Protistology 17 (1): 3–15 (2023) | doi:10.21685/1680-0826-2023-17-1-1

Protistology

ORIGINAL ARTICLE

Observations on some planktonic dinophysoid dinoflagellates (Dinophysales, Dinophyta) from the Mexican Pacific, including the description of a new species, *Dinofurcula pseudoultima* sp. nov., and taxonomic and distribution notes about the genera *Latifascia* and *Triposolenia*†

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| Submitted May 17, 2022 | Accepted January 18, 2023 |

Summary

Dinoflagellates are an important component of marine phytoplankton in terms of diversity, biomass, and ecological role as primary and secondary producers. Dinophysoids are thecate dinoflagellates with solitary cells divided in two halves, sagittal suture, reduced epitheca, and prominent cingular and sulcal lists. During the analyses of phytoplankton samples from the tropical Mexican Pacific, specimens of rare and little-known dinophysoid species were found, including a new species, *Dinofurcula pseudoultima* sp. nov., as well as *Dinofurcula ventralis, Latifascia inaequale, Triposolenia bicornis, Triposolenia depressa* and *Triposolenia longicornis* that were studied using basically light microscopy, and scanning electron microscopy for one species. All species are heterotrophic forms, with food vacuoles and no chloroplasts. The new species *Dinofurcula pseudoultima* is a small cell with a characteristic domed epitheca, an epithecal crest and a triangular dorsoposterior process, differing in cell shape and size from the closely related species *Dinofurcula ultima. Dinofurcula ventralis* in our samples was almost identical in shape and size to the original description. Detailed observations of *Latifascia inaequalis* showed important plates that

† This paper is dedicated to the memory of Juan Carlos Hernández-Becerril (1968–2022), brother of the senior author (DUH-B).

https://doi.org/10.21685/1680-0826-2023-17-1-1

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characterize this species, particularly H_1 (first hypothecal plate); the left sulcal list does not belong entirely to the left half, as originally described. *Triposolenia longicornis* had a shape and size very similar to the original description and, surprisingly, it was found in one coastal station. *Dinofurcula ventralis* and *Triposolenia longicornis* are illustrated since these are their original findings, and together with *Latifascia inaequalis* they represent new records in the Mexican Pacific. *Triposolenia bicornis* and *Triposolenia depressa* are firstly illustrated for the Mexican Pacific. New taxonomic combinations are proposed within the genus *Latifascia*.

Key words: dinoflagellates, dinophysoids, morphology, new records, new species, Mexican central Pacific, phytoplankton

Introduction

Dinoflagellates are an important component of marine phytoplankton all over the world in terms of diversity, biomass and productivity. They integrate part of a complicated food web, as about half of the extant species are photosynthetic and the other half are mixotrophic, phagotrophic and even parasitic (Gómez, 2012a). In the Mexican Pacific, the diversity of planktonic dinoflagellates is very high and includes an important fraction of tropical and subtropical forms (Hernández-Becerril, 1988a, 1988b; Hernández-Becerril et al., 2008; Esqueda-Lara and Hernández-Becerril, 2010; Hernández-Becerril et al., 2021). The group of the so-called dinophysoid dinoflagellates (order Dinophysales) encompasses a diverse assemblage of characteristic solitary thecate forms divided in two halves with a sagittal suture, lateral compression, reduction of epitheca, large or elongated hypotheca, and variable development of cingular and sulcal lists (Sournia, 1986; Fensome et al., 1993; Steidinger and Tangen, 1997; Hernández-Becerril et al., 2008). Species of some dinophysoid genera are heterotrophs and/or have symbiotic relationships with Cyanobacteria and picoeukaryotes (Sournia, 1986; Tarangkoon et al., 2010; Daugbjerg et al., 2013). Most dinophysoids are planktonic forms; they are particularly diverse in tropical areas (Kofoid and Skogsberg, 1928; Hernández-Becerril et al., 2008; Zinssmeister et al., 2017; Estrella et al., 2020).

The genus *Dinofurcula* Kofoid et Skogsberg, proposed in 1928 (Kofoid and Skogsberg, 1928), is considered as a dinophysoid, and its two historical species, *Dinofurcula ultima* (Kofoid) Kofoid et Skogsberg (the type species) and *D. ventralis* Kofoid et Skogsberg, have been rarely reported since their original description, despite their very characteristic shape (Hernández-Becerril and Bravo-Sierra, 2004; Ochoa and Baylón, 2005). There is a third species, the recently described *Dinofurcula tricornuta* Gómez (Gómez, 2022). This genus includes species with a unique "molariform" shape in lateral view, posterior processes, and in the type species, the sulcus is displaced to the right half. According to previous reports, these species prefer subsurface to deeper water layers and their populations are not too dense (Gómez, 2022).

The genus *Heteroschisma* Kofoid et Skogsberg (another dinophysoid) was originally established by Kofoid and Skogsberg (1928), with the description of *Heteroschisma inaequale* Kofoid et Skogsberg (the type species) and *H. aequalae* Kofoid et Skogsberg. These descriptions based on two main morphological characteristics such as the presence of an unusually large first hypothecal plate (H_1) in the left hypothecal half, and the left sulcal list (LSL) belonging to the left half in its entire extension. Later, the name *Heteroschisma* was replaced by *Latifascia* Loeblich et A.R. Loeblich III (Loeblich Jr. and Loeblich III, 1966), with the consequent nomenclatural changes. There are two accepted species, *Latifascia inaequalis* (Kofoid et Skogsberg) Loeblich et A.R. Loeblich III and *L. subantarctica* (Balech) Okolodkov (Guiry, 2022), but the species *Heteroschisma aequale* has not been transferred to *Latifascia*. Currently, *Heteroschisma encompasses* either four species (Gómez, 2005) or six species (Guiry, 2022), and *Latifascia* – only two (Gómez, 2012b; Guiry, 2022).

The dinophysoid genus *Triposolenia* Kofoid was first described by Kofoid (1906), including five species, among which *Triposolenia truncata* Kofoid is the type species. Other species were described later (Kofoid, 1907; Kofoid and Skogsberg, 1928), and until now, we may count 10 species, including the most recently described, *Triposolenia fallax* Hernández-Becerril et Meave del Castillo (Hernández-Becerril and Meave, 1999). The main morphological feature is the "tripoid" character, or the presence of three extensions: an anterior part and two posterior extensions or processes in lateral view (Kofoid, 1906). All species of the genus are considered rare to extremely rare, as some species were described based on only one specimen (Hernández-Becerril and Meave, 1999). They are distributed in tropical to subtropical regions and preferably in deep waters (Kofoid, 1907; Kofoid and Skogsberg, 1928; Dolan et al., 2019).

