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Note on the morphology of two planktonic diatoms: *Chaetoceros bacteriastroides* and *C. seychellarus*, with comments on their taxonomy and distribution

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HERNÁNDEZ-BECERRIL, D. U., 1993. **Note on the morphology of two planktonic diatoms: *Chaetoceros bacteriastroides* and *C. seychellarus*, with comments on their taxonomy and distribution.** Two planktonic species of diatoms, *Chaetoceros bacteriastroides* and *C. seychellarus*, have been studied by light and electron microscopy. Important features that may be used as taxonomic characters are described. A new subgenus, *Bacteriastroidea*, is proposed to include *C. bacteriastroides*, because of its unique characteristics within the genus. The taxon is considered to be a link between the genera *Bacteristrum* and *Chaetoceros*. Morphological and taxonomic affinities between *C. seychellarus* and other related species of *Chaetoceros* subgenus *Chaetoceros* section *Borealia*, are noted, and a phylogenetic sequence is suggested. Some general evolutionary tendencies are discussed. The known distribution of *C. bacteriastroides* and *C. seychellarus* is revised: both species are restricted to warm waters, but while *C. bacteriastroides* shows an Indo-Pacific distribution, *C. seychellarus* is found in all three oceans.

ADDITIONAL KEY WORDS:—*Chaetoceros* – diatoms – distribution – morphology – taxonomy.

CONTENTS

INTRODUCTION

Studies on the morphology and taxonomy of several species of the diatom genus *Chaetoceros* Ehrenberg have been carried out using light (LM) and electron microscopy (both TEM and SEM), contributing comments and proposals to its

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classification, as well as description of new species of the genus (Hernández-Becerril, 1989, 1991).

Two fairly uncommon, tropical planktonic species of the genus were studied: *C. bacteriastroides* Karsten and *C. seychellarus* Karsten. The first species was found in very small numbers in samples from coasts off Baja California and the Indian Ocean and *C. seychellarus* was encountered rarely in the Gulf of California and also in the Indian Ocean. Both species were originally described from the Indian Ocean by Karsten (Karsten, 1907). *Chaetoceros bacteriastroides* is a rarely recorded species; apart from the original description, there are two other records from the central Pacific Ocean, including the electron microscopy study by Fryxell (1978). The present study shows it to be sufficiently different from species in the existing subgenera to warrant its removal to a new subgenus, *Chaetoceros* subgenus *Bacteriastroidea*. *Chaetoceros seychellarus* is also a rarely cited species, the most recent record from the Gulf of California (Gárate Lizárraga, Siqueiros Beltrones & Lechuga Devéze, 1990); but this is the first electron microscope study of the species.

MATERIAL AND METHODS

This study is based on preserved marine plankton samples collected in different seasons from the Gulf of California, coast off Baja California, and the Indian Ocean. The locations where the two species were encountered are given in Table 1.

The material was rinsed and/or cleaned (Hernández-Becerril, 1991). Identification, selection, measurements and preliminary observations were made in LM. Either drops of material or isolated specimens were prepared

TABLE 1. Position of samples used for this study

	Area	Cruise	Source
Chaetoceros bacteriastroides	Coasts off Baja California 26°14'N, 114°29'W 26°32'N, 114°40'W	CICIMAR-CIB (8508)	CIB (1985)
	Coasts off Baja California 26°25'N, 114°17'W	CIB-CICIMAR (8605)	CIB (1986)
	Indian Ocean 01°51'S, 67°46'E 07°01'S, 67°20'E	Discovery (1964)	IOS (1964)
Chaetoceros seychellarus	Gulf of California 27°31'N, 111°20'W 27°49'N, 111°55'W	GOLCA (8606)	CICIMAR (1986)
	Gulf of California 23°08'N, 109°27'W	CORTES II	ICML (1985)
	Indian Ocean 07°01'S, 67°20'E	Discovery (1964)	IOS (1964)

CIB, Centro de Investigaciones Biológicas de Baja California Sur, A.C. (La Paz, B.C.S., Mexico); CICIMAR, Centro Interdisciplinario de Ciencias Marinas (La Paz, B.C.S. Mexico); ICML, Instituto de Ciencias del Mar y Limnología, NMA (Estación Mazatlán, Sin., México); IOS, Institute of Oceanographic Sciences (Wormley, Surrey, U.K.).

conventionally for SEM (Phillips 501, at 10–12 kV) study. Only cleaned material was used for TEM (JEOL 1200 EX) observations.

