

Morphology and taxonomy of three little-known marine planktonic *Chaetoceros* species (Bacillariophyceae)

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Three marine planktonic species of the diatom genus *Chaetoceros* were studied by light and electron microscopy, from net samples collected from different tropical and subtropical areas: coasts of Baja California, the Gulf of Tehuantepec (both in the Pacific Ocean), the Gulf of Mexico (the Atlantic Ocean) and the Indian Ocean. Two of the species, *Chaetoceros pseudodichaeta* and *C. pseudoaurivilli*, were originally described by Ikari in 1926 from Japanese waters. This is the second record of them. *C. pseudodichaeta* is superficially similar to *C. dichchaeta* but detailed morphology differs, especially that of the intercalary setae, which are four-sided in cross-section, with long spines at the edges, and a pattern of two striae between two costae. *Chaetoceros pseudoaurivilli* is a distinctive species with a characteristic dome-shaped protuberance on terminal valves and the presence of various rimoportulae on, at least, terminal valves of the chain. Finally, *C. pseudosymmetricus* is a species only reported twice in the Indian Ocean. Its distinctive character is the heteropolarity of terminal setae: one is coarse, long and strongly curved, and the other is delicate, shorter and smoothly curved. It also has a single rimoportula on terminal valves only. The three species are regarded as rare, and consequently our knowledge of their distribution is rather poor. Additional taxonomic comments are provided for the three species.

Key words: *Chaetoceros*, distribution, morphology, planktonic diatoms, taxonomy

Introduction

The great species diversity of the diatom genus *Chaetoceros* Ehrenberg as well as the wide morphological variability in some species have been pointed out earlier (Evensen & Hasle, 1975; Rines & Hargraves, 1988; Hernández-Becerril, 1996). The large number of species (approximately 400 names, following Hasle & Syvertsen, 1996) has led to infrageneric classifications, into subgenera (*Chaetoceros*, *Hyalochaete* and *Bacteriastroidea*, e.g. Hasle & Syvertsen, 1996; Hernández-Becerril, 1993b, 1996) and sections (19–20, following Hernández-Becerril, 1996, or up to 21–22 according to recent proposals by Hernández-Becerril & Flores Granados, 1998). During the examination of plankton material for a current study of *Chaetoceros* species, more than 45 taxa (species, varieties and forms) have been analysed, some being described as new species (Hernández-Becerril, 1991a, 1992a) and others studied using modern techniques (e.g. electron microscopy) for the first time (Hernández-Becerril, 1992b, 1993a, 1996; Hernández-Becerril *et al.*, 1993).

The present report covers the morphology and taxonomy of three rare and little-known species. *Chaetoceros pseudodichaeta* Ikari was originally described in 1926 (Ikari, 1926) from Japanese waters; after this initial description there have been no further documented reports.

Chaetoceros pseudoaurivilli Ikari was also described in the same paper (Ikari, 1926), with no further record until now. Finally, *Chaetoceros pseudosymmetricus* Steeman-Nielsen, depicted from the Indian Ocean (Steeman-Nielsen, 1931), is a very rare species, apparently reported only twice from the region. Comments and proposals are made on the taxonomic position of these three species.

Materials and methods

This study is based on analysis of preserved marine plankton samples (mainly using nets, 54 and 64 μm mesh), collected on different dates and seasons from coasts off Baja California and the Gulf of Tehuantepec, in the Pacific Ocean of Mexico, the Gulf of Mexico, in the Atlantic Ocean, and in the Indian Ocean (Table 1).

The material was rinsed or cleaned following conventional methods (e.g. Hasle, 1978). Species identification, selection, measurements and preliminary observations were made by light microscopy (LM; Olympus CH, phase contrast). Drops of water samples or isolated specimens were prepared for scanning electron microscopy (SEM; Philips 501, at 10–12 kV), as recorded in Hernández-Becerril (1996). For transmission electron microscopy (TEM; JEOL 1200 EX), only cleaned material was used.

