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The genus *Chaetoceros* (Bacillariophyta) from Peter the Great Bay, Sea of Japan

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Abstract

Several studies in the Sea of Japan have dealt with the taxonomy, morphology and ecology of *Chaetoceros* species. In this study, a total of 33 *Chaetoceros* taxa was recorded between 1991 and 2004 from the phytoplankton of Peter the Great Bay, in the northwestern part of the Sea of Japan. This investigation was based on light and electron microscopy. *Chaetoceros minimus* is a new record for the Pacific Ocean, *C. compressus* var. *hirtisetus* is a new record for the seas of Russia, and *C. socialis* f. *radians* is a new record for the northwestern Sea of Japan. Diagnostic descriptions, illustrations and distribution are provided for all 33 *Chaetoceros* taxa from the study area.

Keywords: *Chaetoceros*; diatoms; morphology; Sea of Japan.

Introduction

The diatom genus *Chaetoceros* Ehrenberg is one of the most diverse and widespread groups among marine phytoplankton. Its species are distributed globally and they often dominate in coastal ecosystems (Evensen and Hasle 1975, Guillard and Kilham 1977, Rines and Hargraves 1988, Hernández-Becerril 1996, Hasle and Syvertsen 1997, Bérard-Therriault et al. 1999). The predominance of the genus *Chaetoceros* in the Sea of Japan, recorded from the Early Miocene, is also typical of the modern diatom phytoplanktonic assemblages (Zjuze 1959). Few studies have been performed on the genus *Chaetoceros* in the Sea of Japan. However, *Chaetoceros* species have been reported as winter, spring and summer dominant elements of the phytoplanktonic assemblages in the region (Kiselev 1934, Orlova 1984, Konovalova 1987, Shevchenko et al. 2004). Morphological studies of some *Chaetoceros* taxa have been made by Orlova (1987), Orlova (1988), Konovalova et al. (1989) and Orlova and Selina (1993).

Identification at the species level within the genus *Chaetoceros* is often not an easy task and mainly based on gross morphology investigated by light microscopy (LM). Some morphological characters of taxonomical value can only be detected in detail using electron microscopy (EM). The main objective of this study is to provide new information on the morphology, taxonomy and distribution of *Chaetoceros* taxa in Peter the Great Bay, Sea of Japan.

Materials and methods

Phytoplankton samples were collected at 17 stations in Peter the Great Bay, Sea of Japan, between September 1991 and October 2004 (Figure 1, Table 1). A total of 421 quantitative and qualitative samples were taken with a 4-l sampling bottle from 0.5, 2 and 6 m depths and by a 20 μm net hauled in the upper 5 m of the water column. Water samples were preserved in a Lugol's solution with sodium acetate and buffered formaldehyde. Phytoplankton samples were concentrated following the sedimentation method of Utermöhl (1958) or by a reverse filtration, using a 2 μm Nuclepore membrane (Pleasaton, USA) as described by Sukhanova (1983).

The routine observation and identification of *Chaetoceros* species were made using an Olympus BX 41 light microscope (Olympus, Tokyo, Japan), operating with brightfield optics. Phytoplankton samples were cleaned of organic matter and prepared following the method described by Hasle and Fryxell (1970) for transmission (TEM) and scanning (SEM) electron microscopy. Some cleaned phytoplankton material was dried onto formvar-coated grids and examined with a TEM (JEM-100, JEOL, Tokyo, Japan), while other material was concentrated and dried on Nuclepore filters. For observation of whole cells, some material was dehydrated in ethanol (25, 50, 75, 96% for 10 min in each solution and twice in absolute alcohol for 30 min), concentrated on Nuclepore filters and dried in open air. Filters were attached on metallic stubs, coated with gold and examined with a SEM (Leo-430, Carl Zeiss, Cambridge, UK).

Terminology of the diatom valves follows the works of Anonymous (1975) and Ross et al. (1979), with a specific terminology for *Chaetoceros* proposed by Rines and Hargraves (1988) and Hernández-Becerril (1996).

Results

A total of 33 taxa of *Chaetoceros* have been identified for Peter the Great Bay (Sea of Japan) since the first phytoplankton sampling was made in September 1991. Five of these species (*C. affinis*, *C. atlanticus*, *C. decipiens*, *C. didymus* and *C. salsugineus*) were studied previously in detail for their morphology (Orlova 1987, 1988, Orlova

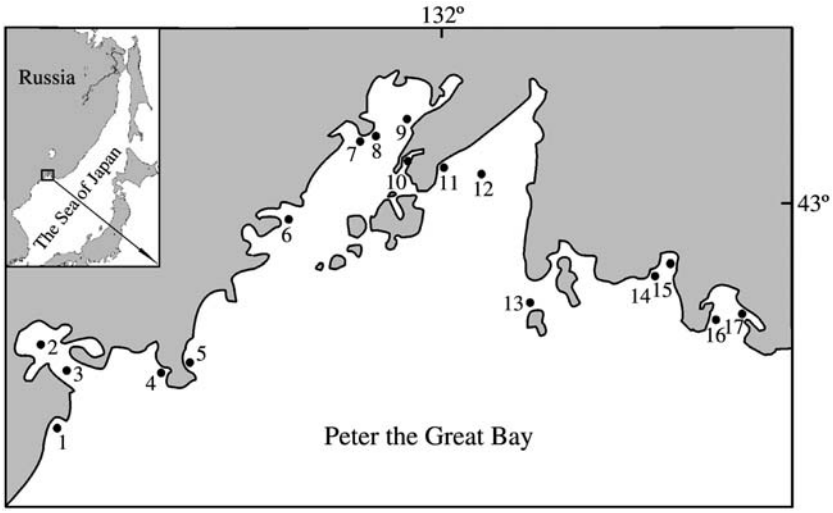


Figure 1 Location of the sampling stations in Peter the Great Bay, Sea of Japan.

and Selina 1993). Short diagnostic descriptions are given for all species observed during this study. The data on cell dimensions (width of cell measured along apical axis and cell height on the pervalvar axis) are presented in Table 2. Seasonal occurrences of *Chaetoceros* species in Peter the Great Bay are provided in Table 3.

Subgenus *Chaetoceros* (*Phaeoceros* Gran)

Cells large and robust. Setae long, thick and covered with spines. Small and numerous chloroplasts also present in the setae. One rimoportula on each valve. Resting spores known only for *C. eibenii*. Mainly oceanic.

Chaetoceros atlanticus Cleve var. *atlanticus* (Figures 2–4)

References Cleve (1873), p. 11, pl. 2, fig. 8; Evensen and Hasle (1975), p. 157, figs 6–11; Koch and Rivera (1984), p. 63, figs 1–5; Orlova (1987), p. 68, pl. I, figs 5–7; Takano (1990), p. 282; Bérard-Therriault et al. (1999), p. 42, pl. 23, figs d, e, pl. 24, fig. d.

LM Colony straight and robust. Cells rectangular in girdle view with valve slightly concave or flat with a central undulation, mantle high. Cells elliptical in valve view. Foramina wide and hexagonal. Terminal and intercalary setae similar, long, thick, with long basal part. Setae cross over at the colony axis, diverge at an angle of 45° from the colony axis (Figure 2).

EM Valve and mantle perforated by numerous small poroids (Figure 3). Valve edge with a hyaline rim. Rimoportula centrally located with an external simple tube and an internal elliptical hole. Setae four-sided in cross-section, perforated with poroids, bearing spines (Figure 4).

Distribution *Chaetoceros atlanticus* occurred at all stations from winter to summer with up to 8000 cells l^{-1} in spring; not rare.

Chaetoceros atlanticus var. *neapolitanus* (Schröder) Hustedt (Figure 5)

References Hustedt (1930), p. 645, fig. 366; Hernández-Becerril (1996), p. 4, pls 2, 3.

Table 1 Position of the sampling stations in Peter the Great Bay, Sea of Japan.

Station no.	Sampling date	No samples	Latitude N	Longitude E
1	June–July 1996	6	42°08′	130°48′
2	July 1993	3	42°39′	130°45′
3	July 1996	1	42°36′	130°49′
4	August–December 1979	86	42°36′	131°10′
5	July 1993	2	42°35′	131°15′
6	March 1992	1	43°01′	131°35′
7	June 1992	1	43°09′	131°44′
8	September 1991	1	43°12′	131°45′
9	January 1996–May 1998	296	43°11′	131°54′
10	June 1992	1	43°06′	131°53′
11	September 1991	1	43°10′	132°05′
12	May 1996	1	42°05′	132°10′
13	September 1994	1	42°47′	132°20′
14	July 1992	1	42°52′	132°43′
15	August 1993	1	42°54′	132°44′
16	September–October 2004	2	42°45′	132°55′
17	September–October 2004	16	42°45′	133°02′

Table 2 Morphometric data of *Chaetoceros* taxa in Peter the Great Bay, Sea of Japan.

Taxa	Cell size Axis (μm)	
	Apical	Pervalvar
Subgenus *Chaetoceros*		
C. atlanticus var. *atlanticus*	18–40	25–45
C. atlanticus var. *neapolitanus*	7–10	6–25
C. concavicornis	12–30	20–30
C. convolutus	15–30	20–35
C. peruvianus	15–35	15–40
C. rostratus	15–25	10–35
Subgenus *Hyalochaete*		
C. affinis	10–30	12–30
C. anastomosans	10–16	10–20
C. compressus var. *compressus*	20–35	10–35
C. compressus var. *hirtisetus*	10–25	10–35
C. constrictus	15–25	15–30
C. curvisetus	10–30	12–35
C. debilis	12–30	10–25
C. decipiens	20–50	20–45
C. diadema	20–40	20–35
C. didymus	10–35	8–12
C. diversus	10–12	6–18
C. furcillatus	10–20	8–15
C. laciniosus	10–25	15–25
C. lorenzianus	15–50	10–55
C. messanensis	12–35	6–40
C. minimus	2–8	6–24
C. protuberans	10–35	8–12
C. pseudocrinitus	8–25	10–45
C. pseudocurvisetus	15–35	15–30
C. radicans	12–22	12–20
C. salsugineus	3–7	4–9
C. socialis f. *socialis*	5–10	5–10
C. socialis f. *radians*	5–12	5–16
C. subtilis	4–12	8–20
C. teres	10–35	15–50
C. tortissimus	14–25	–
C. vanheurckii	10–30	15–30

Synonym *Chaetoceros neapolitanus* Schröder (1900), p. 29, pl. 1, fig. 4.

LM Colony straight. Cells rectangular and elongate in girdle view, mantle low. Foramina high and hexagonal. Setae long, thick, with long basal part. Setae cross over at the colony axis, diverge almost perpendicularly to the colony axis (Figure 5).

EM Valve and mantle perforated by small poroids. Rimoportula in the central part of the valve. Setae four-sided in cross-section, perforated with poroids, bearing spines (Hernández-Becerril 1996).

Remarks *Chaetoceros atlanticus* var. *neapolitanus* differs from *C. atlanticus* var. *atlanticus* by the foramina shape and divergence of the setae. Also the *C. atlanticus* var. *neapolitanus* cells are more elongate and smaller in comparison to *C. atlanticus* var. *atlanticus* cells.

Distribution *Chaetoceros atlanticus* var. *neapolitanus* was found at stations 1 and 4 in summer, with about 100 cells l^{-1}; very rare.

***Chaetoceros concavicornis* Mangin (Figures 6–9)**

References Mangin (1917), p. 704, figs 5 (l), 6, 7; Evensen and Hasle (1975), p. 158, figs 15–22; Hernández-Becerril (1996), p. 21, pl. 15, figs 4, 5; Bérard-Therriault et al. (1999), p. 44, pl. 26, fig. e, pl. 27, figs a, c-e; Horner (2002), p. 69; Gogorev (2004), p. 88, tabs I, II, figs 1–7.

LM Colony straight and short. Cells heterovalvate with the anterior valve convex and broadly elliptical, and the posterior valve flat, mantle high. Foramina reduced and slightly elongated. Terminal and intercalary setae similar, thick, heavy, with short basal part. Setae arise near to the center on the anterior valve and raised closer to the cell corners on the posterior valve. All setae directed toward the posterior end of the colony.

EM Valves perforated by poroids (Figure 7). Girdle bands not distinguishable (Figure 6). Rimoportula located eccentrically with an externally tube-like structure and an internally elliptical hole (Figure 7). Setae four-sided in cross-section and transversely striated with two rows of poroids between the costae, bearing large spines on the edges (Figures 8 and 9).

Distribution *Chaetoceros concavicornis* occurred at stations 1, 4 to 9, and 13 to 15 in winter, spring and summer at about 1000 cells l^{-1}; rare.

***Chaetoceros convolutus* Castracane (Figures 10–12)**

References Castracane (1886), p. 78; Fryxell and Medlin (1981), p. 9, figs 6–8, 43–49; Koch and Rivera (1984), p. 67, figs 23–35; Hernández-Becerril (1996), p. 21, pl. 15, figs 1–3; Bérard-Therriault et al. (1999), p. 45, pl. 27, fig. b, pl. 28, figs a, b; Horner (2002), p. 70; Gogorev (2004), p. 93, tab. IV.

LM Colony short and straight, sometimes twisted. Cells heterovalvate with anterior valve convex and posterior valve flat, mantle high. Foramina very narrow and almost absent. Terminal and intercalary setae similar, thick, with short basal part. Setae arise from near to the center and are bent toward the posterior end of the colony.