Terminology follows that proposed by Anonymous (1975) and Ross *et al.* (1979). In addition, specific terminology for *Chaetoceros* was taken from Rines & Hargraves (1988) and modified by Hernández-Becerril (1991).

OBSERVATIONS

Genus Chaetoceros *Ehrenberg subgenus* Bacteriastroidea Hernández-Becerril
Subgenus ***Bacteriastroidea*** Hernández-Becerril **subgen. nov.**

Valvae cylindraceae, omnibus valvis intercalaribus paria tria setarum praeditis, paribus duobus valde deminutis et pari uno crasso et bene evoluto. Prominentiae regulares in marginem valvarum intercalarium prasentia. Rimoportulae non nisi in valvis terminalibus praesentia; cellulae chromatophoris binis.

TYPUS: *C. bacteriastroides* Karsten

Valves cylindric, each intercalary valve possessing three pairs of setae, some of them (two pairs) very reduced, the other setae usually thick and well developed. Regular projections (outgrowths) on the edge of the intercalary valves. Rimoportula only present on terminal valves; two chomatophores per cell.

Chaetoceros bacteriastroides Karsten, *Wissenschaftliche Ergebnisse der deutsche Tiefsee-Expedition "Valdivia" 1898–1899, II.***2:** 390 (1907).

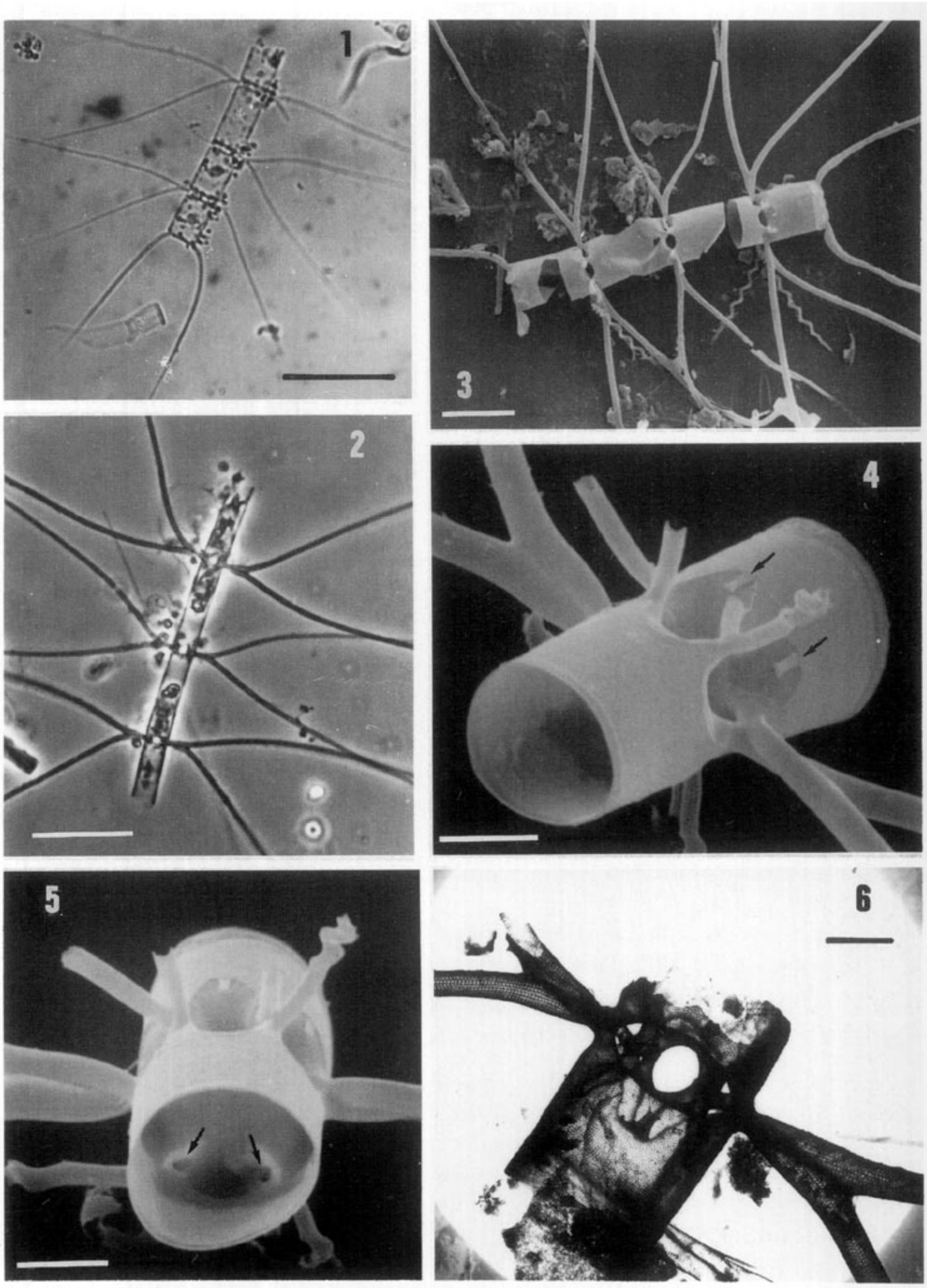
SYNONYM: *Chaetoceros bacteriastroides* Karsten forma *bacteriastroides* Thorrington-Smith, *Nova Hedwigia, Beiheft* **31:** 825 (1970).

