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A morphological study of *Chaetoceros* species (Bacillariophyta) from the plankton of the Pacific Ocean of Mexico

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CONTENTS

SYNOPSIS. An analysis of 65 preserved marine plankton samples from waters of the Pacific Ocean of Mexico was undertaken in order to investigate the morphology of species of the diatom genus *Chaetoceros* Ehrenb. Forty-six *Chaetoceros* taxa were recorded from the samples. Of these, 35 were studied using light, scanning and transmission electron microscopy; a further 11 species were also recorded as present in the material, but these have been treated elsewhere. Most of the taxa studied are characteristic of warm-water regions. Their morphology is discussed, especially where it differs from that previously described. Most of the taxa are illustrated by light and electron micrographs. A new section, *Peruviana* Hern.-Bec., within subgenus *Chaetoceros* (*Phaeoceros*), is proposed. New observations by electron microscopy are contributed for the following taxa: *C. atlanticus* var. *neapolitanus*, *C. atlanticus* var. *skeleton*, *C. brevis*, *C. compressus*, *C. densus*, *C. denticulatus*, *C. distans*, *C. pendulus*, and *C. vistulae*. Phylogenetic relationships with other genera and aspects of distribution and biogeography are also revised.

INTRODUCTION

General

Chaetoceros species are an important and often abundant component of the marine phytoplankton community; however, the great number of species makes positive identification difficult. The major characters traditionally used for identification at the species level are: the form and relative length of the chain, the frustule shape (girdle and valve views) and size, the structure and size of the girdle and valve mantle, the orientation and form of the setae, and the number of chloroplasts. Evensen & Hasle (1975) found that the structure and size of the rimoportula is another important feature for identifying species. Hargraves (1979) considered that resting spores can also aid identification, although these are limited to species belonging to subgenus *Hyalochaete*.

Many *Chaetoceros* species from the plankton of temperate and cold waters have been described and studied using electron microscopy (EM). However, tropical and subtropical species have been less studied using such modern techniques.

This work is a study of the morphology and taxonomy of some species of the genus *Chaetoceros* which were encountered in tropical and subtropical areas, in order to present a systematic account of the species from those regions and contribute to the taxonomy of the genus.

Historical background and taxonomic relationships

The genus *Chaetoceros* was erected by Ehrenberg (1844), who described the type species, *C. dichaeta*, as well as three allied genera: *Dicladia*, *Goniothecium*, and *Syndendrium*; the last two were at spore stage and all three are now considered to be synonyms of *Chaetoceros* (VanLandingham, 1968). Later, Brightwell (1856) provided an emended description of *Chaetoceros*, including two new species. Schütt (1895) described a new genus, *Peragallia*, which is also now considered to be a synonym of *Chaetoceros* (probably *C. peruvianus* Brightw.).

Gran (1897) divided *Chaetoceros* into two subgenera: *Phaeoceros* and *Hyalochaete* (Hendey, 1964, has correctly substituted *Chaetoceros* for *Phaeoceros*, as this subgenus contains the type species). Ostenfeld (1903) divided the subgenera into 16 sections (two in *Chaetoceros* and 14 in *Hyalochaete*); further additions were made by Gran (1905). Recent additions to the classification include the proposal of section *Coarctata* within subgenus *Chaetoceros* (Hernández-Becerril, 1991*a*), section *Conspicua* within subgenus *Hyalochaete* (Hernández-Becerril et al., 1993), and the proposal for a new subgenus, *Bacteriastroidea* (Hernández-Becerril, 1993*a*). The present infrageneric classification includes three subgenera and 19 sections (including the one proposed here): four in subgenus *Chaetoceros* and 15 in subgenus *Hyalochaete*.

According to VanLandingham (1968) there are 177 species of *Chaetoceros*, including one fossil, four described as spore stages, and five from freshwater environments, together with 36 infraspecific taxa: 19 varieties and 17 forms. However, Hargraves (1979) considered that this number was an overestimation and some species should be regarded as forms or varieties of others.

Chaetoceros exhibits little variation in its general structure. The subgenera may be distinguished by the following features:
I. *Chaetoceros* (*Phaeoceros*)–robust species; one pair of setae per valve; setae thick and strong, most with chloroplasts and spines; resting spores known only in one species.
II. *Hyalochaete* – delicate species; one pair of setae per valve; setae thin and fragile, usually lacking chloroplasts; resting spores in most of the species.
III. *Bacteriastroidea* – fairly robust species; three pairs of setae per valve (two pairs reduced), lacking chloroplasts; resting spores unknown.

Evensen & Hasle (1975) noted that the rimoportulae in subgenus *Hyalochaete* are shorter and less prominent than those in subgenus *Chaetoceros*, and are confined to terminal cells.

The genus *Chaetoceros* has been considered to belong to the family Chaetoceraceae Smith, together with *Bacteriastrum* Shadbolt and *Acanthoceros* Honigm. (Simonsen, 1979). However, Round et al. (1990) placed *Chaetoceros* within the family Chaetocerotaceae Ralfs, with *Bacteriastrum* and *Gonioceros* H. Perag. & Perag., although Crawford et al. (1994) later transferred the two *Gonioceros* species to the genus *Attheya* West, leaving the family with only two genera: *Chaetoceros* and *Bacteriastrum*. Other workers have included only *Chaetoceros* in Chaetoceraceae (e.g. Lebour, 1930; Hendey, 1964), but it is evident, however, that *Chaetoceros* and *Bacteriastrum* are closely related (Fryxell, 1978; Simonsen, 1979). *Acanthoceros* is now placed within its own family, Acanthoceratacea R.M. Crawford (Round et al., 1990).

In Simonsen's (1979) classification, Chaetoceraceae is placed within the suborder Biddulphiineae, order Centrales. In Round et al. (1990) Chaetocerotaceae is placed within the order Chaetocerotales, subclass Chaetocerotophycidae (both taxa proposed by Round & Crawford in Round et al., 1990); the present study follows this latter classification.

Recent studies with electron microscopy

Studies of *Chaetoceros* using electron microscopy began with Okuno (1951), when he published microphotographs of *C. criophilus* Castrac. Helmcke & Krieger (1953) also made TEM observations of *Chaetoceros* species, as did Hendey et al. (1954). Desikachary & Bahadur (1954) provided a study of the genus, although gave few details. Desikachary (1956) attempted to summarize the electron microscopy studies (mainly TEM) made on diatoms up to that time. However, his list of 11 species of *Chaetoceros* did not include *C. densus* Cleve, which had been studied previously by Hendey et al. (1954). Okuno (1956) provided additional information on some partially described species. Later, Hendey (1959) prepared another list, this time including 19 species of *Chaetoceros* studied using TEM and especially with regard to the cell wall. Okuno (1970) continued to provide more information on *Chaetoceros*, while Blasco (1970) made a detailed study of *C. didymus* Ehrenb. Other observations combining LM and TEM were made during the study of life cycles (Hargraves, 1972; Stosch et al., 1973) and morphology (Duke et al., 1973).

The most important recent contribution to our knowledge of the genus *Chaetoceros* was made by Evensen & Hasle (1975), who studied 14 species (four in subgenus *Chaetoceros* (*Phaeoceros*), 10 in subgenus *Hyalochaete*) using SEM and TEM. Later, Fryxell (1978) studied three species of Chaetoceraceae, including two *Chaetoceros* species, with SEM. Hargraves (1979) provided an important contribution on the resting spores of *Chaetoceros* by combining LM, SEM, and TEM. Fryxell & Medlin (1981) studied three *Chaetoceros* species using LM and SEM, especially with regard to chain formation. Navarro (1982) listed and figured 25 species and one variety of *Chaetoceros* using LM, but gave no new data on their cell structure. Takano (1983) described a new species, *C. salsugineus* Takano, accompanied by electron micrographs. Koch & Rivera (1984) studied nine species of subgenus *Chaetoceros* (*Phaeoceros*), two of them not previously studied with EM. Additional observations have been made recently on valve development (Li & Volcani, 1985), morphology (Rogerson et al., 1986; Giuffré & Ragusa, 1988; Hernández-Becerril, 1991*a*, *b*, 1992*a*, 1993*a*; Moreno Ruiz et al., 1993), taxonomy (Rines & Hargraves, 1986; Hernández-Becerril et al., 1993), and resting spores (Stockwell & Hargraves, 1986).

One of the latest contributions to the knowledge of the genus was made by Rines & Hargraves (1988), who gave an account of species encountered in Rhode Island, U.S.A., using LM, but also discussing important taxonomic points within the genus as a whole. Other studies with EM involve the discovery of more than one rimoportula per valve (Rines & Hargraves, 1990; Hernández-Becerril, 1991*a*, *c*; Hernández-Becerril et al., 1993) and the description of new species (Hernández-Becerril, 1991*c*, 1992*b*).

MATERIALS AND METHODS

Source of material

This study was carried out using preserved marine plankton samples, some collected by the author, but the majority supplied by the following colleagues: R. Cortés-Altamirano (ICMyL-UNAM), S. Gómez-Aguirre (IB-UNAM), and institutions: CIB and CICIMAR (La Paz, B.C.S., Mexico).

Sixty-five samples were obtained from the tropical-subtropical Pacific Ocean of Mexico: 29 from the Gulf of California, 31 from off the coast of Baja California, five from off the Pacific coast of Mexico (see Table 1).

Methods

All material prepared for light and electron microscopy was rinsed at least five times with distilled water. Permanent slides for light microscopy were made from the rinsed and cleaned material. The method for cleaning diatoms followed that used by Simonsen (1974) and Hasle (1978), which is basically the oxidation of the organic material (using KMnO4) followed by acid treatment (HCl). Identification, preliminary observations, and measurements were made with an Olympus CH light microscope, phase contrast, and an Olympus Bh with attached camera, phase contrast, bright field and differential interference contrast.

Rinsed and cleaned material was used for SEM. Drops of the prepared material were put onto coverslips, air-dried, and then coated with gold in a coating unit. Some previously identified specimens were isolated with the aid of a micropipette, and afterwards the above method was followed. Critical point drying was used for a few samples, after rinsing and dehydration. The scanning electron microscope used was a Phillips 501, usually operated at 10–12 kv.

For transmission electron microscope studies, only cleaned material was used. This was carefully placed with a micropipette onto copper, Formvar-coated grids, air-dried, and then observed directly. The instrument was a JEOL 1200 EX.

Terminology

The terminology adopted in this study generally follows that proposed by Anonymous (1975) and Ross et al. (1979). Specific terminology for *Chaetoceros* follows Brunel (1966, 1972) and Rines & Hargraves (1988). However, the following terms used in this paper have been modified from those cited (Hernández-Becerril, 1991*a*, *c*, 1992*a*):

- The term chain is used instead of colony, as colony implies a more complex organization with some interaction between its members.
- Chains are arbitrarily considered short if the number of cells in them is less than 10, long if 11 cells or more. Usually, there is no overlap between these two categories, as species are typically long-chained or short-chained.
- The term heteropolar is applied in the sense of Rines & Hargraves (1988), where the two ends of a chain or the two valves of a cell are markedly different from each other (Pl. 1, Figs 3a, b). Thus, to distinguish each end the terms anterior and posterior are used: the anterior end having valves with curved setae, directed towards the chain or cell, and the posterior end with setae directed away from the chain or cell.
- Girdle view is regarded as the broad girdle view, unless otherwise stated (Pl. 1, Fig. 1).
- 'Aperture' is the space between sibling cells in a chain (Pl. 1, Fig. 1). This is described as narrow if it is less than 5 µm, and as wide if more than 5 µm. A few species show a rather wide range of variation in the size of aperture and in these cases the average measurement is given. The term aperture is

Table 1 Plankton samples used for this study.

Sample no.	Location	Cruise	Source
	Coast of Baja California	CICIMAR-CIB 8508	CIB
01	26° 41' N 112° 39' W		
02	25° 53' N 112° 58' W		
03	25° 43' N 113° 17' W		
04	26° 10' N 113° 09' W		
05	26° 00' N 113° 18' W		
06	25° 50' N 113° 46' W		
07	26° 27' N 113° 19' W		
08	26° 18' N 113° 38' W		
09	26° 07' N 113° 57' W		
10	26° 25' N 113° 50' W		
11	–		
12	26° 14' N 114° 29' W		
13	26° 52' N 114° 01' W		
14	26° 24' N 114° 20' W		
15	26° 32' N 114° 40' W		
	Gulf of California	GOLCA 8606	CIB
16	27° 28' N 111° 25' W		
17	27° 45' N 110° 53' W		
18	27° 31' N 111° 20' W		
19	27° 49' N 111° 55' W		
20	27° 59' N 111° 36' W		
21	28° 13' N 111° 14' W		
22	28° 24' N 111° 52' W		
23	28° 38' N 112° 28' W		
	Coast of Baja California	CIB-CICIMAR 8605	CIB
24	26° 25' N 114° 17' W		
25	26° 35' N 113° 58' W		
26	26° 15' N 114° 36' W		
27	26° 29' N 113° 34' W		
28	26° 19' N 113° 48' W		
29	26° 03' N 113° 39' W		
30	26° 13' N 113° 19' W		
31	26° 23' N 113° 00' W		
32	25° 47' N 112° 38' W		
33	25° 37' N 112° 57' W		
34	25° 09' N 113° 05' W		
35	24° 45' N 112° 25' W		
36	24° 01' N 112° 23' W		
37	24° 19' N 112° 34' W		
38	23° 55' N 111° 05' W		
39	23° 27' N 111° 12' W		
	Gulf of California	GOLCA 8411	CICIMAR
40–49	–		
	Gulf of California	CORTES II (1985)	ICML
50	25° 02' N 108° 32' W		
51	25° 33' N 110° 59' W		
52	26° 51' N 110° 06' W		
53	28° 10' N 112° 48' W		
54	29° 12' N 112° 31' W		
55	29° 48' N 114° 20' W		
56	31° 17' N 114° 22' W		
57	28° 09' N 111° 41' W		
58	26° 59' N 111° 50' W		
59	23° 08' N 109° 27' W		
60	21° 38' N 106° 31' W		
	Pacific Ocean coast of Mexico	CORTES II (1985)	ICML
61	21° 28' N 105° 20' W		
62	22° 45' N 108° 53' W		
63	20° 49' N 105° 41' W		
64	15° 46' N 95° 38' W	Author	Author
65	17° 22' N 102° 51' W	Author	Author

CIB = Centro de Investigaciones Biológicas de Baja California Sur, A.C., La Paz, B.C.S., Mexico.
CICIMAR = Centro Interdisciplinario de Ciencias del Mar (IPN), La Paz, B.C.S., Mexico.
ICML = R. Cortés-Altamirano, Instituto de Ciencias del Mar y Limnología (UNAM), Estación Mazatlán, Sin., Mexico.

chosen in preference to 'foramen' (e.g. Rines & Hargraves, 1988), because the foramen represents a structure in the valve, while the aperture is not considered to be a valve structure.

- Setae have been named according to their position in the chain and their position in the cell (Brunel, 1966). However, this terminology is only partly followed here, as it is very complex. i) Position in the chain: 'terminal' is used in the sense of Takano (1983) as the setae in the terminal valve, not the terminal cell, in the chain; 'intercalary' refers to setae of the intercalary valves and cells, including the internal valve of the terminal cell; 'special' is used to describe intercalary setae which are thicker and larger than the others, fused, and with bigger spines. ii) Position in the cell: 'isovalvar', the setae in the same valve; 'heterovalvar', the setae in different valves (Pl. 1, Fig. 1).
- The term 'annulus' (Stosch, 1977) is used to name the 'central hyaline field', as used by Evensen & Hasle (1975) and the 'central area' in the sense of Okuno (1956).
- The measurements given for *Chaetoceros* species are: apical axis (typically the width in the broad girdle view, abbreviated a.a.), pervalvar axis (p.a.), and aperture (ap.) (Pl. 1, Figs 1, 2).

SYSTEMATIC ACCOUNT

Thirty-five taxa belonging to the genus *Chaetoceros* are described, the taxonomic arrangement following the traditional classification (e.g. Hustedt, 1930; Cupp, 1943; Hendey, 1964; Rines & Hargraves, 1988). The local distribution (in the material studied) is indicated by the sample numbers (see Table 1).

CHAETOCEROS Ehrenb. in *Ber. Akad. Wiss. Berlin* **1844**: 200 (1844). Type species: *Chaetoceros dichaeta* Ehrenb.

I. Subgenus **CHAETOCEROS** (*Phaeoceros* Gran)

1. Section **ATLANTICA** Ostenf.

Centre of valve with prominent, tubular protrusion of the rimoportula. Apertures wide.

1. **Chaetoceros atlanticus** var. **neapolitanus** (Schröd.) Hust.

Hustedt, 1930: 645, fig. 366; Hendey, 1937: 290; Cupp, 1943: 104, fig. 59-Be, non d; Sournia, 1968: 46.

Chaetoceros neapolitanus Schröd.

Schröder, 1900: 29, pl. 1, fig. 4; Hendey, 1964: 119, pl. 16, fig. 3.

Pls 2, 3.

LM. Chains straight, short, rather robust. In girdle view, cells rectangular, the pervalvar axis being longer, the corners smooth, slightly curved. Valve face slightly convex, bearing a process in the middle, mantle low, lines of girdle straight; apertures wide, hexagonal. In valve view, cells elliptical, the setae not diverging widely. Terminal and intercalary setae undifferentiated, generally thick, robust, and spine-bearing; intercalary setae arise from the valve corners, curving smoothly at an angle of about 45° from the chain axis, terminal setae arise at a similar angle from the corners. Numerous small chloroplasts present in cell and setae. Measurements: 7–13 µm a.a., 17–25 µm p.a., 24–30 µm ap. (Pl. 2, Figs 1, 2)

EM. The general morphology of this species is relatively simple. The valve face, mantle, and setae bases are irregularly perforated by small poroids, although weak costae are sometimes apparent close to the bases of the setae (Pl. 2, Figs 3–6; Pl. 3, Fig. 4). The valve edge shows a hyaline rim and in the mantle rows of thickening run parallel to the lines of the girdle insertion (Pl 3, Figs 1, 2). Rimoportulae are present in each valve in the chain, located in the centre of the valve face. Externally, these are simple tubes open to the outside (Pl. 3, Figs 1–3). The structure of the setae changes at their very base and also distally. They are circular in cross-section at the base, perforated by poroids as in the valve (Pl. 3, Figs 1, 2). They then curve and fuse with sibling setae, beyond which point they become thicker, square in cross-section, and spine-bearing; the spines run in rows along each edge and the areola pattern comprises two striae between two costae (Pl. 2, Fig. 7; Pl. 3, Figs 5–7).

DISTRIBUTION. 29, 42, 63.

REMARKS. See following variety.

2. **Chaetoceros atlanticus** var. **skeleton** (F. Schütt) Hust.

Hustedt, 1930: 643, fig. 365; Cupp, 1943: 104, fig. 59-Bb, c; Sournia, 1968: 46.

Chaetoceros skeleton F. Schütt

Schütt, 1895: 45, pl. 5, fig. 19; Peragallo & Peragallo, 1897–1908: 482, pl. 134, fig. 9.

? *Chaetoceros polygonus* F. Schütt

Schütt, 1895: 46, pl. 5, fig. 24; Hustedt, 1920: pl. 323, figs 6, 8; Lebour, 1930: 114, fig. 80; Hendey, 1964: 120, pl. 14, fig. 1 (non *C. polygonus* F. Schütt sensu Hust., 1920: pl. 322, figs 5, 6 = *C. atlanticus* var. *neapolitanus* (Schröd.) Hust.).

Pls 4, 5.

LM. Chains straight, short, delicate. In girdle view, cells octagonal, the apical axis being longer. Valve face convex, bearing a short, cylindrical process, mantle very low, lines of girdle straight; apertures wide. In valve view, cells elliptical, the setae only slightly diverging. Setae thick, coarse, bearing minute spines; terminal setae essentially undifferentiated from intercalary setae, the latter diverging and curving more widely, almost parallel to the chain axis. Several small chloroplasts present in cell and setae. Measurements: 10–17 µm a.a., 8–11 µm p.a., 8–10 µm ap. (Pl. 4, Figs 1, 2)

EM. The valves are not as heavily silicified as those of var. *neapolitanus*, but the structure is otherwise similar to that described above. The costa pattern becomes more apparent in this variety and radiates from the centre of the valve (Pl. 4, Fig. 4). A hyaline rim is also present on the valve edge and thickenings in the mantle run along the lines of the girdle (Pl. 4, Fig. 6). Each valve bears a rimoportula, located in the centre (Pl. 5, Fig. 3). This resembles that of the preceding variety, but is shorter (Pl. 4, Figs 4, 6; Pl. 5, Fig. 1). Inside the rimoportula is a simple hole without a well-developed labiate structure (Pl. 5, Fig. 2). The structure of the setae is the same as that described for *C. atlanticus* var. *neapolitanus*. One remarkable character is the presence of thicker, large poroids at the base of the setae below the point of fusion (Pl. 5, Fig. 6). The areola pattern also comprises two striae between two costae and this is still apparent close to the tip, which is sharp (Pl. 5, Figs 4, 5, 7).

DISTRIBUTION. 42, 45, 48, 52.

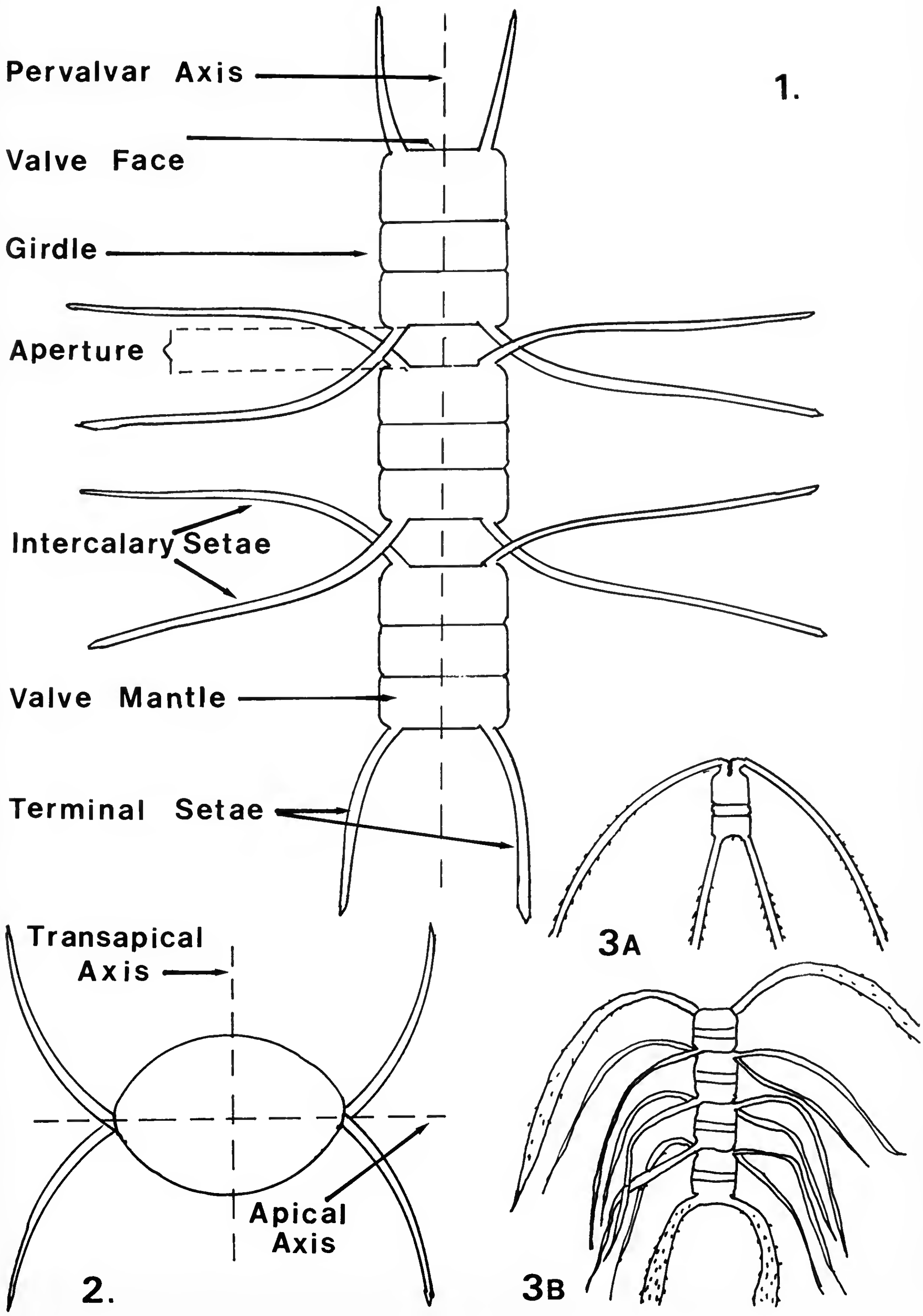

Plate 1 Fig. 1: diagram illustrating terminology used to describe a typical chain of *Chaetoceros* (broad girdle view). Fig. 2: valve view of a species of *Chaetoceros*. Figs 3a, 3b: examples of a heterovalvar species: *C. peruvianus* (3a), and a heteropolar species: *C. coarctatus* (3b).

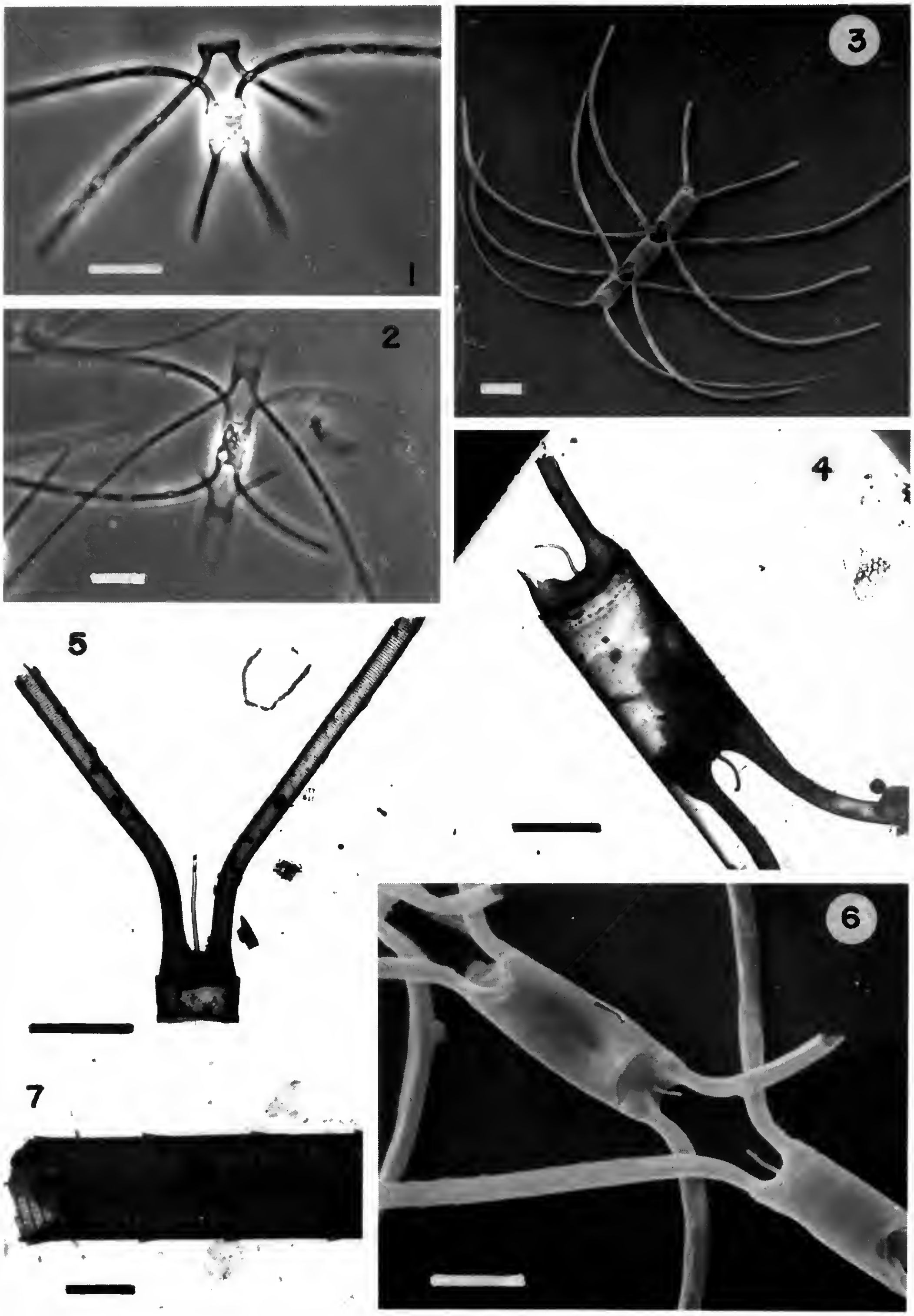

Plate 2 *Chaetoceros atlanticus* var. *neapolitanus*. Figs 1, 2: typical chains. LM. Fig. 3: complete chain. SEM. Fig. 4: whole cell. TEM. Fig. 5: valve showing setae and rimoportula. TEM. Fig. 6: detail of chain. SEM. Fig. 7: detail of seta. TEM. Figs 1–3, bar = 20 μm; Figs 4–6, bar = 10 μm; Fig. 7, bar = 2 μm.

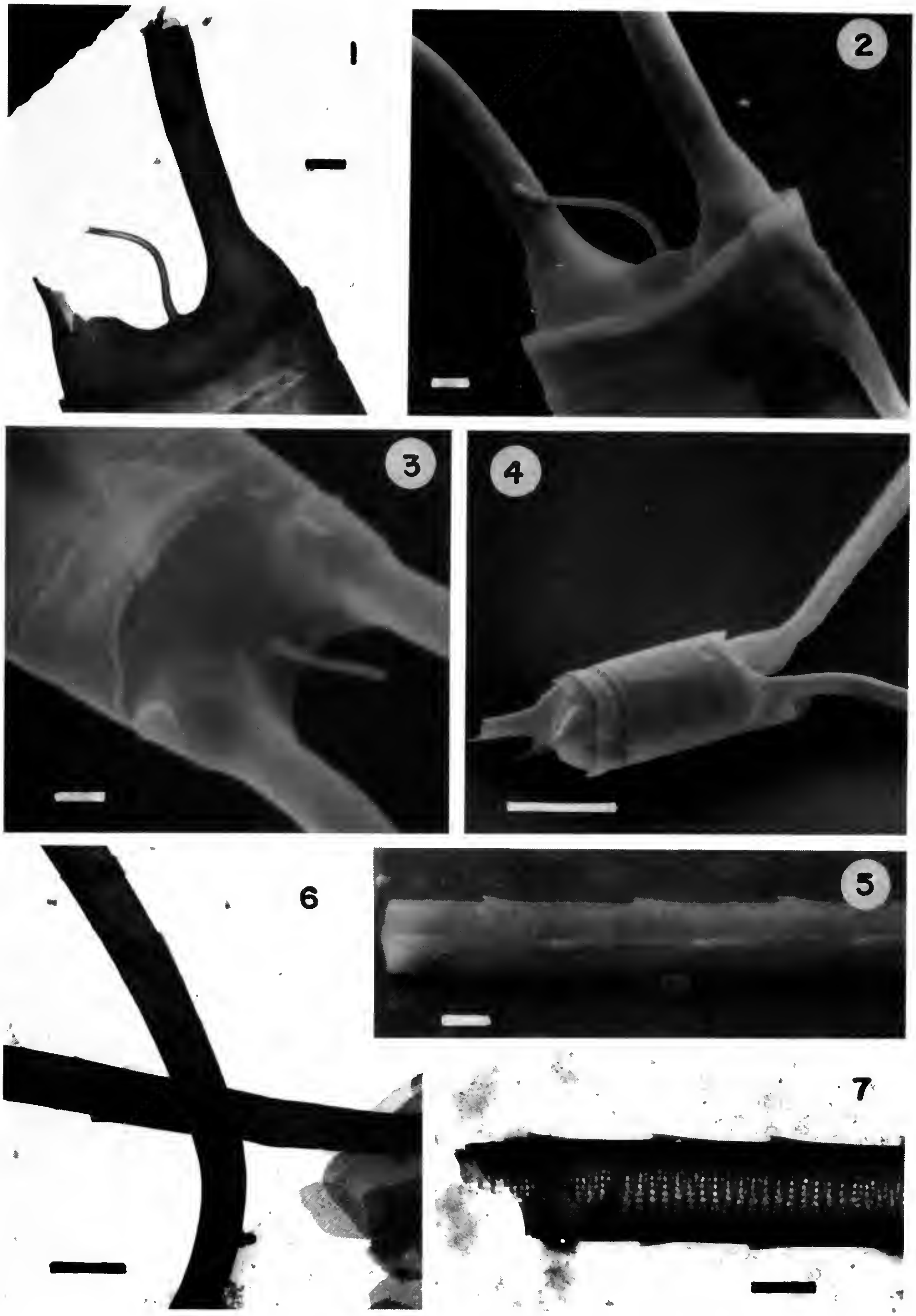

Plate 3 *Chaetoceros atlanticus* var. *neapolitanus*. Fig. 1: part of valve with broken seta and rimoportula. TEM. Fig. 2: part of valve showing setae and rimoportula. SEM. Fig. 3: detail of rimoportula. SEM. Fig. 4: another cell showing some thickening in the mantle. SEM. Fig. 5: seta with rows of spines. SEM. Fig. 6: fusion of two sibling setae. TEM. Fig. 7: seta showing poroid areolae. TEM. Figs 1–3, 5, 7, bar = 2 μm; Fig. 4, bar = 10 μm; Fig. 6, bar = 5 μm.

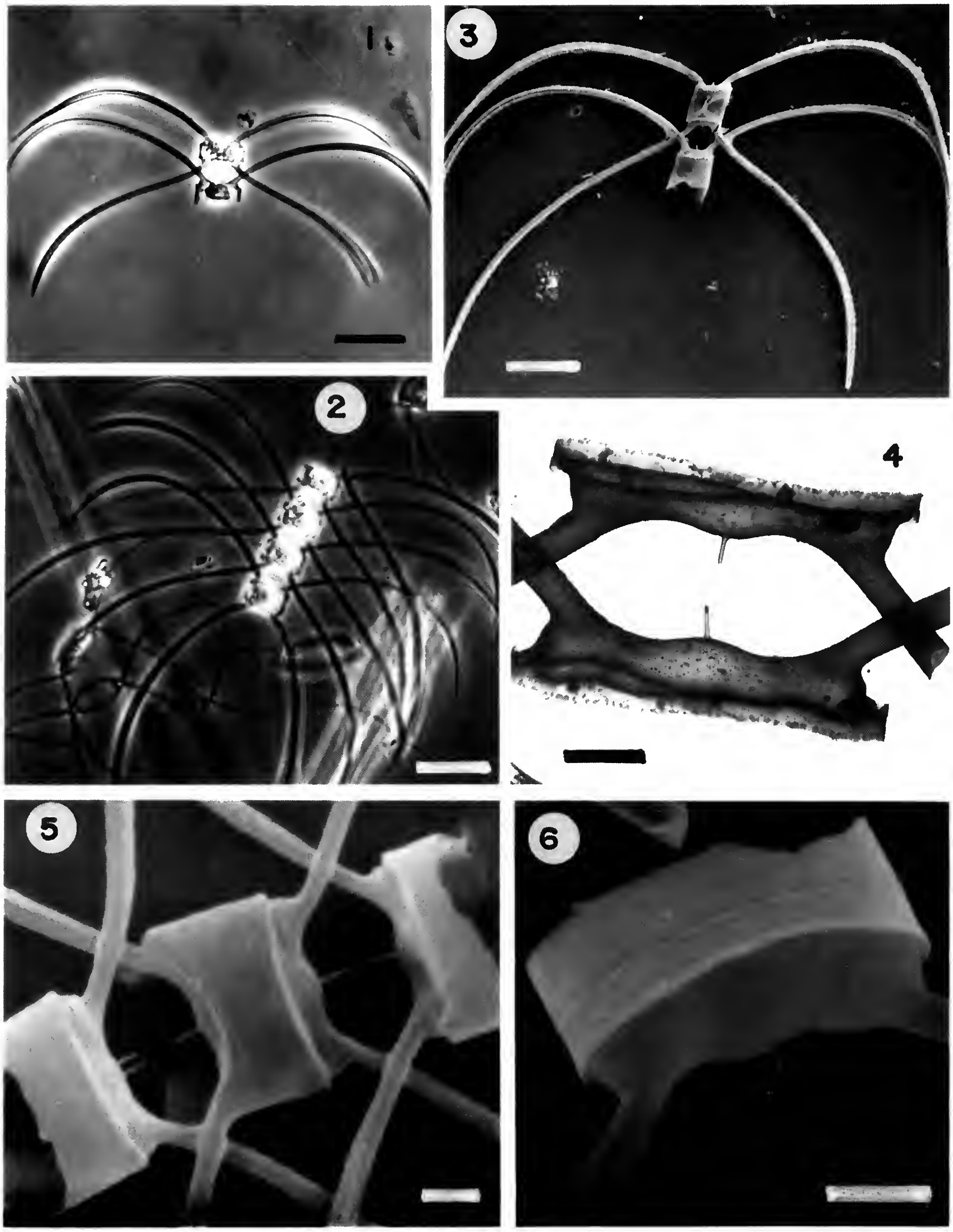

Plate 4 *Chaetoceros atlanticus* var. *skeleton*. Figs 1, 2: part of chain and complete chain, respectively. LM. Fig. 3: part of chain. SEM. Fig. 4: two sibling valves showing rimoportulae. TEM. Fig. 5: detail of chain. SEM. Fig. 6: one valve showing hyaline rim and thickening in mantle. SEM. Figs 1–3, bar = 20 μm; Figs 4–6, bar = 5 μm.

REMARKS. *Chaetoceros atlanticus* var. *neapolitanus* and var. *skeleton* are morphologically very similar to the type, as indicated by Evensen & Hasle (1975) and Koch & Rivera (1984), and their taxonomic position is in little doubt. They differ in having a more temperate or subtropical distribution. Contrary to Simonsen's (1974) opinion that distinction 'seems to be senseless' between these two taxa, I consider that their taxonomic separation should be retained.

3. **Chaetoceros dichaeta** Ehrenb.

Ehrenberg, 1844: 200; Hustedt, 1920: pl. 326, fig. 8; Hustedt, 1930: 648, fig. 367; Hendey, 1937: 291, pl. 6, figs 9, 10; Cupp, 1943: 106, fig. 60; Hendey, 1964: 119, pl. 13, fig. 1; Okuno, 1970: pl. 652; Evensen & Hasle, 1975: 157, figs 1–5; Koch & Rivera, 1984: 64, figs 6–12.

Chaetoceros janischianus Castrac.

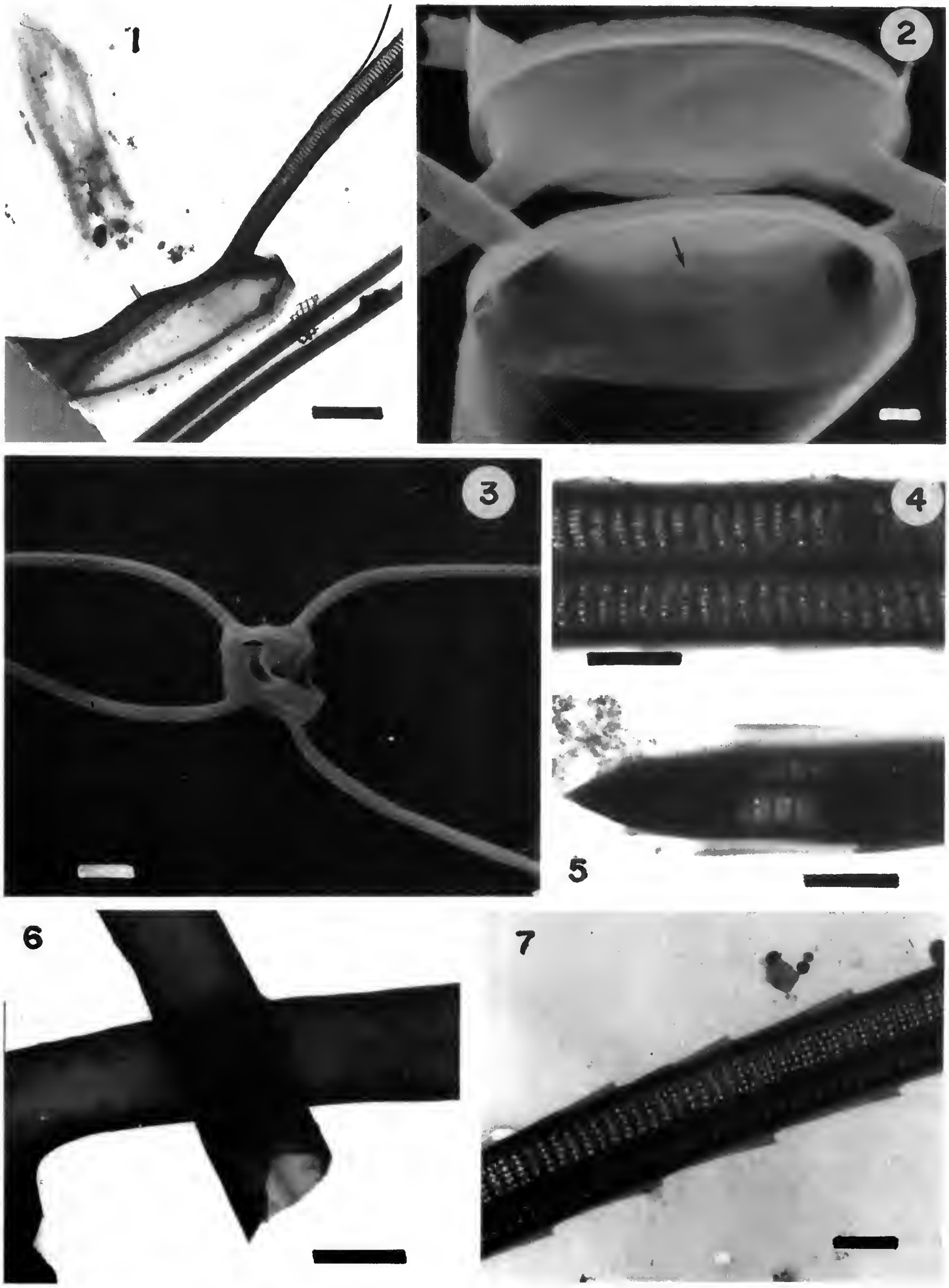

Plate 5 *Chaetoceros atlanticus* var. *skeleton*. Fig. 1: terminal valve. TEM. Fig. 2: inside view of valve showing rimoportula internally. SEM. Fig. 3: single cell. SEM. Fig. 4: detail of seta with poroid areolae. TEM. Fig. 5: tip of seta. TEM. Fig. 6: point of fusion in two sibling setae. TEM. Fig. 7: detail of another seta. TEM. Fig. 1, bar = 5 µm; Figs 2, 4–7, bar = 2 µm; Fig. 3, bar = 10 µm.

