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# PARMALES (CHRYSOPHYCEAE) FROM THE GULF OF TEHUANTEPEC, MEXICO, INCLUDING THE DESCRIPTION OF A NEW SPECIES, *TETRAPARMA INSECTA* SP. NOV., AND A PROPOSAL TO THE TAXONOMY OF THE GROUP[1]

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**There are few studies dedicated to species of the Order Parmales all over the world. All 12 taxa described are part of the marine ultraplankton (less than 5 μm). Analysis of filtered samples from the Gulf of Tehuantepec yielded specimens of two taxa of the group. One is a new species, belonging to the genus *Tetraparma*. *Tetraparma insecta* sp. nov. is solitary and spherical (2.8–3.8 μm diameter), and all plates lack ornamentations or knobs, the walls are smooth, and only the plate junctions are seen. The shield plates are convex and show a conspicuous rim, some of them with an indentation. This species shows superficial similarities with *Tetraparma pelagica*, the other species described of the genus, and is very similar to siliceous forms, previously found, with no formal name. The other species is the taxon *Triparma laevis* form *mexicana* (Kosman) stat. nov., earlier described for Mexican waters, which has an irregular ala, the shield plates have knobs at the center, the triradiate plates show a "Y"-shaped keel, and the walls of plates and ala show minute granules. *Tetraparma insecta* was distributed widely in the study area and was relatively abundant, reaching a density of 4 × $10^4 \cdot L^{-1}$, with an evident preference for subsurface waters (10–20 m depth), whereas *T. laevis* form *mexicana* was rare and scarce. Both species seem to be restricted to tropical–subtropical waters. We discuss the taxonomy of Parmales, especially concerning the category of subspecies within the group. Parmales is a widespread group in cold and tropical waters.**

***Key index words:*** **Mexican Pacific Ocean; new species; Parmales; taxonomic proposal; *Tetraparma*; *Triparma***

The order Parmales, class Chrysophyceae, was established by Booth and Marchant (Booth and Marchant 1987, 1988, Lee 1999), with a total of seven species and four subspecies, and encompasses a small group of tiny and solitary cells, generally 2 to 5 μm in diameter, each with a chloroplast and a silicified cell wall composed of five to eight plates. A new subspecies of Parmales, as well as several forms (with no formal taxonomic category), were described more recently by Kosman et al. (1993).

Species of Parmales were first described as resting stages or cysts of other groups, including choanoflagellates, but detailed studies of the group revealed their algal affinity (Marchant and McEldowney 1986, Mann and Marchant 1989), and finally they were placed within the Chrysophyceae (Booth and Marchant 1987, Preisig 1994). Because of their size, members of Parmales belong in the marine ultraplankton fraction (or pico/nanoplankton fraction, of less than 5 μm).

The geographical distribution of this group has been mainly reported from cold oceanic and neritic regions, especially the subarctic Pacific and Antarctic waters (Booth et al. 1980, 1981, 1982, Silver et al. 1980, Buck and Garrison 1983, Nishida 1986, Marchant and McEldowney 1986, Takahashi et al. 1986, Kosman et al. 1993, Smith and Hobson 1994). There are only a few reports of Parmales from tropical and subtropical regions. Silver et al. (1980) recorded species of Parmales from the bottom waters of the equatorial Pacific, and Kosman et al. (1993) recorded species from surface waters of the subtropical Gulf of California (Sea of Cortés), Mexico. Other possible findings in subtropical areas were made by Norris (1971) from the Indian Ocean.

Here we deal with the occurrence of species of Parmales in a tropical area (the Gulf of Tehuantepec, in the Mexican Pacific). We describe a new species, provide data on abundance and distribution, and discuss the taxonomy of some taxa of this group, with a new taxonomic proposal.

## MATERIALS AND METHODS

Our observations are based entirely on field samples collected in the R/V "El Puma" during the cruise PACMEX III (6–17 April 2000) from the Gulf of Tehuantepec, Pacific Ocean of Mexico. The study area is located between 13° and 16° N and 92° and 96° W (Fig. 1). This area has traditionally been considered as a very rich and productive system, where wind-forced upwellings play an important role in maintaining this high productivity.

Bottle samples (4 L) were taken regularly at 10, 20, and 30 m (samples from 5, 30, and 50 m were occasionally collected) from 14 fixed stations to collect the "preservable" fraction of the phytoplankton (i.e. diatoms, thecate dinoflagellates, coccolithophorids, and silicoflagellates). The samples were then filtered (Millipore 0.45-μm pore size Millipore, Mexico City, Mexico) by pump, washed with 10 mL of distilled water, and dried. Variables obtained included *in situ* continuous temperature, salinity, and dissolved oxygen measurements, with a CTD instrument (CTD, Mark IIIC-WOCC, General Oceanics, Miami, FL, USA), in vertical profiles. Temperature and salinity data for stations where Parmales were found are given in Table 1.