non Chaetoceros pseudocurvisetus Mangin, *Bulletin de la Societé Botanique de France,* **57:** 350 (1910).
non Chaetoceros bacteriastroides forma *imbricatus* (Mangin) Thorrington-Smith, *Nova Hedwigia, Beiheft* **31:** 825 (1970).
non Chaetoceros bacteriastroides forma *parvi-torosum* Thorrington-Smith, *Nova Hedwigia, Beiheft* **31:** 826 (1970).

ICONES: Karsten (1907) p. 390, pl. 44, figs 2 a–c; Fryxell (1978) p. 68, figs 18–21; Thorrington-Smith (1970) p. 825, pl. 2 fig. 4.

Description in LM (Figs 1, 2). The chains are straight, usually long and robust. The cells are cylindrical, in girdle view the cells appear rectangular with smooth corners and long pervalvar axis. The aperture between the cells is narrow and the valve face is slightly concave with two projections (pegs) on the edge connecting with similar pegs on the sibling valves. The valve mantle is high. In valve view the valves are circular. The setae are thick and coarse, the terminal setae differing from the intercalary ones in direction, as the terminal setae are directed toward the chain axis and the intercalary setae project almost perpendicularly to the chain axis. Two chromatophores occur in the centre of the cells. Measurements: 10–14 μm apical axis, 19–25 μm pervalvar axis.

Description in EM. The valves appear to be fairly lightly silicified (Figs 3–6), as are most of the species within *Chaetoceros* subgenus *Hyalochaete.* They are regularly perforated by rows of poroids running along the pervalvar axis radiating from a



Figures 1–6. *Chaetoceros bacteriastroides*. Fig. 1. Part of a chain, with terminal cell, LM. Fig. 2. Middle part of a chain, LM. Fig. 3. A short complete chain (four cells), SEM. Fig. 4. Sibling valves showing two pairs of reduced setae and two pairs of well-developed setae. Arrows point to the outgrowths on the edge of the valve, SEM. Fig. 5. Inside view of a valve showing the bases of reduced setae (arrows), SEM. Fig. 6. Sibling valves with main setae joined for a short distance, TEM. Figs 1, 2: scale bars = 50 μm. Fig. 3: scale bar = 20 μm. Figs 4–6: scale bars = 5 μm.

conspicuous annulus (Figs 6, 7). On the edge of the valves some projections arise between the bases of the setae (Figs 4, 6). The rimoportula is only located on the terminal valves, being a slit-like structure with a short protrusion to the outside and no true labiate structure inside (Fig. 9).

Each intercalary valve has three pairs of setae, two of which are reduced (Figs 4, 5). Some of the reduced setae have a spiral pattern and apparently all of them are open externally (Figs 3–5). The terminal valves have just four small projections on the edges, probably corresponding with the reduced setae of the intercalary valves (Figs 8, 9). The well-developed setae are rather thick (in contrast with most species of *Chaetoceros* subgenus *Hyalochaete*). Intercalary setae fuse to those of sibling valves and remain joined for a short distance before diverging (Figs 4, 6, 13). The terminal setae are slightly thicker near their base (Fig. 10), but both intercalary and terminal setae are circular in cross-section and have irregularly distributed spines (Figs 11, 12); the wall is perforated by rows of poroids running longitudinally (Figs 11, 13). Distally the spines become larger. The tip is flattened or truncated and heavily spined (Figs 14, 15). The reduced setae seem to have the same morphology as the main ones.