During the study of phytoplankton net and filtered samples from various oceanographic cruises carried out along the tropical Mexican Pacific, specimens of six species of dinophysoid dinoflagellates were found, described and illustrated by light microscopy (LM), and scanning electron microscopy (SEM) (only one species): two species of the genus *Dinofurcula, Dinofurcula pseudoultima* sp. nov. (a new species) and *D. ventralis*, as well as *Latifascia inaequalis, Triposolenia bicornis, Triposolenia depressa* and *Triposolenia longicornis*. Their distribution is also discussed here. *Dinofurcula ventralis* and *Triposolenia longicornis* are illustrated since we present their original findings. Additionally, these two species and *Latifascia inaequalis* represent new records in the Mexican Pacific, whereas *Triposolenia bicornis* and *Triposolenia depressa* are firstly illustrated for the Mexican Pacific.

Material and methods

Net phytoplankton samples obtained during four oceanographic cruises in the tropical coasts of the tropical Mexican Pacific were studied. The study area is located between 20°27’ N and 16°20’ N, and 100°06’ W and 106°15’ W. The cruises were carried out on board the R/V “El Puma” and corresponded to “MareaR VIII” (31 March - 11 April, 2016), “MareaR IX” (18-30 April, 2017), “MareaR X” (13-24 April, 2018), and “MareaR XI” (2-13 April, 2019) (Hernández-Becerril et al., 2021). Phytoplankton samples were collected using the nets with 54 and 64 µm mesh in vertical hauls from 100 to 120 m depth at 47 stations and were preserved with formaldehyde (4% final concentration). Additionally, a 3 L bottle sample from one location (Station 32: 15° 27’ N, 94° 22’ W) from the Gulf of Tehuantepec, Mexican Pacific (oceanographic cruise PACMEX III, 6-17 April, 2000), which had been filtered through 0.45 µm pore size filters and washed with 30 ml of distilled water, was used to study the new species of *Dinofurcula*.

Samples were analyzed by light microscopy; either raw (not rinsed) or rinsed aliquots were studied. The equipment used was a light microscope Olympus, BX40, and attached camera Hitachi KP-D50 Color digital. Specimens of rare dinoflagellates were found and specifically aliquots containing these specimens were treated using sodium hypochlorite, following recommendations by Taylor (1978) and Taylor et al. (2003), for making the theca transparent. In addition, a small piece (about 1 cm^2) of the filter from the Gulf of Tehuantepec was mounted on a stub, dried, and coated with gold to be studied by scanning electron microscopy (SEM); the equipment used was a JEOL 1200 EX scanning electron microscope (Hernández-Becerril and Bravo-Sierra, 2004).

Terminology followed recommendation by Kofoid (1906), Kofoid and Skobgsberg (1928), and Balech (1967, 1980, 1988) for *Dinofurcula, Heteroschisma* (*Latifacia*) and *Triposolenia*. Measurements made of the specimens considered total length (length), total cell depth (dorsovental distance, depth), width of the body (width), and length of antapical processes.

Results

Morphological descriptions

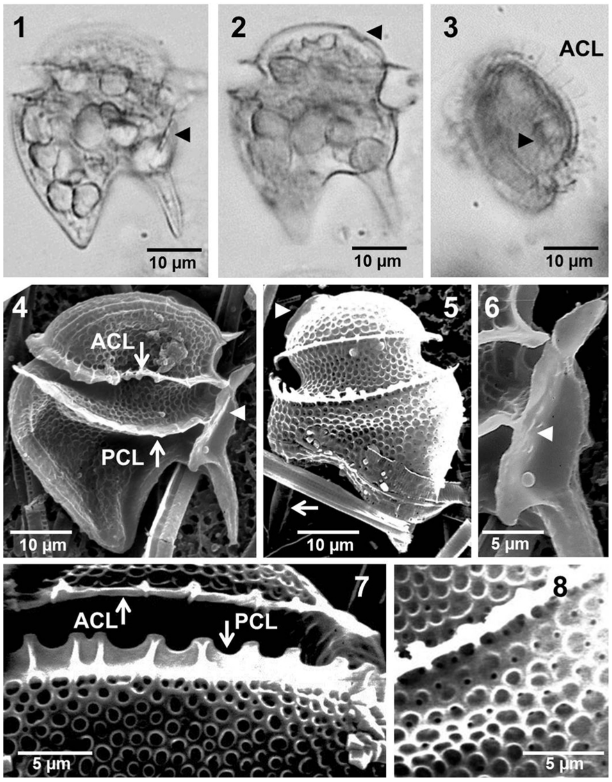
Genus *Dinofurcula* Kofoid et Skogsberg

Dinofurcula pseudoultima Hernández-Becerril sp. nov. (Figs 1-8).

Synonyms: *Dinofurcula* cf. *ultima* (Kofoid) Kofoid et Skogsberg *sensu* Hernández-Becerril and Bravo-Sierra, 2004, p. 342, figs 2-7; *Dinofurcula* cf. *ventralis* Kofoid et Skogsberg *sensu* Ochoa and Baylyn, 2005, p. 378, figs 2, 3.

Diagnosis: Solitary, small-sized cells with molariform shape in lateral outline and strongly compressed laterally. High and domed epitheca, protruding over the cingular lists. Excavated and wide cingulum. Hypotheca elongated, bifurcated, with two processes, the dorsoposterior triangular and the ventroposterior thinner and horn-like. Cingular lists wide, with ribs. Sulcus located laterally, on the right side, sulcal lists poorly developed. A short crest present in the left epithecal plate. Cells with no chloroplasts but food vacuoles present.

