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Species of the planktonic diatom genus *Skeletonema* (Bacillariophyta) from the Mexican Pacific Ocean

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Abstract – After the recent revisions of the diatom genus *Skeletonema*, our knowledge on its diversity has greatly improved, although its taxonomy has become more complicated, especially with the descriptions of cryptic or semicryptic species, which make species recognition difficult. The combination of different observation techniques (LM, SEM and TEM) and/or the use of molecular tools are now required for an accurate identification. In this paper, we studied numerous phytoplankton samples collected with nets or bottles from locations along the Mexican Pacific, and provided observations on the morphospecies of *Skeletonema*. Four taxa were found using LM, SEM and TEM: *Skeletonema* sp. aff. *japonicum* and *Skeletonema* cf. *marinoi*, *S. pseudocostatum* and *S. tropicum*. Some features of the chains, cells, valves, terminal or intercalary fultoportulae and rimoportulae, and cingular bands, are given for each species. The taxon named here *Skeletonema* cf. *marinoi* showed particular characters (ribs-like structures), not previously described, on the fultoportulae of terminal valves, which arise suspects of the presence of new species within the species complex. We annotate *Skeletonema pseudocostatum* as a new record from the Mexican Pacific, where only three species have been previously recorded. The species *Skeletonema costatum*, traditionally considered as abundant, frequent and widely spread all over the region, was not recognized in our samples.

Diatoms / Mexican Pacific Ocean / Morphology / Phytoplankton / *Skeletonema*

Résumé – Les espèces de la diatomée du genre *Skeletonema* (Bacillariophyta) de l'Océan Pacifique du Mexique. Après les récentes révisions du genre *Skeletonema* par certains auteurs, la taxonomie du genre est devenue plus compliquée avec la découverte d'espèces cryptiques ou demicryptiques. Il est dorénavant nécessaire de tenir compte de certaines caractéristiques morphologiques de façon très détaillée (uniquement avec microscopie électronique à balayage et transmission) et/ou des techniques de biologie moléculaire. Dans cet article nous avons étudié de nombreux échantillons recueillis avec des filets de plancton et des bouteilles à divers endroits dans le Pacifique du Mexique, pour l'identification des espèces planctoniques du genre *Skeletonema*. Quatre taxa ont été trouvés à l'aide de ML, MEB et MET : *Skeletonema* sp. aff. *japonicum* and *Skeletonema* cf. *marinoi*, *S. pseudocostatum* and *S. tropicum*. Les détails morphologiques des espèces,

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comme les valves, fultoportulées et rimoportulées terminale et intercalaire, copulées de cingulum, sont fournis. Le taxon nommé ici comme *Skeletonema* cf. *marinoi* a montré des caractères particuliers (structures ressemblant à des côtes), qui n'ont pas été décrits, sur les fultoportulées des valves terminales, par consequent nous suspectons la présence d'une nouvelle espèce pseudocryptique au sein de ce complexe d'espèces. Nous reportons la présence de *Skeletonema pseudocostatum* sur le Pacifique mexicaine, ou seulement trois espèces ont été documentées à ce jour. L'espèce *Skeletonema costatum*, supposément, fréquente et abondante dans le Pacifique du Mexique, n'a pas été détecté dans cette étude et nous considérons qu'elle avait été incorrectement identifiée auparavant.

Diatomées / Océan Pacifique mexicain / Morphologie / Phytoplancton / *Skeletonema*

INTRODUCTION

The diatom genus *Skeletonema* Greville *emend*. Sarno *et* Zingone is currently constituted by planktonic forms, mainly marine, and widespread all over the world. Globally, species of *Skeletonema* are numerically important in coastal areas, where they may produce non-toxic "blooms" (Smayda, 1973), or even red tides (Wang *et al.*, 1993), moreover they may also cause fish escape reactions and fish and benthic invertebrates mortality due to oxygen depletion, produced by unknown allelopathic substances, that interact with seaweeds and some dinoflagellates and rahidophytes forming HAB (Zacaroni & Scaravelli, 2007; Granéli *et al.*, 2008). Abundances and seasonality of *Skeletonema* species have been studied for long time series (Borkman & Smayda, 2009) in certain areas.

