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Planktonic Silicoflagellates (Dictyochophyceae) from the Mexican Pacific Ocean

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One hundred and sixty Formalin-preserved net samples were collected from different zones in the Mexican Pacific Ocean during 11 cruises and other surveys (1984–1999) to study the composition of silicoflagellates. A few bottle samples from a coastal zone containing living material were also analyzed. Observations were made by light and scanning electron microscopy. We describe five taxa of silicoflagellates: four species and one variety, including some morphological variants (traditionally considered as recognized species or varieties). Living specimens of *Dictyocha californica* were also studied, from which we consider it to be an extant species. *Dictyocha calida* may also be regarded as an extant species, as it is very characteristic and readily distinguished, with no intergrades with related taxa, but no living cells or cells with chloroplasts were found. A discussion of morphological variation of some species within the group and the characters of the siliceous skeleton as taxonomic criteria are given. The most ubiquitous species was *Dictyocha fibula* (and its related 'species' or varieties), found in most of the locations sampled, whereas *D. californica* and *D. fibula* var. *robusta* are regarded as neritic, warm water forms.

Introduction

Silicoflagellates are a small group of microscopic marine flagellates with numerous discoid golden-brown chloroplasts, and belonging to the class Dictyochophyceae (Order Dictyochales), of the Division Heterocontophyta (Hoek *et al*. 1995, Lee 1999). The cells range from 20 to 100 μm in size, they possess chlorophylls *a* and *c*, one single external flagellum (with mastigonemes) per cell, and an external, basket-like siliceous skeleton (Van Valkenburg 1980). Ultrastructural details show the chloroplasts with an internal pyrenoid and thylacoids arranged in bands of three, whereas the nucleus is surrounded by Golgi bodies (Moestrup and Thomsen 1990, Jeffrey and Vesk 1997).

Although the forms with siliceous skeleton are the dominant ones, some naked forms have also been found (Jochem and Babenerd 1989, Larsen and Moestrup 1989, Moestrup and Thomsen 1990). The taxonomy of the group is based on the shape of the siliceous skeleton: shape and type of the basal ring, basal and lateral rods, apical bridge, number of apical spines of the basal ring and the presence of apical and supporting spines.

There is considerable morphological plasticity and variation in the skeleton, which seems to be related to environmental conditions (Frenguelli 1935, Deflandre 1952, Van Valkenburg and Norris 1970, Van Valkenburg, 1971 a, 1971 b, 1980, Boney 1973). This fact has led to the erection of a number of species, mainly from fossil material. However, strong controversy exists on the number of extant genera and species. Some authors claim that there are two genera and three extant species, others consider only one genus (*Dictyocha* Ehrenberg) and three extant species (Deflandre 1952, Moestrup and Thomsen 1990, Henriksen *et al*. 1993), whereas the most recent literature describes and illustrates eight species (Throndsen 1997).

Silicoflagellates occur in all oceans, usually in low numbers, and as they are photosynthetic algae, they play an important role in the plankton food-webs, especially in some cold and polar areas. They are also known to be sensitive to temperature, therefore some of them are considered indicators of water masses (Travers and Travers 1968). Because of their rich fossil record, silicoflagellates are also very valuable in biostratigraphy studies and for the dating of marine sediments. Some species may cause anoxia by bloom formation (Fanuko 1989).

In Mexican waters, studies devoted to silicoflagellates are rather scarce, and mainly concentrated on the Gulf of California (Murray and Schrader 1983, Pérez-Cruz and Molina-Cruz 1988), and some localities of the Mexican Pacific Ocean (Hernández-Becerril 1987). In an attempt to contribute to the knowledge of the phytoplanktonic diversity in Mexico, in this paper we deal with species of silicoflagellates found in parts of the Mexican Pacific Ocean. We also discuss some taxonomic matters regarding the group.