Description: Solitary cell of small size, with a “molariform” shape in lateral view (Figs 1, 2, 4, 5), and strongly compressed laterally (Fig. 3). The



Figs 1–8. *Dinofurcula pseudoultima*, LM and SEM. **Figs 1, 2**. Cell in right lateral view, showing the general outline and details as the displaced sulcus and a notch indicating the location of the epithecal crest (*arrowheads*), respectively; food vacuoles are apparent, LM. **Fig. 3**. Cell in apical view, showing the epitheca with the ACL with ribs and the epithecal crest (*arrowhead*), LM. **Fig. 4**. Cell in right lateral view showing the domed epitheca, cingulum and sulcus displaced to the right (*arrowhead*), SEM. **Fig. 5**. Left lateral view with the epithecal crest (*arrowhead*), wide cingulum and its lists, and the ventroposterior process (*arrow*), SEM. **Fig. 6**. Detail of the left sulcal list (*arrowhead*), SEM. **Figs 7, 8.** Details of the cingular lists and their ribs, and the theca ornamentation, SEM.

epitheca is relatively high and domed (8–10.5 µm height), and protrudes over the anterior cingular list (ACL), the cingulum is wide and excavated (4.5–7 µm wide), the hypotheca is elongated and bifurcated, the dorsoposterior process with a triangular shape, whereas the ventroposterior one is an elongated and thin horn-like process (Figs 1, 2, 4, 5). The maximum separation between the two tips of the posterior processes ranges between 14 and 18 µm.

There is an indentation in the epitheca closer to the ventral side (Fig. 2), which is interpreted as an epithecal crest (Figs 3, 5). This crest runs parallel to the suture line of the epitheca and extends for about one third of the cell's total depth (Fig. 5).

The cingulum has wide lists at both the anterior and posterior edge, each with numerous ribs (width of cingular lists 3.5–5 µm) (Figs 3–5, 7, 8). The sulcus has a lateral position in right lateral view as a characteristic longitudinal furrow, and it extends between the two posterior processes of the hypotheca (Figs 1, 4, 6). The right and left sulcal lists appear not very prominent (Figs 1, 6). The sulcus is 3.5–5.5 µm wide, with lists being 2.6–3.8 µm wide.

The theca is ornamented by irregularly round to ovoid areolae of different sizes, many of them randomly perforated by very small pores (Figs 7, 8). These areolae are absent in the ventroposterior process (Figs 4, 6).

The cells studied showed many large food vacuoles, but no chloroplasts (Figs 1, 2).

Measurements: 31–36.5 µm length, 25.4–29 µm total depth, 13 µm length of processes (Table 1). Seven specimens were measured.

Holotype: As the species is not kept in culture and is impossible to preserve, we are considering the ICN article 40.5, which mentions that "the type of a name of a new species ... of microscopic algae... may be an effectively published illustration if there are technical difficulties of specimen preservation or if it is impossible to preserve a specimen that would show the features attributed to the taxon by the author of the name".

Iconotype: Specimens illustrated in Figures 1, 2, 4 and 5.

Type locality: Material obtained from a coastal location in the tropical Mexican Pacific (20° 17' 50" N, and 106° 04' 15" W).

Etymology: The species name is related to the original confusion with *Dinofurcula ultima*.

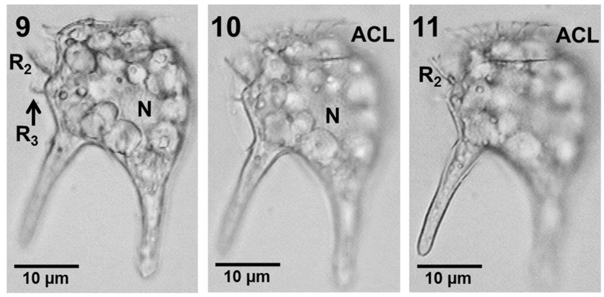
Dinofurcula ventralis Kofoid et Skogsberg (Figs 9–11).

Kofoid and Skogsberg, 1928, p. 205, figs 28, 2–4.

Description: Cell of small to medium size, similar to *D. ultima*, also of a "molariform" shape in lateral view and strongly compressed laterally, with two asymmetric posterior horn-like processes (Fig. 9). Epitheca low and bumped, not protruding over the anterior cingular list, with wide cingulum; hypotheca elongated and bifurcated (Fig. 9). The dorsoposterior process is slightly wider and longer than the ventroposterior one (Figs 9–11). The hypothecal ventral margin is sinuous and the dorsal margin is convex (Figs 9, 10).

The anterior cingular list (ACL) is well developed and shows several ribs, whereas the posterior cingular list (PCL) is significantly less conspicuous (Figs 10, 11). The left sulcal list (LSL) was observed, which is narrow and short, supported by three ribs, R_2 being the longest and strongest, whereas R_1 and R_3 are very short (Figs 9-11). No chloroplasts were found, but many food vacuoles (more than 10) and the nucleus were located close to the centre of the hypotheca (Figs 9, 10).

Measurements: 54 µm length, 36 µm total depth, 32.5 µm body depth, 26 µm length of processes (Table 1). Only one specimen observed.



Figs 9–11. *Dinofurcula ventralis*, LM. Three different focuses of a cell in left lateral view, exhibiting posterior processes, centric nucleus (N), LSL with ribs (mainly R_2 and R_3) and ACL with ribs; food vacuoles are shown.

Genus *Latifascia* Loeblich Jr. et Loeblich III (= *Heteroschisma* Kofoid et Skogsberg)

Latifascia inaequalis (Kofoid et Skogsberg) Loeblich et A.R. Loeblich, III (Figs 12–27)

Loeblich Jr. and Loeblich III, 1966, p. 38.

Synonym: *Heteroschisma inaequale* Kofoid et Skogsberg

Kofoid and Skogsberg, 1928, p. 38, text-fig. 1(3), pl. 1, figs 1, 2; Balech, 1988, p. 37, pl. 4, figs 9, 10, 12.