Type material of the three species was not examined, but original figures have been redrawn (Figs 21–23). Terminology adopted here generally follows the

Table 1. Collection data for samples used for this study

Species	Location	Area	Cruise/Date
<i>Chaetoceros pseudodichaeta</i>	21°30'N, 91°00'W 15°12' N, 93°15' W	Gulf of Mexico Gulf of Tehuantepec	JS 02/87 FIQUIMBI 11/89
<i>Chaetoceros pseudoauriivilli</i>	26°14'N, 114°29'W 15°30'N, 94°30'W	Gulf of California Gulf of Tehuantepec	CICIMAR 88/85 MIMAR-V 05/89
<i>Chaetoceros pseudosymmetricus</i>	01°5 1'S, 67°46'E	Indian Ocean	Discovery 64

proposals by Anonymous (1975) and Ross *et al.* (1979). In addition, specific terminology for *Chaetoceros* was taken from Brunel (1966), Rines & Hargraves (1988) and Hernández-Becerril (1991b, 1996).

Observations

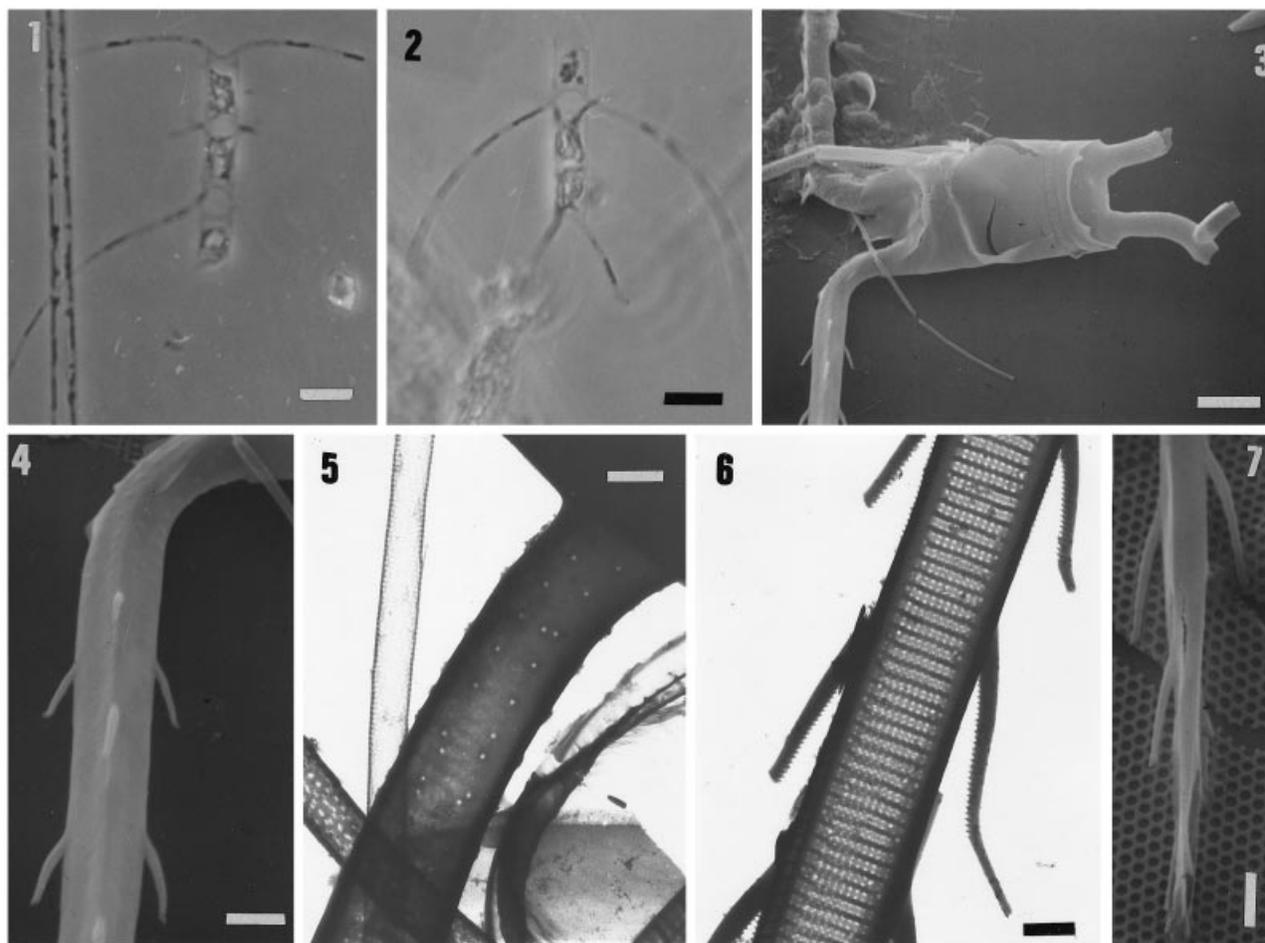
Chaetoceros pseudodichaeta Ikari (Figs 1–7, 21) Ikari, 1926, p. 517, fig. 1a–c

