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A Taxonomic Account of *Ceratium* (Dinoflagellates) in Vietnamese Waters

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ABSTRACT: Fifty-two species of *Ceratium* are reported from Vietnamese waters. All species are described and illustrated by light microscopy, and some species were also examined by scanning electron microscopy. The largest diversity of *Ceratium* was found in South Central Vietnam and its offshore islands, while the lowest diversities were found in North and South east Vietnam, presumably due to low salinity and high turbidity in the delta of the Red River in the north and the outflow of the Mekong River in the south.

KEY WORDS: *ceratium* taxonomy, Vietnam.

INTRODUCTION

Species of *Ceratium* Schrank are common elements of marine phytoplankton. They are distinctive and easily recognized by their heavily armoured cells and their 2-3 horns. Gomez (2005) recognized 63 marine species of *Ceratium*. The largest diversity of the group is found in subtropical and tropical oceans, but assignment to species is generally difficult as the morphological features used to identify species can be extremely variable (Lopez, 1966; Sournia, 1967; Dowidar, 1983; Taylor, 1976; Huisman, 1989). Graham and Bronikovsky (1944) described the morphology and provided illustrations of 57 *Ceratium* species in the Pacific and North Atlantic. Chaghtai and Saifullah (1988) reported 51 species in the waters of Saudi Arabia with descriptions and detailed pictures, and McDermott and Raine (2006) described 28 species of this genus in the waters of Ireland.

In Vietnamese waters, Hoang (1963) found 39 species and 6 forms of *Ceratium* in Nha Trang Bay, and Shirota (1966) illustrated 30 species from South Central Vietnam. However, most reports from Vietnam are lists of species that are not accompanied by species descriptions or illustrations (e.g., Boonyapiwat, 2000; Doan-Nhu and Nguyen-Ngoc, 2008; Doan-Nhu *et al.*, 2008; Nguyen-Ngoc *et al.*, 2008).

Recently, Gomez *et al.* (2010) created a new genus, *Neoceratium,* with the type species being *N. furca*

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for the marine species previously assigned to *Ceratium*, and proposed 76 new combinations in the new genus. This was based on DNA studies which showed a clear distinction between the freshwater and marine species of *Ceratium*. This distinction is supported also by both recent and earlier morphological observations where it was demonstrated that the freshwater species of the *Ceratium* have 6 cingular plates, whereas marine species have only 5 cingular plates (Gomez *et al.*, 2010, and references therein). These observations support the separation of the marine species into a separate genus which is required because the type of *Ceratium* is a freshwater species. Therefore, Gomez *et al.* (2010) created the new generic name, *Neoceratium*, arguing that previously published legitimate names should be rejected in order "to avoid potential confusion derived from the use of previous subgeneric names" (Gomez *et al.,* 2010). This argument was challenged by Calado and Huisman (2011) who argued that *Neoceratium* is illegitimate according to ICBN art. 52.1 (McNeill *et al.*, 2006). Calado and Huisman (2011) basically agree with the taxonomic conclusion of Gomez *et al.* (2010), that the marine species should be recognized as a separate genus, but they conclude that the correct name for this genus is *Tripos* Bory, 1823. The view that *Neoceratium* is illegitimate is followed here, but a taxonomic revision of the genus is outside the scope of this paper; as such, all species described in the present account are assigned to *Ceratium*.

The present work was funded by the National Foundation For Science and Technology Development (NAFOSTED, MOST, Vietnam) and conducted as part of the project "Climate change and estuarine ecosystems in Vietnam". From the climate change perspective it may serve as a base-line study of the diversity of *Ceratium* in Vietnamese waters, which may allow for comparisons of biodiversity in studies completed in the future.

MATERIALS AND METHODS

Phytoplankton samples

Phytoplankton samples were collected from Vietnamese waters (Fig. 1) by national/local projects and international cooperative programmes between Vietnam with the Philippines, Denmark, and Germany from 1995 to 2011. About 500 samples were analysed for species diversity of *Ceratium*, and all samples are stored in 4% formalin, at the Institute of Oceanography, Nha Trang, Vietnam.

Data on seasonal occurrences of *Ceratium* in northern and southern parts of Vietnam were added by Mr. Chu Van Thuoc from the Institute of Marine Environment and Resource, and Ms. Do Thi Bich Loc from the Center of Environment and Climate Change (Institute of Marine Technology, HCMC).

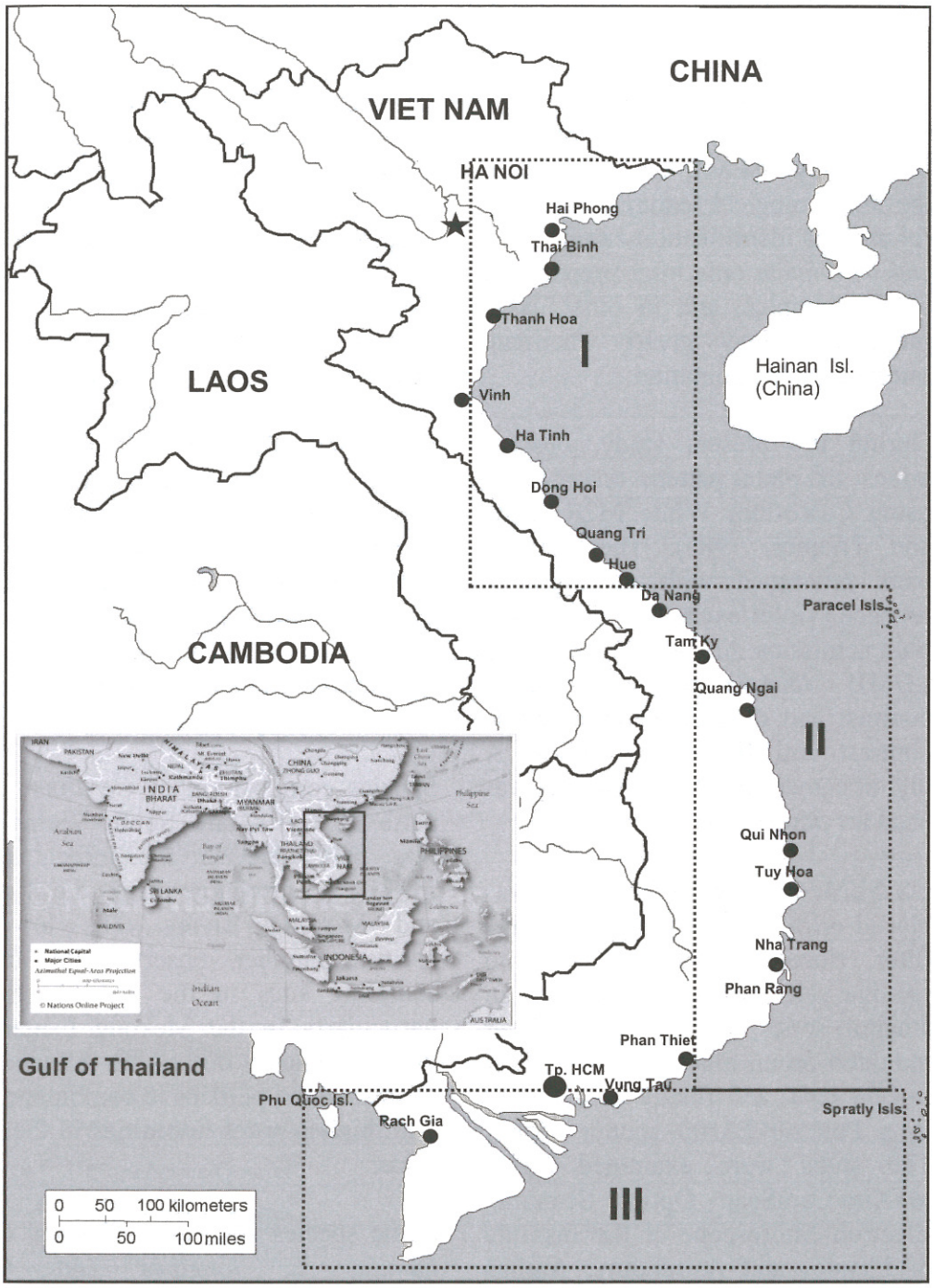


Figure 1. Map showing the position of Vietnam in the South East Asian Region and Vietnamese coastal waters with three distribution zones of *Ceratium* species: - Zone I. Tonkin Gulf and North & Mid-Central Viet Nam; Zone II. South Central Vietnam; and Zone III. Southeast & Southwest Vietnam.

Identifying species

The net samples were examined by light microscopy (LM) and in some cases also by scanning electron microscopy (SEM). Observation of the morphological features important for species identification can in some cases be made only after preparation of the samples, and in other cases preparation may greatly facilitate microscopic examination.

During the present study, observations of plate pattern were made using Calcofluor White M2R (Fritz and Triemer, 1985). The samples were examined with an epifluorescence (violet excitation *c.* 430 nm, blue emission *c.* 490 nm) Leica LDMB microscope with phase contrast and differential interference contrast and fluorescent optics. A digital camera (Olympus DP-71) was used for photography.

For SEM, one drop of the sample was placed on a 5 μm carbon membrane filter, rinsed in distilled water to remove salt, dehydrated through an ethanol series, air dried, the filter mounted on an aluminium stub with carbon tape, and finally gold coated in a Polaron E5100 sputter coater. The stubs were examined on a MaXim/CamScan Optics Scanning Electron Microscope at the Institute of Physics and Astronomy, Aarhus University, Denmark.

The preparation techniques, methods of observation, terminology and keys applied in identification of species in this present study are followed by Jörgensen (1920), Graham and Bronikovsky (1944), Wood (1954), Sournia (1967), Taylor (1976), Chaghtai and Saifullah (1988), Huisman (1989), McDermott and Raine (2006), Okolodkov (2010).

RESULTS AND DISCUSSION

List of Ceratium species

Fifty-two species of *Ceratium* were found along the Vietnamese coast in three zones (Table 1). All species in zone 1 and zone 3 are also found in zone 2. Some species such as *C. arietinum*, *C. axiale*, *C. azoricum*, *C. belone*, *C. bigelowii*, *C. cephalotum*, *C. dens*, *C. digitatum*, *C. ehrenbergii*, *C. gravidum*, and *C. hexacanthum* were recorded only in zone 2 (Tab. 1).

Species composition of *Ceratium* in parts of North and South Vietnam was poor due to the effects of freshwater discharge from the Red and Mekong Rivers. The lower species number observed at the sampling sites in the zone 1 and particularly in the Mekong Estuary was presumably due to the influence of freshwater, perhaps in combination with higher water turbidities in these areas.

Some species such as *C. biceps*, *C. humile*, *C. longipes* and *C. bucephalum*, *C. euarcuatum*, *C. pavillardii* and *C. pulchellum* are listed by Boonyapiwat (2000), but they were not seen in our samples. Freshwater species found in river

mouths or in estuaries in rainy periods are not included in the list.