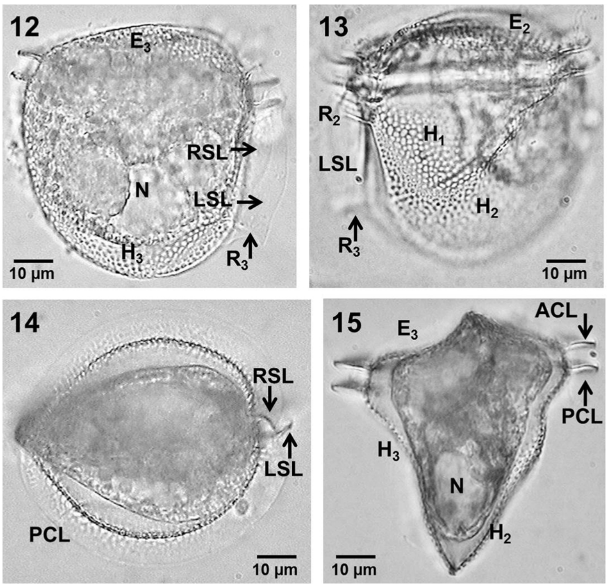
Description: Cell of medium size, with a broad ovate, "phalacromoid" shape in lateral view (Figs 12, 13). The epitheca is relatively high, as it protrudes from the cingular lists and is domed; the hypotheca is large and semi spheric, rounded at the antapical margins and with straighter ventral margin (Figs 12, 13). Both cingular lists are wide and well developed; the posterior cingular list has incipient and short areolae-like ornamentations (instead of true ribs) sticked to the bases of this list (Fig. 14). In left lateral view, the large first hypothecal plate (H1) is clearly visible, it occupies almost a half of the hypotheca (Fig. 13).

The left sulcal list (LSL) is wide and long, reaching almost to the end part of the hypotheca, supported by three ribs (R_1–R_3) where R_2 (the intermediate one) is closer to R_1, and R_3 is the longest one (Figs 12, 13). The right sulcal list (RSL) is less developed, reaching to the middle of the hypotheca, and has no ribs (Fig. 12).

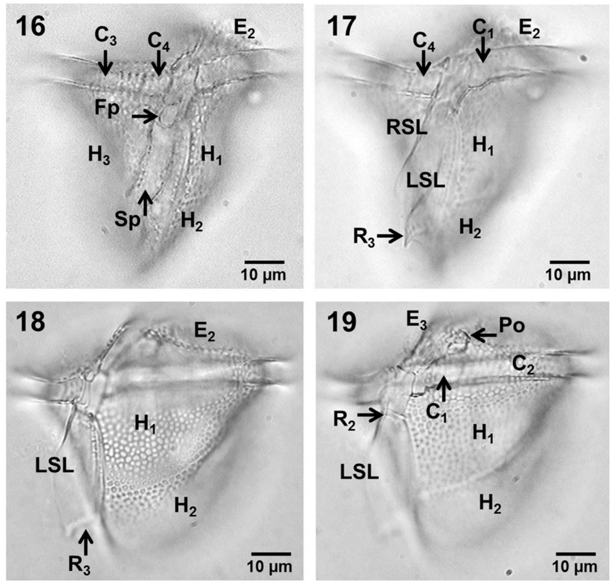
In ventral view, the cell appears asymmetrically biconical, with very pointed apical and antapical ends, a conspicuous inflation of the left hypothecal half, and convex hypothecal half (Fig. 15). This ventral view shows details of the RSL and the LSL,

Table 1. Morphological characters and geographic distribution of the known *Dinofurcula* species. Data from Kofoid and Skogsberg (1928), Gómez (2022), and this study (*). Processes are ventro-posterior (v-p), short posterior (s p) and long posterior (l p). All measurements are given in µm.

Species	*D. pseudoultima*	*D. tricornuta*	*D. ultima*	*D. ventralis*
Length	31–36.5*	53–57	61.3–63.6	56.5–60.7 54*
Depth	25.4–29*	30	39–39.7	31.1–36 36*
Epitheca height	8–10.5*	17–20	–	–
Cingulum width	4.5–7*	5	–	5*
Length of processes	13*	25 (v–p) 10–11 (s p) 15 (l p)	–	26*
Separation of processes	14–18*	–	–	27*
Geographic area	Tropical Mexican Pacific, Peruvian coasts	Marmara Sea (Mediterranean)	Eastern tropical Pacific	Eastern tropical Pacific



Figs 12–15. *Latifascia inaequalis*, LM. **Figs 12, 13**. Cell in right and left lateral view, respectively, showing the nucleus, RSL, LSL and its ribs (R_2 and R_3) and some important plates, including H_1 and H_2. **Fig. 14.** Cell in antapical view, with the wide PCL, reduced RSL and larger LSL. **Fig. 15**. Cell in ventral view, showing cingular lists (ACL and PCL), nucleus and some large plates.



Figs 16–19. *Latifascia inaequalis*, LM. **Figs 16, 17**. Ventral view of the cell with relevant plates, the flagellar pore (Fp) and sulcal lists (RSL and LSL). **Figs 18, 19**. Detail of cell in ventro- left lateral view, showing the LSL and two ribs, and important plates, including H_1 and H_2.

the large flagellar pore and the posterior sulcal plate (Sp), as well as the cingular plates (C_1–C_4) and some epithecal (E_2) and hypothecal plates (H_1–H_3) (Figs 16, 17). Other intermediate view shows the triangular shape of the H_1 and the conspicuous apical pore (Po) (Figs 18, 19).

A thecal dissociation allowed to observe the upper part of the LSL (between R_1 and R_2) sticked to the H_1, indicating that the LSL does not belong in its entire extension to the left half of the cell (Fig. 20), and some smaller epithecal plates (E_1 and E_4), the apical plates (A1 and A_2), and the apical pore (Po) (Figs 21-24). The recognized sulcal plates are the posterior (Sp) and the right ones (Sd): the Sp is long and tongue-shaped, with four longitudinal rows of small poroids and a forked upper part, whereas the Sd is completely forked (Figs 25-27).

The theca is ornamented with regularly distributed areolae of various sizes and shapes, with three rows of areolae along the cingulum. No chloroplast was observed.

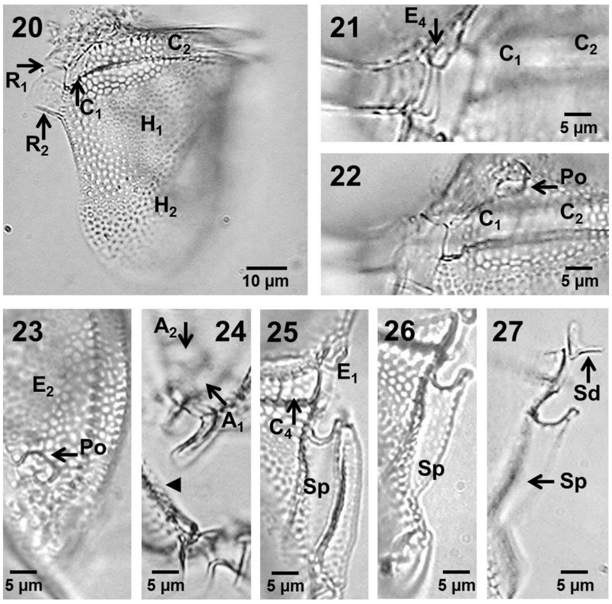
Measurements: 64.5 µm length, 58 µm body depth, 69 µm total depth, 51.6 µm width. One specimen studied.