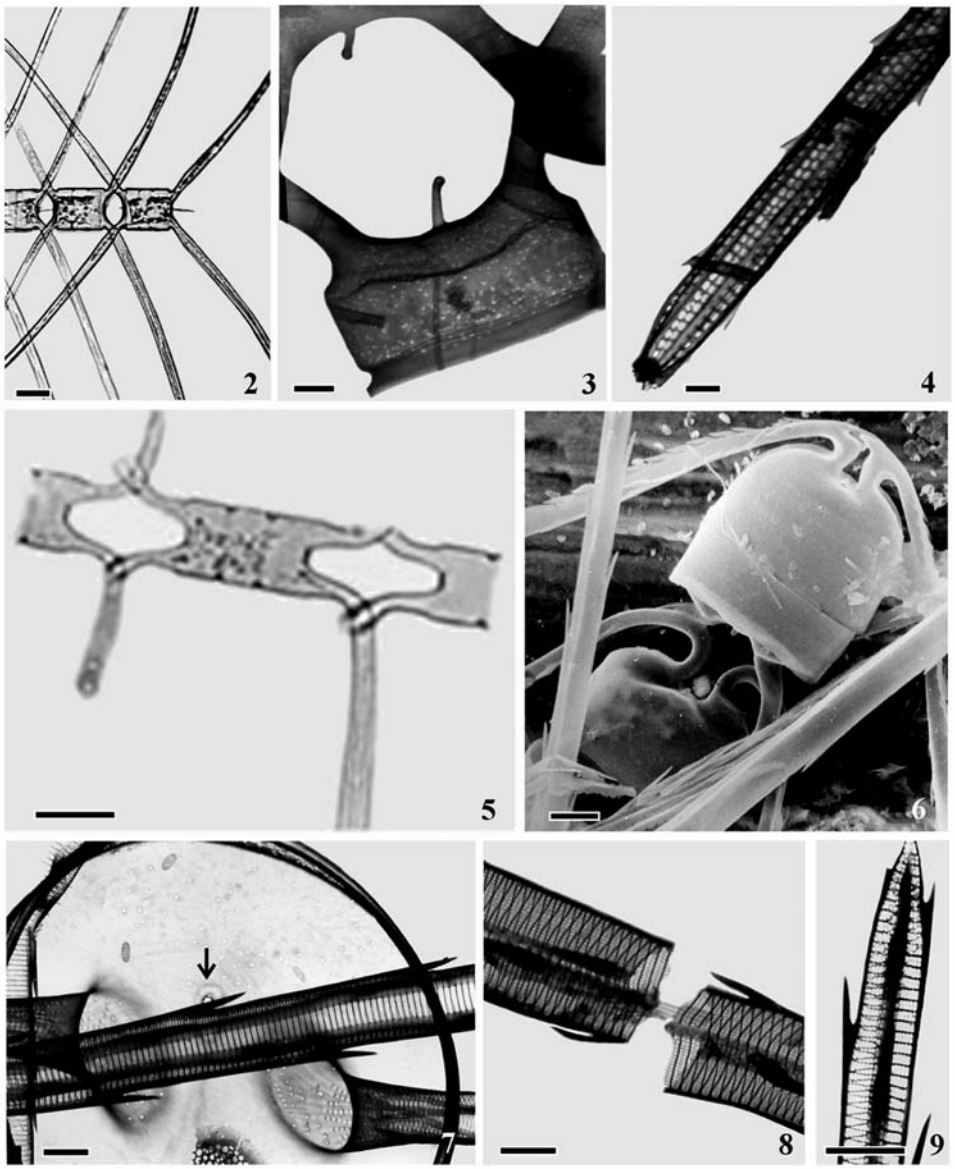
EM Valves perforated by poroids (Figure 11). Girdle zone clearly distinguishable (Figure 10). Sibling valves held together by prehensors on setae of posterior valves (Fryxell and Medlin 1981, Hernández-Becerril 1996, Gogorev 2004). Rimoportula stellate, round structure internally (Figure 12). Setae four-sided in cross-section, bearing large spines and perforated with poroids.

Remarks *Chaetoceros convolutus* and *C. concavicornis* are very similar in gross morphology. Differences in LM are the shape of the foramina and a clearly distinguishable girdle zone for *C. convolutus*. Both species can be distinguished under electron microscopy by the presence of prehensors and a stellate rimoportula in *C. convolutus*.

Table 3 Seasonal occurrence of *Chaetoceros* taxa in Peter the Great Bay, Sea of Japan, and their worldwide geographical distribution.

Taxa	January	February	March	April	May	June	July	August	September	October	November	December	Geography
Subgenus *Chaetoceros*													
C. atlanticus var. *atlanticus*	■	■	■	■	■	■	■	■					C
C. atlanticus var. *neapolitanus*								■					W
C. concavicornis		■	■	■	■	■	■	■					N, T
C. convolutus	■	■	■	■	■							■	C
C. peruvianus	■			■		■	■	■	■	■	■	■	C
C. rostratus								■					W
Subgenus *Hyalochaete*													
C. affinis	■	■	■	■	■	■	■	■	■	■	■	■	C
C. anastomosans							■	■	■				W, T
C. compressus var. *compressus*	■	■	■	■	■	■	■	■	■	■	■	■	N, T
C. compressus var. *hirtisetus*					■	■							T
C. constrictus				■	■	■	■		■	■	■		T
C. curvisetus							■	■	■	■	■		C
C. debilis	■	■	■	■	■				■	■	■	■	N, T
C. decipiens	■	■	■	■	■	■	■	■	■	■	■	■	C
C. diadema	■	■		■	■			■	■	■		■	C
C. didymus	■	■	■	■	■	■	■	■	■	■	■	■	C
C. diversus								■	■				W
C. furcillatus			■	■		■							N
C. laciniosus							■	■	■	■	■		T
C. lorenzianus					■	■		■	■	■	■		W, T
C. messanensis								■					W
C. minimus					■	■							T
C. protuberans					■	■	■	■	■	■			W, T
C. pseudocrinitus	■	■	■	■	■						■	■	N, T
C. pseudocurvisetus							■	■					W
C. radicans		■		■		■	■	■	■	■	■	■	C
C. salsugineus						■	■	■	■	■	■		T
C. socialis f. *socialis*	■	■	■	■	■		■	■	■	■	■		C
C. socialis f. *radians*		■	■	■						■	■	■	N, T
C. subtilis						■	■	■	■	■			T
C. teres	■	■	■	■	■					■	■		N, T
C. tortissimus	■			■	■						■	■	T
C. vanheurckii						■	■		■				T

C: cosmopolitan; N: north cold-water; T: temperate; W: tropical warm-water.



Figures 2–9 *Chaetoceros* taxa from Peter the Great Bay.
Figures 2, 5, LM; Figures 3, 4, 7–9, TEM; Figure 6 SEM. Scale bars=10 μm (Figures 2, 5); 5 μm (Figures 3, 6, 7); 1 μm (Figures 4, 8, 9).
(2–4) *Chaetoceros atlanticus* var. *atlanticus*. (2) Part of a colony. (3) Sibling valves in girdle view with long, tube-like rimoportulae. (4) Seta with spines and straight rows of poroids. (5) *Chaetoceros atlanticus* var. *neapolitanus*, broken colony. (6–9) *Chaetoceros concavicornis.* (6) Two cells of a colony. (7) Internal view of valve with elongated rimoportula (arrow) and setae crossing through the valve center. (8) Broken four-sided seta showing spines and rows of poroids. (9) Tip of a seta.

Distribution *Chaetoceros convolutus* was found at stations 1, 4, 6 to 10 and 13 to 15 in winter and spring with up to 10 000 cells l^{-1} in spring; not rare.

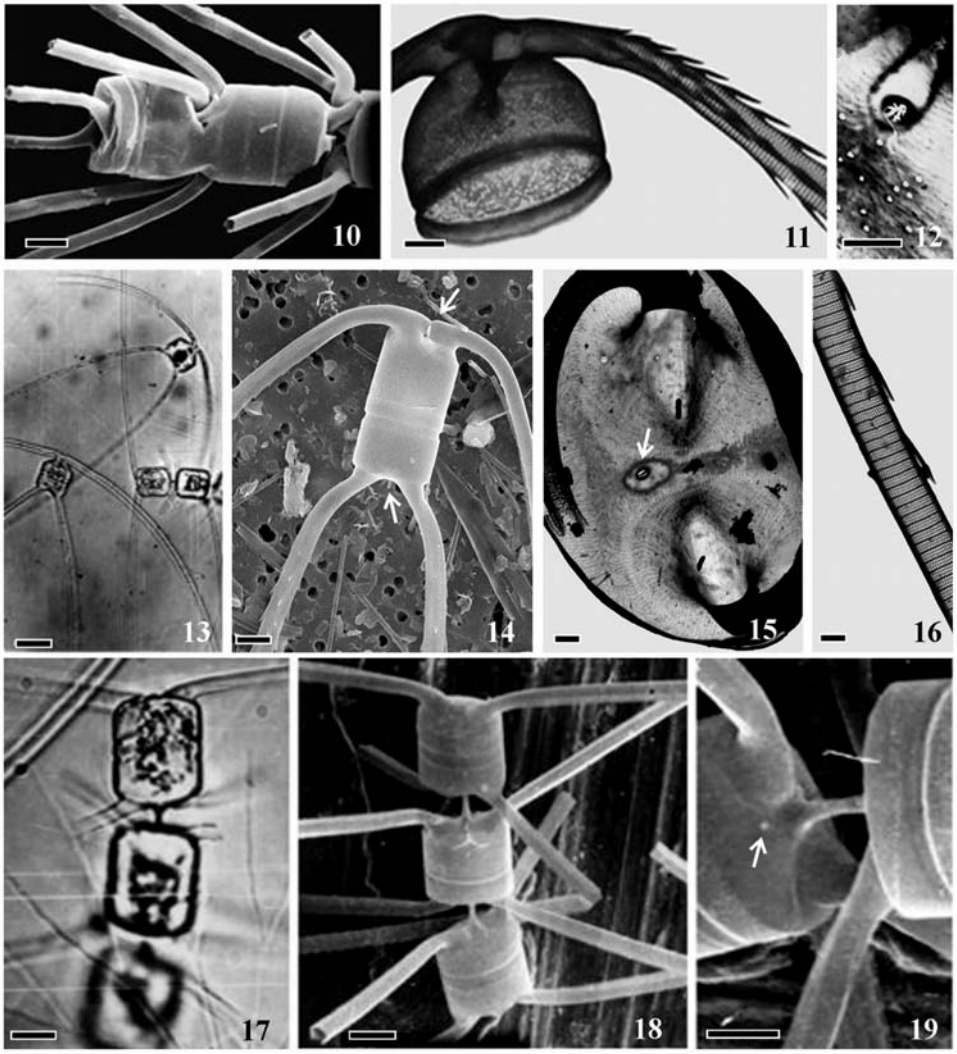
Chaetoceros peruvianus Brightwell (Figures 13–16)

References Brightwell (1856), p. 107, pl. 7, figs 16–18; Koch and Rivera (1984), p. 69, figs 36–47; Hernández-Becerril 1996, p. 22, pls 16, 17; Hernández-Becerril and Granados (1998), p. 511, fig. 24.

LM Cells solitary and heterovalvate. Cells cylindrical in girdle view. Terminal and intercalary setae similar, long, thick, with short basal part. Anterior setae fuse together after a short base in the valve center, posterior setae arise near to the corners, all directed toward the posterior end of the cell (Figure 13).

EM Anterior valve convex and posterior valve flat or concave, mantle high (Figure 14). Valves perforated by poroids. Rimoportula eccentrically located within the annulus, protruding externally in a tube and opening internally as a simple hole (Figure 15). Setae four-sided in cross-section, bearing spines and transversely striated with three rows of poroids between the costae (Figure 16).

Remarks *Chaetoceros peruvianus* cells from Peter the Great Bay appeared to be considerately larger (Table 2)



Figures 10–19 *Chaetoceros* taxa from Peter the Great Bay.
Figures 13, 17, LM; Figures 11, 12, 15, 16, TEM; Figures 10, 14, 18, 19, SEM. Scale bars=10 μm (Figures 10, 13, 14, 17, 18); 5 μm (Figures 11, 19); 1 μm (Figures 12, 15, 16).
(10–12) *Chaetoceros convolutus*. (10) Part of a colony with setae. (11) Valve showing the insertion of the setae. (12) Stellate rimoportula. (13–16) *Chaetoceros peruvianus*. (13) Solitary cells. (14) Cell in girdle view, note the insertion of the setae and the rimoportulae (arrows). (15) Valve with rimoportula (arrow). (16) Seta with spines and rows of poroids. (17–19) *Chaetoceros rostratus*. (17) Cells in a colony. (18) Sibling valves with long, central linking process, and setae. (19) Sibling valves showing the insertion of the setae and the small rimoportula (arrow).

than reported in the literature (Cupp 1943, Hernández-Becerril 1996, Hasle and Syvertsen 1997).

Distribution *Chaetoceros peruvianus* was present throughout the year at stations 1 to 16 with up to 10 000 cells l^{-1} in mid-summer; not rare.

Chaetoceros rostratus Lauder (Figures 17–19)

References Lauder (1864), p. 79, tab. 8, fig. 10; Giuffré and Ragusa (1988), p. 503; Rines and Hargraves (1988), p. 55, figs 105–107; Hernández-Becerril (1996), p. 16, pls 11, 12; Hernández-Becerril and Granados (1998), p. 509, figs 19–23.

LM Colony short and straight. Cells hexagonal in girdle view with a process at valve center connecting sibling cells, mantle high. Intercalary and terminal setae similar, thick, straight, with short basal part. Setae not touching each other, but arising close to the corners and diverging perpendicularly to the colony axis (Figure 17).

EM Valve elliptical. Connecting processes thin and long, absent at the terminal valve (Figure 18). Rimoportula slightly eccentric (Figure 19). Setae four- or five-sided in cross-section, bearing large spines on the edges.