Tab. 1. List of *Ceratium* species in Vietnamese waters. See Fig. 1 for zoning. The numbers 1-12 refer to the months of the year. Y refers to species that occurred throughout the year.

Ord.	Species names	Zone 1	Zone 2	Zone 3
1	*C. arietinum* Cleve	3, 8, 12	5, 8, 12	
2	*C. axiale* Kofoid		4, 7, 8	
3	*C. azoricum* Cleve		4, 7	
4	*C. belone* Cleve		2-4, 7, 12	
5	*C. bigelowii* Kofoid		7, 12	
6	*C. breve* (Ostenfeld & Schmidt) Schröder	6, 8, 12	3-4, 8, 12	
7	*C. candelabrum* (Ehrenberg) Stein	4-5	Y	4-5, 7
8	*C. carriense* Gourret		3-4, 8	4-5
9	*C. cephalotum* (Lemmermann) Jörgensen		4,7, 11-12	
10	*C. concillians* Jörgensen		4	4-5
11	*C. contortum* (Gourret) Cleve	12	4, 7, 6, 9, 12	
12	*C. contrarium* (Gourret) Pavillard	x	4, 7	
13	*C. declinatum* Kofoid	x	7	
14	*C. deflexum* (Kofoid) Jörgensen	8, 12	3, 8, 12	
15	*C. dens* Ostenfeld & Schmidt		Y	
16	*C. digitatum* Schutt		3-4, 7	
17	*C. ehrenhbergii* (Kofoid)		4	
18	*C. extensum* (Gourr.) Cleve	8, 12	Y	
19	*C. falcatum* (Kofoid) Jörgensen	8, 12	8, 12	2, 4-5, 8
20	*C. furca* (Ehrenberg) Clap. & Lachmann	Y	Y	Y
21	*C. fusus* (Ehrenberg) Dujardin	Y	Y	Y
22	*C. geniculatum* (Lemmermann) Cleve		4, 7, 12	
23	*C. gibberum* Gourret	11-12	Y	
24	*C. gravidum* Gourret		3-4, 8-9, 12	
25	*C. hexacanthum* Gourret		4, 7, 12	
26	*C. horridum* (Cleve) Gran	8, 12	3-5, 8, 12	4-5, 7, 9
27	*C. incisum* (Karsten) Jörgensen		3-4, 7, 12	
28	*C. inflatum* (Kofoid) Jörgensen	11-12	4, 7, 12	
29	*C. kofoidii* Jörgensen	12, 1-2	8, 12	3-5

Tab. 1. List of *Ceratium* species in Vietnamese waters. See Fig. 1 for zoning. The numbers 1-12 refer to the months of the year. Y refers to species that occurred throughout the year (Continued).

Ord.	Species names	Zone 1	Zone 2	Zone 3
30	*C. limulus* Gourret		4, 7, 12	
31	*C. lineatum* (Ehrenberg) Cleve		4, 12	2, 4-5, 8
32	*C. longipes* (Bailey) Gran		4, 7-8, 12	
33	*C. longirostrum* Gourret		4, 8, 12	4-6
34	*C. longissinum* (Schroder) Kofoid		4, 7-8	
35	*C. lunula* (Schimpe) Jörgensen	8, 12	4, 8, 12	5-6, 9
36	*C. macroceros* (Ehrenberg) Cleve	8, 12	Y	9
37	*C. massiliense* (Gourret) Jörgensen	8, 12	8, 12	
38	*C. minutum* Jörgensen	7-9	4, 7	6-7, 9
39	*C. paradoxides* Cleve		4, 7	
40	*C. pavillardii* Jörgensen		4, 5	
41	*C. pentagonum* Gourret	1-2, 12	Y	3,5
42	*C. platycorne* Daday		2-4	
43	*C. praelongum* (Lemmermann) Kofoid		7, 12	
44	*C. pulchellum* Schroder	8, 12	8, 12	
45	*C. ranipes* Cleve		1, 4, 7-8, 12	
46	*C. schroeteri* Schroder		1,3, 4, 7	
47	*C. setaceum* Jörgensen		8	
58	*C. symmetricum* Pavillard	8, 12	8, 12	
49	*C. teres* Kofoid	8, 12	Y	3, 5, 9
50	*C. trichoceros* (Ehrenberg) Kofoid	3-4, 8-9, 12	Y	1, 3, 9
51	*C. tripos* (O.F. Muller) Nitzsch	3-4, 6, 9, 12	Y	1, 3, 9
52	*C. vulture* Cleve	3, 4, 9, 12	Y	1, 9
	Number of species	**25**	**52**	**18**

Taxonomic description

Subgenus *Archaeceratium* Jörgensen

Ceratium gravidum Gourret, 1883 Figs. 2a-c

Taxonomic remarks: Cells are 400-450 µm long and 200 µm wide, with smooth surface. Epitheca flat rounded (Figs. 2a-b) to spatula like (Fig. 2c), larger than hypotheca without apical horn. Hypotheca quadrilateral with two

thin antapical horns. The left divergent is longer than the right which is straight or converging. Apical pore present (Figs. 2a-c).
Two varieties are indentified: - *C. gravidum* var. *latum* (Fig. 2b) and – *C. gravidum* var. *angustum* (Fig. 2c).
Distribution: Widely distributed, common in warm temperate and tropical waters.

Ceratium schroeteri Schröder, 1906 Figs. 3a-d
Taxonomic remarks: Cells are 250-270 µm long and body is 40-45 µm wide. Epitheca elongate, slightly twisted, tapering into apical horn (Figs. 3a-d). Hypotheca short with two large horns curved outward and posteriorly.
Distribution: Tropical waters, but rare species.

Ceratium lanceolatum Kofoid, 1907 Figs. 4a-b
Taxonomic remarks: Medium-sized species, 100-120 µm long and 20-22 µm wide. Body broadly lanceolate (Figs. 4a-b). Epitheca long, sides slightly parallel without apical horn. Hypotheca short, antapical horns lanceolate, the right shorter than the left, both antapical horns wider at the base and tapering to sharp ends (Figs. 4a-b).
Distribution: Pacific and Atlantic oceans. *C. lanceolatum* seem to be found in clean water of coral reefs with high salinity (33-34‰). It was found off the South Central coast of Vietnam. Rare species.

Ceratium praelongum (Lemmermann) Kofoid, 1907 Figs. 5a-c
Basionym: *Ceratium gravidum* var. *praelongum* Lemmermann
Taxonomic remarks: Cells are 200-220 µm long. Body is 50-60 µm wide. Epitheca flat, much larger than hypotheca, without apical horn. Hypotheca rectangular and narrower than epitheca. Antapical horns strong and straight, the right longer than the left and slightly curved outward (Figs.5a-b). Apical pore present.
Distribution: Offshore, warm waters.

Ceratium cephalotum (Lemmermann) Jörgensen, 1911 Fig. 6
Synonym: *Ceratium oviformi* Daday 1888
Taxonomic remarks: Medium-sized species, 150-160 µm in length and 45-50 µm in width. Theca smooth with small pores. Epitheca rounded without apical horn (Fig. 6). Hypotheca quadrangular, narrow with two horns, the right longer than the left.
Distribution: Offshore, common in temperate and tropical waters.

Ceratium digitatum Schütt, 1895 Fig. 7
Taxonomic remarks: Cells are medium-sized, 120-140 µm long. It is very easy to identify by its morphology. Epitheca swollen, sides strongly curved dorsally. Antapical horns are very dissimilar, the right shorter, straight and tapering to a

sharp point; the left horn thick, strongly bent forward and then turned backward (Fig. 7).
Distribution: Common in warm waters, offshore.

Subgenus *Ceratium* (=*Biceratium* [Vanhöffen] Ostenf.)

Ceratium kofoidii Jörgensen 1911 Figs. 8a-c
Synonym: *Ceratium boehmii* Graham, 1944
Taxonomic remarks: Small-sized species. Cells are 80-100 µm long and 20-25 µm wide. Epitheca triangular, tapering into a straight apical horn. The antapical horns are straight and slightly diverging, the left one longer than the right one (Figs. 8a-c). Nucleus is located at the center of the body (Fig. 8a). Theca with numerous pores and weak linear sculpture (Figs. 8b-c)
Distribution: Widely distributed in temperate and tropical waters.

Ceratium lineatum (Ehrenberg) Cleve, 1899 Figs. 9a-d
Synonym: *Ceratium reticulatum* (Pouchet) Cleve, 1903
Taxonomic remarks: Small-sized species, 80-100 µm long and 30-32 µm wide. Epitheca triangular, tapering into a long apical horn. Hypotheca quadrangular with two antapical horns. Antapicals slightly parallel, the left longer than the right (Figs. 9a-b). Theca with numerous large pores and fine striae (Figs. 9c-d).
Distribution: Widely distributed, temperate and tropical waters.

Ceratium setaceum Cleve, 1900 Figs. 10a-b
Taxonomic remarks: Cells are rather long, 220-250 µm. Body pentagonal, similar to *C. pentagonum* but body slender, 40-42 µm wide. Epitheca triangular, apical horn long, straight and thin. Antapical horns short, the left longer than the right and slightly curved inward (Figs. 10a-b). Antapical horns diverging.
Distribution: Common in temperate and tropical waters.

Ceratium teres Kofoid, 1907 Figs. 11-12
Taxonomic remarks: Small species, 120-150 µm long, body hyaline, with many dots (Figs. 11a-b) and very strong linear sculpture (Figs. 12a-b), 35-37 µm wide. Epitheca conical, tapering into a long horn. Hypotheca quadrangular. Antapical horns very small, diverging, the left longer than the right.
Distribution: Widely distributed, common in coastal waters.

Ceratium pentagonum Gourret, 1883 Figs. 13-14
Synonym: *C. subrobustum* (Jörgensen) Steemann Nielsen, 1934
Taxonomic remarks: Body pentagonal, 250-300 µm long and 90-95 µm wide. Theca with linear striae. Epitheca conical, tapering into a short or long horn. Antapical horns short, the left longer and diverging, the right shorter (*C. pentagonum* var. *subrobustum*, Figs. 14a-c).

C. pentagonum var. *tenerum* (Figs. 13a-c) has a smaller body, 60-65 μm wide, pentagonal shape. Apical horn very long and thin. Antapical horns short, its shape looks like *C. teres*. Theca with many large pores and no striae observed.
Distribution: Widely distributed, warm temperate and tropical waters.