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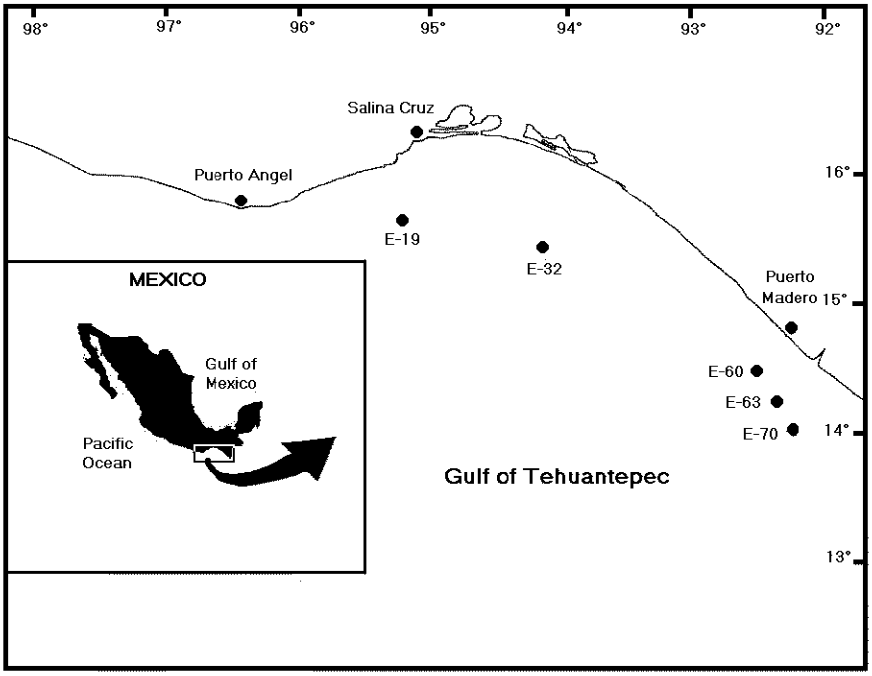


FIG. 1. Map of the study area, showing location of fixed stations in the Gulf of Tehuantepec, Mexico, where species of Parmales were found.

The material in the dried filters was studied by SEM using a small piece of the filters (about 1 cm$^2$) and treated conventionally (mounted and coated with gold). A scanning electron microscope (JEOL 1200 EX MEB JEOL-JSM 35 (JEOL de Mexico, Mexico) was used for our observations. Once a species of Parmales was identified, material was additionally studied by LM in fresh mount of the filters, using immersion oil to clear filters to count the number of cells. We used a small piece of the filter (approximately 1 cm$^2$) and counted cells in a number of fields at 40× and 100× and then calculated the density of cells in 1 L of water, taking into account the number of organisms counted, the total area counted, the total area filtered, and the volume filtered (Bollmann et al. 2002). Recognition of Parmales in LM was based on general appearance of cells: size (2.5–5 μm) and shape (spherical forms). A light microscope (bright field and phase contrast; Zeiss Axiolab Carl Zeiss de Mexico, Mexico) was used for these observations and cell counts.

We used important morphological characters such as the basic construction, symmetry, and ornamentation of cells of Parmales and their plates, following the terminology proposed by Booth and Marchant (1987) to describe the species herein.

TABLE 1. Temperature and salinity data from stations where Parmales were found in the Gulf of Tehuantepec.

| Station | Depth (m) | Temperature (°C) | Salinity (psu) |
|---|---|---|---|
| E-19 | 5 | 21.2 | 34.6 |
| | 30 | 20.3 | 34.5 |
| | 50 | 19.6 | 34.6 |
| E-32 | 10 | 23.4 | 34.5 |
| | 20 | 16.7 | 34.6 |
| | 30 | 14.0 | 34.7 |
| E-60 | 10 | 17.5 | 34.5 |
| | 20 | 16.2 | 34.7 |
| | 30 | 15.2 | 34.7 |
| E-63 | 5 | 19.7 | 34.4 |
| | 10 | 17.5 | 34.5 |
| | 18 | 16.5 | 34.7 |
| E-70 | 10 | 17.3 | 34.5 |
| | 20 | 16.2 | 34.7 |
| | 30 | 15.2 | 34.7 |

Readings obtained from CTD profiles.

## RESULTS

We found specimens of Parmales at only five stations in the study area (Fig. 1). We encountered two taxa of Parmales in our samples, one of which is considered to be a new species, whereas the other was previously described in Mexican waters, but we propose a new taxonomic status for it.