In general, the species of the genus form cylindrical chains connected by marginal processes (fultoportulae) which fuse in sibling valves, with only one rimoportula per valve, and cells having one, two or many chloroplasts (Hasle, 1973; Round *et al.*, 1990; Hasle & Syvertsen, 1997). Some recent studies combining molecular biology and morphological observations have yielded a number of "cryptic or semicryptic species", especially considering that the putative cosmopolitan species *Skeletonema costatum* (Greville) Cleve can be really split in various species (Medlin et al., 1991), distinguished by both molecular characters and very detailed morphological characters, most of them only visible by electron microscopy (Sarno *et al.*, 2005, 2007; Zingone *et al.*, 2005; Kooistra *et al.*, 2008). Critical morphological characters for identifying species have traditionally included cell size (diameter), cells per chain, areolae density, number of fultoportulae per valve, number of chloroplasts per cell, and more recently characters such as shape of fultoportulae in terminal valves and their tip shape, number of connections between sibling fultoportulae, and cingular bands ultrastructure, should also be considered (Sarno *et al.*, 2005; Bergesch *et al.*, 2009; Naik *et al.*, 2010). Recent studies providing morphological descriptions of *Skeletonema* species were carried out in Brazil (Bergesh *et al.*, 2009), Korea (Jung *et al.*, 2009) and India (Naik *et al.*, 2010).

Other attempts to recognize *Skeletonema* species nowadays include the use of molecular tools, such as sequences of the LSU, ITS-1, ITS-2 and 5.8S rDNA (Godhe *et al.*, 2006; Chen *et al.*, 2007a, b; Ellegaard *et al.*, 2008), although the molecular approach (LSU rDNA) for species delimitation not always matches with morphological identification, as shown for *Skeletonema marinoi*/*dohrnii* by Ellegaard *et al.* (2008).

In this paper, we studied numerous phytoplankton samples collected with nets or bottles from diverse locations along the Mexican Pacific, and provided observations on the morphospecies (e.g. species recognized by morphological characters) of the genus *Skeletonema*.

MATERIAL AND METHODS

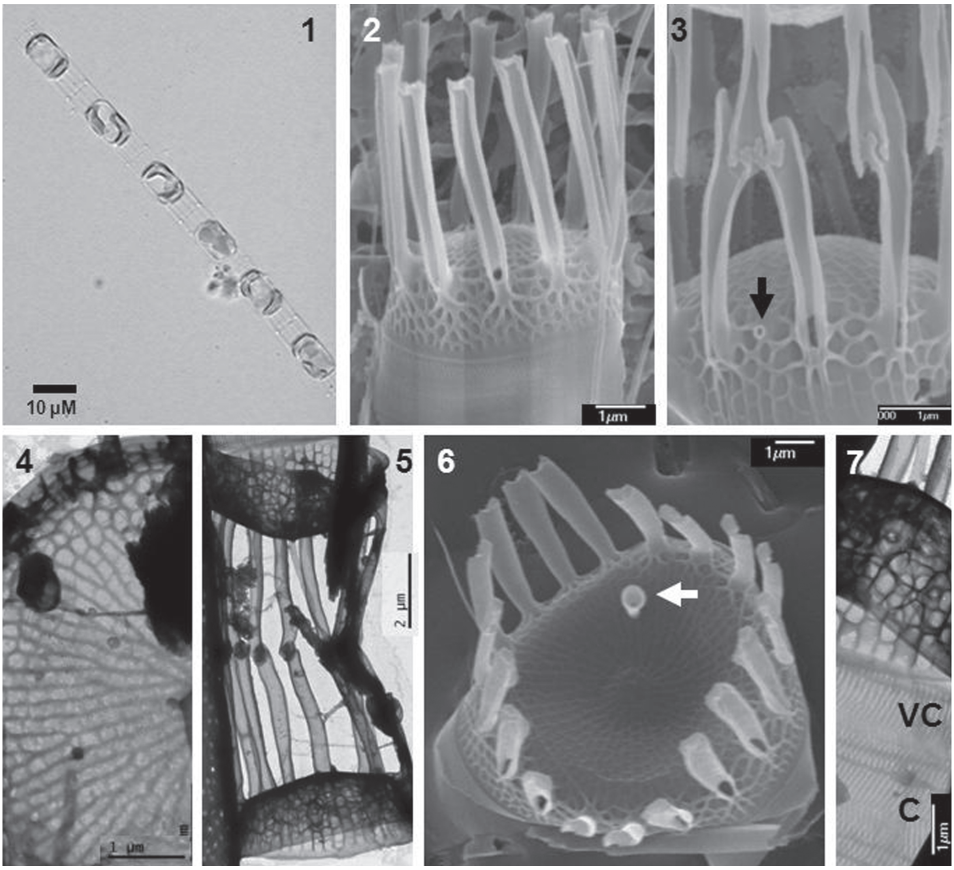
Phytoplankton samples for this study were obtained from various locations and different periods along coasts of the Mexican Pacific Ocean, and were taken by nets (meshes 45-64 μm) in vertical hauls (maximum 100 m) and/or by bottles at different depths. Net samples were fixed with 4% formalin and bottle samples were fixed with Lugol's solution. A total of 68 samples, deposited at the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, were studied.

