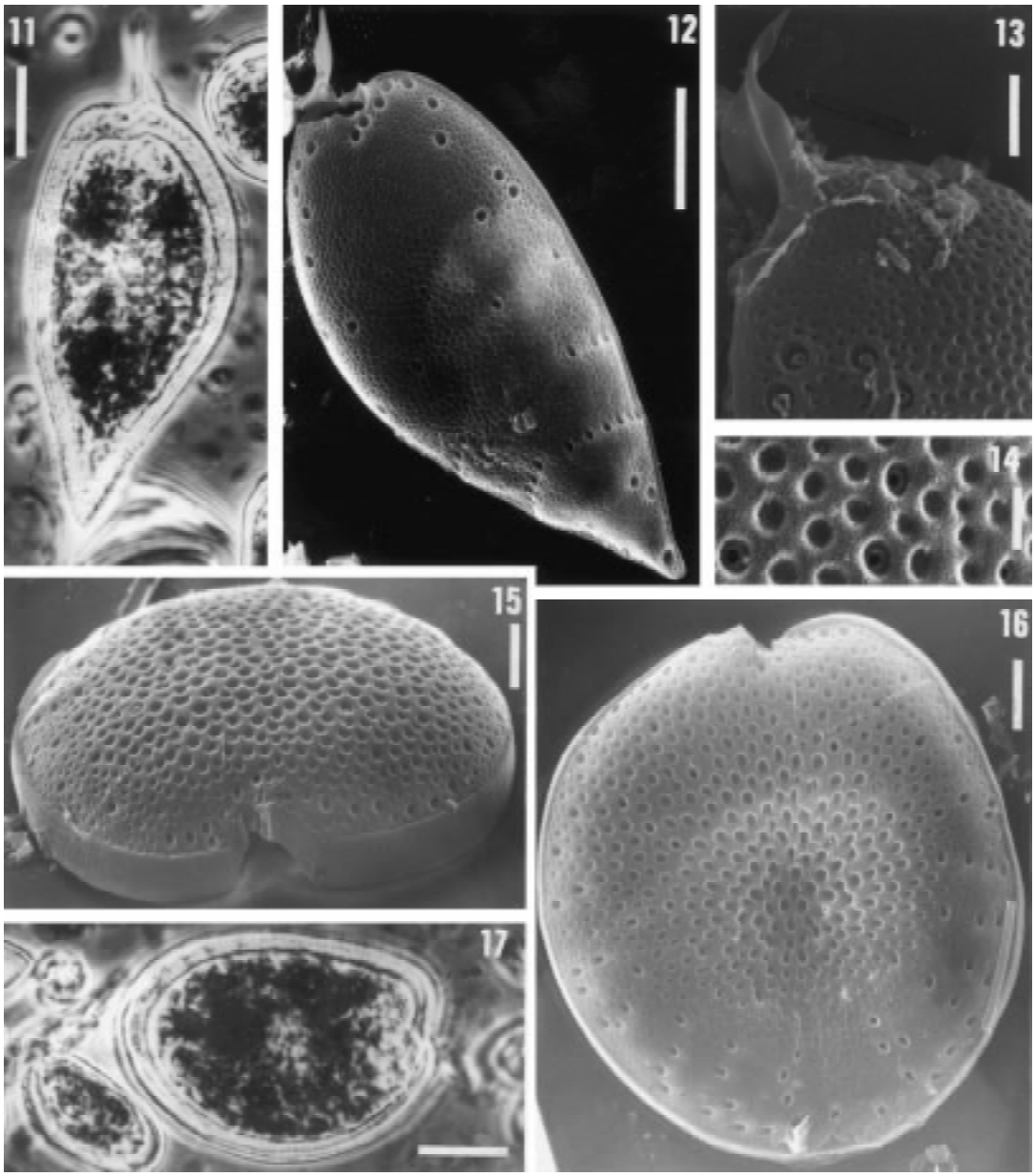
Prorocentrum gracile Schütt, Figures 11–14

Schütt, 1895, pl. 1, Figure 3; Schiller, 1933, 37 pp., Figures 39 a, b; Dodge, 1975, 114 pp., Figure 3 C; Taylor, 1976, 22 pp., pl. 1, Figure 2; Balech, 1988, 32 pp., pl. 4, Figure 2; Hernández-Becerril, 1988a, 424 pp., Figure 2; Steidinger & Tangen, 1997, 423 pp., pl. 8.