The cells form straight chains of three to five cells (Fig. 1); all the chains seen were broken and loose cells and valves were also observed. In girdle view, the cells are rectangular, the perivalvar axis being longer than the apical

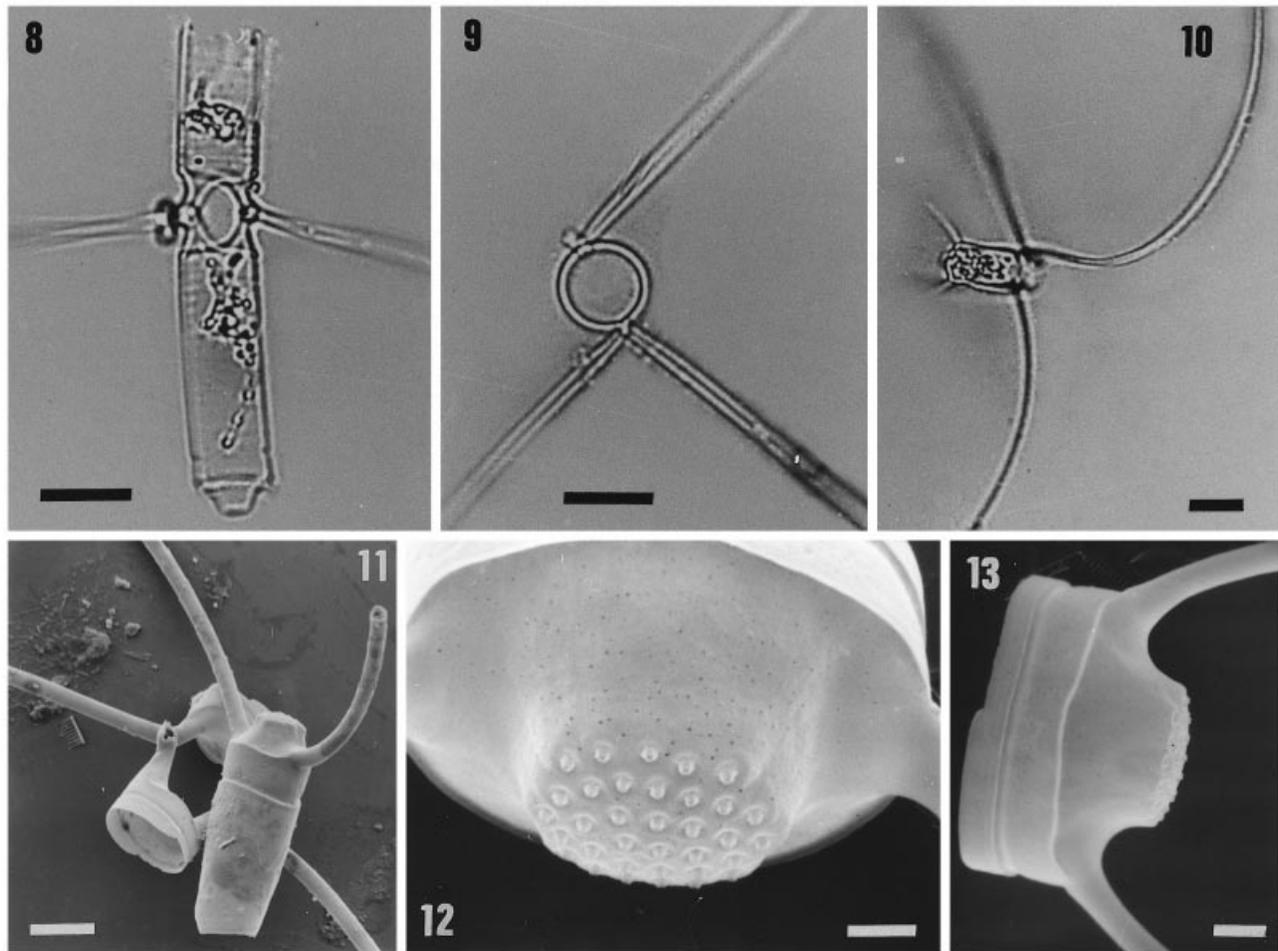
one (Fig. 2). The apertures are wide and rectangular to elliptical in shape (Fig. 2). The cells are elliptical in valve view. The chloroplasts in the cell are round and small, but they are compressed and elongate in the setae (Figs 1, 2).