Genus *Triposolenia* Kofoid

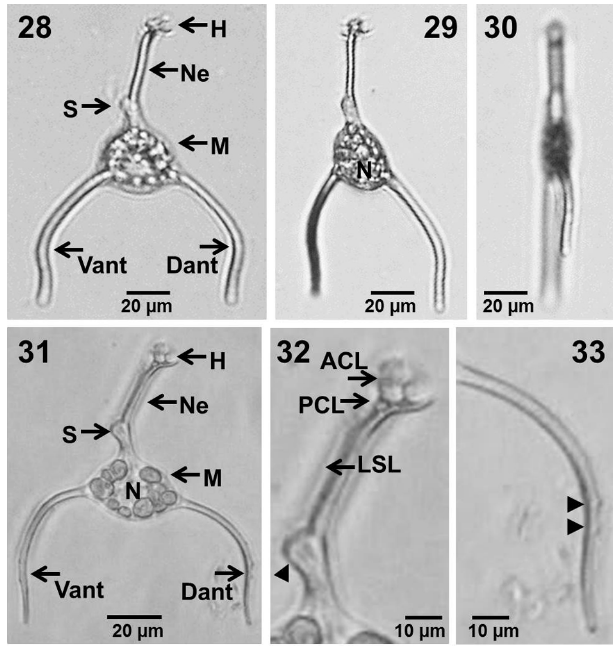
Triposolenia bicornis Kofoid (Figs 28-30)

Kofoid, 1906, p. 105, pl. 15, figs 1, 2; Jörgensen, 1923, p. 41, fig. 62; Kofoid and Skogsberg, 1928, p. 473, fig. 66; Abé, 1967, p. 114, fig. 45; Taylor, 1976, p. 31, pl. 3, fig. 33; Gómez et al., 2011, figs 1 j-m; Iwataki et al., 2012, p. 59; Jung and Kim, 2013, p. 1242, fig. 14; Yang et al., 2014, p. 34, figs 28 a-e; Zinssmeister et al., 2017, fig. 6 i.

Description: Cell solitary and relatively large, with a tripoid feature (e.g. anterior part and two posterior extensions) in left lateral view, and compressed laterally (Figs 28, 30). The head, composed by a flat episome and cingulum, bears poorly developed anterior and posterior cingular lists (Figs 28, 29), and continues with a long, straight and narrow neck, leaned to the dorsal side (about 15°), until reaching a conspicuous shoulder (Figs 28, 29), and then the midbody, which is rather round, with curved anterior and posterior margins (Fig. 28). There are two long and almost symmetric posterior processes (ventral and dorsal antapicals) (Figs 28-30), raising from the posterior extremes of the midbody (Figs 28, 29), slightly curved, with a flexion close to their ends, and short spines or knobs on the external margins of the terminal portion of both antapicals (Figs 28,



Figs 20–27. *Latifascia inaequalis*, LM. **Fig. 20**. Detail of the left half of the cell, with upper part of the LSL (R_1 and R_2) and hypothecal plates H_1 and H_2. Figs **21, 22**. Details of the anterior part of the cell, showing some epithecal and cingular plates and the apical pore complex (Po). **Fig. 23**. Another detail of the apical pore complex (Po). **Fig. 24**. Details of the apical plates and the sagittal suture (arrowhead). **Figs 25–27**. Details of some cingular, epithecal and sulcal plates.



Figs 28–33. *Triposolenia bicornis* and *Triposolenia depressa*, LM. **Figs 28–30**. *Triposolenia bicornis.* Three different views of a cell: left lateral view, intermediate view and dorsal view, respectively. Head (H), neck (Ne), shoulder (S), midbody (M), and ventral and dorsal antapical processes (Vant and Dant, respectively). **Figs 31-33**. *Triposolenia depresssa*. **Fig. 31**. A cell in left lateral view showing main morphological characters. **Fig. 32**. Detail of the small head, neck and shoulder (*arrowhead*). **Fig. 33**. Detail of the dorsal antapical process, with spines or knobs on the external margins (*arrowheads*).

29). The cell showed no chloroplasts but some food vacuoles and a large nucleus close to the center of the midbody (Figs 28, 29).

Measurements: 130 µm length, 35 µm midbody depth, 28 µm neck length, 59 and 57 µm length of ventral and dorsal antapical processes, respectively (Table 2). One specimen found.

Triposolenia depressa Kofoid (Figs 31–33)

Kofoid, 1906, p. 104, pl. 16, figs 3, 4; Kofoid and Skogsberg, 1928, p. 468, figs 64, 65, pl. 14, figs 4-9; Balech 1962, p. 130, pl. 17, fig. 252; Balech 1988, p. 72, pl. 17, fig. 14.

Description: Cell very similar to the precedent, relatively large and with a tripoid feature (Fig. 31). The head is very small, with very poorly developed cingular lists, a straight neck and a prominent shoulder (Fig. 32); the anterior part is, however, more leaned to the dorsal side (about 30°) (Figs 31, 32). The midbody is ovoid, with smoothly curved anterior margins and convex posterior margin, whereas the antapical processes are nearly symmetric, curving broadly (Fig. 31), with short spines or knobs on the external margins of the terminal portion of the antapicals (Fig. 33). A centrally located nucleus was detected but no chloroplasts were found, only many relatively large food vacuoles.

Measurements: 110 µm length, 39 µm midbody depth, 30 µm neck length, 52 and 49 µm length of ventral and dorsal antapical processes, respectively (Table 2). One specimen found.

Triposolenia longicornis Kofoid (Figs 34-38)

Kofoid, 1907, p. 201, pl. 17, fig. 101; Kofoid and Skogsberg, 1928, p. 479, fig. 69 (1-3), pl. 15, figs 1-6.