Materials and Methods

Material used for this study was obtained from various locations on the coast of the Mexican Pacific Ocean: the western coast of Baja California, the Gulf of California, Bahía Banderas and the Gulf of Tehuantepec (Fig. 1, Table I), during eleven oceanographic cruises and local surveys (1984−1999). Tow net (54, 64 and 105 μm mesh) samples were taken and immediately fixed with Formalin (4 %) on board and 169 samples were analyzed at our institute. Additionally, a few bottle samples with living material were collected from Mazatlan, Sinaloa State. (Fig. 1, Table I) and studied.

We used fresh slides (not cleaned material) as well as permanent ones (cleaned material, by treatment with $KMnO_4$ and then HCl) to study silicoflagellates under light microscopy (LM, a Zeiss Axiolab photomicroscope with phase contrast): preliminary identifications, measurements and observations of living and preserved specimens were made. Morphological details were observed by using scanning electron microscopy (SEM, Phillips 501 and JEOL 1200 EX) using either uncleaned or cleaned material.

Terminology, according to various classical proposals, including Van Valkenburg (1971 a) and Poelchau (1976).

Results and Observations

We distinguished five different taxa: four species and one variety (some specimens may be morphological variants − ecoforms or morphotypes? − of well-defined species, such as *Dictyocha fibula*). The taxa are described as follows:

Dictyocha calida Poelchau **Figs 2−4, 13, 14**

Poelchau 1976, p. 169, pl. 1, figs c, d, pl. 3, figs a−f; Murray and Schrader 1983, pl. II, figs 14, 15; Pérez-Cruz and Molina-Cruz 1988, figs 5−10; Desikachary and Prema 1996, pl. 13, fig. 4.