The valves are less heavily silicified than in other members of the subgenus *Chaetoceros*. There is a rim clearly dividing the valve face from the mantle (Fig. 3). The valve face of intercalary valves is nearly flat to slightly convex with no evident external protrusion of the rimoportula. Terminal valves were originally described as carrying a single rimoportula, which has an external tubular structure; this structure was not observed here.

All setae are rather thick. Intercalary setae arise from the apices of the cells, have a short base parallel to the chain



Figs 1–7. *Chaetoceros pseudodichaeta*. Fig. 1. Middle part of a broken chain, with three cells and long intercalary setae. LM. Fig. 2. Terminal part of a chain, showing intercalary and broken terminal setae. LM. Fig. 3. A complete cell from a broken chain. SEM. Fig. 4. Detail of an intercalary seta with prominent spines. SEM. Fig. 5. Base of an intercalary seta, showing its wall perforated by small pores. TEM. Fig. 6. Middle part of an intercalary seta, exhibiting two striae in between two costae, and strong, long spines at the edges. TEM. Fig. 7. Tip of an intercalary seta, with reduced spines. SEM. Scale bars represent: 20 μ m (Figs 1, 2), 5 μ m (Fig. 3), 2 μ m (Figs 4, 7), 1 μ m (Figs 5, 6).



Figs 8–13. *Chaetoceros pseudoaurivilli*. Fig. 8. Terminal part of a chain, with broken terminal setae. LM. Fig. 9. Valve view of a cell, showing three intercalary setae. LM. Fig. 10. Another terminal part of a chain. LM. Fig. 11. Terminal and intercalary valves from a broken chain. SEM. Fig. 12. Detail of the protuberance of a terminal valve, exhibiting numerous rimoportulae. SEM. Fig. 13. Terminal valve with a dome-shaped protuberance. SEM. Scale bars represent: 20 μm (Figs 8–10), 10 μm (Fig. 11), 5 μm (Fig. 13), 2 μm (Fig. 12).

axis and then fuse together. They then diverge perpendicular to the chain axis (Figs 1, 3). Terminal setae differ in direction, for they curve smoothly close to their base and then become parallel to the chain axis (Fig. 2). Intercalary setae are circular in cross-section at their base (Figs 4, 5), perforated by small pores, with no spines, but distally become four-sided, armoured with long saw-toothed spines, arranged either in opposite pairs or alternately, located at the edges (Figs 4, 6), with a pattern of two striae between two costae, perpendicular to the seta axis (Fig. 6). They terminate in a pointed tip, with the spines quite reduced (Fig. 7).

Dimensions: Apical axis 10–13 μm , perivalvar axis 15–20 μm , aperture 8–9 μm , width of setae 2.8–3.5 μm .