*Systematic account*
*Division:* Heterokontophyta
*Class:* Chrysophyceae Christensen
*Order:* Parmales Booth et Marchant
*Family:* Triparmaceae Booth et Marchant
*Genus:* *Tetraparma* Booth

***Tetraparma insecta*** Bravo-Sierra et Hernández-Becerril *sp. nov.*
(Figs. 2, A–F, and 3A)

*Cellula solitaria, immobilis, sphaerica. 2.8–3.8 μm diametro. 8 laminae per cellula: 4 parmae, 4 triradiatae. Paries cellulae expolita, processus carentes. Laminae parmae, 0.89–1.36 μm diametro, circulares, convexae, margines elevatos (0.58 μm) habentibus indentatio conspicua. Laminae triradiatae, 1.9–2.4 μm longitudo, margines elevatos. Species planctonica marina.*

The cells are presumably planktonic, solitary, apparently non-motile and spherical, with dimensions of 2.8–3.8 μm in diameter. They are covered by 8 silicious plates: 4 shield plates and 4 triradiate plates. All plates lack ornamentations, papillae or knobs, the walls are rather smooth, and only the plate junctions are readily seen. The shield plates, 0.89–1.36 μm in diameter, are round and convex and show a conspicuous rim surrounding each of these plates, some of the rims having an indentation; these rims may be as high as 0.58 μm. The triradiate plates, 1.9–2.4 μm of maxi-