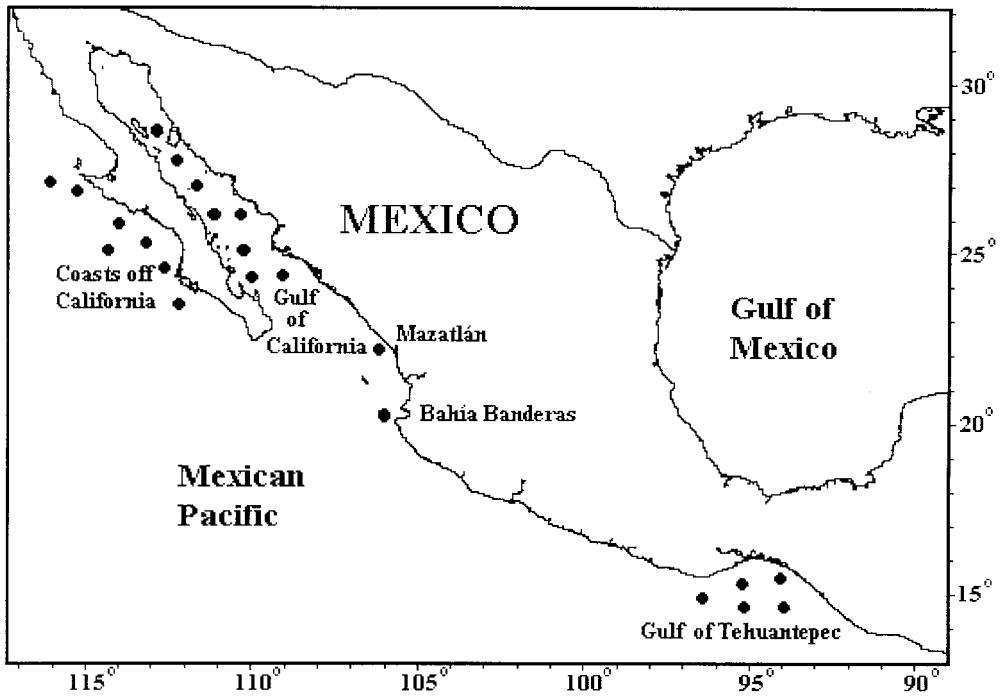
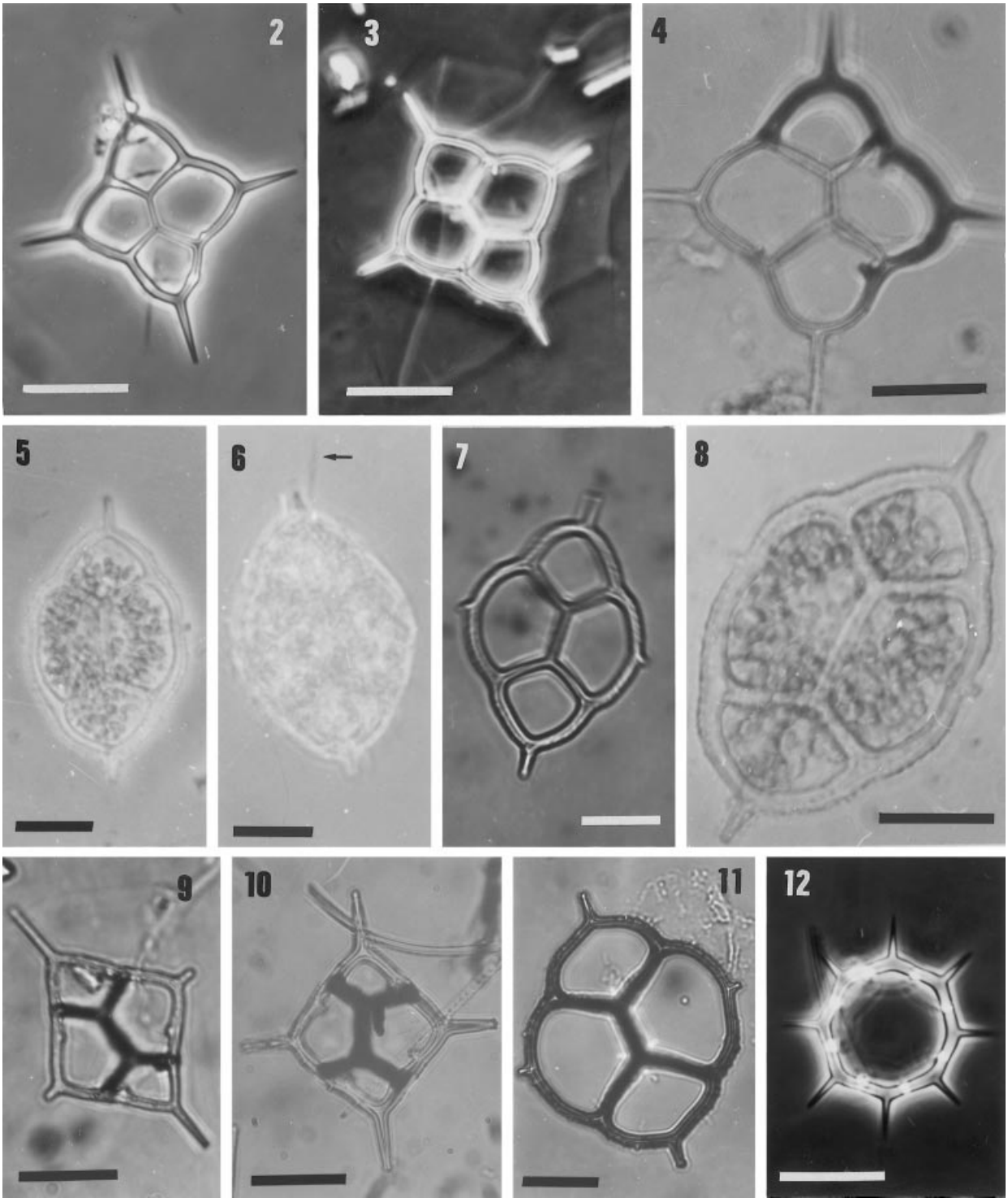


Fig. 1. Map of the Mexican Pacific Ocean showing locations of sampling points.

