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Study of the marine planktonic dinoflagellate *Ceratium divaricatum* (Dinophyceae), a confused and considerably variable species

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SUMMARY

The species *Ceratium divaricatum* (Lemmermann) Kofoid has largely been subject to misidentification and taxonomic confusion. The history of the species is complex: originally illustrated by Bergh (1881) as *Ceratium tripos* var., for which Lemmermann (1899) gave it the name *Ceratium tripos* var. divaricatum; the name *Ceratium divaricatum* was used by Kofoid (1908) with no specification of authors or references. It shows a high degree of morphological variation and development of autotomy of the apical and antapical horns. This great morphological variation has led to misidentifications in routine examinations of phytoplankton materials, and several names have been used for this species, including *Ceratium dens, Ceratium porrectum and Ceratium tripos* var. *ponticum*, as well as *Ceratium balechii*, a proposed new species for intermediate forms. Here, the species is redescribed, on the basis of material from Mexican Pacific coasts. Morphological and ecologic differences exist among this species and other closely related ones. Distribution of *C. divaricatum* is wider than previously documented (mainly because of previous misidentifications): the North Pacific Ocean, from British Columbia in Canada to temperate or subtropical waters of Mexico, and then is interrupted to reappear again in coasts of Peru and Chile, and also in coasts of the Benguela area, the South-west Atlantic Ocean. In tropical and equatorial areas of the Pacific Ocean, a more delicate form occurs, herein proposed as a variety of this species: *Ceratium divaricatum* var. *balechii*. *C. divaricatum* and var. *balechii* may be relatively abundant, even producing non-toxic red tides, in various spots along coasts of the Pacific Ocean (Canada to Mexico). It appears to be a neritic form, with high sensibility to changes in water temperature, and presumably associated to upwelling areas.

Key words: *Ceratium divaricatum*, dinoflagellates, Mexican Pacific, phytoplankton, red tides, taxonomical proposal.

INTRODUCTION

The armored genus *Ceratium* Shrank is one of the oldest genera described for dinoflagellates. It contains a large number of species that are truly planktonic and are widely distributed in all seas and also in continental waters. In the marine habitat, the number of species and infraspecies (varieties or forms) of the genus is approximately 120, plus approximately 85 names that remain in doubt or are possible synonyms (Sournia 1986; Dodge & Marshall 1994). This leads to a rather complex classification, a classification into four subgenera (Sournia 1986), and some taxonomic and nomenclature problems not solved as yet.

The traditional morphological characters of taxonomic value to identify species of this genus are: general shape and size of cells, length, width, direction of apical and antapical horns, and surface ornamentation of the thecae (crests, areolation, veins etc.) (Sournia 1986). However, some of these characters may be variable (Sournia 1966, 1968), such as the direction and relative length of the horns, and the ornamentation of the thecae; relative length of the horns may be affected by the process known as autotomy (Kofoid 1908), whereas the rest of the characters depend of the maturity and life stage of the cells.

Most *Ceratium* species are recognized to have chloroplasts and, therefore, to be photosynthetic forms, although digestive vacuoles have been found in some specimens (e.g. Jacobson 1999); other species have been shown to be bioluminescent. Sexual reproduction is known in very few species, with probable gametes involved (e.g. *Ceratium horridum Gran* and *Ceratium schrankii* Kofoid, von Stosch 1972; Montresor & Tomas 1988, respectively).

The species *Ceratium divaricatum* (Lemmermann) Kofoid has largely been subject to misidentification and taxonomic debate. The history of the species is

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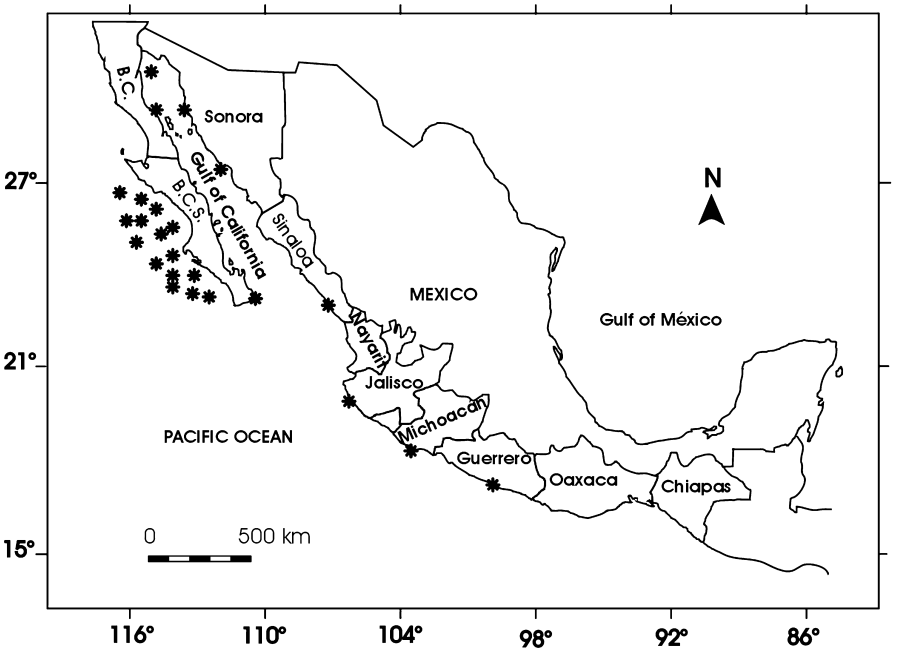