Ceratium belone Cleve, 1900 Figs. 15a-c
Taxonomic remarks: Body long and straight about 600 μm in length and 30 μm in width. Epitheca gradually tapering into very long straight apical horn (Fig. 15a). Hypotheca short and narrow (Figs. 15b-c). Antapical horns straight and parallel, the left longer than the right (Figs. 15a-c).
Wood (1968) documented that the species is 150-200 μm in length.
Distribution: Oceanic, rare tropical species.

Ceratium incisum (Karsten) Jörgensen, 1911 Fig. 16
Synonym: *Ceratium furca incisum* Karsten 1906
Taxonomic remarks: Similar to *C. furca* but with slender body. Epitheca wedge shape, large and narrow, slightly curved dorsally. Cells are 110-135 μm long, and 20-25 μm wide. Hypotheca is short with two horns, the left bent, longer than the right which is straight.
Distribution: Offshore, warm waters.

Ceratium minutum Jörgensen, 1920 Figs. 17a-b
Taxonomic remarks: Small species, 60-70 μm long and 33-34 μm wide. Epitheca convex dorsaly, apical horn short. Hypotheca rectangular, with two short antapical horns, the left longer than the right.
Wood (1954) and Chaghtai & Saifullah (1988) illustrated *C. minutum* with descriptions of *C. ehrenbergii*. Both species are clearly differentiated by their morphology (see Fig. 17 and Fig. 18 for comparing).
Distribution: Worldwide, common in coastal waters.

Ceratium ehrenbergii Kofoid, 1907 Figs. 18a-b
Taxonomic remarks: A small species, 52-54 μm long and 32-34 μm wide, rounded mid-body and short horn. Mid-body with convex margin and very convex dorsal side. Apical and antapical horns are short and slightly divergent. Theca with fine linear striae.
Our illustrations and descriptions are in accordance with those by Kofoid (1907), but Kofoid's species is larger, 90-100 μm long and 50 μm in transdiameter. There is confusion between *C. ehrenbergii* and *C. minutum* (see above, Wood 1954; Chaghtai and Saifullah 1988). On the other hand, the illustrations of our specimen look like microgametes in sexual stages of some *Ceratium* species (see Hoppenrath *et al.*, 2009: p. 176, figs. 71f-h). The ratio between apical horn and cell body is 1:2, while in the microgametes, this ratio is 1:1.2.
Distribution: From tropical to temperate waters. Rare species.

Ceratium candelabrum (Ehrenberg) Stein, 1883 Figs. 19a-d & 77
Synonym: *Peridinium candelabrum* Ehrenberg 1859
Taxonomic remarks: Medium-sized with quadrangular body. It is easy to identify this species because it has a very distinctive shape. Cell body is broad. Epitheca triangular, tapering into apical horn. Hypotheca shorter with two horns, the left longer than the right.
Two varieties are recorded: *C. candelabrum* var. *depressum* (Figs 19a-b) and *C. candelbrum* var. *candelabrum* (Figs. 19c-d).
Distribution: Offshore, widely distributed in warm temperate and tropical waters.

Ceratium furca (Ehrenberg) Claparède et Lachmann, 1859 Figs. 20a-h
Basionym: *Peridinium furca* Ehrenberg, 1836
Taxonomic remarks: Cells are 90-120 µm long and 26-30 µm wide. Theca is linear and has small pores. Epitheca conical, tapering into straight apical horn. Hypotheca is quadrangular with two parallel horns, the left longer than the right. Nucleus is located at the center of the cell body (Figs. 20b, d, g).
Ceratium furca varies much in its morphology leading to different varieties such as *C. furca* var. *magnipes* with antapical horn strongly divergent (Figs. 20b-c); *C. furca* var. *furca* with slender epitheca, tapering into straight apical horn; antapical horns serrated, parallel and slightly divergent (Figs. 20d-e); *C. furca* var. *eugrammum* with robust body with linear striae. Antapical horns parallel.
Distribution: Widely distributed, common in temperate and tropical waters. In Vietnam, *C. furca* occurs through the year along the Vietnamese coast. It is dominant at low salinities (30-32 ‰), causing blooms, but no harm.

Subgenus *Amphiceratium* Vanhöffen

Ceratium extensum (Gourret) Cleve, 1901 Figs. 21a-b
Synonym: *Ceratium biceps* Claparède et Lachmann, 1859
Taxonomic remarks: Cell are very long, longer than1,000 µm. Epitheca shorter than hypotheca. Hypotheca narrow and straight. Left antapical horn very long, right antapical absent.
Distribution: Temperate and tropical waters.

Ceratium fusus (Ehrenberg) Dujardin, 1841 Figs. 22a-b
Synonym: *Peridinium fusus* Ehrenberg, 1834
Taxonomic remarks: Cells are 250-300 µm long. Epitheca is long, tapering into apical horn. Hypotheca tapers into the left antapical horn that may be slightly curved. The right antapical is reduced to a stub.
Distribution: Temperate and tropical waters.

Ceratium bigelowii Kofoid, 1907 Figs. 23a-b

Taxonomic remarks: Cell body is well distinguished with a suboval swollen at the girdle and therefore it is well separated from the horns. Hypotheca very short and narrow. Apical and left antapical horns equal or subequal in length; apical horn slightly curved and the left antapical horn notably continuously curved. Right antapical horn very small and needle-like.
Distribution: Temperate and tropical waters.

Ceratium falcatum (Kofoid) Jörgensen, 1920 Figs. 24a-b

Taxonomic remarks: Similar to *C. longirostrum* and *C. falcatiforme* but left antapical horn strongly bent near the tip. Left antapical horn longer than apical horn, right antapical horn very small.
Distribution: Temperate and tropical waters.

Ceratium falcatiforme Jörgensen, 1920 Fig. 25

Taxonomic remarks: Similar to *C. falcatum* and *C. longirostrum* but apical and left antapical horns more curved. Cell body rather thick. Apical horn slightly bent near the tip and longer than antapical horn. Left antapical horn large, right horn very small.
Distribution: Tropical waters, a new record from Vietnamese waters.

Ceratium longirostrum Grourret, 1883 Fig. 26

Taxonomic remarks: Cells are 500-600 µm long, epitheca longer than hypotheca. Apical horn longer than left antapical which is bent near the tip. The right antapical is very small, needle-like.
Distribution: Very common in tropical waters.

Ceratium geniculatum (Lemmermann) Cleve, 1901 Figs. 27a-d

Taxonomic remarks: Cells spindle-shaped, relatively long. The cell body is long. Epitheca is inflated, tapering into an apical horn. Hypotheca tapers into a long left antapical horn, slightly curved. Apical horn positioned closer to the left side of the cell. A reduced right antapical horn is present.
Distribution: Tropical species.

Subgenus *Tripoceratium* Kofoid

Ceratium arietinum Cleve, 1900 Figs. 28-29

Synonym: *Ceratium bucephalum* Cleve, 1897
Taxonomic remarks: Medium-sized species 150-200 µm long and 60-70 µm wide. The apical horn is curved at its base. Hypotheca is rounded at the base. The distal part of the right antapical horn is perpendicular to the apical horn. Left antapical curved, converging towards the apical horn.
Distribution: Temperate and tropical waters.

Ceratium azoricum Cleve, 1900 Figs. 30a-b

Taxonomic remarks: Medium size, 80-100 long. Epitheca rounded, tapering into a short apical horn which is winged, robust, wide with a slight constriction at the base. Hypotheca is convex at the base. Antapical horns relatively short, curved. Right antapical horn is close to the cell body. Distance between right antapical horn and apical horn is half of left antapical horn and apical horn. These characteristics identify the species.

Distribution: Offshore high-salinity waters in South Central Vietnam.

Ceratium axiale Kofoid, 1907 Figs. 31a-b

Taxonomic remarks: Small species. Epitheca triangular, apical horn curves to the right. Hypotheca rounded at the base. Antapical horns turn forward. Right antapical horn rather long and pressing against apical horn. Left antapical horn shorter than the right and more distant from the cell body.

Distribution: Tropical waters.

Ceratium breve (Ostenfeld et Schmidt) Schröder, 1906 Figs. 32-34, 72-73 & 75-76

Basionym: *Ceratium tripos* var. *breve* Ostenfeld & Schmidt, 1901

Taxonomic remarks: Medium-sized species, 180-220 µm long. Epitheca equal or smaller than hypotheca. Apical horn straight or slightly bent to right. Right antapical curved inward. Left antapical bent at the base, then straight and parallel to apical horn. Species has much variation in morphology (see figs 33-34: LM and 72-73, 75-76: SEM).

Distribution: Temperate and tropical waters.

Ceratium contortum (Gourret) Cleve, 1900 Figs. 35-36 & 83

Basionym: *Ceratium giberrum* var. *contortum* Gourret, 1883

Synonym: *Ceratium longinum* (G. Karst.) Jörgensen, 1911

Taxonomic remarks: Rather large species, 450 µm long. Epitheca oblique on right, apical horn bent to the left and then straight. Hypotheca convex at the base with two long antapical horns. The right longer than the left, the left curved and parallel to apical horn, the right also curved and converging to the apical horn.

Distribution: Widely distributed, common in coastal waters.

Ceratium concilians Jörgensen, 1920 Fig. 37

Taxonomic remarks: Similar to *C. gibberum* in shape. Cell body is small, 200 µm long. Theca surface rather smooth. The apical horn bends strongly to the right. Hypotheca rounded, left antapical horn strongly bent, tip closed.

Distribution: Tropical waters.

Ceratium longissimum (Schröder) Kofoid, 1907 Figs. 38a-b
Taxonomic remarks: Body longer than broad, 500-600 µm long. Epitheca triangular, tapering into very long apical horn, bent dorsally. Hypotheca shorter than epitheca. Antapical horns shorter than apical horn.
Distribution: Temperate and tropical waters.

Ceratium carriense Gourret, 1883 Figs. 39a-b
Taxonomic remarks: Rather large species, 500-700 µm long. Epitheca equal to hypotheca. Epitheca triangular with apical horn long and straight. Hypotheca trapezoidal. Antapical horns are very large and more divergent. Antapical horns directed backward making obtuse angles.
Distribution: Offshore, temperate and tropical waters.

Ceratium declinatum (Karsten) Jörgensen, 1911 Figs. 40-41
Taxonomic remarks: Body longer than broad, 250-300 µm long. Apical horn long, straight. Hypotheca shorter than epitheca, convex at the base. Right antapical horn longer than left and diverging to apical horn.
Distribution: Oceanic species, widely distributed in both temperate and tropical waters.

Ceratium horridum (Cleve) Gran, 1902 Figs. 42-44
Synonyms: *Ceratium tripos* var. *horridum* Cleve, 1896, *Ceratium intermedium* (Jörgensen) Jörgensen, 1905, *Ceratium buceros* Zacharias *emend.* Böhm in Schiller, 1937, *Ceratium batavum* Paulsen, 1908.
Taxonomic remarks: Rather large species, 400-500 µm long. Apical horn straight. Antapical horns parallel, slightly diverging with swollen and clavate ends.
Distribution: Coastal, offshore, widely distributed.