Distribution *Chaetoceros rostratus* was only found at station 4 in summer with about 100 cells l^{-1}; very rare.

Subgenus *Hyalochaete* Gran Cells weakly silicified, variable in size. Setae thin, hair-like, mostly without chloroplasts, smooth or covered with small spines. Chloroplasts one or few plate-like or numerous granules. Terminal valves with one or several rimoportulae. Resting

spores known for most of the species. Mainly in coastal waters.

***Chaetoceros affinis* Lauder (Figures 20–24)**

References Lauder (1864), p. 78, pl. 8, fig. 5; Evensen and Hasle (1975), p. 161, figs 46–54; Rines and Hargraves (1988), p. 59, figs 113, 114; Hernández-Becerril (1996), p. 35, pls 27, 28; Jensen and Moestrup (1998), p. 20, figs 30–43; Bérard-Therriault et al. (1999), p. 42, pl. 22, fig. g, pl. 23, figs b, c; Horner (2002), p. 82.

LM Colony straight and usually long. Cells rectangular in girdle view, slightly concave in the central part, mantle high. Foramina narrow and elliptical. Setae long, thin, with short basal part. Terminal setae thicker than intercalary ones, curving smoothly to the colony axis. Intercalary setae diverge at an angle of 10–30° to the colony axis. Setae cross over at the colony margin. One large chloroplast (Figure 20).

EM Valve face elliptical, with numerous spines, perforated by poroids. Rimoportula centrally located, tube-like structure externally (Figure 22). Terminal setae polygonal in cross-section, bearing large spines. Intercalary setae circular in cross-section, with rows of small spines and regular poroids (Figure 23).

Resting spores spiny, primary valve dome-shaped convex (Figure 21), secondary valve convex with one row of poroids between the mantle and the valve face (Figure 24).

Distribution *Chaetoceros affinis* occurred at all stations throughout the year with blooms in mid-summer and early autumn with up to 1.5×10^6 cells l^{-1}; not rare.

***Chaetoceros anastomosans* Grunow (Figures 25–30)**

References Grunow (1882) *In* Van Heurck (1880–1885), pl. 82, figs 6–8; Hernández-Becerril and Granados (1998), p. 517, figs 53, 54; Hernández-Becerril and Aké-Castillo (2001), p. 57, figs 1–6; Horner (2002), p. 79.

Synonyms *Chaetoceros externus* Gran (1897), p. 25, pl. 3, figs 44, 45. *Chaetoceros anastomosans* var. *externa* (Gran) Hustedt (1930), p. 743, fig. 430.

LM Colony straight or slightly curved. Cells rectangular in girdle view with elongate corners, mantle inconspicuous. Foramina wide, elongated and octagonal. Setae long, thin, straight, thinner at the base and thicker distally, with long basal part. Sibling intercalary setae not crossing, connected by bridges; diverge almost perpendicularly to the colony axis (Figure 25). Two chloroplasts per cell (Hernández-Becerril and Aké-Castillo 2001).

EM Valve elliptical to round, flat, with a pattern of costae radiating from the annulus to the margins (Figures 26, 27). Rimoportula centrally located, internally slit-like structure (Figure 27). Setae round in cross-section, with rows of small pores and spines spirally arranged, and larger pores distributed randomly (Figures 28, 29).

Resting spores with equal convex valves, smooth (Figure 30).

Remarks According to the literature, the resting spores of *Chaetoceros anastomosans* bear numerous spines (Hustedt 1930, Cupp 1943, Oku and Kamatani 1997). Our observations revealed that the surface of the resting spores of specimens from Peter the Great Bay are smooth.

Distribution *Chaetoceros anastomosans* was found at stations 4, 14 and 15 in summer and autumn at about 100 000 cells l^{-1} in late summer; rare.

***Chaetoceros compressus* Lauder var. *compressus* (Figures 31–34)**

References Lauder (1864), p. 78, pl. 8, figs 6a, b; Rines and Hargraves (1988), p. 64, figs 131–134, 218; Hernández-Becerril (1996), p. 32, pls 25, 26.

LM Colony straight or slightly twisted, usually long. Cells rectangular in girdle view, mantle low. Foramina from narrow to wide. Two types of intercalary setae: special intercalary setae long, thick, twisted, bearing large spines, diverge parallel to the colony axis and common intercalary setae, thinner, diverge almost perpendicularly to the colony axis. Terminal setae diverge widely and subsequently become parallel to the colony axis. Setae with long basal part, cross over inside the colony margin. Several chloroplasts (Figure 31).

EM Valve face flat to convex, elliptical (Figure 32). Rimoportula small tube-like structure, eccentrically located (Hernández-Becerril 1996). Setae circular in cross-section, bearing spines, common intercalary setae perforated by large pores and spiral rows of small poroids (Figures 33, 34).

Resting spores smooth, with primary valve highly convex and secondary valve slightly convex (Cupp 1943, Rines and Hargraves 1988).

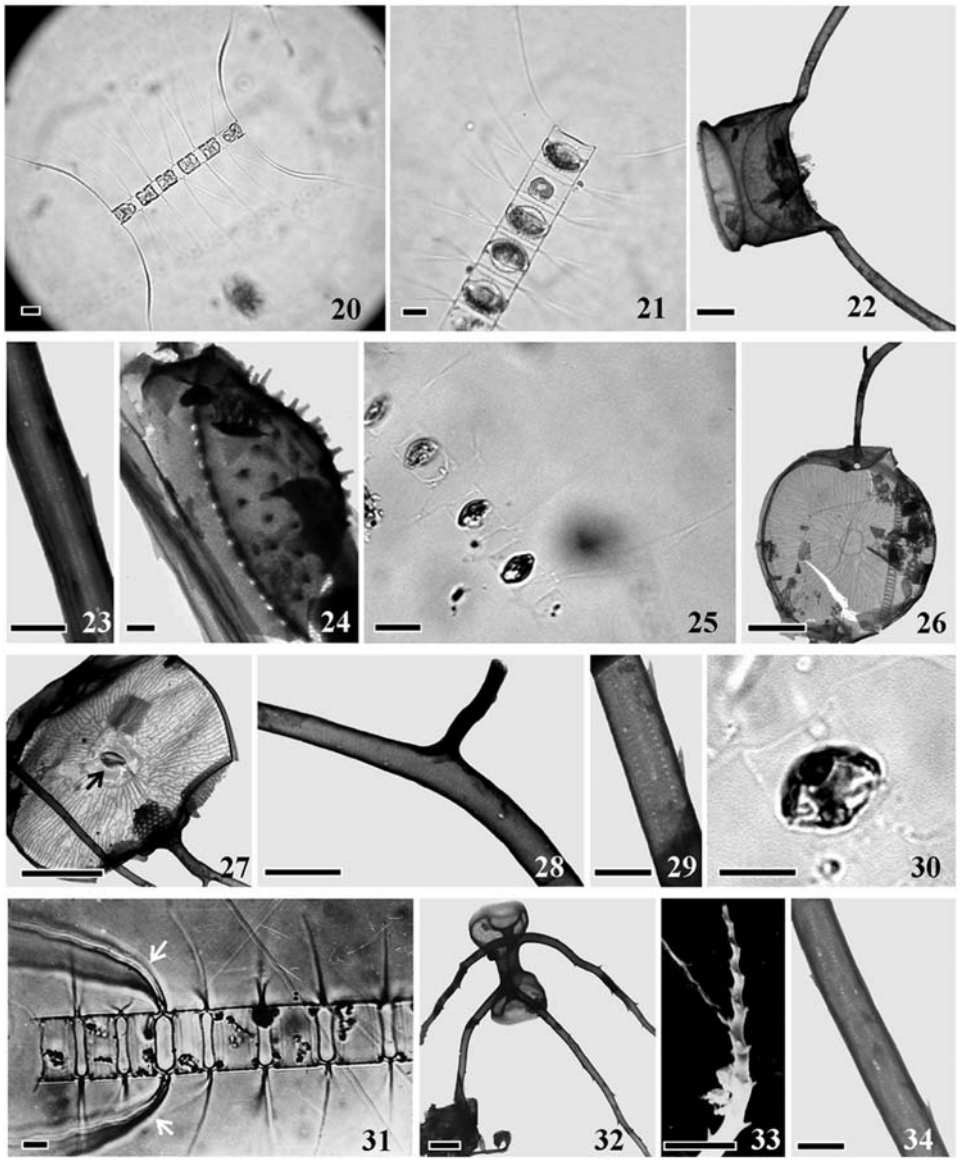
Distribution *Chaetoceros compressus* was found at all stations throughout the year with maximum values up to 900 000 cells l^{-1} in late summer and autumn; not rare.

***Chaetoceros compressus* var. *hirtisetus* Rines *et* Hargraves (Figures 35–39)**

Reference Rines and Hargraves (1990), p. 121, figs 1–29.

Synonym *Chaetoceros* sp. "C", Rines and Hargraves (1988), p. 104, figs 212–217.

LM Colony relatively long, straight or twisted. Cells rectangular in girdle view, mantle low (Rines and Hargraves 1990). Foramina narrow with a central constriction. Intercalary setae of two different types, the common setae long, thin, and the special setae thicker and shorter, with large spines, spirally twisted. Terminal setae shorter and thinner than the others, with spiral pattern of large spines. Setae cross over inside the colony margin.



Figures 20–34 *Chaetoceros* taxa from Peter the Great Bay.
Figures 20, 21, 25, 30, 31, LM; Figures 22–24, 26–29, 32, 34, TEM; 33, SEM. Scale bars=10 μm (Figures 20, 21, 25, 30–32), 5 μm (Figures 22, 26, 27), 1 μm (Figures 23, 24, 28, 29, 33, 34).
(20–24) *Chaetoceros affinis*. (20) A complete colony. (21) Part of colony with resting spores. (22) Terminal valve of a colony with spines and tube-like rimoportula. (23) Seta with spines and large poroids. (24) Secondary valve of a resting spore covered with spines. (25–30) *Chaetoceros anastomosans*. (25) Part of a colony with resting spores. (26) Intercalary valve. (27) Terminal valve with slit-like rimoportula (arrow). (28) Structure of a seta close to the bridge. (29) Seta with spines and rows of poroids. (30) Smooth resting spore. (31–34) *Chaetoceros compressus* var. *compressus*. (31) Cells in a colony with special setae (arrows). (32) Sibling valves with special setae. (33) Distal end of a special seta. (34) Common intercalary seta with spiral rows of spines and poroids.

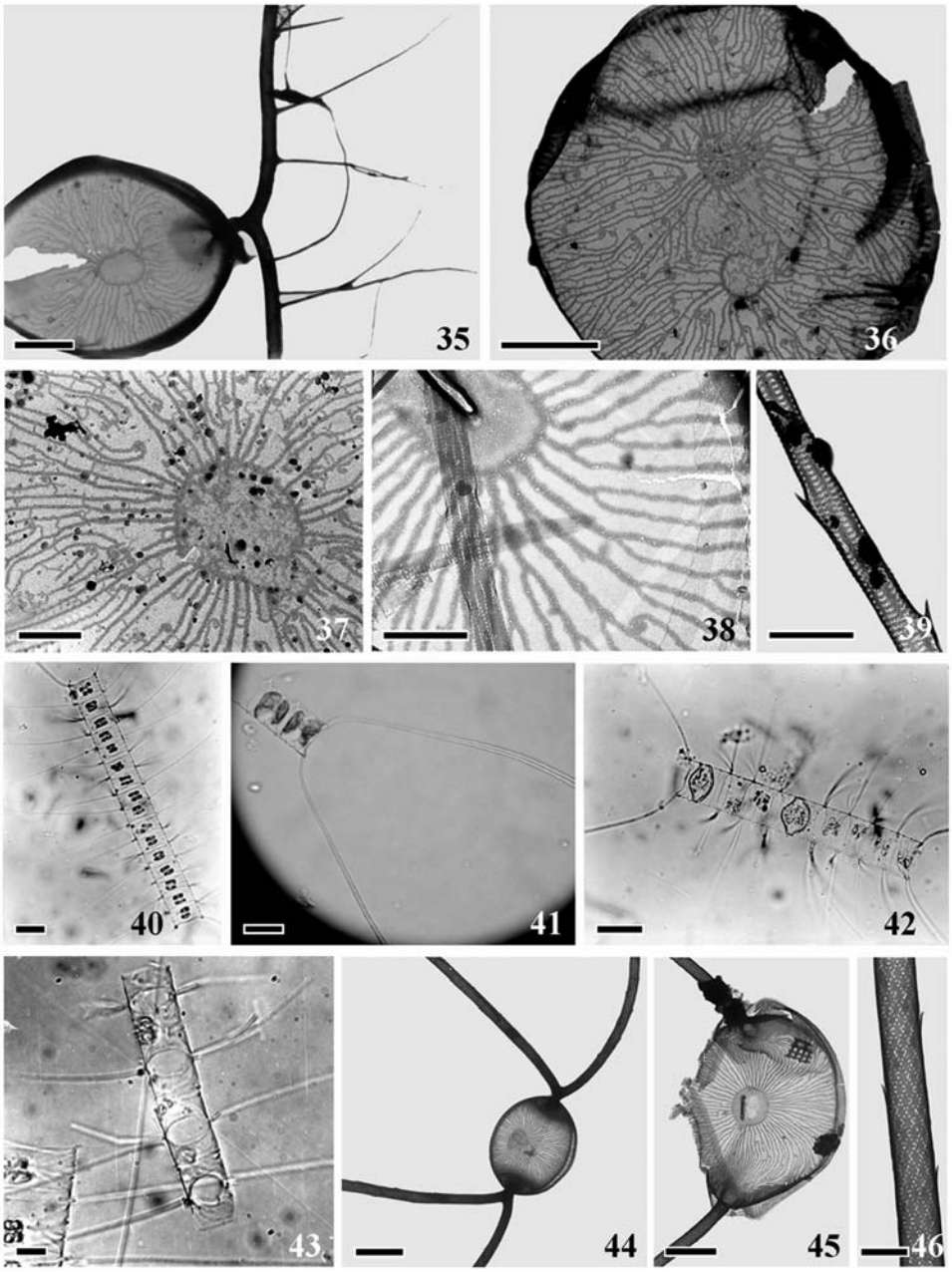
Chloroplasts small and numerous (Rines and Hargraves 1990).