Fig. 1. Map of Mexico, with States of the Pacific Ocean and locations of samples for the present study.

complex: it was originally illustrated by Bergh (1881) as *Ceratium tripos* var., for which Lemmermann (1899) later gave it the name *Ceratium tripos* var. *divaricatum*. The name *C. divaricatum* was used by Kofoid (1908), with no specification of authors or references, but showing a high degree of morphological variation and development of autotomy, especially of the apical and antapical horns. Schiller (1937) placed this species as a synonym of *Ceratium porrectum* (Karsten) Jörgensen. The great morphological variation has led to misidentifications in routine examinations of phytoplankton materials, and several names have been involved, such as *Ceratium dens* Ostenfeld et Schmidt, *Ceratium porrectum*, *Ceratium tripos* (Müller) Nitzsch, *Ceratium tripos* var. *ponticum* Jörgensen (Allen 1941; Muñoz & Avaria 1980; Hernández-Becerril 1985; Balech 1988; Licea *et al*. 1995; Cortés Altamirano & Núñez-Pastén 2000), as well as *Ceratium balechii* (sic) Meave, Okolodkov et Zamudio (Meave *et al*. 2003), a proposed new species, for intermediate forms of this species. The name *C. divaricatum* has been used in studies of phytoplankton from the eastern Pacific Ocean (e.g. Wailes 1928; Reid *et al*. 1985; Horner 2002).

A study of this species, including a redescription, based on material from Mexican Pacific coasts and the proposal for a new variety of *C. divaricatum* are made herein, together with a comparison with closely related species, and the distribution of all these species is presented and discussed.

MATERIALS AND METHODS

The present study is based on analysis of preserved marine plankton samples (using nets of 54 and 64 μm mesh), collected on various cruises in different seasons (August 1985, June and July 1986) from coasts off Baja California and the Gulf of California, and more recently (June 1996, 1999; and various dates in 2002 and 2003) from other coastal locations in the tropical Pacific Ocean of Mexico: points of coasts in the States of Sinaloa, Jalisco, Michoacán and Guerrero (Fig. 1).

The material was rinsed and permanent and temporary slides were prepared, following conventional methods. Species identification, measurements and preliminary observations were made by light microscopy (Olympus CH, phase contrast). Drops of material or isolated specimens were prepared for scanning electron microscopy (Philips 501, at 10–12 kV), as recorded earlier (Hernández-Becerril 1989).

Terminology followed typical proposals (Fensome *et al*. 1993; Steidinger & Tangen 1997).

OBSERVATIONS AND RESULTS

Systematic account

Ceratium divaricatum (Lemmermann) Kofoid, 1908 var. divaricatum (Figs. 2a–e,g,3a–j); Kofoid (1908), p. 379, figs 30,31; Wailes (1928), pl. 2, fig. 8; Hernández-Becerril (1989), p. 42, figs 24,49; Horner (2002), p. 137 (as Ceratium divaricatum Lemmermann).

Synonyms:

Ceratium tripos var. *sensu* Bergh (1881, p. 204, pl. 13, fig. 21).

Ceratium tripos var. *divaricatum* Lemmermann (1899, p. 363).

Ceratium *furca* var. *divaricata* Lemmermann, *sensu*

Jörgensen (1911, p 37, pl. 4, fig. 77a,b).

Ceratium tripos (var. *ponticum*) f. *divaricatum* (Lemm.)

Jörgensen (1920, fig. 49).

Non:

Ceratium dens Ostenfeld and Schmidt (1901, p. 165, fig. 16); Jörgensen (1911, p. 31, fig. 58); Sournia (1968, p. 457, fig. 80).

Ceratium tripos porrectum Karsten (1907, pl. 51, fig. 6a,b).

Ceratium porrectum (Karsten) Jörgensen (1911, p. 34, fig. 63); Schiller (1937, p. 389, fig. 427a); Sournia (1968, p. 425, fig. 46).

Ceratium tripos var. *ponticum* Jörgensen (1920, p. 49, figs 37,38).