Genus Chaetoceros *Ehrenberg subgenus* Chaetoceros (Phaeoceros *Gran*)

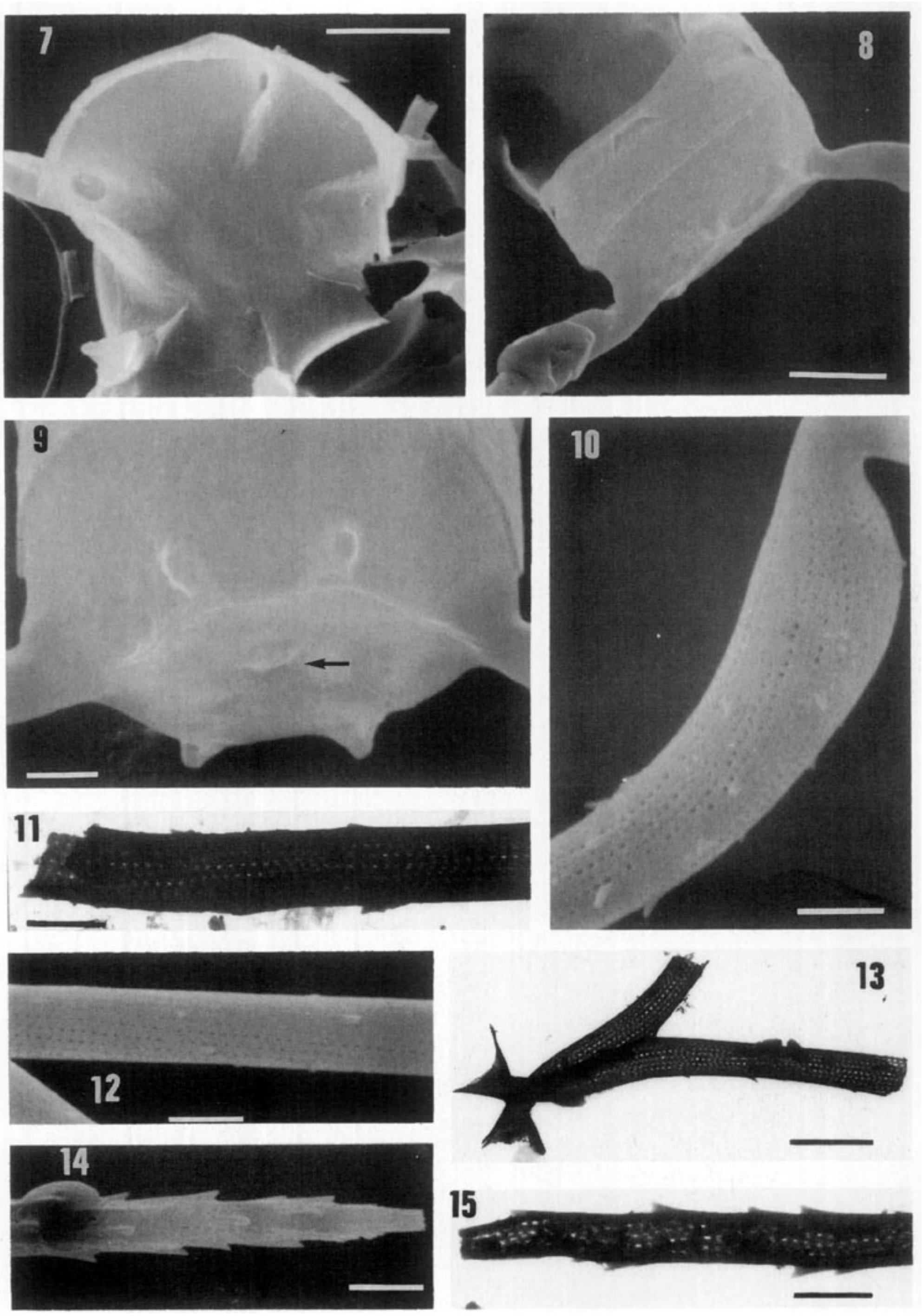
Section *Borealia* Ostenfeld

Chaetoceros seychellarus Karsten, *Wissenschaftliche Ergebnisse der deutsche Tiefsee-Expedition "Valdivia" 1898–1899, II.* **2:** 387 (1907).
= *Chaetoceros borealis* Bailey *sensu* Desikachary *et al.* (1987, pl. 355, fig. 1, pl. 356, fig. 1).

ICONES: Karsten, (1907) p. 387, pl. 43, figs 4 a–e; Hustedt (1920) pl. 327, figs. 12, 13; Hendey (1937) p. 296; Simonsen (1974) p. 32.