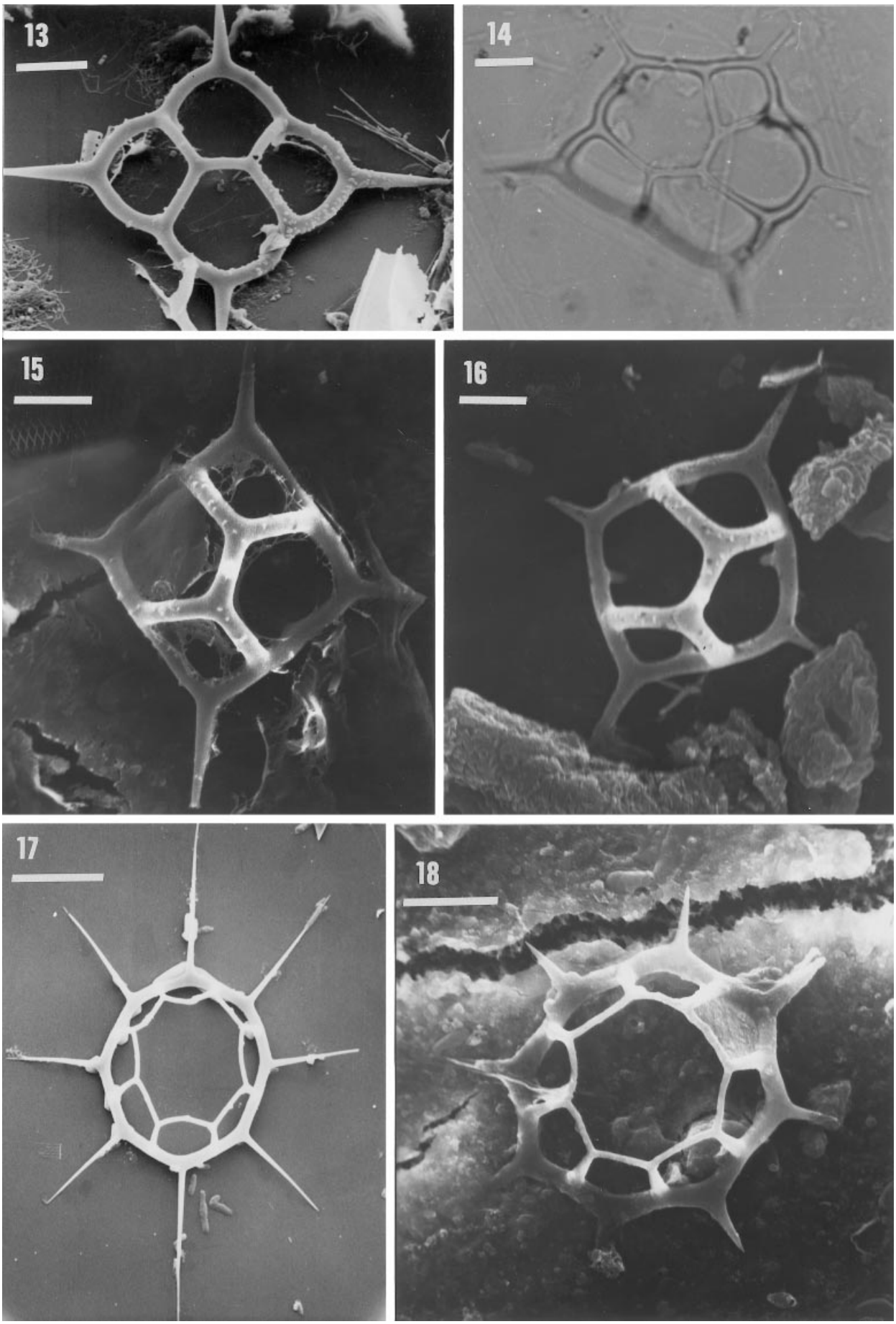
Table I. Occurrence of taxa of silicoflagellates in selected areas of the Mexican Pacific Ocean (see Fig. 1).

Taxa	Coast of Baja California	Gulf of California	Coast of Mazatlan	Bahia Banderas	Gulf of Tehuantepec
Dictyocha calida		X			X
Dictyocha californica	X	X	X	X	
Dictyocha fibula	X	X	X	X	X
Dictyocha fibula var. *robusta*		X			X
Dictyocha octonaria	X	X	X	X	

Specimens have siliceous skeletons which are rhomboid or sub-quadrate in shape, with four radial spines of equal length: the general appearance is quite symmetrical (dimensions: 52−58 μm length, 51−54 μm width). The basal rods are slightly curved and the basal windows appear rounded. The apical bridge and lateral rods are more delicate, if compared with the basal rods, and the apical bridge has no apical spine. There are short supporting spines near the junction of the basal and lateral rods.