Castracane, 1886: 77.
Pls 6, 7.

LM. Chains straight, of variable length. In girdle view, cells rectangular, nearly octagonal, corners smooth. Valve face generally flat, with a thin, cylindrical process at the centre, mantle low, lines of girdle straight; apertures very wide. In valve view, cells nearly circular or elliptical. Setae thick, coarse; intercalary setae curve smoothly and fuse further out from the cells than terminal setae; terminal setae curve towards the chain axis. Numerous, small chloroplasts present in cell and setae. Measurements: 6–11 μm a.a., 11–12 μm p.a., 13–22 μm ap. (Pl. 6, Figs 1, 2)

EM. Short chains were observed (Pl. 6, Fig. 3). The valve appears to be lightly silicified and perforated by small poroids thoughout; no costae were observed (Pl. 6, Figs 4–6). Hair-like structures are present on the valve edge, some relatively long, others shorter (Pl. 7, Fig. 1). Hyaline rims occur on the edge of the valve and in the mantle. The presence of thickening was also noted in this species (Pl. 6, Fig. 6). The rimoportula consists of a simple, cylindrical tube, open to the outside, and with no labiate structure inside (Pl. 7, Figs 1–3, 5). Setae differ from the preceding varieties of *C. atlanticus* chiefly in the areola pattern, which has longitudinal rows of big poroids (Pl. 7, Figs 3, 6, 8), but no costae. Their polygonal shape in cross-section is also different, with five or six sides, and the rounded tips have a small hole (an opening?) (Pl. 7, Figs 4, 7).

DISTRIBUTION. 12, 48.

REMARKS. Evensen & Hasle (1975) commentated on the presence of weak costae in the valves of this species, a characteristic not found in the material used for this study. The hair-like structures on the valve edge have been found by some authors (e.g. Evensen & Hasle, 1975; Koch & Rivera, 1984). These same authors have also stated that the seta in *C. dichaeta* is circular in cross-section, which differs from my observations where it has clearly been seen as polygonal.

2. Section **BOREALIA** Ostenf.

Tubular rimoportula usually absent. Apertures narrow.

4. **Chaetoceros octagonus** Hern.-Bec.

Hernández-Becerril, 1992*b*: 218, figs 1, 3–15.

DISTRIBUTION. 7, 12.

5. **Chaetoceros densus** Cleve

Cleve, 1901: 299; Meunier, 1913: 14, pl. 1, figs 14–28; Hustedt, 1920: pl. 325, fig. 9; Hustedt, 1930: 651, fig. 368; Lebour, 1930: 115, fig. 81; Cleve-Euler, 1951: 96, figs 184a–c; Hendey et al., 1954: 28, pl. 1, fig. 1; Hendey, 1964: 120, pl. 17, fig. 1; Drebes, 1974: 64, figs 48a, b; Rines & Hargraves, 1988: 50, figs 100, 101.
Chaetoceros borealis var. *densa* Cleve
Cleve, 1897: 20, pl. 1, figs 3, 4.
Pls 8, 9.

LM. Chains straight, usually long, robust. In girdle view, cells rectangular or nearly eight-sided, with smooth corners and constrictions at girdle zones; apertures narrow. Valve face flat or slightly convex, mantle high, lines of girdle straight. In valve view, cells elliptical, the setae diverging at an angle of about 30° from the apical axis. Setae thick, coarse, bearing spines; terminal setae differ from intercalary setae only in direction of divergence, intercalary setae arising almost parallel to the apical axis, terminal setae curving to the chain axis. Numerous, small chloroplasts present in cell and setae. Measurements: 38–45 μm a.a., 32–48 μm p.a., 3–4 μm ap. (Pl. 8, Fig. 1)

EM. The valves follow the general pattern of structure for the genus: heavily silicified and perforated by poroids, but here a weak costa pattern is observed and the poroids become scarse close to the valve centre (Pl. 8, Figs 2–4). The annulus is an oblong hyaline field in the valve centre (Pl. 9, Figs 2–4). The rimoportula is located at the very centre of the valve, being a simple hole inside with a small protrusion outside (Pl. 8, Fig. 5; Pl. 9, Figs 1–4). At the very base of the setae, the wall is perforated by a fine mesh of poroids, resembling a certain type of areola (Pl. 9, Figs 1, 4). The setae are almost circular close to the base, but become four-sided after a short distance (Pl. 9, Figs 5, 6). They bear rows of alternate spines on the edges and the areola pattern is of one stria between two costae (Pl. 8, Figs 6, 7; Pl. 9, Figs 5, 6).

DISTRIBUTION. 16, 42, 45, 48.

REMARKS. This species is closely related to *C. borealis* Bailey, an opinion which may be confirmed by comparing Evensen & Hasle's (1975) observations of *C. borealis* with those made in this study on *C. densus*. However, two major differences between these species are the position of the rimoportula (in *C. densus* it is central and in *C. borealis* it is located to one side) and the presence of poroids in the setae bases, characteristic of *C. densus* but lacking in *C. borealis*.

6. **Chaetoceros tetrastichon** Cleve

Hernández-Becerril, 1992*a*: 367, figs 1–8.

DISTRIBUTION. 12.

7. **Chaetoceros seychellarus** G. Karst.

Hernández-Becerril, 1993*a*: 121, figs 16–27.

DISTRIBUTION. 18, 19, 45, 48, 63.

8. **Chaetoceros denticulatus** Lauder

Lauder, 1864: 79, pl. 8, fig. 9; Hustedt, 1920–1921: pl. 324, fig. 7, pl. 337, fig. 7; Allen & Cupp, 1935: 135, fig. 53; Subrahmanyan, 1946: 129, figs 188–190; Sournia, 1968: 47, pl. 3, fig. 24; Simonsen, 1974: 31; Desikachary & Prema, 1987: pl. 258, fig. 5.
Chaetoceros nanodenticulatus Okamura
Okamura, 1907: 91.
Chaetoceros denticulatus f. *angusta* Hust.
Hustedt, 1920: pl. 324, fig. 5
Chaetoceros denticulatus f. *lata* Hust.
Hustedt, 1920: pl. 324, fig. 6.
Pl. 10.

LM. Chains straight, of variable length, robust. In girdle view, cells octagonal, with smooth corners and constrictions at girdle level. Valve face conical, mantle high, lines of girdle straight; apertures wide. In valve view, cells elliptical, the setae diverging at an angle of about 15–20° from the apical axis. Setae arise from close to the valve centre, thick and coarse, with a tooth-like projection near the base in contact with that of the sibling setae.

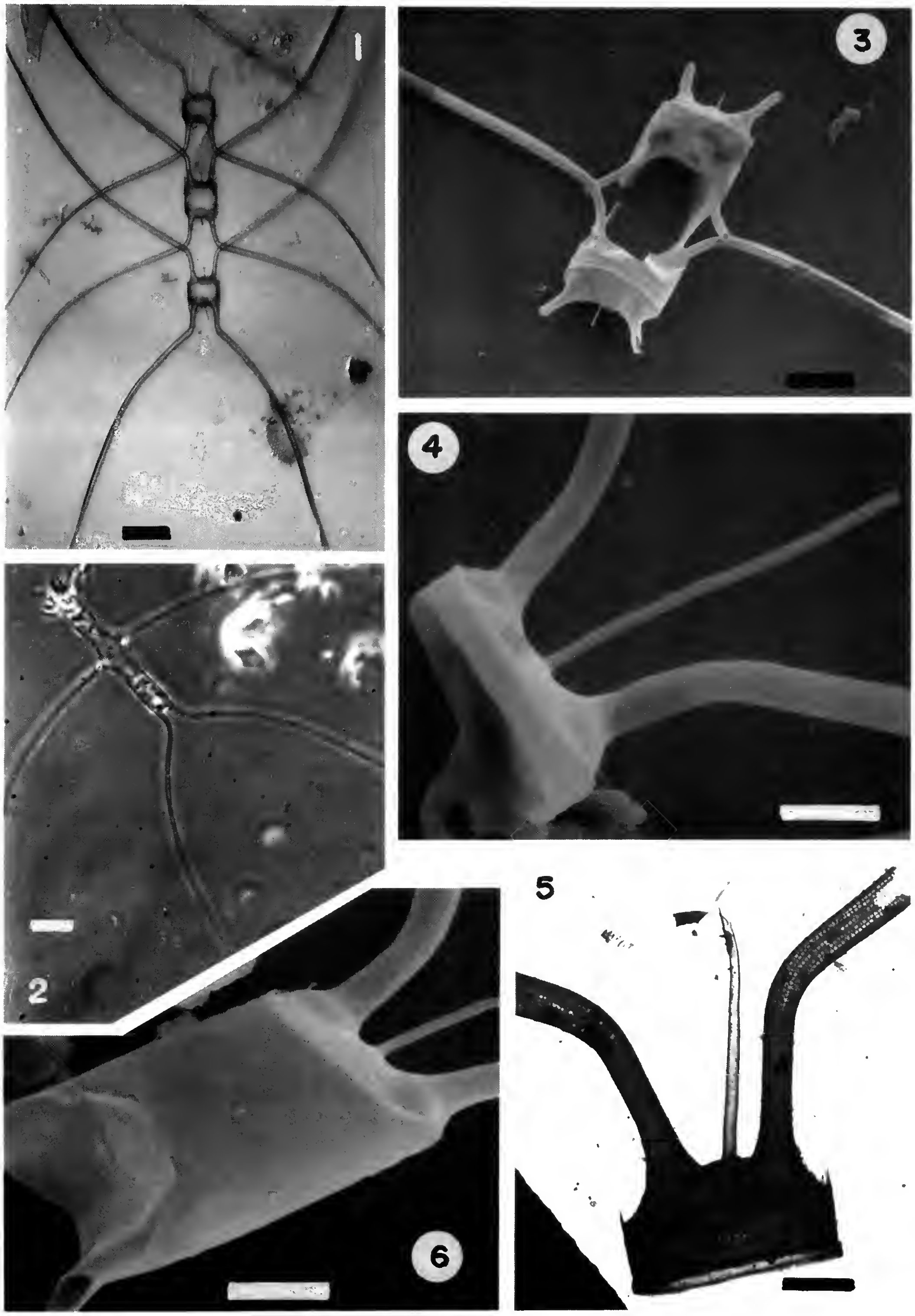

Plate 6 *Chaetoceros dichaeta*. Figs 1, 2: typical chains. LM. Fig. 3: part of chain. SEM. Fig. 4: valve with long, central rimoportula. SEM. Fig. 5: another valve showing rimoportula and setae. TEM. Fig. 6: complete cell. SEM. Figs 1, 2, bar = 20 μm; Fig. 3, bar = 10 μm; Figs 4–6, bar = 5 μm.

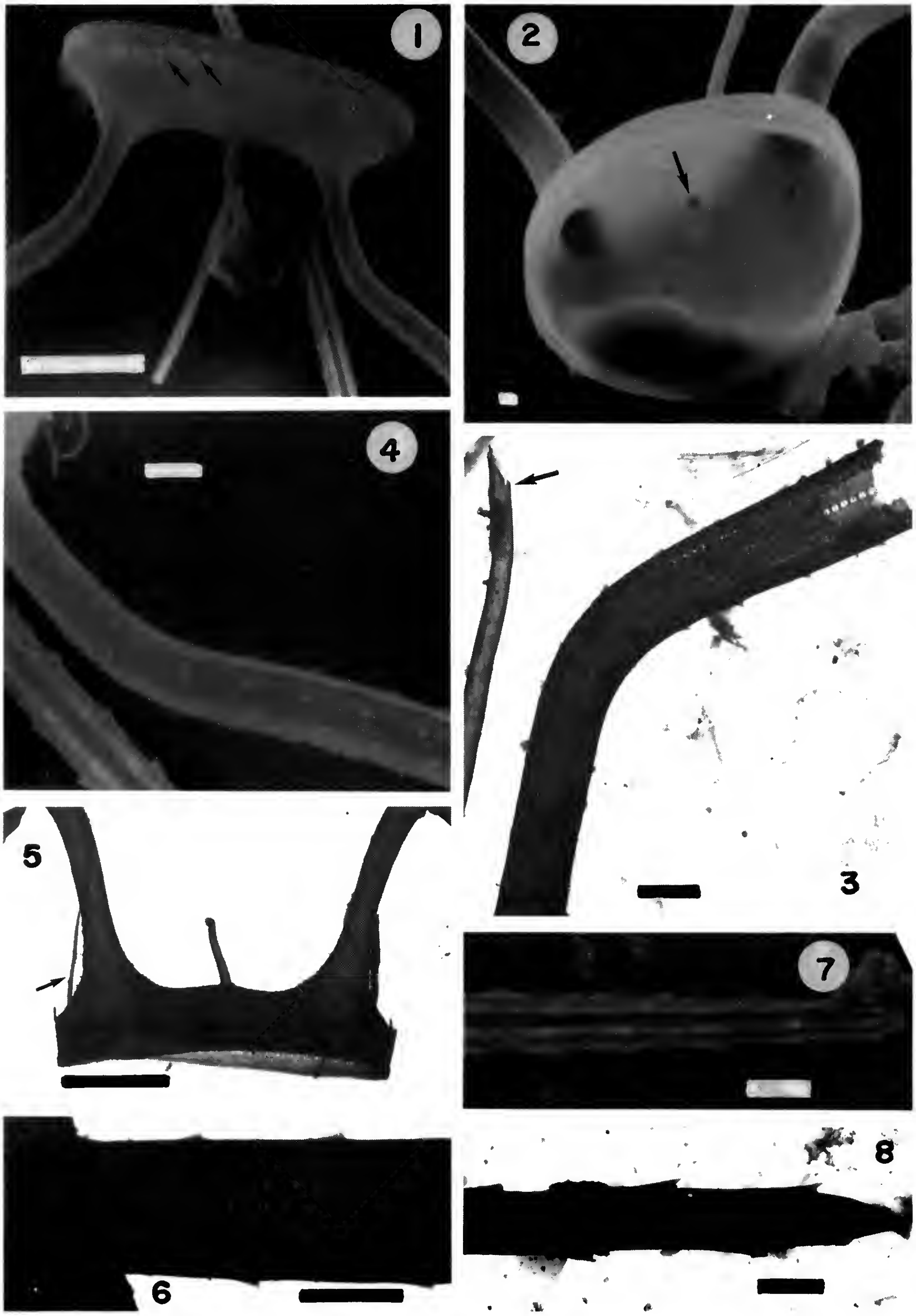

Plate 7 *Chaetoceros dichaeta.* Fig. 1: valve showing hair-like structures (arrows). SEM. Fig. 2: inside view of valve. Arrow indicates the rimoportula internally. SEM. Fig. 3: detail of rimoportula (arrow) and broken seta. TEM. Fig. 4: base of seta. SEM. Fig. 5: valve with long hair-like structures (arrow). TEM. Fig. 6: poroid areolae in seta. TEM. Fig. 7: tip of seta. SEM. Fig. 8: tip of seta. TEM. Figs 1, 5, bar = 5 µm; Figs 2–4, 6–8, bar = 2 µm.

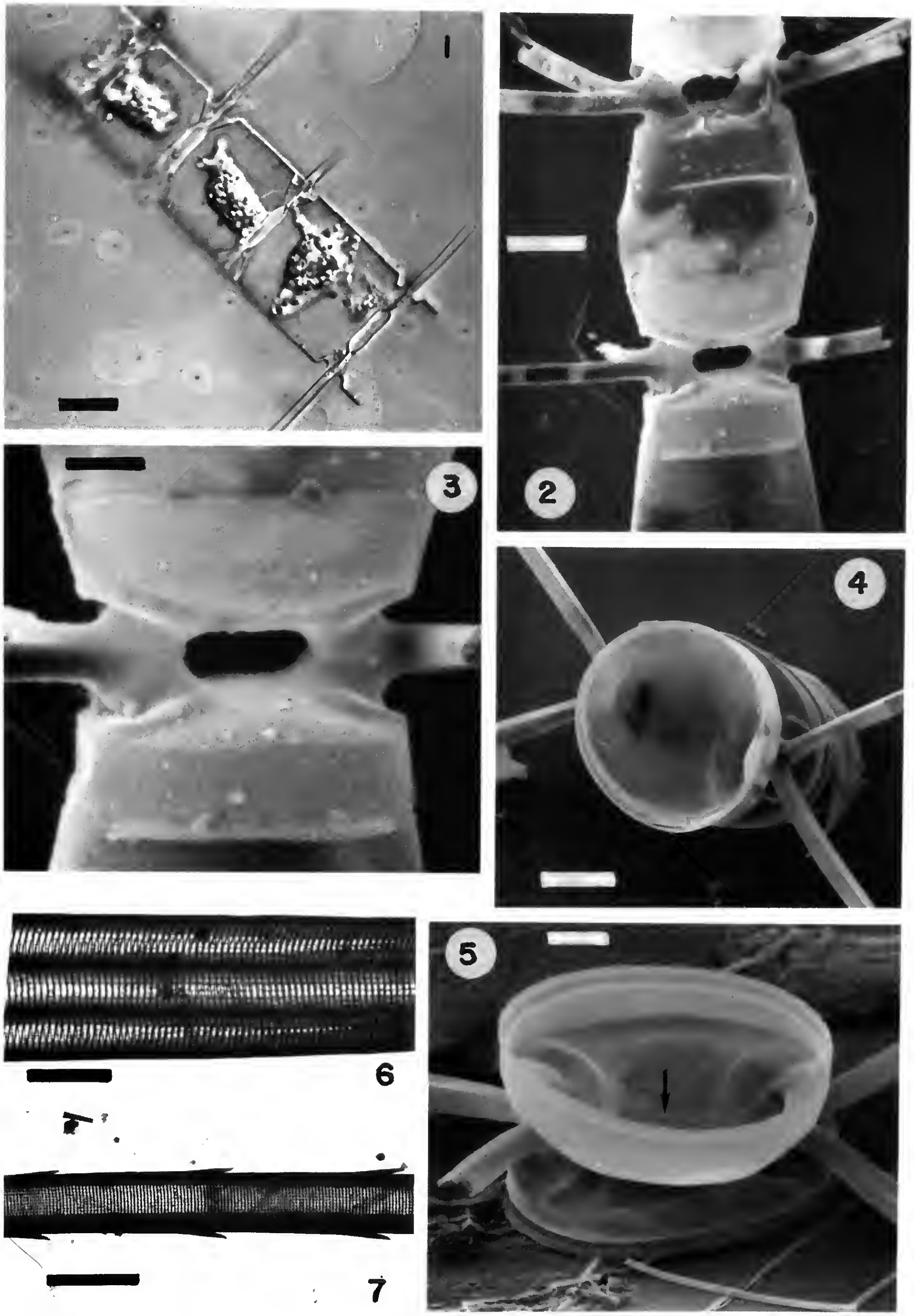

Plate 8 *Chaetoceros densus*. Fig. 1: typical chain. LM. Fig. 2: part of chain. SEM. Fig. 3: detail of two valves. SEM. Fig. 4: inside view of valve. SEM. Fig. 5: inside view of valve showing rimoportula internally. SEM. Fig. 6: detail of seta base with poroid areolae and no spines. TEM. Fig. 7: another seta with spines. TEM. Fig. 1, bar = 20 µm; Figs 2, 4, bar = 10 µm; Figs 3, 5, 7, bar = 5 µm.

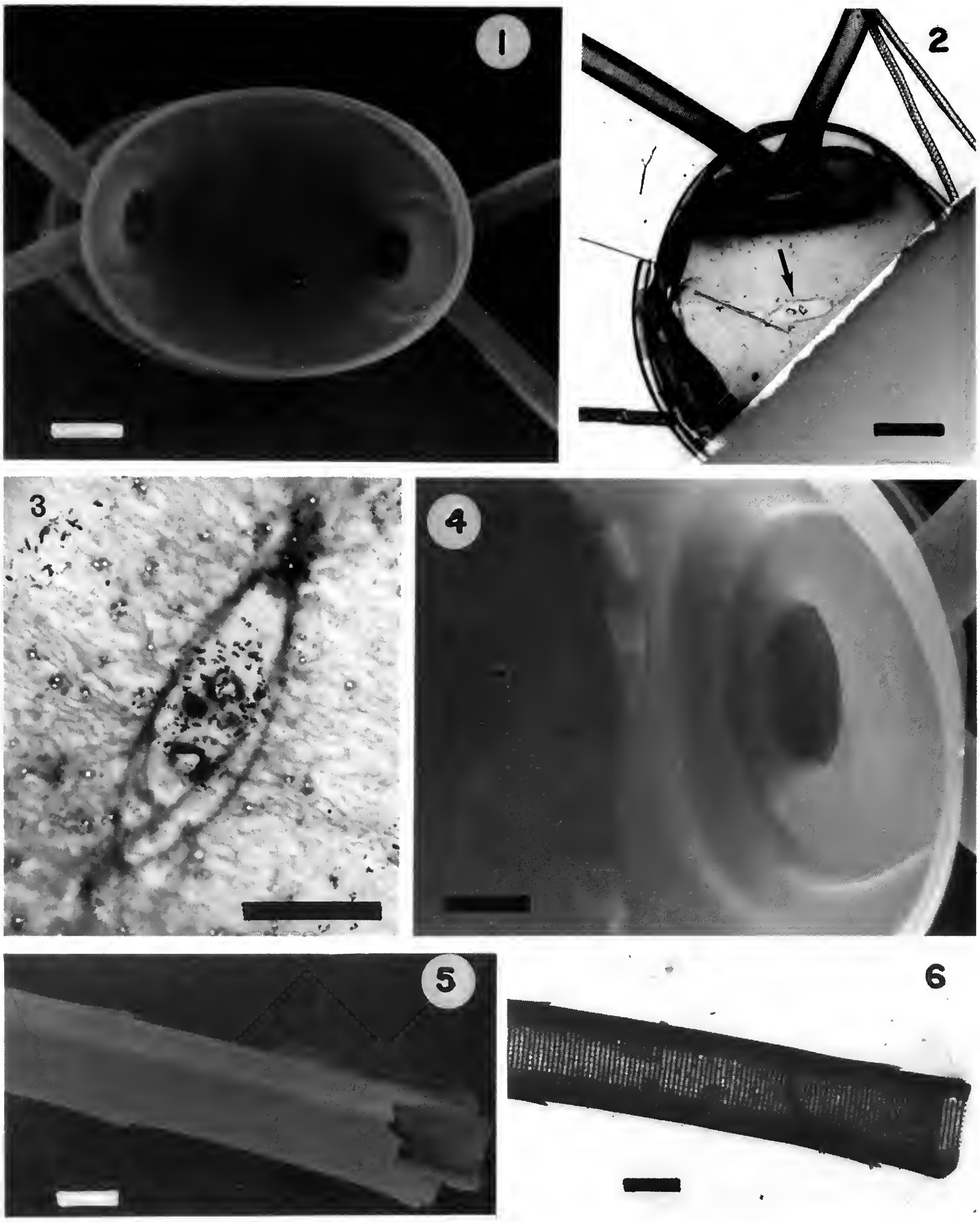

Plate 9 *Chaetoceros densus*. Fig. 1: inside view of valve. SEM. Fig. 2: valve with central annulus and rimoportula (arrow). TEM. Fig. 3: detail of annulus and rimoportula. TEM. Fig. 4: internal view of rimoportula (left) and seta base with mesh of fine poroids. SEM. Fig. 5: broken seta. SEM. Fig. 6: seta with poroid areolae and spines. TEM. Figs 1, 2, bar = 5 µm; Figs 3–6, bar = 2 µm.

Terminal and intercalary setae differ only in orientation. Several chloroplasts present in cell and setae. Measurements: 31–36 µm a.a., 28–36 µm p.a., 6–9 µm ap. (Pl. 10, Figs 1, 2)

EM. This species has the general pattern of a perforated valve without apparent costae. The valve face is reduced, conical, and with an excentric annulus (Pl. 10, Figs 3–5, 7). The rimoportula is at the centre of the annulus and has a simple hole inside (with no labiate structure) as well as an external projection, a spine-like structure that is present only in terminal valves (Pl. 10, Figs 5, 7). The setae bases are circular in cross-section and very wide, occupying a large area of the valve face. Sibling setae are fused at the point where a tooth-like structure occurs, which suggests that this structure is used for forming chains (Pl. 10, Fig. 4). The morphology of the terminal setae does not appear to vary. Although spines are lacking at the base of the setae, they have been shown to be present at distal parts. The wall has a poroid areola pattern, with one stria between two costae (Pl. 10, Fig. 6).

DISTRIBUTION. 65.

REMARKS. Although two forms of this species have been described or illustrated, as well as the separate entity *C.*

Plate 10 *Chaetoceros denticulatus*. Figs 1, 2: part of chain and two sibling valves, respectively. LM. Fig. 3: two sibling valves. SEM. Fig. 4: detail of tooth-like structure in the setae. SEM. Fig. 5: another valve showing rimoportula and tooth-like structures in the setae. SEM. Fig. 6: base of setae. SEM. Fig. 7: internal view of rimoportula (arrow). SEM. Fig. 1, bar = 20 µm; Figs 2, 3, bar = 10 µm; Figs 4, 5, 7, bar = 5 µm; Fig. 6, bar = 2 µm.

nanodenticulatus, it is reasonable to think that *C. denticulatus* presents a wide range of variation and that those taxa should be considered synonymous, as claimed by Simonsen (1974).

It is interesting to note that *C. denticulatus* forms chains using a tooth-like structure. This character has not previously been reported within *Chaetoceros*.

9. **Chaetoceros rostratus** Lauder

Lauder, 1864: 79, pl. 8, fig. 10; Hustedt, 1921: pl. 337, fig. 8; Allen & Cupp, 1935: 136, fig. 55; Léger, 1973: 14, figs 2, 3; Navarro, 1982: 316, fig. 40; Giuffré & Ragusa, 1988: 504, figs 1–22.

Chaetoceros glandazii L. Mangin
Mangin, 1910: 346, fig. 2; Hendey, 1964: 121, pl. 9, fig. 4.

Chaetoceros rostratus var. *glandazii* (L. Mangin) F.J.R. Taylor
Taylor, 1966: 439, pl. 2, fig. 12.

Pls 11, 12.

LM. Chains straight, usually short. In girdle view, cells hexagonal with a process in the centre of the valve connecting sibling cells, corners smooth; sibling cells not touching at the corners, but as setae diverge they leave apparent apertures, which may be narrow or wide. Valve face conical, mantle high, lines of girdle straight. In valve view, cells nearly circular to elliptical. Setae thick, spine-bearing, arising close to the corners but diverging almost perpendicularly to the chain axis, meeting sibling setae, apparently without fusing. Several chloroplasts present in cell and setae. Measurements: 9–20 µm a.a., 22–34 µm p.a. (Pl. 11, Figs 1, 2)

EM. Valves are thickly silicified and regularly perforated by poroids. Some have a costa pattern radiating from the centre (Pl. 11, Fig. 5; Pl. 12, Fig. 3), while in others these costae are either very weak or non-existent (Pl. 11, Fig. 4). The poroids become denser in the mantle, arranged in rows between costae running parallel to the pervalvar axis. The processes connecting sibling cells are solid and may be short and thick or longer and thinner (Pl. 11, Figs 3–6; Pl. 12, Figs 2–4); terminal valves lack the linkage process (Pl. 12, Fig. 1). To one side of these processes there is a small, round rimoportula (Pl. 12, Figs 2, 4). In the same intercalary cell of the chain the two valves are twisted, so the setae arise without meeting the corresponding sibling setae (Pl. 11, Fig. 6; Pl. 12, Fig. 2). The seta structure is similar to that described earlier for *C. atlanticus* var. *neapolitanus* (p. 4); setae are four-sided with rows of spines along each edge, an areolate, poroid wall, and two stria between pairs of costae (Pl. 12, Figs 6, 7).

DISTRIBUTION. 51, 65.

REMARKS. Controversy has arisen concerning the identity of *C. glandazii* and its relationship to *C. rostratus* (e.g. Giuffré & Ragusa, 1988). These authors believe that *C. glandazii* is a good species. However, the arguments for maintaining it as a separate taxon seem confused. Although no type material has been studied, I concur with authors such as Hustedt (1930) in placing *C. glandazii* as a synonym of *C. rostratus*, unless further studies indicate otherwise.

Another interesting point has been mentioned by Rines & Hargraves (1988) and concerns the manner in which *C. rostratus* forms chains through linking processes and the taxonomic significance that this holds. Rines & Hargraves noted that in this character *C. rostratus* differs from the many other species in section *Borealia*, but any taxonomic changes are pending, awaiting a major revision of the genus. Whether solitary cells (Pl. 12, Fig. 5) should be considered as distinct forms is better left for future research as information from culture studies is required.

10. **Chaetoceros danicus** Cleve

Cleve, 1889: 55; Peragallo & Peragallo, 1897–1908: 479, pl. 127, fig. 1; Hustedt, 1930: 659, fig. 373; Lebour, 1930: 124, fig. 89; Gran & Angst, 1931: 470, fig. 51; Cupp, 1943: 109, fig. 65; Cleve-Euler, 1951: 96, figs 185a–d; Okuno, 1956: 187, pl. 3, figs 1–5; Hendey, 1964: 122, pl. 10, fig. 5; Brunel, 1970: 88, pl. 11, figs 1–6; Okuno, 1970: pl. 651; Drebes, 1974: 66, fig. 51; Koch & Rivera, 1984: 71, figs 53–56; Rines & Hargraves, 1988: 49, figs 95–99.

Pls 13, 14.

LM. Cells solitary or united to form very short chains, 2–3 cells long. In girdle view, cells rectangular with small constrictions at girdle level. Valve face flat, with a small process in the centre, mantle high, lines of girdle straight; apertures very narrow, when present. In valve view, cells elliptical, the setae diverging at an angle of about 15° from the apical axis. Setae straight, rather thick, bearing spines, arising from the corners almost parallel to the apical axis. Numerous small chloroplasts present in cell and setae. Measurements: 15–22 µm a.a., 16–28 µm p.a. (Pl. 13, Figs 1, 2)

EM. The valve is perforated by poroids but lacks costae. The poroids become fewer around the centre of the valve and at the base of the setae; the valve appears thicker at these parts (Pl. 13, Figs 5–7; Pl. 14, Figs 2, 3). The annulus is inconspicuous or appears without clear boundaries (Pl. 13, Fig. 5). Thickenings are present in the mantle, in rows parallel to the lines of the girdle (Pl. 14, Fig. 1). The single rimoportula is central, oblong or slit-like, with a small projection outside and a simple hollow inside (Pl. 13, Fig. 7; Pl. 14, Figs 2–4). The setae are circular in cross-section at the base, without spines or areolae, but further from the base they become four-sided, with rows of spines on the edges and single rows of poroids between costae (Pl. 14, Figs 5–7). Close to the tip the spines become larger; the tip itself is rather flattened (Pl. 14, Fig. 8). In chains, the sibling setae fuse above a short, free base and then diverge again more widely (Pl. 13, Fig. 6).

DISTRIBUTION. 17, 42.

REMARKS. This is a very well-known species which has been widely studied (e.g. Okuno, 1956, 1970; Koch & Rivera, 1984).

3. Section **PERUVIANA** Hern.-Bec., **sectio nova**

Cellulae in catenas vel solitariae. Valvae in cellula, dissimile. Setae robustae, in planitie catena divergentes, versus idem terminus. Rimoportula in uterque valva, lateralis valvaris.

Cells solitary or in chains, heterovalvar. All setae robust, pointed towards the same end. Rimoportula present in every valve, excentrically placed.

The first attempt to group the species now placed in this section was made by Mangin (1919), who suggested a number of criteria on which to base the inclusion of taxa. The species included are: *Chaetoceros aequatorialis* Cleve, *C. concavicornis* L. Mangin, *C. convolutus* Castrac., *C. criophilus* Castrac., *C. curvatus* Castrac., *C. pendulus* G. Karst., and *C. peruvianus* Brightw.

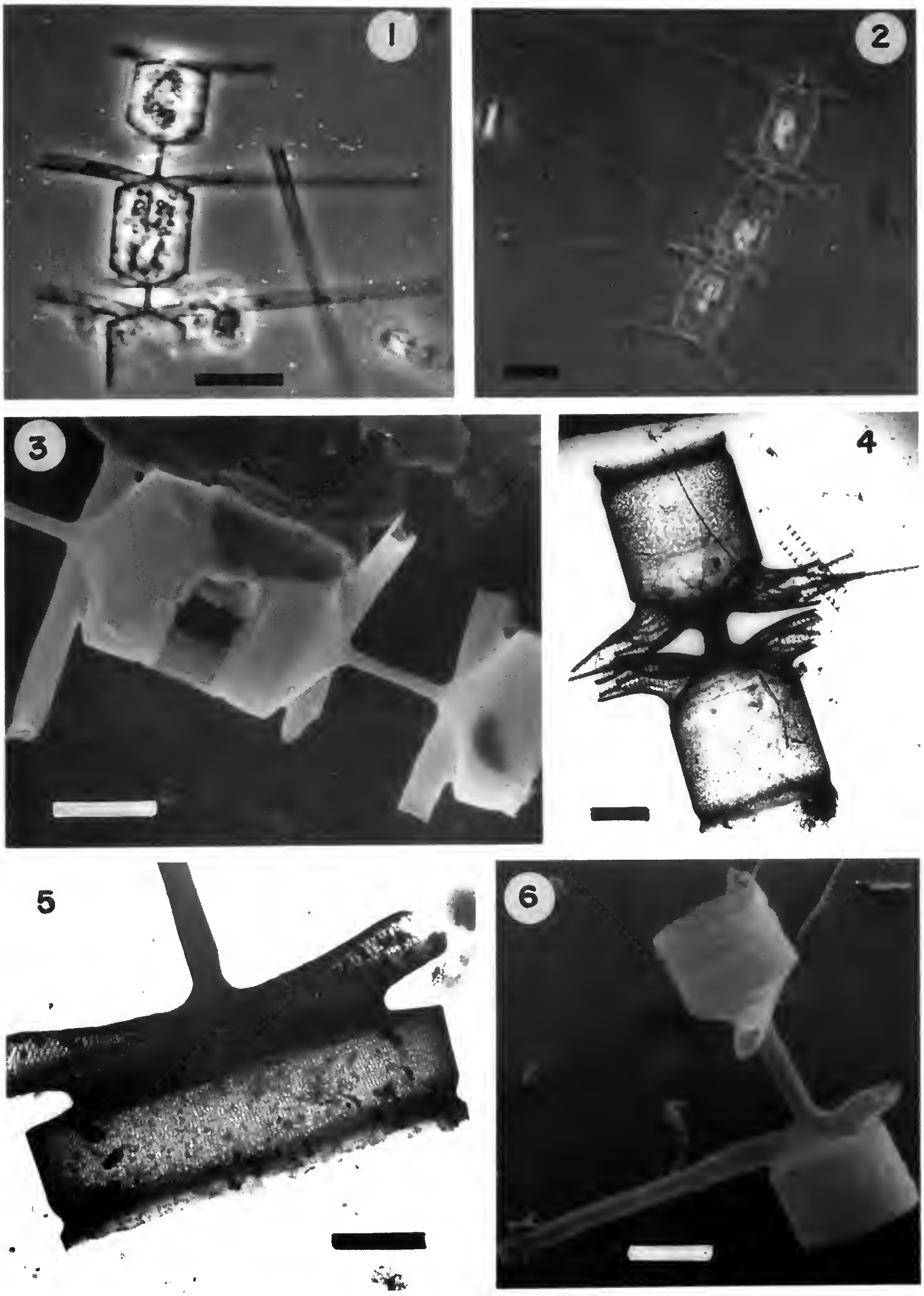

Plate 11 *Chaetoceros rostratus*. Figs 1, 2: typical chains. LM. Fig. 3: part of chain. SEM. Fig. 4: two sibling valves with short linking process. TEM. Fig. 5: valve with longer linking process. TEM. Fig. 6: sibling valves twisted in relation to each other. SEM. Figs 1, 2, bar = 20 µm; Figs 3, 6, bar = 10 µm; Figs 4, 5, bar = 5 µm.

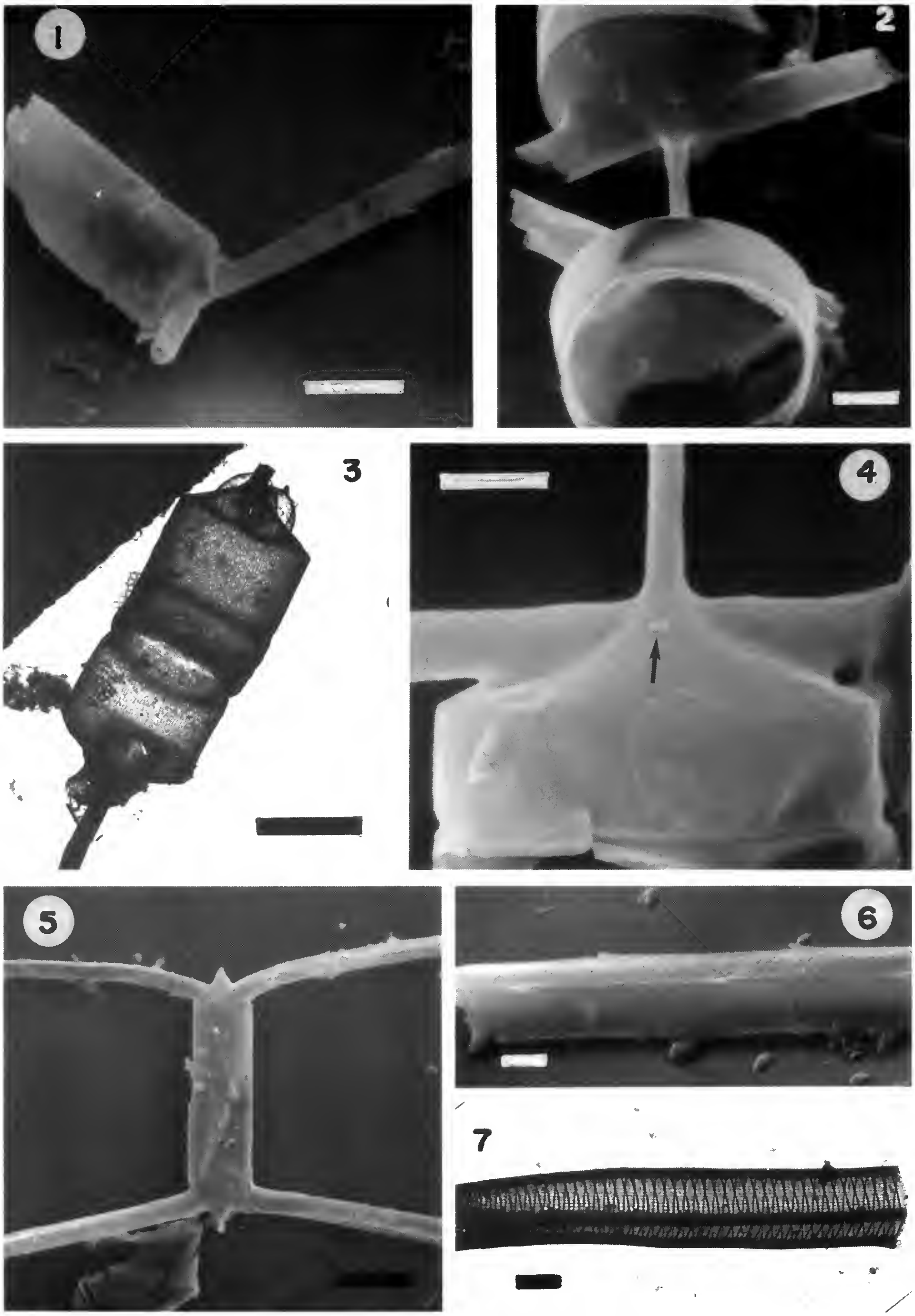

Plate 12 *Chaetoceros rostratus*. Fig. 1: terminal valve without linking process. SEM. Fig. 2: part of chain with inside view. SEM. Fig. 3: complete cell. TEM. Fig. 4: valve showing rimoportula (arrow). SEM. Fig. 5: single cell (solitary?). SEM. Fig. 6: square (in cross-section) seta with rows of spines. SEM. Fig. 7. Base of seta lacking spines but showing poroid areolae. TEM. Figs 1, 3, 5, bar = 10 μm; Figs 2, 4, bar = 5 μm; Figs 6, 7, bar = 2 μm.