Samples were examined either fresh, after rinsing with distilled water, or digested to remove all the organic matter following a potassium permanganate oxidation and a hydrochloric acid protocol (Simonsen, 1974; Hasle 1978). Both unprocessed and cleaned diatom material were examined in light microscopy (LM) using an Olympus BX 40 optical microscope, equipped with a Hitachi KP-D50 color digital camera and a Zeiss Axiolab microscope. For the examination in scanning electron microscopy (SEM), some rinsed or cleaned material was put on coverslips, air-dried and mounted on aluminum stubs, coated with gold (Ion Sputter JFC 1100, JEOL) and observed using a JEOL JSM6360LV SEM. Treated material was also used for observations by TEM (JEOL TEM1200 EXII), following conventional methods.

RESULTS

***Skeletonema* sp. aff. *japonicum* Zingone *et* Sarno** **Figs 1-7**

References: Sarno *et al.*, 2005, p. 158, figs 4 A-J.
Description: Cells arranged in rather long chains (6-22 cells per chain) (Fig. 1). Two chloroplasts per cell were observed (Fig. 1). The valves are flat to convex, with a mantle relatively high (Figs 2, 3, 5, 7). All fultoportulae are open (Figs 2, 3, 5-7), although some fultoportulae of intercalary valves (IF) showed a closed base (Fig. 3). The tips of fultoportulae of terminal valves (TF) are truncated or with a short spine (Figs 2, 6). Each IF connects one or two IF's of the sibling valve in a singular manner (Figs 3, 5). The valves show rectangular, polyedric or elongate areolae (Figs 4, 7). The rimoportula of intercalary valves (IR) is very short with no external tube and is located marginally (Fig. 3, arrow), whereas the rimoportula of terminal valves (TR) occurs between the valve margin and the valve centre, and is more tubular (Fig. 6, arrow). Some details of the cingular bands show valvocopula, copulae, ribs and rows of poroids (Fig. 7).
Measurements: cell diameter 2.6-9 μm, areolae density 30-50 in 10 μm (other morphometric data are also provided in Table 1).



Figs 1-7. *Skeletonema* sp. aff. *japonicum*, LM, SEM and TEM. **1.** A chain of 6 cells containing two chloroplasts per cell, LM. **2.** Terminal valve with high mantle and fultoportulae, SEM. **3.** Intercalary valves showing valve areolae, fultoportulae connected (1:1 or 1:2) and a marginal rimoportula (arrow), SEM. Fig. **4.** Detail of a valve with areolae, TEM. **5.** Two sibling valves showing valve and fultoportulae connected (1:1), TEM. **6.** Valve view of a terminal valve, with fultoportulae and a single eccentric rimportula (arrow), SEM. **7.** Details of the valve mantle and cingulum bands (valvocopula, VC and copulae, C), TEM.

***Skeletonema* cf. *marinoi* Sarno *et* Zingone — Figs 8-15**

References: Sarno *et al.*, 2005, p. 160, figs 5 A-H; Jung *et al.*, 2009, p. 197, figs 2 A-H.

Description: Straight to slightly curved chains of 9-25 cells were found (Fig. 8). The valves are flat and have a mantle variable in height (Figs 9-11, 13, 14). TF may be short or long, open and with the tip flared and jagged margins (Figs 9, 13, 14), whereas IF may also be relatively short to long and are also open, each IF connecting one or two of the sibling valve (Figs 10-12). TR has a long tube, becoming wider at the tip (Figs 13, 14). Close to the tip of TF there are a number (1-5) of short transverse ribs-like structures, depending on the length of the processes (TF) (Figs 9, 13, 14, arrowheads). This character has not been previously

Table 1. Morphological and morphometric characters of the *Skeletonema* species found in the Mexican Pacific Ocean

	Skeletonema sp. aff. *japonicum*	*Skeletonema* cf. *marinoi*	*Skeletonema pseudocostatum*	*Skeletonema tropicum*
Cell diameter (µm)	2.6-9.0	7.2-12.3	2.8-11.0	15.5-27.4
Cells per chain	6-22	9-25	5-18	10-24
Number of chloroplasts	2	–	1-2	4-5
Length of pervalvar axis (µm)	8-16	12-27	15-27	15-25
Areolae in 10 µm	30-50	32-55	35-40	22-26
Fultoportulae in 10 µm	12.6	13.5	10.9	8.9
Distance between fultoportulae (µm)	0.6-1-2	0.6-1.1	0.6-1.4	0.7-1.15
Shape of fultoportulae	Open (IF show closed bases), tips truncated with short spines	Open with tip flared and transverse ribs-like structures	Open, bases tubular and oblique, tips with long spines	Open with tip truncated
Cingular bands ribs in 1 µm	12-13	13-15	14-15	13-14