Figs 2−12. Silicoflagellates found in the Mexican Pacific, LM.
Figs 2−4. *Dictyocha calida*, three different specimens. Figs 5−8. *Dictyocha californica*. Figs 5, 6, 8. Living cells. Fig. 6. Cell with flagellum (arrow). Fig. 7. Complete skeleton. Figs 9, 10. *Dictyocha fibula*, two specimens with slightly different morphologies. Fig. 11. *Dictyocha fibula* var. *robusta*, skeleton. Fig. 12. *Dictyocha octonaria*, whole skeleton. Scale bars = 20 μm.


13
14
15
16
17
18

This species is very characteristic and we found no significant morphological variation in our material. Some aberrant forms, resembling the 'species' *Dictyocha pentagona* (Schulz) Burky *et* Foster, occurred (Fig. 14), but our specimens showed a more delicate structure than those of *D. pentagona*, especially the apical bridge and lateral rods, which have no apical spine, and the basal ring which has smoothly curved basal rods, all of these are characteristics of *D. calida*.

General distribution: Warm (equatorial) waters, a more oceanic form.

Dictyocha californica Schrader *et* Murray **Figs 5–8**

Schrader and Murray 1985, pl. 1, figs 1–4; Pérez-Cruz and Molina-Cruz 1988, figs 1–4.

Synonym: *Dictyocha* sp. A.

Murray and Schrader 1983, figs 1–5.

The skeletons are relatively large (dimensions: 65–80 μm length, 48–55 μm width) and elliptical, with two longer radial spines in the major axis, and the two other spines (in the minor axis) are reduced. The general appearance of the skeleton is coarse. The basal windows closer to the longer radial spines are nearly rhomboid and more reduced than the others. The basal rods are robust, angled to curved, with those rods parallel to the apical bridge more linear. The lateral rods and the apical bridge are more delicate, the apical bridge being slightly oblique. There is no apical spine nor supporting spines.

We observed living specimens having a single flagellum and numerous chloroplasts (Figs 5, 6, 8). All of the protoplast is confined to the siliceous skeleton. We did not notice any significant morphological variation in the material studied.

General distribution: In the eastern Pacific Ocean, most possibly a coastal form.

Dictyocha fibula Ehrenberg **Figs 9, 10, 15, 16**

Gemeinhardt 1930, p. 47, fig. 37 a; Frenguelli 1935, pl. 2, figs 1, 4; Throndsen 1997, p. 632, pl. 6.

Synonyms (?):

Dictyocha epiodon Ehrenberg
Poelchau 1976, p. 170, pl. 1, figs e, f, pl. 4, figs a–d; Murray and Schrader 1983, figs 7–12.

Dictyocha messanensis Haeckel f. *messanensis*
Poelchau 1976, p. 173, pl. 1, figs a, b, pl. 5, figs a, c, d.

Dictyocha messanensis f. *spinosa* Lemmermann
Poelchau 1976, p. 174, pl. 5, figs b, e, f.

Dictyocha fibula var. *messanensis* (Haeckel) Lemmermann
Gemeinhardt 1930, p. 51, fig. 41 a.

Under this name we include many specimens which may be assigned to this species and other possible taxonomic varieties. The siliceous skeleton is square to rhomboid in shape (dimensions: 45–58 μm length, 40–52 μm width), with four radial spines, two of them may be longer (those in the major axis) (Fig. 9). Most specimens look symmetrical regarding the axis of the apical bridge, whereas others are more elongated (var. *messanensis* ?, Fig. 9). The basal rods are as robust as the lateral rods and the apical bridge; the basal rods are rather straight. The apical bridge is parallel or slightly oblique to the major axis, and bears a prominent apical spine. Supporting spines are conspicuous and located close to the junctions of the basal and lateral rods, within the basal windows next to the apical bridge.