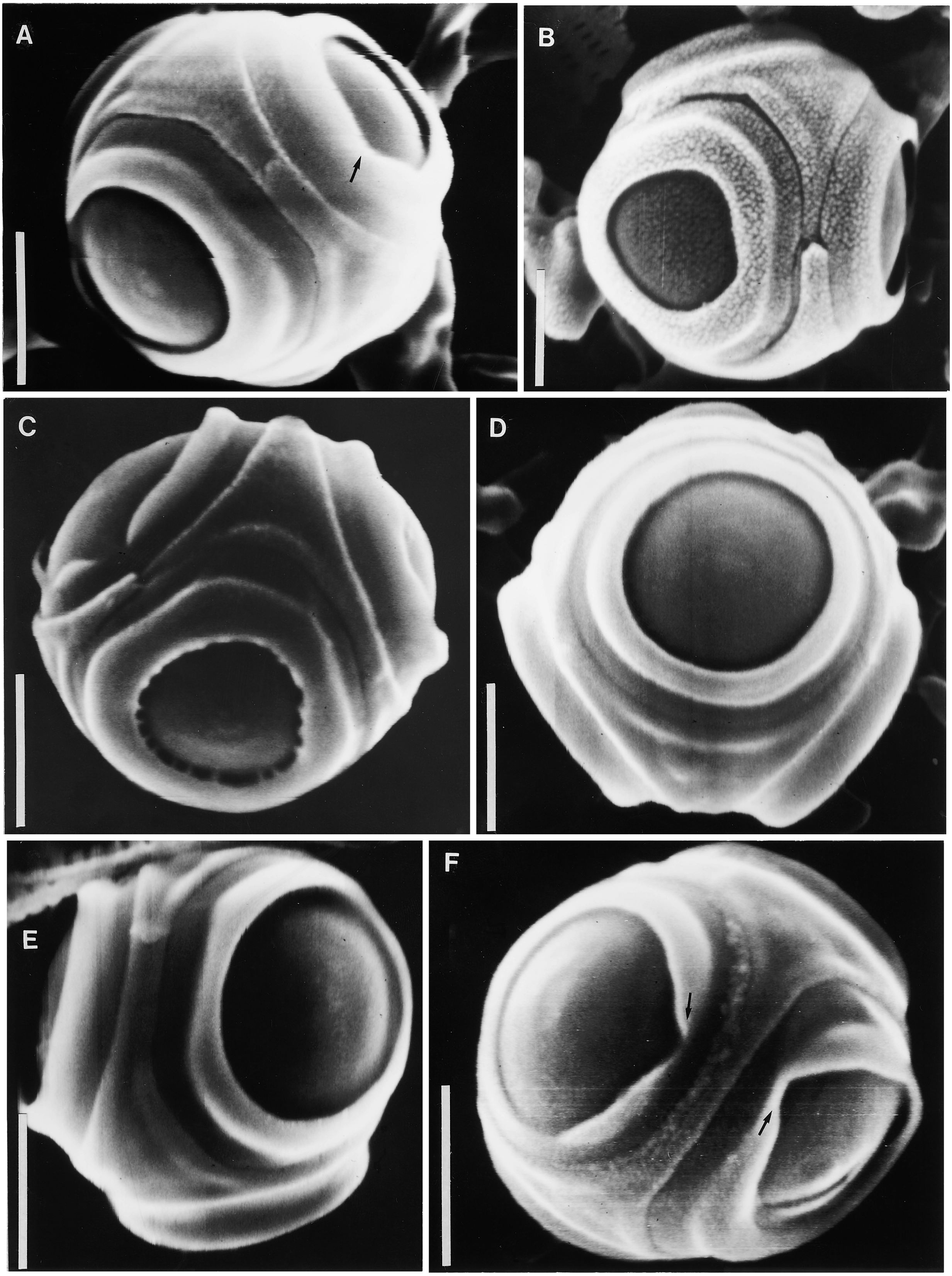


FIG. 2. *Tetraparma insecta* Bravo-Sierra et Hernández-Becerril sp. nov. (A) A cell showing two triradiate and two shield plates, with their junctions, the indentation of one rim surrounding the shield plate is incipient (arrow). (B) Cell exhibiting a shield plate and the junctions of the plates. (C) Another specimen with shield plates, one showing an indentation of the rim surrounding one shield plate. (D) A cell with a big round shield plate. (E) Another cell, with five plates, also showing the height of the rim surrounding the shield plates. (F) Cell with two big shield plates and two well-developed indentations of the rim (arrows). Scale bars, 1 μm.