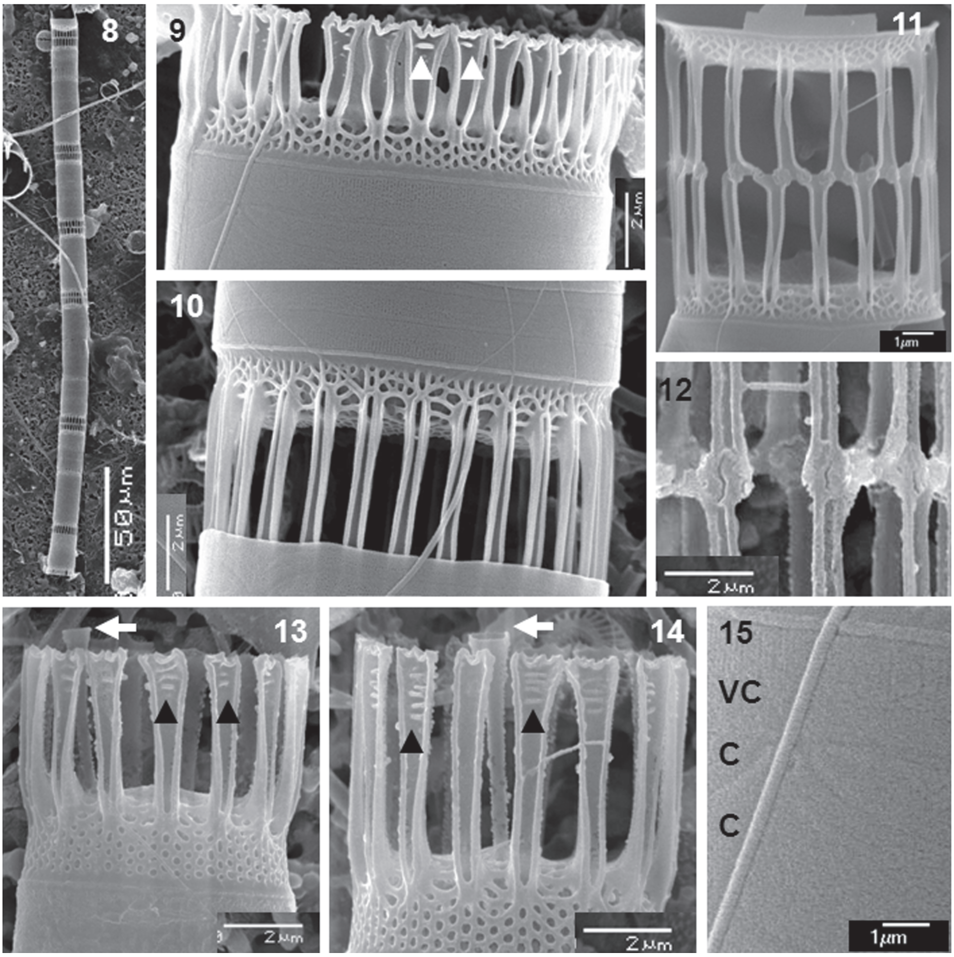
described and might be important in the near future, if the combination of molecular and morphological studies demonstrates this fact. Cingular bands (valvocoupa and copulae) show ligula and antiligula, and longitudinal rows of tiny poroids (Fig. 15).
Measurements: cell diameter 7.2-12.3 µm, areolae density 32-55 in 10 µm (Table 1).

***Skeletonema pseudocostatum* Medlin *emend.* Zingone *et* Sarno** **Figs 16-25**

References: Medlin *et al.*, 1991, p. 522; Sarno *et al.*, 2005, p. 162, figs 7, A-I.
Description: Chains relatively long and straight, with 5-18 cells were found (Figs 16, 17). Usually there are one or two chloroplasts per cell (Fig. 16). Valves are flat to convex, with a relatively high valve mantle (Figs 18, 19, 21, 22). All TF's are open, although their bases are more tubular and oblique to the cell axis, forming an angle (Fig. 20, arrowhead), and their tips have a long spine (Figs 18, 19). Each IF fuses to one of the sibling valve (Figs 21-23). The TR is nearly marginal, and has a long tube, with an inflated tip (Figs 18, 19), whereas the IR is also almost marginal, but very short (Fig. 23, arrow). Cingular bands exhibit perpendicular rows of minute poroids (Figs 24, 25).
Measurements: cell diameter 2.8-11 µm, areolae density 35-40 in 10 µm (Table 1).