Chaetoceros pseudoaurivilli Ikari (Figs 8–13, 22) Ikari, 1926, p. 522, fig. 5a–e

Straight chains consisting of three to six cells, most of them broken, were observed (Figs 8, 11). The cells are rectangular in girdle view, with their perivalvar axis much longer than the apical axis. The aperture is rather wide and elliptical. The terminal valves show a singular dome-shaped protuberance (Figs 8, 10–13). In valve view, the valves are circular to subcircular (Fig. 9).

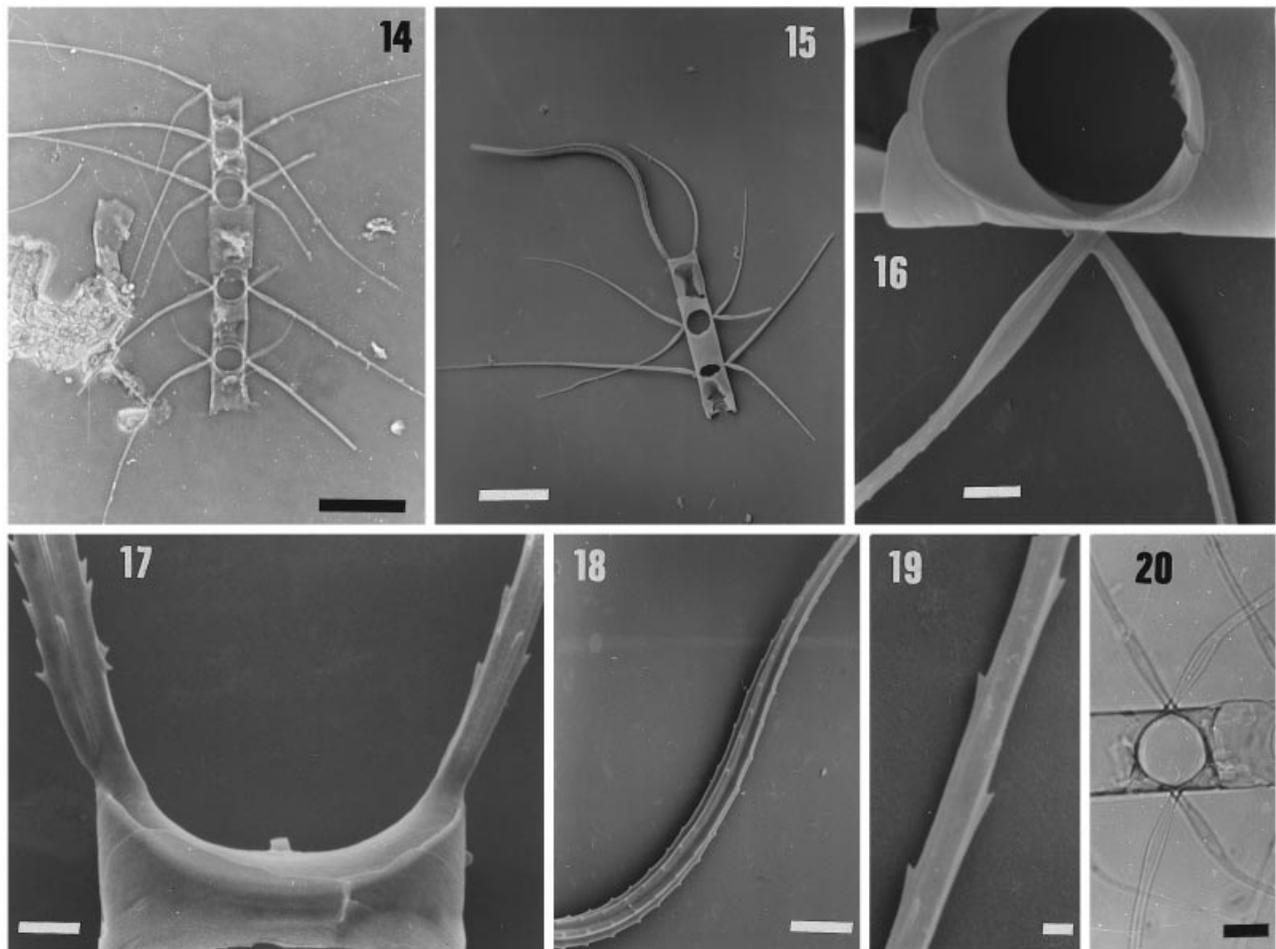
The valves are heavily silicified, finely perforated by small pores (Fig. 12). The intercalary valves have a low mantle and a flat face. The terminal valves have a higher mantle than that of intercalary valves (Fig. 11), the protuberance occupying the valve face and bearing numerous rimoportulae (31–34) on the top; these are simple short tubular structures, each with a slit orientated at random and placed on depressions in the valve (Fig. 12). The girdle is composed of several bands.