Description in LM (Figs 16, 17). The chains are straight, long and robust. In girdle view the cells are rectangular with smooth corners and constrictions at girdle level, the pervalvar axis being longer than the apical one. The aperture is narrow, the valve face is flat or slightly convex and the valve mantle is high. In girdle view the valves are elliptical, with the setae curving toward the transapical axis. The setae are very thick, coarse and have spines; they arise very close to the corners and curve smoothly toward the chain axis. Numerous small and round chromatophores are present in the cells and the setae. Measurements: 15–29 μm apical axis, 33–42 μm pervalvar axis, 7–9 μm aperture.

Description in EM. The valves appear heavily silicified (Figs 18, 19, 22), being perforated by evenly spaced poroids, but lack costae in both valve face and mantle (Fig. 20); some external thickenings form a row parallel to the line of girdle insertion in the mantle and others are scattered close to the valve margin (Figs 20, 23, 26). The annulus is easily seen in the valve face and eccentric (Figs 21, 23, 26). One rimoportula occurs on each valve in the chain (e.g. intercalary or terminal); as the rimoportula is related to the annulus position, this is also placed to one side on the valve. The annulus is a simple hole inside, with a very short projection to the outside (Figs 23, 26). The aperture between cells is often found to be occluded by a thin wall, perhaps occurring in dividing cells (Fig. 22).



Figures 7–15. *Chaetoceros bacteriastroides*. Fig. 7. Inside view of an intercalary valve showing the central annulus, SEM. Fig. 8. Terminal valve, SEM. Fig. 9. Detail of terminal valve. Note the rimoportula (arrow) and pegs on the valve edge, SEM. Fig. 10. Base of a terminal seta, SEM. Fig. 11. Middle part of an intercalary seta, TEM. Fig. 12. An intercalary seta near its base, SEM. Fig. 13. Two sibling setae fused for a short distance, TEM. Fig. 14. Tip of a seta, SEM. Fig. 15. Tip of a seta, TEM. Figs 7, 8, 13: scale bars = 5 μm. Figs 9–12, 14, 15: scale bars = 2 μm.