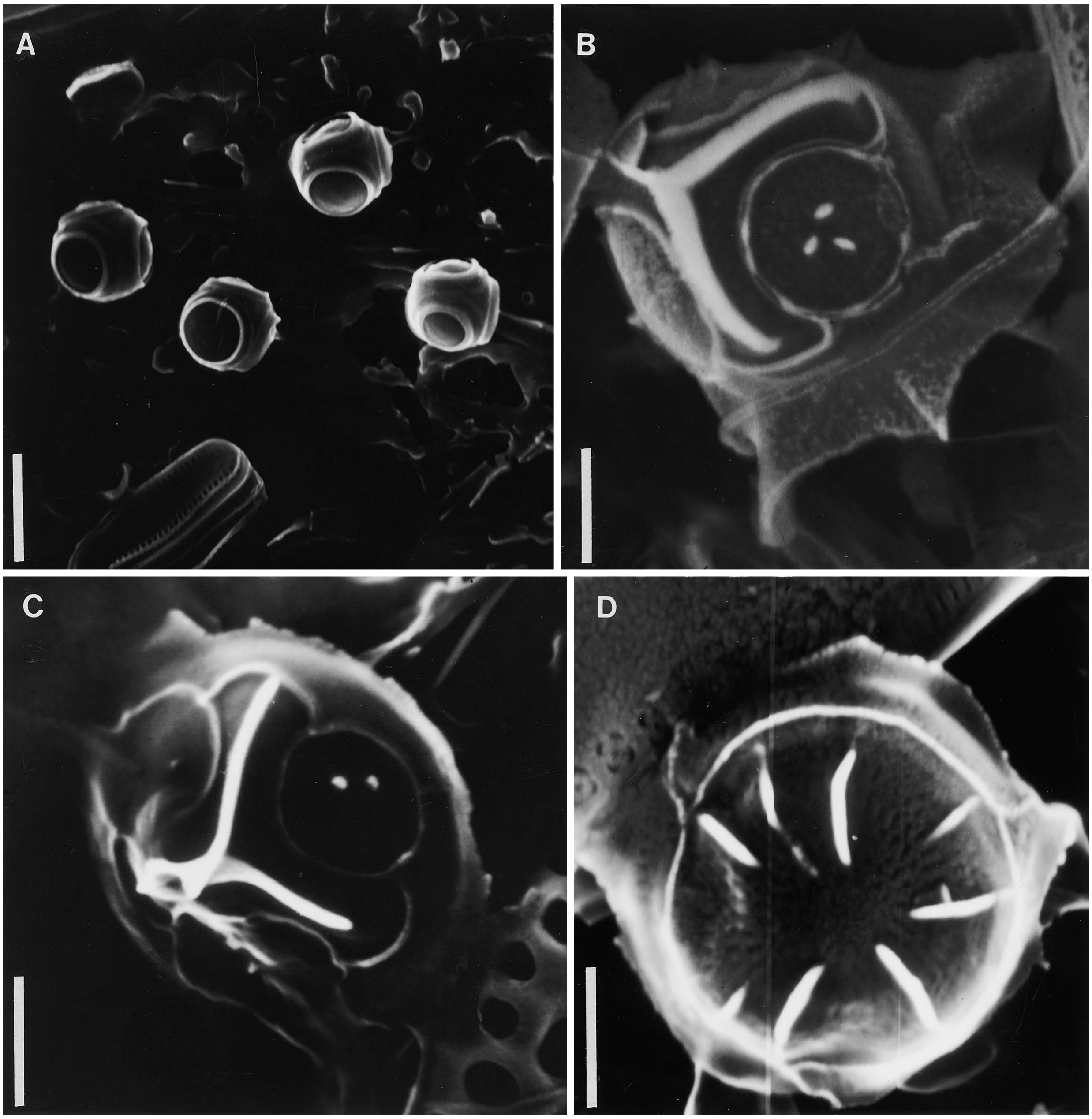


FIG. 3. (A) *Tetraparma insecta* Bravo-Sierra et Hernández-Becerril sp. nov., four different cells, to show relative high abundance. (B) *Triparma laevis* form *mexicana* (Kosman) Hernández-Becerril et Bravo-Sierra stat. nov., a cell showing a triradiate plate with its triradiate keel, three shield plates (one with three conspicuous knobs at center), and an ala ("wing") with four ribs. (C) Another cell with a triradiate plate and keel and shield plates (one with two knobs at center). (D) Ventral plate of a specimen, with poroids ("elongate areolation") and eight costae or venations. Scale bars: (A) 3 μm; (B–D) 1 μm.

mum length, have raised margins. No considerable morphological variation was detected.

*Holotype.* Slide containing the species are to be deposited in the Herbario Nacional de México (Instituto de Biología, UNAM), MEXU Colección Ficológica (Phycological Collection), No. 1494. Iconotype: Fig. 2A.

*Etymology.* The species name *insecta* refers to the general appearance of the cells, with the big round shield plates resembling the eyes of an insect.

*Type locality.* Gulf of Tehuantepec, in the tropical Mexican Pacific Ocean. Specimens of *Tetraparma insecta* were first found at Station 32, located at 15° 27.24′ N, 94° 22.91′ W.

*Distribution and abundance.* The species was relatively abundant at five stations in the Gulf of Tehuantepec (Fig. 1, Table 1). At the moment, we can say that *T. insecta* seems to be restricted to tropical–subtropical waters. The species may be considered as relatively abundant in the study area. Abundance of this species was as high as $4 \times 10^4 \cdot L^{-1}$ in one station, although species of diatoms and coccolithophorids were even more abundant.

The vertical distribution of this species indicates preference for inhabiting a subsurfacial layer, between 10 and 50 m, mostly 10–20 m, all cases being above the main thermocline. No specimens were found at surface samples (e.g. between 0 and 5 m). Table 1 provides temperature and salinity data for stations and depths where samples were taken.

*Genus. Triparma* Booth et Marchant

***Triparma laevis*** *Booth* ***form mexicana*** (Kosman) Hernández-Becerril et Bravo-Sierra stat. nov. (Fig. 3, B–D)
*Triparma laevis Booth* subsp. *mexicana* Kosman (Kosman et al. 1993, p.117, Figs. 1–10)

The earlier description of this taxon (Kosman et al. 1993) completely agrees with our finding. The cells found are considered to be planktonic, solitary, most probably non-motile, and subspherical, with 2.8–4.3 μm in diameter. Cells are covered by eight plates: three shield plates, one triradiate plate, one ventral plate, and three girdle plates. There is a conspicuous ala ("wing") dividing the cell in two hemispheres; the ala is irregular and has various (five or more) ribs and spine-like projections. The maximum width of this ala is 0.93 μm. The shield plates are round and nearly flat, with their margins slightly undulate and one to three small knobs at the center; diameter of the shield plates ranges from 0.93 to 1.3 μm. The triradiate plates show a "Y"-shaped keel, which is raised ("triradiate keel"); the maximum length of these plates is 1.8 μm. The ventral plates are round or nearly round, flat or slightly convex, with a diameter of 2.1–2.3 μm, and poroids ("elongate areolae") in their wall, and with strong costae or venations (up to eight per plate). The walls of plates and ala show minute granules. Plate junctions are distinctly distinguished.

*Distribution and abundance.* This taxon was rather rare and scarce in the Gulf of Tehuantepec: it occurred in very few samples: Stations E-19 and E-70 (Fig. 1, Table 1). However, its distribution has widened from the Gulf of California (where it was originally described) to southern waters, the Gulf of Tehuantepec, but it is apparently restricted to tropical–subtropical waters. Density of cells was very low, as very few cells were encountered.

## DISCUSSION

*Parmales in Mexican waters.* This is the second report of Parmales in Mexican waters; the first one was made in the Gulf of California (Sea of Cortés) by Kosman et al. (1993), where at least two taxa were found and described: *T. laevis* form *mexicana* and *T. retinervis* Booth. With the finding of *T. insecta*, we can count three species occurring in Mexican waters; however, we consider that the number of taxa of Parmales in Mexican waters could increase, as researchers use specific methods for studying small cells. At the moment, we have been unable to find any other species of the group in other areas of the Mexican Pacific and the Gulf of Mexico.