Description

Cells are solitary and robust, of medium to relatively large size: 140–206 μm length, 60–69 μm width at the cingulum, 75–130 μm length of apical horn (Fig. 2a–e,g). The body shows a certain degree of morphological variation, ranging from triangular to irregularly pentagonal (Fig. 2a–d). The epitheca is triangular, developing an apical horn of wide base, straight, sometimes winged, tapering toward the end (Fig. 2a–d). The hypotheca is rhomboid, with the antapical margins flat or slightly curved and very often continuous with the right antapical horn; in some specimens the cingulum is much lower and, therefore, the right margin reduces considerably, giving the hypotheca a completely asymmetric shape (Figs 2b,3b,f). The left antapical horns are generally more developed than the right ones, but very often both have different degrees of development (Figs 2b,d,g,3a,b,g,h). The plates of the theca are readily distinguished, both cingular lists are poorly developed, and the sulcus is very large and excavated (Fig. 2d,e). The surface of the theca has pores and strong venations, which run parallel to the horns or are scattered with no particular arrangement (Fig. 2b,d,e). Some deeper alveoli may be found in some specimens (Fig. 2e).

The antapical horns (Ant H) may be truncated, but when they are more developed, their tips are pointed (Fig. 2a,c–e,g). The left Ant H are curved and directed oblique to the apical horn, whereas the right Ant H are more smoothly curved or nearly straight, directed perpendicular to the apical horn; in some specimens the right Ant H is completely reduced or absent (Figs 2a–e,g,3a–j). Both apical and antapical horns may have their margins serrate; the left Ant H may have a wing (Fig. 2a,b,e). Length of both apical and antapical horns is very variable, and direction of antapical horns is also a variable character (Figs 2b–d,g,3a–j).

Some morphotypes assigned to this species are particularly different, regarding their body shape and also direction and length of the antapical horns (Fig. 3k,l).

Distribution in the present study

Found in many net samples, sometimes relatively abundant (no cell counts were made), from Baja California to Mazatlán, Sinaloa (Fig. 1). It was absent in samples more to the south of the Mexican Pacific (Jalisco, Michoacan, Guerrero; Fig. 1).

DISCUSSION

Morphology and taxonomic relationships

The shape of *C. divaricatum* is characteristic, although it shows a marked morphological variation, particularly in the shape of the body and the length and direction of the apical and antapical horns (e.g. Kofoid 1908) (Figs 2a–e,g,3a–l,o). It appears coarser and more robust when compared to species of similar shape, those among which it is very often misidentified: *C. dens*, *C. porrectum*, and *C. tripos* var. *ponticum* (Table 1, Fig. 4). This is the kind of species that, because of its size and shape (and abundance, sometimes), cannot be ignored.

There are certain morphological differences with closely related species, such as the shape of the body, which is somewhat irregular in *C. divaricatum*, whereas in *C. dens* it is more regular (triangular) and delicate, smaller in relation to the horns, and in *C. porrectum* it is more elongate. *C. tripos* var. ponticum has a more defined, rather pentagonal body, with well defined base of the apical horn (Jörgensen 1920; fig. 48) (Table 1, Fig. 4).

The other important morphological characters differing in such species are the shape, length and direction of the apical, but particularly antapical horns. *C. dens* has a very distinctive right Ant H, longer and slightly thinner than the left one, and directed in an angle of 45–50° with regard to the apical horn; this pattern is completely opposed to the pattern in *C. divaricatum*, with the left Ant H more developed than the right one. In *C. porrectum* the two antapical horns, of about the same length, are directed obliquely to the apical horn. *C. tripos* var. *ponticum* has well developed antapical horns: the left Ant H is curved, almost oblique to the apical horn, whereas the right Ant H curves more smoothly and is also oblique to the apical horn (Table 1, Fig. 4).

Ceratium divaricatum has been misidentified more often as *C. dens* (Hernández-Becerril 1985; Ochoa & Gómez 1997; Pech-Pacheco *et al*. 1999; Cortés Altamirano & Núñez-Pastén 2000). Balech (1988) also described *C. dens* for specimens that clearly are *C. divaricatum* (pl. 69, figs 3–5). Evidently, the closely related species are those with which *C. divaricatum* has been confused or misidentified: *C. dens*, *C. porrectum* and *C. tripos* var. *ponticum*. However, the species *C. dens*, apparently similar to *C. divaricatum*, may be less related phylogenetically, for *C. dens* belongs to the Section Densa,