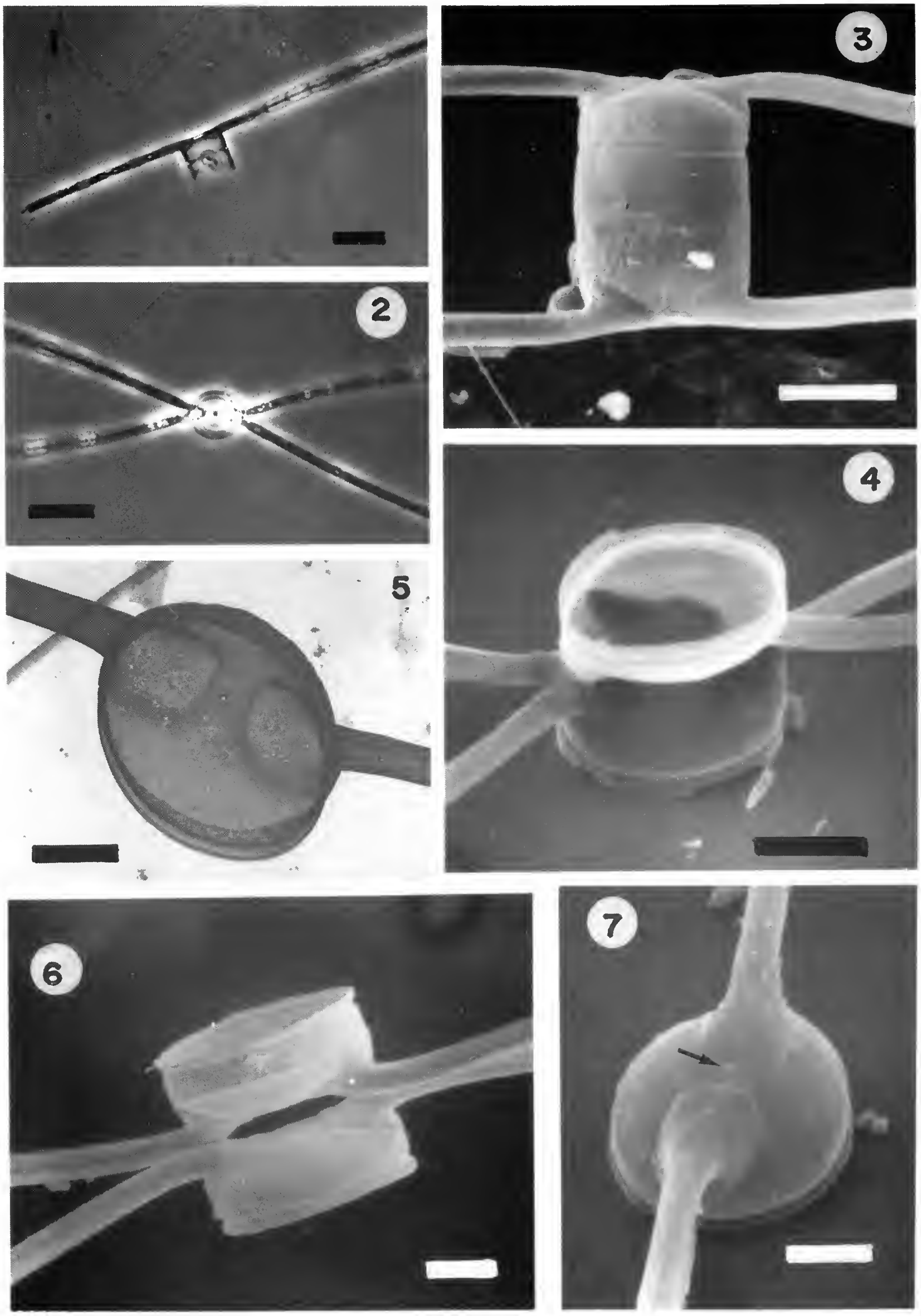

Plate 13 *Chaetoceros danicus*. Figs 1, 2: valves in girdle and valve view, respectively. LM. Fig. 3: complete cell. SEM. Fig. 4: valves of two sibling cells. SEM. Fig. 5: valve showing presence of rimoportula. TEM. Fig. 6: sibling valves. SEM. Fig. 7: another single valve with rimoportula (arrow). SEM. Figs 1, 2, bar = 20 μm; Figs 3, 4, bar = 10 μm; Figs 5–7, bar = 5 μm.

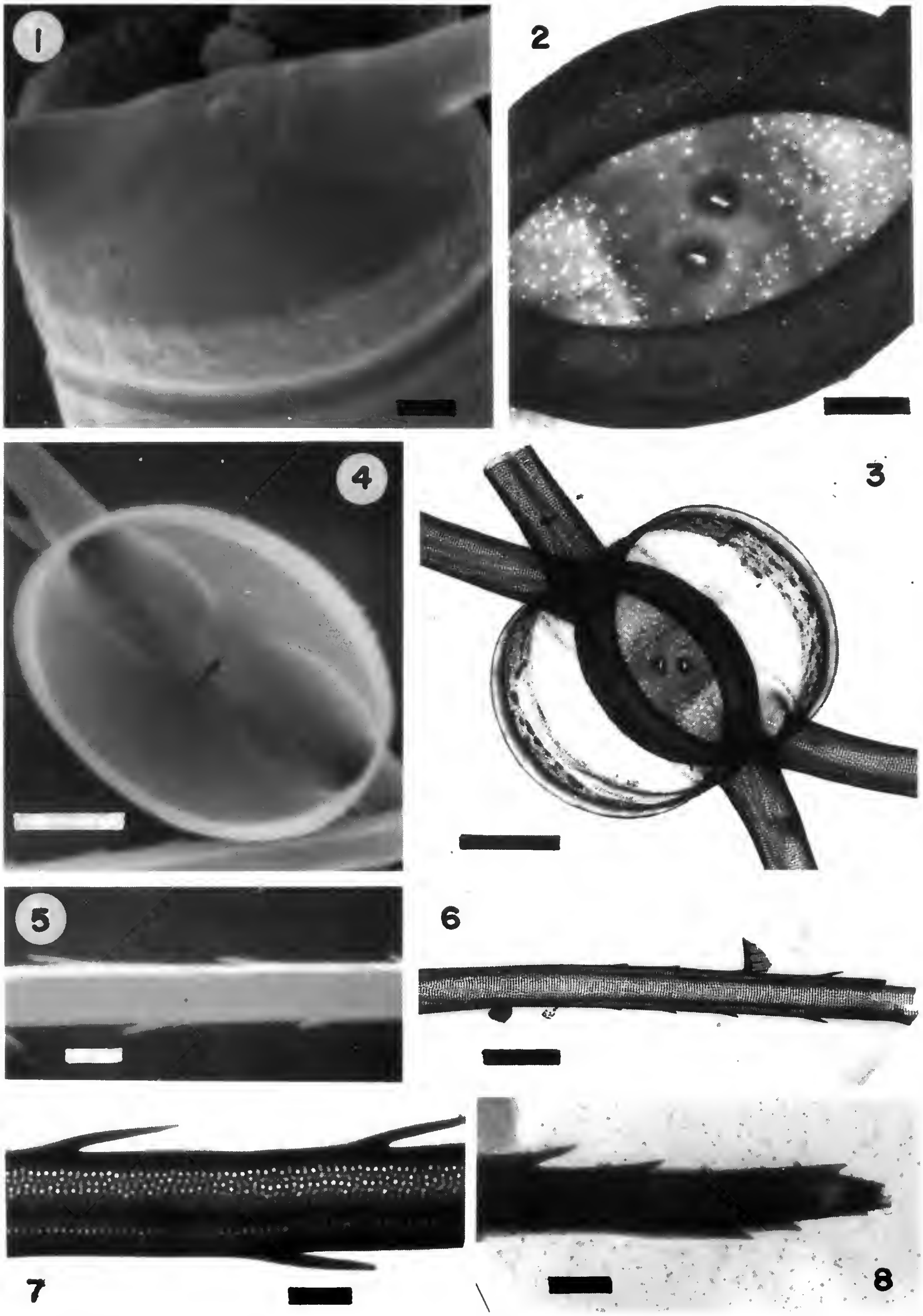

Plate 14 *Chaetoceros danicus*. Fig. 1: valve with thickenings and rimoportula. SEM. Fig. 2: two valves with rimoportula but no apparent annulus. TEM. Fig. 3: two valves with thickenings. TEM. Fig. 4: detail of rimoportula internally (arrow). SEM. Fig. 5: middle part of seta with spines. SEM. Fig. 6: base and distal part of seta. TEM. Fig. 7: another view of middle part of seta. TEM. Fig. 8: tip of seta. TEM. Figs 1, 2, 5, 7, 8, bar = 2 µm; Figs 3, 4, 6, bar = 5 µm.

11. **Chaetoceros concavicornis** L. Mangin

Mangin, 1917: 704, figs 5(I), 6, 7; Hustedt, 1930: 665, fig. 376; Gran & Angst, 1931: 469, fig. 50; Cupp, 1943: 109, figs 66a–c; Hendey, 1964: 122, pl. 9, fig. 1; Brunel, 1970: 90, pl. 12, figs 1–5; Evensen & Hasle, 1975: 158, figs 15–22.
Chaetoceros criophilus Gran, non *C. criophilus* Castrac. sensu Gran, 1905: 71, fig. 85.
Chaetoceros concaviformis (sic) L. Mangin sensu A. Cleve, 1951: 96, figs 182a–c.
Pl. 15, Figs 4, 5.

LM. Chains straight, rather short (3–9 cells), relatively robust. In girdle view, cells cylindrical, heterovalvar, the anterior valve rounded, the posterior valve more rectangular. Apertures very small, elongated (in the chain axis). In valve view, cells elliptical. Setae of the anterior valve arise from near the centre of the valve face and diverge; setae of the posterior valve are borne close to the corners and diverge. Distinct terminal setae apparently not present. Many small, rounded chloroplasts present in the cell (also reported within the setae). Measurements: 15–16 μm a.a., 35–39 μm p.a., 4–5 μm ap. (Pl. 15, Fig. 4)

EM. One posterior valve was observed by SEM and seems to be heavily silicified. No distinct valve face was noticed as the bases of the setae are placed closely and are slightly raised (Pl. 15, Fig. 5). The most outstanding character is the presence of 'prehensors' close to the setae bases on the posterior valve (Pl. 15, Fig. 5); these structures should hold the sibling setae, as described for *C. convolutus* Castrac. (see p. 22). No further details of the setae were observed.

DISTRIBUTION. 11, 15.

REMARKS. This species has been studied previously using EM (Evensen & Hasle, 1975); their details of the setae (e.g. structure of the wall, tip, etc.) augment the observations made here, although they did not report the presence of prehensors.

12. **Chaetoceros convolutus** Castrac.

Castracane, 1886: 78; Hustedt, 1930: 668, fig. 378; Gran & Angst, 1931: 468, fig. 49; Hendey, 1937: 293; Cupp, 1943: 110, fig. 67; Cleve-Euler, 1951: 96, figs 183a–c; Hendey, 1964: 122, pl. 8, fig. 1; Brunel, 1970: 91, pl. 13, figs 1–3; Fryxell & Medlin, 1981: 9, figs 6–8, 43–48; Rines & Hargraves, 1988: 47, fig. 94.
Pl. 15, Figs 1–3.

LM. Chains straight, mostly short (2–8 cells), robust. In girdle view, cells cylindrical, heterovalvar, the anterior valve more

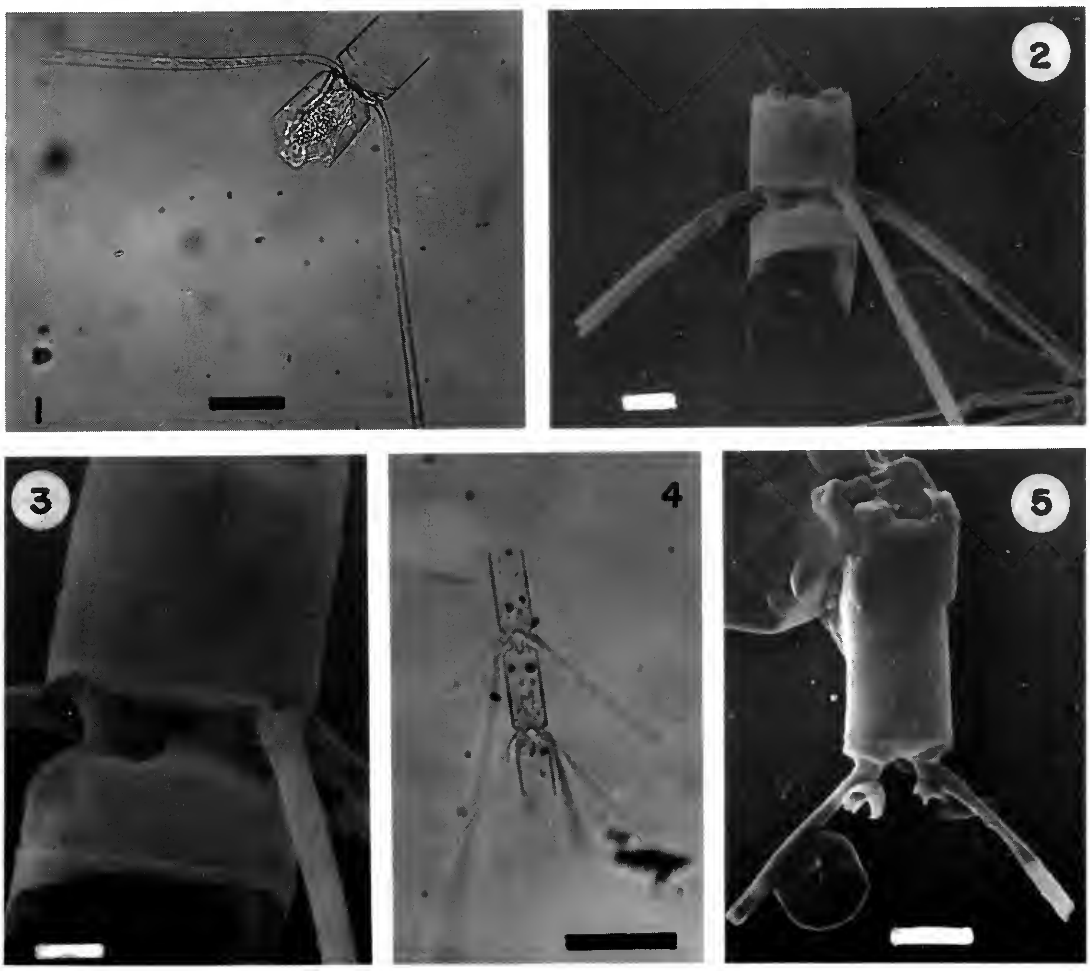

Plate 15 *Chaetoceros convolutus* (Figs 1–3) and *C. concavicornis* (Figs 4, 5). Fig. 1: broken chain with two valves. LM. Fig. 2: two sibling valves in chain. SEM. Fig. 3: detail of valves showing prehensor holding sibling seta. SEM. Fig. 4: typical chain. LM. Fig. 5: valve showing prehensors on setae. SEM. Figs 1, 4, bar = 50 μm; Fig. 2, bar = 20 μm; Figs 3, 5, bar = 10 μm.

rounded than the rectangular posterior valve. Apertures very narrow or almost absent; girdle zone very conspicuous. In valve view, cells subcircular or elliptical. Setae becoming thicker and spine-bearing at distal parts; those of the anterior valve arising close to the centre and diverging widely; those of the posterior valve arising from close to the corners and spreading. Numerous chloroplasts present in the cell and setae. Measurements: 22–42 μm a.a., 28–34 μm p.a. (Pl. 15, Fig. 1)

EM. Two sibling intercalary valves were observed (Pl. 15, Fig. 2). They appear to be heavily silicified and perforated by small, randomly distributed poroids (Pl. 15, Fig. 3). The rounded anterior valve shows no clear valve face and the setae bases occupy most of the centre of this area. An external protrusion of the rimoportula was noticed on one side of the posterior valve (the rectangular one) (Pl. 15, Fig. 3); no further observations were made on the corresponding rimoportula of the anterior valve. There is no apparent fusion of the sibling setae, but at the setae bases on the posterior valve some sort of prehensors develop (one per seta) and hold the setae arising from the sibling anterior valve (Pl. 15, Fig. 3). Sibling setae then diverge opposite each other. The setae become thicker and four-sided distally, with rows of spines at the edges (Pl. 15, Fig. 3).

DISTRIBUTION. 12.

REMARKS. *Chaetoceros concavicornis* and *C. convolutus* show a particular type of chain-formation, namely the possession of prehensors to hold sibling setae in the chain, which was first described by Fryxell & Medlin (1981), at least for *C. convolutus*. Fryxell & Medlin (1981) also discussed the difficulty of distinguishing between these two species.

13. **Chaetoceros peruvianus** Brightw.

Brightwell, 1856: 107, pl. 7, figs 16–18; Hustedt, 1930: 671, fig. 379, 380; Allen & Cupp, 1935: 136, fig. 56; Hendey, 1937: 296, pl. 13, fig. 6; Cupp, 1943: 113, fig. 68a–c; Okuno, 1956: 191, pl. 8, fig. 1–8; Hendey, 1964: 123, pl. 9, fig. 3; Okuno, 1970: pls 655, 656; Koch & Rivera, 1984: 69, figs 36–47; Desikachary et al., 1987: pl. 354, fig. 4; Rines & Hargraves, 1988: 53, figs 108–112.

Chaetoceros peruvianus f. *robusta* (Cleve) Hust.
Hustedt, 1930, p. 673, fig. 381a.

Chaetoceros peruvianus f. *gracilis* (Schröd.) Hust.
Hustedt, 1930: 672, fig. 381b.

Chaetoceros chilensis Krasske
Krasske, 1941: 266, pl. 4, fig. 3.

Pls 16, 17.

LM. Cells solitary, robust, heterovalvar. In girdle view, cells cylindrical, with rounded corners and constrictions at girdle zones. Anterior valve face reduced, mostly occupied by the setae bases, mantle variable in depth, lines of girdle straight; posterior valve face flat. In valve view, cells elliptical. Setae thick, coarse, long, bearing spines; setae of anterior valves fused together after a very short, free base, then diverging widely towards the pervalvar axis; setae of posterior valves arising close to the corners of the valve, then also diverging towards the pervalvar axis. Small chloroplasts present in cell and setae. Measurements: 13–22 μm a.a., 20–36 μm p.a. (Pl. 16, Fig. 1)

EM. The valves are heavily silicified (Pl. 16, Fig. 2) and perforated by poroids. In the centre of some anterior valves a pattern of weak costae runs parallel to the transapical axis (Pl. 16, Figs 3–6). No costae were seen in posterior valves (Pl. 17, Fig. 3). The annulus is oblong, placed to one side of the valve, and the rimoportula occurs at its centre (Pl. 17, Fig. 2). The rimoportula is a simple hole inside but projects externally as a flattened tube (Pl. 16, Fig. 4); in posterior valves the rimoportula appears to be open to the outside and it is relatively shorter and more cylindrical (Pl. 17, Fig. 3). The rimoportulae in both valves are apparently located to the same side. Anterior setae fuse together over the valve centre, forming an interlocking tooth-like structure (Pl. 17, Fig. 1), before twisting slightly and showing the common structure, as mentioned for most of the species within subgenus *Chaetoceros*. The setae are marked with longitudinal ridges at the base and are generally four-sided; spines are also present in rows and there are three striae between costae (Pl. 17, Figs 5–8).

DISTRIBUTION. 3, 6, 7, 10, 15–18, 23, 24, 26, 36, 42, 45, 48, 58, 64.

REMARKS. Previous EM observations are confirmed here. However, despite Koch & Rivera's (1984) statements about the variation in the number of striae between costae, it is clear from their figures and my own observations that the areola pattern shows no change in this aspect; Koch & Rivera's (1984) interpretations were based on setae observed at different angles, such that it appears the intercostal striae may number more than three. Ratkova (1974) tried to show that differences exist between *C. chilensis* and *C. peruvianus*, but her observations do not seem to be conclusive.

14. **Chaetoceros pendulus** G. Karst.

Karsten, 1905: 118, pl. 15, figs 7, 7a; Hendey, 1937: 295; Cupp, 1943: 114, fig. 69.

Pls 18, 19.

LM. Cells solitary, heterovalvar. In girdle view, cells almost rectangular, with smooth corners and constricted at the girdle zones, the apical axis being relatively longer. Anterior valve convex, mantle very low, lines of girdle straight; posterior valve depressed at centre. In valve view, cells elliptical. Setae thick, long, bearing spines distally; those of anterior valve arise diagonally, then curve to the pervalvar axis, directed almost parallel to the setae from the posterior valve, which simply curve smoothly towards the pervalvar axis. Several small chloroplasts present in cell and setae. Measurements: 15–19 μm a.a., 10–17 μm p.a. (Pl. 18, Figs 1, 2)

EM. The valves are fairly heavily silicified (Pl. 18, Figs 3, 4, 6), perforated by small poroids (Pl. 18, Fig. 5), and show a pattern of weak costae arranged in rows following the apical axis close to the base of the setae (Pl. 19, Fig. 2). A small number of slightly stronger costae are present in the centre of the valve, running transapically and leading to the excentric annulus. In the centre of this annulus a rimoportula is found, comprising a simple oblong hole internally, with a connection close to it, and a very short, flattened tube projecting externally (Pl. 19, Figs 1–3). The rimoportulae of both the posterior and the anterior valves are at the same side of the cell, the one in the posterior valve located in a depressed area of the valve (Pl. 18, Figs 4, 5). The setae bases are circular and simply perforated. Setae become four-sided, with large spines running in rows along each edge; their walls are poroid, with three striae between costae (Pl. 19, Figs 4–7). The tips are very sharp, without any opening to the outside (Pl. 19, Fig. 8).

DISTRIBUTION. 24, 48, 50.

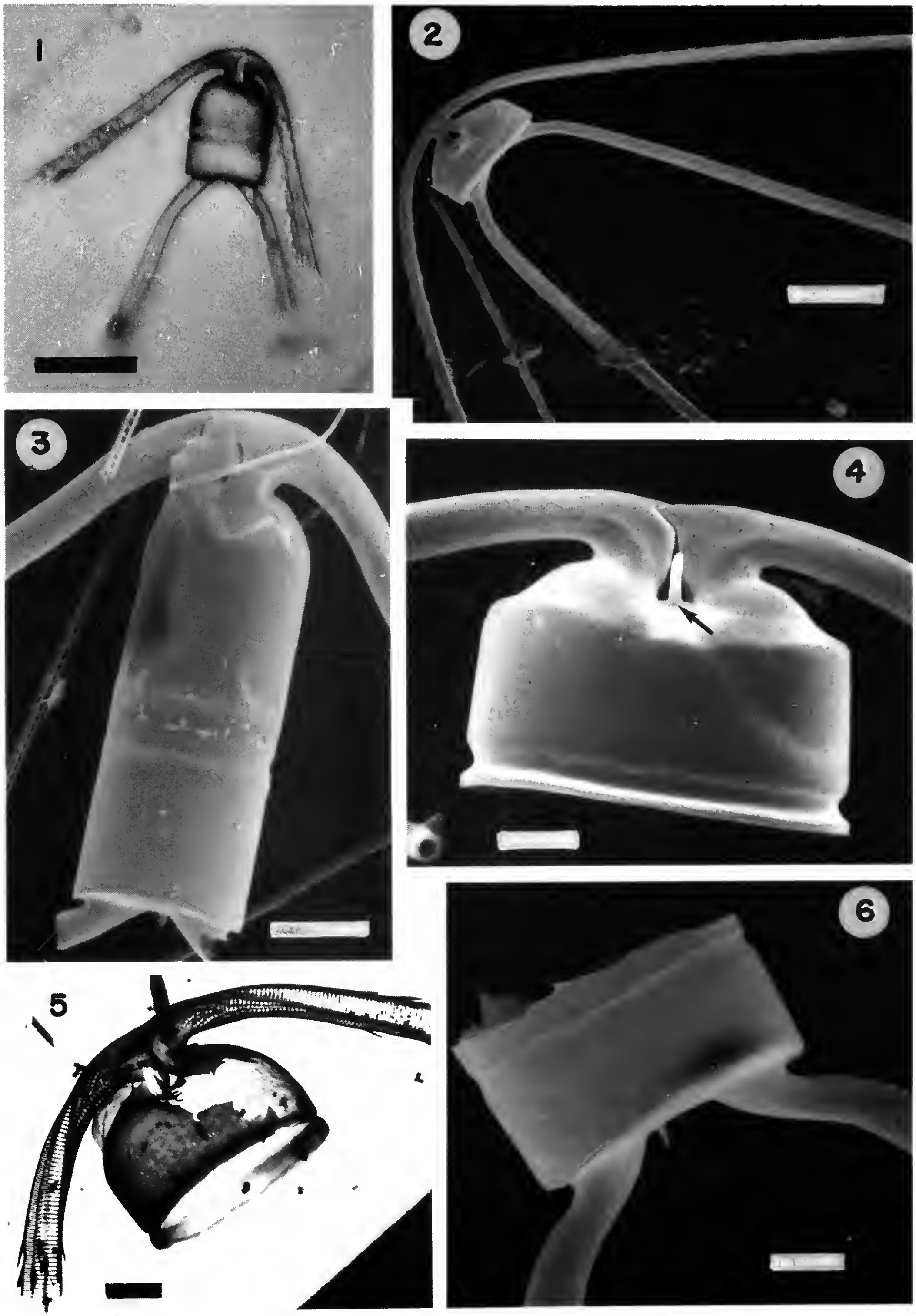

Plate 16 *Chaetoceros peruvianus*. Fig. 1: complete cell. LM. Fig. 2: complete cell. SEM. Fig. 3: another cell with various girdle bands. SEM. Fig. 4: anterior valve showing rimoportula (arrow). SEM. Fig. 5: another partially broken anterior valve. TEM. Fig. 6: detail of posterior valve. SEM. Figs 1, 2, bar = 20 μm; Figs 3–6, bar = 5 μm.

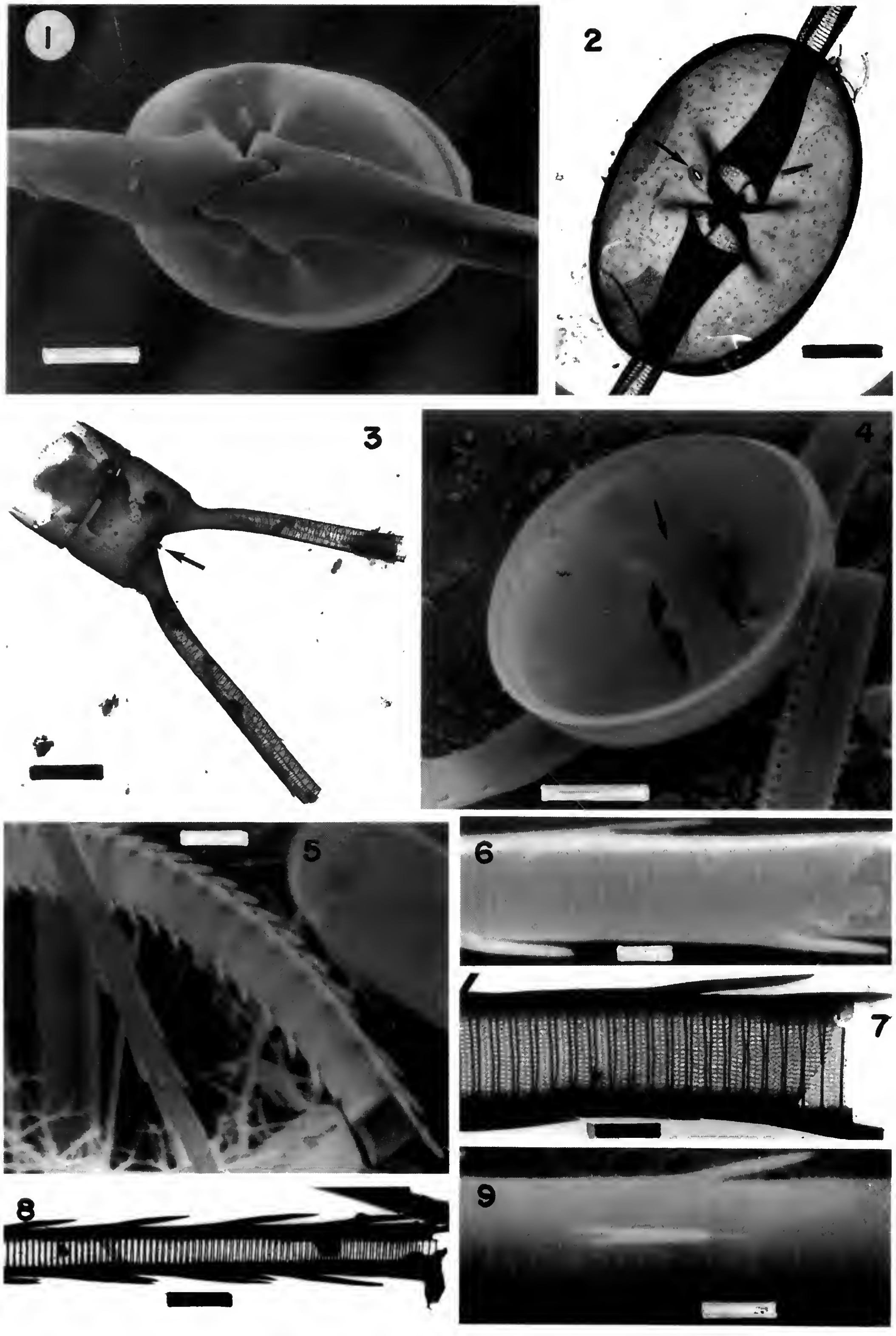

Plate 17 *Chaetoceros peruvianus*. Fig. 1: anterior valve showing interlocking of setae. SEM. Fig. 2: anterior valve with excentric annulus and rimoportula (arrow). TEM. Fig. 3: posterior valve with rimoportula (arrow). TEM. Fig. 4: internal view of rimoportula (arrow). SEM. Fig. 5: square (in cross-section) seta. SEM. Figs 6, 9: middle part of seta with spines. SEM. Figs 7, 8: middle part of seta. TEM. Figs 1, 2, 4, 5, 9, bar = 5 μm; Fig. 3, bar = 10 μm; Figs 6–8, bar = 2 μm.

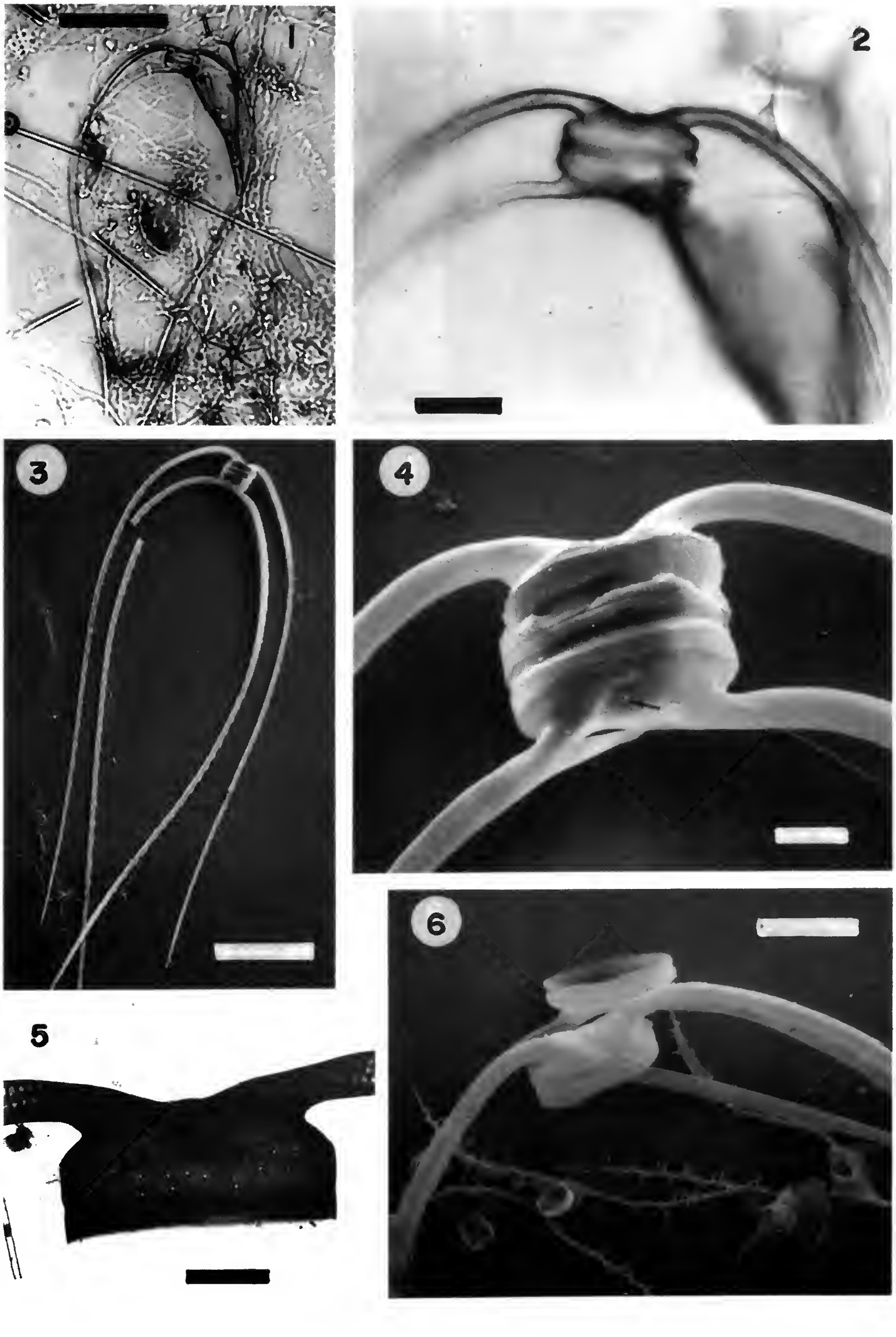

Plate 18 *Chaetoceros pendulus*. Figs 1, 2: solitary cells. LM. Fig. 3: complete cell. SEM. Fig. 4: detail of cell showing rimoportula (arrow) at posterior valve. SEM. Fig. 5: valve with setae bases. TEM. Fig. 6: anterior and posterior valves separated. SEM. Figs 1, 3, bar = 50 μm; Figs 2, 6, bar = 10 μm; Figs 4, 5, bar = 5 μm.

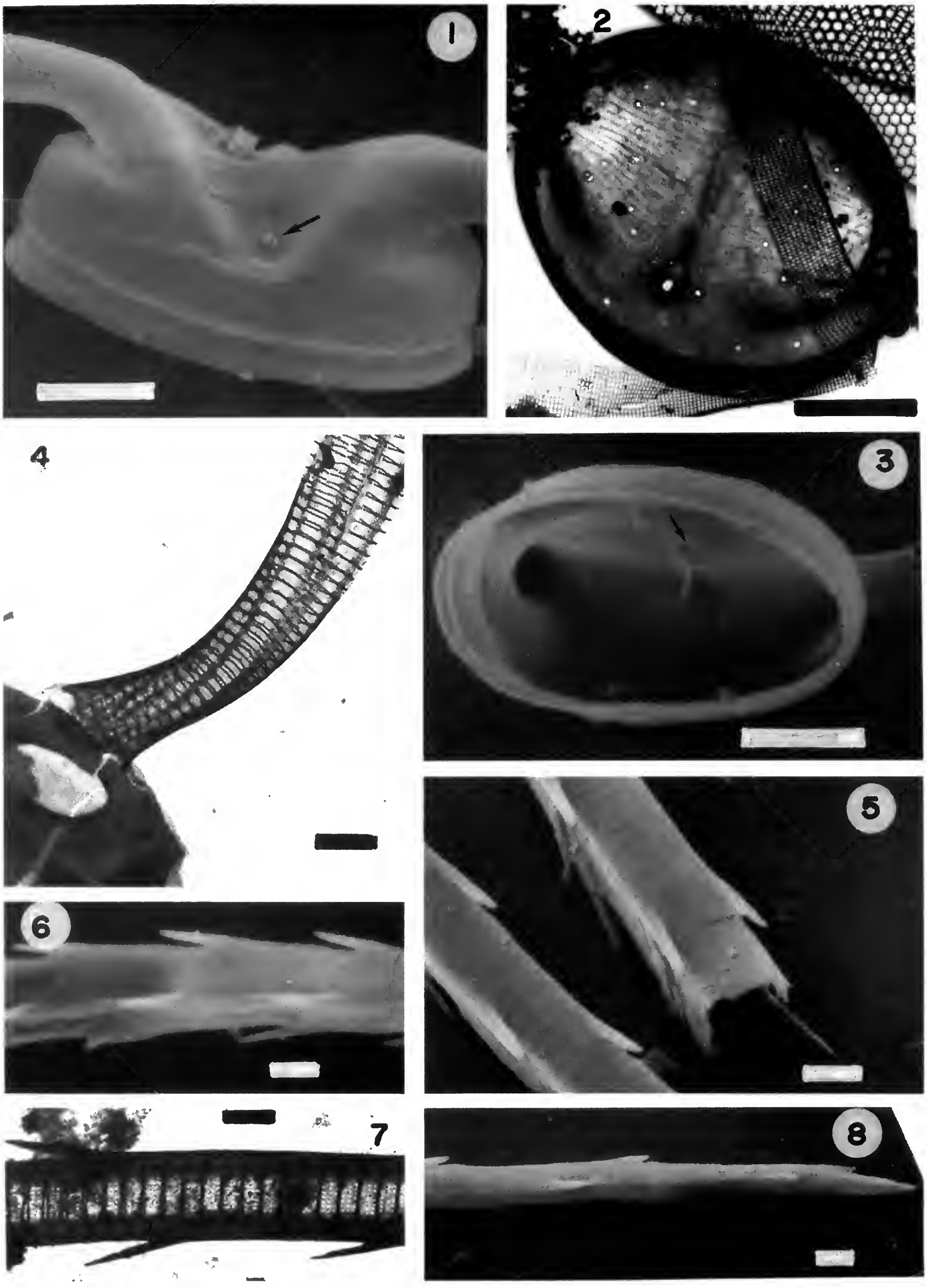

Plate 19 *Chaetoceros pendulus*. Fig. 1: anterior valve showing excentric rimoportula. SEM. Fig. 2: another anterior valve with excentric annulus and rimoportula. TEM. Fig. 3: inside view of valve. Arrow indicates rimoportula. SEM. Fig. 4: base of seta. TEM. Fig. 5: four-sided (in cross-section) seta. SEM. Fig. 6: middle part of seta. SEM. Fig. 7: middle part of seta with spines. TEM. Fig. 8: tip of seta. SEM. Figs 1–3, bar = 5 μm; Figs 4–8, bar = 2 μm.

REMARKS. This species is closely related to *C. aequatorialis* Cleve and further studies may reveal that they are conspecific. Cleve (1873*a*: pl. 2, fig. 9) figured one specimen forming a short chain (two cells), accompanied by a rather poor description. The species described here is identified as *C. pendulus* since this has previously been reported from the area where the present material was collected (Cupp, 1943) and because chains were not found in this material. However, if both species are indeed conspecific, the name *C. aequatorialis* would have priority.

4. Section **COARCTATA** Hern.-Bec.

Chains heteropolar, usually very robust. Numerous small rimoportulae present in each valve.

15. **Chaetoceros coarctatus** Lauder

Hernández-Becerril, 1991*a*: 282, figs 1–13.

DISTRIBUTION. 7, 16, 17, 19, 20, 23, 41, 44, 45, 48, 49.

II. Subgenus **HYALOCHAETE** Gran

5. Section DICLADIA (Ehrenb.) Gran

Terminal and intercalary setae similar. Chloroplasts numerous.

Some authors (Lebour, 1930; Cupp, 1943; Hendey, 1964) have included *C. decipiens* Cleve within section *Oceanica* Ostenf. because it lacks resting spores. However, I consider that *C. decipiens* and *C. lorenzianus* Grunov are closely related, and I include the former in this section.

16. **Chaetoceros decipiens** Cleve

Cleve, 1873*b*: 11, pl. 1, figs 5a, b; Peragallo & Peragallo, 1897–1908: 485, pl. 131, figs 3, 4, 8; Hustedt, 1930: 675, fig. 383; Gran & Angst, 1931: 470, fig. 52; Cupp, 1943: 115, figs 70–A, 70–Ba, b; Cleve-Euler, 1951: 98, figs 188a, b; Hendey et al., 1954: 29, pl. 1, fig. 4; Okuno, 1956: 191, pl. 7, figs 1–8; Hendey, 1964: 123, pl. 12, fig. 2; Brunel, 1970: 99, pl. 21, figs 1–4, pl. 22, figs 1–5; Drebes, 1974: 69, fig. 52; Evensen & Hasle, 1975: 161, figs 55–69; Navarro, 1982: 309, fig. 22; Rines & Hargraves, 1988: 75, figs 148, 152.
Pls 20, 21.

LM. Chains straight, often long. In girdle view, cells rectangular, with sharp corners. Valve face nearly flat or slightly concave, mantle high, lines of girdle straight; apertures rather wide. In valve view, cells elliptical, the setae straight, following the apical axis. Setae relatively thick, with minute striae along their length; terminal setae slightly thicker than intercalary setae and also differing in their direction. Intercalary setae arise from the corners and fuse immediately with sibling setae, remaining joined for a short distance before diverging again at an angle of about 10–15° from the apical axis. Small chloroplasts present at the centre of the cell. Measurements: 18–40 µm a.a., 17–24 µm p.a., 5–10 µm ap. (Pl. 20, Figs 1, 2)

EM. The valve morphology of this species may be considered as typical for most of the species within subgenus *Hyalochaete*: the valves do not appear to be as heavily silicified as those of species placed in subgenus *Chaetoceros* (Pl. 20, Figs 3, 4; Pl. 21, Figs 3, 4). Another general characteristic of the valves is the presence of an annulus from which a weak costal pattern radiates (Pl. 20, Figs 4, 5). There are small poroids between the costae. A hyaline rim is often found on the edge of some terminal valves (Pl. 21, Fig. 5). Also, short, hair-like filaments of solid appearence become visible in apical areas of some intercalary valve mantles (Pl. 20, Fig. 6; Pl. 21, Fig. 2). Thin walls with a simple, perforated structure appear to connect the corners (apical areas) of intercalary sibling valves (Pl. 21, Fig. 2). A rimoportula is present only on terminal valves; each shows a very small projection to the outside and is centrally placed within the annulus (Pl. 21, Fig. 5). The setae are circular at the base (Pl. 21, Fig. 1), but become polygonal (6–8 sides) distally, with spines running in rows along each edge and rather large perforations in the sides (Pl. 21, Figs 2, 6, 7). Terminal setae are thicker than intercalary setae, with relatively bigger spines, but smaller holes (Pl. 21, Fig. 6). The tips are truncated (Pl. 21, Fig. 7).