Ceratium gibberum Gourret, 1883 Figs. 45a-b & 80
Synonyms: *Ceratium tripos* var. *megaceras* Pouchet, 1883; *Ceratium concilians* Jörgensen f. *dispar* (Pouchet) Böhm, 1931
Taxonomic remarks: Cells are 250-300 µm long and 100-120 µm wide. Apical horn is asymmetrical and straight. Right antapical horn is strongly curved and touches the epitheca. Left antapical horn is smoothly curved and divergent.
Distribution: Widely distributed in temperate and tropical waters.

Ceratium dens Ostenfeld and Schmidt, 1901 Fig. 46
Synonym: *Ceratium dens* var. *reflexa* Schmidt 1901
Taxonomic remarks: Body broader than long, 100-120 µm in length. Epitheca triangular, tapering to a straight apical horn. Hypotheca oblique. Left antapical horn short. Right antapical horn long and divergent.
Distribution: Temperate and tropical waters.

Ceratium lunula (Schimper) Jörgensen, 1911 Fig. 47
Synonym: *Ceratium tripos lunula* Schimper ex G. Karst., 1906
Taxonomic remarks: Body broader than long. Epitheca rectangular, tapering into a short apical horn. Hypotheca shorter than epitheca. Antapical horns are longer than apical horn, symmetrical and convergent.
Distribution: Temperate and tropical waters.

Ceratium symmetricum Pavillard, 1905 Figs. 48a-c
Taxonomic remarks: Body longer than broad, 300 µm in lenght. Apical horn straight or slightly bent. Antapical horns converge towards the apical horn. Hypotheca smoothly rounded at the base and of symmetrical appearance.
Distribution: Temperate and tropical waters.

Ceratium limulus Gourret, 1883 Figs. 49 & 74
Taxonomic remarks: Cells are 100-120 µm long. Epitheca longer than hypotheca. Apical horn short, blunt. Hypotheca rounded at the base. Antapical horns symmetrical and parallel to apical horn. Thecal surface rather rough.
Distribution: Warm waters.

Ceratium paradoxides Cleve, 1900 Figs. 50a-c
Taxonomic remarks: Similar to *C. limulus*. Cells are 100-120 µm long. Thecal surface is rough with reticulations. Epitheca longer than hypotheca. Apical horn is short and straight. Antapical horns are slightly bent and parallel to apical horn.
Distribution: Warm temperate waters, this species is uncommon in tropical waters.

Ceratium hexacanthum Gourret, 1883 Figs. 51-52
Synonym: *Ceratium reticulatum* (Pouchet) Cleve, 1903
Taxonomic remarks: Cells are 250-350 µm long. Epitheca triangular, tapering into a long, straight or slightly bent apical horn. Hypotheca is convex at the base. Antapical horns are bent. Theca surface is characterised by its polygonal pattern.
Distribution: Coastal and offshore, common in warm waters.

Ceratium tripos (O. F. Müller) Nitzsch, 1817 Figs. 53-58 & 78
Basionym: *Cercaria tripos* O. F. Müller, 1781
Taxonomic remarks: Cell size is variable. It can form chains. Epitheca triangular, tapering into straight apical horn. Antapical horns are well developed and parallel to the apical horn. Figs. 54-58 show different varieties of *C. tripos*.
Distribution: Temperate and tropical waters.

Ceratium macroceros (Ehrenberg) Vanhöffen, 1897 Figs. 59a-b
Basionym: *Peridinium macroceros* Ehrenberg, 1840
Taxonomic remarks: Rather large species with long antapical horns. Epitheca oblique, tapering into straight apical horn. Antapical horns arise behind the transverse girdle, pointing backward, then curving more, not parallel with the apical horn. Figures 59a-b show *C. macroceros* var. *gallicum*.
Distribution: Cold temperate to tropical waters.

Ceratium contrarium (Gourret) Pavillard, 1905 Fig. 60
Basionym: *Ceratium tripos* var. *contrarium* Gourret, 1883
Synonym: *Ceratium trichoceros* (Ehrenberg) Kofoid var. *contrarium* (Gourret) Schiller, 1937
Taxonomic remarks: Cells are 200-220 μm long. Body small, with very thin horns. Similar to *C. trichoceros* but antapical horns rather curved. Apical horn long and straight. Antapical horns arising below the base. They are strongly curved inward about halfway to the tips.
Distribution: Warm coastal and oceanic species.

Ceratium trichoceros (Ehrenberg) Kofoid, 1908 Figs. 61a-b
Synonym: *Peridinium trichoceros* Ehrenberg, 1860
Taxonomic remarks: Cells are 300-500 μm long. Body small with long thin horns. Epitheca triangular, tapering into a long straight apical horn. Hypotheca quadrangular, antapical horns long, slightly divergent.
Distribution: Very common in temperate and tropical waters.

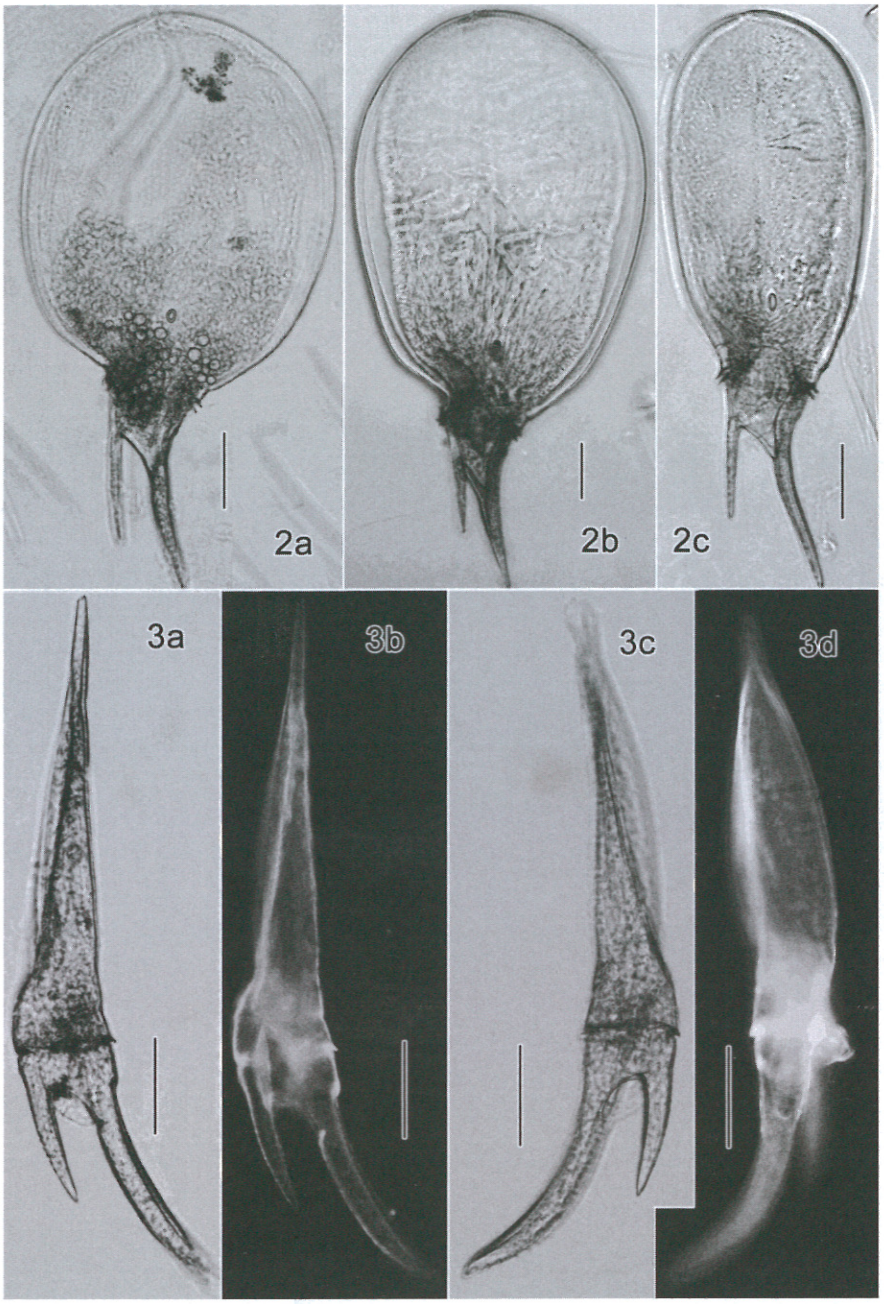
Ceratium ranipes Cleve, 1900 Figs. 62 & 82
Taxonomic remarks: Cells are 400-500 μm long. Epitheca rounded, tapering into a long apical horn which is bent. Hypotheca triangular, antapical horns bent, with five "fingers" at the tips. "Fingers" vary much in shape and size.
Distribution: Offshore, warm temperate and tropical waters.

Ceratium massiliense (Gourret) Jörgensen, 1911 Figs. 63-64 & 81
Basionym: *Ceratium tripos* var. *massiliense* Gourret 1883
Taxonomic remarks: Rather large species, 400-500 μm long. Similar to *Ceratium carriense* but antapical horns less divergent. Epitheca triangular, tapering into long, straight apical horn. Hypotheca quadrangular. Antapical horns arising at right angles to each other then bending, diverging or slightly parallel to apical horn. Spines present on antapical horns. *C. massiliense f. armatum* (Figs. 63a-b) and *C. massiliense var. protuberans* (Figs. 64a-b) are recorded in North and central Vietnam, not found in South of Vietnam.
Distribution: Temperate and tropical waters.