***Skeletonema tropicum* Cleve** **Figs 26-31**

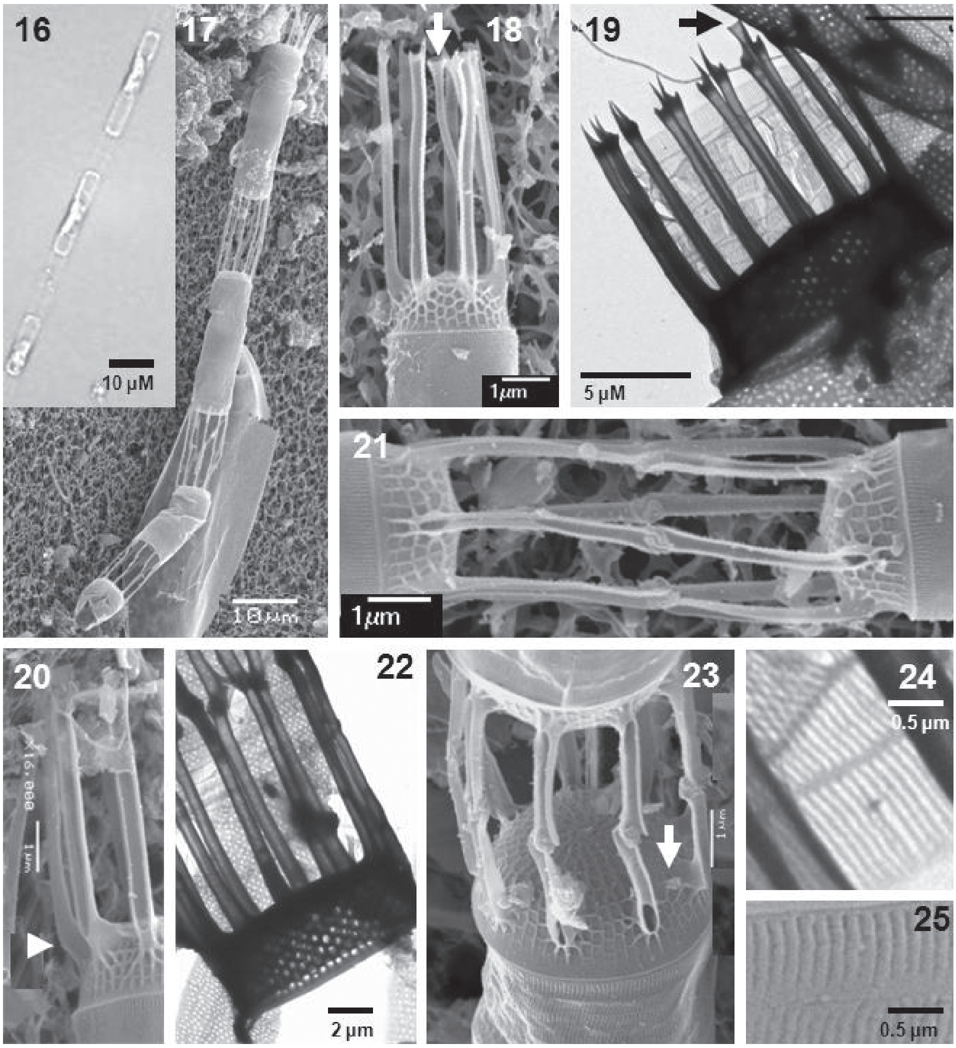
References: Sarno *et al.*, 2005, p. 166, figs 9 A-H; Jung *et al.*, 2009, p. 202, Figs 4 A-H.
Description: Relatively long and straight chains of this species were encountered (although some were found broken), with 10-24 cells (Figs 26, 27). Cells showed more than two chloroplasts per cell (usually 4-5) (Fig. 26). The valves are flat to slightly convex and have a relatively low mantle (Figs 27-29, 31). IF's are relatively