The setae are coarse, arising from the apices of the valves. The intercalary setae fuse together and diverge widely after a short base, then curve smoothly perpendicular to the chain axis (Figs 10, 11). The terminal setae are directed, almost straight or slightly curved, to the chain axis (Fig. 11). All setae are circular in cross-section at the base.

Dimensions: Apical axis 13–31 μm , perivalvar axis 45–48 μm , aperture 9–12 μm , width of setae 3–3.8 μm .

Chaetoceros pseudosymmetricus Steeman-Nielsen (Figs 14–20, 23) Steeman-Nielsen, 1931, p. 4, fig. 3

Synonym: *Chaetoceros affine* [sic] Lauder f. *pseudosymmetricus* (Steeman-Nielsen) Thornington-Smith, 1970, p. 827, pl. 4, fig. 1a–c.



Figs 14–20. *Chaetoceros pseudosymmetricus*. Fig. 14. Middle part of a broken chain. LM. Fig. 15. Terminal part of a chain, with intercalary and terminal setae. SEM. Fig. 16. Detail of intercalary valves and setae. SEM. Fig. 17. Terminal valve, exhibiting heteropolar terminal setae and a short external process of the rimoportula on the valve face. SEM. Fig. 18. Thicker terminal seta with a polyhedral shape and small spines. SEM. Fig. 19. Intercalary seta with small spines in spiral. SEM. Fig. 20. Detail of the anterior, showing apertures and inflation of intercalary setae. LM. Scale bars represent: 50 μm (Figs 14, 15), 10 μm (Figs 18, 20), 5 μm (Figs 16, 17), 2 μm (Fig. 19).

The cells form straight and short chains of three to seven cells (Figs 14, 15). The cells are rectangular in girdle view and narrowly elliptical in valve view. The apertures are oval, relatively narrow to wide (Figs 14–16). The valves are delicate, more weakly silicified than in most species of the subgenus *Chaetoceros*, with concave faces, very low mantles, and rims which clearly divide face from mantle (Figs 16, 17). The terminal valves have a short flattened tube outside, protruding from the single rimoportula, located in the centre (Fig. 17), whereas the intercalary valves lack this structure.

The intercalary setae emerge from the apices of the valves and fuse immediately to the sibling setae. After fusion, they become inflated for a short distance and then gradually taper to the tip (Fig. 16). These setae are directed obliquely to the chain axis (Figs 14, 15, 20), either curving smoothly or becoming straight. They are four-sided in cross-section and have minute spirally arranged spines (Fig. 19). The terminal setae are heteropolar (Fig. 15): one is quite thick, very long, strongly curved, polyhedral (five sides) and armoured with spines at the edges (Fig. 18); the tip is truncated. The other is more similar to the intercalary

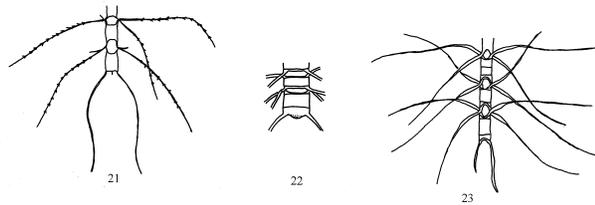
ones: thinner and shorter, smoothly curved, four-sided in cross-section, and also with spirally arranged spines at the edges.