Cells are medium-sized, elongate and lanceolate. The anterior end is rounded and the posterior end in pointed. There is an anterior spine which is long, sigmoid and winged. Poroids distributed all over the thecae. Large pores follow a typical pattern: one or two postmedian rows of 3–6 pores radiating from the center, closer to the posterior end and the margins of the thecae; the thecae are sometimes slightly arisen at



Figures 3–10. *Prorocentrum* species, LM and SEM. Figures 3–5. *Prorocentrum lebourae*.
Figure 3. One cell in lateral view, LM.
Figure 4. Another cell in apical view, showing two small projection close to the periflagelar area, SEM.
Figure 5. Complete cell in lateral view, SEM.
Figure 6. *Prorocentrum dactylum*, a cell in lateral view, LM.
Figures 7–10. *Prorocentrum dentatum*.
Figure 7. Five cells in lateral view, LM.
Figure 8. A complete cell in lateral view, SEM.
Figure 9. Another cell in side view, showing the suture band, SEM.
Figure 10. Cell in apical view, exhibiting the periflagelar area, SEM. Scale bars= 20 μm (Figure 3), = 10 μm (Figures 4–7), = 5 μm (Figures 8–10).



Figures 11–17. *Prorocentrum* species, LM and SEM. Figures 11–14. *Prorocentrum gracile*.
Figure 11. A cell in lateral view, LM.
Figure 12. Another cell in lateral view, showing large pores on the theca, SEM.
Figure 13. Anterior part of a cell, with a prominent spine, SEM.
Figure 14. Detail of the theca surface with poroids and larger pores, SEM.
Figures 15 and 16. *Prorocentrum lenticulatum*.
Figure 15. A cell in apical view, SEM.
Figure 16. Cell in lateral view, with some larger pores on the periphery of the theca, SEM.
Figure 17. *Prorocentrum maximum*, one cell in lateral view, LM. Scale bars= 10 μm (Figures 11, 12 and 17), = 5 μm (Figures 13, 15 and 16), = 2 μm (Figure 14).

these rows of pores. Other pores scattered close to the posterior end and one larger pore at the very end of the theca. Some pores are close to the anterior end. The pores are placed in the middle of depressions. Suture lines or bands are also arisen. Length: 42–51 μm, width: 23–25 μm, length of spine: 8–11 μm.

Distribution: This species is widely distributed in the Mexican Pacific, but not abundant.

Prorocentrum lebourae Schiller, Figures 3–5

Schiller, 1928, 62 pp., Figure 23; Schiller, 1933, 33 pp., Figure 34; Dodge, 1975, 111 pp., Figure 2 F, as *P. compressum* (Bailey) Abé ex Dodge.

The cells are ovate to subcircular, with rounded margins, compressed in side view. Anterior end with a depression and one or two short spines, the right spine slightly larger than the left one. Thecae with poroids evenly distributed and the pores which are replacing the correspondant poroid are scattered randomly. A peripheral row of slightly larger pores is present. Some specimens exhibit no poroids in a field close to the posterior end. Other pores are arranged in postmedian radial rows of 4–6 pores toward the posterior end. Length: 34–57 μm, width: 31–47 μm.

Distribution: Widely distributed along the Gulf of California, although not very common. This is the first record of the species in the Mexican Pacific.

Remarks: Measurements (45 μm length, 40 μm width) originally given by Schiller (1928, 1933) fit well with those found here. Dodge (1975) has reduced this species to a synonym of *Prorocentrum compressum*, but the shape and size of the cells in *P. lebourae*, as well as the pores arrangement, clearly differ from the former.

Prorocentrum lenticulatum (Matzenauer) Taylor, Figures 15, 16

Taylor, 1976, 23 pp., pl. 1, Figures 11, 12.

Synonym: Exuviaella lenticulata Matzenauer

Matzenauer, 1933, 438 pp., Figures 1 a, b.