DISTRIBUTION. 15–17, 20, 23, 31, 35, 36, 42, 52.

REMARKS. See remarks under *C. lorenzianus* Grunov (p. 31).

17. **Chaetoceros decipiens** f. **singularis** Gran

Gran, 1904: 536, pl. 17, fig. 7; Cupp, 1943: 117, fig. 70–Bc, d.
Pl. 24, Figs 1, 2.

LM & EM. Cells solitary. The morphology is typically the same as that of the type, with setae diverging at an angle of about 10–20° from the pervalvar axis. Valves and setae are as described above. Two snail-like structures were found at the base of the setae (Pl. 24, Figs 1, 2).

DISTRIBUTION. 17, 23, 42, 45.

REMARKS. It is unclear whether this taxon should be considered as a form of *C. decipiens* or if it is only part of the life cycle of the species.

18. **Chaetoceros lorenzianus** Grunov

Grunow, 1863: 157, pl. 5, fig. 13; Peragallo & Peragallo, 1897–1908: 484, pl. 130, figs 1, 2, pl. 131, fig. 1, non 3; Hustedt, 1930: 679, fig. 385; Gran & Angst, 1931: 471, fig. 53; Allen & Cupp, 1935: 137, fig. 58; Cupp, 1943: 118, fig. 71; Subrahmanyan, 1946: 131, figs 199, 202–204, 206–209, non 198; Cleve-Euler, 1951: 98, figs 187a–d; Okuno, 1956: 190, pl. 6, figs 1–7; Hendey, 1964: 124, pl. 16, fig. 1; Brunel, 1970: 105, pl. 18, figs 1–4, pl. 19, figs 1–4; Navarro, 1982: 312, fig. 34; Desikachary & Prema, 1987: pl. 262, figs 3, 4 (non *C. lorenzianus* Grunov sensu Helmcke & Krieger, 1954: pl. 124 = *C. decipiens* Cleve).
Pls 22, 23.

LM. Chains straight, of variable length. In girdle view, cells rectangular with sharp corners, the pervalvar axis generally longer. Valve face flat or slightly convex in the centre, mantle high, lines of girdle straight; apertures variable in size. In valve view, cells elliptical. Setae relatively thick, marked with striae; intercalary setae arise from the valve corners, diverging at an angle of about 15–20° from the apical axis; terminal setae curve towards the chain axis. Several, small chloroplasts present in the cell. Measurements: 13–25 µm a.a., 8–50 µm p.a., 8–12 µm ap. (Pl. 22, Fig. 1)

EM. The valve structure is similar to that in *C. decipiens* (Pl. 22, Fig. 2), but the costae are more marked and stronger (Pl. 22, Figs 3–6). The costae converge at the apices, making the valve thicker. Small poroids are scattered between the costae. The girdle structure differs slightly from that of the valve in lacking costae,

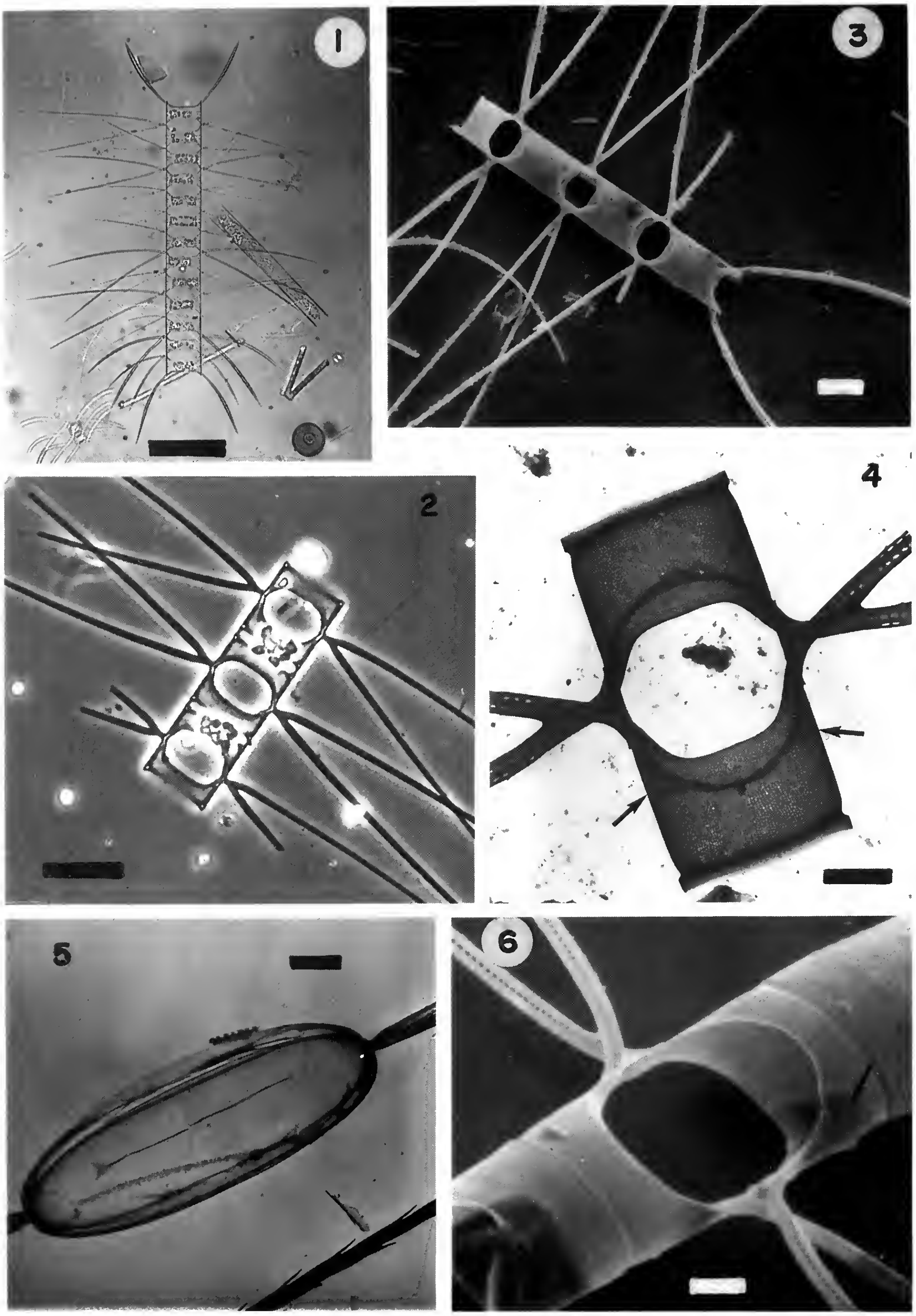

Plate 20 *Chaetoceros decipiens*. Figs 1, 2: complete chain and part of chain, respectively. LM. Fig. 3: part of chain. SEM. Fig. 4: sibling valves, the lower showing some filaments (arrows). TEM. Fig. 5. valve view of valve with central annulus. TEM. Fig. 6: sibling cells, one showing filaments in mantle (arrow). SEM. Fig. 1, bar = 100 μm; Figs 2, 3, bar = 20 μm; Figs 4–6, bar = 5 μm.

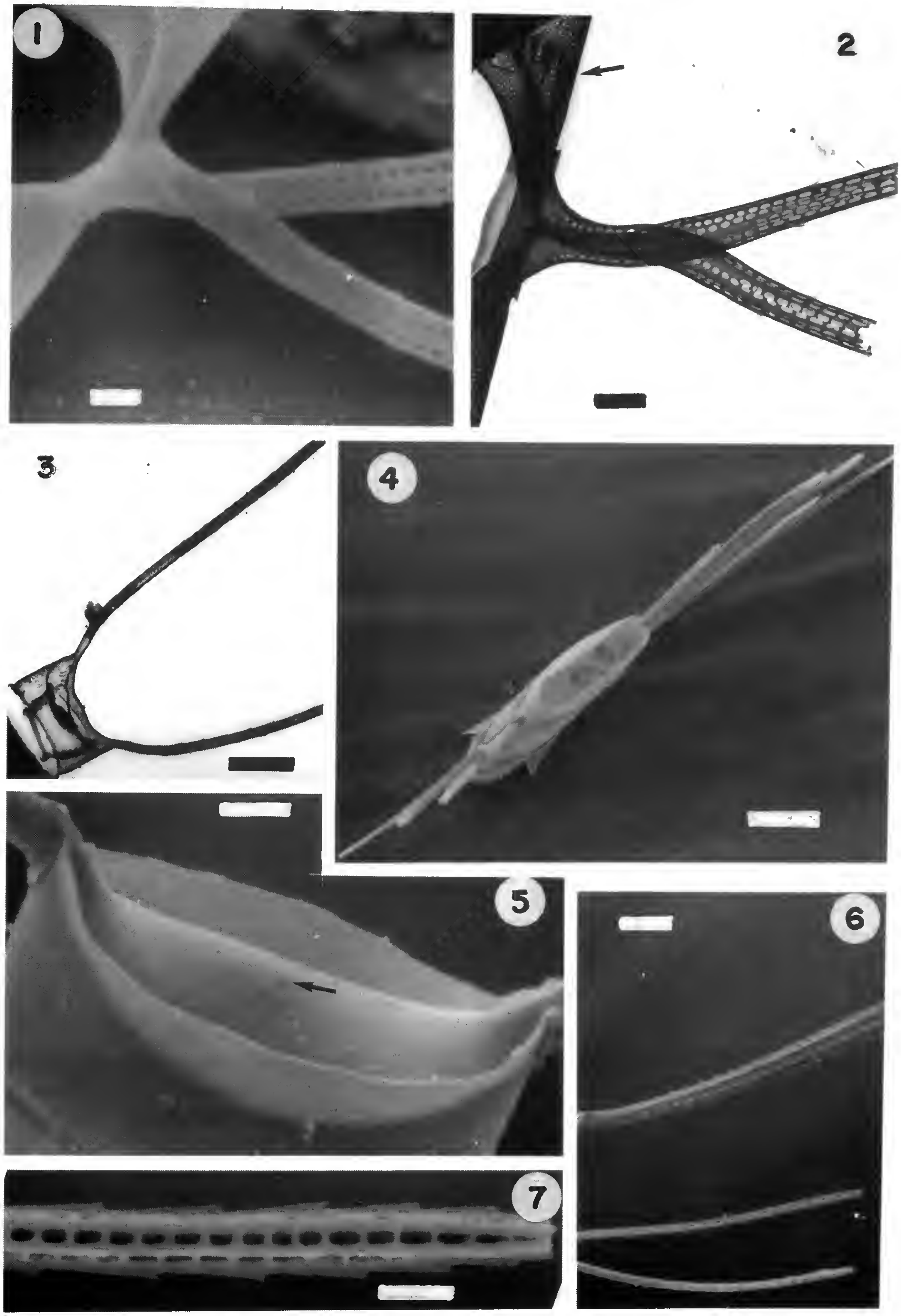

Plate 21 *Chaetoceros decipiens.* Fig. 1: base of setae. SEM. Fig. 2: base of setae joined for a short distance. Arrow indicates filaments on mantle. TEM. Fig. 3: terminal valve. TEM. Fig. 4: valve view of chain. SEM. Fig. 5: terminal valve with central rimoportula. SEM. Fig. 6: terminal seta (upper) and intercalary setae (lower). SEM. Fig. 7: tip of seta. SEM. Figs 1, 2, 5, 7, bar = 2 μm; Figs 3, 4, 6, bar = 10 μm.

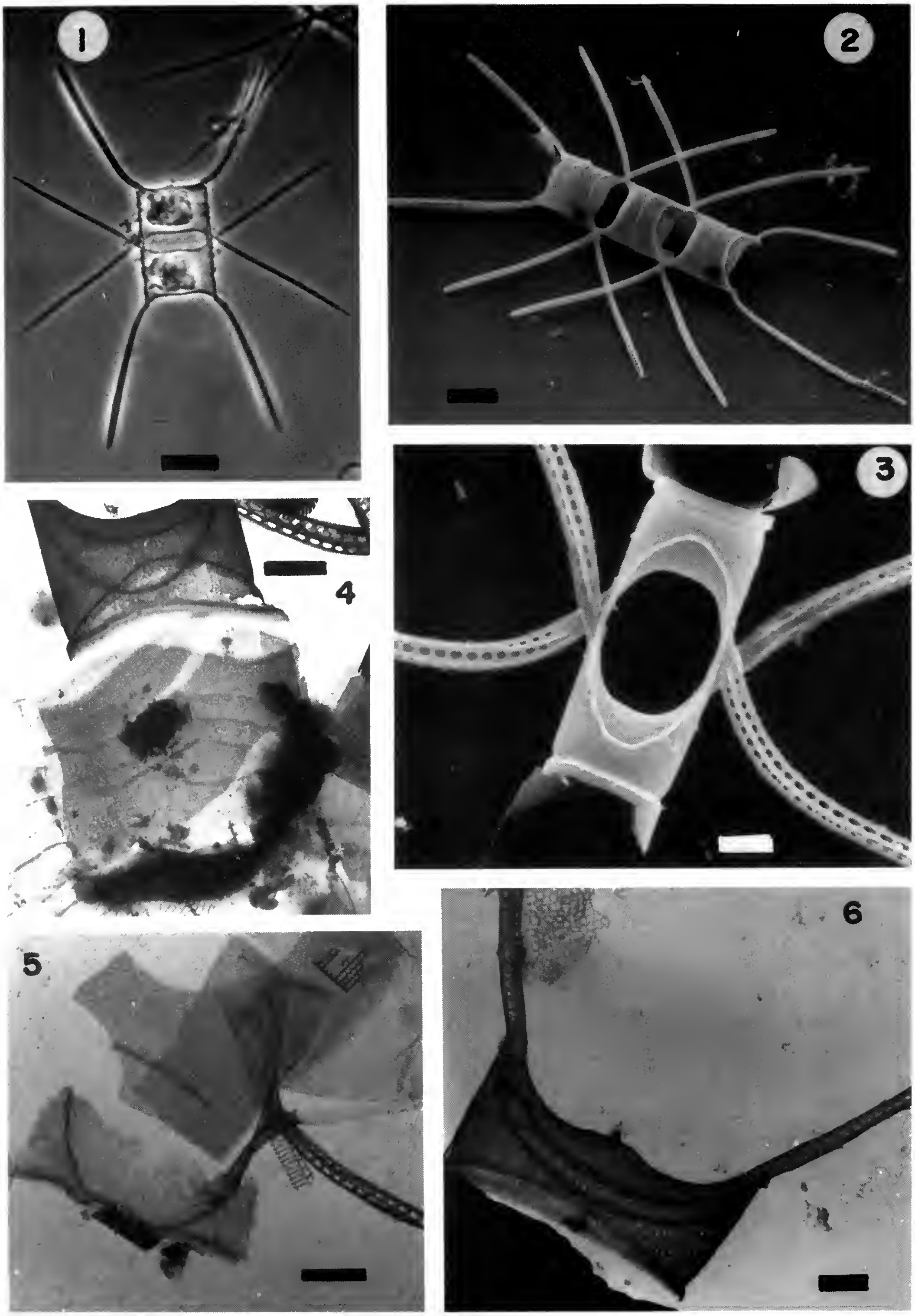

Plate 22 *Chaetoceros lorenzianus*. Fig. 1: typical chain. LM. Fig. 2: complete chain. SEM. Fig. 3: sibling valves. SEM. Fig. 4: valve with several girdle bands. TEM. Fig. 5: broken valve showing base of setae. TEM. Fig. 6: terminal valve with rimoportula. TEM. Figs 1, 2, bar = 20 µm; Figs 3, 4, 6, bar = 5 µm; Fig. 5, bar = 10 µm.

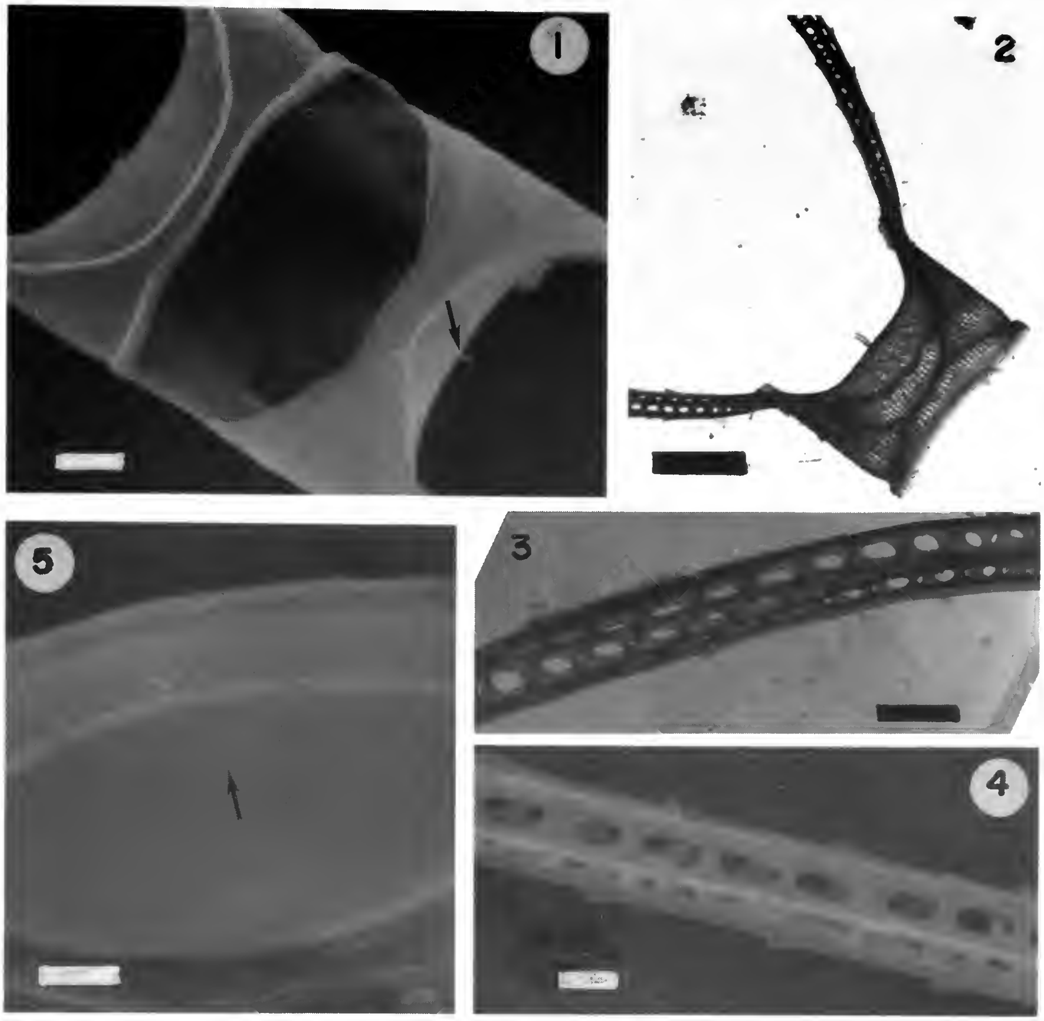

Plate 23 *Chaetoceros lorenzianus*. Fig. 1: terminal cell with rimoportula at terminal valve (arrow). SEM. Fig. 2: terminal valve with tube-like rimoportula. TEM. Fig. 3: middle part of seta. TEM. Fig. 4: middle part of seta. SEM. Fig. 5: inside view of valve showing rimoportula with labiate structure. SEM. Fig. 1, bar = 5 µm; Fig. 2, bar = 10 µm; Figs 3–5, bar = 2 µm.

but with rows of poroids that follow the pervalvar axis (Pl. 22, Fig. 4). The rimoportulae are found only on terminal valves, located in the centre, again coinciding with the annulus. Each consists of a relatively short or longer cylindrical tube open to the outside and with a true labiate structure inside (Pl. 23, Figs 1, 2, 5). The structure of the setae is very like that of *C. decipiens* and it is difficult to determine any differences between them (Pl. 23, Figs 3, 4). No resting spores were observed.

Distribution. 12, 15, 18, 23, 42, 45, 48, 53.

Remarks. Okuno (1956) studied *C. decipiens* and *C. lorenzianus* and illustrated the major differences between them. Apparently, *C. lorenzianus* presents a stronger costal pattern and lacks the fine poroids which occur in the valves of *C. decipiens* (Evensen & Hasle, 1975). Furthermore, following the observations made in this study, it can be appreciated that the distinctive structure of the rimoportulae, with that of *C. lorenzianus* projected externally in a short tube and that of *C. decipiens* being rather reduced, could be an important distinguishing character, as could the distinctive presence of filaments in *C. decipiens*, which are absent in *C. lorenzianus*. The presence of resting spores in *C. lorenzianus* is a useful character for identification. However, the possibility that both are stages in the life cycle of one species calls for further investigation (see also Evensen & Hasle, 1975).

19. **Chaetoceros lorenzianus** f. **forceps** Meunier

Meunier, 1913: 20, pl. 2, figs 12–18; Brunel, 1970: 106, pl. 20, figs 1–3.

Pl. 24, Figs 3–6.

Lm & em. This is a solitary, non chain-forming form of *C. lorenzianus*, which has the same basic characteristics regarding valve and seta morphology (Pl. 24, Figs 3–6). No resting spores were found.

Distribution. 23.

Remarks. Brunel (1970) has shown that this form is indeed able to create resting spores which are identical to those of the type species.

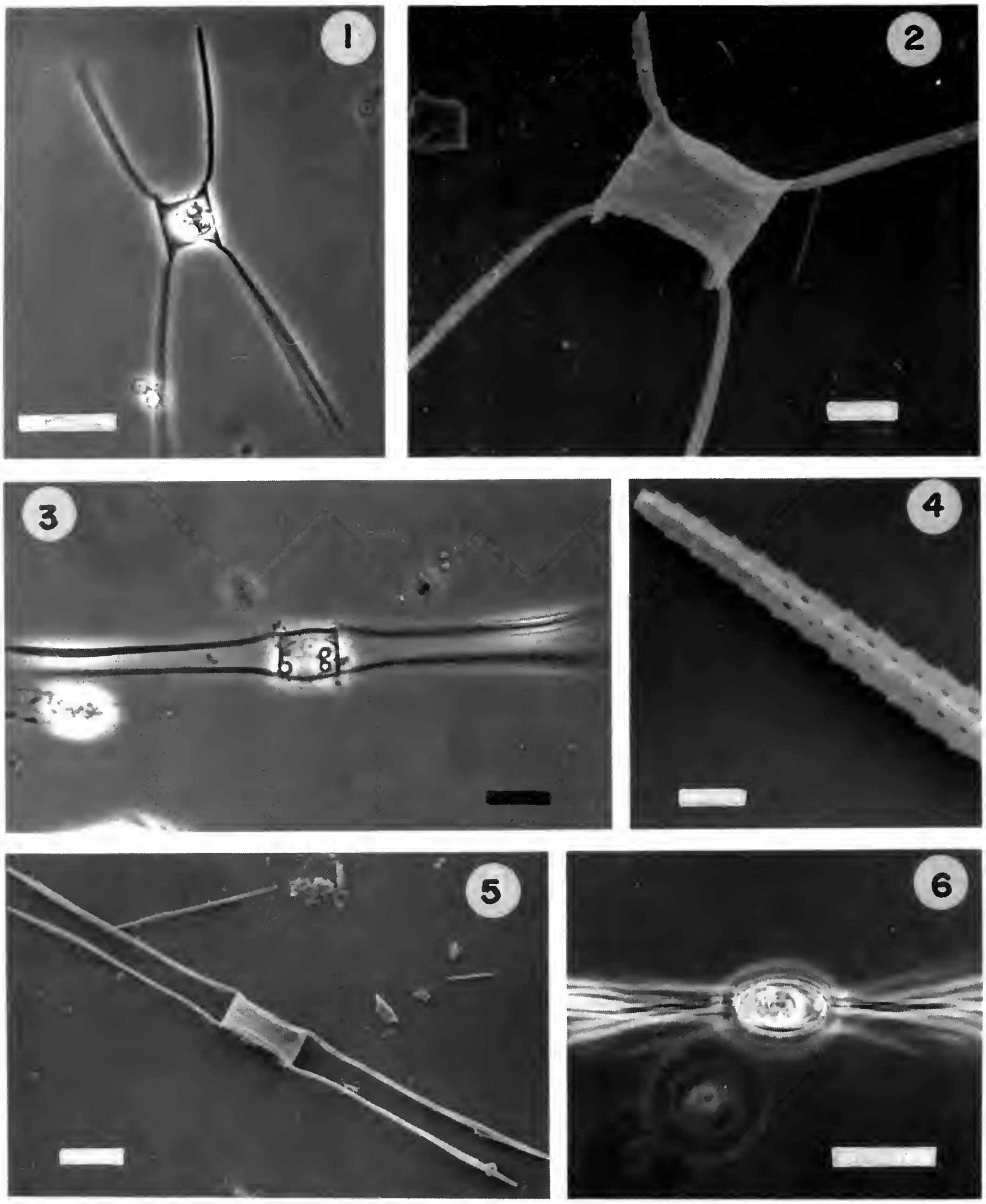

Plate 24 *Chaetoceros decipiens* f. *singularis* (Figs 1, 2) and *C. lorenzianus* f. *forceps* (Figs 3–6). Fig. 1: complete cell. LM. Fig. 2: complete cell. SEM. Fig. 3: complete cell. LM. Fig. 4: detail of seta tip. SEM. Fig. 5: complete cell. SEM. Fig. 6: cell in valve view. LM. Fig. 1, bar = 50 µm; Fig. 2, bar = 10 µm; Figs 3, 5, 6, bar = 20 µm; Fig. 4, bar = 2 µm.

6. Section **CYLINDRICA** Ostenf.

Valves nearly circular (cylindrical). Apertures narrow. Terminal setae not thicker than other setae. Chloroplasts numerous.

20. **Chaetoceros bermejensis** Hern.-Bec.

Hernández-Becerril, 1991*c*: 522, figs 1–14.

DISTRIBUTION. 42, 45.

7. Section **COMPRESSA** Ostenf.

Valves compressed. Intercalary setae of two types: thin, common setae and thicker, twisted special setae.

21. **Chaetoceros compressus** Lauder

Lauder, 1864: 78, pl. 8, fig. 6; Peragallo & Peragallo, 1897–1908: 488, pl. 134, fig. 8; Hustedt, 1930: 684, fig. 388; Gran & Angst, 1931: 472, fig. 55; Allen & Cupp, 1935: 138, fig. 60; Cupp, 1943: 119, fig. 74; Subrahmanyan, 1946: 134, fig. 218; Cleve-Euler, 1951: 99, figs 191b, c, non a; Hendey et al.,

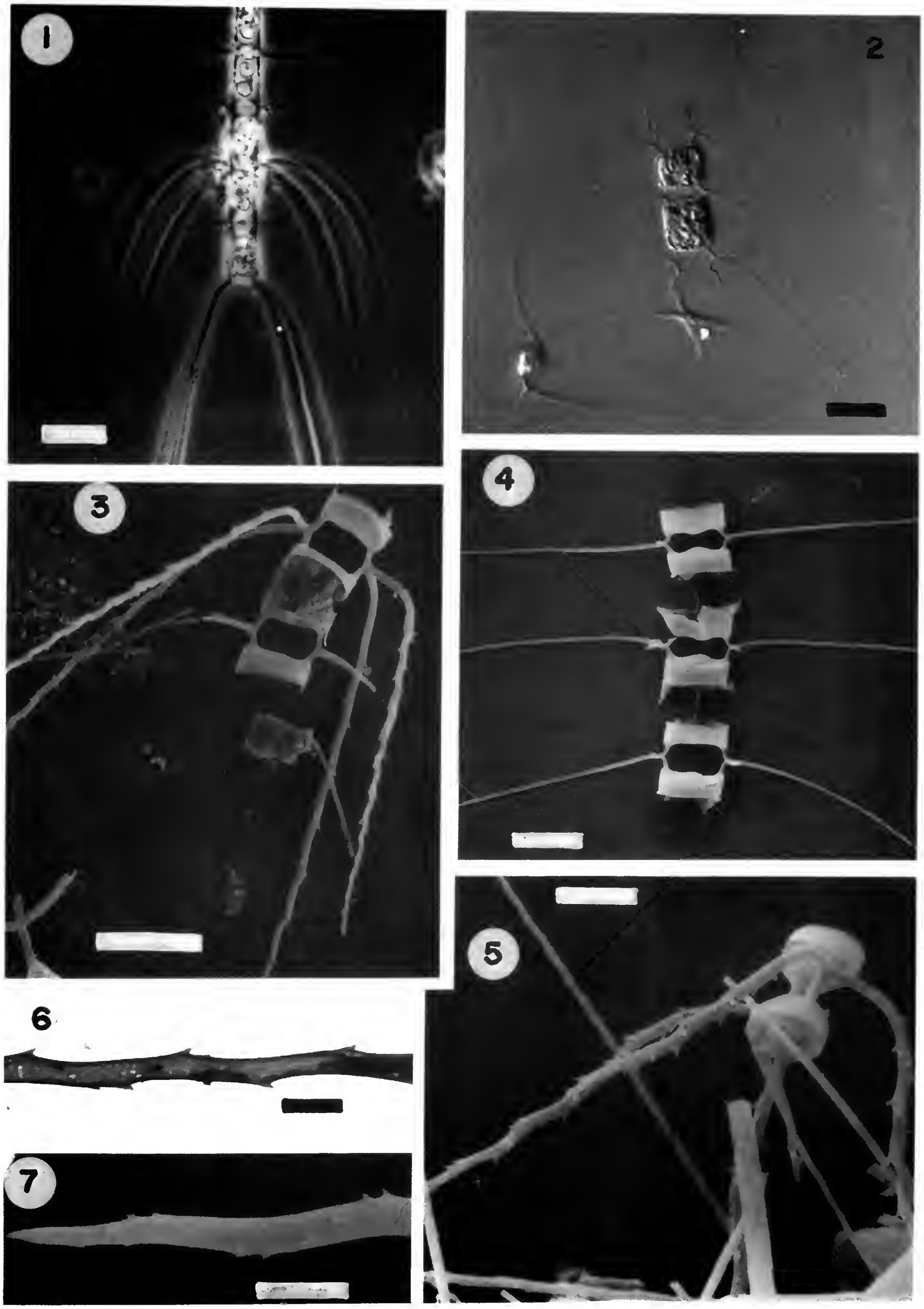

Plate 25 *Chaetoceros compressus*. Figs 1, 2: typical chain and part of chain, respectively. LM. Fig. 3: part of chain with special setae. SEM. Fig. 4: another part of chain. SEM. Fig. 5: sibling valves with special setae. SEM. Fig. 6: middle part of special seta. TEM. Fig. 7: tip of special seta. SEM. Figs 1–4, bar = 20 μm; Fig. 5, bar = 10 μm; Figs 6, 7, bar = 5 μm.

1954: 29, pl. 1, fig. 3, non fig. 5; Hendey, 1964: 125, pl. 15, fig. 5; Brunel, 1970: 110, pl. 25, figs 1–4; Drebes, 1974: 72, figs 56a, b; Navarro, 1982: 309, fig. 15; Desikachary et al., 1987: pl. 258, fig. 2; Rines & Hargraves, 1988: 64, figs 131–134, 218.
Pls 25, 26.

LM. Chains variable, straight or slightly twisted, generally long and delicate. In girdle view, cells rectangular to square, with sharp corners. Valve face convex, mantle low, lines of girdle straight; apertures of variable width. In valve view, cells elliptical. Terminal and intercalary setae differ, the former thicker and coarser. Special intercalary setae often present, longer and with larger spines than other intercalary setae. Common intercalary setae diverging at random. Various small chloroplasts present in the cell. Measurements: 10–21 μm a.a., 10–24 μm p.a., 6–7 μm ap. (Pl. 25, Figs 1, 2)

EM. The valve is usually weakly silicified (Pl. 25, Figs 3, 4), with a conspicuous annulus from which weak costae radiate (Pl. 25, Fig. 4; Pl. 26, Fig. 1). The rimoportula is a rather excentric, hollow structure and occurs in the annulus (Pl. 26, Figs 1, 2). The setae arise from close to the corners of the valve (Pl. 26, Fig. 1); they have a spiral pattern of spines running longitudinaly, as well as small poroids perforating the wall (Pl. 25, Fig. 6). The spines on special setae are larger than those on common intercalary setae (Pl. 25, Figs 3, 5; Pl. 26, Figs 3–5, 7). All setae are circular in cross-section and the tips are very pointed (Pl. 25, Fig. 7; Pl. 26, Fig. 6).

DISTRIBUTION. 1, 7, 17, 23, 52, 53.

REMARKS. This species exhibits a wide range of forms during its life cycle, which makes positive identification difficult.

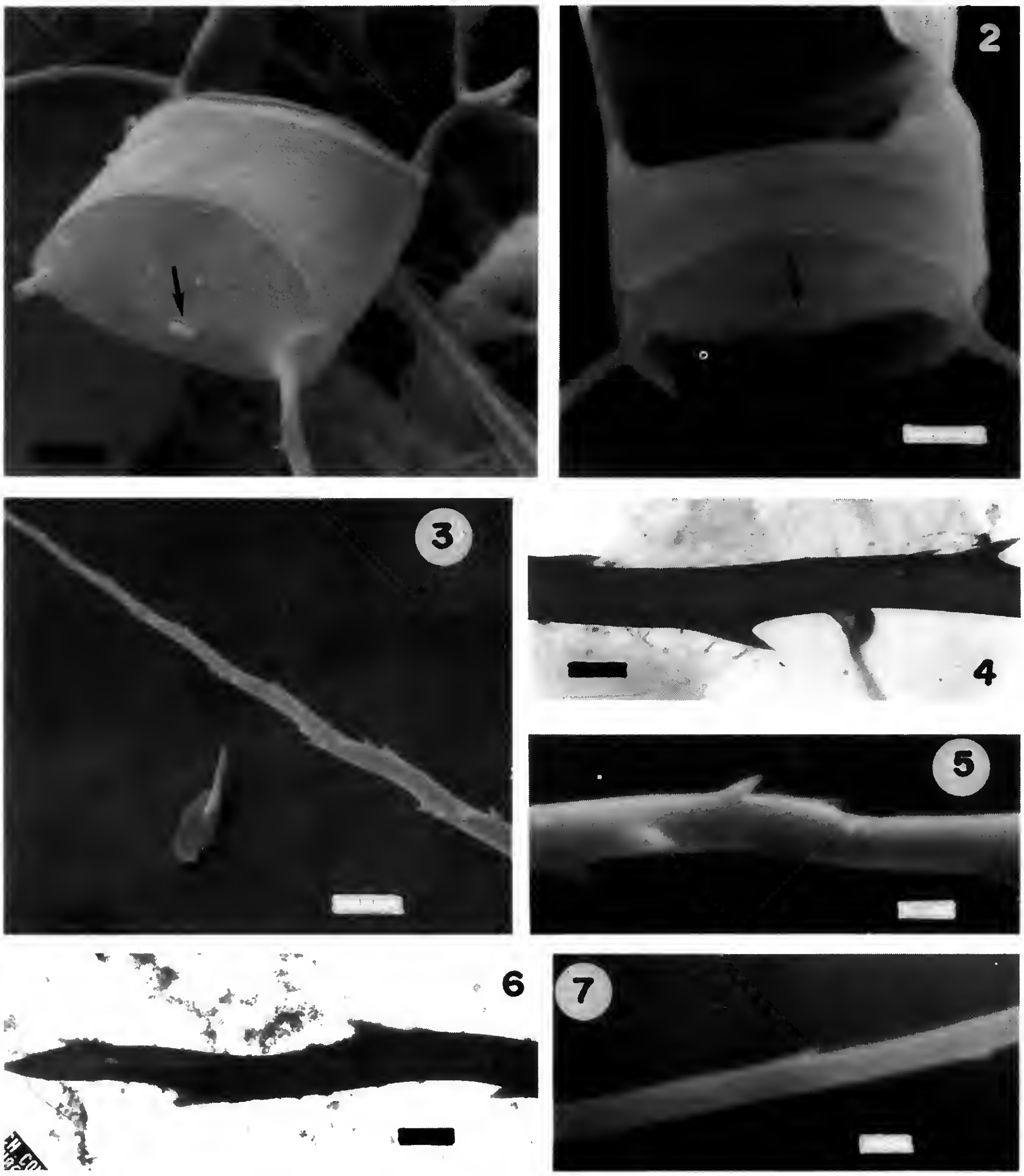

Plate 26 *Chaetoceros compressus*. Fig. 1: terminal cell with rimoportula (arrow) at terminal valve. SEM. Fig. 2: terminal cell showing rimoportula (arrow). SEM. Fig. 3: detail of special seta. SEM. Fig. 4: middle part of special seta. TEM. Fig. 5: middle part of special seta. SEM. Fig. 6: tip of special seta. TEM. Fig. 7: middle part of intercalary (common) seta. SEM. Figs 1–3, bar = 5 μm; Figs 4–7, bar = 2 μm.

8. Section **PROTUBERANTIA** Ostenf. emend. Hern.-Bec.

A large protuberance present in the centre of the valve. Two chloroplasts per cell.

In the light of recent observations, mainly on *C. protuberans* Lauder whose resting spores lack setae (Lechuga-Devéze & Hernández-Becerril, 1988), this section can no longer be regarded as having resting spores with long setae ('two long horns', Lebour, 1930)

22. **Chaetoceros didymus** Ehrenb.

Hernández-Becerril, 1991*b*: 290, figs 1–12.

DISTRIBUTION. 23, 40, 42, 52, 55, 64.

23. **Chaetoceros protuberans** Lauder

Hernández-Becerril, 1991*b*: 290, figs 14–25.

DISTRIBUTION. 4, 7, 8, 13, 23, 41, 44–46, 48.

9. Section **CONSTRICTA** Gran

Cells constricted. Terminal setae thicker than other setae. Chloroplasts one or two. Resting spores with spines on both valves.

24. **Chaetoceros constrictus** Gran

Gran, 1897: 17, pl. 1, figs 11–13, pl. 3, fig. 42; Peragallo & Peragallo, 1897–1908: 491, pl. 134, fig. 5; Hustedt, 1930: 694, fig. 395; Cupp, 1943: 122, fig. 76; Cleve-Euler, 1951: 100, figs 193a–c; Hendey, 1964: 126, pl. 9, fig. 2; Brunel, 1970: 112, pl. 26, figs 1, 2; Rines & Hargraves, 1988: 67, figs 128–130.
Pl. 29, Fig. 6.

LM. Chains straight, relatively short. In girdle view, cells rectangular with sharp corners, showing a conspicuous constriction at girdle zones. Valve face slightly concave, leaving a narrow, lanceolate aperture. Intercalary setae orientated close to the apical axis; terminal setae thicker, directed to the chain axis. Two chloroplasts present in each cell, placed at the valve faces. Measurements: 16–18 μm a.a., 13–15 μm p.a., 2 μm ap. (Pl. 29, Fig. 6)

EM. No observations were made.

DISTRIBUTION. 24, 41, 48, 52.

REMARKS. See next species.

25. **Chaetoceros vanheurcki** Gran

Gran, 1897: 18; Gran & Angst, 1931: 476, fig. 60; Cupp, 1943: 123, fig. 77.
Pl. 29, Figs 4, 5.

LM. Chains straight, of variable length, delicate. In girdle view, cells rectangular, with sharp corners, mantle low. Apertures oblong, narrowing at the centre. Intercalary setae directed close to the apical axis; terminal setae slightly thicker, orientated to the chain axis. Two? chloroplasts present. Measurements: 15–16 μm a.a., 9–12 μm p.a., 2–3 μm ap. (Pl. 29, Fig. 4)

EM. A few observations made using SEM show valves which are not heavily silicified, with clear constrictions near to the girdle (Pl. 29, Fig. 5). There appears to be no rimoportula on intercalary valves and therefore it is assumed that this structure is only located on terminal valves. The intercalary setae arise from the very apex of the valves and fuse immediately to the corresponding sibling valve (Pl. 29, Fig. 5).

DISTRIBUTION. 12, 48.

REMARKS. The two species studied within section *Constricta* have traditionally been separated by the morphology of the resting spores. The resting spores of *C. vanheurckii* have long spines present on the secondary valve, in contrast to *C. constrictus*, which has short-spined resting spores. This is another case where cultures and life cycle studies are required to show whether or not morphological variation is present in these two species, and to define the important morphological characters used to distinguish between them. The direction of the intercalary setae (e.g. in *C. constrictus* they diverge more widely than in *C. vanheurckii*) may not be a character of sufficient taxonomic value to separate them.

10. Section **STENOCINCTA** Ostenf.

Terminal setae curved, thicker than other setae. One chloroplast. Resting spores with numerous spines or processes on both valves.

26. **Chaetoceros affinis** Lauder var. **affinis**

Lauder, 1864: 78, pl. 8, fig. 5; Peragallo & Peragallo, 1897–1908: 478, pl. 129, fig. 3, pl. 130, fig. 3; Hustedt, 1930: 695, fig. 396; Gran & Angst, 1931: 479, fig. 63; Cupp, 1943: 125, figs 78–A(1), 78–A(2); Cleve-Euler, 1951: 105, fig. 212; Hendey, 1964: 127, pl. 18, fig. 2; Okuno, 1956: 186, pl. 1, figs 1–5; Hendey, 1964: 127, pl. 18, fig. 3; Brunel, 1970: 114, pl. 27, fig. 1; Drebes, 1974: 75, fig. 58a; Evensen & Hasle, 1975: 161, figs 46–54; Rines & Hargraves, 1988: 59, figs 113, 114.
The numerous synonyms are listed by Hustedt (1930) and VanLandingham (1968).
Pls 27, 28.