The importance of this group in the phytoplankton has been neglected in Mexican waters, because Parmales are a group of very tiny forms, which may be easily overlooked in routine phytoplankton analysis. The method used here is typical for studying the "preservable" fraction of the phytoplankton, such as diatoms, thecate dinoflagellates, coccolithophorids, and silicoflagellates, and basically it has been used to study living and fossil coccolithophorids by micropaleontologists (Bollmann et al. 2002). This method actually underestimates the contribution by fragile "phytoflagellates," such as forms of naked dinoflagellates, prasinophytes, cryptophytes, other haptophytes, and also some picoplanktonic forms. We were able to obtain specimens of Parmales, because they have a relative hard cover. The "classic" traditional method of the inverted microscope (Utermöhl) has also been used for most phytoplankton analyses in Mexico, but this can hardly be useful for studying the very small Parmales species.

*Comparison of* Tetraparma insecta *with other Parmales forms.* The new species described herein belongs undoubtedly to the Order Parmales, the Family Triparmaceae, and the genus *Tetraparma*. The size and shape of the cells, together with the number and shape of the plates, are characteristic of the genus. There is only one species previously described of the genus *Tetraparma: Tetraparma pelagica* Booth et Marchant (Booth and Marchant 1987), originally found in Antarctic waters, at the surface, but also found in other cold water regions (Kosman et al. 1993).

*Tetraparma insecta* differs from *T. pelagica* by the almost perfect spherical shape, the smooth cell walls, the absence of any ornamentations in the plates, and the big round shield plates. In contrast, most cells of *T. pelagica* exhibit very small papillae covering all the plates, whereas other cells show a strong pattern of areolation in the shield plates (Booth and Marchant 1987, Figs. 2, 3, and 5). Additionally, the shield plates in cells of *T. pelagica* also carry a very characteristic centric process or knob. Furthermore, cells of *T. pelagica* appear to be smaller (2.2–2.8 μm in diameter) than those of *T. insecta*.

These morphological differences, together with ecological features (i.e. *T. insecta* is found in tropical–subtropical waters, whereas *T. pelagica* has been encountered in cold waters: Antarctic and more recently in Arctic waters [Kosman et al. 1993]), are considered sufficient to propose a new species separate from *T. pelagica*.

Another form with no formal taxonomic name, depicted as a siliceous cyst, obtained from 2900 m depth in the Equatorial Pacific Ocean (Silver et al. 1980), is most probably the closest related taxon to *T. insecta*. These forms should be considered as a species or taxon of Parmales. Both forms are very similar to each other: they are about the same shape (spherical) and size (between 3 and 4 μm in diameter) and share the basic morphological structure, including relatively smooth cell walls. The main point of difference is the supposed shield plates, which are rather raised and dome-shaped in the cysts of Silver et al. (1980, Fig. 3) and have a short papilla-like projection at the center.

Finally, there is another nanoplanktonic siliceous form described by Stradner and Allram (1982a) found in sediments from a tropical location (Stradner and Allram 1982b) and also closely related to *T. insecta*. It is similar in morphology to *T. insecta* in terms of shape and size. However, the presumed shield plates are different from those of *T. insecta*, being "domed, hat-shaped plates," and these plates are surrounded by considerably raised margins (Stradner and Allram 1982a, Figs. 1–4).

These three entities, namely *T. insecta* and the two forms previously found by Silver et al. (1980) and Stradner and Allram (1982a), were found in tropical waters of a same region and could in fact belong to only one species or taxon, if intergrades in morphology are detected in the near future.

*Taxonomic proposal.* Taxa of Parmales have been proposed as species and subspecies (Booth and Marchant 1987, Kosman et al. 1993). Kosman et al. (1993) listed the taxa within the Parmales, with 12 taxa: 7 species and 5 subspecies. In Table 2 we list all taxa known of the group, with morphological characters and distribution information.

Morphological differences have been considered as important characters in distinguishing subspecies in Parmales. Some of these morphological characters show no intergrades between species and subspecies and are features that can be clearly used to separate distinct entities. In botany, and especially in phycology, the taxonomic category subspecies is not very common or used; most taxa under the category of species are considered either "varieties" and/or "forms."

Considering general concepts of ranks or categories, especially revised for "variety" and "form" in other algal groups such as dinoflagellates (Taylor 1976) and diatoms (Sundström 1986), and based on our observations presented here, we suggest that subspecies of Parmales be revised and categories of species, varieties, and forms be used instead of subspecies. Some of these subspecies may be considered to be raised to the species level, because some morphological characters show important differences regarding the nominal species, whereas in other taxa the rank of form should be used, if we assume that morphological characters such as ornamentation of cell wall might be the result of different growth pattern under varying conditions, particularly temperature.