Description: Cell of comparatively large size, tripoid in left lateral view and compressed laterally (Fig. 34). The head shows fairly developed anterior and posterior cingular lists (Fig. 36), and there is a long, straight and narrow neck, leaned to the dorsal side (approximately 25–30°), a prominent

Table 2. Morphological characters and geographic distribution of the three *Triposolenia* species studied here. Data from Kofoid and Skogsberg (1928) (*) and this study. All measurements are given in µm.

Species	*T. bicornis*	*T. depressa*	*T. longicornis*
Length	120–153* 130	92–122* 110	210–243* 230
Midbody depth	35	39	69
Head	Small, fairly developed lists	Very small, poorly developed lists	Medium, well- developed lists
Neck length Inclination	28 15°	30 30°	58 25–30°
Shoulder	Conspicuous	Prominent	Prominent
Antapicals Ventral Dorsal Spines	 60 57 +	 52 49 +	 130 134 –
Geographic area	Tropical and subtropical Pacific, Atlantic and Indian Oceans	Eastern tropical and subtropical Pacific, south Atlantic	Eastern tropical Pacific, Mediterranean

shoulder (Figs 34, 36), and the triangular midbody with straight or slightly curved anterior margins and convex posterior margin (Fig. 35). The two posterior processes are very long and almost symmetric (Figs 34, 37, 38), raising from the posterior extremes of the midbody (Figs 34, 35); the processes curve broadly, with no conspicuous spines or knobs and are truncate (Figs 37, 38). The cell had no chloroplasts, but many food vacuoles, and a large nucleus close to the posterior margin of the midbody (Figs 34, 35).

Measurements: 230 µm length, 69 µm midbody depth, 58 µm length neck, 130 and 134 µm length of ventral and dorsal antapical processes, respectively (Table 2). Only one specimen studied.

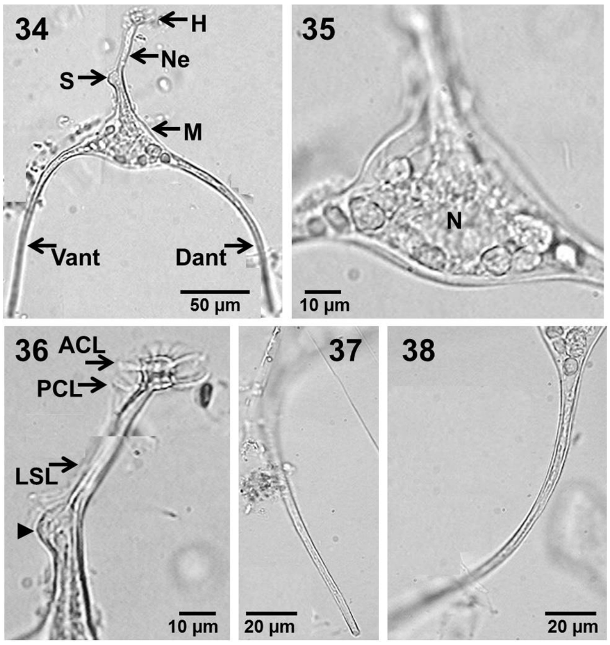
Discussion

The new species *Dinofurcula pseudoultima* Hernández-Becerril sp. nov.

The description of *Dinofurcula pseudoultima* as a new species is based on the observations by LM and SEM, where both cell shape and size were different from those of the closely related species *Dinofurcula ultima* (the type species of the genus) (Hernández-Becerril and Bravo-Sierra, 2004, figs 2-7). The name previously conferred to that species was *Dinofurcula* cf. *ultima* (Hernández-Becerril and Bravo-Sierra, 2004). We now realize that the specimens found in the Gulf of Tehuantepec (southern part of the Mexican Pacific), are identical and consistent in morphology to those found more recently in net samples from the oceanographic cruises “MareaR” (2016–2019), and it also includes the specimen found in Peruvian waters (Ochoa and Baylyn, 2005). We are dealing with a new species, different from *Dinofurcula ultima*. Ochoa and Baylyn (2005) had recorded *Dinofurcula* cf. *ventralis* from Peruvian coasts, but their description (including measurements) and illustrations show high similarity with specimens of *Dinofurcula* cf. *ultima*, as found and described by Hernández-Becerril and Bravo-Sierra (2004), and in the current study.

Here, we also complement previous observations that included details of the sulcus displaced to the right half of the cell, the reduced RSL with a couple of very incipient ribs, and the more extended LSL with 4 to 5 short ribs, as a continuation of the PCL, as well as the finding of an apical crest-like structure on the left epithecal plate (E_2), running in parallel to the suture line (Hernández-Becerril and Bravo-Sierra, 2004, figs 2-7; figs 1-3, 5 in this study).

The main differences between *Dinofurcula pseudoultima* and *D. ultima* are the following: (1) Cell shape. *D. ultima* shows a relatively low epitheca, slightly protruding over the cingular lists, with a large bump toward the ventral side, which is different from the relatively high and domed epitheca present in *D. pseudoultima*. Additionally, the posterior processes are both very elongate and horn-like in *D. ultima*, whereas in *D. pseudoultima*, only one process (the ventroposterior one) is relatively similar, although shorter, and the other (the dorsoposterior one) is consistently triangular. (2) Size of the cells. *D. ultima* was described with a total length of 61.3 to 63.6 µm and greatest depth of 39-39.7 µm, in contrast to *D. pseudoultima*, which yielded measurements of 31–36.5 µm length and 25.4–29 µm depth (Table 1). (3) The presence of the epithecal crest parallel



Figs 34–38. *Triposolenia longicornis*, LM. **Fig. 34**. A complete cell in left lateral view, showing important parts of the species, as indicated previously. **Fig. 35**. Detail of the midbody, with the nucleus. **Fig. 36**. Detail of the head, neck and shoulder (*arrowhead*), with the ACL, PCL and LSL. **Figs 37, 38**. Details of the two antapical processes.

to the suture line in *D. pseudoultima*, which is absent (or unknown) in *D. ultima*. This crest found in *D. pseudoultima* was interpreted as the bump toward the ventral end in the original description and illustration of *D. ultima* (Hernández-Becerril and Bravo-Sierra, 2004), but it is now clear that these are two different structures that belong to different species. Both species share the unique character of the sulcus displacement to the right half of the cell, and the continuation of the PCL into the LSL.