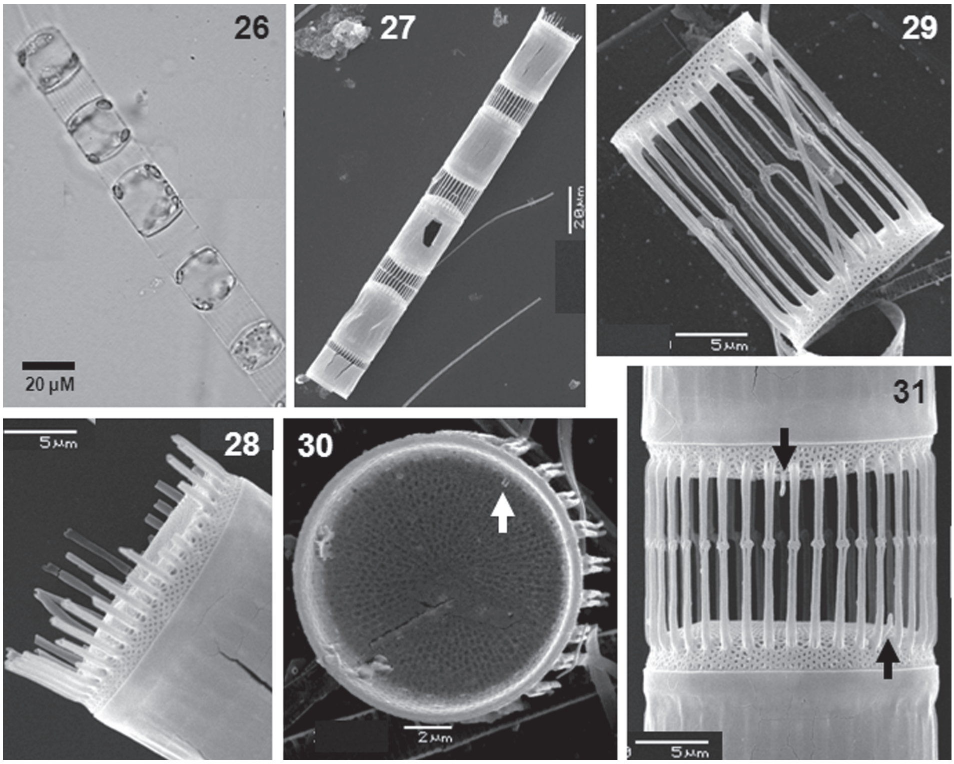
Figs 8-15. *Skeletonema* cf. *marinoi*, SEM. **8.** A long and slightly curved chain of the species. **9.** Terminal valve exhibiting mantle, cingulum and short fultoportulae with some short transverse ribs-like structures (arrowheads). Fig. **10.** Intercalary valves with open fultoportulae. **11.** Intercalary valves with fultoportulae joining the corresponding of sibling valves (1:1 or 1:2). **12.** Fultoportulae of intercalary valves connected 1:1. **13, 14.** Terminal valves of a same chain, showing longer fultoportulae with ribs-like structures (arrowheads) and rimoportulae (arrows). **15.** Cingular bands (valvocupula, VC and copulae, C), showing ligula and antiligulae.

long and open, and each may connect with only one or two of the other IF of the sibling valve (Figs 29, 31), whereas TF's appeared shorter (Fig. 28 shows TF's probably broken). TR was located at the valve margin and showed an internal labiate structure (Fig. 30), whereas the IR's were thin with a short tubular structure and also marginal (Fig. 31).

Measurements: cell diameter 15.5-27.4 µm, areolae density 22-26 in 10 µm (Table 1).



Figs 16-25. *Skeletonema pseudocostatum*, LM, SEM and TEM. **16.** Part of a thin chain, LM. **17.** Terminal part of a chain, SEM. **18.** Terminal valve with fultoportulae and a single, long rimoportula (arrow), SEM. **19.** Terminal valve with fultoportulae having pointed spines and a single rimportula (arrow), TEM. **20.** Terminal valve showing open fultoportulae with their bases tubular and oblique to the cell axis (arrowheads), SEM. **21.** Intercalary valves showing mantle, areolae and fultoportulae connected 1:1, SEM. **22.** Intercalary valves with details of the connections between fultoportulae, TEM. **23.** Intercalary valves with fultoportulae connected 1:1, and a single short tube of rimoportula (arrow), SEM. **24, 25.** Some details of cingular bands (rows of poroids), TEM and SEM, respectively.



Figs 26-31. *Skeletonema tropicum*, LM and SEM. **26.** Part of a straight chain with five cells and various chloroplasts per cell, LM. **27.** A broken chain with four cells, SEM. **28.** Terminal valve with its fultoportulae, SEM. **29.** Two loose intercalary valves, showing connections between fultoportulae, SEM. **30.** Internal view of a terminal valve, with fultoportulae and the labiate structure of the marginal rimoportula (arrow), SEM. **31.** Intercalary valves exhibiting mantle, cingulum, fultoportulae connections 1:1, and short external tubular structures of rimoportulae (arrows), SEM.

DISCUSSION

The genus *Skeletonema* in Mexican Pacific waters has been considered to be constituted by only two species: *S. costatum* and *S. tropicum* (Hernández-Becerril, 1987). In a previous morphological and ecological study on species of the genus, made in a coastal lagoon from the Gulf of Mexico (Atlantic Ocean), Aké-Castillo *et al.* (1995) included these two species as well as other brakish species.

However, after the recent revisions of the genus using both molecular and morphological characters, more than 10 species are currently recognized in the world Ocean (Sarno *et al.*, 2005, 2007; Zingone *et al.*, 2005; Kooistra *et al.*, 2008). Furthermore, most of the morphological characters used to distinguish species required an observation by electron microscopy: shape of fultoportulae in terminal valves and their tip shape, number of connections between sibling fultoportulae, and cingular bands ultrastructure.

The only species that appears to be relatively easy to accurately identify within the genus (even using only LM) is *Skeletonema tropicum*, mainly due to the combination of (1) large size (long chains and cell diameter), and (2) number of chloroplasts per cell (more than 2, mostly 4-5).