EM Valve broadly elliptical or round, flat or slightly convex, with a pattern of costae radiating from the annulus to the margins (Figures 35–37). One or several annuli present on intercalary valves (Figures 35, 36). Rimoportula simple tube externally, slit-like structure internally (Figure 38). The common intercalary setae bearing small spines, perforated with poroids (Figure 39), and with capilli at the proximal part. Setae circular in cross-section.

Resting spores with equal convex valves. Primary valve with long bifurcate spines, originating at the mantle and secondary valve smooth (Rines and Hargraves 1990).

Remarks *Chaetoceros compressus* var. *hirtisetus* shows similarity to *C. compressus* var. *compressus* and *C. radicans*. *C. compressus* var. *hirtisetus* is distinguishable from *C. compressus* var. *compressus* by the presence of capilli on the setae, and from *C. radicans* by the number of chloroplasts and presence of heavy twisted intercalary setae.

Distribution *Chaetoceros compressus* var. *hirtisetus* occurred at stations 9, 14 and 15 in spring and summer with 100 cells l^{-1} in summer; rare.



Figures 35–46 *Chaetoceros* taxa from Peter the Great Bay.
Figures 40–43, LM; Figures 35–39, 44–46, TEM. Scale bars=10 μm (Figures 40–44), 5 μm (Figures 35, 36, 45), 1 μm (Figures 37–39, 46).
(35–39) *Chaetoceros compressus* var. *hirtisetus*. (35) Valve showing capilli on intercalary setae. (36) Valve with costae and two annuli. (37) Part of intercalary valve showing structure of annulus and pattern of costae. (38) Part of terminal valve with rimoportula. (39) Intercalary seta with spines and perforated by poroids. (40–42) *Chaetoceros constrictus.* (40) A complete colony. (41) Part of a colony, note long terminal setae. (42) Colony with some resting spores. (43–46) *Chaetoceros curvisetus*. (43) Cells in a colony. (44) Valve with costae. (45) Terminal valve with rimoportula. (46) Intercalary seta with spines and spirally arranged poroids.

Chaetoceros constrictus Gran (Figures 40–42)

References Gran (1897), p. 17, pl. 1, figs 11–13, pl. 3, fig. 42; Rines and Hargraves (1988), p. 67, figs 128–130; Hernández-Becerril (1996), p. 65, pl. 29, fig. 6; Jensen and Moestrup (1998), p. 31, figs 89–94; Bérard-Therriault et al. (1999), p. 44, pl. 29, figs e, f, pl. 30, figs a, b, d.

LM Colony straight. Cells rectangular in girdle view, with constriction in girdle zone, mantle high. Foramina narrow and lanceolate (Figure 40). Intercalary setae long, thin, without basal part, diverge almost perpendicularly to the colony axis. Terminal setae thicker than intercalary setae, almost parallel to the colony axis (Figure 41). Setae cross over at the colony margin. Two chloroplasts per cell.

EM Rimoportula centrally located, externally short tube-like structure and internally labiate structure (Jensen and Moestrup 1998).

Resting spores spiny, with broadly convex primary valve, secondary valve tightly convex (Figure 42).

Distribution *Chaetoceros constrictus* was found at all stations from spring to autumn with about 1×10^6 cells l^{-1} in mid-summer; not rare.

***Chaetoceros curvisetus* Cleve (Figures 43–46)**

References Cleve (1889), p. 55; Evensen and Hasle (1975), p. 159, figs 23–26; Rines and Hargraves (1988), p. 71, figs 141, 142; Hernández-Becerril (1996), p. 53, pls 42, 43, figs 1–5; Jensen and Moestrup (1998), p. 37, figs 114–116.

LM Colony curved and relatively long. Cells rectangular in girdle view, mantle low. Foramina wide and elliptical. Intercalary and terminal setae similar, long, thin, with short basal part. Setae cross over at the colony margin, curve to the same direction, almost perpendicularly to the colony axis. One chloroplast (Figure 43).

EM Valve face concave, elliptical, with sharp radiating costate pattern (Figures 44, 45). Rimoportula centrally located tube-like structure (Figure 45). Setae circular in cross-section, perforated by small poroids and bearing spiral rows of spines (Figure 46).

Resting spores spiny, with broadly convex primary valve and almost flat secondary valve (Rines and Hargraves 1988).

Distribution *Chaetoceros curvisetus* occurred at stations 1 to 16 in summer and autumn at about 1×10^6 cells l^{-1} in late summer; not rare.

***Chaetoceros debilis* Cleve (Figures 47–52)**

References Cleve (1894), p. 13, pls 1, 2; Evensen and Hasle (1975), p. 159, figs 27–32; Rines and Hargraves (1988), p. 72, figs 143–147; Takano (1990), p. 286; Hernández-Becerril (1996), p. 58, pls 46, 47; Jensen and Moestrup (1998), p. 37, figs 117–121; Bérard-Therriault et al. (1999), p. 46, pl. 30, figs c, e-g; Horner (2002), p. 80.

LM Colony long and spirally twisted. Cells rectangular in girdle view, mantle low. Foramina narrow. Setae long, thin, with short basal part. Terminal setae thicker than intercalary setae, perpendicular to the colony axis. Intercalary setae diverge at an angle above 30–70° from the colony axis. Setae cross over slightly outside the colony margin. One chloroplast (Figure 47).

EM Valve elliptical, with costae radiating from eccentric annulus (Figures 48, 49). Rimoportula in the eccentrically positioned annulus, externally flat tube-like structure (Figure 49). Setae circular in cross-section, perforated with poroids, bearing spirally located spines (Figure 50).

Resting spores with equal convex valves, primary valve with two long spines (Figure 51). Other type of resting spores: primary valve with two undulations, secondary valve flat and smooth (Figure 52).

Remarks Resting spores of *Chaetoceros debilis* from the study area are quite variable. The presence or absence of spines and two undulations on the primary valve of resting spores was studied and discussed by Hargraves (1979). *C. debilis* can be confused with *C. curvisetus* and *C. pseudocurvisetus* which form spirally twisted colonies also. The main differences between these species are the shape of foramina, the form of resting spores, as well as the form and location of the rimoportula.

Distribution *Chaetoceros debilis* was found at all stations from autumn to spring with up to 500 000 cells l^{-1} in late spring; not rare.

***Chaetoceros decipiens* Cleve (Figures 53–58)**

References Cleve (1873), p. 11, fig. 5; Evensen and Hasle (1975), p. 161, figs 55–69; Rines and Hargraves (1988), p. 75, figs 148, 149, 152; Hernández-Becerril (1996), p. 27, pls 20, 21; Hernández-Becerril and Granados (1998), p. 511, figs 26–28; Jensen and Moestrup (1998), p. 37, figs 122–131; Bérard-Therriault et al. (1999), p. 46, pl. 32; Horner (2002), p. 71.

LM Colony long and straight. Cells rectangular in girdle view with valve face concave, mantle high. Foramina narrow. Setae long, thick, straight, without basal part. Sibling intercalary setae fuse in proximal part, diverge at an angle over 10–25° from the colony axis. Terminal setae thicker and shorter than intercalary setae, broadly diverge from cell angles and curve parallel to the colony axis. Setae cross over at the colony margin. Several small chloroplasts (Figure 53).

EM Valve elliptical. Hair-like filaments visible in apical areas of intercalary valve mantle (Figure 55). Rimoportula small tube-like structure, eccentrically located (Figure 56). Intercalary setae fuse for a distance of 10–20 μm before diverging (Figure 54). Setae polygonal in cross-section (6–8 sides), perforated with poroids, bearing small spines (Figures 57, 58).

Resting spores unknown.

Distribution *Chaetoceros decipiens* occurred at all stations throughout the year with 500 000 cells l^{-1} in spring; not rare.

***Chaetoceros diadema* (Ehrenberg) Gran (Figures 59–63)**

References Gran (1897), p. 20, pl. 2, figs 16–18; Rines and Hargraves (1988), p. 76, figs 150, 151, 153; Hernández-Becerril (1996), p. 38, pls 34, 35; Jensen and Moestrup (1998), p. 39, figs 132–141; Gogorev and Makarova (1999), p. 40, pl. 1, figs 8–10, pl. 2, figs 1, 2; Bérard-Therriault et al. (1999), p. 47, pls 33, 34, fig. a; Horner (2002), p. 84.

Synonym *Chaetoceros subsecundus* (Grunow) Hustedt (1930), p. 709, fig. 404.

LM Colony straight or slightly twisted. Cells rectangular in girdle view, mantle high. Foramina narrow with central constriction. Setae short, thick, with short basal part. Terminal setae thicker than intercalary setae. Setae cross over at the colony margin (Figure 59). One chloroplast per cell (Jensen and Moestrup 1998).

EM Valve face flat or concave, broadly elliptical, with weak costae radiating dichotomously and bearing solid or branched spines. Long process situated on the margin of some intercalary valves (Figure 60). Annulus centrally situated (Figure 61). Rimoportula located in an annulus, short tube-like structure externally, labiate structure internally (Jensen and Moestrup 1998). Setae polygonal in cross-section, bearing spines (Figure 62).

Resting spores have dissimilar valves. Primary valve broadly convex with dichotomous branches and spines in the central part, secondary valve centrally inflated, smooth (Figures 59, 63).

Distribution *Chaetoceros diadema* occurred at stations 1 to 5, 9, 11, 12, 14, and 15 throughout the year with 10 000 cells l^{-1} in late spring; not rare.

Chaetoceros didymus Ehrenberg (Figures 64–70)

References Ehrenberg (1845), p. 75; Rines and Hargraves (1988), p. 77, figs 154–163; Takano (1990), p. 288; Hernández-Becerril (1991), p. 290, figs 1–12; Jensen and Moestrup (1998), p. 141, figs 142–144, 146; Bérard-Therriault et al. (1999), p. 47, pl. 34, figs e, g; Horner (2002), p. 75.

Synonyms *Chaetoceros didymus* var. *anglica* (Grunow) Gran (1905), p. 80, fig. 95. *Chaetoceros didymus* f. *singularis* Takano (1960), p. 182, fig. 2b.

LM Colony straight, usually long. Cells rectangular in girdle view with raised corners, valve with a protuberance in the center, mantle low. Foramina panduriform, wide or narrow, with central constriction. Intercalary and terminal setae similar: long, coarse, straight, with short basal part. Intercalary setae diverge at about 25–45° to the colony axis, terminal setae almost parallel to the colony axis. Setae cross over at the colony margin. Two chloroplasts per cell (Figure 64).

EM Valve elliptical, perforated with small poroids (Figure 66). Long branched capilli at the edge of the valve and at the setae base (Figures 65, 66). Rimoportula centrally located, externally tube-like structure surrounded by small spines (Figure 67). Setae four-sided in cross-section, perforated with poroids, bearing spines (Figure 68).

Resting spores smooth, paired, held together by short thick curved setae. Primary valves with one or two undulations (Figure 69) or with central high protuberance (Figure 70), secondary valves concave.

Remarks According to Hargraves (1979), Stockwell and Hargraves (1986), Rines and Hargraves (1988) and Hernández-Becerril (1991), the primary valve of *Chaetoceros didymus* resting spores is dome-shaped. The primary valve of resting spores of specimens from Peter the Great Bay have a high protuberance in the center.

Distribution *Chaetoceros didymus* was found at stations 1 to 16 throughout the year with about 10 000 cells l^{-1}; not rare.

Chaetoceros diversus Cleve (Figures 71–73)

References Cleve (1873), p. 9, tab. 2, fig. 12; Hernández-Becerril (1996), p. 46, pls 36–39.

Synonym *Chaetoceros laevis* Leuduger-Fortmorel (1892), p. 38, pl. 6, fig. 2.

LM Colony short and straight. Cells rectangular in girdle view, mantle high. Foramina very narrow or almost absent. Two kinds of intercalary setae present, basal part short. Common intercalary setae short, thin, straight, diverge at an angle over 30–50° to the colony axis. Special intercalary setae long and thick, curved strongly, proximally diverge at an angle of 45°, distally parallel to the colony axis. Terminal setae morphologically similar to common intercalary setae, parallel to the colony axis. Setae cross over outside at the colony margin. One chloroplast per cell (Figure 71).

EM Valve elliptical, flat or concave, weakly silicified. Rimoportula small tube-like structure, centrally located (Hernández-Becerril 1996). Setae polygonal in cross-section, perforated with poroids, bearing spines (Figure 73).

Resting spores unknown.

Distribution *Chaetoceros diversus* occurred at stations 1 to 4 in summer and autumn with about 100 cells l^{-1}; very rare.