Although *D. ultima* was described having a "finely reticulate" theca ornamentation and the illustrations showed that character (Kofoid and Skogsberg, 1928, pl. 5, figs 4, 6), it is not absolutely certain whether both species share this character. In particular, the illustrations by SEM (Figs 7, 8) showed the regular reticulation (areolae and pores) of the theca (except in the dorsal margin and the tips of the two processes) as was recorded also in *D.* cf. *ultima* (now *D. pseudoultima*) (Hernández-Becerril and Bravo-Sierra, 2004, figs 2-7).

We may now count with four species of *Dinofurcula*, with the two species found and described here (*Dinofurcula pseudoultima* and *D. ventralis*) plus *D. ultima* and *D. tricornuta*, the latter recently described from the Marmara Sea (Mediterranean Sea) (Gómez, 2022).

Morphology and taxonomy of the other species

Another species of *Dinofurcula*, also found in this study, *Dinofurcula ventralis*, was depicted here for first time since the original description of the genus, and it was almost identical in shape and size to the original illustration and description (Kofoid and Skogsberg, 1928). Thus, the species is illustrated for the first time since nearly a century ago.

In contrast to both *Dinofurcula pseudoultima* and *D. ultima, D. ventralis* does not show the sulcus displaced to the right side of the cell. We additionally confirmed that the epitheca is bumped, not protruding over the ACL, which is well developed and has apparent ribs; the two posterior processes are about the same shape and length, and R_2 is the longest and most conspicuous rib of the LSL.

Ochoa and Baylón (2005) recorded *Dinofurcula* cf. *ventralis* from Peruvian coasts, but their description, measurements and illustrations show high similarity with specimens of *Dinofurcula* cf. *ultima*, as found and described by Hernández-Becerril and Bravo-Sierra (2004), and in the current study, which is considered to be a new species, *Dinofurcula pseudoultima*. The four known species of the genus *Dinofurcula* are compared in Table 1.

The genus *Heteroschisma* (now *Latifascia*) was originally erected considering important distinctive morphological characteristics such as: (1) the presence of an unusually large first hypothecal plate (H1) in the left hypothecal half, and (2) the left sulcal list belonging to the left half in its entire extension (Kofoid and Skogsberg, 1928). Balech (1967) discussed these two characters and he had another opinion considering that the left sulcal list had a different structure than presumably related species of the genera *Dinophysis* Ehrenberg or *Phalacroma* Stein. This in fact is shown also in our paper: the left sulcal list (LSL) does not belong in its entire extension to the left half of the cell (see Fig. 16). Additionally, Balech (1967) suggested another evident and distinctive morphological character in *Heteroschisma*, which is the location and structure of the apical pore, and later Balech (1980) mentioned that the apical region became more complicated and was formed by three plates. The latter character was shown also in this study (see Figs 14, 17, 18).

If we consider all described *Heteroschisma* species as part of *Latifascia,* for nomenclatural reasons

(Loeblich Jr. and Loeblich III, 1966; Zinssmeister et al., 2017), the following nomenclature changes are proposed here:

Genus *Latifascia* Loeblich Jr. et Loeblich III
(= *Heteroschisma* Kofoid et Skogsberg)
Latifascia aequalis (Kofoid et Skobgsberg) Hernández-Becerril nov. comb.
Basonym: *Heteroschisma aequale* Kofoid et Skogsberg
Kofoid and Skogsberg, 1928, p. 36, pl. 1, figs 7, 8, fig. 1: 1, 2.

Latifascia longialata (Gaarder) Hernández-Becerril nov. comb.
Basonym: *Phalacroma longialata* Gaarder
Gaarder, 1954, p. 53, figs 70a.
(non *Dinophysis longialata* Gran et Braarud)
Synonyms: *Heteroschisma longialata* (Gaarder) Balech
Balech, 1967, p. 98, pl. III, figs 62-69.
Dinophysis fortunata Sournia
Sournia, 1973, p. 13.

Latifascia pirum (Gaarder) Hernández-Becerril nov. comb.
Basonym: *Phalacroma pirum* Gaarder
Gaarder, 1954, p. 54, figs 70 b, c.
Synonym: *Heteroschisma pirum* (Gaarder) Balech
Balech, 1967, p. 95, pl. III, figs 47-54.

There is one additionally listed species of *Heteroschisma, H. globulus* (Schütt) Schiller (Gómez, 2005; Guiry, 2022). However, according to Balech (1967), this species should not be considered as a true representative of *Heteroschisma* because it is very poorly known and, therefore, it is neither included in *Latifascia*.

Concerning the *Triposolenia* species studied here, we confirm the high similarity between *Triposolenia bicornis* and *T. depressa*, both species found in this study (Table 2). Balech (1988) discussed this similarity earlier. The main differences are size of head, leaning of the anterior part, shoulder prominence, midbody shape, and curvature of the antapical processes. *Triposolenia bicornis* has, in comparison with *T. depressa*, a larger head, less leaning of the anterior part (15° versus 30°), shoulder not so protuberant, the midbody is more rounded and the antapical processes are almost straight, with a flexion close to their ends. Additionally, *Triposolenia bicornis* is slightly larger than *T. depressa* (Table 2).

The specimen analyzed in this study and identified as *Triposolenia longicornis* had a very similar shape and size as in the original descriptions (Kofoid, 1907; Kofoid and Skogsberg, 1928). Its large size and characteristic shape, with the two long and smoothly curved antapical extensions, lead to no confusion about its identity, although it is superficially similar to *T. fatula* Kofoid, but much larger. It is illustrated in this paper for first time ever since its original description, illustration and further study in the early last century (Kofoid, 1907; Kofoid and Skogsberg, 1928).

The phylogeny of the genera *Dinofurcula* and *Latifascia* (or *Heteroschisma*) has not been resolved for obvious reasons (e.g. only scarce material is available from field samples or in successful cultures). However, there is one approach to the molecular phylogenies of one *Triposolenia* species, *T. bicornis*, which claded together with species of *Amphisolenia* Stein, as expected because both genera belong to the same family, Amphisoleniaceae Lindemann (Gómez et al., 2011).

Ecology and distribution

All species found in this study may be considered as "shade-forms" ("shade-flora") (Sournia, 1982; Gómez et al., 2011; Dolan et al., 2019; Gómez, 2022), as they have been detected deep in the water column since their original description (Kofoid, 1907; Kofoid and Skogsberg, 1928; Gómez, 2022). As previously described and also shown here, these species lack chloroplasts and show food vacuoles. Thus, considering their distribution in deep waters, they represent potential predators to phytoplanktonic cells of about same size or smaller, or they may have symbiotic relationships (Tarangkoon et al., 2010; Daugbjerg et al., 2013), especially in the case of *Triposolenia longicornis*.