Cells ovate to subcircular in valve view, lenticular and flattened in side view. A slight depression is evident in the theca center in some specimens. Anterior end excavated, with no spine nor process. Poroids regularly distributed in the thecae, except at the postmedian part, close to the posterior end, where the thecae become smooth, also with some radial rows of pores and others arranged peripherally, following the margins of the thecae. Other pores are scatterd on the thecae. Length: 35–40 μm, width: 29–32 μm.

Distribution: Found in few stations in the Gulf of California, in very low numbers.

Prorocentrum maximum (Gourret) Schiller, Figure 17

Schiller, 1933, 41 pp., Figures 44 a–c; Dodge, 1975, 117 pp., Figures 4 C, D, pl. 3 F.

Cells ovate, one margin nearly straigth and the other more rounded. Both ends rounded, the anterior end has a concavity and a small spine. Pattern of pores not seen. Length: 36 μm, width: 24 μm.

Distribution: Present in some points in the Gulf of California and the bay of Mazatlán.

Remarks: Other *Prorocentrum* species have been reduced to synonyms of *P. maximum*, including *P. mexicanum* (Dodge, 1975). Not much information has been provided on the morphological variation of this species.

Prorocentrum mexicanum Osorio-Tafall, Figures 18–20

Osorio-Tafall, 1942, 440 pp., pl. 34, Figures 3 and 8; Faust, 1990, 549 pp., Figures 5–12; Steidinger & Tangen, 1997, 424 pp., pl. 8.

Synonym: Prorocentrum rhathymum Loeblich, Sherley & Schmidt

Fukuyo, 1981, 968 pp., Figures 5–7 and 47.

Cells are ovate with rounded margins in valve view, elliptical in apical view. Anterior end concave, with a small, winged spine on one side, close to the concavity. Specimens studied have smooth thecae, without poroids, but rows of pores (4–5) radiating from the center, obliquely to the margin. Some other pores close to the margins and one further row perpendicular to the margins, close to the anterior concavity. Length: 31–36 μm, width: 17–21 μm.

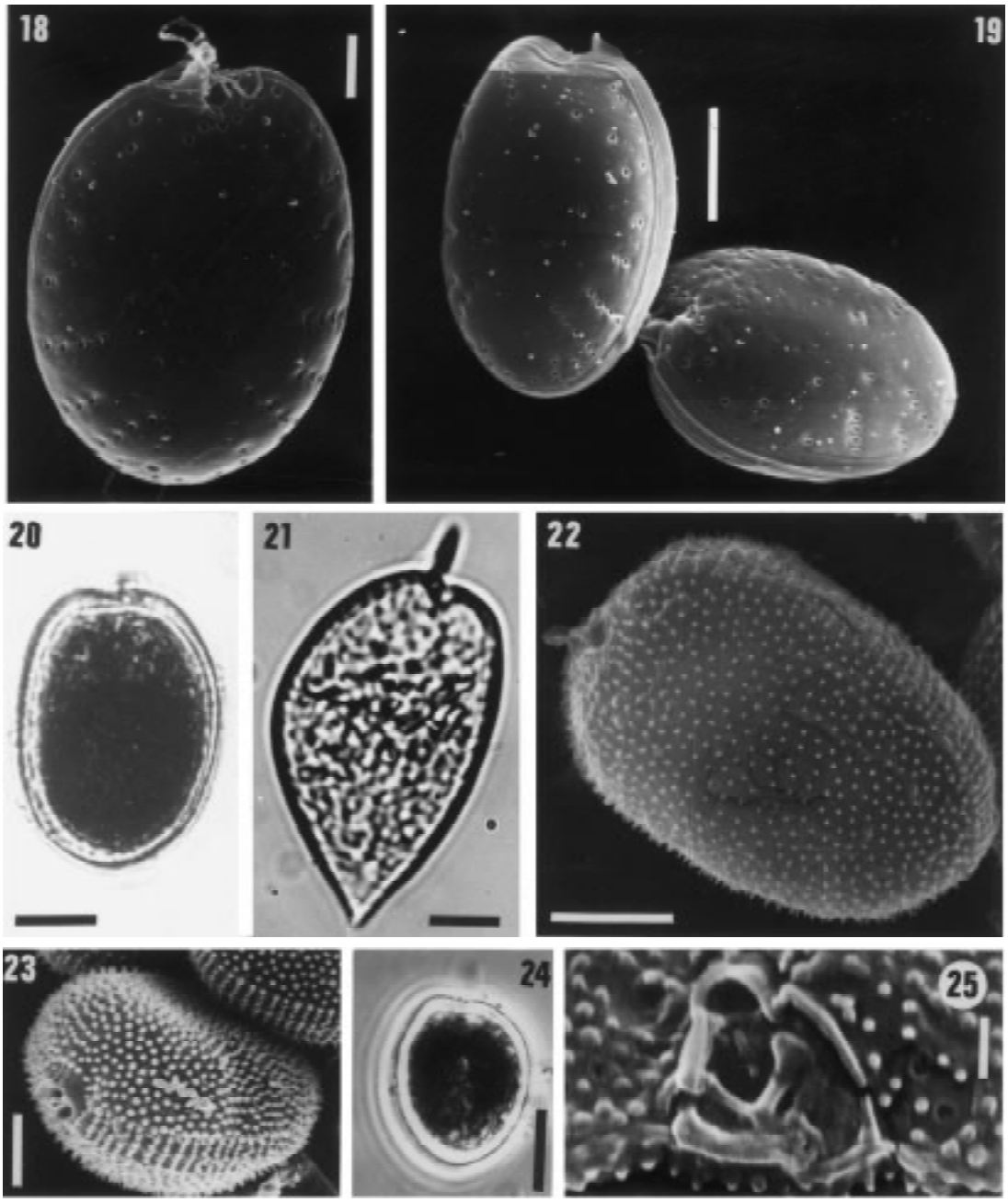
Distribution: Ocurring in some points of the Gulf of California and also in Acapulco.