Dimensions: Apical axis 19–26 μm , perivalvar axis 28–32 μm , aperture 7–16 μm , width of intercalary setae (including the inflated part) 1.5–3.1 μm , width of thick terminal seta 4–5.6 μm , width of delicate terminal seta 2.5–3 μm .

Discussion

Chaetoceros pseudodichaeta

Chaetoceros pseudodichaeta belongs to the subgenus *Chaetoceros* (*Phaeoceros*), as all its characters fit into the circumscription of this subgenus (e.g. chains and appendages robust, possession of small and numerous chloroplasts in cells and setae, presence of rimoportulae on every valve in the chain). The cells in the chain are linked by fusion of setae, as in most *Chaetoceros* species (although other modes of linking cells have been shown, e.g. Fryxell & Medlin, 1981; Hernández-Becerril, 1992a). As regards its classification into a section of this subgenus, the



Figs 21–23. Fig. 21. *Chaetoceros pseudodichaeta*. Fig. 22. *C. pseudoaurivilli*. Figures redrawn from Ikari's (1926) originals (figs 1c and 5e, respectively). Fig. 23. *C. pseudosymmetricus*. Figure redrawn from Steeman-Nielsen's (1931) original.

placement by Yamaji (1966) of *C. pseudodichaeta* into the section *Atlantica*, together with closely allied species, especially *C. dichchaeta* Ehrenberg (possibly its closest related species) seems to be correct.

C. pseudodichaeta closely resembles *C. dichchaeta*, in particular by the shape of the chain, and can easily be confused with it in routine analysis (e.g. using light microscopy). However, *C. pseudodichaeta* differs by the distinctive long and strong spines in the intercalary setae, which are less evident in *C. dichchaeta*. *C. pseudodichaeta* also has well-developed tubular external processes on terminal valves only, whereas in *C. dichchaeta* every valve of the chain carries a single such structure. In his description of this species Ikari (1926) emphasized that the terminal setae had no spines like those found in the intercalary ones (also illustrated, e.g. Fig. 21).

The detailed morphology of the intercalary seta wall is undoubtedly remarkably different between the two species. In *C. pseudodichaeta*, besides the large spines at the edges of the setae, the setae are four-sided in cross-section and have a pattern of two striae in between two costae, perpendicular to the seta direction, whereas *C. dichchaeta* has polyhedral (more than four-sided) setae and no costae nor striae (Koch & Rivera, 1984; Hernández-Becerril, 1996). However, Evensen & Hasle (1975) described the setae as being circular in cross-section in TEM and with 'single rows of holes running parallel to the main axis'. Ikari (1926) described and illustrated terminal setae with no spines, whereas spines were found in intercalary setae (Fig. 21).

C. pseudodichaeta is known in Japan only from its first description (Ikari, 1926) and was listed by Yamaji (1966). The present report from tropical to subtropical waters (coasts of Baja California and the Gulf of Tehuantepec) is probably the second for the species, which might be regarded as a coastal form. On the other hand, *C. dichchaeta* has mostly been reported from the Antarctic and southern cold waters (Hustedt, 1930; Koch & Rivera, 1984; Hasle & Syvertsen, 1996), although more delicate and more weakly silicified forms (ecoforms?) appear in subtropical waters (Hernández-Becerril, 1996; Hernández-Becerril & Flores Granados, 1998).

Chaetoceros pseudoaurivilli

The original description of *Chaetoceros pseudoaurivilli* (Ikari, 1926) included one illustration of long chains of 20 cells or more (fig. 5d). In the material studied here, only

short or broken chains were observed, but there is no doubt that the species dealt with in this study is *C. pseudoaurivilli*, basically because the terminal valves have the typical protuberance and multiple rimoportulae. The specimens studied here are longer (45–48 μm) than those originally described (which were, in the perivalvar axis, 15–30 μm); several girdle bands may contribute to the size. In this species the cells are united in the chain by fusion of setae.