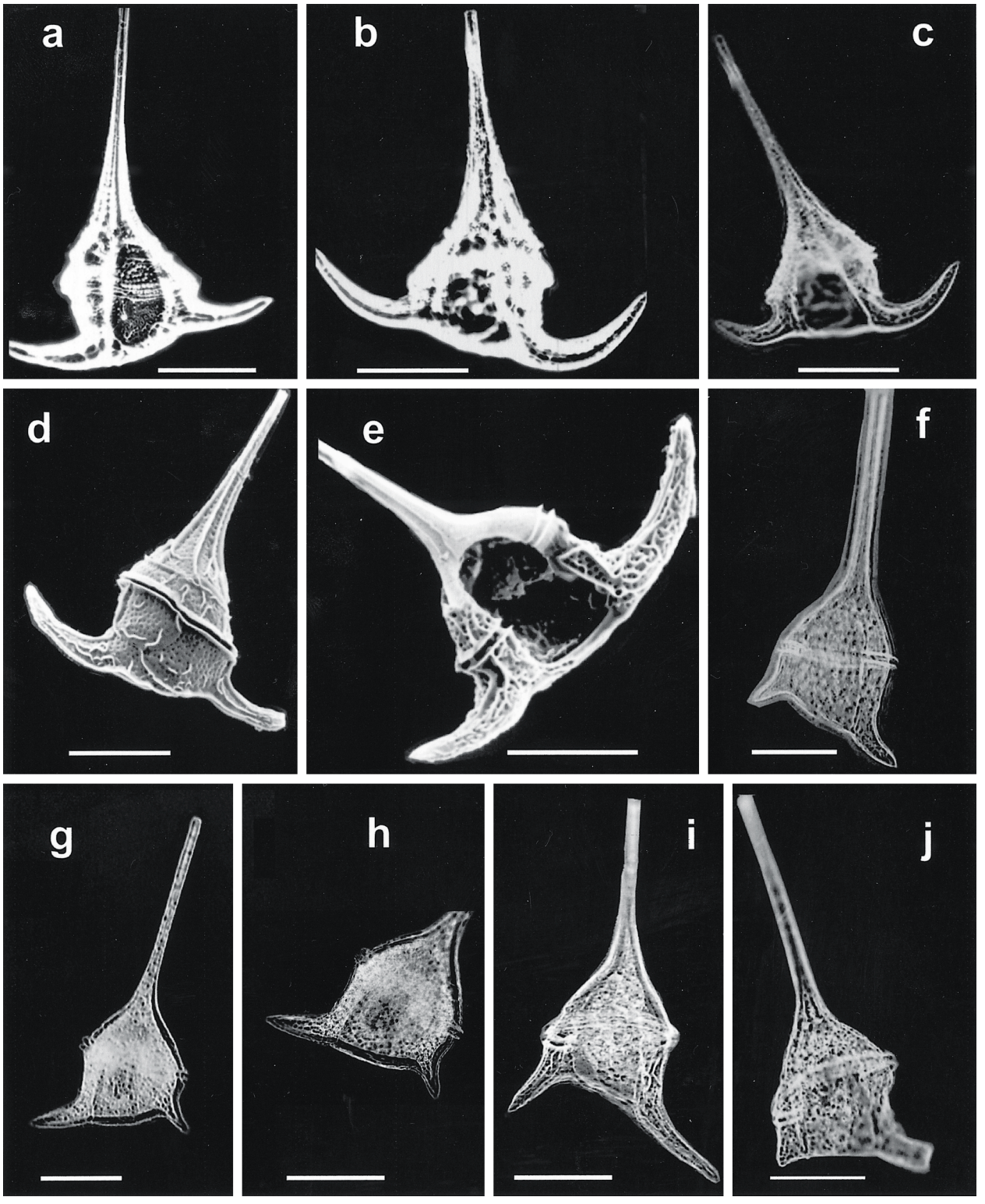

Fig. 2. (a)–(j). *Ceratium divaricatum* var. *divaricatum and Ceratium divaricatum* var. *balechii*, light microscopy and scanning electron microscopy. (a,d,g) *Ceratium divaricatum* var. *divaricatum*, dorsal view, (b,c,e) Ventral view, (f,i,j) *Ceratium divaricatum* var. *balechii*, ventral view, and (h) Dorsal view. Scale bars = 50µm.

precisely because of the typical shape of the body and the feature of the right Ant H.

Specimens with similar morphological characters of *C. divaricatum* were also found in our material, but these forms are much more delicate and elongate, with no marked ornamentation and no serrate margins of apical and antapical horns. Their distribution (see below) is also different. These forms may be considered