LM. Chains straight, usually long, robust. In girdle view, cells rectangular, slightly constricted at girdle zones. Valve face concave, mantle high, lines of girdle straight; apertures narrow. In valve view, cells elliptical. Terminal and intercalary setae differ: terminal setae thicker, smoothly curved; intercalary setae diverging at an angle of about 15–30° from the apical axis. One chloroplast present at the centre of each cell. Measurements: 18–25 μm a.a., 10–22 μm p.a., 4–6 μm ap. (Pl. 27, Fig. 1)

EM. Short chains (Pl. 27, Fig. 3) and loose valves were observed. The valves are irregularly perforated by poroids and some show a weak costal pattern radiating from the centre (Pl. 27, Figs 2, 4, 5, 7). The rimoportula is centrally located, comprising a flattened, tube-like structure externally with a true labiate structure internally (Pl. 28, Figs 1, 2). The morphology of the terminal and intercalary setae differ. The terminal setae bear regular rows of large spines which run parallel to their main axis, with rows of poroids also running along the same axis, as well as a scattering of relatively larger poroids. These setae are polygonal in cross-section (Pl. 28, Figs 3–5). Intercalary setae have rows of smaller spines and poroids in a spiral pattern, and are rather circular in cross-section (Pl. 27, Fig. 6; Pl. 28, Figs 6, 7).

DISTRIBUTION. 18, 23, 24, 42, 45, 64.

REMARKS. The morphology, as described here, is similar to that recorded by Evensen & Hasle (1975) for *C. affinis* from

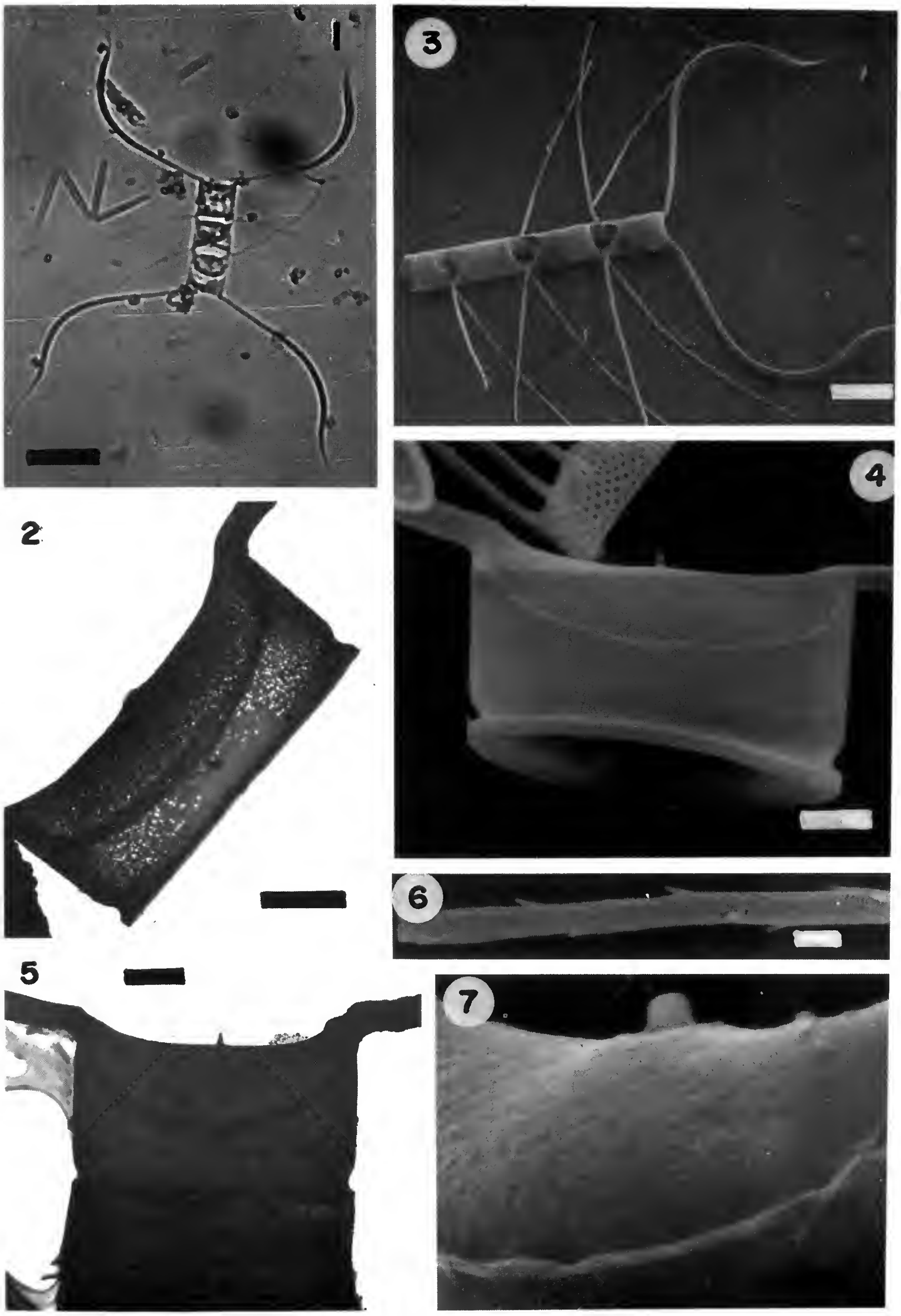

Plate 27 *Chaetoceros affinis* var. *affinis*. Fig. 1: typical chain. LM. Fig. 2: single terminal valve. TEM. Fig. 3: part of chain. Note difference between terminal and intercalary setae. SEM. Fig. 4: terminal valve showing rimoportula. SEM. Fig. 5: terminal valve with rimoportula. TEM. Fig. 6: middle part of intercalary seta. SEM. Fig. 7: valve face (terminal valve) with rimoportula. SEM. Figs 1, 3, bar = 50 µm; Figs 2, 4, 5, bar = 5 µm; Figs 6, 7, bar = 2 µm.

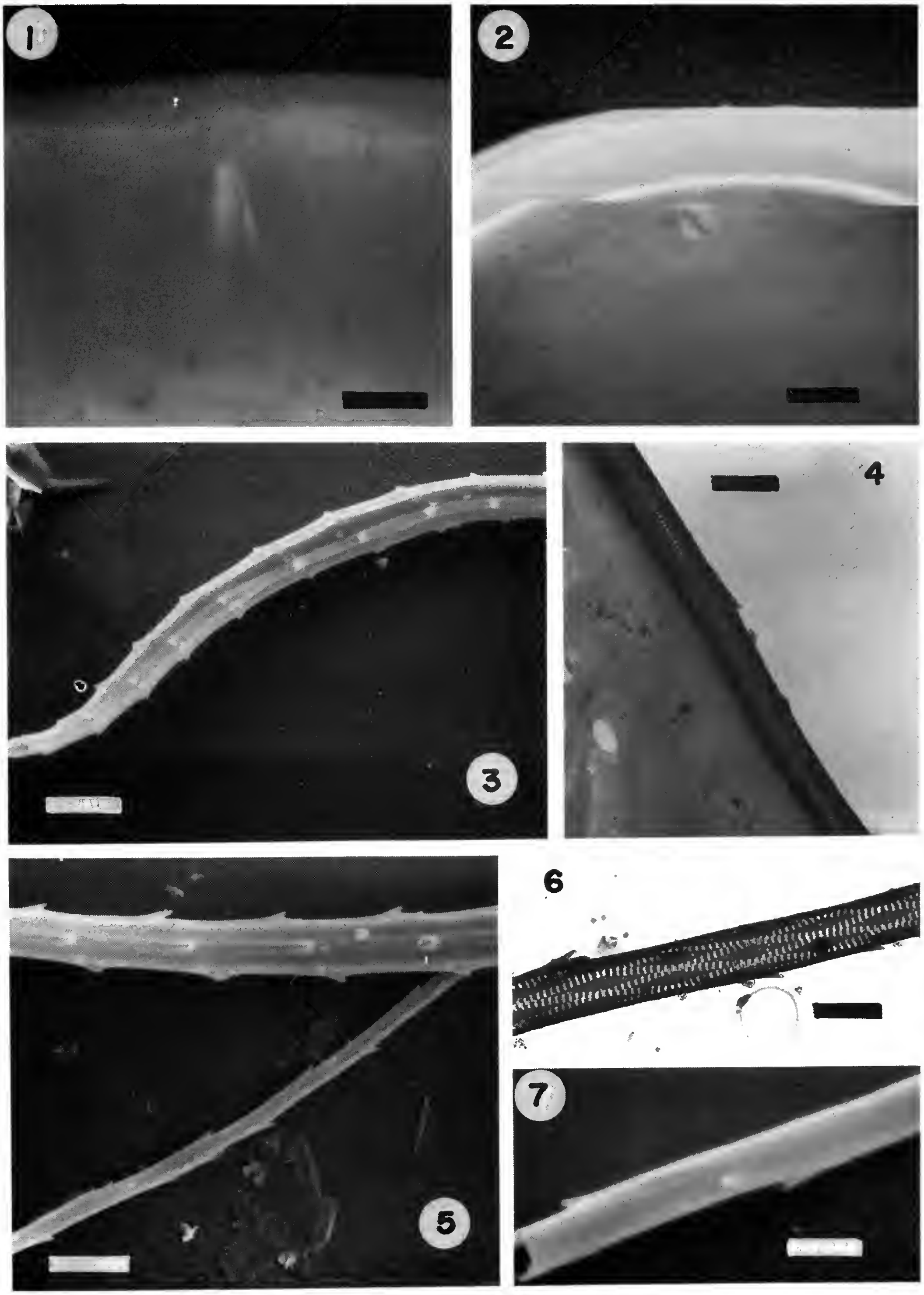

Plate 28 *Chaetoceros affinis* var. *affinis*. Fig. 1: terminal valve with external view of rimoportula. SEM. Fig. 2: internal view of rimoportula. Note labiate structure. SEM. Fig. 3: complete terminal seta. SEM. Fig. 4: middle part of terminal seta. TEM. Fig. 5: terminal seta (above) and intercalary seta (below). SEM. Fig. 6: middle part of intercalary seta. TEM. Fig. 7: intercalary seta close to tip. SEM. Figs 1, 2, 6, 7, bar = 2 μm; Figs 3–5, bar = 5 μm.

Californian cultures. They claimed to have found at least two taxa included in *C. affinis*, as currently delimited.

27. **Chaetoceros affinis** var. **willei** (Gran) Hust.

Hustedt, 1930: 697, fig. 398; Cupp, 1943: 126, fig. 78c; Cleve-Euler, 1951: 105, fig. 213; Brunel, 1970: 116, pl. 27, fig. 2; Drebes, 1974: 75, fig. 58b.

Chaetoceros willei Gran

Gran, 1897: 19, pl. 4, fig. 47; Hendey, 1964: 126, pl. 18, fig. 4.

Pl. 29, Figs 1–3.

LM. Chains straight, short, delicate. In girdle view, cells rectangular, with sharp corners, mantle high; apertures very narrow. In valve view, cells elliptical. Terminal setae thicker than intercalary setae, lying *c*. 25–30° from the chain axis. Intercalary setae arise either parallel to the apical axis or at an angle of 15–25° from this axis. One chloroplast present at the centre of the cell. Measurements: 10–12 μm a.a., 17 μm p.a. (Pl. 29, Fig. 1)

EM. Valves not heavily silicified (Pl. 29, Fig. 2). No details of the costae pattern were observed. The rimoportula is not prominent (as in var. *affinis*) and is presumably located only on terminal valves. The terminal setae are slightly thinner than those of var. *affinis* and have spiral rows of minute spines (Pl. 29, Fig. 3).

DISTRIBUTION. 23.

REMARKS. It is shown here that the morphology of var. *willei* is clearly similar to that of the type (var. *affinis*). This is the reason for considering the former species *C. willei* as a variety of *C. affinis*. However, further studies, especially by EM, are required for those varieties (and synomyms) of *C. affinis* which are not well known (e.g. var. *circinalis* (Meunier) Hust., *C. schuetti* Cleve, etc.). Observations on the resting spores may show significant differences that warrant separation into separate species.

28. **Chaetoceros paradoxus** Cleve

Hernández-Becerril, 1993*b*: 170, figs 1–14.

DISTRIBUTION. 17, 23, 24, 42, 50, 52.

11. Section **LACINIOSA** Ostenf.

Apertures wide. Chloroplasts one or two.

29. **Chaetoceros distans** Cleve

Cleve, 1873*a*: 9, pl. 2, figs 11a, b; Gran & Yendo, 1914: 9, fig. 10; Hustedt, 1921: pl. 337, figs 3–6, pl. 338, fig. 8 (non *Chaetoceros distans* var. sensu Cleve, 1894: 14, pl. 2, fig. 2 = ? *C. laciniosus* F. Schütt).

Pls 30, 31.

LM. Chains straight, of variable length. In girdle view, cells rectangular, with sharp corners. Valve face flat or slightly convex, mantle low, lines of girdle curved (convex); apertures wide. In valve view, cells elliptical or nearly circular. Intercalary setae usually thin, arising from the corners, then diverging almost parallel to the apical axis or curving smoothly towards the chain axis. Terminal setae arise straight, then curve to the chain axis. One chloroplast present at the centre of the cell. Measurements: 20–30 μm a.a., 30–37 μm p.a., 18–24 μm ap. (Pl. 30, Fig. 1)

EM. The chain is delicate (Pl. 30, Fig. 2) and the valves are thinly silicified (Pl. 30, Fig. 5), having the typical pattern of a conspicuous central annulus and radiating costae (Pl. 30, Figs 3, 4, 6), with some poroids between the costae (Pl. 31, Figs 1, 4). The costae join together at apical zones close to the base of the setae, making the valve thicker at this point (Pl. 39, Figs 3, 6). A hyaline rim appears on the edge of some valves (Pl. 30, Figs 4, 6). The rimoportula is a flattened hollow at the centre of the annulus (Pl. 31, Figs 3, 4). The intercalary setae have a rather long base (Pl. 31, Fig. 2), being circular throughout, with small spines in spiral rows and poroids distributed in the wall with no apparent pattern (Pl. 31, Figs 5–8). Terminal setae differ in direction.

DISTRIBUTION. 7, 15, 23, 28, 42, 48, 58, 64.

REMARKS. The question of whether or not this species is conspecific with *C. laciniosus* F. Schütt cannot be answered here, because studies of the life cycle are needed. The general structure appears to be the same (see Evensen & Hasle, 1975 for observations on *C. laciniosus*). One distinctive character is found in the girdle insertion; the lines of girdle in *C. distans* are curved, whereas in *C. laciniosus* they are straight (Gran & Yendo, 1914). Ikari (1928) indicated that 'the basal part' of the setae is shorter in *C. laciniosus* than in *C. distans*. These characters may not be sufficient to separate them, and in that case the name *C. distans* would have priority over *C. laciniosus*. VanLandingham (1968) cited *C. distans* as a synonym of *C. dichaeta*.

30. **Chaetoceros brevis** F. Schütt

Schütt, 1895: 38, pls 4, 5, figs 4a, b; Hustedt, 1930: 707, figs 403a, b; Allen & Cupp, 1935: 141, fig. 70; Cupp, 1943: 129, fig. 82; Cleve-Euler, 1951: 103, figs 205a–c, non d; Hendey, 1964: 127, pl. 9, fig. 5; Brunel, 1970: 120, pl. 27, fig. 3, non pl. 29, figs 1, 2; Navarro, 1982: 309, fig. 12.

Pls 32, 33.

LM. Chains straight, generally short and delicate. In girdle view, cells rectangular or square, with sharp corners. Valve face convex, with a slight protuberance, mantle high, lines of girdle straight; apertures wide. In valve view, cells elliptical, with setae diverging only slightly from the apical axis. Setae thin, delicate, arising from the corners of the valves. Intercalary setae diverge almost parallel to the apical axis at an angle of about 15°, or curve towards the main axis, as do the terminal setae. One large, central chloroplast per cell. Measurements: 15–28 μm a.a., 22–29 μm p.a., 8–10 μm ap. (Pl. 32, Fig. 1)

EM. The chains are linked by fusion of the setae (Pl. 32, Figs 2, 3). The valves are weakly silicified, with the flattened, hollow rimoportula coinciding with the slightly excentric annulus (Pl. 32, Figs 4–6; Pl. 33, Figs 1, 2). The setae are circular in cross-section, with spirals of spines and rows of poroids; terminal and intercalary setae appear to be similar (Pl. 33, Figs 3–5).

DISTRIBUTION. 17, 23.

12. Section **DIADEMA** (Ehrenb.) Ostenf. emend. Gran

One chloroplast. Resting spores with spines on one valve.

31. **Chaetoceros diadema** (Ehrenb.) Gran

Gran, 1905: 84, figs 102a, b; Lebour, 1930: 139, fig. 102; Gran & Angst, 1931: 478, fig. 61; Cleve-Euler, 1951: 103, figs 207a–g; Hendey, 1964: 128, pl. 10, fig. 1; Brunel, 1970: 122, pl.

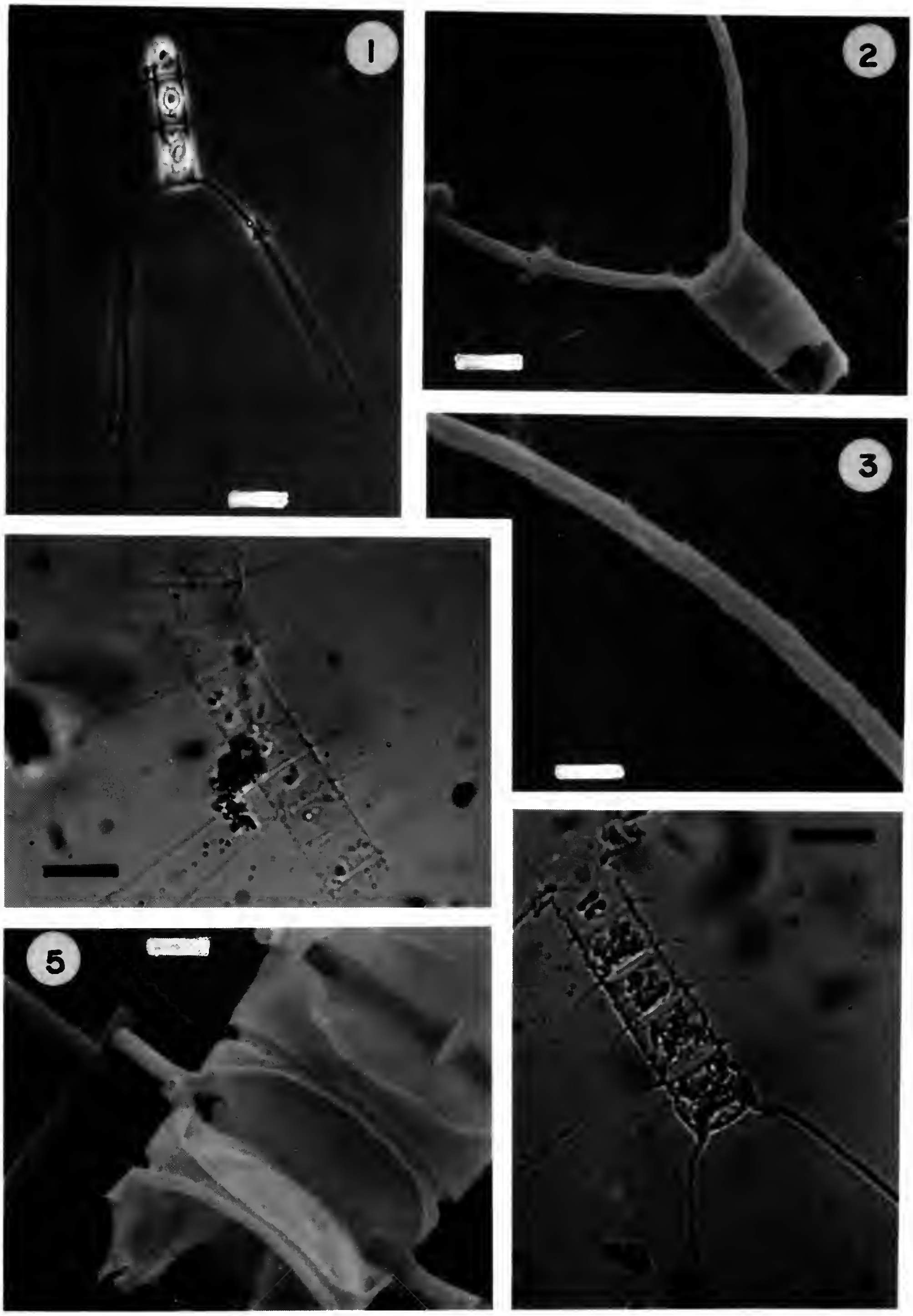

Plate 29 *Chaetoceros affinis* var. *willei* (Figs 1–3), *C. vanheurcki* (Figs 4, 5), and *C. constrictus* (Fig. 6). Fig. 1: terminal part of chain. LM. Fig. 2: terminal valve. SEM. Fig. 3: detail of terminal seta. SEM. Fig. 4: middle part of chain. LM. Fig. 5: sibling valves showing constrictions at girdle zones and broken setae. SEM. Fig. 6: part of chain. LM. Figs 1, 4, 6, bar = 20 µm; Fig. 2, bar = 10 µm; Figs 3, 5, bar = 5 µm.

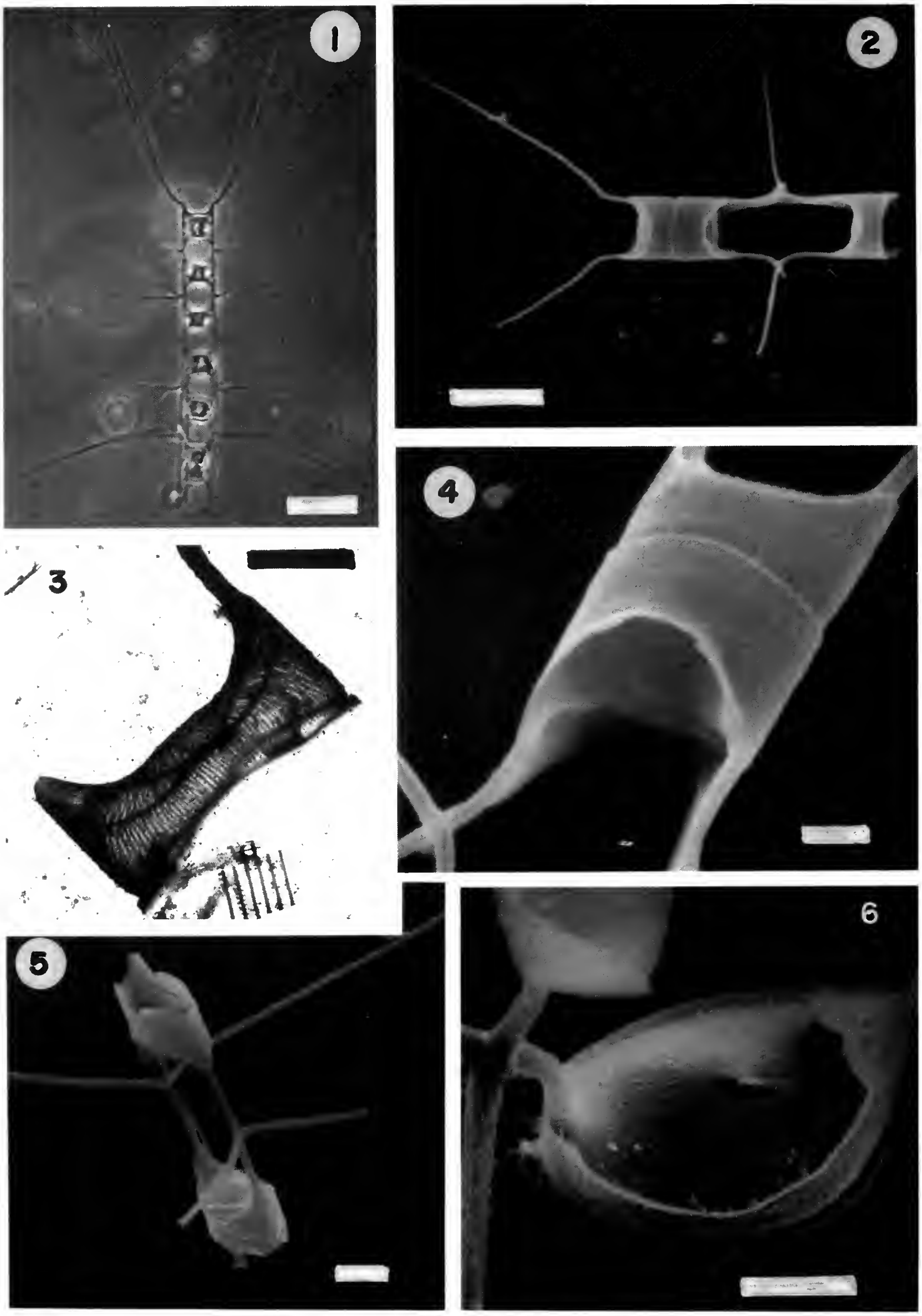

Plate 30 *Chaetoceros distans*. Fig. 1: complete chain. LM. Fig. 2: part of chain. SEM. Fig. 3: single valve. TEM. Fig. 4: cell showing annulus and costae on valve face. SEM. Fig. 5: two sibling valves with rather wide aperture. SEM. Fig. 6: valve face with central annulus and radiating costae. SEM. Fig. 1, bar = 50 μm; Figs 2, 5, bar = 20 μm; Figs 3, 4, 6, bar = 5 μm.

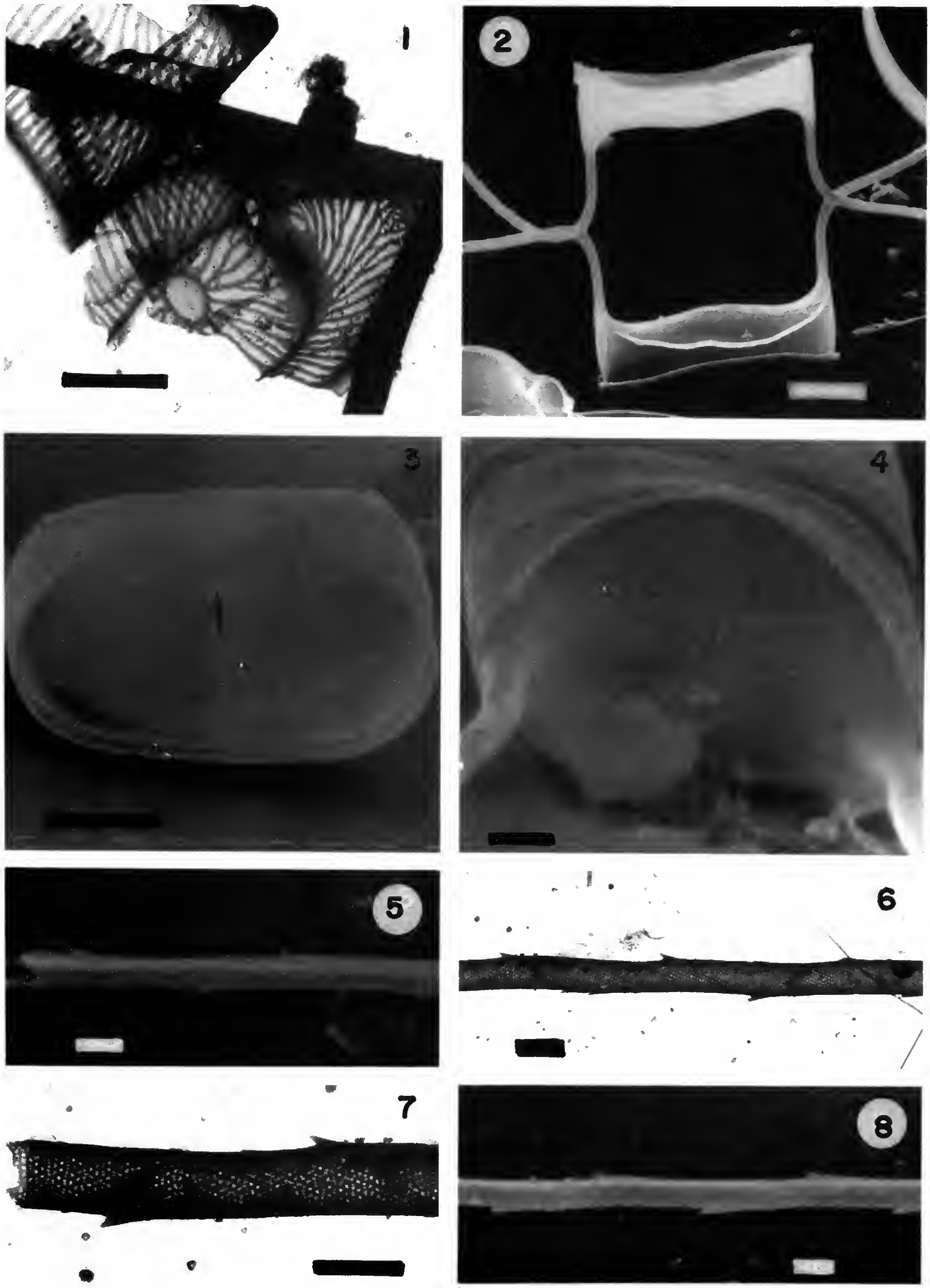

Plate 31 *Chaetoceros distans*. Fig. 1: view of valve with annulus and costae. TEM. Fig. 2: sibling valves showing wide aperture and fusion of setae. SEM. Fig. 3: Internal view of rimoportula (arrow). SEM. Fig. 4: external view of rimoportula. SEM. Fig. 5: middle part of intercalary seta. SEM. Figs 6, 8: middle part of intercalary seta. Note randomly distributed poroids. TEM. Fig. 7: middle part of intercalary seta. SEM. Figs 1, 3, bar = 5 µm; Fig. 2, bar = 10 µm; Figs 4–8, bar = 2 µm.

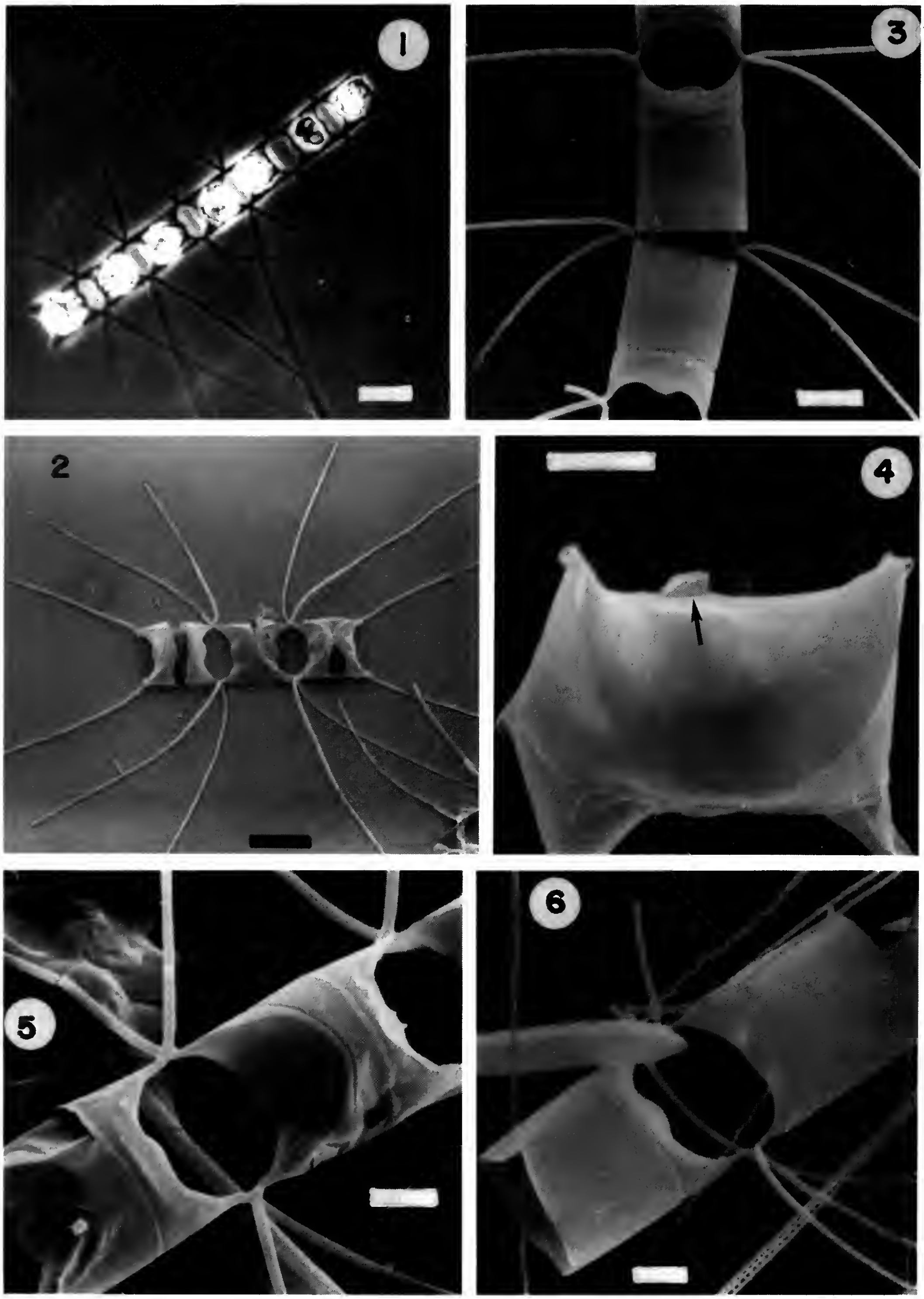

Plate 32 *Chaetoceros brevis*. Fig. 1: typical chain. LM. Fig. 2: short chain. SEM. Fig. 3: part of chain. SEM. Fig. 4: terminal valve showing rimoportula. SEM. Fig. 5: sibling cells showing fusion of setae. SEM. Fig. 6: two sibling valves. SEM. Figs 1, 2, bar = 20 μm; Fig. 3, bar = 10 μm; Figs 4–6, bar = 5 μm.

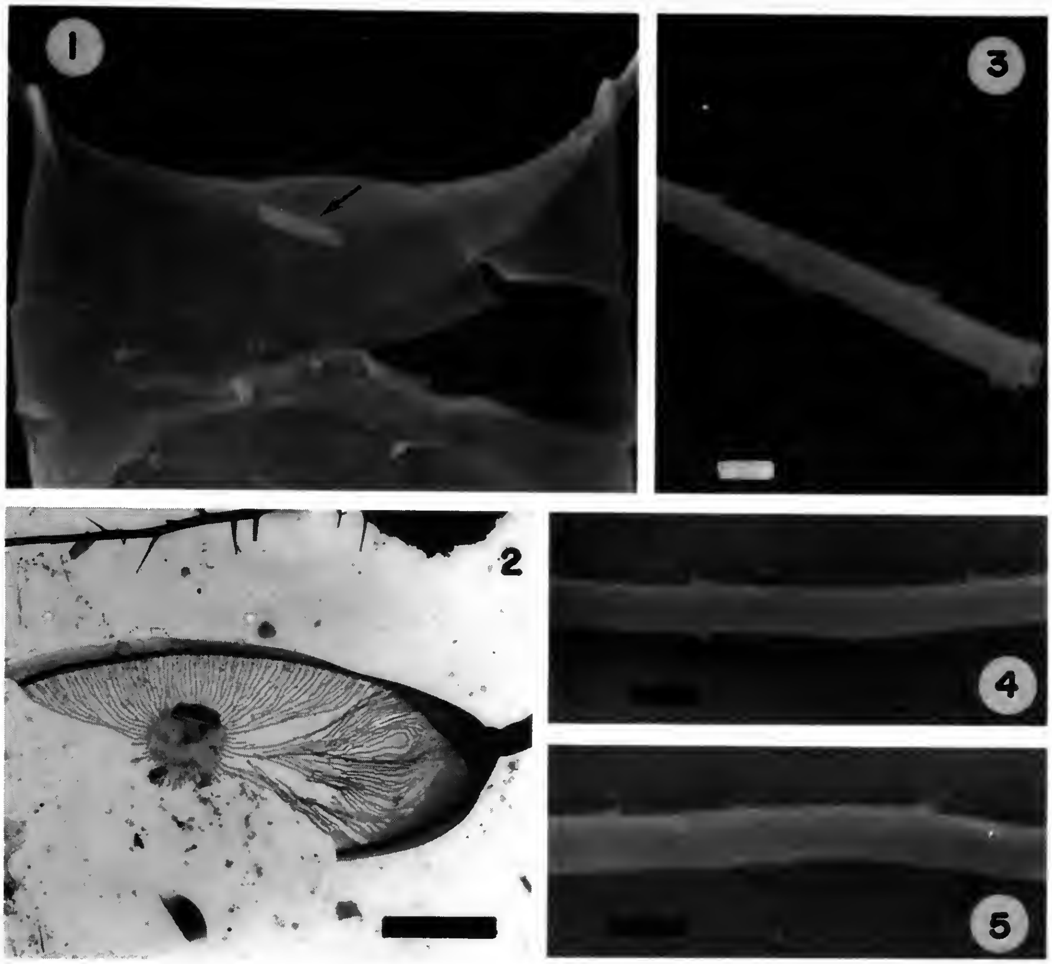

Plate 33 *Chaetoceros brevis*. Fig. 1: terminal valve with excentric rimoportula (arrow). SEM. Fig. 2: terminal valve showing rimoportula. TEM. Fig. 3: detail of seta close to tip. SEM. Fig. 4: middle part of intercalary seta. SEM. Fig. 5: middle part of terminal seta. SEM. Figs 1, 3–5, bar = 2 µm; Fig. 2, bar = 5 µm.

27, fig. 4, pl. 30, figs 1–5; Hargraves, 1972: 249, figs 2A–M, 3–14; Drebes, 1974: 77, figs 60, 61; Rines & Hargraves, 1988: 76, figs 150, 151, 153.

Chaetoceros subsecundus (Grunov) Hust.

Hustedt, 1930: 709, fig. 404; Cupp, 1943: 130, fig. 83.

Chaetoceros diadema Ehrenb. sensu Meunier, 1913: 33, pl. 5, figs 1–9.

Pls 34, 35.

LM. Chains straight or slightly twisted, long, delicate. In girdle view, cells rectangular, with sharp corners. Valve face flat or slightly concave, mantle low, lines of girdle straight; apertures of variable width. Setae thin, arising from close to the corners. Terminal setae thicker, directed to the chain axis; intercalary setae diverging at random. One central chloroplast per cell. Resting spores with one valve flattened, the other concave, bearing many spines at the centre. Measurements: 24–42 µm a.a., 20–38 µm p.a., 5–8 µm ap. (Pl. 34, Figs 1, 2)

EM. The valves are lightly silicified (Pl. 34, Figs 3, 4), with a central or slightly excentric annulus (Pl. 34, Fig. 6) from which weak costae radiate, with no poroids between (Pl. 34, Figs 5, 6; Pl. 35, Figs 1, 4). Small spines which appear to be solid and branched are sometimes found on the valve face (Pl. 34, Figs 3, 5; Pl. 35, Figs 3, 5). Also evident is the presence of a hyaline rim on the valve edge and some snail-like projections on the apical regions of the mantle (Pl. 35, Fig. 2). The rimoportula is a hollow structure with a very short projection to the outside (Pl. 35, Fig. 6). Setae are circular at the base, becoming four-sided distally with spines on the edges. The walls of the setae are regularly perforated by longitudinal rows of poroids; terminal setae do not differ in structure from other setae, but are thicker (Pl. 35, Figs 7, 8). No resting spores were examined.

DISTRIBUTION. 52, 58.

REMARKS. All Hargraves' (1972) observations are confirmed here.

32. **Chaetoceros seiracanthus** Gran

Gran, 1897: 21, pl. 3, figs 39–41; Peragallo & Peragallo, 1897–1908: 479, pl. 133, figs 7, 8; Hustedt, 1930: 711, fig. 405; Gran & Angst, 1931: 478, fig. 62; Cleve-Euler, 1951: 104, fig. 209; Hendey, 1964: 129, pl. 15, fig. 1; Rines & Hargraves, 1988: 92, fig. 199.

LM. Chains straight, fairly short (6 cells). In girdle view, cells nearly rectangular, mantle low, with constrictions at girdle zones. Valve face flat or concave; apertures relatively wide.

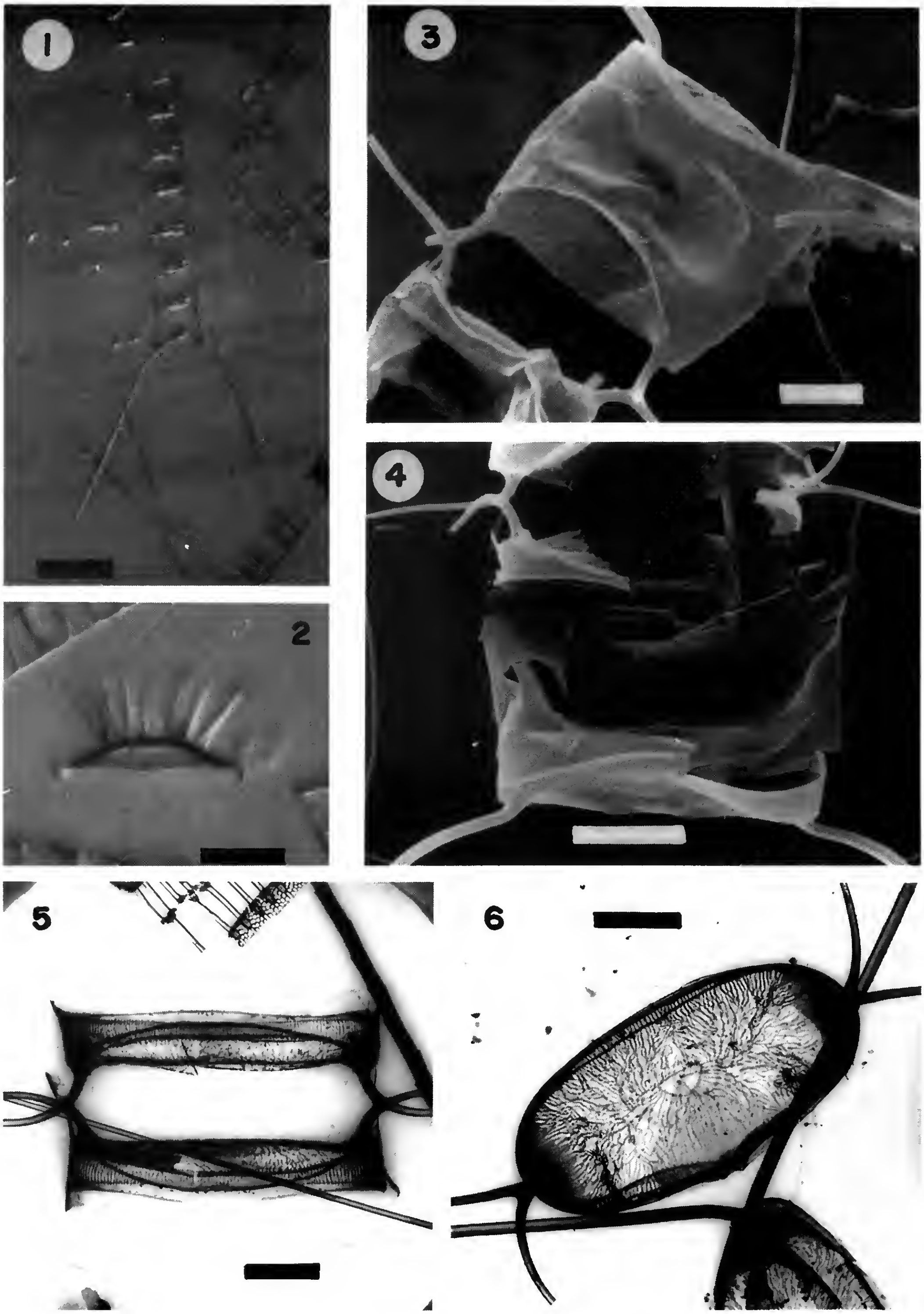

Plate 34 *Chaetoceros diadema*. Fig. 1: part of chain. LM. Fig. 2: typical resting spore. LM. Fig. 3: terminal cell of chain. SEM. Fig. 4: another terminal cell. SEM. Fig. 5: two sibling valves with costae. TEM. Fig. 6: valve view of valve showing central annulus and costae. TEM. Fig. 1, bar = 50 μm; Fig. 2, bar = 20 μm; Figs 3–6, bar = 10 μm.