There is a considerable morphological variation in specimens found in our study, but we did not find 'spinous' forms (*Dictyocha epiodon* ?).

General distribution: Widely distributed in all oceans, regarded as a more oceanic form.

Dictyocha fibula var. ***robusta*** Schrader *et* Murray **Fig. 11**

Schrader and Murray 1985, pl. 1, figs. 9–10; Pérez-Cruz and Molina-Cruz 1988, figs 23–28.

Synonym: *Dictyocha* sp. B

Murray and Schrader 1983, pl. II, figs 6–10.

A well characterized taxon, which has a very robust skeleton, subcircular to broadly elliptical in shape (dimensions: 65–76 μm length, 56–62 μm width). Skeletons look coarse and rather symmetrical. The radial spines are longer in the major axis, as the other spines are reduced. The basal ring is constricted at the junction of the lateral and basal rods; the basal rods are smoothly curved. The windows next to the apical bridge are larger than those opposite the apical bridge, which are more rhomboid in shape. The lateral rods and the apical bridge are as delicate as the basal rods. The apical bridge is parallel or slightly oblique and shows no conspicuous apical spine. Supporting spines are inconspicuous or absent.

There was no particular morphological variation in specimens studied.

Figs 13–18. Silicoflagellates found in the Mexican Pacific, SEM.
Figs 13, 14. *Dictyocha calida*. Fig. 13. Skeleton. Fig. 14. Aberrant form, showing five apical spines. Figs 15, 16. *Dictyocha fibula*. Two complete skeletons. Figs 17, 18. *Dictyocha octonaria*. Fig. 17. Rather elongated form with long apical spines. Fig. 18. Form with reduced apical spines. Scale bars = 10 μm.

General distribution: In the Eastern Pacific Ocean, a rather coastal form.

Dictyocha octonaria Ehrenberg **Figs 12, 17, 18**

Gemeinhardt 1930, p. 69.

Synonyms:

Dictyocha speculum var. *octonarius* (Ehrenberg) Joergensen
Gemeinhardt 1930, p. 69, fig. 59.

Octactis pulchra Schiller
Poelchau 1976, p. 177, pl. 6, figs h–i. Murray and Schrader 1983, pl. I, figs. 1–6; Pérez-Cruz and Molina-Cruz 1988, figs 29–33.

Octactis octonaria (Ehrenberg) Hovasse
Throndsen 1997, p. 641, pl. 6.

Distephanus pulchra (Schiller) Ling *et* Takahashi
Ling and Takahashi 1985, p. 80, pl. 1, figs 1–9, pl. 2, figs 1–7.

The specimens have a nearly circular to slightly elliptical skeleton (octagonal basal ring) with usually eight radial spines (specimens having seven or nine were also found) which are variable in length (38–52 μm in diameter). The radial spines on the axis of elongation may be slightly longer. The apical ring, supported by lateral rods arising from the basal ring between the radial spines, is more delicate than the basal ring. No apical spines or supporting spines were seen in our material.

The apical ring may be missing, probably due to breakage, or may be shorter. This fact and the relative length of the basal spines are the major source of morphological variation.

General distribution: Widely distributed in all oceans, the species may be oceanic or coastal.

Discussion

Our observations of the material collected from locations of the Mexican Pacific Ocean indicate the presence of five taxa, as four species and one variety. This is a lower number of taxa considering that in the Gulf of California previous works (Murray and Schrader 1983, Pérez-Cruz and Molina-Cruz 1988) have shown the occurrence of eight taxa, including *Dictyocha calida*, *D. californica*, *D. epiodon*, *D. fibula* var. *robusta*, *D. minima* Schrader *et* Murray, *D. messanensis* var. *messanensis*, *D. speculum* Ehrenberg (as *Distephanus speculum* [Ehrenberg] Haeckel) and *D. octonaria* (as *Distephanus pulchra*). From these taxa, only *Dictyocha minima* and *D. speculum* are well-characterized, with no major intergrades with other taxa, but they did not appear in our samples. The absence of *Dictyocha speculum* may be explained by the fact that it is a species which lives in the relatively cold waters of the California Current (Murray and Schrader 1983). Furthermore, we consider *Dictyocha epiodon* and *D. messanensis* var. *messanensis* to be rather synonyms (morphological variants) of *Dictyocha fibula*, but were referred to as 'recognized species' in previous works.