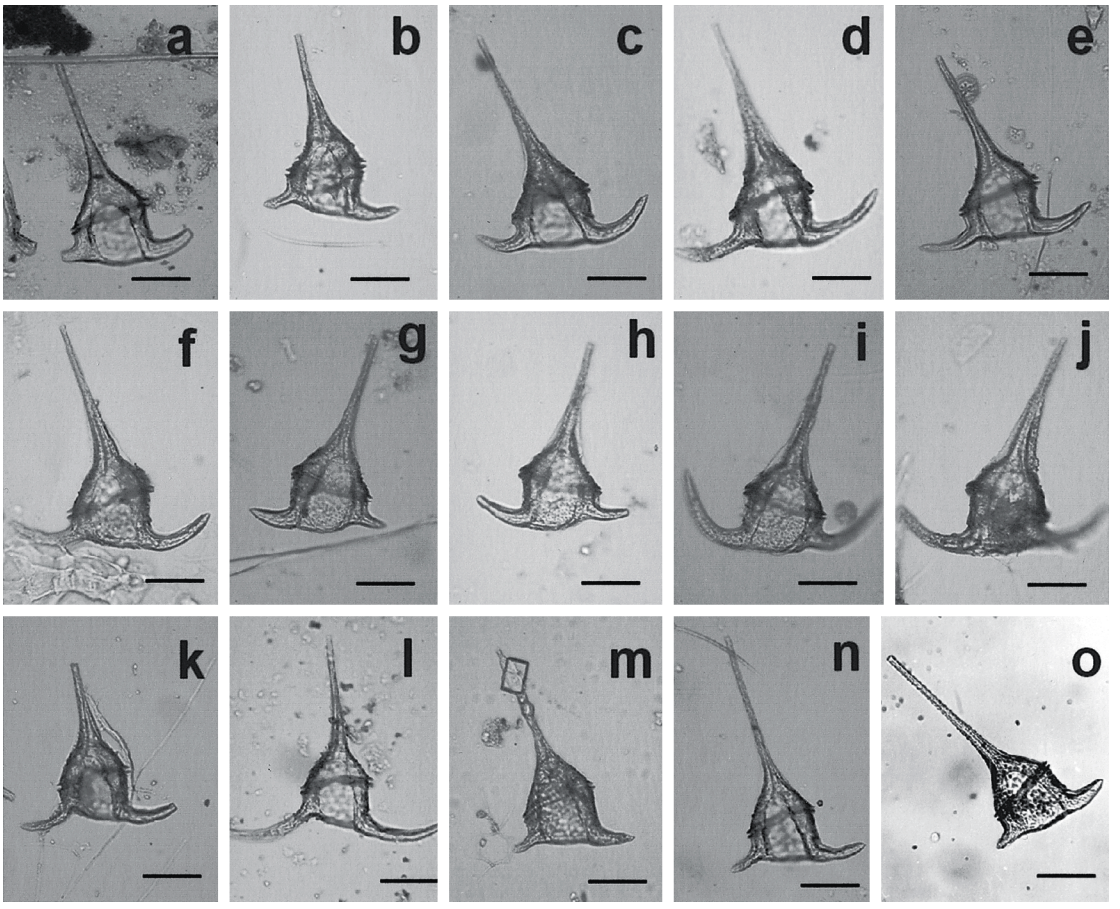

Fig. 3. (a)–(o). Morphological variation of *Ceratium divaricatum* var. *divaricatum* and *Ceratium divaricatum* var. *balechii*, light microscopy. (a–f,o) *Ceratium divaricatum* var. divaricatum, ventral view, (g–j) Dorsal view, (k,l) Two morphotypes assigned to *Ceratium divaricatum* var. *divaricatum*, and (m,n) *Ceratium divaricatum* var. *balechii*, ventral view. Scale bars = 50µm.

to belong to *C. balechii*, described recently from waters of the southern Mexican Pacific, for which a high morphological variation was also documented (Meave *et al*. 2003). *C. divaricatum* looks coarser in general appearance compared to *C. balechii* and, additionally in *C. balechii*, both antapical horns are very short, straight and pointed, and the left Ant H is directed nearly parallel or in an angle of about 10° to the apical horn (Table 1, Fig. 4). All these characters might be sufficient to define another species, but we could detect some intergrades between *C. divaricatum and C. balechii* (Figs 2f,j,3m,n).

The effect of environmental conditions, basically water temperature, on the morphological variants of *Ceratium* species was discussed by Sournia (1966, 1968). He proposed a number of taxonomic varieties for warm-water and cold-water forms, which do differ from each other (Sournia 1966). It is believed that cold-water (psychrophiles) are generally organisms more robust than warm-water forms, which are more delicate and finer (Sournia 1968). This is an important element in making a taxonomic proposal in the present paper.

Taking into account both morphological characters and ecologic preferences, we are proposing that *C. balechii* may be considered as a variety of *C. divaricatum*, as follows:

Ceratium divaricatum var. *balechii* (Meave, Okolodkov et Zamudio) Hernández-Becerril (Figs 2f,h–j,3m,n)

Basyonim: *Ceratium balechii* Meave, Okolodkov et Zamudio (2003, p. 83, fig. 11d–f (non 11a–c, *C. divaricatum* var. *divaricatum*), fig. 12 a–e).

Recognition of *C. divaricatum* as well as all other related species may rely (and it should be completely confident) on morphological characters, but it would also be useful to separate these species more accurately, for routine examinations or for non-expert personnel, and quickly on the basis of molecular techniques. Morphological characters as well as ecologic features (mainly distribution) are considered together here, to help separate different taxonomic entities.