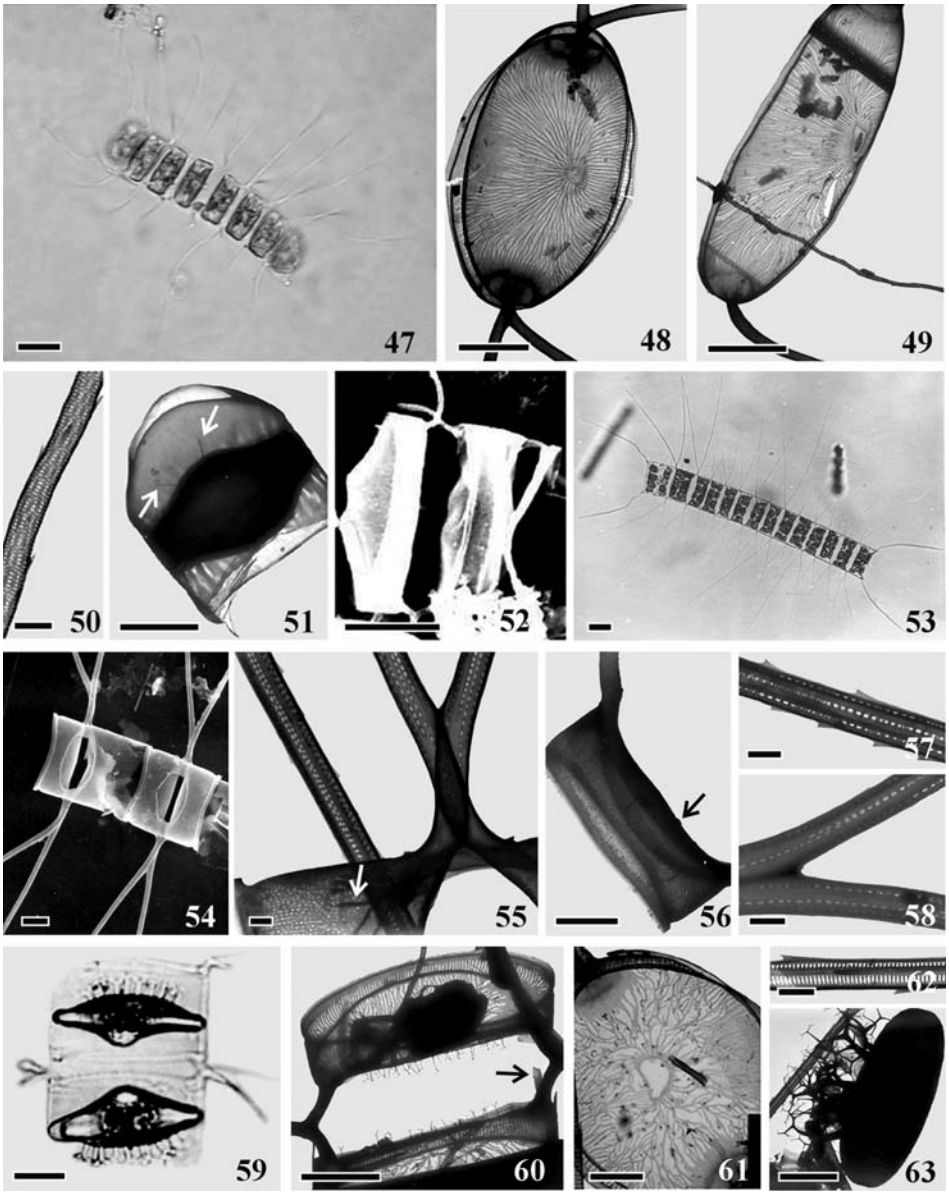
Chaetoceros furcillatus Bailey (Figures 74–79)

References Bailey (1856), p. 3, pl. 1, fig. 4; Bérard-Therriault et al. (1999), p. 48, pl. 35; Peterson et al. (1999), p. 257, figs 2–14.

LM Colony straight. Cells rectangular in girdle view, mantle low. Foramina narrow with central constriction. Setae long and thin, diverge at an angle of 45° to the colony axis. Setae cross over slightly outside at the colony margin (Figure 74). One chloroplast per cell (Peterson et al. 1999).

EM Valve face flat or with central elevation. Rimoportula not observed.

Resting spores paired or non-paired, smooth or spiny. Paired resting spores unite together by a specialized valve, bearing heavy, smooth and straight setae, which fuse together at the base before becoming bifurcate (Figures 75–77). Setae of non-paired resting spores smooth, long and straight (Figures 78, 79). Primary valves domed, covered with long spines (Figures 77, 78) or smooth (Figures 75, 79). Secondary valves slightly convex and smooth.



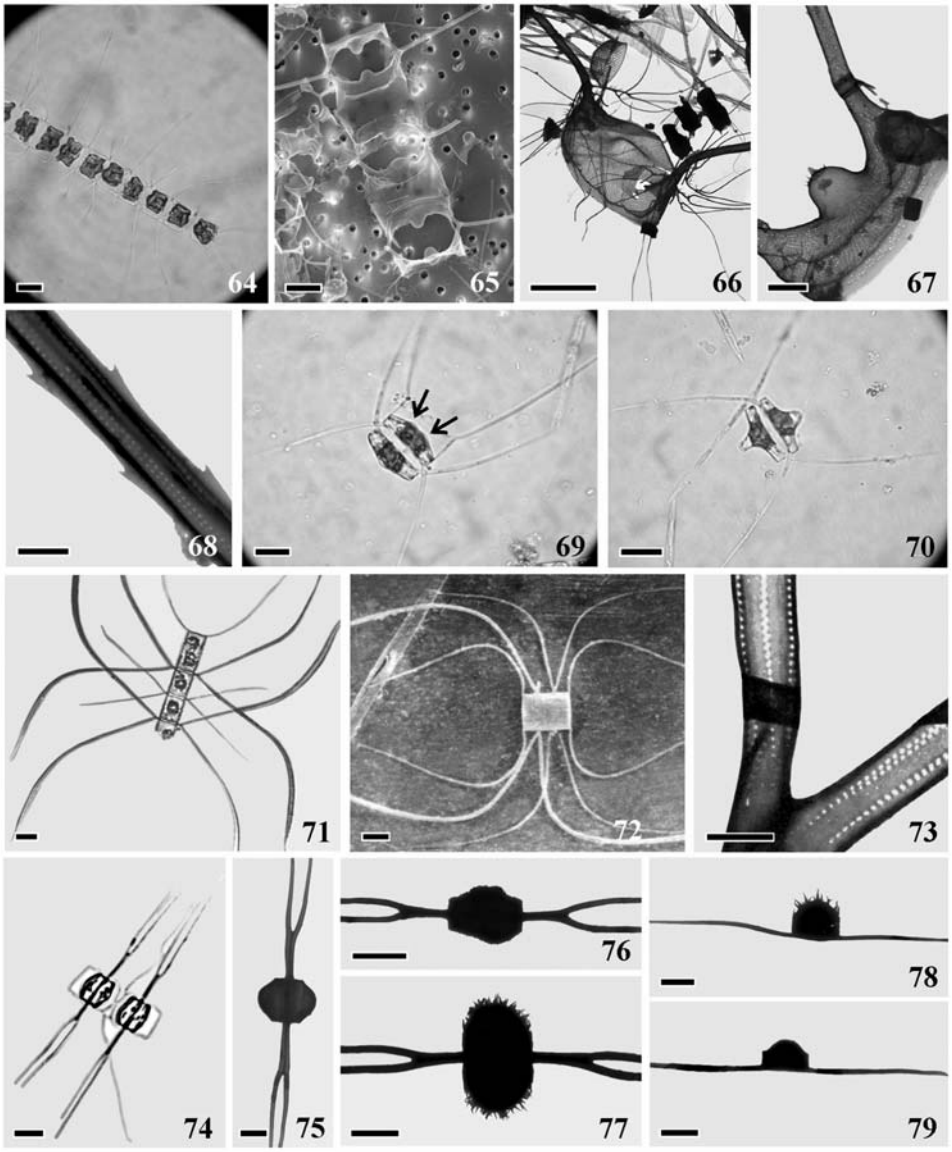
Figures 47–63 *Chaetoceros* taxa from Peter the Great Bay.
Figures 47, 53, 59, LM; Figures 48–51, 55–58, 60–63, TEM; Figures 52, 54, SEM. Scale bars=10 μm (Figures 47, 51–54, 56, 59, 60, 63); 5 μm (Figures 48, 49, 61); 1 μm (Figures 50, 55, 57, 58, 62).
(47–52) *Chaetoceros debilis*. (47) Cells in a colony. (48) Intercalary valve showing the insertion of setae. (49) Terminal valve with rimoportula. (50) Intercalary seta with spines and poroids. (51) Primary valve of resting spore with two spines (arrows). (52) Smooth resting spores with two undulations on primary valves. (53–58) *Chaetoceros decipiens*. (53) A complete colony. (54) Sibling cells in girdle view, note narrow foramina and fused of intercalary setae. (55) Intercalary valves, note filaments on mantle (arrow). (56) Girdle view of terminal valve shoving rimoportula (arrow). (57) Seta with straight rows of poroids and spines. (58) Fused setae over a distance of 10–20 μm. (59–63) *Chaetoceros diadema*. (59) Two resting spores in a colony. (60) Sibling valves showing valve face covered with straight or branched spines, note one long process at margin (arrow). (61) Valve with costae. (62) Seta with rows of spines and poroids. (63) Resting spore with dichotomously branched spines.

Remarks The morphology of vegetative cells lacks unique, characteristic features, thus positive identification is difficult without the resting spores. According to Stockwell and Hargraves (1986), Peterson et al. (1999), the primary valves of *Chaetoceros furcillatus* resting spores are smooth or covered with short ridges. In the phytoplankton samples from Peter the Great Bay, we observed resting spores with long spines (Figures 77, 78) and with raised ridges (Figure 76) on the primary valve.

Distribution *Chaetoceros furcillatus* was found at stations 7, 8, 11, and 12 in spring and summer with about 200 cells l^{-1}; very rare.

Chaetoceros laciniosus Schütt (Figures 80–83)

References Schütt (1895), p. 38, pl. 4, fig. 5; Evensen and Hasle (1975), p. 160, figs 42–45; Rines and Hargraves (1988), p. 83, figs 167–169; Jensen and Moestrup



Figures 64–79 *Chaetoceros* taxa from Peter the Great Bay.
Figures 64, 69–71, 74, LM; Figures 66–68, 73, 75–79, TEM; Figures 65, 72, SEM. Scale bars=10 μm (Figures 64–66, 69–72, 74–79); 5 μm (Figure 67); 1 μm (Figures 68, 73).
(64–70) *Chaetoceros didymus*. (64) Part of a colony. (65) Part of a colony showing panduriform foramina. (66) Intercalary valve with long branched capilli at the edge. (67) Terminal valve with rimoportula surrounded by spines. (68) Seta with spines and straight rows of poroids. (69, 70) Paired resting spores showing two undulations on the primary valve (arrows). Note primary valves with high undulations in Figure 70. (71–73) *Chaetoceros diversus*. (71, 72) Cells in a colony. (73) Distal part of intercalary seta. (74–79) *Chaetoceros furcillatus*. (74) Two resting spores in a colony. (75–77) Paired resting spores, primary valve smooth in Figure 75, with ridges in Figure 76, and with long spines in Figure 77. (78, 79) Non-paired resting spores, primary valve with long spines in Figure 78 and smooth in Figure 79.

(1998), p. 46, figs 153–158; Bérard-Therriault et al. (1999), p. 49, pl. 37; Horner (2002), p. 77.

Synonym *Chaetoceros distans* Cleve (1894), p. 14, pl. 2, fig. 2.

LM Colony long and straight. Cells rectangular in girdle view with elongate corners, mantle high. Foramina very wide with central compression. Setae long, thin, with long basal part. Terminal setae longer and thicker than intercalary setae. Intercalary setae almost perpendicular to the colony axis, diverge distally parallel to the colony axis, terminal setae parallel to the colony axis. Setae cross over at the colony margin. Possibly one chloroplast per cell (Figure 80).

EM Valve face flat or slightly concave, elliptical, with costae radiating from valve central part. Rimoportula flat and elongated tube externally, eccentrically located (Evensen and Hasle 1975). Setae circular in cross-section, with spirally located spines and poroids (Figure 83).

Resting spores with dissimilar valves. Primary valve highly convex, secondary valve slightly convex, both smooth (Rines and Hargraves 1988) or primary valve covered with long spines and smooth secondary valve (Jensen and Moestrup 1998).

Distribution *Chaetoceros laciniosus* occurred at stations 2 to 17 in summer and autumn with about 80 000 cells l^{-1} in autumn; not rare.

***Chaetoceros lorenzianus* Grunow (Figures 84–89)**

References Grunow (1863), p. 157, pl. 5, fig. 13; Rines and Hargraves (1988), p. 85, figs 178–180, 183; Hernández-Becerril (1996), p. 27, pls 22, 23; Jensen and Moestrup (1998), p. 48, figs 160–165; Bérard-Therriault et al. (1999), p. 50, pl. 38, figs a, b, d, e; Horner (2002), p. 72.

LM Colony straight of variable length. Cells rectangular in girdle view with elongate corners, mantle low. Foramina wide, octagonal or hexagonal. Setae long, thick, without basal part. Terminal setae shorter than intercalary setae. Intercalary setae perpendicular or diverge at an angle of 20–70° to the colony axis, terminal setae almost parallel to the colony axis. Setae cross over at the colony margin (Figure 84). Chloroplasts small and numerous (Rines and Hargraves 1988).

EM Valve face flat, elliptical, with costae radiating from a central annulus. Hair-like filaments visible in apical area of intercalary valve mantle (Figure 85). Some terminal valves with two elongate structures arising from the corners toward the central part (Figure 86). Rimoportula centrally located, tube-like structure externally (Figure 86). Setae polygonal in cross-section, with large poroids and straight row of spines (Figures 87, 88).

Resting spores with dissimilar valves: primary valve with two conical protuberances finishing with dichotomously branched spines, secondary valve with central inflation, smooth (Figure 89).

Remarks *Chaetoceros lorenzianus* can be confused with *C. decipiens*. The main differences between species are a distinctive structure of the rimoportula, the presence of resting spores and an elongate process on some terminal valves in *C. lorenzianus* and the fused setae in *C. decipiens*.