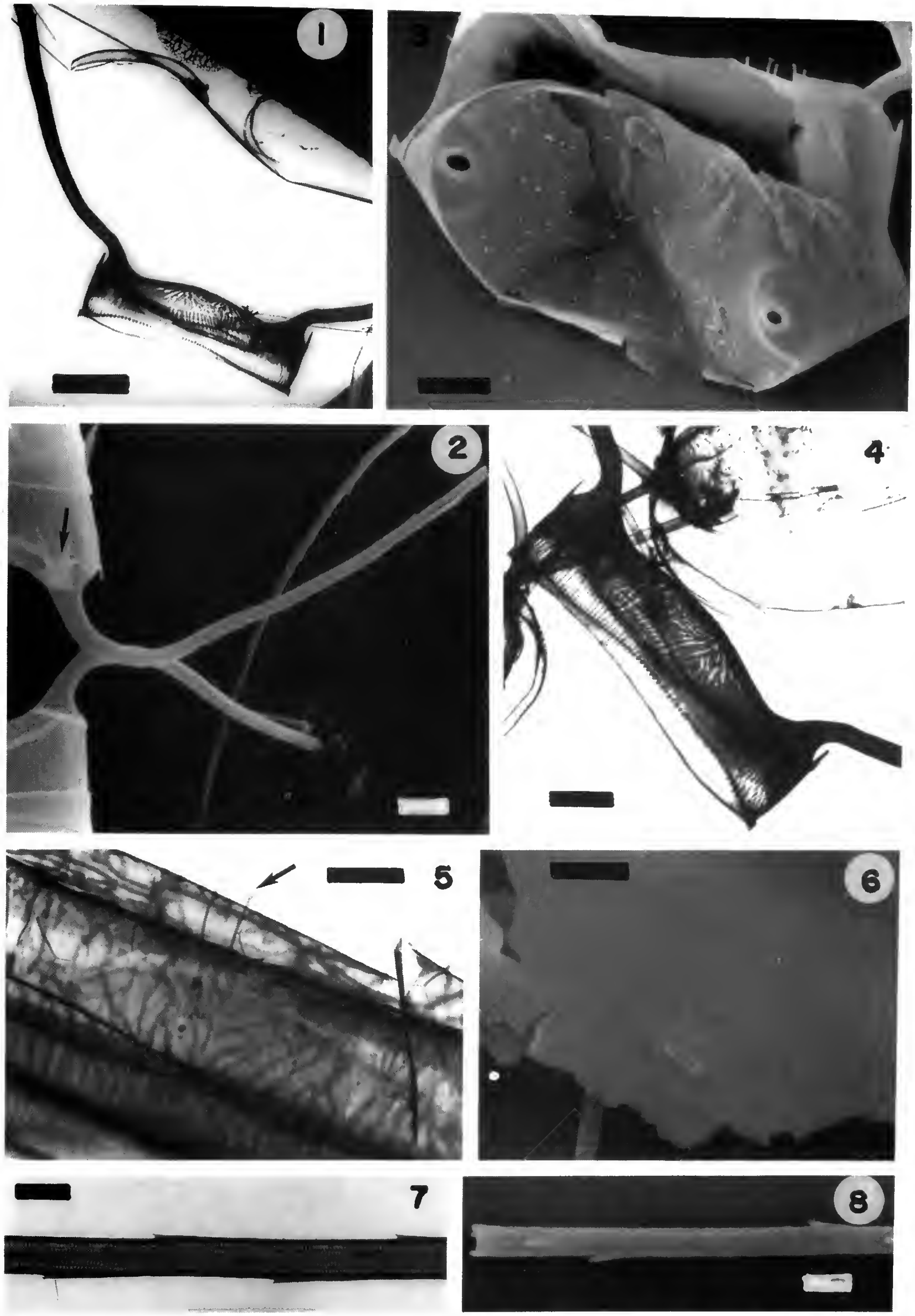

Plate 35 *Chaetoceros diadema*. Fig. 1: terminal valve with snail-like structures in apical regions. TEM. Fig. 2: fusion of sibling setae. Note snail-like structure (arrow). SEM. Fig. 3: valve face showing small spines. SEM. Fig. 4: closer view of terminal valve. TEM. Fig. 5: detail of valve face with some spines (arrow). TEM. Fig. 6: rimoportula at terminal valve. SEM. Fig. 7: middle part of seta. TEM. Fig. 8: middle part of seta. SEM. Fig. 1, bar = 10 µm; Figs 2–4, bar = 5 µm; Figs 5–8, bar = 2 µm.

Sibling cells not touching at the corners, the setae arising from close to the corners and meeting corresponding sibling setae. Setae thin; intercalary setae diverging either randomly or in parallel to the apical axis; terminal setae with similar morphology, directed towards the chain axis. One chloroplast per cell. Measurement: 14–19 µm a.a., 12–17 µm p.a., 4–8 µm ap.

EM. No observations were made.

DISTRIBUTION. 23.

13. Section **DIVERSA** Ostenf.

Short chains. Intercalary setae of two types, as in section *Compressa*, but special setae not twisted. One chloroplast. Resting spores unknown.

33. Chaetoceros diversus Cleve

Cleve, 1873*a*: 9, pl. 2, fig. 12; Peragallo & Peragallo, 1897–1908: 487, pl. 135, fig. 4; Hustedt, 1930: 716, fig. 409; Allen & Cupp, 1935: 142, fig. 71; Cupp, 1943: 132, fig. 87; Subrahmanyan, 1946: 142, figs 241–243, non 235; Cleve-Euler, 1951: 101, fig. 197; Hendey, 1964: 130, pl. 17, fig. 4; Navarro, 1982: 312, figs 26, 27; Desikachary & Prema, 1987: pl. 257, figs 1, 2, 4, 6, pl. 262, figs 1, 2; Moreno et al., 1993: 420, figs 2–28.

Chaetoceros laevis Leud.-Fortm.

Leuduger-Fortmorel, 1892: 38, pl. 6, fig. 2.

Pls 36–39.

LM. Chains straight, short. In girdle view, cells rectangular or nearly square. Valve face slightly concave, mantle high, lines of girdle straight; apertures very narrow. In valve view, cells elliptical. Different kinds of setae present; intercalary setae thin and short; terminal setae thicker, directed to the chain axis. Special intercalary setae curve strongly, thicker and longer than other setae. One large chloroplast present in the centre of the cell. Measurements: 10–22 µm a.a., 7–19 µm p.a., 2 µm ap. (Pl. 36, Fig. 1; Pl. 38, Fig. 1)

EM. The chains are short and joined by fusion of the setae (Pl. 36, Figs 2, 3; Pl. 38, Figs 2, 3). The same general pattern of morphology as shown by most species belonging to subgenus *Hyalochaete* is present in this species, although there is no clear annulus (Pl. 37, Figs 2, 3). The costae become apparent and slightly thicker close to the mantle edge (Pl. 37, Fig. 3; Pl. 38, Fig. 6). The apertures are sometimes covered by a thin wall and a hyaline rim is found on the edge of some valves (Pl. 36, Fig. 4; Pl. 38, Figs 4, 6). One small, circular rimoportula is commonly located at the centre of terminal valves; this is short, hollow, and slightly projected to the outside (Pl. 37, Fig. 2; Pl. 38, Fig. 5). Girdle bands show no costae, but their walls are randomly perforated by small poroids (Pl. 38, Figs 4, 6). All setae appear to have essentially the same structure: circular at the base (Pl. 36, Figs 5, 6) and polygonal distally, with spines running in rows and the walls perforated by poroids arranged in rows (Pl. 37, Figs 4–7; Pl. 39, Figs 3–7). Other, bigger poroids are randomly distributed (Pl. 37, Figs 4, 7). Special setae are also polygonal, but much thicker (Pl. 37, Figs 4, 5, 8; Pl. 39, Figs 4, 6, 7).

DISTRIBUTION. 17, 22, 23, 48, 51.

REMARKS. Many authors (e.g. Hustedt, 1930; Cupp, 1943) have discussed the identity of *C. laevis* and its relationship to *C. diversus*. The main differences between the two taxa are the direction and structure of the setae, but apparently these characters are very variable (Moreno et al., 1993). Resting spores may provide new evidence for maintaining the two taxa as separate species, but none has yet been reported. On the basis of my observations and taking into account a recent report (Moreno et al., 1993) where no significant differences in structure between the species were seen, *C. laevis* is considered here as a synonym of *C. diversus*. Another closely related species is *C. rudis* Leud.-Fortm., which was poorly described and illustrated.

34. Chaetoceros messanensis Castrac.

Castracane, 1875: 394, pl. 6, fig. 1; Peragallo & Peragallo, 1897–1908: 488, pl. 129, fig. 1; Hustedt, 1930: 718, fig. 410; Hendey, 1937: 304; Cupp, 1943: 133, figs 89A–B; Cleve-Euler, 1951: 101, figs 198a–c; Hendey, 1964: 129, pl. 12, fig. 3; Okuno, 1970: pl. 654; Evensen & Hasle, 1975: 162, figs 70–74; Desikachary & Prema, 1987: pl. 261, figs 1, 4, 5.

Chaetoceros furca Cleve

Cleve, 1897: 21, pl. 1, fig. 10.

Pls 40, 41.

LM. Chains straight, usually short, but sometimes long. In girdle view, cells rectangular, with sharp corners. Valve face flat or slightly concave, mantle low, lines of girdle straight; apertures wide. In valve view, cells elliptical. Setae of three different kinds; terminal setae thin and short, one curved strongly, the other diverging widely; common intercalary setae also thin and slightly diverging; special setae thicker, fusing two sibling setae together for a considerable distance from the chain, then diverging opposite each other, bearing minute spines at the ends. One central chloroplast present. Measurements: 20–32 µm a.a., 12–18 µm p.a., 5–12 µm ap. (Pl. 40, Fig. 1)

EM. Most of the chains observed were broken (Pl. 40, Figs 2, 3). The valves have a pattern of strong, sometimes branched costae which radiates from the thickened centre and may be parallel to the apical axis (Pl. 40, Figs 4, 5; Pl. 41, Fig. 2). Two or three rows of poroids are evident between the costae. Hyaline rims may be found on the edge of some valves (Pl. 41, Figs 1, 2). The rimoportula is excentric and consists of a flattened and elongated tube with a short external projection (Pl. 41, Figs 1, 3). Terminal and intercalary setae (common type) are circular throughout, with spirals of spines and poroids. Special setae appear to be more heavily silicified, but like the other setae are circular and are somewhat sparsely perforated by randomly spaced poroids (Pl. 41, Fig. 7). When the setae finally diverge, they bear spines in spirals, with both relatively large and small poroids scattered at random (Pl. 41, Figs 4–6). Their tips appear to be open to the outside.

DISTRIBUTION. 40, 42, 44, 45, 48, 65.

REMARKS. All previous observations made by Okuno (1970) and Evensen & Hasle (1975) are confirmed here and no additional new findings are reported. The position of this species within section *Diversa* should, however, be considered carefully because *C. messanensis* appears to be distinct from *C. diversus*; the latter develops special setae not only in intercalary valves, but also in terminal valves, and the terminal valve in *C. messanensis* shows a rather large external projection of the rimoportula and a pattern of costae, lacking in *C. diversus*.

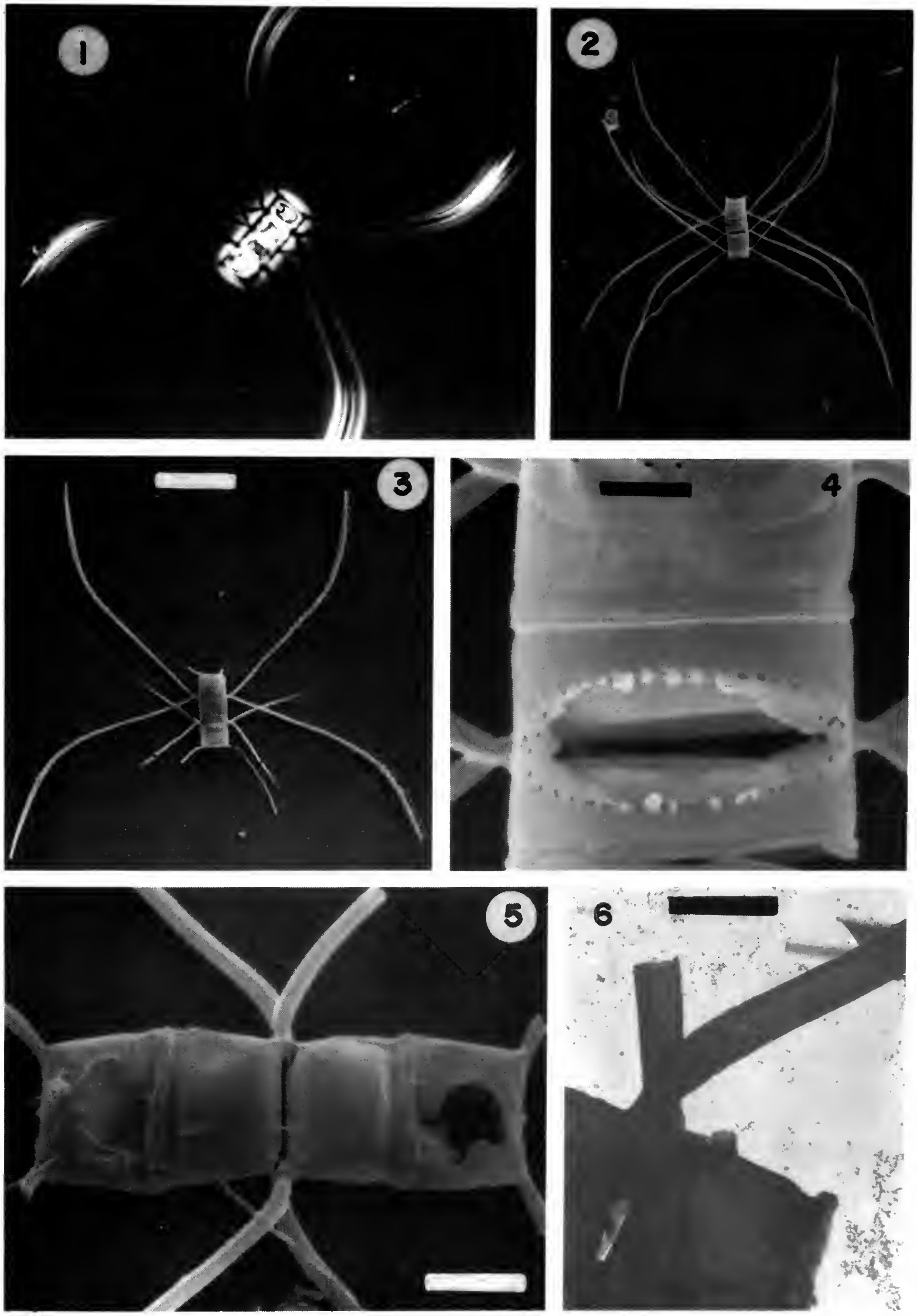

Plate 36 *Chaetoceros diversus*. Fig. 1: complete chain. LM. Figs 2, 3: complete chains. SEM. Fig. 4: cell in girdle view. Note partially occluded aperture. SEM. Fig. 5: chain of two cells. SEM. Fig. 6: detail of fusion of setae. TEM. Fig. 1, bar = 20 µm; Figs 2, 3, bar = 50 µm; Figs 4, 6, bar = 5 µm; Fig. 5, bar = 10 µm.

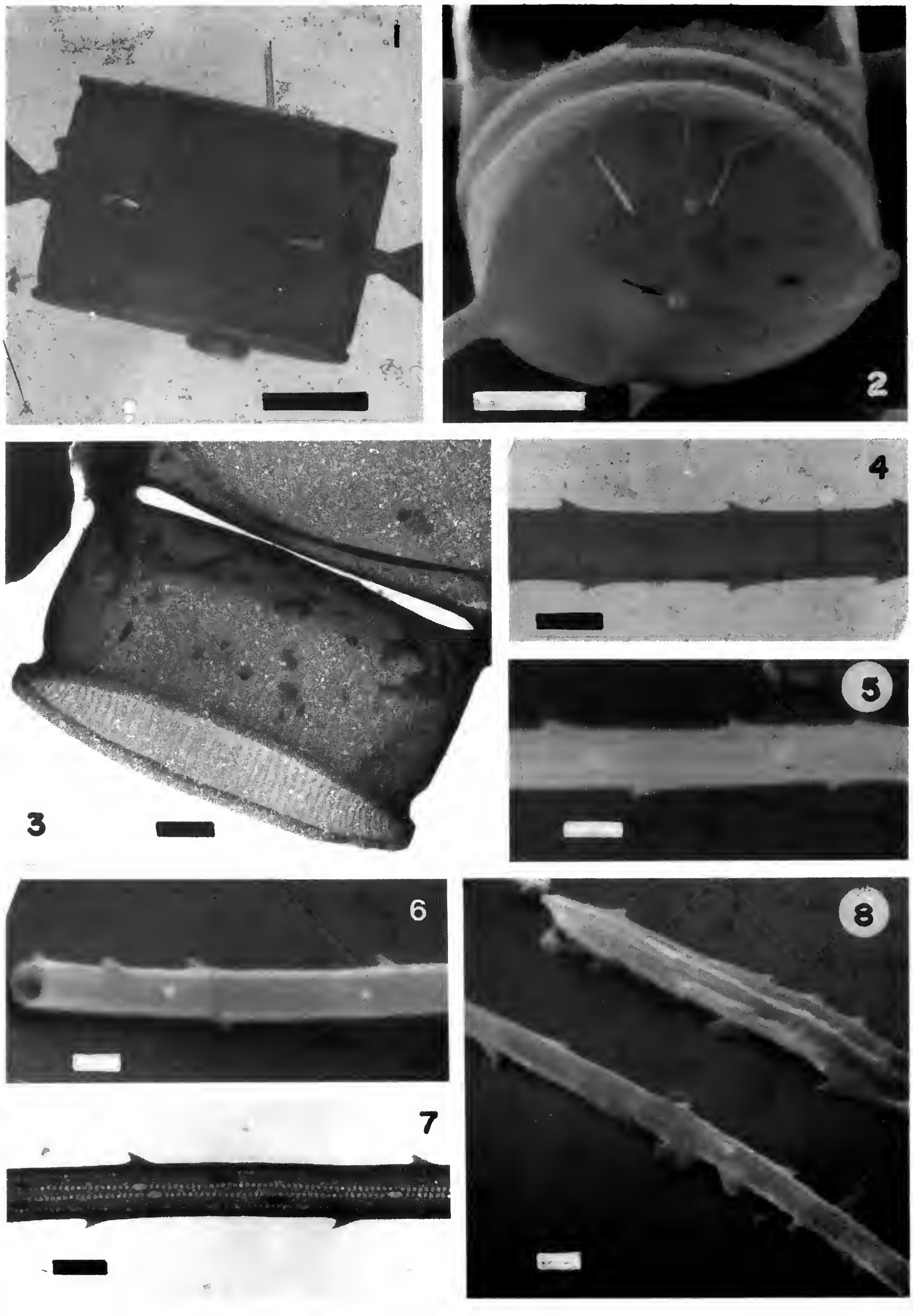

Plate 37 *Chaetoceros diversus*. Fig. 1: sibling valves showing very narrow aperture. TEM. Fig. 2: terminal valve showing rimoportula (arrow). SEM. Fig. 3: valve showing weak costae. TEM. Fig. 4: middle part of special seta. TEM. Fig. 5: middle part of special seta. SEM. Fig. 6: seta close to tip. SEM. Fig. 7: seta close to tip. TEM. Fig. 8: special seta (above) and intercalary seta (below). SEM. Figs 1, 2, bar = 5 µm; Figs 3–8, bar = 2 µm.

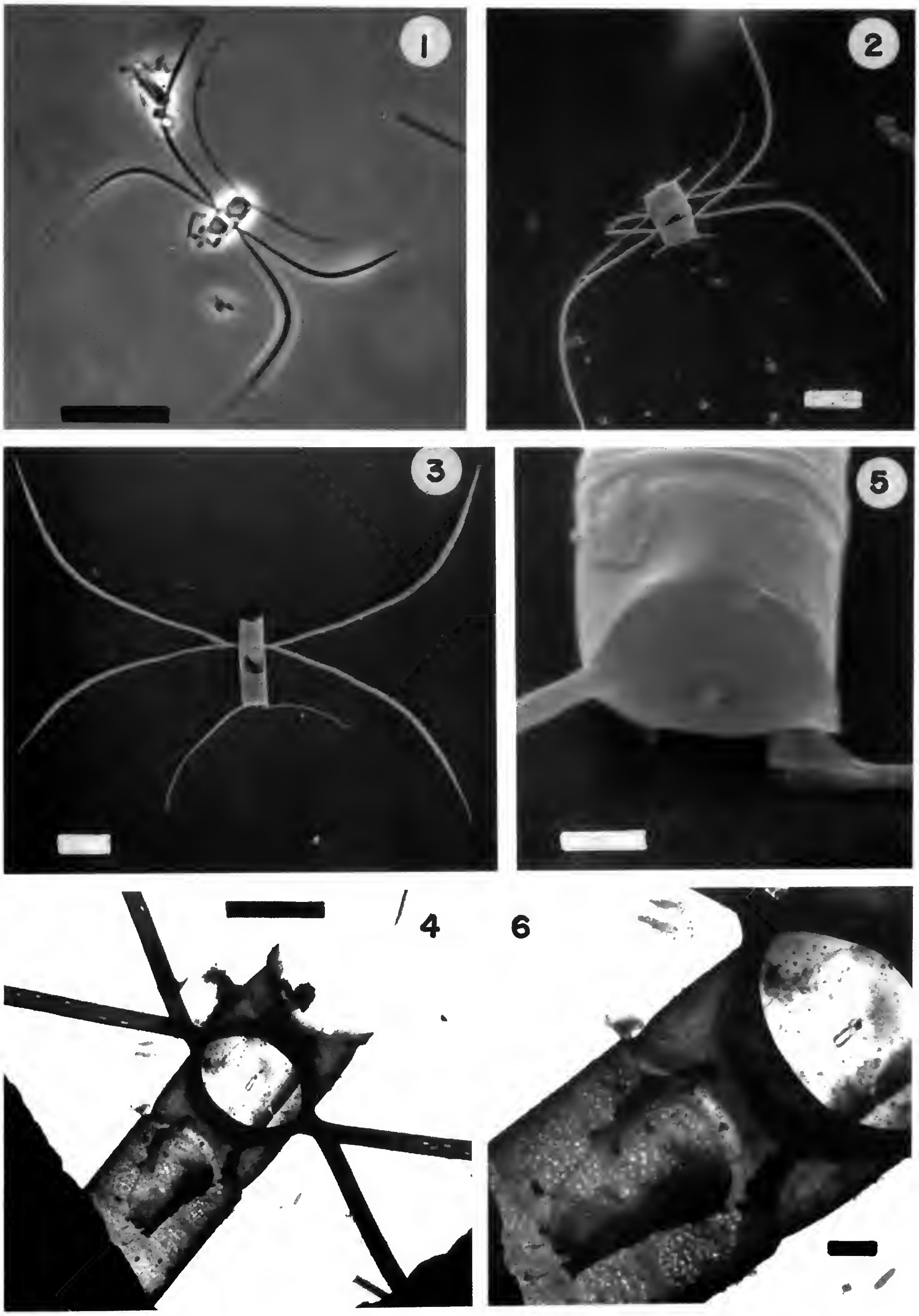

Plate 38 *Chaetoceros diversus*. Fig. 1: typical chain. LM. Figs 2, 3: two chains. SEM. Fig. 4: two sibling valves with aperture covered by thin wall. TEM. Fig. 5: terminal valve with rimoportula. SEM. Fig. 6: detail of valve and girdle bands. TEM. Fig. 1, bar = 50 µm; Figs 2, 3, bar = 20 µm; Fig. 4, bar = 10 µm; Figs 5, 6, bar = 5 µm.

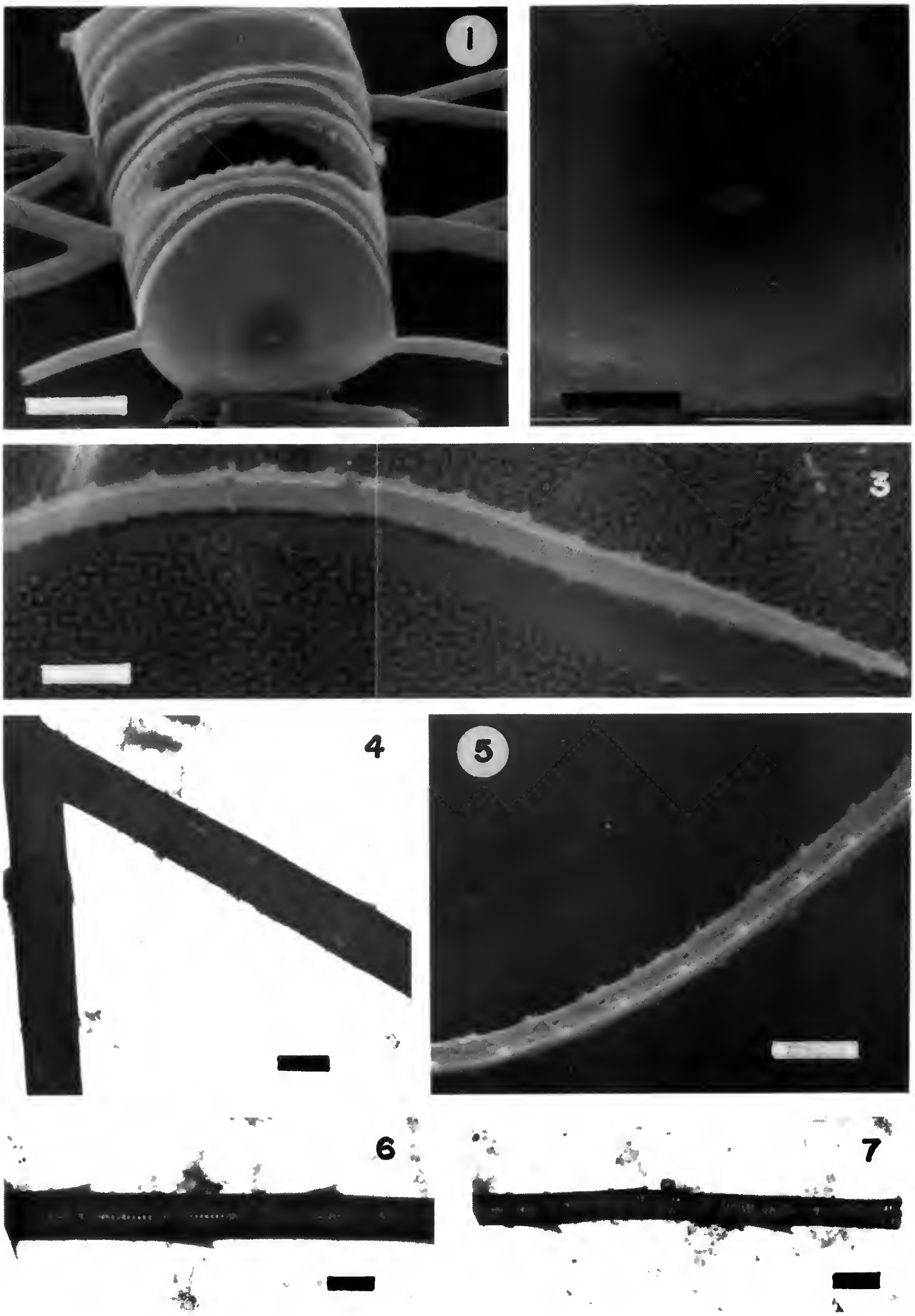

Plate 39 *Chaetoceros diversus.* Fig. 1: part of chain showing rimoportula. SEM. Fig. 2: detail of annulus and rimoportula. SEM. Fig. 3: complete special seta. SEM. Fig. 4: base of special seta. TEM. Fig. 5: view of special seta. SEM. Fig. 6: middle part of special seta. TEM. Fig. 7: special seta close to tip. SEM. Figs 1, 3, 5, bar = 5 μm; Figs 2, 4, 6, 7, bar = 2 μm.

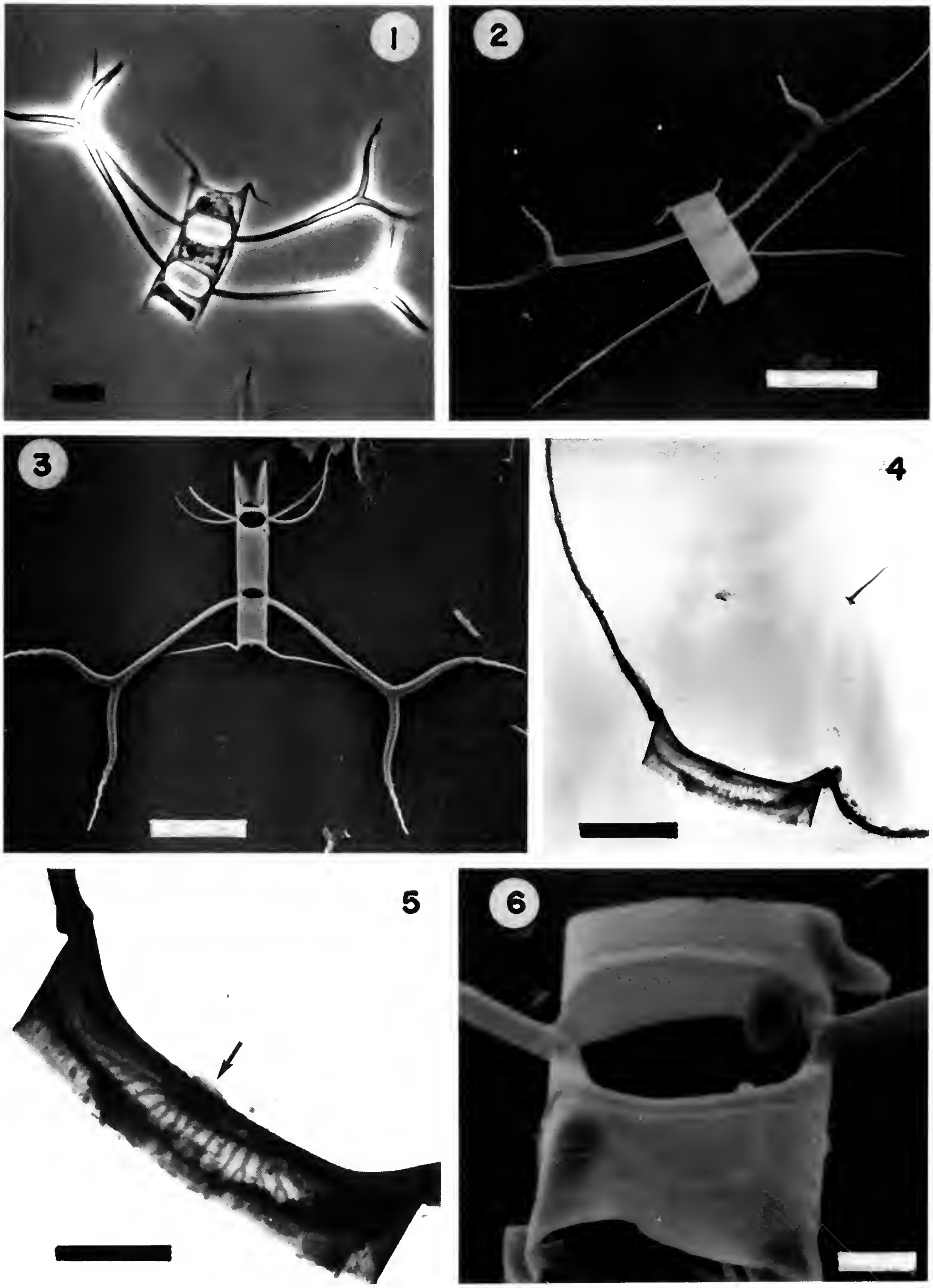

Plate 40 *Chaetoceros messanensis*. Fig. 1: view of typical chain. LM. Fig. 2: part of chain. SEM. Fig. 3: part of chain. Note special setae. SEM. Fig. 4: terminal valve. Note direction of terminal setae. TEM. Fig. 5: detail of terminal valve with rimoportula (arrow). TEM. Fig. 6: sibling valves, the lower showing several girdle bands. SEM. Fig. 1, bar = 20 µm; Figs 2, 3, bar = 50 µm; Fig. 4, bar = 10 µm; Figs 5, 6, bar = 5 µm.

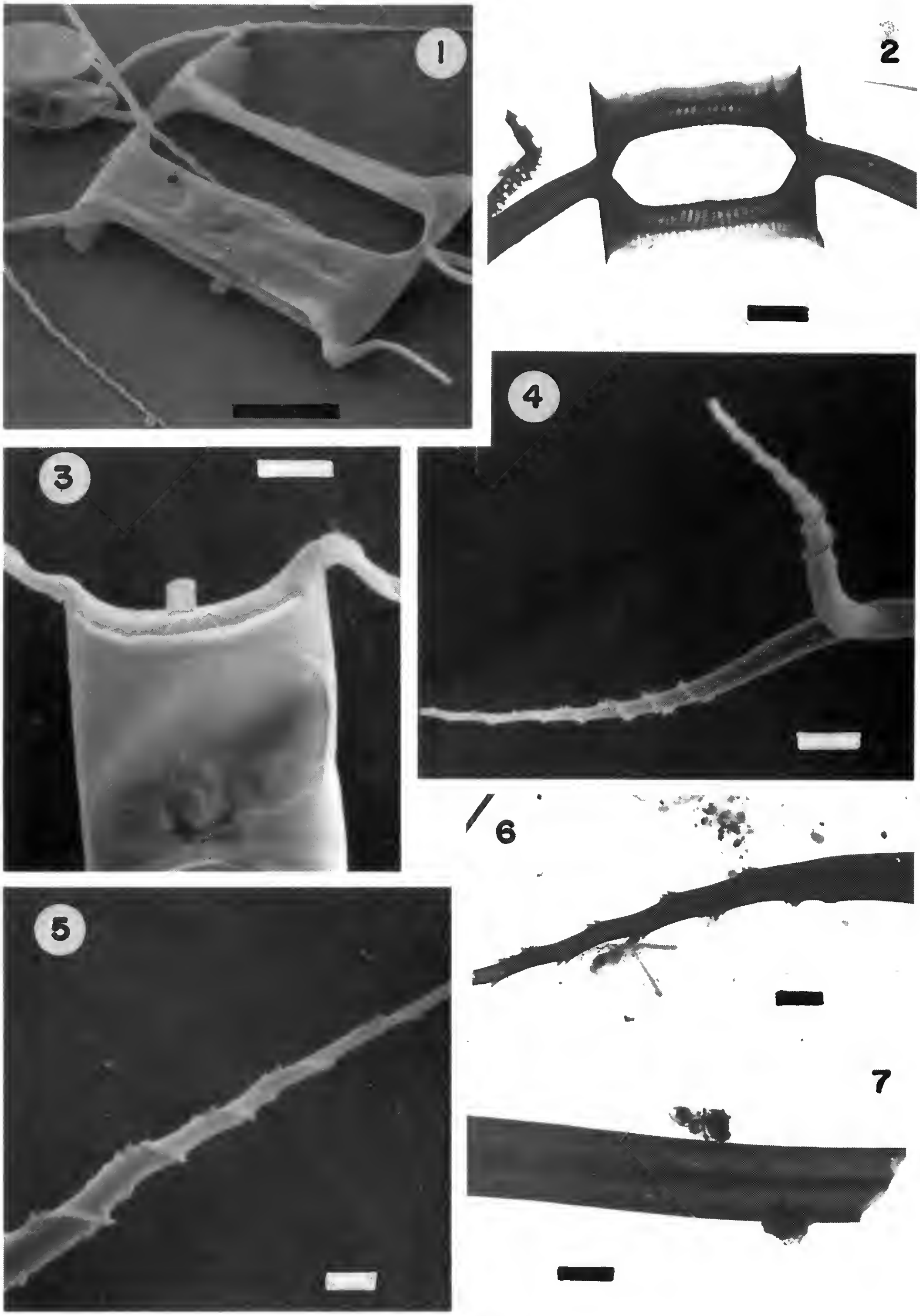

Plate 41 *Chaetoceros messanensis*. Fig. 1: terminal valve showing flattened, tubular rimoportula. SEM. Fig. 2: sibling valves with costae. TEM. Fig. 3: terminal valve with prominent rimoportula. SEM. Fig. 4: special setae as they diverge. SEM. Fig. 5: detail of special seta. Note spirals of spines. SEM. Fig. 6: tip of special seta (apparently open, or broken?). TEM. Fig. 7: middle part of special seta. The two sibling setae are fused together. TEM. Fig. 1, bar = 10 μm; Figs 2–4, bar = 5 μm; Figs 5–7, bar = 2 μm.

14. Section **BREVICATENATA** Gran

Small forms. Chains straight. Terminal setae thinner than other setae. Chloroplasts one or two.

35. **Chaetoceros pseudocrinitus** Ostenf.

Ostenfeld, 1901: 300, fig. 11; Hustedt, 1930: 733, fig. 422; Gran & Angst, 1931: 480, fig. 64; Hendey, 1937: 304; Cleve-Euler, 1951: 106, figs 217a–c; Hendey, 1964: 132, pl. 14, fig. 2; Rines & Hargraves, 1988: 87, figs 174, 177, 219.

LM. Chains straight or somewhat twisted, fairly long. In girdle view, cells rectangular, with sharp corners touching sibling valves. Valve face flat or convex; apertures very narrow. Intercalary setae very thin, arising at random from the valve corners; terminal setae essentially similar, but longer and orientated to the chain axis. One chloroplast per cell. No resting spores seen. Measurements: 10–12 µm a.a., 9–12 µm p.a., 1–2 µm ap.

EM. No observations were made.

DISTRIBUTION. 53.

REMARKS. Brunel (1970) has already pointed out the difficulty in identifying the species commonly placed in section *Brevicatenata*, and the poor present state of our knowledge of them. Brunel (1970) and Rines & Hargraves (1988) discussed the close relationship between *C. crinitus* F. Schütt, *C. ingolfianus* Ostenf., and *C. pseudocrinitus*. Furthermore, Rines & Hargraves (1988) considered *C. ingolfianus* to be merely a synonym of *C. pseudocrinitus*. Investigations of their life cycle, as well as observations using EM, are strongly recommended to elucidate this problem.

36. **Chaetoceros wighami** Brightw.

Brightwell, 1856: 108, pl. 7, figs 19–36; Peragallo & Peragallo, 1897–1908: 491, pl. 134, fig. 4; Hustedt, 1930: 724, fig. 414; Cupp, 1943: 136, fig. 91; Cleve-Euler, 1951: 107, figs 221a–c; Hendey, 1964: 131, pl. 11, fig. 3.
Pl. 43, Fig. 6.

LM. Chains straight, short, delicate. In girdle view, cells rectangular, the pervalvar axis being, corners sharp. Valve face concave, mantle low; apertures narrow, elliptical or oblong. In valve view, cells elliptical. Intercalary setae thin, long, emerging from the corners of the valves and diverging following the apical axis; terminal setae curving smoothly at the base, then directed to the chain axis. One chloroplast per cell. Measurements: 6–8 µm a.a., 12–17 µm p.a., 3–4 µm ap. (Pl. 43, Fig. 6)

EM. No observations were made.

DISTRIBUTION. 51.

REMARKS. Rines & Hargraves (1988) have discussed previous claims about the close relationship between *C. wighami* and *C. amanita* A. Cleve, the latter being a fresh- or brackish-water form.

15. Section **CURVISETA** Ostenf. emend. Gran

Chains generally curved. Setae generally directed to the same side. One chloroplast.