Table 1. Comparative morphological characteristics and distribution of *Ceratium divaricatum* var. *divaricatum and* closely related taxa

	Ceratium divaricatum var. *divaricatum*	*Ceratium divaricatum* var. *balechii*	*Ceratium dens*	*Ceratium porrectum*	*Ceratium tripos* var. *ponticum*
General appearance	Robust. coarse	Fine, delicate	Coarse	Fine to slightly coarse	Fine to coarse
Epitheca,	Irregular	Triangular	—	—	—
Apical horn base	Continuous	Well defined	Continuous	—	Well defined
Apical horn length	Very variable	Very variable	Variable	—	Large, variable?
Antapical horn	Left (+), right (–), reduced or absent Pointed or truncate	Left (+), right (–), reduced or absent Pointed or truncate	Right (+), thinner, oblique. Pointed	Approximately same length. Pointed	Approximately same length. Pointed
Theca margins	Serrate and wings	Rather smooth	Rather smooth	Rather smooth	Rather smooth
Theca ornaments	Venation and alveolae	Slight venation and alveolae	Slight venation	Slight venations	Slight venation
Distribution	North-east and south-east Pacific, Southeast Atlantic	Tropical and equatorial east Pacific	Trop Indo-west Pacific, Red Sea	Tropical Indian and Atlantic	Mediterranean Sea
Remarks	Harmless, red tides producers	Harmless, red tides producers	Endemic	—	—
References†	1–9	10, 11	12–16	17	18

†References numbers are given in legend of Figure 5. —, no information available.