Distribution *Chaetoceros lorenzianus* was found at stations 9, 14 and 15 from spring to autumn with 10 000 cells l^{-1}; rare.

***Chaetoceros messanensis* Castracane (Figures 90–92)**

References Castracane (1875), p. 394, pl. 6, fig. 1; Evensen and Hasle (1975), p. 162, figs 70–74; Hernández-Becerril (1996), p. 46, pls 40, 41.

LM Colony straight. Cells rectangular in girdle view, mantle low. Foramina wide, elliptical or hexagonal. Setae with short basal part. Three kinds of setae present: special intercalary setae long and thick, strongly silicified, fuse for a distance and then diverge; common intercalary setae long and thin; terminal setae short and thin. Common intercalary setae diverge at an angle of 30–90°, special sibling intercalary setae diverge at an angle of 45° to the colony axis. One terminal seta curved and perpendicular, the second terminal seta diverges at an angle of 60–70° to the colony axis. Setae cross over at the colony margin. One chloroplast per cell (Hernández-Becerril 1996).

EM Valve elliptical, heavily silicified, with costae radiating from a central annulus. Rimoportula flat and elongated tube externally, centrally located (Figure 92). Setae circular in cross-section, distally bearing spines arranged in spirals.

Resting spores unknown.

Distribution *Chaetoceros messanensis* occurred at stations 5 and 12 in summer at about 200 cells l^{-1}; very rare.

***Chaetoceros minimus* (Levander) Marino, Giuffré, Montresor *et* Zingone (Figures 93–96)**

References Marino et al. (1991), p. 318, figs 1–9; Bérard-Therriault et al. (1999), p. 50, pl. 19, figs a, e.

Synonym *Rhizosolenia minima* Levander (1904), table 1, figs 7, 8.

LM Solitary cells, very small and weakly silicified. In girdle view, cells cylindrical with rounded corners, mantle high. One or two setae per valve, long and thin, diverge almost parallel to the colony axis. One chloroplast.

EM Valve face elliptical, costae radiating from central annulus (Figure 95). Girdle zone clearly visible (Figures 93, 94). Long spine on the margin of some intercalary valves. Rimoportula in the centrally located annulus, small, tube-like structure externally (Figure 96). Setae four-sided in cross-section, perforated with small poroids, bearing spines.

Resting spores ellipsoidal. Primary valve with protuberances and knobs, secondary valve with numerous small knobs and a strong stud-like central protuberance (Marino et al. 1991).

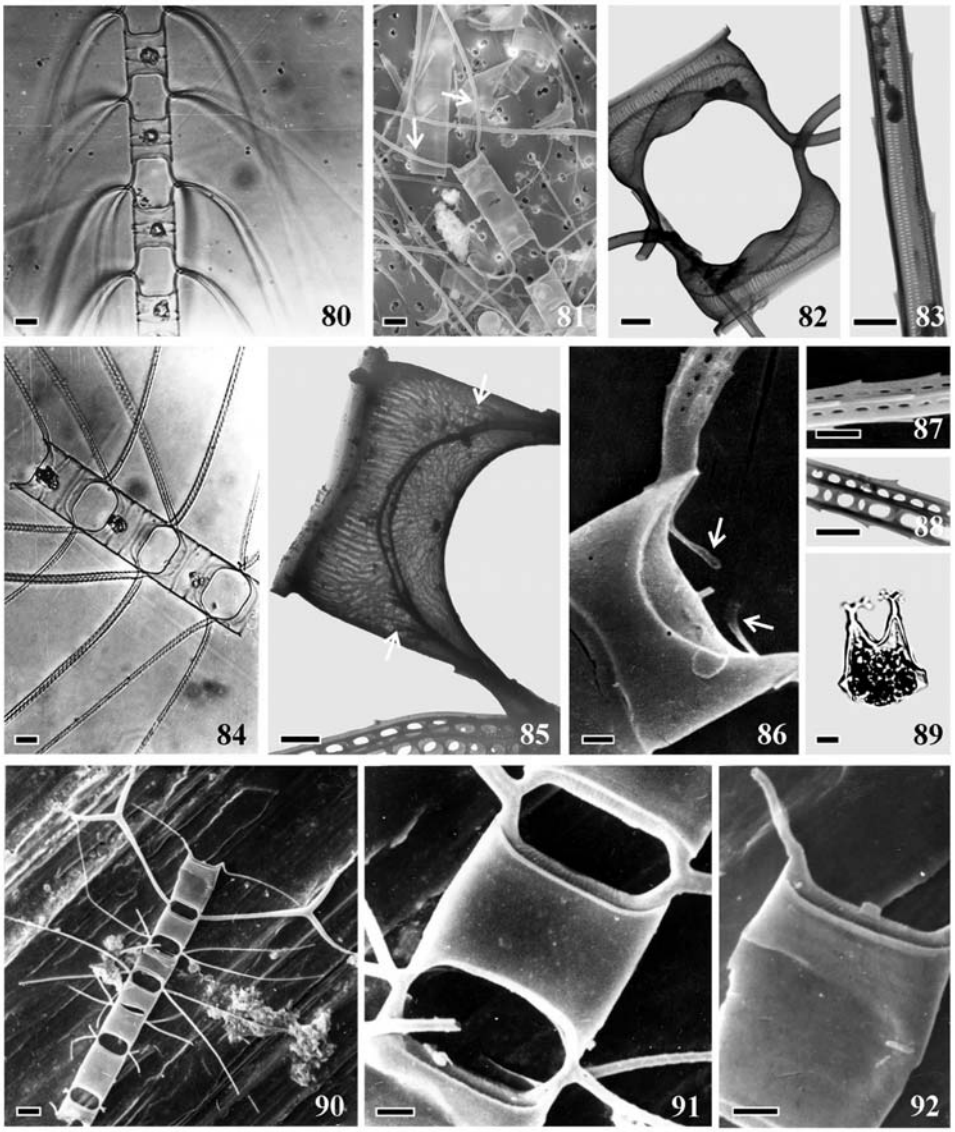
Distribution *Chaetoceros minimus* was only found at station 9 in spring and summer with 1000 cells l^{-1}; very rare.

***Chaetoceros protuberans* Lauder (Figures 97–100)**

References Lauder (1864), p. 79, pl. 8, fig. 11; Lechuga-Devéze and Hernández-Becerril (1988), p. 79, figs 2, 3; Hernández-Becerril (1991), p. 294, figs 14–28.

Synonym *Chaetoceros didymus* var. *protuberans* (Lauder) Gran and Yendo (1914), p. 72, fig. 5.

LM Colony straight and long. Cells rectangular in girdle view, with a protuberance in the center, mantle high. Foramina wide with a central constriction. Intercalary and terminal setae similar: long, thick, with long basal part. Intercalary setae diverge at an angle of about 45–90° from the colony axis, terminal setae almost parallel to the colony axis. Setae cross over outside the colony margin. Two chloroplasts per cell (Figure 97).



Figures 80–92 *Chaetoceros* taxa from Peter the Great Bay.
Figures 80, 84, 89, LM; Figures 82, 83, 85, 88, TEM; Figures 81, 86, 87, 90–92, SEM. Scale bars=10 μm (Figures 80, 81, 84, 89, 90); 5 μm (Figures 82, 85, 86, 91, 92); 1 μm (Figures 83, 87, 88).
(80–83) *Chaetoceros laciniosus*. (80) Part of a colony. (81) Cells in a colony with terminal setae (arrows). (82) Sibling valves showing insertion and crossing of setae, note large foramen. (83) Intercalary seta with spines and rows of poroids. (84–89) *Chaetoceros lorenzianus*. (84) Cells in a colony. (85) Intercalary valve, note hair-like filaments in apical area (arrows). (86) Terminal valve showing rimoportula and elongate processes arising from the corners of the valve (arrows). (87, 88) Four-sided setae with spines and poroids. (89) Resting spore. (90–92) *Chaetoceros messanensis*. (90) A complete colony, note special intercalary setae. (91) Cells in colony showing wide foramina. (92) Terminal valve with rimoportula.

EM Valve elliptical, perforated with small poroids. Long process on the margin of intercalary valves (Figure 98). Rimoportula tube-like structure externally, centrally located (Figure 99). Setae four-sided in cross-section, perforated with poroids, bearing spines (Figure 100).

Resting spores not observed.

Remarks *Chaetoceros protuberans* is closely related in morphology to *C. didymus*. The main differences are the possession of capilli on the bases of setae either in terminal and intercalary valves, a ring of small spines surrounding the rimoportula at the terminal valves (*C. didymus*), the presence of a process on the margin of some intercalary valves (*C. protuberans*) and the morphology of the resting spores. Resting spores were examined here for *C. didymus* only, revealing paired resting spores with specialized setae. Non-paired resting spores were studied by Stockwell and Hargraves (1986) and were detected in the life cycle of *C. protuberans* by Lechuga-Devéze and Hernández-Becerril (1988).

Distribution *Chaetoceros protuberans* was found at stations 9 to 12 from spring to autumn at about 10 000 cells l^{-1}; rare.

Chaetoceros pseudocrinitus Ostenfeld (Figures 101–108)

References Ostenfeld (1901), p. 300, fig. 11; Rines and Hargraves (1988), p. 87, figs 174, 177, 219; Jensen

and Moestrup (1998), p. 49, figs 176–188; Bérard-Therriault et al. (1999), p. 51, pl. 45, figs b, c.

LM Colony straight or slightly twisted and long. Cells rectangular in girdle view, mantle low. Foramina narrow, slit-like. Setae similar, long and thin, without basal part. Intercalary setae diverge at an angle of 45–70° to the colony axis, terminal setae diverge broadly from cell angles and curve parallel to the colony axis. Setae cross over at the colony margin. One chloroplast per cell (Figure 101).

EM Valve face flat, elliptical to round, with costae eccentrically radiating from the position of the annulus (Figures 102, 103). Rimoportula flat, slit-like structure externally (Figure 102). Setae circular in cross-section, with spiral row of spines and small poroids (Figure 104). Spine at the base of the intercalary seta (Figure 105).

Resting spores with dissimilar valves. Primary valve highly convex, secondary valve slightly convex, both bearing spines (Figure 106).

Distribution *Chaetoceros pseudocrinitus* occurred at stations 1 to 15 from winter to spring with up to 800 000 cells l^{-1} in spring; not rare.

Chaetoceros pseudocurvisetus Mangin (Figures 107–109)

References Mangin (1910), p. 350, figs 3II, 4II; Fryxell (1978), p. 68, figs 22–26; Rines and Hargraves (1988), p. 89, figs 185–191; Takano (1990), p. 290; Hernández-Becerril (1996), p. 53, pls 44, 45.

LM Colony curved and long. Cells rectangular in girdle view, intercalary valves with two processes connecting sibling valves, mantle low. Main foramina wide elliptical; in the margin projection, two small round foramina. Setae similar, long, thin, with short basal part. Intercalary setae diverge at an angle of 35–80° to the colony axis, terminal setae at an angle of 55–60° to the colony axis. Setae cross over at the colony margin, directed away from the curvature of the colony. One chloroplast per cell (Figure 107).

EM Valve broadly elliptical. Rimoportula flattened-tube structure externally (Hernández-Becerril 1996). Setae circular in cross-section, perforated with poroids, bearing spiral rows of spines (Figure 109).

Resting spores with valves equally convex, both valves sheathed and smooth (Rines and Hargraves 1988).

Distribution *Chaetoceros pseudocurvisetus* was only found at station 9 in summer with about 200 cells l^{-1}; very rare.

Chaetoceros radicans Schütt (Figures 110–114)

References Schütt (1895), p. 48, fig. 27; Fryxell and Medlin (1981), p. 8, figs 9–15, 29–42; Rines and Hargraves (1988), p. 90, figs 192–198; Hernández-Becerril (1996), p. 58, pls 48, 49; Bérard-Therriault et al. (1999), p. 51, pls 40, 46, fig. d; Horner (2002), p. 81.

Synonym *Chaetoceros scolopendra* Cleve (1896), p. 30, figs 4–6.

LM Colony straight, curved or slightly twisted, medium length. Cells rectangular in girdle view, sibling cells not touching each other, mantle low. Foramina narrow. Setae long, thin, without basal part. Long spines (capilli) occurring at the intercalary setae only. Intercalary and terminal setae diverge nearly perpendicular to the colony axis. Setae cross over at the colony margin. One chloroplast per cell (Rines and Hargraves 1988).

EM Valve broadly elliptical, flat, with costae radiating from eccentric annulus (Figure 110). Rimoportula flattened-tube structure externally, slit-like structure orientated along apical axis internally (Figure 111). Setae circular in cross-section, bearing randomly distributed spines of variable length, except at the base, perforated with small poroids (Figures 110–113).

Resting spores in pairs: primary valve dome-shaped, smooth, secondary valve flattened, smooth. Sibling setae of resting spores fuse at a short distance, after diverging bent around the cell (Figure 114).

Distribution *Chaetoceros radicans* occurred at stations 3 to 15 throughout the year with about 150 000 cells l^{-1} in early summer; not rare.

Chaetoceros salsugineus Takano (Figures 115–117)

References Takano 1983, p. 2, figs 1–15; Orlova and Selina (1993), p. 124, figs 2–21; Orlova and Aizdaicher (2000), p. 13, fig. 3; Trigueros et al. (2002), p. 527, figs 2–18.

LM Cells solitary or joined in short colonies. Cells rectangular in girdle view, mantle high. Foramina narrow. Setae very long, thin, with short basal part. Intercalary and terminal setae diverge at an angle of 40–50° to the colony axis. Setae cross over at the colony margin. One chloroplast per cell (Figure 115).