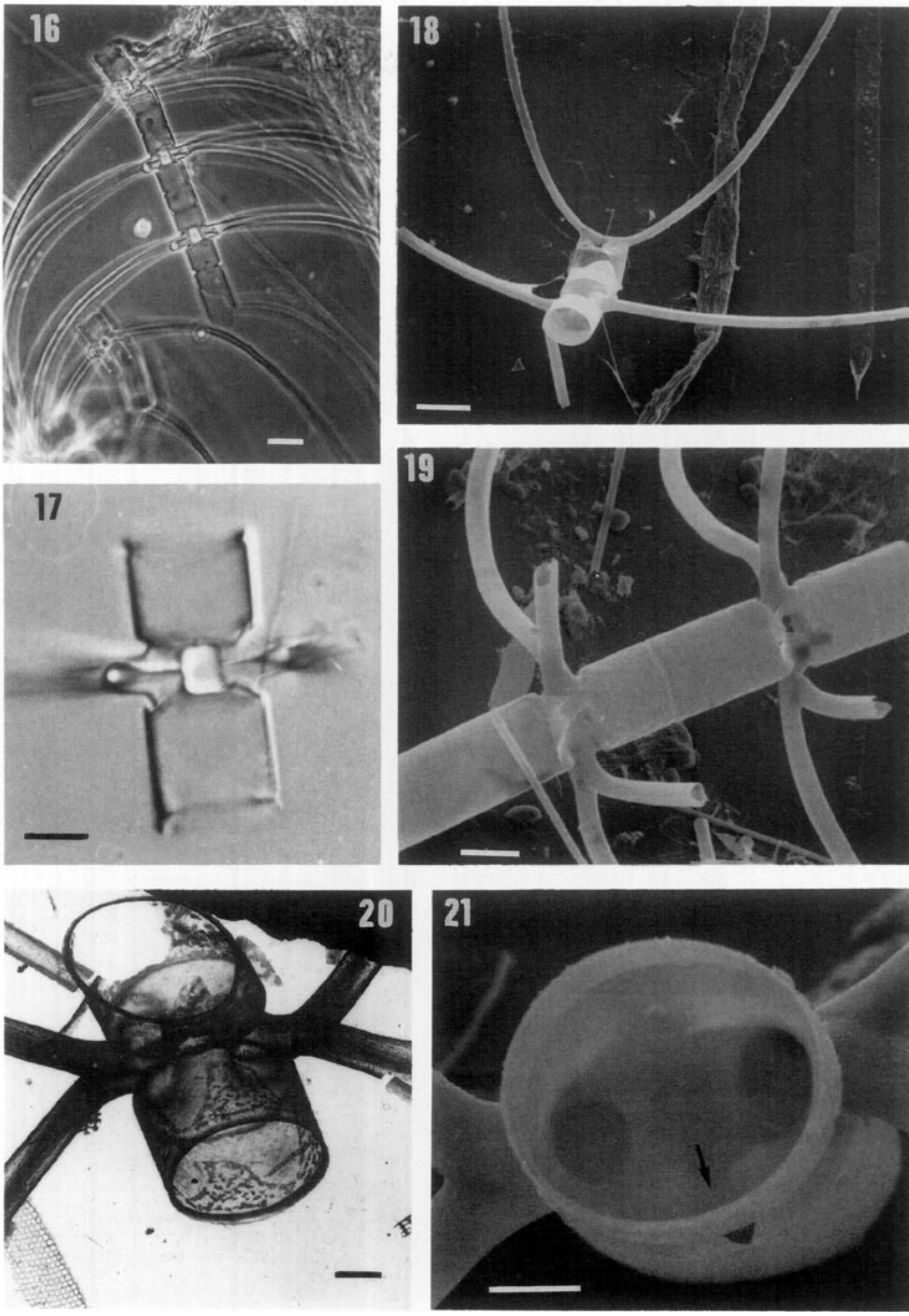
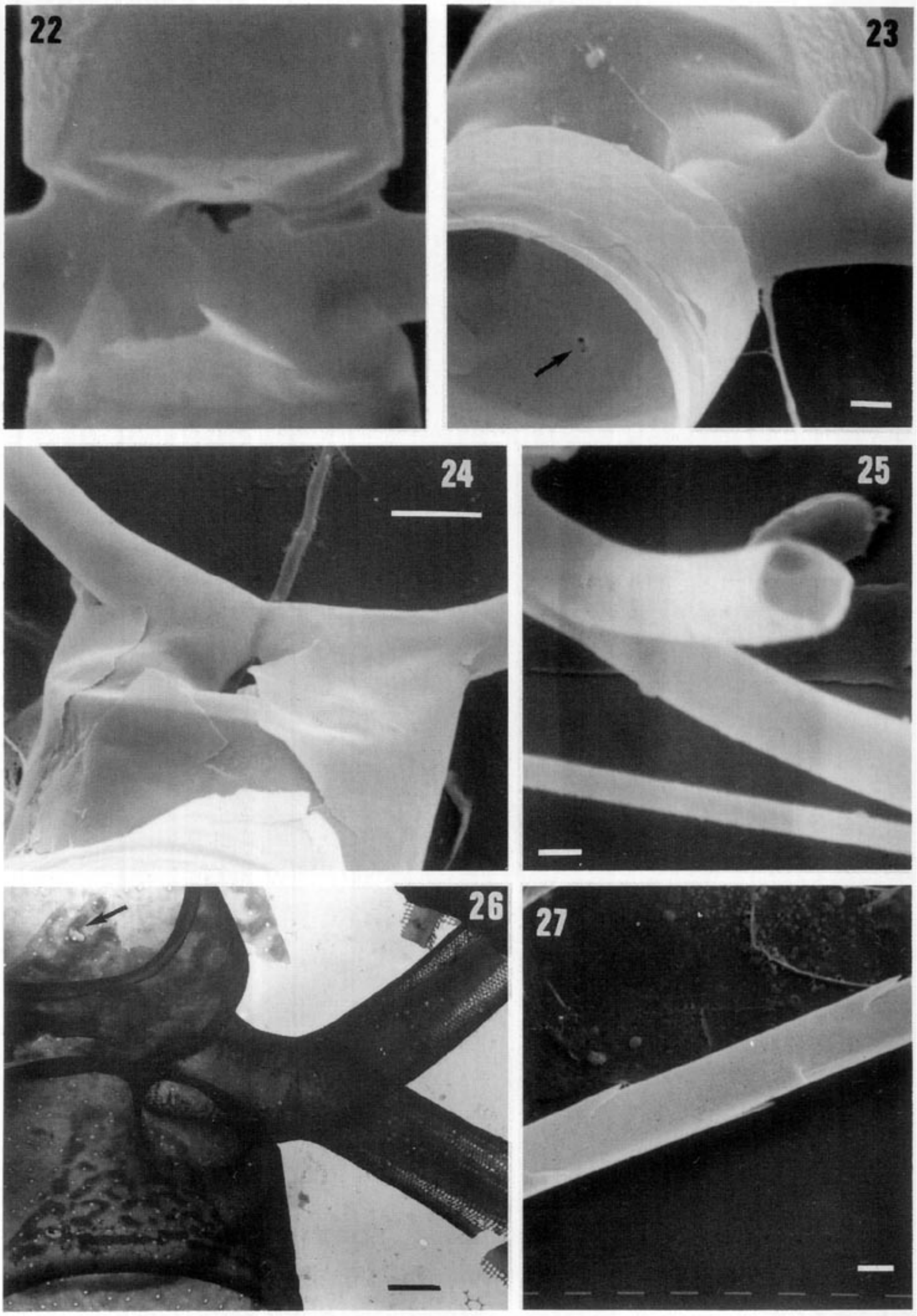