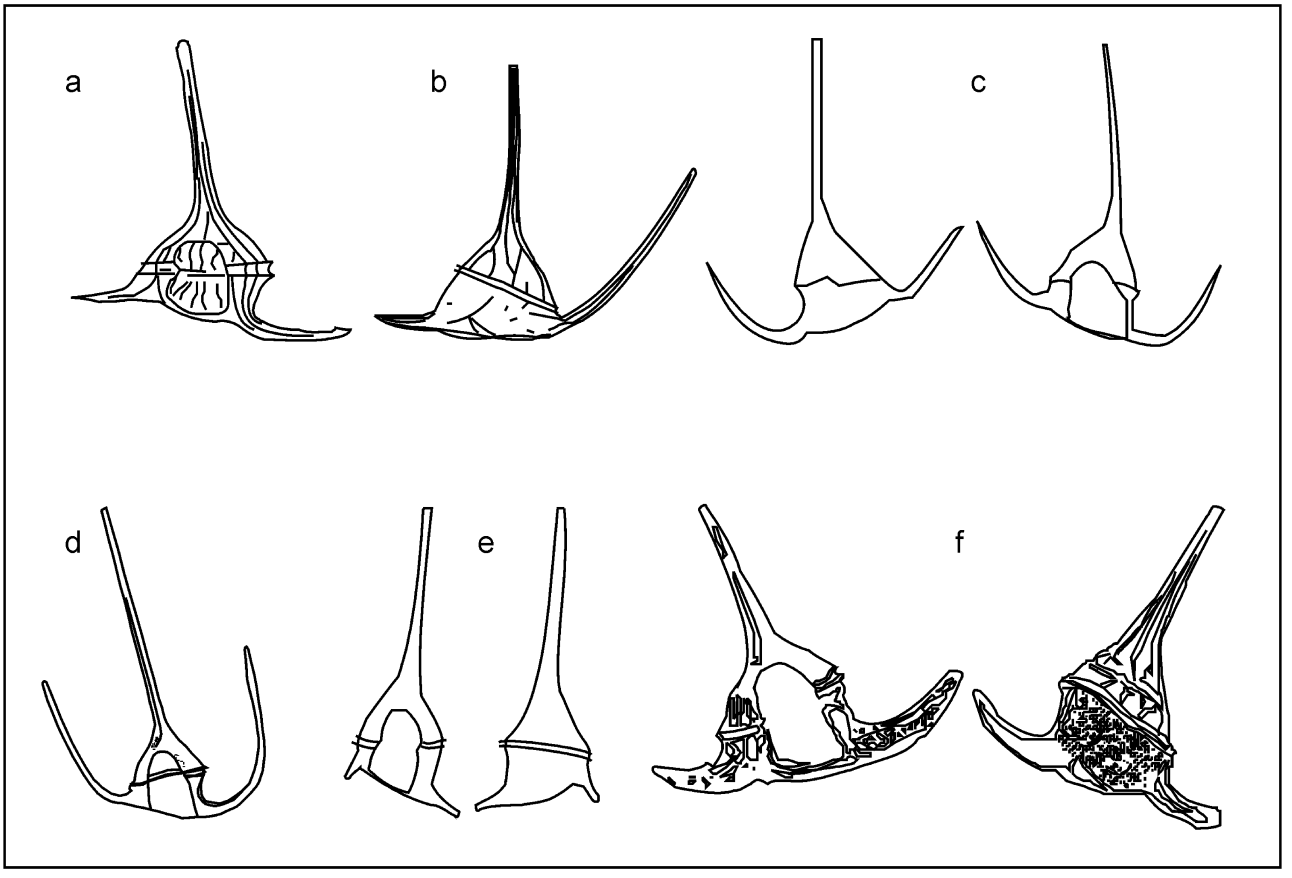

Fig. 4. (a)–(f). Original figures (redrawn) of (a) *Ceratium tripos* var. (Bergh 1881), (b) *Ceratium dens* (Ostenfeld & Schmidt (1901), (c) *Ceratium porrectum* (Karsten 1907), (d) *Ceratium tripos* var. *ponticum* (Jörgensen 1920), (e) *Ceratium balechii* (Meave *et al*. 2003), and (f) drawings of *Ceratium divaricatum* var. *divaricatum* from scanning electron microscopy micrographs.

World distribution

The distribution of *C. divaricatum* is not well known, as it has commonly been misidentified as *C. dens* (see Taylor & Pollinger 1987, p. 444), but may be wider than actually documented. Taylor and Pollinger (1987) mentioned a distribution in the North Pacific, various reports indicate a distribution from British Columbia in