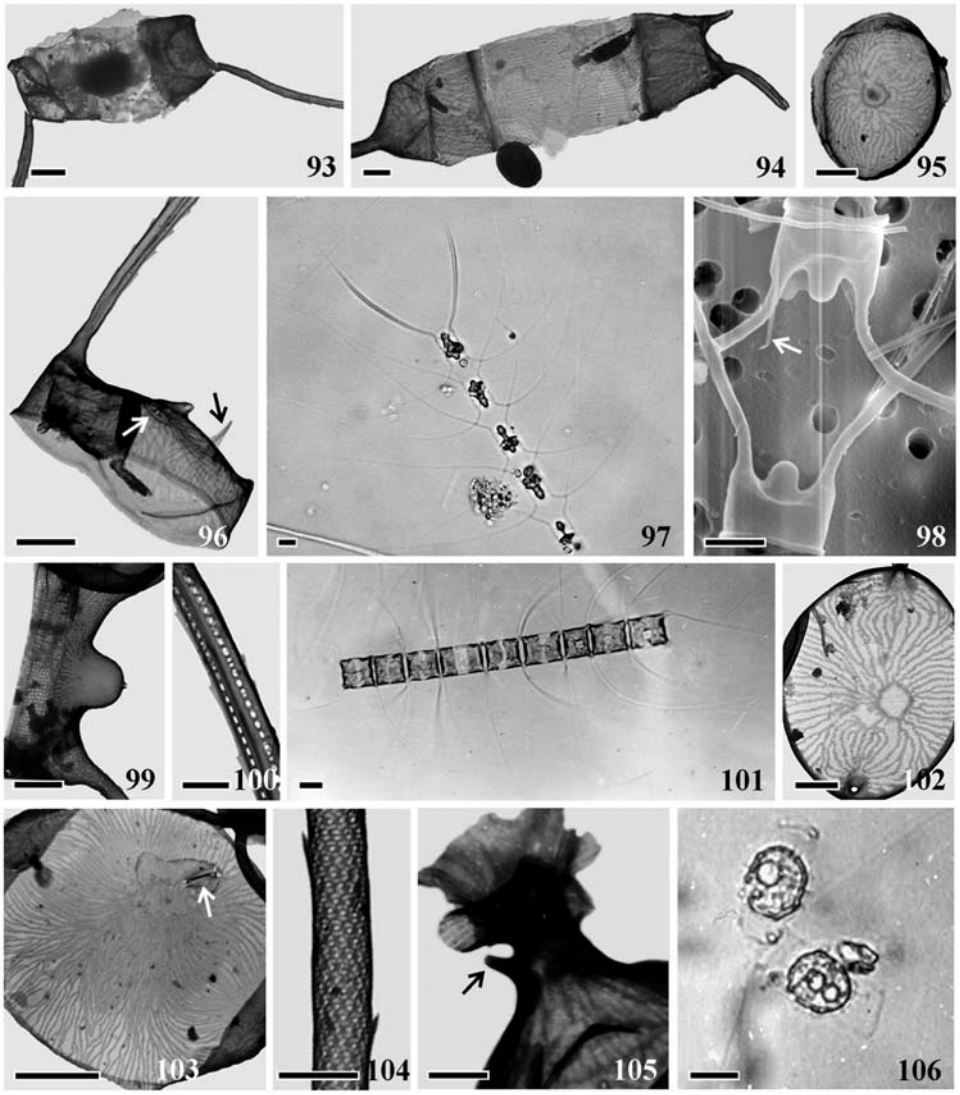
EM Valve face broadly elliptical to circular, perforated with fine pores; thick costae radiating from a central annulus and continuing to the mantle. Rimoportula centrally located, long tube-like structure externally, slit-like structure internally (Figures 116, 117). Setae circular in cross-section, perforated with spiral rows of poroids, bearing small spines.

Resting spores unknown.

Distribution *Chaetoceros salsugineus* was found at all stations in summer and autumn with maximum abundance of 12×10^6 cells l^{-1} in summer; not rare.

Chaetoceros socialis Lauder f. *socialis* (Figures 118–123)

References Lauder (1864), p. 77, pl. 8, fig. 1; Evensen and Hasle (1975), p. 160, figs 33–39; Rines and Hargraves (1988), p. 95, fig. 207; Takano (1990), p. 292; Hernández-Becerril (1996), p. 63, pls 50, 51; Bérard-Therriault et al. (1999), p. 52, pl. 42; Horner (2002), p. 86.



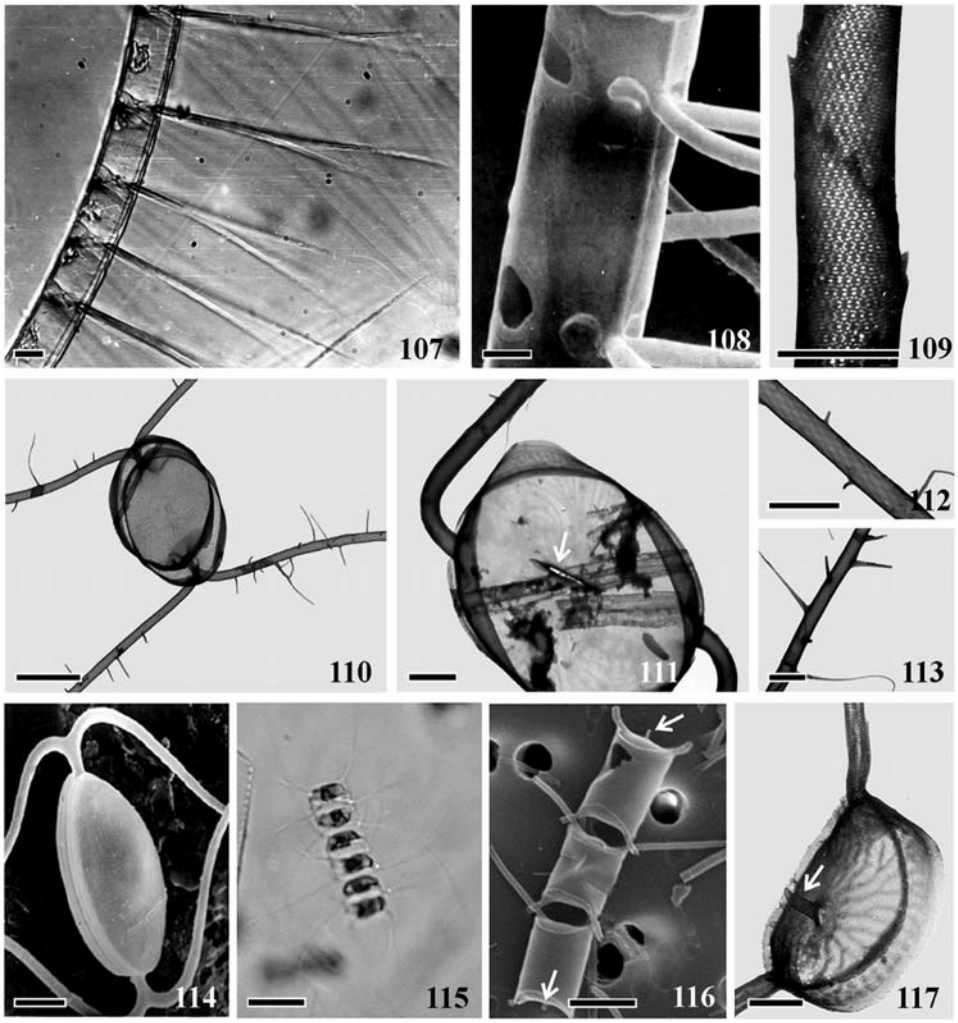
Figures 93–106 *Chaetoceros* taxa from Peter the Great Bay.
Figures 97, 101, 106, LM; Figures 93–96, 99, 100, 102–105, TEM; Figure 98, SEM. Scale bars=10 μm (Figures 97, 98, 101, 106); 5 μm (Figures 99, 102, 103); 1 μm (Figures 93–96, 100, 104, 105).
(93–96) *Chaetoceros minimus*. (93) A single cell with one chloroplast. (94) A cell with two setae per valve. (95) Intercalary valve showing radiate costae. (96) Terminal valve with small rimoportula (white arrow) and with a single spine (black arrow). (97–100) *Chaetoceros protuberans*. (97) Part of a colony. (98) Sibling valves with prominent central protuberance, note long process on the margin (arrow). (99) Terminal valve with rimoportula. (100) Four-sided intercalary seta with spines and row of poroids. (101–106) *Chaetoceros pseudocrinitus*. (101) Cells in a colony. (102) Intercalary valve with costae. (103) Terminal valve with eccentric rimoportula (arrow). (104) Seta with spines and poroids. (105) Base of intercalary seta with a spine (arrow). (106) Resting spores covered with spines.

LM Cells united in short colony, joined by long setae, sometimes forming spherical colonies, embedded in mucus. Cells rectangular in girdle view, mantle low. Foramina wide and hexagonal. Setae long, thin, with short basal part. Two setae diverge at an angle of 20–50° to the apical axis, two setae perpendicular to the axis colony. Setae cross over outside the colony margin. One chloroplast per cell (Figure 118).

EM Valve flat, elliptical, with costae dichotomously radiating from central annulus (Figures 119, 120). Rimoportula flat and elongated tube externally and slit-like structure internally, centrally located (Evensen and Hasle 1975). Setae circular in cross-section, with spiral rows of poroids and small spines, perforated with large poroids (Figure 121).

Resting spores smooth or with spines on primary valve. Smooth spores with dissimilar valves: primary valve strongly convex with a thick rim ornamented with rounded poroids, secondary valve less convex (Figure 122). Resting spores with primary valve bearing short spines in the central part and secondary valve smooth, have equal convex valves (Figure 123).

Distribution *Chaetoceros socialis* f. *socialis* was present at stations 1 to 15 throughout the year with up to 100 000 cells l^{-1} in spring; not rare.



Figures 107–117 *Chaetoceros* from Peter the Great Bay.
Figures 107, 115, LM; Figures 109–113, 117, TEM; Figures 108, 114, 116, SEM. Scale bars=10 μm (Figures 107, 108, 110, 115); 5 μm (Figures 111, 114, 116); 1 μm (Figures 109, 112, 113, 117).
(107–109) *Chaetoceros pseudocurvisetus*. (107) Cells in a colony. (108) Sibling cells showing the insertion of the setae and small foramina. (109) Seta with spines and poroids in quincunx. (110–114) *Chaetoceros radicans*. (110) Sibling valves with long spines on setae. (111) Terminal valve with rimoportula (arrow). (112, 113) Setae with long spines. (114) Paired resting spore. (115–117) *Chaetoceros salsugineus*. (115) Cells in a colony. (116) Colony of three cells, note rimoportulae on terminal valves (arrows). (117) Terminal valve with costae and long rimoportula (arrow).

Chaetoceros socialis f. *radians* (Schütt) Proschkina-Lavrenko (Figures 124–127)

References Proschkina-Lavrenko (1963), p. 113, pl. 21, figs 8–15; Hargraves (1979), p. 106, figs 42–47; Jensen and Moestrup (1998), p. 56, figs 207–215.

Synonyms *Chaetoceros radians* Schütt (1895), p. 41, pl. 4, fig. 10; Evensen and Hasle (1975), p. 160, figs 40, 41. *Chaetoceros socialis* f. *vernalis* Proschkina-Lavrenko (1953), p. 51, figs 3f–j.

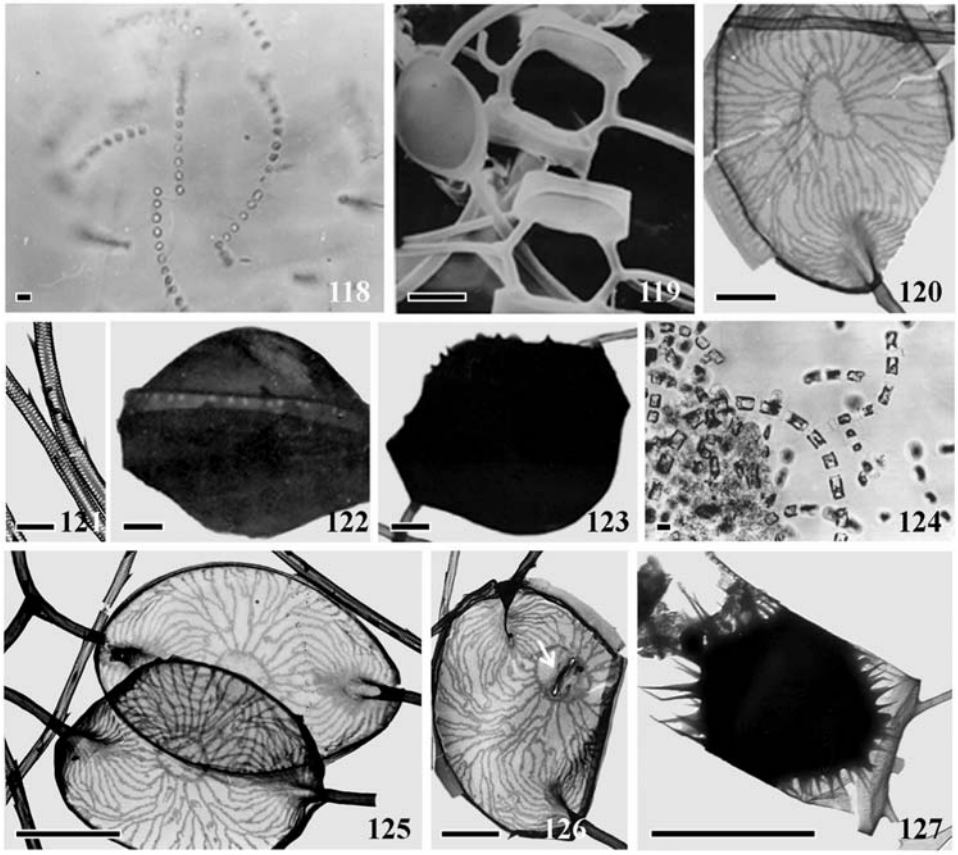
LM Cells in colony of various length, long and twisted, short and straight, or curved. Cells rectangular in girdle view, mantle low. Foramina wide. Setae long, thin, with short basal part. Two setae diverging at an angle of 20–50° to the apical axis, two setae perpendicular to the axis colony. Setae cross over outside the colony margin. One chloroplast per cell (Figure 124).