Remarks: Faust (1990) found specimens with poroid thecae and mentioned that young cells of the species have smooth thecae, whereas older cells 'become rugose'. Details of the periflagelar area were not observed here.

Prorocentrum micans Ehrenberg, Figure 21

Ehrenberg, 1833, 307 pp.; Schiller, 1933, 35 pp., Figure 37; Dodge, 1975, 112 pp., Figure 3 A, pl. 2 A–C; Taylor, 1976, 23 pp.; Balech, 1988, 32 pp., pl. 4, Figure 1; Steidinger & Tangen, 1997, 424 pp., pl. 8.

Cells rather large, oval-lanceolate, with one margin rounded and the other nearly straight. Theca considerably wider from the middle toward the anterior end. Posterior end is very pointed, anterior end is concave with a prominent spine. One valve is excavated. Pattern of pores are similar to that of *P. gracile*: two oblique or radial rows (of up to six pores) in the third



Figures 18–25. *Prorocentrum* species, LM and SEM.
Figures 18–20. *Prorocentrum mexicanum*.
Figure 18. A complete cell in lateral view, showing one flagellum at the anterior end, SEM.
Figure 19. Two specimens, one with a small, winged spine at the anterior end, SEM.
Figure 20. A cell in lateral view, LM.
Figure 21. *Prorocentrum micans*, one cell in lateral view, LM.
Figures 22–25. *Prorocentrum minimum*.
Figure 22. Cell in lateral view, with minute spines on the theca, SEM.
Figure 23. One cell in apical view, with denser minute spines on the theca and showing the suture band, SEM.
Figure 24. A cell in lateral view, LM.
Figure 25. Detail of the periflagelar area, also exhibiting small pores surrounding this area, SEM. Scale bars= 10 μm (Figures 19–21 and 24), = 5 μm (Figures 18, 22 and 23), = 2 μm (Figure 25).

part of the theca, closer to the rounded margin; some other radial rows close to the straight margin of the theca, and various scattered pores are close to the margins. Length: 40–57 μm, width: 26–30 μm, length of spine: 7–9 μm.

Distribution: Widely distributed in the Mexican Pacific.

Remarks: This species is similar to *P. gracile* (see above) and in many cases, confusion between bot species may occur. *P. micans* is larger, with one margin of the valve more inflated and a pattern of pores slightly different.