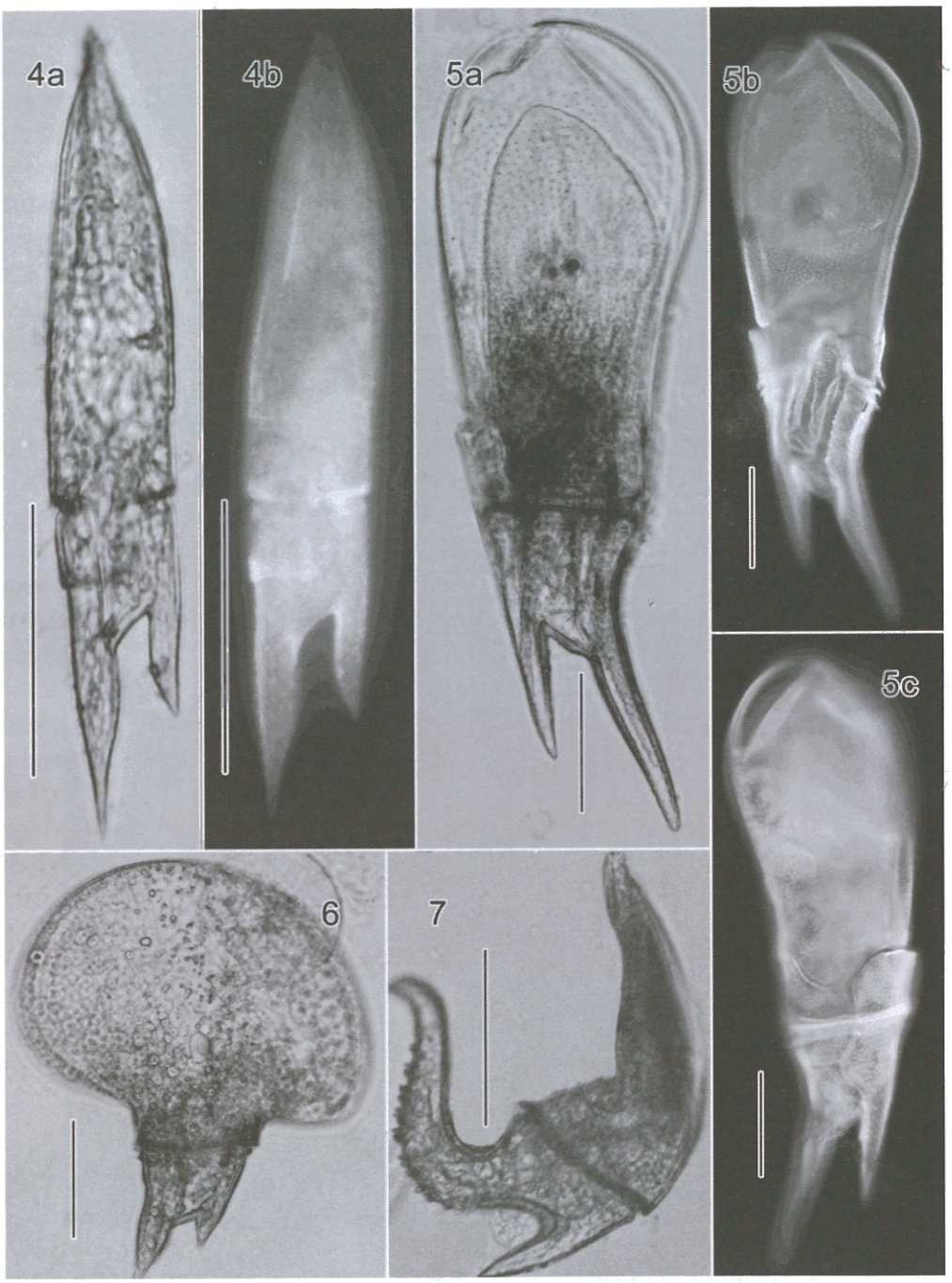
Ceratium deflexum (Kofoid) Jörgensen, 1911 Fig. 65
Basionym: *Ceratium macroceros* var. *deflexum* Kofoid, 1907
Taxonomic remarks: Cells are 200-250 µm long. Similar to *C. macroceros* in body shape, but antapical horns are clearly deflected compared to the base of the body. Epitheca triangular, tapering into straight apical horn. Hypotheca oblique, antapical horns parallel with apical horn.
Distribution: Temperate to tropical waters.

Ceratium vultur Cleve, 1900 Figs. 66a-b, 70a-b & 79
Synonyms: *Ceratium sumatranum* (Karsten) Jörgensen 1911; *Ceratium recurvum* (Jörgensen) Reinecke 1973
Taxonomic remarks: Large-sized species often found in chains. Epitheca short and broad. Apical horn short, straight or slightly bent. Hypotheca triangular. Antapical horns well developed and strongly diverging. Strongly developed wings and spines on apical and antapical horns.
There are two varieties found in Vietnamese waters, *C. vulture* var. *japonica* forma *robustum* (Figs. 66a-b and 79) and *C. vulture* var. *submatranum* (Figs. 70a-b),
Distribution: Temperate and tropical waters.

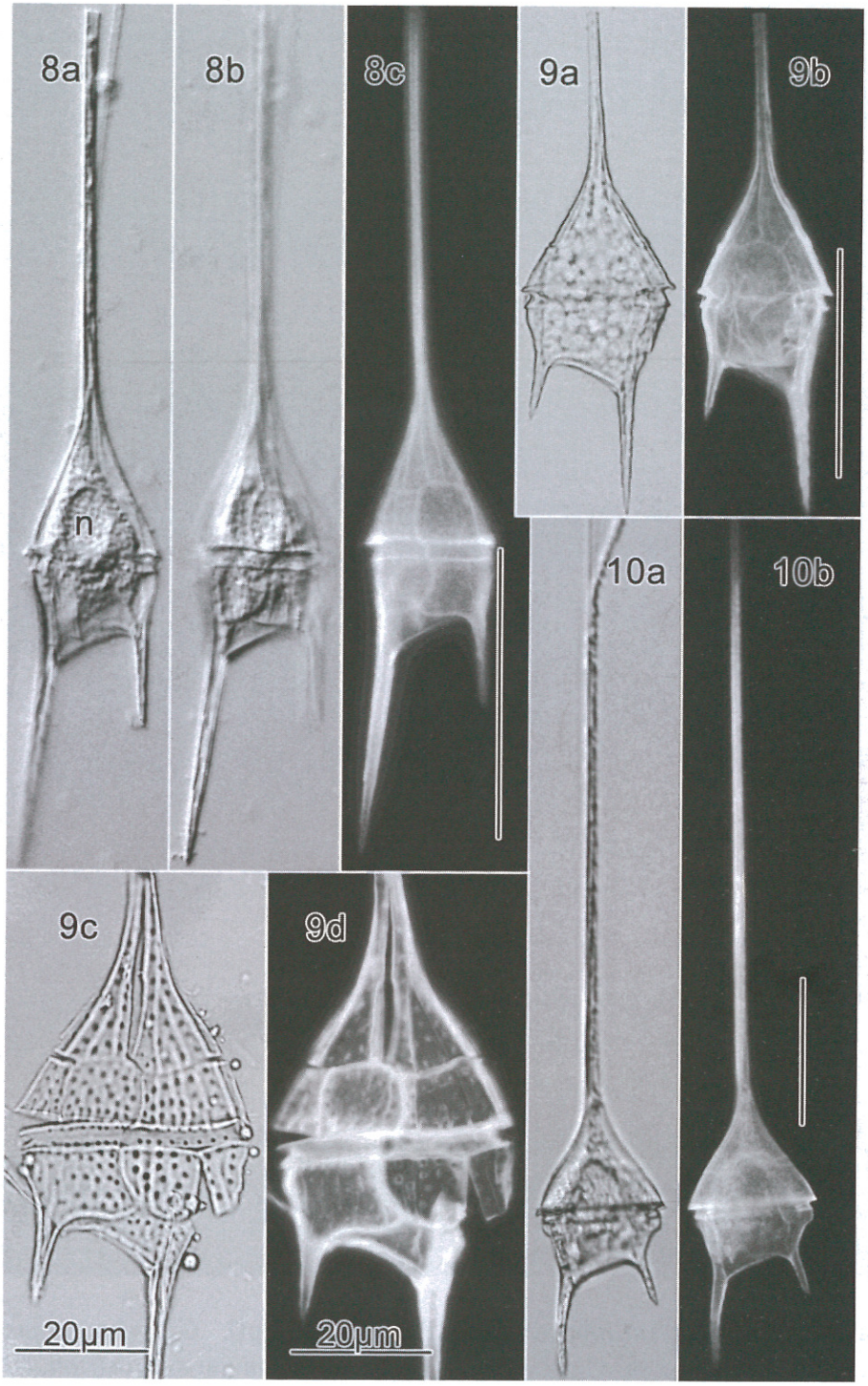
Ceratium platycorne Daday, 1888 Figs. 67-69
Taxonomic remarks: Cells are 150-250 µm long. Epitheca rounded, tapering into straight apical horn. Hypotheca convex at the base. Antapical horns flat, flipper-shaped. Spines present on antapical horns. Figures 67-69 show the different varieties of *C. platycorne*.
Distribution: Offshore, warm waters.



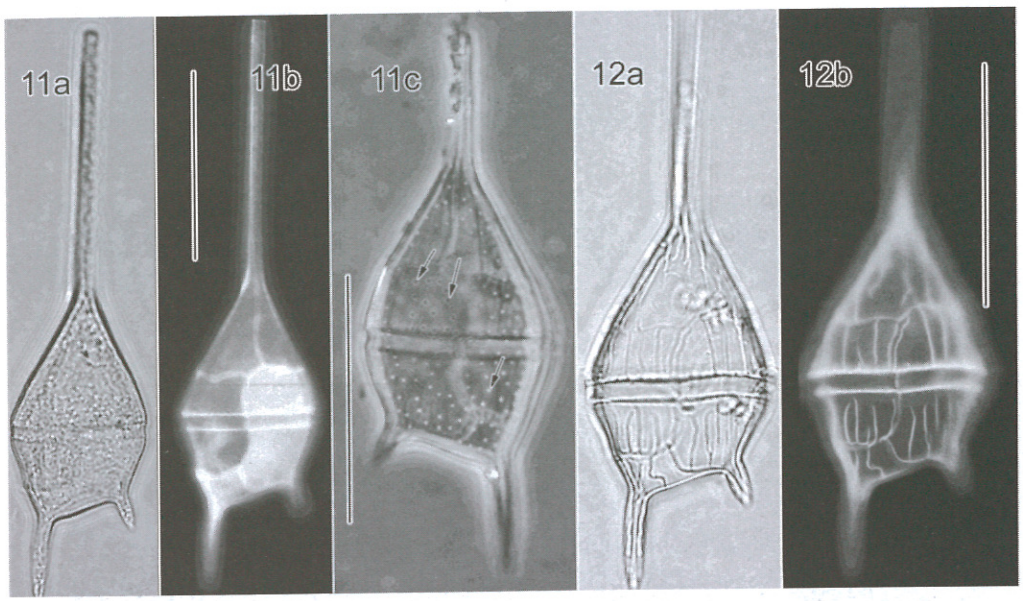
Figures 2-3. ***Archaeceratium***: – 2a (LM-BF). *Ceratium gravidum,* - 2b (BF). var. *latum*, and 2c (BF). var. *angustum*, - all in ventral view with the ventral pore (arrows); Figs 3a&c (LM-BF) and 3b&d (LM-Epi): *Ceratium schroeteri,* - in ventral view (3a&c), and in dorsal view (3c&d). All scale bars = 50 μm. LM: light microscope, BF: bright field, Epi: Epifluorescent, DIC: differential interference contrast, PC: phase contrast. These abbreviations are applied for all following figure legends.