One concrete taxonomic proposal is referred to the subspecies *Triparma laevis* Booth subsp. *mexicana* Kosman, for which a new status of form is proposed, *Triparma laevis* form *mexicana* (Kosman) Hernández-Becerril et Bravo-Sierra stat. nov. The major feature that distinguishes this form from the nominal species is basically ornamentation, which could be caused by differences in environmental conditions, thus denoting phenotypic variants, for which the term form is used (Taylor 1976, Sundström 1986).

We still do not know much about life cycles and morphological variation in natural populations of Parmales, and although some attempts have been made to culture species of this group (Taniguchi et al., 1995), no observations of living cells or molecular studies have been done.

TABLE 2. List of taxa of Parmales, including new taxonomic proposals, with data on their morphological and distribution characters.

| Species | Cell size (μm) | Sheild plates (μm) | Morphological and distribution characters |
|---|---|---|---|
| *Pentalamina corona* Marchant | 5–5.8 | 3.6–4.6 | Five plates. Polar.[a] |
| *Tetraparma pelagica* Booth et Marchant | 2.2–2.8 | 1.7–2.2 | Eight plates: 4 triradiate and 4 shield plates, with elongate reolae, with papillae and areolae. Subpolar.[a,b] |
| *Tetraparma insecta* Bravo-Sierra et Hernández-Becerril | 2.8–3.8 | 0.89–1.36 | Rims surrounded shield plates. Tropical.[c] |
| *Triparma columnacea* Booth | 2.3–4.7 | 1.0–1.8 | Eight plates: 3 shield plates, 1 triradiate, 3 girdle plates and 1 ventral plate. Areolation coarse. Subpolar.[a] |
| *Triparma columnacea* subsp. *alata* Marchant | 3.5–4.2 | 1.6–2.2 | All plates with coarse venation, small knobs at center of plate in shield plates. Subpolar.[a] |
| *Triparma retinervis* Booth | 2.7–4.5 | 1.4–2.2 | Areolation fine. Temp.-trop.[a,b] |
| *Triparma retinervis* subsp. *crenata* Booth | 2.4–3.9 | 1.2–2.0 | Presence of spines that may be curved in plates. Temp.-trop.[a,b] |
| *Triparma laevis* Booth | 2.2–3.1 | 1.4–2.0 | Plates smooth (without areolae). Subpolar.[a,b] |
| *Triparma laevis* Booth subsp. *pinnatilobata* Marchant | 3.0–3.6 | 2.4–2.6 | Shield plates smooth with raised margin, short processes in center of plate (1 to 3). Subpolar.[a,b] |
| *Triparma laevis* Booth subsp. *ramispina* Marchant | 2.5–3.2 | 1.8–2.0 | "Hinge-like" structures between girdle and shield plate. Subpolar.[a] |
| *Triparma laevis* form *mexicana* (Kosman) Hernández-Becerril et Bravo-Sierra | 2.8–4.3 | 0.9–1.5 | Different ventral plate keel patterns, knobs in shield plates. Subtropical.[b,c] |
| *Triparma strigata* Booth | 3.1–3.8 | 1.8–2.8 | All plates with long processes, scattered to fairly dense. Subpolar.[a] |
| *Triparma verrucosa* Booth | 3.2–3.9 | 1.9–2.4 | All plates with short, densely spaced processes. Subpolar.[a] |

[a]Booth and Marchant (1987).
[b]Kosman et al. (1993).
[c]Present study.

*Abundance and distribution of Parmales.* The species *T. insecta* appeared relatively abundant (up to $4 \times 10^4 \cdot L^{-1}$) in a rich phytoplankton community, with diatoms and coccolithophorids being important contributors in number and diversity. Historically, studies of phytoplankton in the same area have shown that diatoms are very important numerical (and most probably in term of biomass) contributors.

Parmales are unusually regarded as the most abundant phytoplankton group in warm, stratified, and oligotrophic waters. They often bloom in Antarctic waters (Silver et al. 1980, Booth et al. 1981, 1982) and are relatively abundant in the North Pacific, where densities of $3 \times 10^4 \cdot L^{-1}$ were found (Booth and Marchant 1987).

It is now confirmed that Parmales species are more widely distributed than earlier reports suggested and are not restricted to cold or polar waters. However, we still do not know the distribution patterns of the species of this group. *Tetraparma insecta* appeared in the extant plankton, and its closest relatives were collected in sediment samples from the same region, the equatorial/tropical Pacific Ocean, showing the restricted distribution of the species.