37. **Chaetoceros curvisetus** Cleve

Cleve, 1889: 55; Peragallo & Peragallo, 1897–1908: 479, pl. 129, figs 4–6; Hustedt, 1930: 737, fig. 428; Cupp, 1943: 137, fig. 93; Subrahmanyan, 1946: 143, figs 238, 244–246; Cleve-Euler, 1951: 100, figs 194a–d; Hendey, 1964: 133, pl. 17, fig. 6; Drebes, 1974: 79, figs 63a, b; Evensen & Hasle, 1975: 159, figs 23–26; Navarro, 1982: 309, figs 18, 19; Desikachary et al., 1987: pl. 502, fig. 7; Rines & Hargraves, 1988: 71, figs 141, 142 (non *Chaetoceros curvisetus* Cleve sensu Hustedt, 1920: pl. 327, figs 9, 10 = *C. pseudocurvisetus* L. Mangin).
Chaetoceros secundus Cleve sensu Gran & Angst, 1931: 481, fig. 66.
Pls 42, 43, Figs 1–5.

LM. Chains curved, usually long. In girdle view, cells rectangular, with sharp corners. Valve face concave, mantle low, lines of girdle straight; apertures wide. In valve view, cells nearly circular to elliptical, the setae curving to the same direction. Intercalary setae rather thin, arising from the valve corners and diverging in the apical plane transapically; terminal setae slightly shorter, directed to the chain axis. One central chloroplast present. Resting spores spineless, with one valve flat, the other convex. Measurements: 15–22 µm a.a., 19–25 µm p.a., 12–17 µm ap. (Pl. 42, Figs 1, 2)

EM. The chains are linked by fusion of the setae (Pl. 42, Figs 3, 4). The valve pattern follows the general morphology for *Hyalochaete* species (Pl. 42, Figs 4–6; Pl. 43, Fig. 2), but in this species there is also a hyaline rim on the valve edge (Pl. 42, Fig. 5). The annulus may be central or excentric (Pl. 43, Figs 1, 2). The rimoportula is a flattened, hollow structure, located near the centre of the annulus (Pl. 43, Fig. 3). The setae bear a spiral pattern of spines and rows of poroids in the wall, as well as some scattered, larger poroids (Pl. 43, Figs 4, 5). Although terminal setae have the same morphology as intercalary setae, they are slightly twisted at the base.

DISTRIBUTION. 23, 42, 48, 50, 64.

REMARKS. All previous observations (Evensen & Hasle, 1975) on this species are confirmed here.

38. **Chaetoceros pseudocurvisetus** L. Mangin

Mangin, 1910: 350, figs 3II, 4II; Gran & Yendo, 1914: 22, figs 12a, b; Hustedt, 1930: 739, fig. 427; Allen & Cupp, 1935: 142, fig. 73; Cupp, 1943: 138, fig. 94; Hendey, 1964: 134, pl. 18, fig. 1; Fryxell, 1978: 68, figs 22–26; Navarro, 1982: 316, figs 37–39.
Pls 44, 45.

LM. Chains curved, short or long. In girdle view, cells rectangular, with smooth corners and processes near the corners connecting sibling cells in the chain. Valve face concave, mantle low, lines of girdle straight or slightly concave; main apertures narrow, elliptical, with two small apertures present at corners beside the main aperture. In valve view, cells nearly circular to elliptical, the setae parallel and curving in the same direction or curving in opposite directions. Setae generally thin, arising from the valve corners and curving transapically (girdle view); terminal setae differ in their direction, diverging to the chain axis. One large, central chloroplast present. Measurements: 13–21 µm a.a., 16–22 µm p.a., 4–6 µm ap. (Pl. 44, Figs 1, 2)

EM. Partially broken chains were observed (Pl. 44, Figs 3, 5). The valves are not heavily silicified and have the same general pattern described earlier (e.g. for *C. decipiens*). However, in this

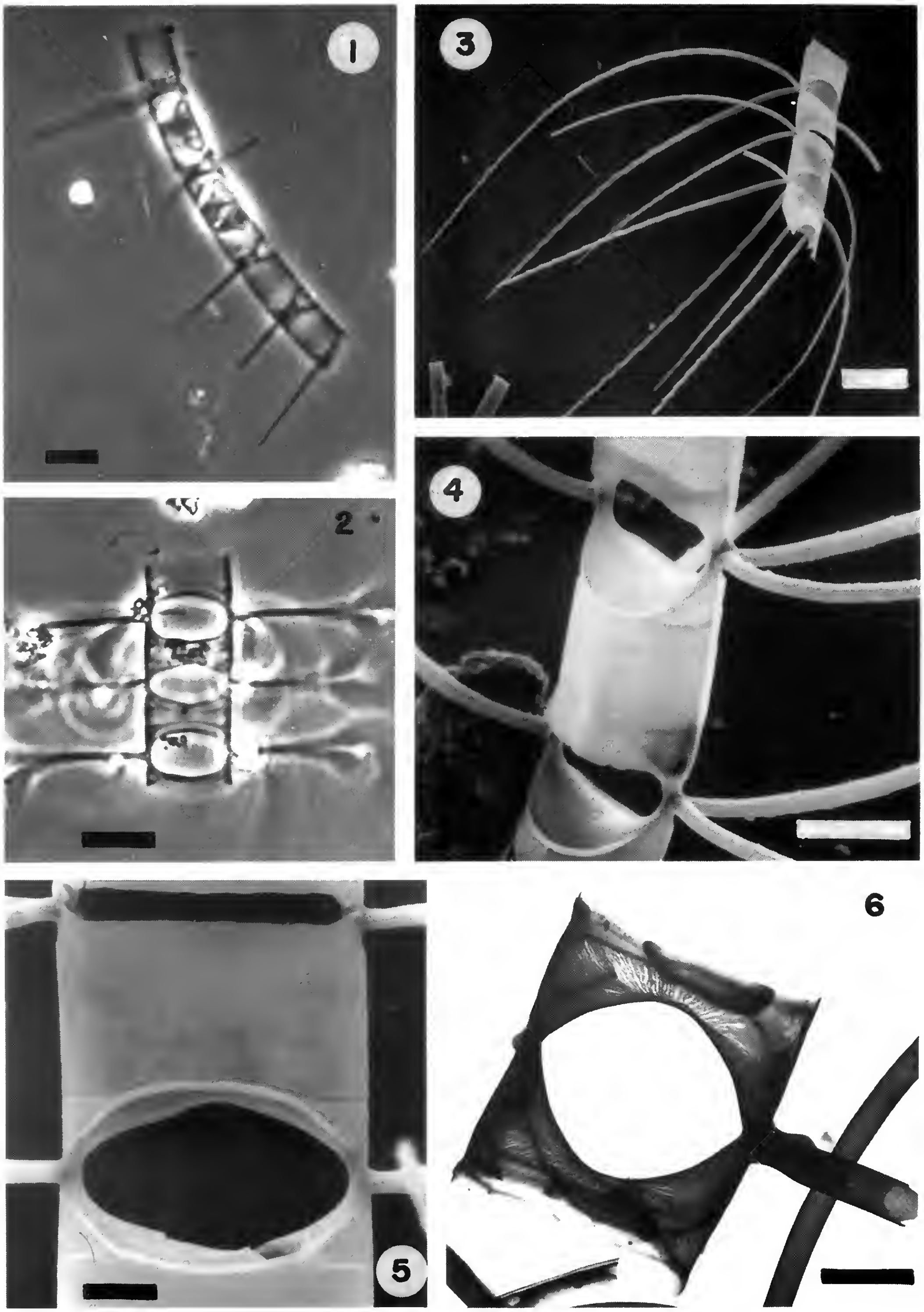

Plate 42 *Chaetoceros curvisetus*. Fig. 1: chain in narrow girdle view. LM. Fig. 2: chain in broad girdle view. LM. Fig. 3: part of chain. SEM. Fig. 4: detail of cells. SEM. Fig. 5: sibling cells showing aperture, hyaline rim on valve edge, and girdle bands. SEM. Fig. 6: two sibling valves. TEM. Figs 1–3, bar = 20 μm; Fig. 4, bar = 10 μm; Figs 5, 6, bar = 5 μm.

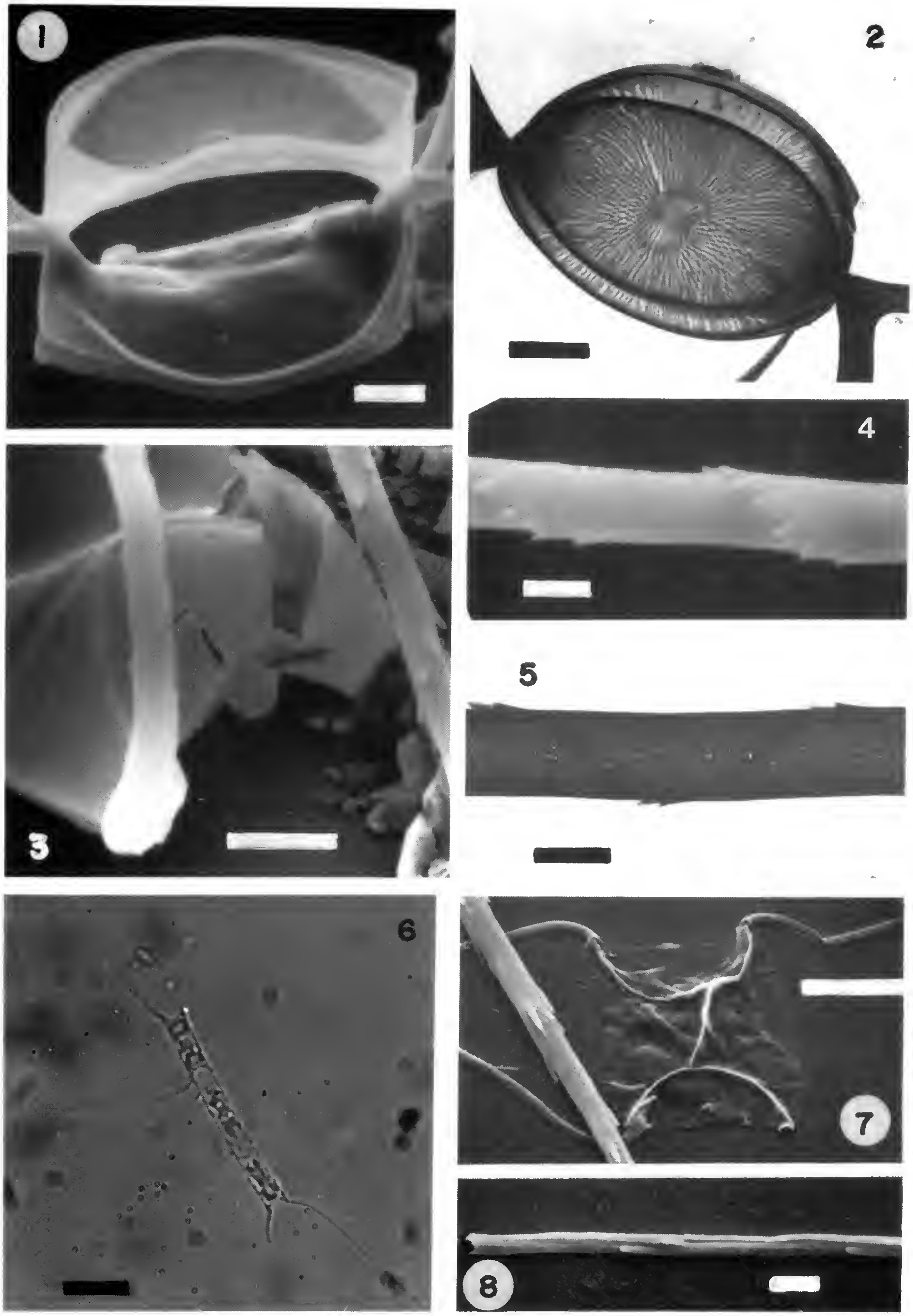

Plate 43 *Chaetoceros curvisetus* (Figs 1–5), *C. wighami* (Fig. 6), and *C. gracilis* (Figs 7, 8). Fig. 1: sibling valves with central annulus. SEM. Fig. 2: valve view of valves with central annulus and radiating costae. TEM. Fig. 3: terminal valve showing rimoportula (arrow). SEM. Fig. 4: middle part of seta. Note spirals of spines. SEM. Fig. 5: middle part of seta showing spirals of small poroids and larger, scattered poroids. TEM. Fig. 6: typical chain. LM. Fig. 7: collapsed cell showing setae and rimoportulae (one on each valve). SEM. Fig. 8: detail of seta. SEM. Figs 1–3, bar = 5 µm; Figs 4, 5, 8, bar = 2 µm; Fig. 6, bar = 20 µm; Fig. 7, bar = 10 µm.

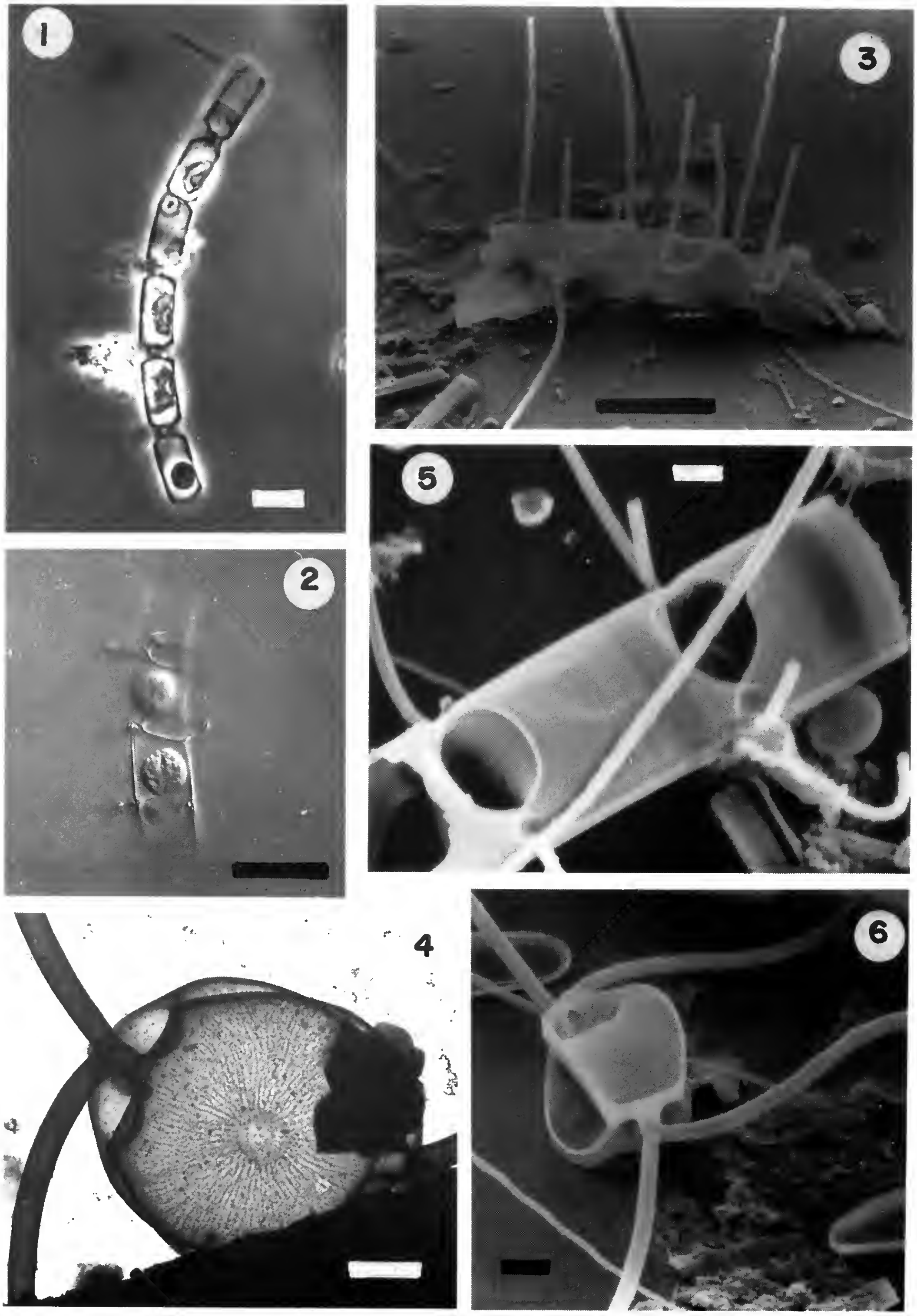

Plate 44 *Chaetoceros pseudocurvisetus*. Fig. 1: typical chain in narrow girdle view. LM. Fig. 2: chain in broad girdle view. LM. Fig. 3: part of chain. SEM. Fig. 4: valve showing annulus and costae. TEM. Fig. 5: part of chain showing small apertures in apical areas. SEM. Fig. 6: two sibling valves. SEM. Figs 1–3, bar = 20 μm; Figs 4–6, bar = 5 μm.

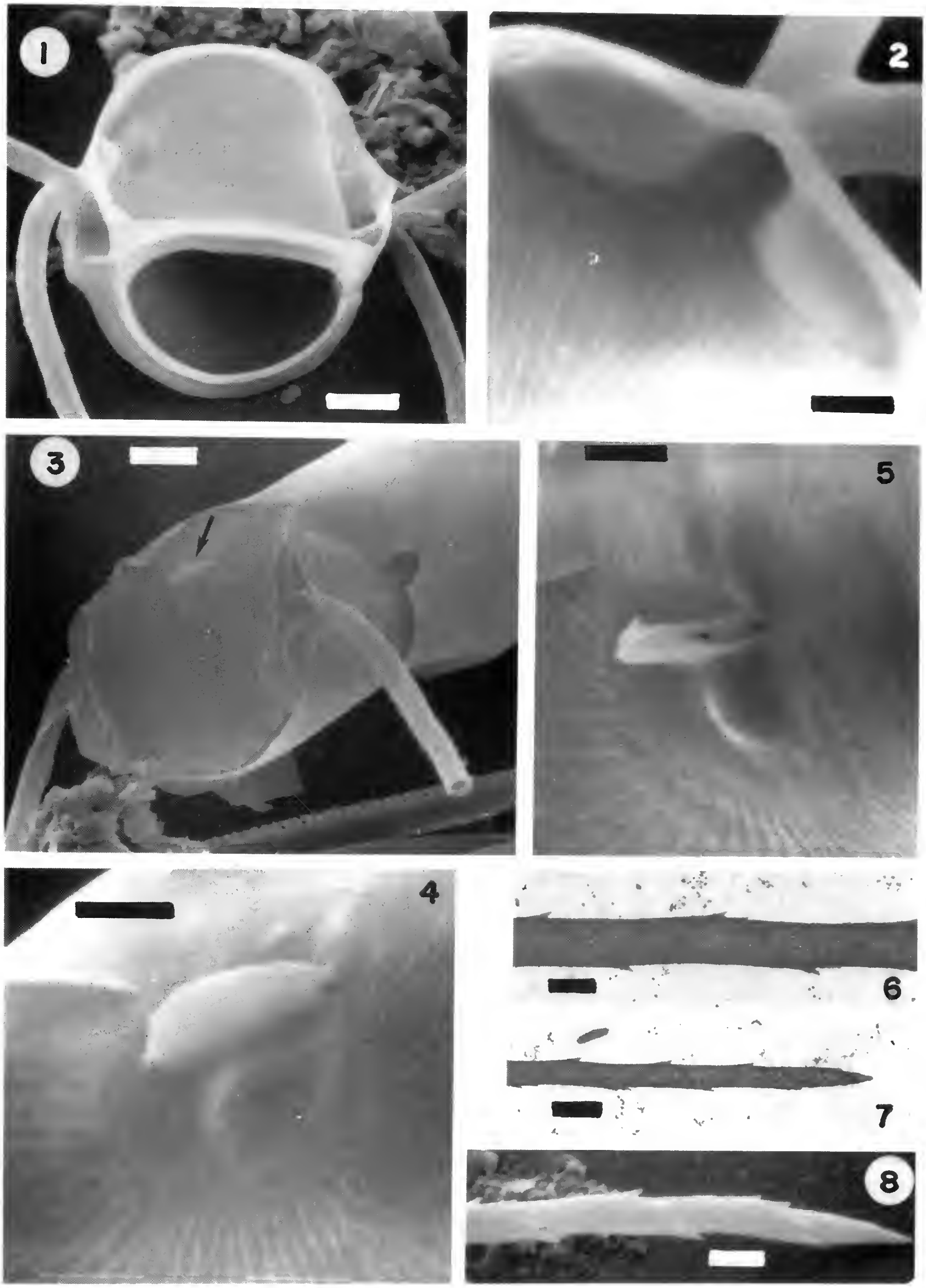

Plate 45 *Chaetoceros pseudocurvisetus*. Fig. 1: sibling valves showing annulus and small apertures at apices. SEM. Fig. 2: detail of apical areas from inside. SEM. Fig. 3: terminal cell with excentric rimoportula (arrow). SEM. Fig. 4: detail of rimoportula. Note small raised area in centre of annulus. SEM. Fig. 5: another view of rimoportula. SEM. Fig. 6: middle part of seta. TEM. Fig. 7: tip of seta. TEM. Fig. 8: tip of seta. Note spirals of spines. SEM. Figs 1, 3, bar = 5 µm; Figs 2, 4–8, bar = 2 µm.

species no poroids could be observed (Pl. 44, Fig. 4). At the edge of the valve, close to where the setae arise, there are four small apertures which are formed by four processes that connect sibling cells (Pl. 44, Fig. 6). Inside there are two depressions, each without costae or thickenings on the apex (Pl. 44, Fig. 6; Pl. 45, Figs 1, 2). The setae arise between. The rimoportula coincides with the annulus which is located slightly to one side of the valve (Pl. 45, Fig. 3). The rimoportula consists of an elongate hollow which protrudes to the outside. Close to the rimoportula there is a small, round, raised area at the very centre of the annulus (Pl. 45, Figs 4, 5). The setae show the same pattern as *C. curvisetus*, being circular throughout (Pl. 45, Figs 6–8). The tips are sharply pointed.

DISTRIBUTION. 45, 64.

REMARKS. The morphology of this species, as described here, is consistent with Fryxell's (1978) observations, although new information is presented for the rimoportula.

39. **Chaetoceros debilis** Cleve

Cleve, 1894: 13, pl. 1, fig. 2; Meunier, 1913: 43, pl. 7, figs 1–11; Hustedt, 1930: 740, fig. 428; Gran & Angst, 1931: 481, fig. 65; Hendey, 1937: 305; Cupp, 1943: 138, fig. 95; Hendey, 1964: 133, pl. 14, fig. 7; Brunel, 1970: 130, pl. 32, figs 1–6; Drebes, 1974: 81, figs 64a, b; Evensen & Hasle, 1975: 159, figs 27–32; Rines & Hargraves, 1988: 72, figs 143, 147.
Pls 46, 47.

LM. Chains curved and twisted, generally long. In girdle view, cells rectangular, with sharp corners, the apical axis usually longer. Valve face flat or concave, mantle low, lines of girdle straight; apertures rather wide. In valve view, cells elliptical, with all setae curving smoothly in the same direction (in the apical plane, transapically). Intercalary setae thin; terminal setae shorter and slightly thicker. One central chloroplast present. Measurements: 17–28 μm a.a., 5–15 μm p.a., 5–8 μm ap. (Pl. 46, Figs 1, 2)

EM. The chains are curved and slightly twisted (Pl. 47, Figs 3, 4). The valves appear to be thinly silicified, with the same basic morphology as other species of subgenus *Hyalochaete*. The annulus is commonly excentric (Pl. 46, Fig. 5). The costae may be branched at times (Pl. 47, Fig. 4) and hyaline rims are found on the edges of some valves (Pl. 47, Figs 1, 2). The rimoportula resembles that of *C. curvisetus*, but is perhaps more excentrically positioned (Pl. 47, Figs 1–5). The setae are circular in cross-section and follow the pattern of *C. curvisetus*. Terminal setae are thicker and shorter than other setae, polygonal at the base and with no spines (Pl. 47, Figs 6–8). The setae tips are flattened.

DISTRIBUTION. 23, 24, 28, 52.

REMARKS. The three species studied here from section *Curviseta* are closely related. All observations made here agree with those made previously (e.g. Evensen & Hasle, 1975).

16. Section **ANASTOMOSANTIA** Ostenf.

Chains mostly loose. Setae united by a bridge.

40. **Chaetoceros rectus** Hern.-Bec.

Hernández-Becerril, 1992*b*: 219, figs 2, 16–29.

DISTRIBUTION. 23, 24.

17. Section **FURCELLATA** Ostenf.

Chains generally loose, without differentiated terminal setae. One chloroplast.

41. **Chaetoceros radicans** F. Schütt

Schütt, 1895: 48, pl. 5, fig. 27; Hustedt, 1930: 746, fig. 431; Gran & Angst, 1931: 483, fig. 67; Cupp, 1943: 141, fig. 97; Brunel, 1970: 132, pl. 33, figs 1–4, pl. 34, figs 1, 2; Hendey, 1964: 134, pl. 14, fig. 4; Drebes, 1974: 82, fig. 66; Fryxell & Medlin, 1981: 8, figs 9–15, 29–42; Rines & Hargraves, 1988: 90, figs 192–198.
Pls 48, 49.

LM. Chains straight, curved or slightly twisted, generally long, delicate. In girdle view, cells rectangular to oblong, with rounded corners, the sibling cells not touching. Valve face convex (dome-shaped), mantle low to high, lines of girdle straight; apertures narrow. In valve view, cells elliptical, with setae diverging in the transapical axis. Setae thin, bearing numerous small spines; they arise from the corners of the valves and diverge nearly perpendicular to the chain axis. Intercalary and terminal setae undifferentiated. One large chloroplast in the centre of the cell. Measurements: 13–24 μm a.a., 10–22 μm p.a., 3–5 μm ap. (Pl. 48, Fig. 1)

EM. The chains are delicate and slightly twisted (Pl. 48, Fig. 2). The valves are weakly silicified (Pl. 48, Fig. 3), having a quite apparent, centrally placed annulus (Pl. 48, Fig. 4). Some costae converge at the apical regions, making the valve slightly thicker (Pl. 49, Figs 2, 3). No poroids were seen, or they were too small to be detected. A hyaline rim is present on the edge of most of the valves (Pl. 48, Fig. 6; Pl. 49, Fig. 4). The rimoportula is slightly excentric and consists of a flattened and elongated hollow orientated in the apical axis or diagonal, being a tubular structure to the outside (Pl. 49, Figs 2–5). The setae are orientated to the transapical axis in opposition to each other, especially on terminal valves (Pl. 49, Figs 1, 2, 5). The setae seem to be circular throughout, developing spines which are sometimes branched, usually after fusion with adjacent setae (Pl. 48, Fig. 5); these spines appear to be solid (Pl. 49, Fig. 6). It is not possible to distinguish any particular pattern of spine distribution, so they are probably positioned at random (Pl. 48, Figs 3, 4, 6; Pl. 49, Fig. 7). The setae walls are simply perforated by minute poroids and appear thicker than those of the valves (Pl. 49, Fig. 6).

DISTRIBUTION. 7, 11, 17, 18, 23, 28, 40–42, 44, 45, 48, 52.

REMARKS. All Fryxell & Medlin's (1981) observations on this species agree with those presented here; however, no details of the resting spores are reported in this study. The rimoportula of the specimens given as *C. radicans* by Helmcke & Krieger (1954: pl. 125) is completely different from that described here, so it is possible their figure does not correspond with this species.

42. **Chaetoceros filiferus** G. Karst.

Hernández-Becerril, 1993*b*: 170, figs 15–28.

DISTRIBUTION. 42, 45, 48.

18. Section **SOCIALIA** Ostenf.

Cells in irregular chains. One chloroplast. Resting spores variable.

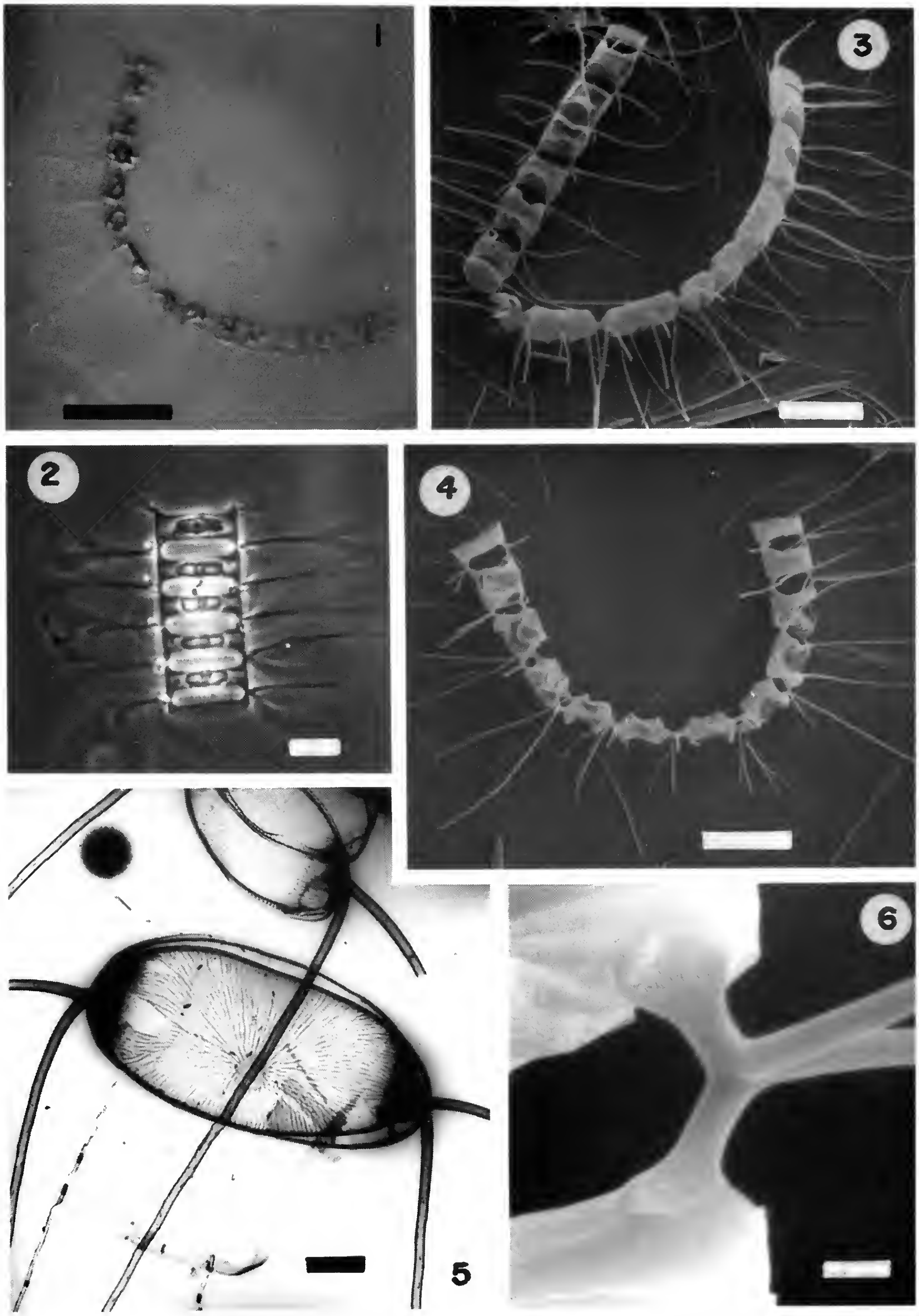

Plate 46 *Chaetoceros debilis*. Fig. 1: typical chain. LM. Fig. 2: chain in broad girdle view. LM. Fig. 3: two chains. SEM. Fig. 4: another chain. SEM. Fig. 5: valve showing slightly excentric annulus and costae. TEM. Fig. 6: detail of fusion of setae. SEM. Figs 1, 3, 4, bar = 50 μm; Fig. 2, bar = 20 μm; Fig. 5, bar = 5 μm; Fig. 6, bar = 2 μm.

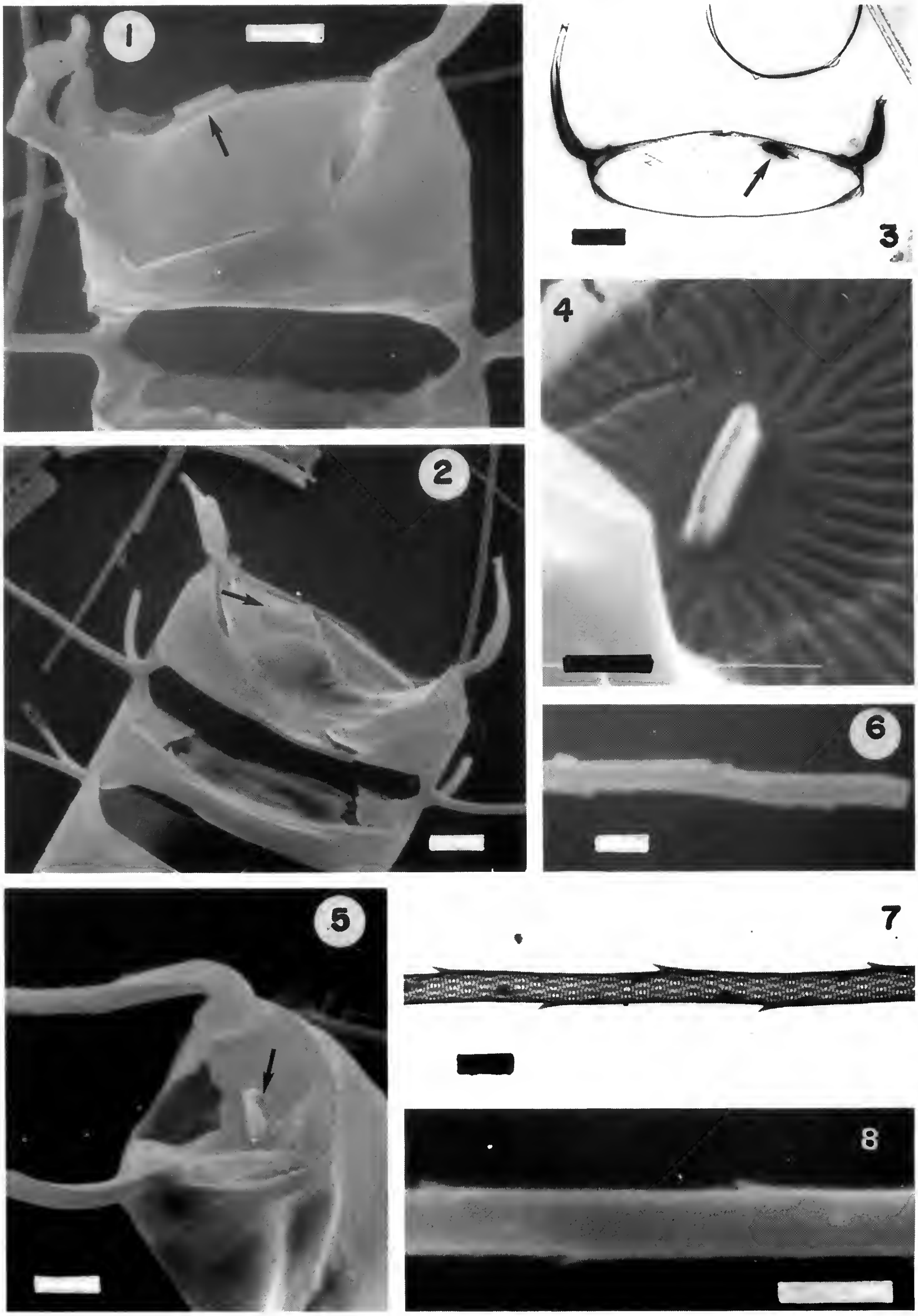

Plate 47 *Chaetoceros debilis*. Fig. 1: terminal cell with excentric rimoportula (arrow). SEM. Fig. 2: terminal cell showing rimoportula (arrow). Note short, thick terminal setae. SEM. Fig. 3: partially broken terminal valve. Arrow indicates rimoportula. TEM. Fig. 4: detail of rimoportula. SEM. Fig. 5: terminal valve with elongate rimoportula (arrow). SEM. Fig. 6: seta close to tip. SEM. Fig. 7: middle part of seta. TEM. Fig. 8: middle part of seta. SEM. Figs 1–3, 5, bar = 5 μm; Figs 4, 6–8, bar = 2 μm.

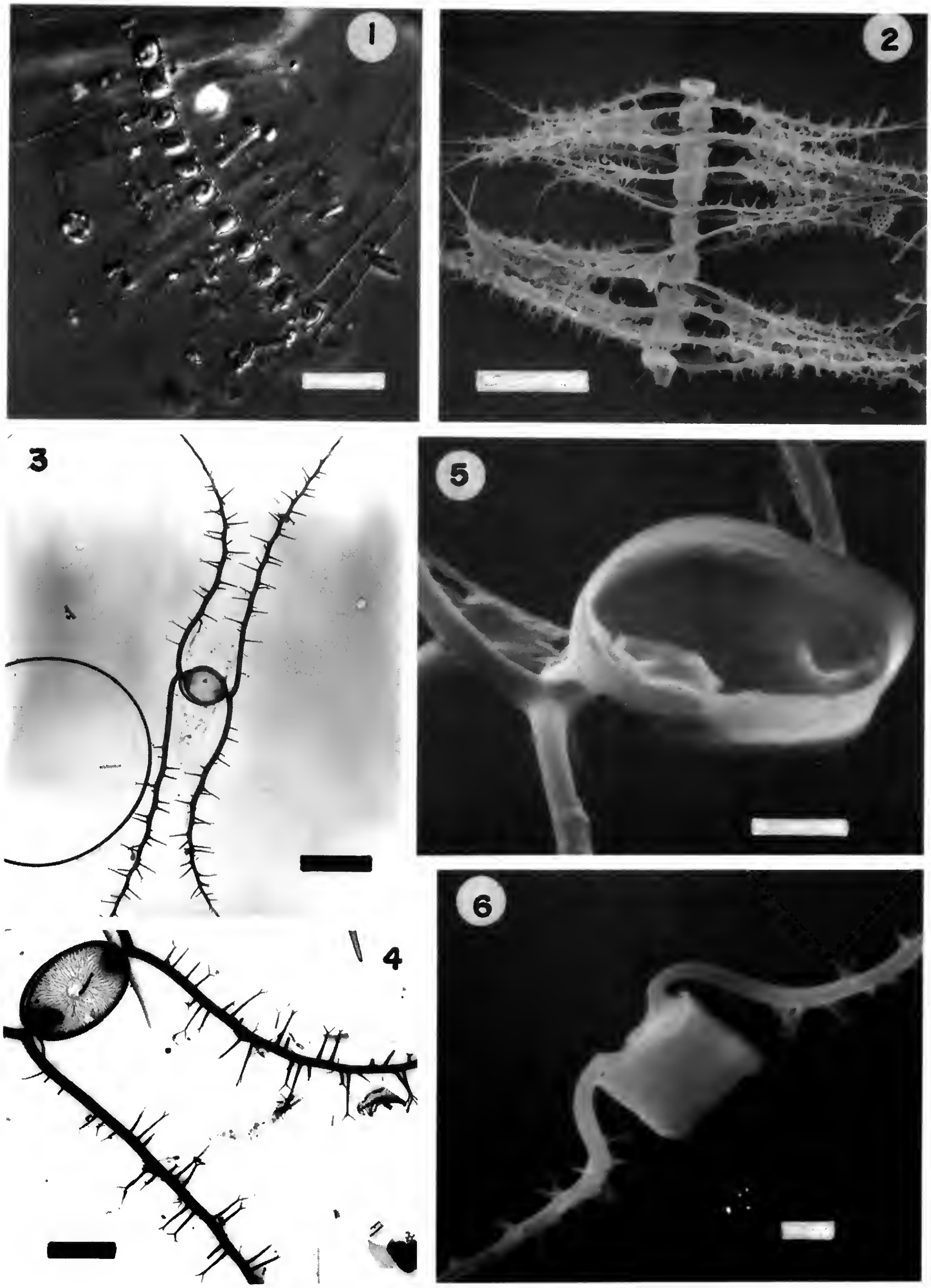

Plate 48 *Chaetoceros radicans*. Fig. 1: typical chain. LM. Fig. 2: part of chain. SEM. Fig. 3: complete cell in valve view. TEM. Fig. 4: detail of valve. TEM. Fig. 5: internal view of valve. SEM. Fig. 6: terminal valve. SEM. Figs 1, 2, bar = 50 µm; Fig. 3, bar = 20 µm; Fig. 4, bar = 10 µm; Figs 5, 6, bar = 5 µm.