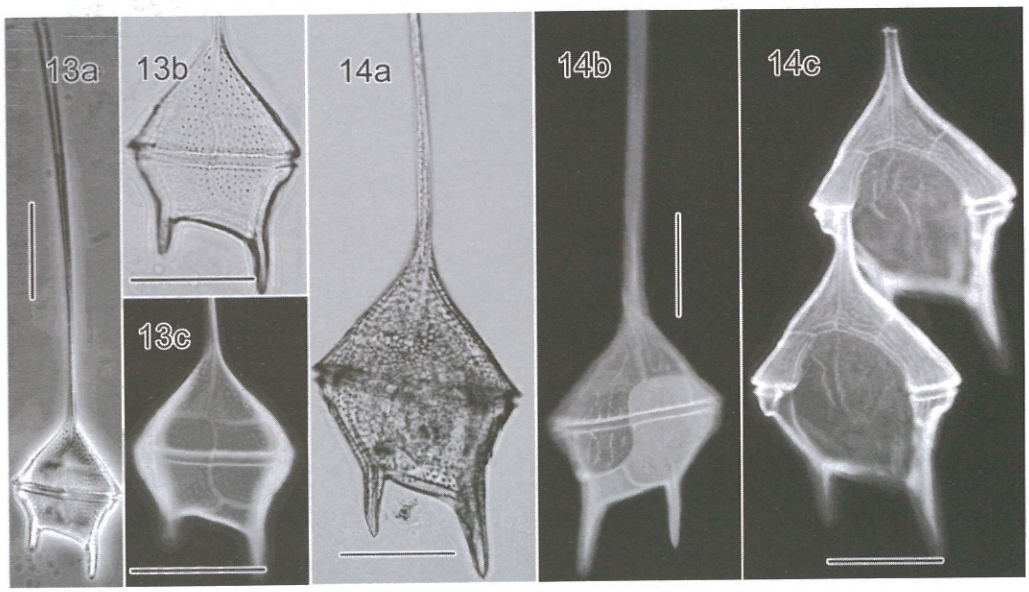
Figures 4-7. ***Archaeceratium***: - 4a (BF)-4b (Epi). *Ceratium lanceolata* in dorsal view; - Figs 5a (BF) & 5b&c (Epi). *C. praelongum,* - in ventral view (5a&b), and in dorsal view (5c); - 6 (BF). *C. cephalotum*; and - 7 (BF). *C. digitatum*. All scale bars = 50 µm.



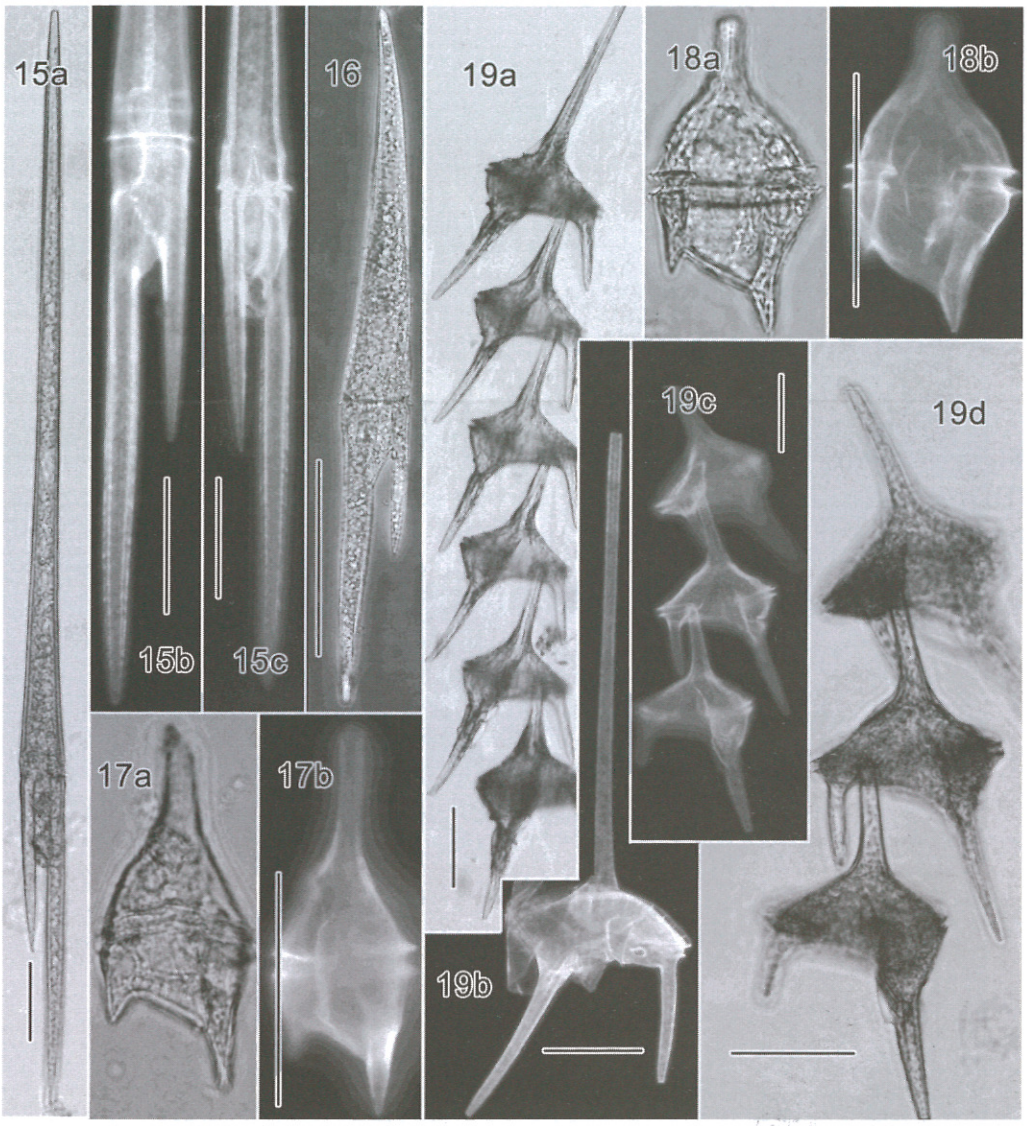
Figures 8-10. ***Biceratium***: – 8a&b (DIC) and 8c (Epi). *Ceratium kofoidii* in dorsal view; - 9a (BF), 9b&d (Epi) and 9c (DIC). *C. lineatum* in ventral view (9a&b), in high magnification showing large pores and fine lined sculpture of theca (9c&d); - 10a (BF)&b (Epi): *C. setaceum* in dorsal view. All scale bars = 50 µm.



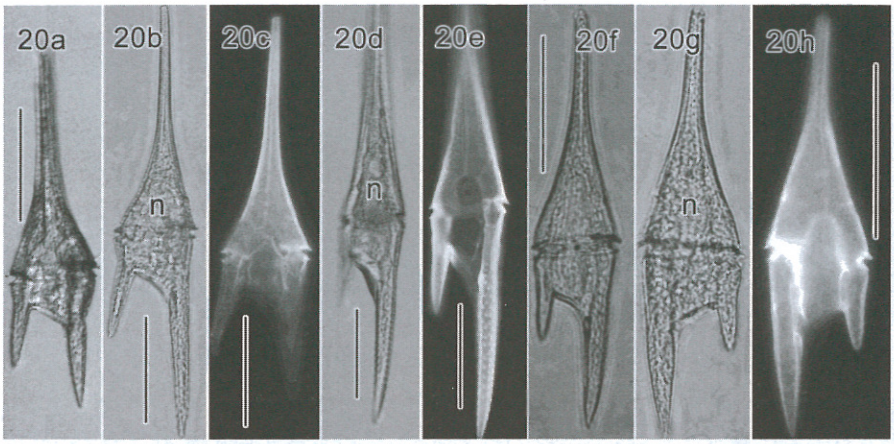
Figures 11-12. ***Biceratium***: - 11-12 (DIC) & (Epi). Different cells of *Ceratium teres* in dorsal view; Figs 11a (BF), 11b (Epi), and 11c (PC): Thecal plates with tiny dots; Figs 12a (PC)-b (Epi): Cell body with strong linear sculpture.



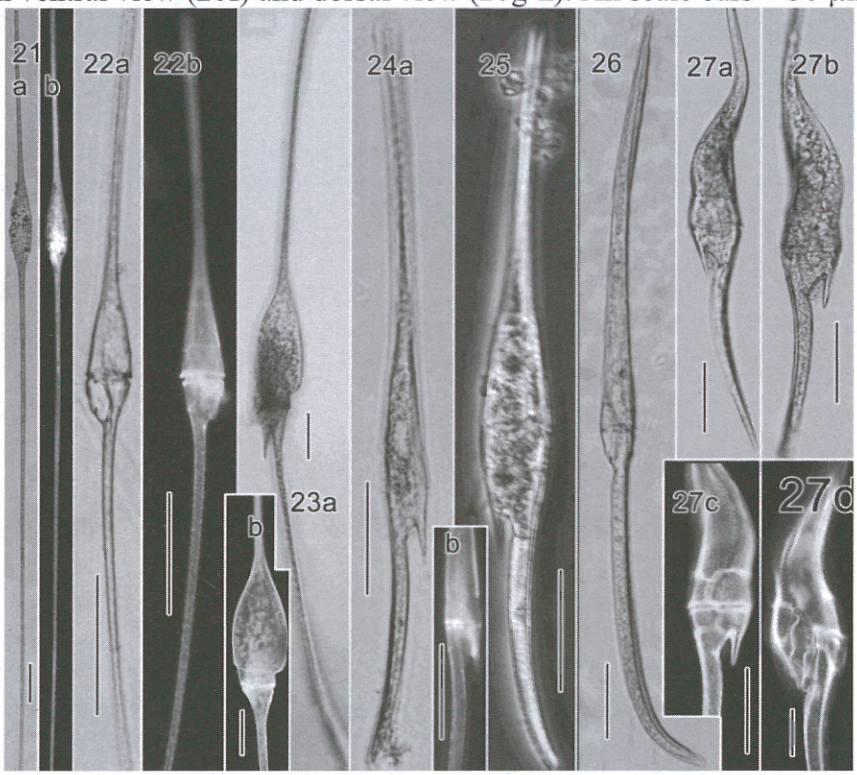
Figures 13-4. ***Biceratium***: - 13a-b(PC) & c (Epi). *C. pentagonum* var *setaceum*, cells in dorsal view; - 14a-c. *C. pentagonum* var *subrostrum*, (BF) & c (Epi), cells in dorsal view and 14b(Epi). All scale bars = 50 µm.