EM Valve flat, elliptical to round, with costae radiating dichotomously from eccentrically located annulus to margins (Figures 125, 126). Rimoportula tube-like structure externally, slit-like structure internally (Figure 126). Setae circular in cross-section, perforated with large poroids and spiral rows of small poroids, bearing small spines.

Resting spores with valves equally convex, covered with long spines. Spines on secondary valve longer and thicker than on the primary valve (Figure 127).

Remarks *Chaetoceros socialis* f. *radians* is closely related morphologically to *C. socialis* f. *socialis*. The presence of spines on *C. socialis* f. *radians* resting spores and their absence on *C. socialis* f. *socialis* resting spores is the main difference between the taxa.

Distribution *Chaetoceros socialis* f. *radians* occurred at stations 9, 15 to 17 from autumn to spring to about 1000 cells l^{-1}; not rare.



Figures 118–127 *Chaetoceros socialis* f. *socialis* and f. *radians* from Peter the Great Bay.
Figures 118, 124, LM; Figures 120–123, 125–127, TEM; Figure 119, SEM. Scale bars=10 μm (Figures 118, 124, 127); 5 μm (Figures 119, 125); 1 μm (Figures 120, 121–123, 126).
(118–123) *Chaetoceros socialis* f. *socialis*. (118) Cells in colonies. (119) Sibling valves showing the insertion and crossing of setae and large foramina. (120) Intercalary valve with costae. (121) Setae with spines and poroids. (122) Smooth resting spore. (123) Spiny resting spore. (124–127) *Chaetoceros socialis* f. *radians*. (124) Cells in colonies. (125) Intercalary valves. (126) Terminal valve with eccentric rimoportula (arrow). (127) Resting spore covered with long spines.

Chaetoceros subtilis Cleve (Figures 128–133)

References Cleve (1896), p. 28–33; Rines and Hargraves (1988), p. 96, figs 204–206; Jensen and Moestrup (1998), p. 58, figs 216, 217; Bérard-Therriault et al. (1999), p. 53, pl. 41, figs e, f; Horner (2002), p. 83.

LM Colony short. Cells rectangular in girdle view, sibling cells fit tightly together, mantle high. No foramen. Setae long, thin, with short basal part. Terminal setae thicker than intercalary setae. Setae not crossing over, diverge at an angle of 45° to the apical axis, directed toward one end of the colony. One chloroplast per cell (Figure 128).

EM Intercalary valve face flat with costae radiating from a central annulus (Figure 130). Anterior valve convex and posterior valve concave (Figures 131, 132). Rimoportula centrally located, tube-like structure externally, labiate structure internally (Figures 131, 132). Setae circular in cross-section, perforated by spirally arranged poroids, bearing rows of spines (Figure 133).

Resting spores with valves unevenly convex, covered with spines (Hendey 1964).

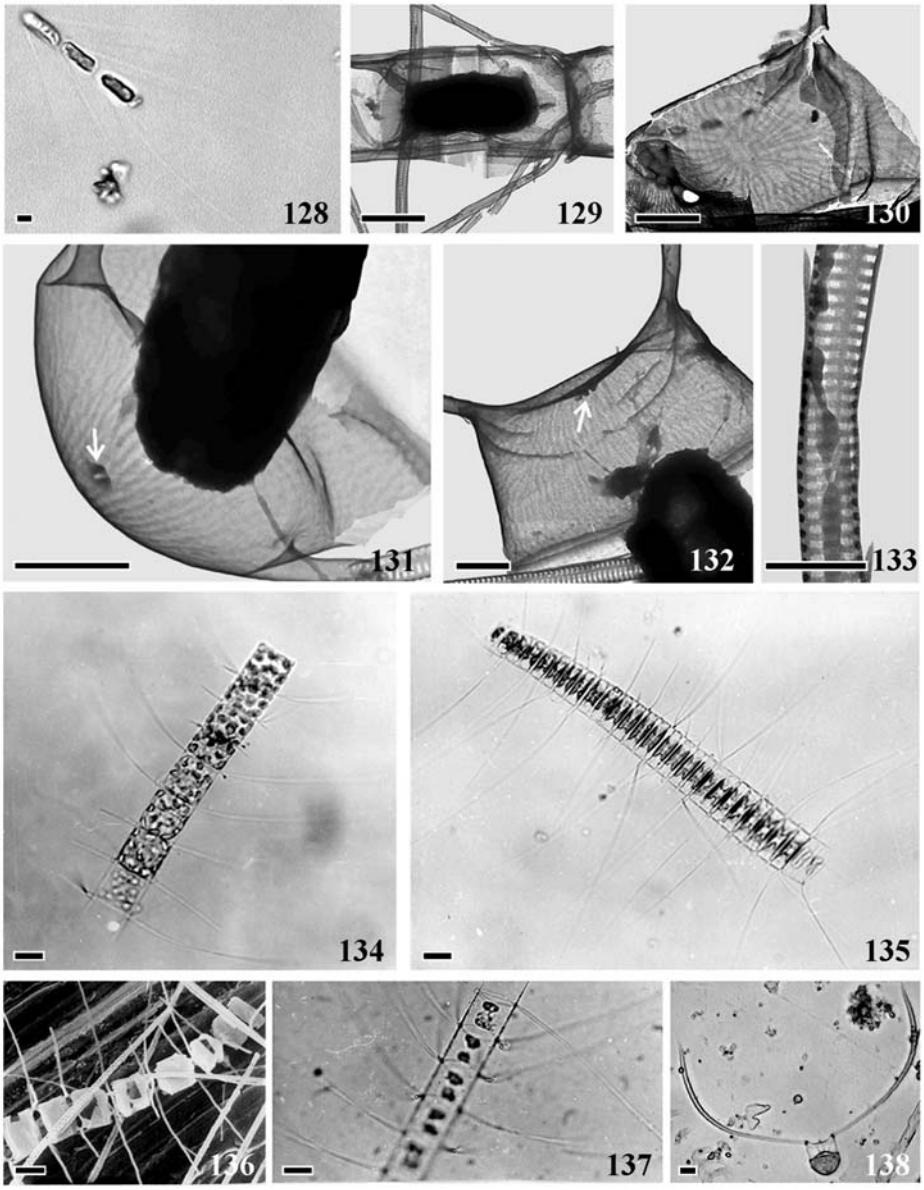
Distribution *Chaetoceros subtilis* was found at stations 14 and 15 in summer and autumn with up to 10 000 cells l^{-1}; rare.

Chaetoceros teres Cleve (Figure 134)

References Cleve (1896), p. 30, fig. 7; Rines and Hargraves (1988), p. 102, fig. 203; Hernández-Becerril and Granados (1998), p. 511, figs 29–34; Jensen and Moestrup (1998), p. 58, figs 218, 219; Bérard-Therriault et al. (1999), p. 53, pl. 43; Makarova and Gogorev (2000), p. 82, pls 4, 5; Horner (2002), p. 74.

LM Colony straight, of a medium length. Cells almost square in girdle view, mantle low. Foramina very narrow to almost absent. Setae similar, long, thin, without basal part, bearing spines. Intercalary and terminal setae diverge almost perpendicular to the colony axis. Setae cross over at the colony margin. Numerous small chloroplasts.

Resting spores with dissimilar valves. Primary valve convex, smooth and secondary valve slightly convex sometimes with ring of long spines (Rines and Hargraves 1988, Bérard-Therriault et al. 1999, Horner 2002).



Figures 128–138 *Chaetoceros* taxa from Peter the Great Bay.
Figures 128, 134, 135, 137, 138, LM; Figures 129–133, TEM; Figure 136, SEM. Scale bars=10 μm (Figures 128, 134–138); 5 μm (Figure 129); 1 μm (Figures 130–133).
(128–133) *Chaetoceros subtilis*. (128) A complete colony. (129) Sibling cells fitting closely together, note one chloroplast. (130) Intercalary valve. (131) Anterior terminal valve with rimoportula (arrow). (132) Posterior terminal valve with rimoportula (arrow). (133) Seta with spines and poroids. (134) *Chaetoceros teres*, cells in a colony. (135, 136) *Chaetoceros tortissimus*, cells in colonies. (137, 138) *Chaetoceros vanheurckii*. (137) Cells in a colony. (138) Terminal cell with resting spore.

Distribution *Chaetoceros teres* was found at stations 6, 8 and 9 from autumn to spring at about 3000 cells l^{-1}; not rare.

***Chaetoceros tortissimus* Gran (Figures 135, 136)**

References Gran (1900), p. 122, pl. 9, fig. 25; Rines and Boonruang (2004), p. 297.

LM Colony twisted and generally long. Cells rectangular in girdle view, mantle low. Foramina narrow. Setae long and thin, with short basal part. Intercalary setae diverge perpendicularly to the colony axis, terminal setae almost parallel to the colony axis. Setae cross over inside the colony margin. One chloroplast per cell (Figure 135).

EM Sibling cells not touching one another (Figure 136). Rimoportula not seen.
Resting spores unknown.

Remarks There is a high variability in cells size in this species (Hustedt 1930, Cupp 1943, Hendey 1964, Drebes 1974, Hasle and Syvertsen 1997, Rines and Boonruang 2004). Specimens from Peter the Great Bay (Table 2) were bigger than those usually described in the literature.

Distribution *Chaetoceros tortissimus* only occurred at station 9 from autumn to spring with about 100 cells l^{-1}; very rare.

***Chaetoceros vanheurckii* Gran (Figures 137, 138)**

References Gran (1897), p. 18; Horner (2002), p. 76.

LM Colony straight. Cells rectangular in girdle view, mantle low. Foramina narrow and lanceolate. Rimoportula tube-like structure, centrally located. Intercalary setae long, thin, diverge in an angle of 40–60° to the colony axis. Terminal setae long, thick, broadly divergent and parallel to the colony axis. Setae cross over at the colony margin. Two chloroplasts per cell (Figure 137).

Resting spores spiny with dissimilar valves, primary valve broadly convex, secondary valve with central undulation and three long spines (Figure 138).

Remarks *Chaetoceros vanheurckii* is very similar to *C. constrictus*, distinguished from *C. constrictus* only by the presence of long spines on the resting spore secondary valve.

Distribution *Chaetoceros vanheurckii* was found only at station 4 in summer and autumn with up to 1000 cells l^{-1}; rare.

Discussion

A total of 59 taxa belonging to the genus *Chaetoceros* are known for the Sea of Japan (Orlova et al. 2003), and of these 33 were found in Peter the Great Bay during this study. A majority of the recorded *Chaetoceros* (27 taxa) belong to the subgenus *Hyalochaete*, while only 6 taxa belong to the subgenus *Chaetoceros* (*Phaeoceros*). Three *Chaetoceros* taxa were new records for the Pacific Ocean (*C. minimus*), the Russian seas (*C. compressus* var. *hirtisetus*) and the northwestern sector of the Sea of Japan (*C. socialis* f. *radians*).

The genus *Chaetoceros* is an important component of the phytoplankton assemblages in Peter the Great Bay. Blooms of *C. affinis, C. constrictus, C. curvisetus* and *C. salsugineus* were observed in summer with abundances exceeding 1×10^6 cells l^{-1} and comprised 50% of the total phytoplankton abundance. The dominant species in the winter-spring season were *C. debilis, C. decipiens* and *C. pseudocrinitus*, with a spring abundance reaching 800 000 cells l^{-1}, comprising 98% of the total phytoplankton abundance.

Chaetoceros was common throughout the year in the study area (Table 3). Temperate and north-temperate *Chaetoceros* species prevailed (15 taxa). Cosmopolitan taxa accounted for 10 species, warm-temperate and warm water taxa included 7 species. Only one cold-water species, *C. furcillatus*, was found in Peter the Great Bay. *Chaetoceros debilis, C. pseudocrinitus, C. convolutus* and *C. teres* were predominant in the cold winter-spring season, while *C. affinis*, *C. compressus*, *C. decipiens* and *C. didymus* were common throughout the year. Moreover, *Chaetoceros debilis, C. decipiens*, *C. convolutus*, *C. affinis* and *C. didymus* are widespread globally and prevail in the plankton of the Far East Seas of Russia (Shevchenko and Orlova 2003), as well as in the temperate seas of the world (Rines and Hargraves 1988). *Chaetoceros atlanticus* f. *neapolitanus, C. diversus*, *C. messanensis*, *C. pseudocurvisetus* and *C. rostratus* were found in summer in low abundance. These species are more common in tropical and subtropical regions (Hernández-Becerril 1996, Hernández-Becerril and Granados 1998).

The region of Peter the Great Bay lies within the temperate zone. Therefore, the occurrence of a considerable number of warm-water *Chaetoceros* species may be explained by some particular oceanographical and climatic conditions. Tropical species might be introduced to the waters of Peter the Great Bay from the south by the warm Tsusima Current. Conversely, cold-water species might be introduced to the study area by the Primorskoe Current from the north (Adrianov and Kussakin 1998). The region of Peter the Great Bay coincides with a transitional zone of phytogeographical areas in the western part of the Pacific Ocean, including the South verge of the arcto-boreal region (approximately 42–45° N) and North verge of the tropical region (approximately 30–35° N) (Semina 1974).

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