Prorocentrum minimum (Pavillard) Schiller, Figures 22—25

Schiller, 1933, 32 pp., Figures 33 a, b; Dodge, 1975, 117 pp., Figures 4 E, F, pl. 3 A–D; Balech, 1988, 33 pp., pl. 4, Figure 7; Steidinger & Tangen, 1997, 425 pp., pl. 9.

Cells rather small and oval, subcircular to circular in valve view, flattened in side view. It has a short spine, mostly at anterior end. Thecae are evenly covered by minute spines (specimens showed a wide range of spines density on the thecae). Large pores are apparent surrounding the periflagellar area, whereas smaller pores occur scattered with no clear pattern. The periflagellar area is flat and has an apical collar; the flagellar pore is large. Length: 14–19 μm, width: 12–16 μm.

Distribution: Found in some stations of the Gulf of California and forming blooms ('red tides') in shrimp farms close to the bay of Mazatlán, reaching densities of 282 191 cels ml^{-1} (Cortés & Agraz, 1994).

Remarks: This species is closely related to *P. balticum* (Lohman) Loeblich III, but differs mainly in size (*P. balticum* is slightly smaller), shape and surface ornamentation. *P. minimum* presents a considerable morphological variation, which probably has lead to give several names to different morphotypes (see Hulburt, 1965; Faust, 1974). Observations on the periflagellar area of this species, made by Honsell & Talarico (1985), are confirmed here.

Prorocentrum robustum Osorio-Tafall, Figure 26

Osorio-Tafall, 1942, 439 pp., pl. 34, Figures 9 and 10.

The cells are ovate to subcircular, both margins rounded. The anterior end is slightly excavated, with a long and winged spine, whereas the posterior end is rounded. Pore pattern was not apparent. Length: 32–38 μm, width: 26–28 μm, length of spine: 5 μm.

Remarks: Measurements found in this study are similar to those provided by Osorio-Tafall (1942), when this species was first described; our Figure 26 is identical to Osorio-Tafall's Figure 10. *P. robustum* was placed as a synonym of *P. scutellum* Schröder by Dodge (1975), whereas *P. scutellum* shows a more acute porterior end, a more developed wing on the anterior spine and it is larger, *P. robustum* has a rounded posterior end.

Prorocentrum rostratum Stein, Figure 32

Stein, 1883, pl. 1, Figures 16 and 17; Dodge, 1975, 112 pp., Figures 3 F, G; Balech, 1988, 185 pp., pl. 4, Figure 8; Steidinger & Tangen, 1997, 425 pp., pl. 8.

Cells are medium-sized, very elongated and lanceolate, with nearly parallel or slightly inflated margins and a posterior end pointed. The anterior end is rounded in one side, whereas the other has a relatively long process. Pattern of pores not observed. Length: 48–50 μm, width: 12 μm, length of spine: 7 μm.

Distribution: Encountered in very low numbers and few stations in the Gulf of California.

Prorocentrum sigmoides Böhm, Figures 30, 31

Böhm, 1933, 398 pp., Figure 1; Osorio-Tafall, 1942, 438 pp., pl. 35, Figures 18 and 19.