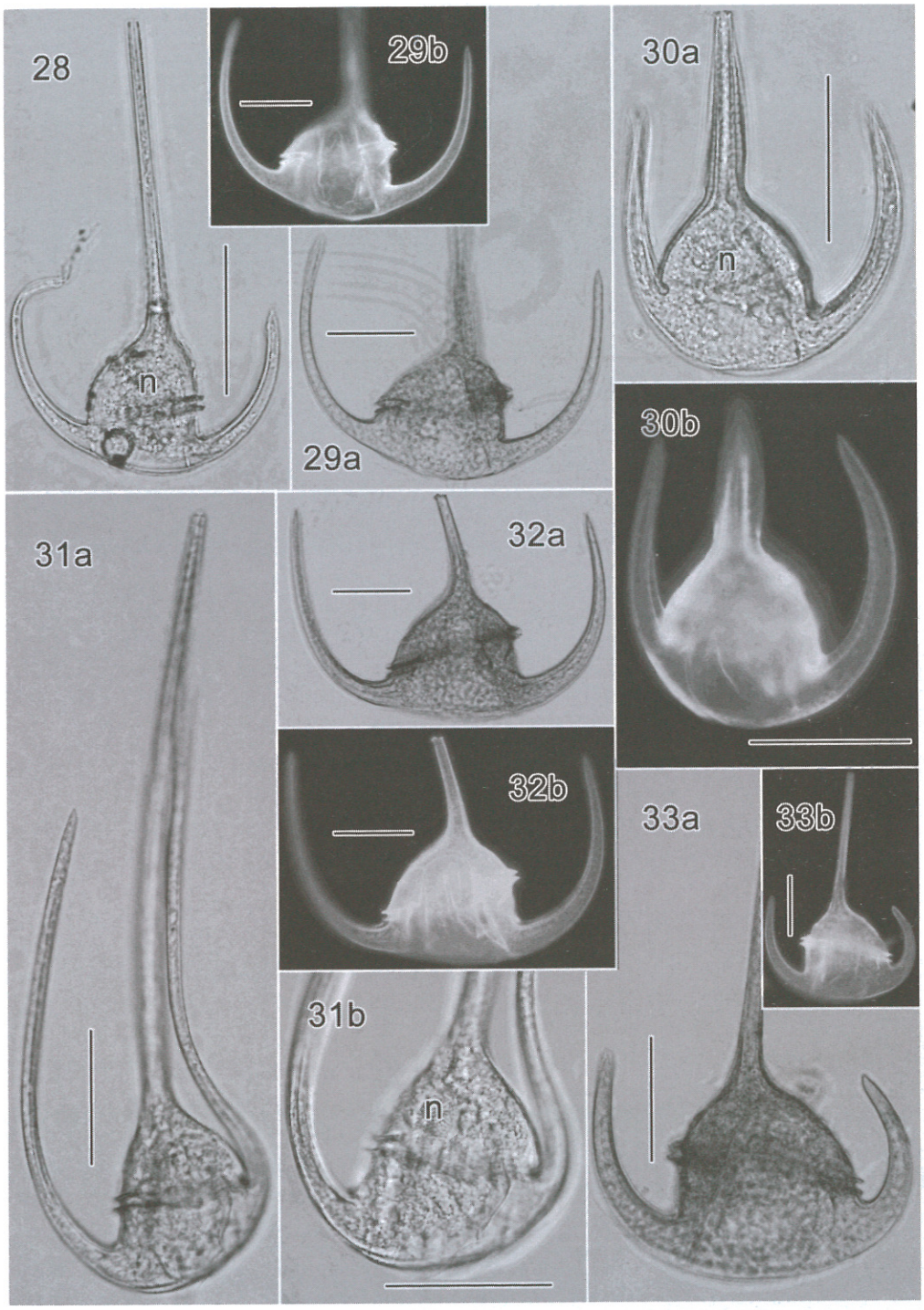
Figures 15-19. ***Biceratium***: - 15a (LM) & 15b-c (Epi). *Ceratium belone*, cells in ventral view (15a&c) and in dorsal view (15b); - 16 (PC). *C. incisum*; - 17a (BF) - b (Epi). *C.* cf. *minutum* cell in ventral view; - 18a (BF) – b(Epi). *C. ehrenbergii*, cell in ventral view; 19a&d (BF) and 19b&c (Epi). *C. candelabrum*. All scale bars = 50 µm.



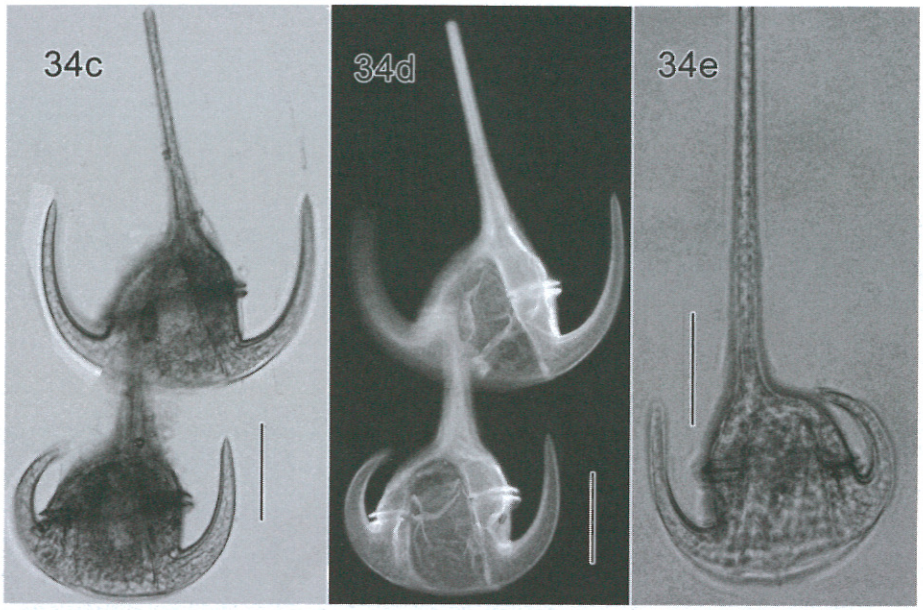
Figures 20a-h. *Biceratium*: - 20a (BF). *Ceratium furca* in ventral view; - 20b (BF)-c (Epi). *C. furca* var. *magnipes* in ventral view; 20d-e (BF). *C. furca* var. *furca* in ventral view; - 20f-g (BF) and 20f (Epi). *C. furca* var *eugrammum*, cells in ventral view (20f) and dorsal view (20g-h). All scale bars = 50 µm.



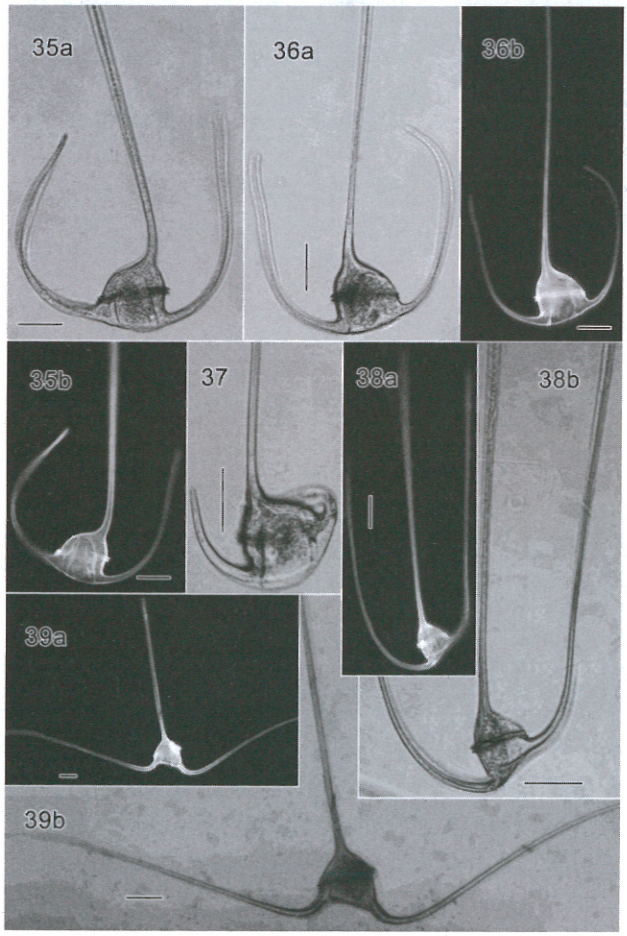
Figures 21-27. *Amphiceratium*: - 21a (BF) - b (Epi). Cell of *C. extensum* in ventral view; - 22a(BF)-b (Epi). *C. fusus* in ventral view (22a) and in dosal view (22b); - 23a (BF)-b (Epi). *C. bigelowii* in dorsal view (24a) and in lateral view (23b); - 24a (DIC) – b (Epi). *C. falcatum* in dorsal view; - 25 (PC). *C. falcatiforme* in ventral view; 26 (BF). *C. longirostrum* in ventral view; 27a-b (BF) and 27c-d (Epi). *C. geniculatum* in ventral view (27a&d), and in dorsal view (27b&c). All scale bars = 50 µm.