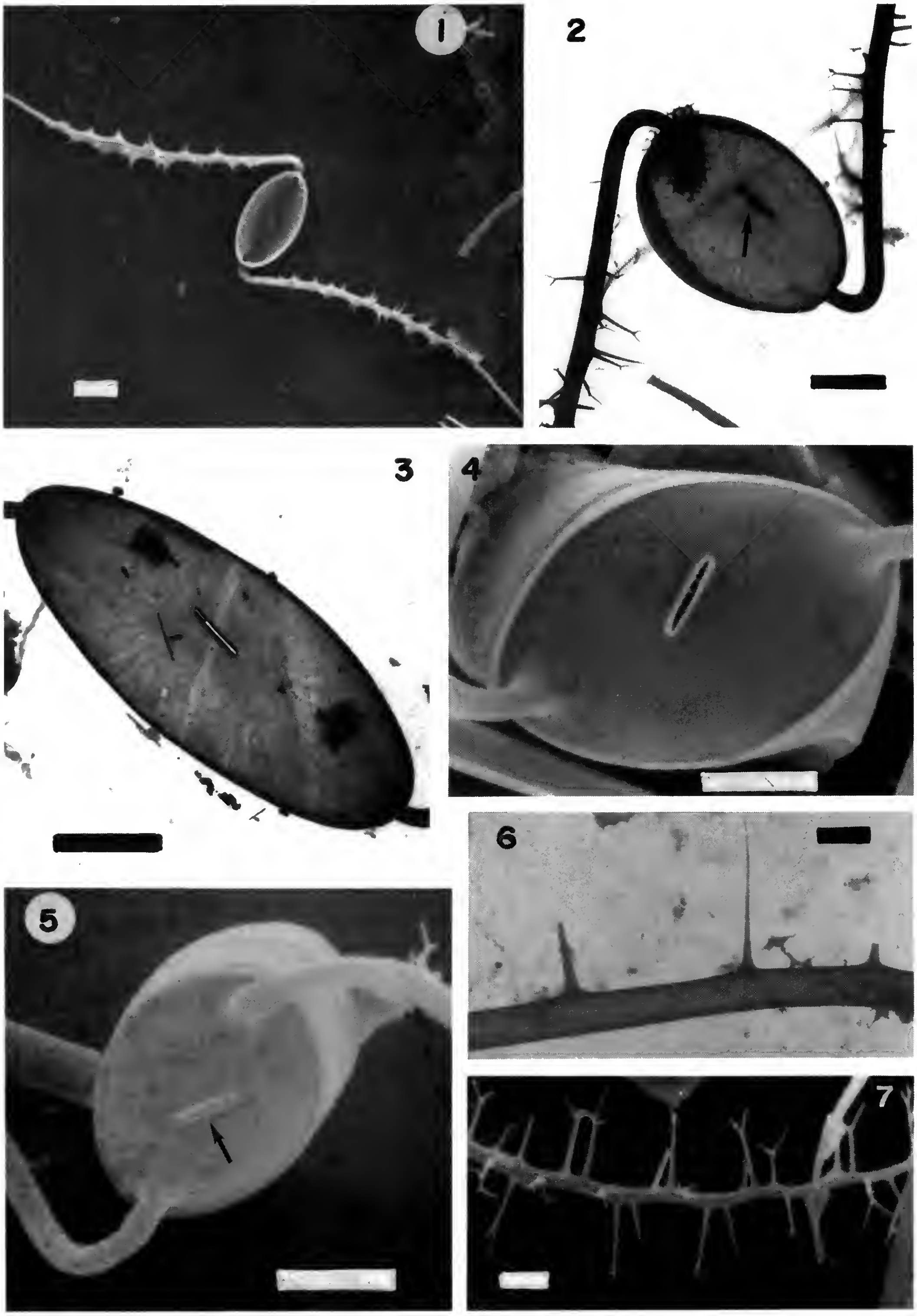

Plate 49 *Chaetoceros radicans*. Fig. 1: terminal valve in valve view. SEM. Fig. 2: another terminal valve. Arrow indicates rimoportula. TEM. Fig. 3: detail of valve showing rimoportula. TEM. Fig. 4: rimoportula at terminal valve. SEM. Fig. 5: flattened, hollow rimoportula (arrow). SEM. Fig. 6: detail of seta close to base. TEM. Fig. 7: middle part of seta. SEM. Fig. 1, bar = 10 μm; Figs 2–5, bar = 5 μm; Fig. 6, bar = 2 μm.

43. **Chaetoceros socialis** Lauder var. ?

Lauder, 1864: 77, pl. 8, fig. 1; Meunier, 1913: 46, pl. 7, figs 26–29; Gran & Angst, 1931: 486, fig. 70; Cupp, 1943: 143, fig. 100; Subrahmanyan, 1946: 143, figs 256, 251?; Cleve-Euler, 1951: 102, figs 199a–e; Brunel, 1970: 135, pl. 29, figs 3, 4, pl. 36, figs 1–3, pl. 37, figs 1–3; Evensen & Hasle, 1975: 160, figs 33–39.
Pls 50, 51.

LM. Cells gathered in short chains or clumps, joined through long setae. In girdle view, cells rectangular, with smooth corners which do not touch sibling cell corners. Valve face concave, mantle low, lines of girdle straight; when present, apertures narrow to wide. In valve view, cells elliptical, the setae curving smoothly, sometimes one longer and straight, following the apical axis. All setae thin, bearing small spines. One chloroplast present at the centre of the cell. Measurements: 10–18 µm a.a., 8–12 µm p.a., 6–7 µm ap. (Pl. 50, Fig. 1)

EM. Chains or clumps seem to be joined by special long setae (Pl. 50, Fig. 2). The valves are thinly silicified (Pl. 50, Figs 3–6). The previous characteristic of an annulus with a costae pattern radiating from it, is also present in this species (Pl. 51, Fig. 1). Rows of fine poroids are found between the costae (Pl. 51, Fig. 1). No rimoportulae were seen; however, it is assumed that one is present just in terminal valves, because in intercalary valves the rimoportula was absent. The setae arise from close to the valve corners and following a short base meet and fuse with sibling setae (Pl. 50, Fig. 6; Pl. 51, Figs 2, 3). They are circular throughout, generally developing spines after fusion (Pl. 50, Fig. 5; Pl. 51, Fig. 3); the spines run in spirals and the walls are perforated by spiral rows of fine poroids, as well as some scattered, bigger poroids (Pl. 51, Fig. 7, 8). One seta is longer than the others; it is spineless, with longitudinal rows of poroids and also randomly scattered bigger poroids (Pl. 51, Fig. 6). Resting spores are generally paired, connected by spineless setae (Pl. 51, Figs 4, 5). One valve is strongly convex with processes radiating from the centre; the other valve is slightly concave and smooth (Pl. 51, Figs 4, 5).

DISTRIBUTION. 42, 52.

REMARKS. Hargraves (1979) mentioned the possibility that more than one taxa are involved in the species currently known as *C. socialis*, mainly due to the range of resting spores found and also the arrangement of the chains. The taxon identified here indeed belongs to *C. socialis*, but it is probably a variety of it. On the other hand, Evensen & Hasle (1975) discussed the difference in structure between the long seta and the others: the long seta lacks spines and the pattern of poroids is straight, distinct from the 'normal' setae. This seta would be involved in the chain formation mechanism 'by sticking together near the tip with setae from other chains or cells' (Evensen & Hasle, 1975).

19. Section **SIMPLICIA** Ostenf.

Cells generally solitary, small and fragile.

44. **Chaetoceros gracilis** F. Schütt

Schütt, 1895: 42, fig. 13; Hustedt, 1930: 758, fig. 440; Gran & Angst, 1931: 487, fig. 71; Cupp, 1943: 143, fig. 101; Cleve-Euler, 1951: 108, figs 225a–e; Hendey, 1964: 137, pl. 14, fig. 6.
Pl. 43, Figs 7, 8.

LM. Cells solitary, small and fragile. In girdle view, cells rectangular, with concave valve face. No clear distinction at girdle zones. In valve view, cells elliptical. Setae very thin, long and delicate, orientated towards the apical axis or smoothly curved. Two chloroplasts are placed opposite the sides of the cell, at girdle zones. Measurements: 7–9 µm a.a., 11–12 µm p.a.

EM. The valves are delicate, very thinly silicified (Pl. 43, Fig. 7). There was no apparent annulus or costae pattern (perhaps not resolved at the magnifications used); however, a minute external protrusion of the rimoportula was found at the centre of the valve face (Pl. 43, Fig. 7). The edges of the valve face show a rim (Pl. 43, Fig. 7). Setae borne on the apices of the valves appear to be circular at the base, becoming polygonal away from the valve, with minute spines (in spirals?) (Pl. 43, Fig. 8).

DISTRIBUTION. 23, 50, 51.

REMARKS. Rines & Hargraves (1988) have thoroughly discussed the problems arising when dealing with species of section *Simplicia* (e.g. they may or may not be single cells, the descriptions are incomplete, etc.). These authors recommend that *C. gracilis* is treated 'with extreme caution'.

45. **Chaetoceros vistulae** Apstein

Apstein, 1909: 136, fig. 2; Ostenfeld, 1912: 10, fig. 24; Hustedt, 1930: 762, fig. 443; Cupp, 1943: 144, fig. 102.
Pl. 52.

LM. Cells solitary, fragile. In girdle view, cells rectangular, with sharp corners, the pervalvar axis being longer. Valve face flat or slightly concave, mantle low, lines of girdle straight. In valve view, cells elliptical. Setae thin, long, arising from corners of the valves, directed towards the pervalvar axis, at an angle of about 10–20° from this axis. One large chloroplast present in each cell, placed centrally. Measurements: 6–9 µm a.a., 20–27 µm p.a. (Pl. 52, Fig. 1)

EM. Valves extremely weakly silicified (Pl. 52, Figs 2, 3), with annulus and costae well apparent (Pl. 52, Fig. 4). Some spine-like projections arise from the centre of the valve and a hyaline rim appears on the valve edge (Pl. 52, Figs 4, 6). There is one rimoportula per valve, each centrally located and consisting of a flattened tube open to the outside (Pl. 52, Fig. 6). The setae are circular at the very base (Pl. 52, Fig. 4), becoming polygonal (four or five-sided) distally, with rows of minute spines running along each edge and a single longitudinal row of poroids running along each side (Pl. 52, Fig. 5).

DISTRIBUTION. 16, 23, 24, 51.

REMARKS. Details from electron microscopy of the valve (costae) and setae of a closely related species, *C. gracilis*, described above and also by Rogerson et al. (1986), reveal similar morphology to *C. vistulae* as shown here. Apparently, this is a brackish-water species, but it has also been recorded from marine waters (e.g. Cupp, 1943).

III. Subgenus **BACTERIASTROIDEA** Hern.-Bec.

Valves cylindrical. Each valve possessing three pairs of setae, two pairs very reduced, the other pair usually thick. Regular projections (outgrowths) present on the valve edge. Chloroplasts two.

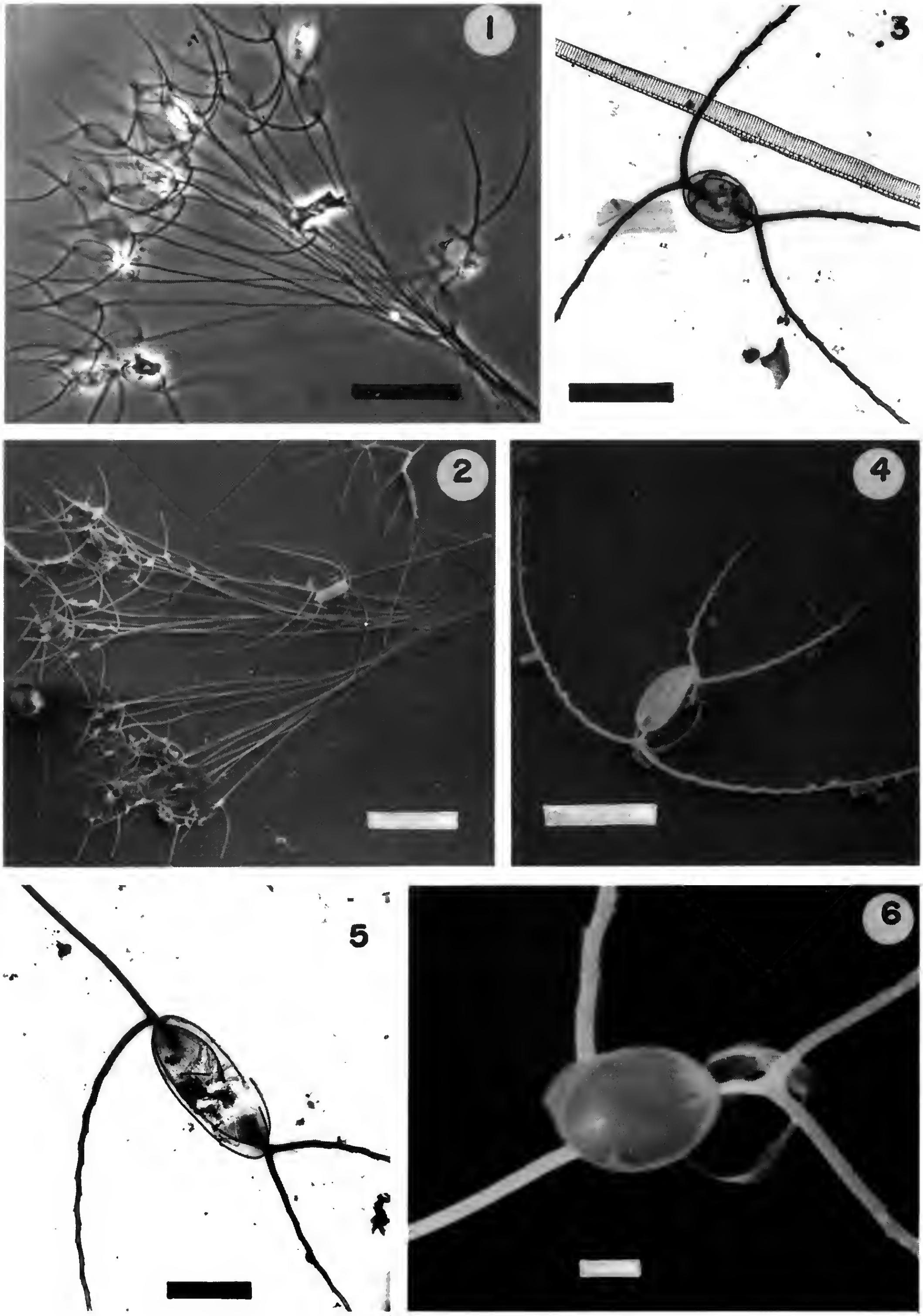

Plate 50 *Chaetoceros socialis* var. ? Fig. 1: complete chain. LM. Fig. 2: part of chain. SEM. Fig. 3: sibling valves. TEM. Fig. 4: sibling valves. Note direction of setae. SEM. Fig. 5: sibling valves. Note direction of setae. TEM. Fig. 6: internal view of valve. SEM. Figs 1, 2, bar = 50 μm; Figs 3, 4, bar = 20 μm; Fig. 5, bar = 10 μm; Fig. 6, bar = 5 μm.

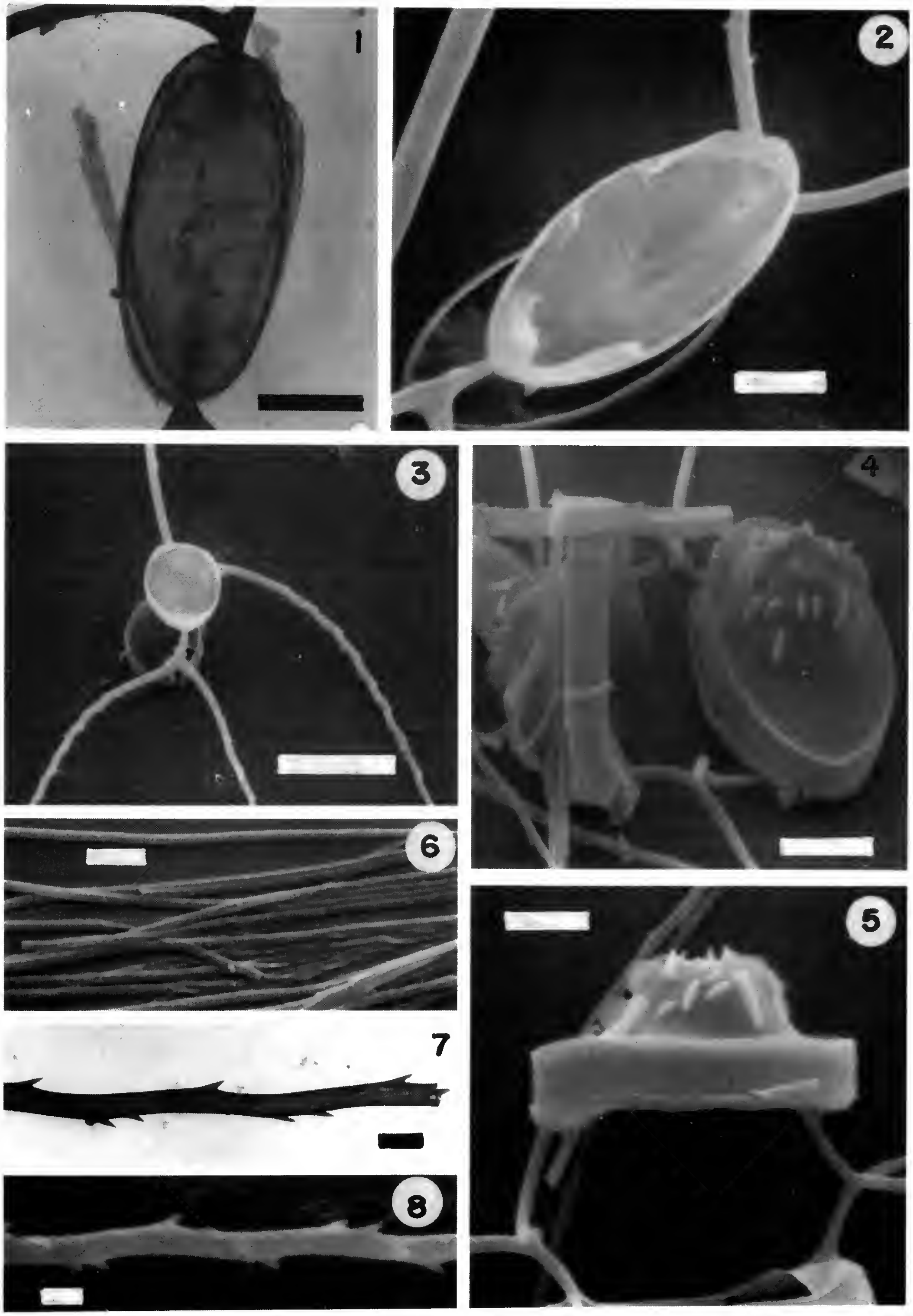

Plate 51 *Chaetoceros socialis* var. ? Fig. 1: detail of valve showing annulus and costae. TEM. Fig. 2: internal view of valve. SEM. Fig. 3: two sibling valves. Note fusion of setae. SEM. Fig. 4: resting spores in pairs. SEM. Fig. 5: girdle view of resting spores. Note processes in upper valve. SEM. Fig. 6: various long setae. SEM. Fig. 7: middle part of seta. TEM. Fig. 8: middle part of seta. SEM. Figs 1, 2, 4, 5, bar = 5 μm; Figs 3, 6, bar = 10 μm; Figs 7, 8, bar = 2 μm.

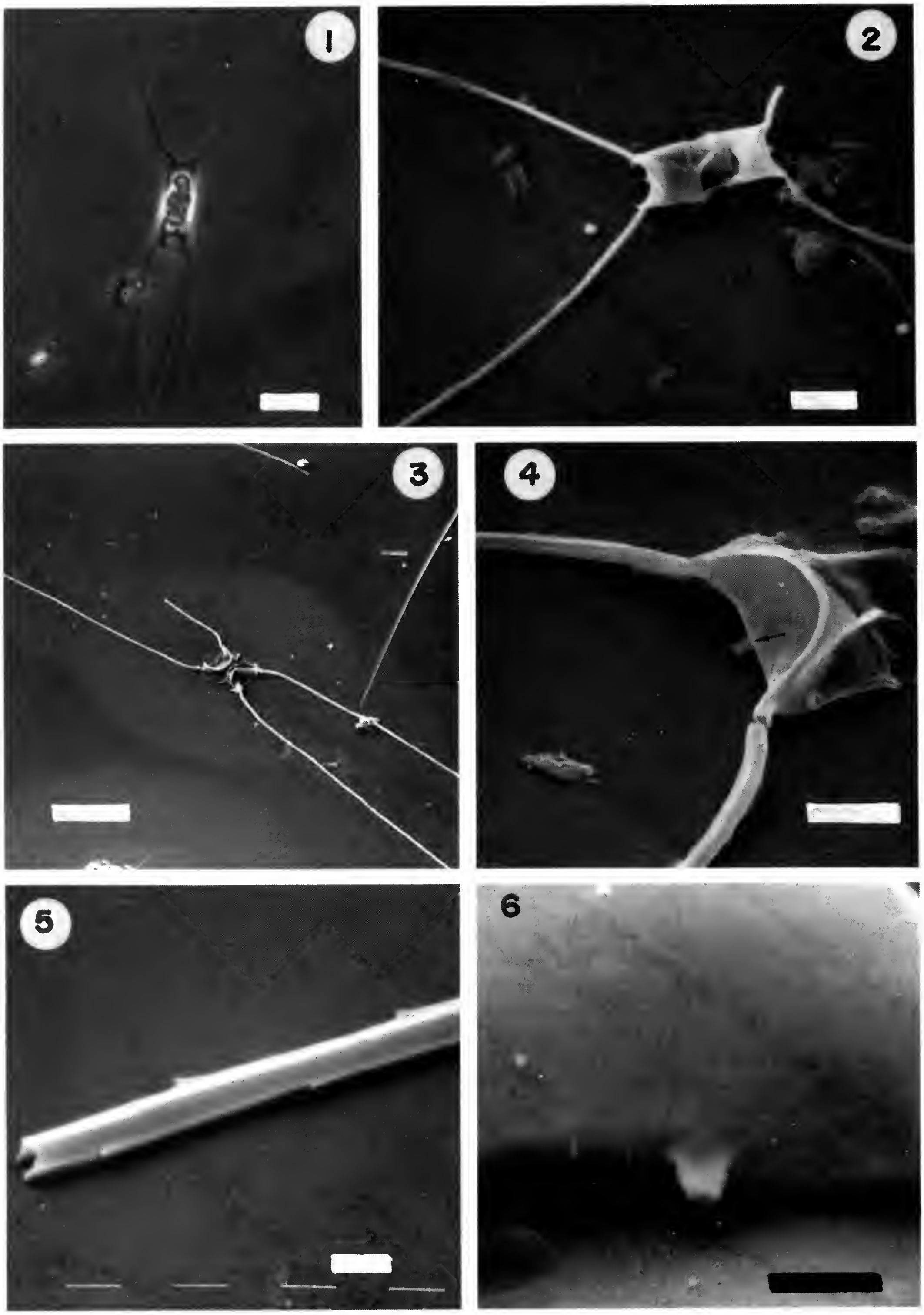

Plate 52 *Chaetoceros vistulae*. Fig. 1: typical cell (solitary). LM. Figs 2, 3: two complete cells. SEM. Fig. 4: detail of valve face. Arrow indicates rimoportula. SEM. Fig. 5: middle part of seta. SEM. Fig. 6: detail of prominent rimoportula and small scattered spines. SEM. Figs 1, 3, bar = 20 µm; Fig. 2, bar = 10 µm; Fig. 4, bar = 5 µm; Figs 5, 6, bar = 2 µm.

46. **Chaetoceros bacteriastroides** G. Karst.

Hernández-Becerril, 1993*a*: 119, figs 1–15.

DISTRIBUTION. 15, 24.

REMARKS. The structure of this species, as already mentioned, differs from the general morphology of species commonly included in the subgenera *Chaetoceros* (*Phaeoceros*) and *Hyalochaete*. This has been taken into account to propose the subgenus *Bacteriastroidea*, where *C. bacteriastroides* remains isolated due to a lack of closely related species.

DISCUSSION

Morphology

General accounts of the morphology of *Chaetoceros* species have been published by several authors, the most recent overview of the genus being provided by Evensen & Hasle (1975). As summarized by Desikachary (1956), the various studies of *Chaetoceros* using TEM have revealed the structure of the cell wall, which is simply perforated by small poroids with some 'vein-like thickenings' in thin-walled species. These findings were complemented by Okuno's (1956) studies, who added observations on the annulus ('central area'), as well as the costae ('vein-like thickenings') radiating from this field (structures usually found in many species of subgenus *Hyalochaete*). Evensen & Hasle (1975) discussed the difference in structure between the cell wall in the main part of the valves and that in the setae, with special emphasis on the morphology of setae and rimoportulae. All these characteristics are confirmed here and there appears to be little new information left to be added to the knowledge of the general morphology of *Chaetoceros*.

Many questions have arisen concerning the function of certain structures in *Chaetoceros*. Evensen & Hasle (1975) emphasized the enigma of the function of the rimoportulae, which at the moment remains a matter for speculation. Ideas put forward for their function in other centric diatoms include differential permeability to certain chemicals (trace elements) (Fryxell & Hasle, 1974), secretion of mucilage pads or stipes for attachment (Crawford, 1975), and role in movement (Andersen et al., 1986; Medlin et al., 1986). Of these hypotheses, only the first might be a possible explanation for their function in *Chaetoceros*.

The presence of multiple rimoportulae in a single valve has recently been found in several species, including *Chaetoceros compressus* var. *hirtisetus* Rines & Hargraves (Rines & Hargraves, 1990), *C. coarctatus* (Hernández-Becerril, 1991*a*), *C. bermejensis* (Hernández-Becerril, 1991*c*), and *C. buceros* G. Karst. (Hernández-Becerril et al., 1993), and this has been related to the evolution of the raphe (Rines & Hargraves, pers. comm.).

The function of the setae has generated more discussion than that of the rimoportulae, as the setae are visible with light microscopy and have been observed since the original type species description was made (Ehrenberg, 1844). Many planktologists have found very elongated or chain-forming species and have believed that in *Chaetoceros* the setae might have the function of conferring buoyancy. This hypothesis seems very likely for some species, but for attached forms, such as *C. dadayi* Pavill. and *C. tetrastichon*, this is clearly not the case (Hernández-Becerril, 1992*a*).

Many species have tiny, delicate setae and it is difficult to see how these could aid buoyancy. Others have very robust setae which must also be heavy and increase the density of the cell. However, very often these setae contain chloroplasts and may therefore increase the photosynthetic capacity of the cell. There is not enough evidence regarding the distribution of robust forms with chloroplasts in the setae (e.g. subgenus *Chaetoceros*) as deep water forms, or more fragile, non chloroplast-bearing forms (e.g. subgenus *Hyalochaete*) as more shallow water forms.

The structure of the setae in species belonging to subgenus *Hyalochaete*, which lack chloroplasts in the setae, reveals a wide range of adaptations for buoyancy; Fryxell (1978) considers that the spiral pattern may be advantageous in relation to buoyancy. The setae of *C. decipiens* and *C. lorenzianus* have perforations along their length which appear to be uncovered even when the organisms are living, and are larger than those in the other species of the subgenus. *C. socialis* var. ?, as described here and previously (Evensen & Hasle, 1975), has one very long, spineless seta which may connect with similar setae to form the chain, although fusion between cells or their parts is rare (Round & Crawford, 1981), but still possible in 'inseparable' chains (Stosch, 1977).

The method of chain formation in *Chaetoceros* has also been discussed (e.g. Rines & Hargraves, 1988). The main ways were outlined by Fryxell (1978) and Fryxell & Medlin (1981) as, for example: fusion of setae (the most typical), fusion of edge valves and setae, holding of setae, and possession of 'prehensors'. More recently, Hernández-Becerril (1992*b*) mentioned yet another special manner of chain formation, which was found in *C. rectus*, a new species described therein. A thin and simple perforated, siliceous wall connects the apices of the sibling valves, so the sibling setae pass through this wall without fusion. Rines & Hargraves (1988) commented on the particular mechanism of chain formation in *C. rostratus*: by fusion of linking spines on the valve face. The valve formation of this species was studied by Li & Volcani (1985), who found that these intercellular linkages are formed by incomplete cytokinesis during cell division, after which silicification occurs and a siliceous septum divides the two adjacent cells.

The different mechanisms of chain formation should be considered as one of the most important points for understanding the great diversity of species in *Chaetoceros*, and one of the main factors in the evolution of the genus. They should also be considered as a valuable taxonomic character, especially when proposals for future classifications are being considered, and in particular those at the sectional level.

Solitary forms are encountered in subgenus *Chaetoceros* (e.g. *C. peruvianus*, *C. pendulus*) and subgenus *Hyalochaete* (e.g. *C. gracilis*, *C. vistulae*). Despite the well-apparent differences, it is possible to make a case for parallel evolution having occurred, with these forms having evolved from a chain-forming ancestor.

With regard to resting spores, it is clear that a number of well-known species can be recognized using this character, but many species (especially those belonging to subgenus *Chaetoceros*) lack resting spores. Also, morphological variation does exist in these structures. The study of the resting spores (including mechanisms of production) will certainly provide evidence to increase our understanding of the biology, ecology, and taxonomy of *Chaetoceros*.

Another aspect, which has not been extensively studied, is intraspecific morphological variation. This is considerable in some taxa and may lead to taxonomic confusion. *C. diversus* has been shown to exhibit a high level of variation, currently involving at least two species (*C. diversus* – *C. laevis*), and perhaps a third (*C. rudis*) (Moreno et al., 1993). Other species are morphologically very similar to closely related taxa and this may cause identification problems. Therefore, further studies on morphological variation and life cycles are highly recommended to elucidate 'valid' or 'currently recognized species'.

The observations made here are summarized in Tables 2 and 3, and general conclusions on the morphology of *Chaetoceros* species can be made from them. Taxa belonging to subgenus *Chaetoceros* are robust forms with large and complex appendages, heavily silicified; valves perforated by poroids, with thickenings or costae in some cases; rimoportula in each valve, central or to one side of the valve, tubular, circular, oval or slit-like; setae polygonal, well-armoured with spines, the wall areolated by rows of poroids or striae and costae pattern.

Taxa belonging to subgenus *Hyalochaete* are less robust and many are delicate and fragile, with delicate and tiny appendages; valves and setae are not thickly silicified, the valve face having an annulus from which a pattern of weak or strong costae radiates and rows of poroids run in between the costae; the rimoportula is present at least on terminal valves, being central or excentric, circular, slit-like or a flattened hollow with a true labiate structure inside; setae generally circular, in a few cases polygonal, with short spines running straight or in a spiral, the wall perforated by rows of poroids, also running straight or in a spiral.

The monotypic subgenus *Bacteriastroidea* is characterized by the presence of three pairs of setae per valve, two of these pairs reduced. A combination of certain other characteristics shown by *Chaetoceros* and *Hyalochaete* species is also present.

Taxonomic relationships

As already stated (p. 2), the genus *Chaetoceros* is included in the family Chaetocerotaceae, together with *Bacteriastrum* and *Gonioceros* (Round et al., 1990), although recent studies (Crawford et al., 1994) have left the family with only two members: *Chaetoceros* and *Bacteriastrum*. Evensen & Hasle (1975) mentioned the difficulty of relating Chaetoceraceae (including *Acanthoceros*, following Simonsen, 1979) to other families, and accordingly that it would be left in 'an isolated taxonomic position'. However, taking into account the two families recently established by Round & Crawford (Round et al., 1990): Acanthocerataceae and Attheyaceae, the family Chaetocerotaceae is more easily related, at least with two genera (*Acanthoceros* and *Attheya*) and their corresponding families. Recent studies made on species of the genus *Attheya* include proposals to transfer two *Gonioceros* species, *G. armatus* (West) Peragallo and *G. septentrionalis* (Østrup) R.M. Crawford, to that genus.

The new subclass, Chaetocerotophycidae, includes the new order Leptocylindrales, with only one family, Leptocylindraceae M. Lebour, 'tentatively placed until further studies can be made' (Round et al., 1990). This inclusion is not convincing to me, as the genus *Leptocylindrus* Cleve is completely different to *Chaetoceros* or *Bacteriastrum*, although superficially similar (in the girdle bands) to *Acanthoceros*.

A new genus closely related to *Chaetoceros* was recently described, namely *Miraltia* D. Marino, Montresor & Zingone (Marino et al., 1987), but it has now been incorporated into *Chaetoceros* (Marino et al., 1991).

Opinions differ on the phylogeny in the family. One view is that the evolutionary trend is from bilateral to radial symmetry (Simonsen, 1979), while another is that the sequence is the opposite (Fryxell, 1978; Fryxell et al., 1986). However, *Bacteriastrum* remains the most closely related genus to *Chaetoceros*, and *C. bacteriastroides* may be an important link in this relationship (see Fryxell, 1978; Hernández-Becerril, 1993*a*).

Classification

The current taxonomic classification has been given above: three subgenera and 19 sections (see p. 2). Rines & Hargraves (1988) recently drew attention to some of the inconsistencies in the traditional classification and the need for a 'contemporary revision'. I fully support this view and also accept that this revision would take some time. However, the present division into three subgenera still seems reasonable and is supported by the various characters mentioned in the summary (p. 2) and by

Table 2 The major characteristics of *Chaetoceros* taxa (subgenera *Chaetoceros* and *Bacteriastroidea*) observed by electron microscopy.

Species	Valve face and mantle	Rimoportula features	Seta structure: cross-section, wall pattern	Remarks on setae
C. atlanticus var. *neapolitanus*	2,4	One, tubular, central	5,7, 2S/2C	–
C. atlanticus var. *skeleton*	2,4	One, tubular, central	5,8, 2S/2C	–
C. dichaeta	1,4	One, tubular, central	6,8, poroids	–
C. octagonus	2	One, circular, central	5,8, 1S/2C	–
C. densus	3,4	One, circular, central	5,7, 1S/2C	–
C. tetrastichon	3	One, slit-like, central	5,7, 3S/2C	–
C. seychellarus	1,4	One, oval, excentric	5,7, 1S/2C	T setae fused
C. denticulatus	1	One, oval, central	5,8?, 1S/2C	–
C. rostratus	3	One, circular, excentric	5,7, 2S/2C	–
C. danicus	2,4	One, oval, central	5,7, 1S/2C	–
C. concavicornis	1 ?	One, spine-like?, excentric	5,7, ?	–
C. convolutus	1	One, spine-like, excentric	5,7, ?	–
C. peruvianus	1	One, spine-like, excentric	5,7, 3S/2C	Ant. T setae fused
C. pendulus	3	One, oval, excentric	5,7, 3S/2C	–
C. coarctatus	1	Numerous, small, central	6,7, 1S/2C	T setae thicker
C. bacteriastroides	2,4	One, slit-like, central	6,8, poroids	XT setae reduced

1 = Valve perforated, no costae, 2 = Valve perforated, weak costae, 3 = Valve perforated, costae, 4 = Thickening (granules), 5 = Setae square (four-sided) in cross-section, 6 = Setae polygonal (more than four sides) in cross- section, 7 = Big spines along edges, 8 = Small spines along edges, S = Striae, C = Costae, T = Terminal, XT = Extra. Taxa of subgenus *Chaetoceros* bear at least one rimoportula on each valve.

Table 3 The major characteristics of *Chaetoceros* taxa (subgenus *Hyalochaete*) observed by electron microscopy.

Species	Valve face and mantle	Rimoportula features	Seta structure: cross-section, wall pattern	Remarks on setae
C. decipiens	2,4	One, hollow, central	7,9, big poroids	T setae thicker
C. decipiens f. *singularis*	2,4	?	7,9, big poroids	–
C. lorenzianus	1,4	One, tubular, central	7,9, big poroids	–
C. lorenzianus f. *forceps*	1,4?	?	7,9	–
C. bermejensis	2,4	Numerous, small, central	6,8, poroids	–
C. compressus	1,4	One, hollow, excentric	6,8, poroids	SP setae thicker
C. didymus	1,5	One, hollow, central	7,9, poroids	T setae thicker
C. protuberans	1,5	One, hollow, central	7,9, poroids	T setae thicker
C. constrictus	–	–	–	–
C. vanheurcki	?	?	6,8?	–
C. affinis var. *affinis*	2,4	One, tubular, central	6,8, poroids	T setae thicker
C. affinis var. *willei*	–	One, excentric	6?,8, poroids?	–
C. paradoxus	1,5?	One, hollow, central	7,9, poroids	–
C. distans	1,4	One, slit-like, central	7,9, poroids	–
C. brevis	1,4	One, hollow, excentric	6,8, poroids	–
C. diadema	1,5?	One, hollow, central	7,9, poroids	–
C. seiracanthus	–	–	–	–
C. diversus	1,4	One, circular, central	6,9, poroids	SP setae thicker
C. messanensis	3,4	One, hollow, excentric	6,8, poroids	SP setae fused
C. pseudocrinitus	–	–	–	–
C. wighami	–	–	–	–
C. curvisetus	1,4	One, hollow, excentric	6,8, poroids	–
C. pseudocurvisetus	1	One, hollow, excentric	6,8, poroids	–
C. debilis	1,4	One, hollow, excentric	6,8, poroids	T setae reduced
C. rectus	2,4	One, beak-like, central	6,8, poroids	–
C. radicans	1	One, hollow, excentric	6, poroids	–
C. filiferus	2,4	One, elongate, central	6,8, poroids	–
C. socialis var. ?	1,4	?	6,8, poroids	One seta very long
C. gracilis	?	One, hollow, central	7,9?, poroids?	–
C. vistulae	1,4	One, tubular, central	7,9, poroids	–

1 = Costae pattern, 2 = Weak costae pattern, 3 = Thick costae pattern, 4 = Poroids between costae, 5 = Poroids at peripheral areas, 6 = Setae circular in cross-section, 7 = Setae polygonal in cross-section, 8 = Spiral pattern of spines, 9 = Longitudinal pattern of spines, SP = Special, T = Terminal. Taxa of subgenus *Hyalochaete* bear at least one rimoportula on terminal valves only.

Evensen & Hasle's (1975) observations. It is hoped that the new findings and observations made in this study will be useful when changes or additions to the present classification are being considered. One new section is proposed: *Peruviana*, to include some heterovalvar species within subgenus *Chaetoceros*.

The general classification, including the taxa studied and listed, plus those placed herein (*) in section *Peruviana*, is given below.

Chaetoceros Ehrenb.

Subgenus *Chaetoceros* (*Phaeoceros* Gran)

I. Section *Atlantica* Ostenf.
C. atlanticus var. *neapolitanus* (Schröd.) Hust.
C. atlanticus var. *skeleton* (F. Schütt) Hust.
C. dichaeta Ehrenb.

II. Section *Borealia* Ostenf.
C. octagonus Hern.-Bec.
C. densus Cleve
C. tetrastichon Cleve
C. seychellarus G. Karst.
C. denticulatus Lauder
C. rostratus Lauder
C. danicus Cleve

III. Section *Peruviana* Hern.-Bec.
C. aequatorialis Cleve *
C. convolutus Castrac.
C. concavicornis L. Mangin
C. criophilus Castrac. *
C. curvatus Castrac. *
C. peruvianus Brightw.
C. pendulus G. Karst.

IV. Section *Coarctata* Hern.-Bec.
C. coarctatus Lauder

Subgenus *Hyalochaete* Gran

V. Section *Dicladia* (Ehrenb.) Gran
C. decipiens Cleve
C. decipiens f. *singularis* Gran
C. lorenzianus Grunov
C. lorenzianus f. *forceps* Meunier

VI. Section *Cylindrica* Ostenf.
C. bermejensis Hern.-Bec.

VII. Section *Compressa* Ostenf.
C. compressus Lauder

VIII. Section *Protuberantia* Ostenf. emend. Hern.-Bec.
C. didymus Ehrenb.
C. protuberans Lauder

IX. Section *Constricta* Gran
C. constrictus Gran
C. vanheurckii Gran

X. Section *Stenocincta* Ostenf.

C. affinis Lauder var. *affinis*
C. affinis var. *willei* (Gran) Hust.
C. paradoxus Cleve

XI. Section *Laciniosa* Ostenf.
C. distans Cleve
C. brevis F. Schütt

XII. Section *Diadema* (Ehrenb.) Ostenf. emend. Gran
C. diadema (Ehrenb.) Gran
C. seiracanthus Gran

XIII. Section *Diversa* Ostenf.
C. diversus Cleve
C. messanensis Castrac.

XIV. Section *Brevicatenata* Gran
C. pseudocrinitus Ostenf.
C. wighami Brightw.

XV. Section *Curviseta* Ostenf. emend. Gran
C. curvisetus Cleve
C. pseudocurvisetus L. Mangin
C. debilis Cleve

XVI. Section *Anastomosantia* Ostenf.
C. rectus Hern.-Bec.

XVII. Section *Furcellata* Ostenf.
C. radicans F. Schütt
C. filiferus G. Karst.

XVIII. Section *Socialia* Ostenf.
C. socialis Lauder var. ?

XIX. Section *Simplicia* Ostenf.
C. gracilis F. Schütt
C. vistulae Apstein

Subgenus *Bacteriastroidea* Hern.-Bec.
C. bacteriastroides G. Karst.

Biogeography

Little effort has been made to assess the world distribution of *Chaetoceros* species, chiefly because many species have been recognized with uncertainty, while others are rather widespread or even cosmopolitan. Some species are, however, restricted to a given region or may be regarded as typically cold-water, warm-water or tropical forms, etc.

The following account of general distribution patterns is based on information widely available in the literature, together with my own observations. The taxa are grouped according to the major regions.

A. *North or south cold-water (occasionally found in temperate regions)*

C. adelianus Manguin
C. atlanticus Cleve
C. borealis Bailey
C. bulbosus (Ehrenb.) Heiden
C. castracanei G. Karst.
C. concavicornis L. Mangin
C. convolutus Castrac.
C. criophilus Castrac.
C. deflandrei Manguin
C. dichaeta Ehrenb.
C. flexuosus L. Mangin
C. gausii Heiden & Kolbe
C. hendeyi Manguin[1]
C. lawii Manguin
C. natatus Manguin[1]
C. neglectus G. Karst.
C. saltans Cleve ?

B. *Temperate to subtropical*

C. affinis Lauder var. *affinis*
C. anastomosans Grunov
C. brevis F. Schütt
C. constrictus Gran
C. curvisetus Cleve
C. danicus Cleve
C. debilis Cleve
C. decipiens Cleve
C. diadema (Ehrenb.) Gran
C. didymus Ehrenb.
C. distans Cleve
C. eibenii Grunov ?
C. filiferus G. Karst.
C. gracilis F. Schütt
C. laciniosus F. Schütt
C. lorenzianus Grunov
C. pelagicus Cleve
C. protuberans Lauder
C. pseudocurvisetus L. Mangin
C. radicans F. Schütt
C. socialis Lauder
C. vistulae Apstein

C. *World-wide warm water (occasionally found in temperate regions)*

C. atlanticus var. *neapolitanus* (Schröd.) Hust.
C. atlanticus var. *skeleton* (F. Schütt) Hust.
C. compressus Lauder
C. costatus Pavill.
C. pendulus G. Karst.[2]
C. peruvianus Brightw.[3]
C. rostratus Lauder
C. messanensis Castrac.

D. *Tropical and subtropical*

C. bacteriastroides G. Karst.?
C. buceros G. Karst.
C. coarctatus Lauder
C. dadayi Pavill.
C. denticulatus Lauder
C. diversus Cleve
C. paradoxus Cleve
C. seychellarus G. Karst.[2]
C. tetrastichon Cleve

[1]Originally described from Antarctic waters (Manguin, 1960), with only one known record. [2]Reported by Manguin (1954) from a cold-water area. [3]Reported by Sournia et al. (1979) from a temperate to cold-water area.

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