Hernández-Becerril (1987) reported five species from three points of the tropical Mexican Pacific Ocean, basically the same species from those recorded here, considering *D. epiodon* as a separate species from *D. fibula*.

The great natural morphological variation found in some taxa (especially *Dictyocha fibula*) may lead to the separation into different taxonomical entities, such as species or varieties. For instance, we encountered specimens having an intergradation (ecoforms or morphotypes?) between the typical *Dictyocha fibula* and *D. epiodon*, and also with (the species or variety) *Dictyocha messanensis*. Additionally, we found few specimens having ill-formed (incomplete) or aberrant skeletons.

The significant morphological variation in silicoflagellates has been widely documented (Frenguelli 1935, Deflandre 1952, Van Valkenburg and Norris 1970, Van Valkenburg 1971 a, 1980, Boney 1973, Van der Spoel *et al*. 1973) and has led to the statement that 'skeletal characters alone either are or are not sufficiently stable to be used as taxonomic base' (Van Valkenburg and Norris 1970). Van Valkenburg and Norris (1970) cultivated a clonal culture of *Dictyocha fibula* which exhibited the characters of at least three genera. Environmental conditions have been proposed to play an important role in determining the morphological plasticity, but no work has been done regarding the genetic diversity of the group.

Although we consider the number of extant species to be low, observations of living cells of the species *Dictyocha californica* may indicate the existence of more than three extant species (as suggested by Moestrup and Thomsen 1990, Henriksen *et al*. 1993). *Dictyocha californica* may be combined in the future, if evidence is found, with *D. fibula* var. *robusta*, although we did not find conspicuous intergrades between the two taxa.

The common presence of skeletons of *Dictyocha calida*, a delicate and apparently well-defined species, in the plankton (even in deep locations), also supports the idea that there are more extant species, although no evidence was found here (e. g. living cells or cells with chloroplasts).

We did not find any naked forms in the living material we examined, and cases of toxicity have not been reported in Mexico.

As regards the distribution of the silicoflagellates in the Mexican Pacific Ocean, we conclude that *Dictyocha californica* and *D. fibula* var. *robusta* are neritic forms, restricted to the coastal zone of warm waters along the Mexican Pacific coasts (they were not detected in western coasts of Baja California). *Dictyocha fibula* (including its morphological vari-

ants) showed the widest distribution in the Mexican Pacific Ocean and was the most common, although not abundant, species in our material.

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References

Boney, A. D. 1973. Observations on the silicoflagellate *Dictyocha speculum* Ehrenb. from the Firth of Clyde. *J. Mar. Biol. Ass. U. K. 53*: 263−268.

Deflandre G. 1952. Classe des Silicoflagellidés. *In*: (P. P. Grassé, ed.) *Traité de Zoologie*: *Anatomie*, *Systematique*, *Biologie*. *Tome* I. *Phylogénie*. *Protozoaires*: *Généralités*. *Flagellés*. Masson et Cie éditeurs, Paris. pp. 425−438.

Desikachary, T. V. and P. Prema. 1996. *Silicoflagellates* (*Dictyochophyceae*). Bibliotheca Phycologica 100, Berlin. pp. 299, 83 pls.

Fanuko, N. 1989. Possible relation between a bloom of *Distephanus speculum* (Silicoflagellata) and anoxia in bottom waters in the Northern Adriatic, 1983. *J. Plankton Res. 11*: 75−84.

Frenguelli, J. 1935. Variaciones de *Dictyocha fibula* en el Golfo de San Matías. *An. Mus. Argent. Cienc. Nat. 38*: 263−381.

Gemeinhardt, K. 1930. Silicoflagellatae. *In*: (I. Rabenhorst, ed.) *Kryptogamen-Flora von Deutschland*, *Österreich und der Schweiz*. Akademische Verlagsgesellschaft, Leipzig. pp. 1−87.