The world´s distribution of the six species studied here and their distribution in the Mexican Pacific is shown in Figure 39. These species are better represented in the tropical and subtropical eastern Pacific Ocean, mainly because of the papers by Kofoid (1906), and especially due to Kofoid (1907), and Kofoid and Skogsberg (1928) who made an extraordinary effort on these regions. Nevertheless, the species have been less studied in the world´s Oceans, with only one record in the Indian Ocean (Taylor, 1976) (Fig. 39).

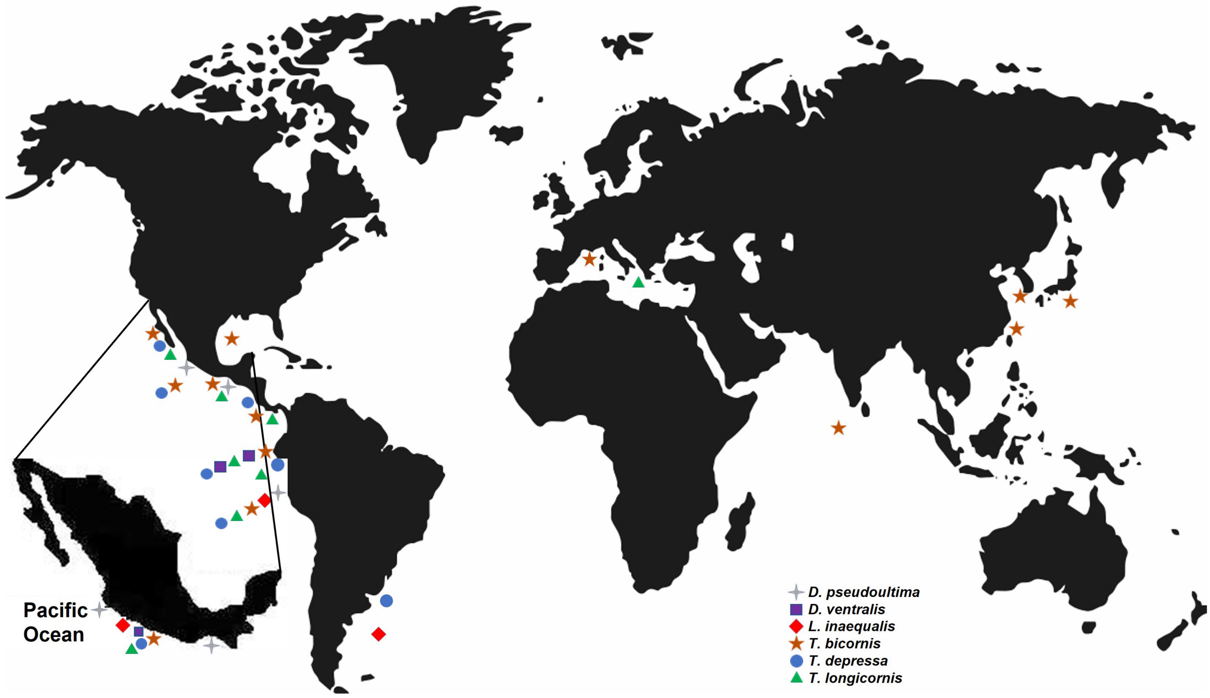


Fig. 39. World and local distribution of the six dinoflagellate species studied here.

Both traditional species of *Dinofurcula, D. ultima* and *D. ventralis*, were originally recorded from the southeastern Pacific (Peruvian current and the south equatorial drift) (Kofoid, 1907; Kofoid and Skogsberg, 1928). The third species, *D. tricornuta*, was recently described from the Marmara Sea (Mediterranean Sea) (Gómez, 2022), in the northern hemisphere. *Dinofurcula pseudoultima* appeared in Mexican tropical waters of the Pacific Ocean, but Ochoa and Baylón (2005) found the same species in the Peruvian coastal waters; therefore, we can conclude that the species is widely distributed in the eastern Pacific Ocean, in both hemispheres. *Dinofurcula ventralis* is a new record for the northern hemisphere and in the Mexican Pacific area (Fig. 39).

Latifascia inaequalis was originally found in the eastern tropical Pacific, in the Peruvian current (sic) (Kofoid and Skogsberg, 1928), and then it has been collected and identified from the southwestern Atlantic Ocean (Balech, 1988). The distribution of this species has been only in the southern hemisphere in both the Pacific and the Atlantic Oceans; therefore, *Latifascia inaequalis* represents a new record in the northern hemisphere and the Mexican Pacific (Fig. 39).

Triposolenia bicornis and *T. depressa* appear to be widely distributed in more tropical and subtropical waters, according to the previous records of both species (e.g. Kofoid, 1906; Jörgensen, 1923; Kofoid and Skogsberg, 1928; Balech 1962; Abé, 1967; Taylor, 1976; Balech 1988; Iwataki et al., 2012; Yang et al., 2014; Zinssmeister et al., 2017) (Fig. 39). *Triposolenia longicornis* was originally collected from the tropical and subtropical regions of the eastern Pacific, including various stations of the “Albatross” expedition: coasts of Baja California, Mexico and the central Mexican Pacific (including Acapulco), the Peruvian current (sic), the Galapagos Islands and the south equatorial drift (sic) (Kofoid, 1907; Kofoid and Skogsberg, 1928) (Fig. 39). Despite of that, this species had not been included in the list of dinoflagellates from the Mexican Pacific (Hernández-Becerril et al., 2003), most probably by omission, and therefore we report it as a new record for that region. The species has been recorded also in the Mediterranean Sea (Gómez, 2003) (Fig. 39). In this study, surprisingly, the species was found in one coastal station, where supposedly upwelling or another physical process may carry deep water to shallower and coastal regions.

Acknowledgments

Partial support for this study was provided by PAPIIT, DGAPA, UNAM (project IN296516). Coordinación de la Investigación Científica (CIC), Universidad Nacional Autynóma de México (UNAM) approved and supported the use of the R/V "El Puma" to carry out the oceanographic cruises "MareaR".

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