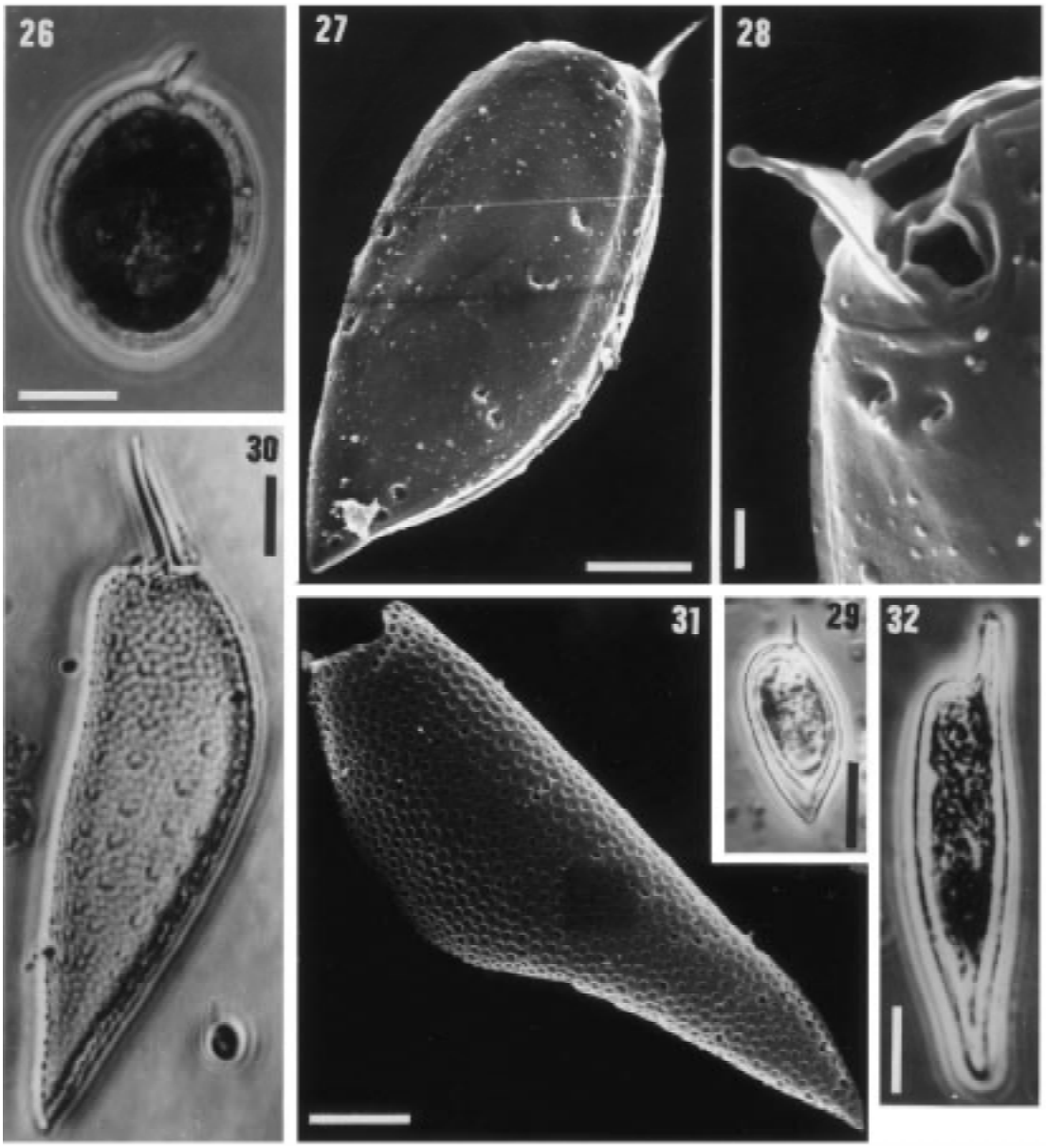
Cells are very elongated, lanceolate and clearly sigmoid. Posterior end pointed. Anterior spine very long, also slightly sigmoid and winged. Poroids spread regurarly on the thecae. Three or four rows of pores on the main axis of the cell: one row of pores (3–5) radiating obliquely toward the more curved margin, closer to the posterior end, at about 3/4 of the cell. Length: 70–73 μm, width: 22–23 μm, length of spine: 16 μm.

Remarks: We consider that this species is a 'currently recognized' one, but not a synonym of *P. gracile*, as regarded by Dodge (1975). The main arguments for this separation are the differences between the two species: the shape of the cell, measurements and the poroid pattern of the thecae. Furthermore, two other species, *P. gibbosum* and *P. arcutum* Issel, have a superficial resemblance to *P. sigmoides*, especially regarding the cell shape, the long apical spine and thecal surface, but the pore pattern is distinct, at least in *P. gibbosum* (Tolomio, 1988), whereas *P. arcuatum* has not been studied in detail.

Prorocentrum triestinum Schiller, Figures 27–29

Schiller, 1928, 57 pp., Figures 16 a–e, pl. 5, Figure 2; Dodge, 1975, 112 pp., Figures 2 A–C; Steidinger & Tangen, 1997, 426 pp., pl. 8.