According to the morphological characters of the species studied (Table 1), we were able to find four taxa, including two taxa for which the identification was not certain: *Skeletonema* sp. aff. *japonicum* and *Skeletonema* cf. *marinoi*, and we reported a new record of *Skeletonema* species in the Mexican Pacific: *Skeletonema pseudocostatum*. The species *Skeletonema tropicum* had been previously recorded (Hernández-Becerril, 1987), whereas *Skeletonema japonicum* had been recently reported from Baja California (Kooistra *et al.*, 2008).

The taxon named here as *Skeletonema* sp. aff. *japonicum* is similar to the species *S. japonicum* in many characters, including the shape and connection manner of the IF (following the original illustrations of Sarno *et al.*, 2005, figs 4 E, G). However, other character such as the ultrastructure of the cingular bands (Fig. 7) does not match completely with the original illustrations.

Another taxon not fully identified, *Skeletonema* cf. *marinoi*, is also similar in most morphological aspects to the species originally described as *S. marinoi* (Sarno *et al.*, 2005), but it has been separated from the closely related species *Skeletonema dohrnii* Sarno *et* Kooistra mainly by the ultrastructure of the cingular bands, although this character was reported as relatively ambiguous (Ellegaard *et al.*, 2008). In this study we reported a high morphological variability for this taxon and the constant presence of a variable number of short transverse ribs-like structures in the TF, a character that was not previously described. We therefore consider that we may have uncovered a new taxon within this species complex and the short transverse ribs-like structures in the TF might represent a new character to distinguish this putative new species that cultures and molecular studies may reveal in the near future.

The presence of the species *Skeletonema costatum* in the Mexican Pacific Ocean cannot be confirmed in this study, although it had been claimed that its distribution was cosmopolitan in tropical to temperate coastal areas. Although various cases of high densities or even blooms caused by *Skeletonema* species have been recorded in the Mexican Pacific coasts, they have been historical attributed to the species *S. costatum*, and in the current taxonomic framework we cannot be certain of the identity of the species causing those proliferations. No bloom case has been reported as toxic or harmful as yet.

The consequences on ecological and physiological studies are enormous, as new concepts and study protocols should be considered if different species of the genus *Skeletonema* are to be separated and taken into account individually (Smayda, 2011). Species of *Skeletonema* could be identified by the combination of methods, including molecular tools (Godhe *et al.*, 2006; Chen *et al.*, 2007a, b; Ellegaard *et al.*, 2008) (possibly molecular probes) and morphological characters (use of microscopy): In our case, observations by electron microscopy are especially necessary, as demonstrated by similar works of Bergesh *et al.* (2009), Jung *et al.* (2009) and Naik *et al.* (2010), in other parts of the world.

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REFERENCES

AKÉ-CASTILLO J., MEAVE DEL CASTILLO M.E. & HERNÁNDEZ-BECERRIL D.U., 1995 — Morphology and distribution of species of the diatom genus *Skeletonema* in a tropical coastal lagoon. *European journal of phycology* 30: 107-115.

BERGESCH M., GARCÍA M. & ODEBRECHT C., 2009 — Diversity and morphology of *Skeletonema* species in Southern Brazil, southwestern Atlantic Ocean. *Journal of phycology* 45:1348-1352.

BORKMAN D.G. & SMAYDA T., 2009 — Multidecadal (1959-1997) changes in *Skeletonema* abundance and seasonal bloom patterns in Narragansett Bay, Rhode Island, USA. *Journal of sea research* 61: 84-94.

CHEN G.F., WANG G.C., ZHANG B.Y. & FAN X.L., 2007a — Nuclear ITS and LSU sequence analysis of *Skeletonema costatum* (Bacyllariophyta)-like species from the China Sea. *Cahiers de biologie marine* 48: 55-65.

CHEN G.F., WANG G.C., ZHANG B.Y. & FAN X.L., 2007b — Morphological and phylogenetic analysis of *Skeletonema costatum*-like diatoms (Bacillariophyta) from the China Sea. *European journal of phycology* 42: 163-175.

ELLEGAARD M., GODHE A., HÄRNSTRÖM K. & MCQUOID M., 2008 — The species concept in a marine diatom: LSU rDNA-based phylogenetic differentiation in *Skeletonema marinoi/dohrnii* (Bacillariophyceae) is not reflected in morphology. *Phycologia* 47: 156-167.

GODHE A., MCQUOID M., KARUNASAGAR I. & REHNSTAM-HOLM A.-S., 2006 — Comparison of three common molecular tools for distinguishing among geographically separated clones of the diatom *Skeletonema marinoi* Sarno *et* Zingone (Bacillariophyceae). *Journal of phycology* 42: 280-291.