Henriksen, P., F. Knipschildt, Ø. Moestrup and H. A. Thomsen. 1993. Autoecology, life history and toxicology of the silicoflagellate *Dictyocha speculum* (Silicoflagellata, Dictyochophyceae). *Phycologia 32*: 29−39.

Hernández-Becerril, D. U. 1987. Especies de fitoplancton tropical del Pacífico Mexicano. I. Diatomeas y Silicoflagelados. *Rev. Lat.-Amer. Microbiol. 29*: 413−426.

Hoek, C. van den, D. G. Mann and H. M. Jahns. 1995. *Algae: an Introduction to Phycology*. Cambridge University Press, Cambridge. pp. 623.

Jeffrey S. W. and M. Vesk. 1997. Introduction to marine phytoplankton pigment signatures. *In*: (S. W. Jeffrey, R. F. C. Mantoura and S. W. Wright, eds) *Phytoplankton Pigments in Oceanography*. UNESCO Pub., Paris. pp. 37−84.

Jochem, F. and B. Babenerd. 1989. Naked *Dictyocha speculum*: a new type of phytoplankton in the Western Baltic. *Mar. Biol. 103*: 373−379.

Larsen, J. and Ø. Moestrup. 1989. *Guide to Toxic and Potentially Toxic Marine Algae*. Fish Inspection Service, Ministry of Fisheries, Copenhagen. pp. 61.

Lee, R. E. 1999. *Phycology*. Cambridge University Press, Cambridge. pp. 614.

Ling, H. Y. and K. Takahashi. 1985. The silicoflagellate genus *Octactis* Schiller 1925: a synonym of the genus *Distephanus*. *Micropaleontology 31*: 76−81.

Moestrup, Ø. and H. A. Thomsen. 1990. *Dictyocha speculum* (Silicoflagellata, Dictyochophyceae), studies on armoured and unarmoured stages. *Biol. Skrift. 37*: 1−56.

Murray, D. and H. Schrader. 1983. Distribution of silicoflagellates in plankton and core top samples from the Gulf of California. *Mar. Micropal. 7*: 517−539.

Pérez-Cruz, L. and A. Molina-Cruz. 1988. El Niño 1983: Efecto sobre la distribución de los silicoflagelados del Golfo de California. *Cienc. Mar. 14*: 9−38.

Poelchau, H. S. 1976. Distribution of Holocene silicoflagellates in North Pacific sediments. *Micropaleontology 22*: 164−193.

Schrader, H. and D. Murray. 1985. Silicoflagellate assemblages in the Gulf of California during the last glacial maximum and the present: oceanographic implications. *Mar. Micropal. 9*: 18−28.

Throndsen, J. 1997. The planktonic marine flagellates. *In*: (C. R. Tomas, ed.) *Identifying Marine Phytoplankton*. Academic Press, San Diego. pp. 591−729.

Travers, A. and M. Travers. 1968. Les Silicoflagellés du Golfe de Marseille. *Mar. Biol. 1*: 285−288.

Van der Spoel, S., G. M. Hallegraeff and R. W. M. Van Soest. 1973. Notes on variation of diatoms and silicoflagellates in the south Atlantic Ocean. *Netherl. J. Sea Res. 6*: 518−541.

Van Valkenburg, S. D. 1971 a. Observations on the fine structure of *Dictyocha fibula* Ehrenberg. I. The skeleton. *J. Phycol. 7*: 113−118.

Van Valkenburg, S. D. 1971 b. Observations on the fine structure of *Dictyocha fibula* Ehrenberg. II. The protoplast. *J. Phycol. 7*: 118−132.

Van Valkenburg, S. D. 1980. Silicoflagellates *In*: (E. Cox, ed.) *Phytoflagellates*. Elsevier North Holland, Inc., New York. pp. 335−350.

Van Valkenburg, S. D. and R. E. Norris. 1970. The growth and morphology of the silicoflagellate *Dictyocha fibula* Ehrenberg in culture. *J. Phycol. 16*: 48−54.