The species is, however, well characterized and cannot be confused with any other species when complete chains or even terminal valves are present, as the protuberance from the terminal valves is conspicuous. Here, some important observations have been made. Although Ikari (1926, fig. 5e) shows the terminal valve with its typical protuberance 'dotted' (Fig. 22), indicating the presence of multiple rimoportulae, this character can only be seen with the use of electron microscopy. If the possession of various rimoportulae on every valve, not only the terminal ones, is confirmed, that character will have considerable taxonomic implications, no matter what the physiological role of those rimoportulae may be. *C. pseudoaurivilli* seems to belong in the subgenus *Chaetoceros*, perhaps in the section *Coarctati*, which currently only has two species, *C. coarctatus* Lauder (Hernández-Becerril, 1991b) and *C. sumatranus* Karsten (Hernández-Becerril, 1999).

Our knowledge of the distribution of *C. pseudoaurivilli* is rather poor. Ikari (1926) regarded it as 'a very rare species'. It occurs in Japan, but is here recorded more widely, from Mexican Pacific coasts (Baja California and Gulf of Tehuantepec) and the Indian Ocean. It seems to be distributed in subtropical to temperate waters, and is probably a coastal form.

Chaetoceros pseudosymmetricus

Chaetoceros pseudosymmetricus is a member of the subgenus *Hyalochaete*, as shown above, having more delicate chains and thinner appendages than in species of the subgenus *Chaetoceros*, weakly silicified valves, no chloroplasts in setae, with rimoportulae on terminal valves only, and intercalary setae fusing together to produce the chains. However, it has never been allocated to any section within the subgenus; it is here assigned to the section *Stenocincta*, for it shares some morphological characters with other species of the section, especially *C. affinis* Lauder.

C. pseudosymmetricus has been regarded as a synonym of *C. affinis* (Thornington-Smith, 1970), but here it is considered a 'currently recognized' species. Both species are, in fact, closely related, but morphological differences do exist, particularly with respect to the setae. Intercalary setae are inflated at the bases in *C. pseudosymmetricus*, but not in *C. affinis* (Evensen & Hasle, 1975; Hernández-Becerril, 1996).

The heteropolarity of terminal setae (Fig. 23) is, itself, the most conspicuous and distinctive morphological character of *C. pseudosymmetricus*, and it is obviously different from *C. affinis*. *C. affinis* also presents polyhedral terminal setae (Hernández-Becerril, 1996), whereas in *C.*

pseudosymmetricus one is long and strongly curved, apparently well developed, and the other is very reduced; the terminal setae differ in direction and length between the two species. The external structure of the rimoportulae on the terminal valves is similar in these two species.

There is considerable morphological variation in *C. affinis* (Hernández-Becerril, 1996), but no intermediates between this species and *C. pseudosymmetricus* have been found. The geographical distribution of these two species also indicates one important difference. *C. affinis* is a well-known cosmopolitan species in temperate and warm-water regions, but *C. pseudosymmetricus* has only been found in the Indian Ocean (Thorrington-Smith, 1970). Because it was first described from below 50 m (Steeman-Nielsen, 1931), the species is considered as a more oceanic 'shade' form.

Conclusions

These three very rare species have not been found or identified in any major classical references (e.g. Hustedt, 1930; Hendey, 1937; Cupp, 1943; Sournia, 1968; Simonsen, 1974), nor in more recent literature (e.g. reviews of diatom material from the Indian Ocean: Desikachary & Prema, 1987; Desikachary *et al.*, 1987, or surveys of the genus *Chaetoceros* in regions of the Atlantic Ocean: Rines & Hargraves, 1988, and in the Pacific Ocean: Hernández-Becerril, 1996). Although it cannot be explained here why these species are so rare, it is suggested that the previous sparse information regarding specific morphological characters, which are further described here, have contributed to our poor knowledge of several *Chaetoceros* species and their distribution. The morphological characters described in this paper have permitted taxonomic proposals regarding allocation of the species studied to certain subgenera and sections of *Chaetoceros*. Suggestions concerning the closest related species have been made, although these relationships may be only superficial.

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