Figure 16–21. *Chaetoceros seychellarus*. Fig. 16. Part of a chain, LM. Fig. 17. Two sibling valves showing the aperture, LM. Fig. 18. Terminal part of a chain, SEM. Fig. 19. Middle part of a chain, SEM. Fig. 20. Two sibling valves showing thickenings on the mantle, TEM. Fig. 21. Inside view of a valve. Arrow points to the eccentric rimoportula, SEM. Figs 16, 18: scale bars = 20 μm. Figs 17, 19: scale bars = 10 μm. Figs 20, 21: scale bars = 5 μm.



Figures 22–27. *Chaetoceros seychellarus*. Fig. 22. Mantle of a valve and the partially occluded aperture, SEM. Fig. 23. Inside view of a valve with the eccentric rimoportula (arrow), SEM. Fig. 24. Anterior terminal valve with its setae fused, SEM. Fig. 25. Detail of a seta: four-sided in cross-section, SEM. Fig. 26. Mantle of a valve, annulus (arrowed), and base of the setae, TEM. Fig. 27. Intercalary seta with rows of spines at its edges, SEM. Figs 22, 24: scale bars = 5 μm. Figs 23, 25–27: scale bars = 2 μm.

The wall at the extreme base of the setae is perforated by a fine mesh of poroids, which resembles the pattern of areolae in other diatoms (Fig. 21). The setae are basically circular in cross-section at their bases (Fig. 23), becoming four-sided with rows of alternate spines running along each edge at distal parts (Figs 25, 27). Their wall shows longitudinal rows of big poroids with transverse striae of very fine poroids and weak costae, following the pattern of one stria between two costae (Fig. 26). The terminal setae have a very short base and then fuse together over the centre of the valve, they then diverge widely (Fig. 24).

DISCUSSION

Morphology, taxonomy and distribution of C. bacteriastroides

The described morphology of this species is consistent with previous EM observations (Fryxell, 1978). All the observations indicate basic differences with regards species of the subgenus *Hyalochaete* Gran (see Evensen & Hasle, 1975; Fryxell & Medlin, 1981; Hernández-Becerril, 1989). *Chaetoceros bacteriastroides* and the species of *Chaetoceros* subgenus *Hyalochaete* are similar in the character of possessing a rimoportula only on terminal valves. However, the valves in *C. bacteriastroides* show no true costae, although they are finely perforated by poroids.

The presence of small (reduced) setae on each intercalary valve in the chain is probably the most outstanding character, and is unique within the genus. The only other taxon showing a similar, but perhaps inconsistent feature is *C. okamurai* Ikari var. *tetraseta* Ikari, which presents four setae on terminal valves of short chains (Ikari, 1928), in contrast to *C. bacteriastroides,* where the terminal valves show no true setae. There are no other characters common to these two species.

The main, well-developed setae show a structure of their own, the terminal setae differing from the intercalary ones only in their direction; some terminal setae were observed to be wider close to the base, a situation which I have not found in Fryxell's paper. The tip of the setae had also not been shown earlier. Another important features is the occurrence of the conspicuous projections ('shoe-horn projections', according to Fryxell, 1978) on the valve margin of the intercalary valves.

Comparing the general morphology and emphasizing important characters, it seems that some of these characters have more affinity to the closely related genus *Bacteriastrum* Shadbolt (see also Fryxell, 1978) than to *Chaetoceros* subgenus *Hyalochaete:* structure of the valves; occurrence of various (more than two per valve) setae on each intercalary valve; presence of outgrowths on the valve edge. *Chaetoceros bacteriastroides* is correctly placed in *Chaetoceros,* because it still fits the general circumscription of the genus, and the bilateral symmetry in *C. bacteriastroides* contrasts to the radial symmetry of the *Bacteriastrum* species. Fryxell (1978) believed the radial symmetry to be primitive condition and the bilateral symmetry advanced; Ikari (1928) and Fryxell (1978) considered *C. bacteriastroides* as the closest link in the sequence from *Bacteriastrum* to *Chaetoceros.*

The creation of a new subgenus, *Chaetoceros* subgenus *Bacteriastroides,* is hereby proposed because there are no known species closely related to *C. bacteriastroides,* and until the forms '*bacteriastroides*', '*imbricatus*', '*parvi-torosum*' described by Thorrington-Smith (1970) are studied by TEM, they cannot be considered as possible members of the subgenus. *Chaetoceros pseudocurvisetus* is not a synonym of *C. bacteriastroides*, as previously discussed by Fryxell (1978).