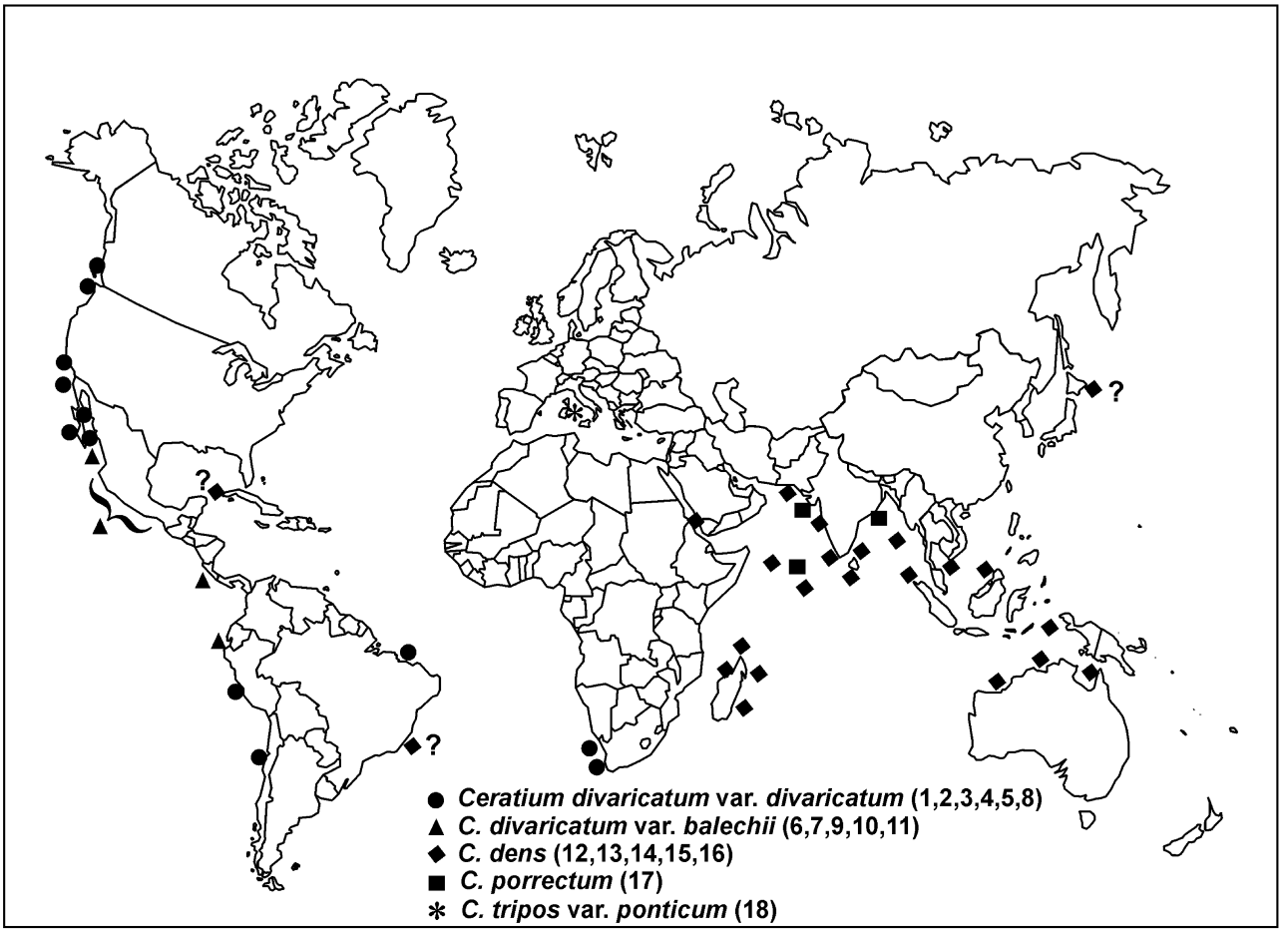

Fig. 5. World distribution of *Ceratium divaricatum* and associated taxa. References for distribution were taken from Table 1. 1: Kofoid (1908), 2: Wailes (1928), 3: Muñoz and Avaria (1980), 4: Reid *et al*. (1985), 5: Hernández-Becerril (1989), 6: Ochoa and Gómez (1997), 7: Cortés Altamirano and Núñez-Pastén (2000), 8: Horner (2002), 9: Botes (2003), 10: Pesantes (1978), 11: Meave *et al*. (2003), 12: Ostenfeld and Schmidt (1901), 13: Subrahmanyan (1968), 14: Krishnamurthy *et al*. (1980), 15: Dowidar (1983), 16: Taylor and Pollingher (1987), 17: Karsten (1907), 18: Jörgensen (1920).

Canada (Wailes 1928), coasts of California and Washington, USA (Allen 1941; Reid *et al*. 1985; Balech 1988; Horner 2002), to coasts of Baja California and Sinaloa, Mexico (Allen 1941; Hernández-Becerril 1985, 1989; Pech-Pacheco *et al*. 1999; Cortés Altamirano & Núñez-Pastén 2000, in one case misidentified as *C. tripos*, and in three cases misidentified as *C. dens*) (Table 1, Fig. 5). Around the Tropic of Cancer may be the southern boundary of the species (Fig. 5).

Then it is also found in coasts of Peru (Ochoa & Gómez 1997; misidentified as *C. dens*) and Chile (Muñoz & Avaria 1980; misidentified as *C. tripos* var. *ponticum*) in the south-east Pacific Ocean. There is a report of the species (under the name *C. dens*) in coasts of the south-east Atlantic Ocean (Benguela) (Botes 2003) (Table 1), and we should also include the record by Balech (1988) under the name *C. dens*, in waters of the south of Brazil (Fig. 5).

This distribution strongly suggests a high sensitivity of *C. divaricatum* to changes in water temperature, and that the species may prefer rather temperate to subtropical waters (when currents may carry the species to these areas) in the Pacific Ocean. Additionally, the areas where *C. divaricatum* is distributed are natural upwelling areas, in both the Pacific and south Atlantic Oceans (Fig. 5). It also appears to be a neritic form.

The species may be relatively abundant, even producing apparently non-toxic red tides, in several spots along coasts of the Pacific Ocean (from Canada to Mexico) (Cortés Altamirano & Núñez-Pastén 2000). *C. divaricatum* (and *C. dens*) has not been recorded from the North Atlantic Ocean (Dodge & Marshall 1994) nor from the Mediterranean Sea (Gómez 2003), but Jörgensen (1920) illustrated specimens named as *C. tripos* (var. *ponticum*) f. *divaricatum*, a synonym of *C. divaricatum*, apparently from Mediterranean waters. Balech (1988) mentioned that the species was absent from the Mediterranean Sea and the Gulf of Mexico.

The closely related species, *C. dens*, is distributed mainly in the tropical Indo-west Pacific region (Karsten

1907; Jörgensen 1911; Sournia 1968; Subrahmanyan 1968; Krishnamurthy *et al*. 1980; Taylor & Pollinger 1987), apparently being an indicator of currents, and it was also reported from the Red Sea (Dowidar 1983) (Fig. 5), but it does not occur in the Atlantic Ocean and the Mediterranean Sea (Sournia 1968), and a record in the Gulf of Mexico (Steidinger 1972) has to be confirmed (Taylor & Pollinger 1987) (Table 1, Fig. 5).

Ceratium porrectum shows a distribution in tropical areas of the Indian (Karsten 1907; Subrahmanyan 1968; Krishnamurthy *et al*. 1980) and Atlantic Oceans (Sournia 1968). *C. tripos* var. *ponticum* was described from the Mediterranean Sea (Jörgensen 1920) (Table 1, Fig. 5).

The taxon *C. divaricatum* var. *balechii* may have an equatorial to tropical distribution, as documented by Meave *et al*. (2003), our own observations made herein, and as indicated by other records that correspond to that variety, for instance in waters of Equator (Pesantes 1978) (Table 1, Fig. 5).

Distribution should be traced more carefully in order to demonstrate that different species have preferences for warmer or colder waters and, therefore, that these species may also be considered as indicator forms.

We conclude that *C. divaricatum* has been the subject of misidentification because of its high morphological variability. Redescription and revision of world distribution made here allow us to approach a taxonomic complex of various species, which makes species identification difficult. According to its morphological and ecologic characters, a new variety is proposed: *C. divaricatum var. balechii*. *Ceratium* species of this complex should be distinguished on the basis of their morphology and ecology, especially distribution and environmental conditions. More studies using modern techniques are recommended to be used in future investigations.

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