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Bollmann, J., Cortés, M. Y., Haidar, A. T., Brabec, B., Close, A., Hofmann, R., Palma, S., Tupas, L., & Thierstein, H. R. 2002. Techniques for quantitative analyses of calcareous marine phytoplankton. *Mar. Micropal.* 44:163–85.

Booth, B. C., Lewin, J. & Norris, R. E. 1980. Siliceous nanoplankton. I. Newly discovered cysts from the Gulf of Alaska. *Mar. Biol.* 58:205–9.

Booth, B. C., Lewin, J. & Norris, R. E. 1981. Silicified cysts in North Pacific nanoplankton. *Biol. Oceanogr.* 1:57–80.

Booth, B. C., Lewin, J. & Norris, R. E. 1982. Nanoplankton species predominant in the subarctic Pacific in May and June 1978. *Deep-Sea Res.* 29:185–200.

Booth, B. C. & Marchant, H. J. 1987. Parmales, a new order of marine Chrysophytes, with descriptions of three new genera and seven new species. *J. Phycol.* 23:245–60.

Booth, B. C. & Marchant, H. J. 1988. Triparmaceae, a substitute name for a family in the Order Parmales (Chrysophyceae). *J. Phycol.* 24:124.

Buck, K. R. & Garrison, D. L. 1983. Protists from the ice-edge region of the Weddell Sea. *Deep-Sea Res.* 30:1261–77.

Kosman, C. A., Thomsen, H. A. & Østergaard, J. B. 1993. Parmales (Chrysophyceae) from Mexican, Californian Baltic, Arctic and Antarctic waters with the description of new subspecies and several new forms. *Phycologia* 32:116–28.

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

Mann, D. G. & Marchant, H. J. 1989. The origins of the diatom and its life cycle. *In* Green, J. C., Leadbeater, B. S. C. & Diver, W. L. [Eds.] *The Chromophyte Algae: Problems and Perspectives.* Systematics Association Special Volume 38. Clarendon Press, Oxford, pp. 307–23.

Marchant, H. J. & McEldowney, A. 1986. Nanoplankton siliceous cysts from Antarctic are algae. *Mar. Biol.* 92:53–7.

Nishida, S. 1986. Nanoplankton flora in southern Ocean, with special reference to siliceous varieties. *Mem. Natn. Inst. Polar Res. Spec. Issue* 40:56–68.

Norris, R. E. 1971. Extant siliceous microalgae from the Indian Ocean. *In* Farinacci, A. [Ed.] *Proceedings of the II Planktonic Conference,* Roma, 1970. Edizioni Tecnoscienza, Roma, pp. 911–9.

Preisig, H. R. 1994. Siliceous structures and silicification in flagellated protists. *Protoplasma* 181:29–42.

Silver, M. W., Mitchell, J. G. & Ringo, D. L. 1980. Siliceous nanoplankton. II. Newly discovered cysts and choanoflagellates from the Weddell Sea Antarctica. *Mar. Biol.* 58:211–7.

Smith, P. J. & Hobson, L. A. 1994. Temporal variations in the taxonomic composition of flagellated nanoplankton in a temperate fjord. *J. Phycol.* 30:369–95.

Stradner, H. & Allram, F. 1982a. Notes on an enigmatic siliceous cyst, Middle America Trench, Deep Sea Drilling Project Hole 490. *In* Lee, M. [Ed.] *Initial Reports of the Sea Drilling Project,* vol. 66 (LXVI) sites 486–493. NSDSP-66. NSF-Univ. California-Scripps Institute of Oceanography, pp. 641–2.

Stradner, H. & Allram, F. 1982b. The nannofossil assemblages of Deep Sea Drilling Project Leg 66, Middle America Trench. *In* Lee, M. [Ed.] *Initial Reports of the Sea Drilling Project,* vol. 66 (LXVI) sites 486–493. NSDSP-66. NSF-Univ. California-Scripps Institute of Oceanography, pp. 589–95.

Sundström, B. G. 1986. *The Marine Diatom Genus* Rhizosolenia. *A New Approach to the Taxonomy.* Doctoral Dissertation, Lund University. 117 pp., 39 pls.

Takahashi, E., Watanabe, K. & Satoh, H. 1986. Siliceous cysts from Kita-No-Set strait, North of Syowa station, Antarctica. *Mem. Natn. Inst. Polar Res. Spec. Issue* 40:84–95.

Taniguchi, A., Suzuki, T. & Shimada, S. 1995. Growth characteristics of Parmales (Chrysophyceae) observed in bag cultures. *Mar. Biol.* 123:631–8.

Taylor, F. J. R. 1976. Dinoflagellates from the International Indian Ocean Expedition. A report on material collected by the R. V. "Anton Bruun" 1963–1964. *Biblioth. Botan.* 132:1–234.