The distribution of *C. bacteriastroides* appears to be restricted to warm waters, mainly close to the equator. The highest latitude record is 26°32'N in coasts off Baja California and is given in this study. It has been only recorded from the Indian and the Pacific Oceans (Indo-Pacific distribution), with no verified report from the Atlantic Ocean. Simonsen (1974) cited it as being tropical/subtropical to temperate and also neritic, the wider range due to the inclusion of *C. psedocurvisetus* as a synonym of *C. bacteriastroides*. *Chaetoceros bacteriastroides* is apparently an oceanic form.

Morphology, taxonomy and distribution of C. seychellarus

The general morphology of *C. seychellarus* resembles that of the related species *C. borealis* Bailey (Evensen & Hasle, 1975) and *C. densus* Cleve (Hernández-Becerril, 1989); three species currently included within the section *Borealia*, subgenus *Chaetoceros* (*Phaeoceros* Gran). *Chaetoceros seychellarus* and *C. borealis* show a similar valve structure and shape, both lacking costae, and possessing granules (or thickenings), as well as the occurrence of a slightly eccentric annulus (and rimoportula). The setae differ, especially in the areolar pattern in the wall structure in both species: *C. seychellarus* has a pattern comprising one stria between two costae, whereas *C. borealis* was observed to have two striae between two costae (Evensen & Hasle, 1975). The main similarities between *C. seychellarus* and *C. densus* are the structure of the valve, with the bases of the setae perforated by a fine mesh of poroids, and the wall of the setae having the pattern of one stria between two costae. The annulus and rimoportula are centric in *C. densus*, but eccentric in *C. seychellarus*.

An important character is *C. seychellarus* is the fusion of the terminal setae in one of the ends of the chain, a character also observed by Karsten (1907: pl. 43, fig. 4d). Neither of the two other mentioned species have this feature, but it has been shown to be present in species of the 'Peruvianus' group (*C. peruvianus* Brightwell, *C. criophilus* Castracane, *C. convolutus* Castracane and *C. concavicornis* Mangin).

Most of the chains of the species included within the section *Borealia* show an evolutionary trend to specialization: some species are short-chained ($<$ 10 cells per chain), and there are several solitary species (*C. peruvianus*, *C. pendulus* Karsten). At the same time they show marked bilateral symmetry (the annulus and rimoportula are eccentric or clearly situated to one side of the valve). There is also a tendency for the chains to be heteropolar, a character seen in several species of the section (*C. tetrastichon* Cleve, *C. dadayi* Pavillard – Hernández-Becerril, 1992), and the same *C. peruvianus* and *C. pendulus* (Koch & Rivera, 1984; Hernández-Becerril, 1989). In *C. tetrastichon* and *C. dadayi* the setae show high specialization (Hernández-Becerril, 1992), which has been observed to attach tintinnids, because of the great associations existing between these two species and the tintinnids. But while different opinions have been claimed, for example, Simonsen (1979) mentioned that the evolutionary trend is from bilateral to radial symmetry, I concur with Fryxell (1978) and Fryxell *et al.* (1986) that the sequence is the opposite.

Following these comments, it is possible to suggest a close taxonomic relationship among some species already mentioned, which belong into the section *Borealia*, and a probable implication in the phylogenetic line, possibly *C. densus* – *C. borealis* – *C. seychellarus* – species of the Peruvianus group. It is clear that further studies are necessary for a more complete phylogenetic picture. No other close taxonomic (and phylogenetic) relationship is apparent: Simonsen (1974) discussed the synonymy of *C. aurivillius* Taylor (*non C. aurvillius* Cleve) with *C. seychellarus*. Many *Chaetoceros* species still remain 'little known' and need to be studied with the modern combination of both light and electron microscopy in order to define the important characters.

As regards to the distribution, *C. seychellarus* shows a distribution restricted to tropical areas, and it is thought to be neritic, though occasionally found in oceanic environs. This species is always rare, usually reported from the Indian and Atlantic Oceans, and this report is only the second record from the Pacific Ocean (within the Gulf of California).

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