Cells small-sized, thecae lanceolate, heart-shaped, with a posterior end pointed, one margin nearly straight or slightly sigmoid and the other is more rounded. In side view, the cells are lenticular. Anterior



Figures 26–32. Figure 26. *Prorocentrum robustum*, a cell in lateral view, showing a prominent anterior spine, LM.
Figures 27–29. *Prorocentrum triestinum*.
Figure 27. Complete cell in lateral view, SEM.
Figure 28. Detail of the anterior end, with the spine, periflagelar area and some pores around this area, SEM.
Figure 29. Cell in lateral view, LM.
Figures 30 and 31. *Prorocentrum sigmoides*.
Figure 30. A cell in lateral view, showing a very long spine, LM.
Figure 31. One theca (right) with poroids ditributed all over the theca, SEM.
Figure 32. *Prorocentrum rostratum*, cell in lateral view, LM. Scale bars= 10 μm (Figures 26, 27, 29, 30–32), = 5 μm (Figure 28).

end slightly excavated with a short, thin and winged spine. Thecae surface is smooth, but have pores located within depressions, distributed peripherally: one row (3–4 pores) is parallel to the rounded margin, closer to the posterior end, some other pores (3–6) surround the periflagellar area. Smaller pores with no depressions are scattered apparently at random. The periflagellar area is slightly excavated, with no particular ornamentation, but with a large flagellar pore. Length: 19–24 μm, width: 9–14 μm, length of spine: 3–5 μm.

Distribution: Species found in blooms, often producing red tides in the bay of Mazatlán, with a maximum density of 31 000 cels ml^{-1}.

Discussion

This is the first survey of the genus *Prorocentrum* in Mexican Pacific waters, although previous papers have dealt with some species of the genus (e.g. Osorio-Tafall, 1942, Hernández-Becerril, 1988a,b). The best studied area regarding planktonic algae is the Gulf of California, where Hernández-Becerril (1987) listed 11 species, including *Prorocentrum balticum*, *P. compressum*, *P. lima* (Ehrenberg) Dodge and *P. vaginulum* (Stein) Dodge, which were not encountered in this study. In addition, *Prorocentrum oblongum* (Schiller) Taylor was found by Licea et al. (1995) in the Gulf of California. The most common and widespread species were *Prorocentrum dentatum*, *P. gracile* and *P. micans*.

Therefore, we currently know 18 species of *Prorocentrum* in the Mexican Pacific. All are planktonic forms, but only *P. mexicanum* has been regarded as epiphytic (but observations by D.U. Hernández-Becerril showed that this species too can be truly planktonic). There are two new records: *Prorocentrum dactylum* and *P. lebourae*. *Prorocentrum mexicanum* and *P. robustum* were originally described in the Mexican Pacific by Osorio-Tafall (1942), while *P. sigmoides* was also reported by him. *Prorocentrum triestinum* has been previously cited in the Gulf of California by Gárate-Lizárraga et al. (1990).

Recent evidence suggests morphological and physiological differences between planktonic and benthic species: pores relate to the production of trichocysts in actively motile cells (in planktonic forms) or to production of mucocysts (in benthic forms) (Fukuyo, 1981; Zhou & Fritz, 1993; McLachlan et al., 1997). Furthermore, Zardoya et al. (1995) showed strong genetic differences between benthic and planktonic species, whereas Grzebyk et al. (1998) encountered two separate groups in nine species of *Prorocentrum*, one formed by benthic and the other by planktonic species.

Some species reported here produced blooms or red tides close to the bay of Mazatlán. These include *Prorocentrum dentatum*, *P. minimum* (in shrimp farms) and *P. triestinum*. *Prorocentrum minimum* has been associated with the production of toxin (Grzebyk et al., 1997) known as venerupin, but this has not been proved (Taylor et al., 1995). *Prorocentrum mexicanum* is also toxic, at least in cultures, producing a hemolytic toxin (Taylor et al., 1995); this species has also produced a red tide (whithout toxicity) in the Gulf of California (Gárate-Lizárraga & Martínez-López, 1997).

Monitoring for red tides caused by potentially toxic *Prorocentrum* species appears warranted and should focus on areas with aquacultural importance within this region, such as shrimp farms or coastal lagoons.

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