GRANÉLI E., WEBER M & SALOMON R.S., 2008 — Harmful algal blooms of allelopathic microalgal species: the role of eutrophication. *Harmful algae* 8: 94-102.

HASLE G.R., 1973 — Morphology and taxonomy of *Skeletonema costatum* (Bacillariophyceae). *Norwegian journal of botany* 20: 109-137.

HASLE G.R., 1978 — Diatoms. *In*: Sournia A. (ed.), *Phytoplankton Manual*. Paris, UNESCO, pp. 136-142.

HASLE G.R. & SYVERTSEN E.E., 1997 — Marine Diatoms. *In*: Tomas, C.R. (Ed), *Identifying Marine Phytoplankton*. San Petersburg, Florida, Academic Press, pp. 5-385.

HERNÁNDEZ-BECERRIL D.U., 1987 — Especies de fitoplancton tropical del Pacífico mexicano. I. Diatomeas y silicoflagelados. *Revista Latinoamericana de microbiología* 29: 415-426.

JUNG S.W., YUN S.M., LEE S.D., KIM Y.-O. & LEE J.H., 2009 — Morphological characteristics of four species in the genus *Skeletonema* in coastal waters of South Korea. *Algae* 24: 195-203.

KOOISTRA W.H.C.F., SARNO D., BALZANO S., GUB H., ANDERSEN R.A. & ZINGONE A., 2008 — Global diversity and biogeography of *Skeletonema* Species (Bacillariophyta). *Protist* 159: 177-193.

LUNDHOLM N., MOESTRUP Ø., HASLE G.R. & HOEF-EMDEN K., 2003 — A study of the *Pseudonitzschia pseudodelicatissima/cuspidata* complex (Bacillariophyceae): what is *P. pseudodelicatissima*? *Journal of phycology* 39: 797-813.

MEDLIN L.K., ELWOOD H.J., STICKEL S. & SOGIN M.L., 1991 — Morphological and genetic variation within the diatom *Skeletonema costatum* Bacillariophyta: evidence for a new species *Skeletonema pseudocostatum*. *Journal of phycology* 27: 514-524.

NAIK R.K., SARNO D., KOOISTRA W.H.C.F., COSTA P.M.D. & ANIL A.C., 2010 — *Skeletonema* (Bacillariophyceae) in Indian waters: a reappraisal. *Indian Journal of marine sciences* 39: 290-293.

ROUND F.E., CRAWFORD R.M. & MANN D.G., 1990 – *The Diatoms. Biology and Morphology of the Genera*. Cambridge, Cambridge University Press, 747 p.

SARNO D., KOOISTRA W.H.C.F., MEDLIN L., PERCOPO I. & ZINGONE A., 2005 — Diversity in the genus *Skeletonema* (Bacillariophyceae). II. An assessment of the taxonomy of *S. costatum*-like species with the description of four new species. *Journal of phycology* 41: 151-176.

SARNO D., KOOISTRA W.H.C.F., BALZANO S., HARGRAVES P.E. & ZINGONE A., 2007 — Diversity in the genus *Skeletonema* (Bacillariophyceae): III. Phylogenetic position and morphological variability of *Skeletonema costatum* and *Skeletonema grevillei*, with the description of *Skeletonema ardens* sp. nov. *Journal of phycology* 43: 156-170.

SIMONSEN, R. 1974 — The diatom plankton of the Indian Ocean Expedition of R/V "Meteor". *Meteor Forschungsergebnisse*, *Reihe D* 19: 1-107.

SMAYDA T.J., 1973 — The growth of *Skeletonema costatum* during a winter-spring bloom in Narragansett Bay, Rhode Island. *Norwegian journal of botany* 20: 219-247.

SMAYDA T.J., 2011 — Cryptic planktonic diatom challenges phytoplankton ecologists. *Proceedings of the national academy of Sciences of the United States of America* 108: 4269-4270.

WANG G.L., HUANG X.Q., JIANG X.S. & HONG J.C., 1993 — The distribution and characteristics of *Skeletonema costatum* red tides occurred in Changjiang Estuary. *Marine sciences* 3: 51-55.

ZACARONI A. & SCARAVELLI D., 2008 — Toxicity of sea algal toxins to humans and animals. *In*: Evangelista V., Barsanti L., M. Frassanito A., Passarelli V. & Gualtieri P. (eds), *Algal toxins*: *Nature*, *occurrence*, *effect and detection*. NATO Science for Peace and Security Series A: Chemistry and Biology. Pisa, Springer, pp. 91-158.

ZINGONE A., PERCOPO I., SIMS P. & SARNO D., 2005 — Diversity in the genus *Skeletonema* (Bacillariophyceae). I. A reexamination of *S. costatum* with the description of *S. grevillei* sp. nov. *Journal of phycology* 41: 140-150.