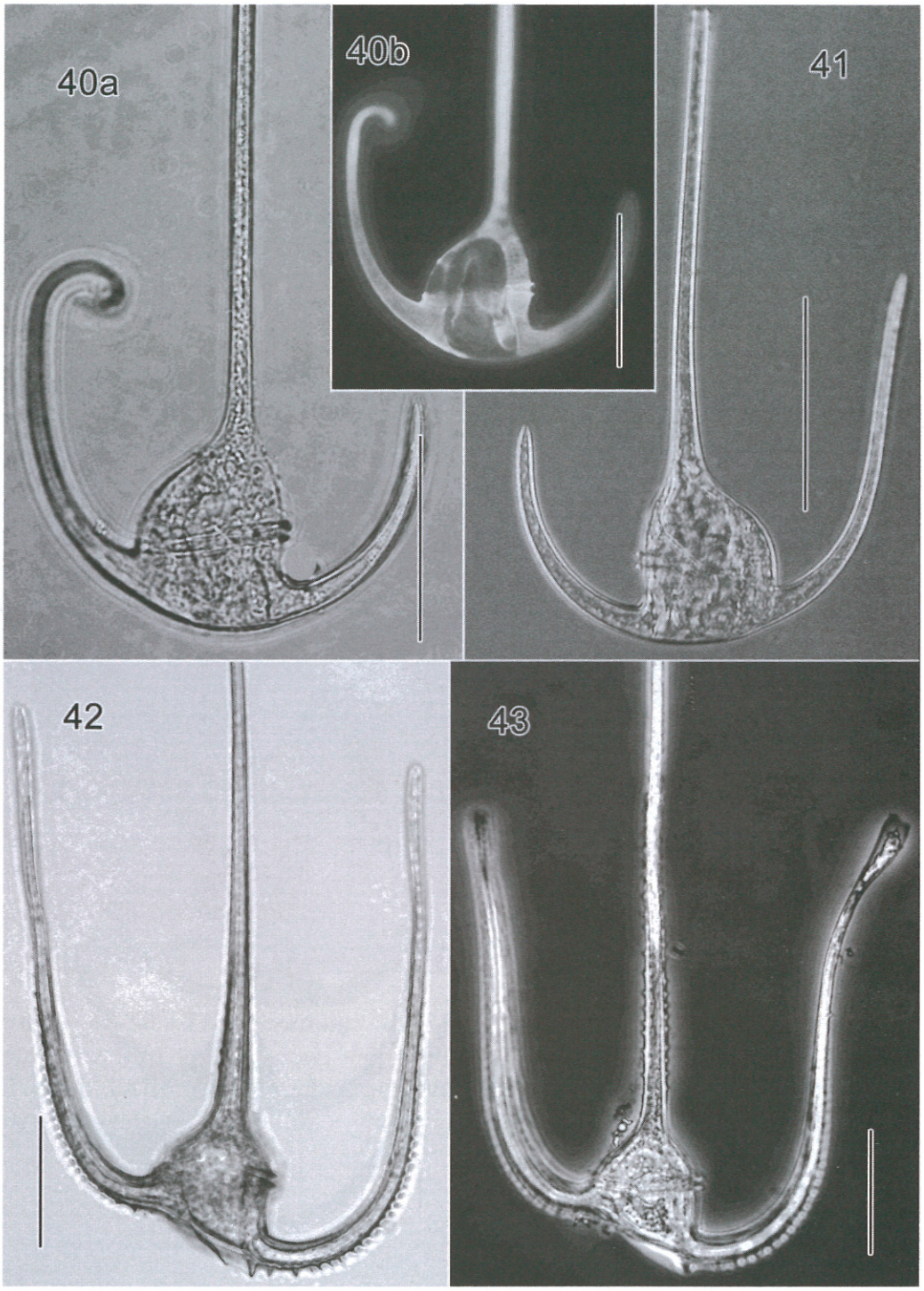
Figures 28-33a-b. ***Tripoceratium***: - 28 (BF) - 29a (Epi)–b (BF). Cell of *C. arietinum* in ventral view (30a-b) and in dorsal view (29); - 31a(BF)-b (Epi). *C. azoricum* in ventral view; - 32a (BF) - b (PC). *C. axiale* in dorsal view; - 33a (DIC) – b (Epi). *C. breve* var. *parallelum* in ventral view; - 34a (BF) – b (Epi). *C. breve* var. *breve* in ventral view. All scale bars = 50 µm.



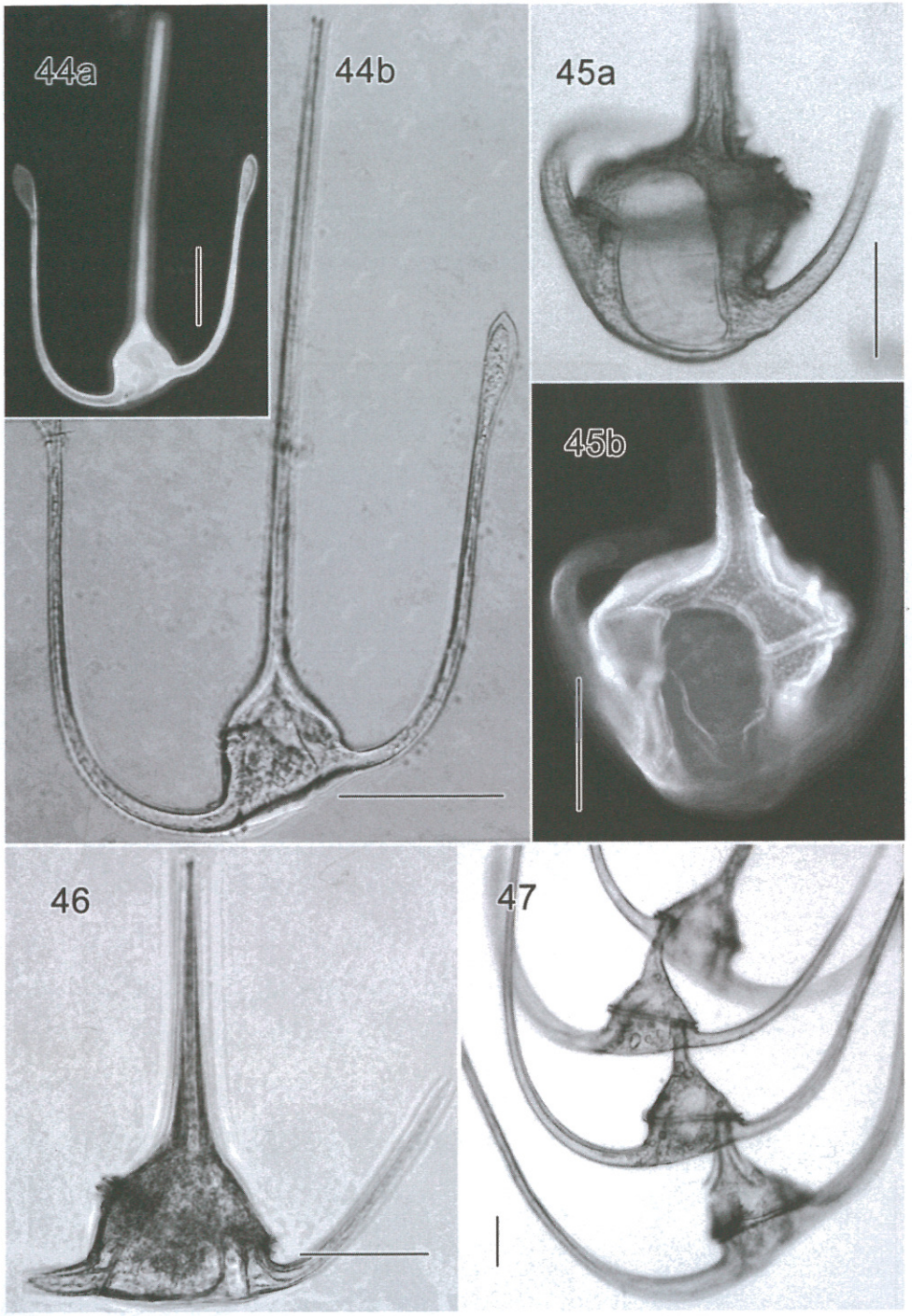
Figures 34c-e. ***Tripoceratium***: - c (BF) - d (Epi). Cell of *C. breve* var. *breve* in ventral view; - e (PC). *C. breve* var. *schmidtii* in ventral view. All scale bars = 50 µm.



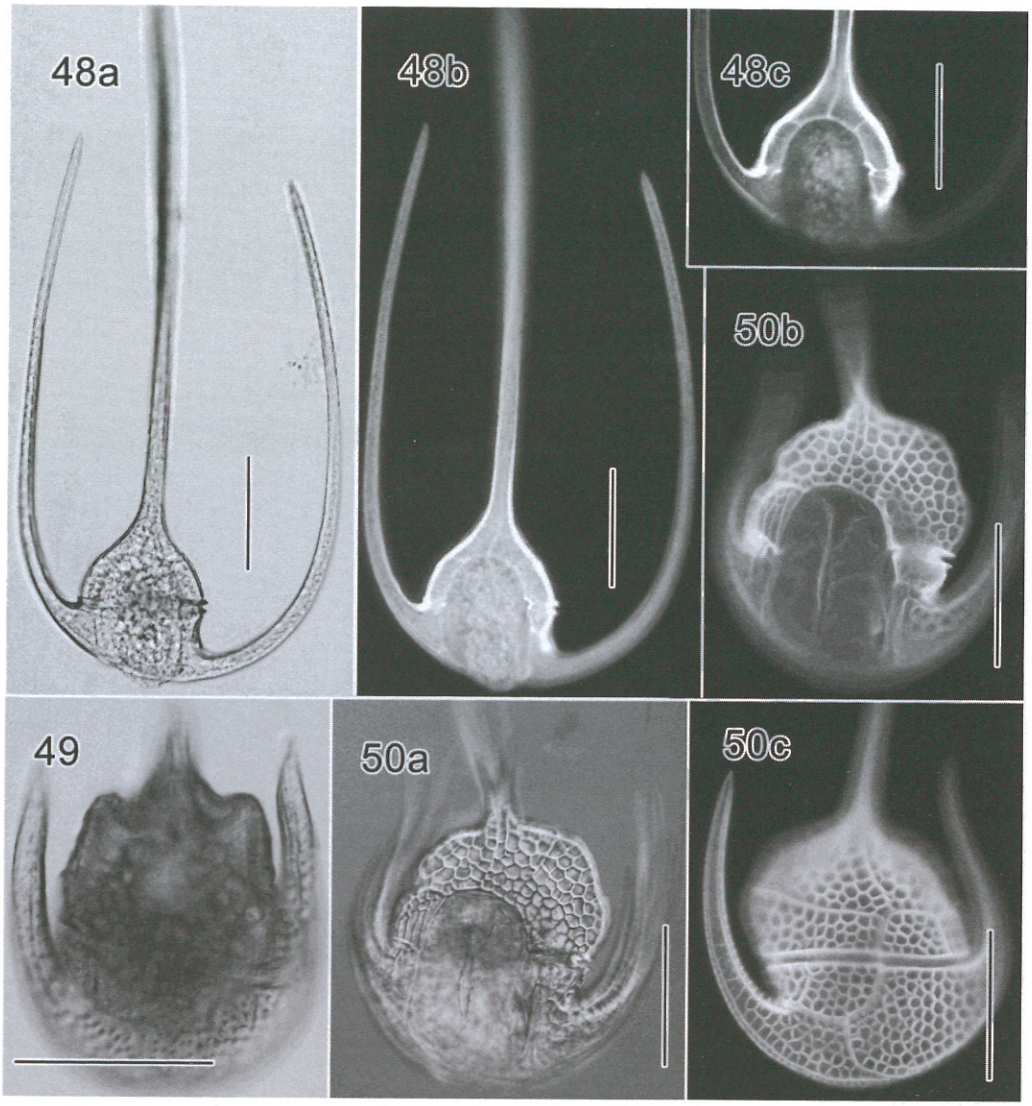
Figures 35-39. ***Tripoceratium***: - 35 a (PC) – b (Epi). Cell of *C. contortum* var. *contortum* in ventral view; - 36a (PC)-b (Epi). *C. contortum* var. *subcontortum* in ventral view; - 37 (PC). *C. concilians* in ventral view; - 38a (Epi) – b (BF). *C. longissimum* in dorsal view; - 39a (Epi) – b (PC). *C. carriense* in ventral view. All scale bars = 50 µm.



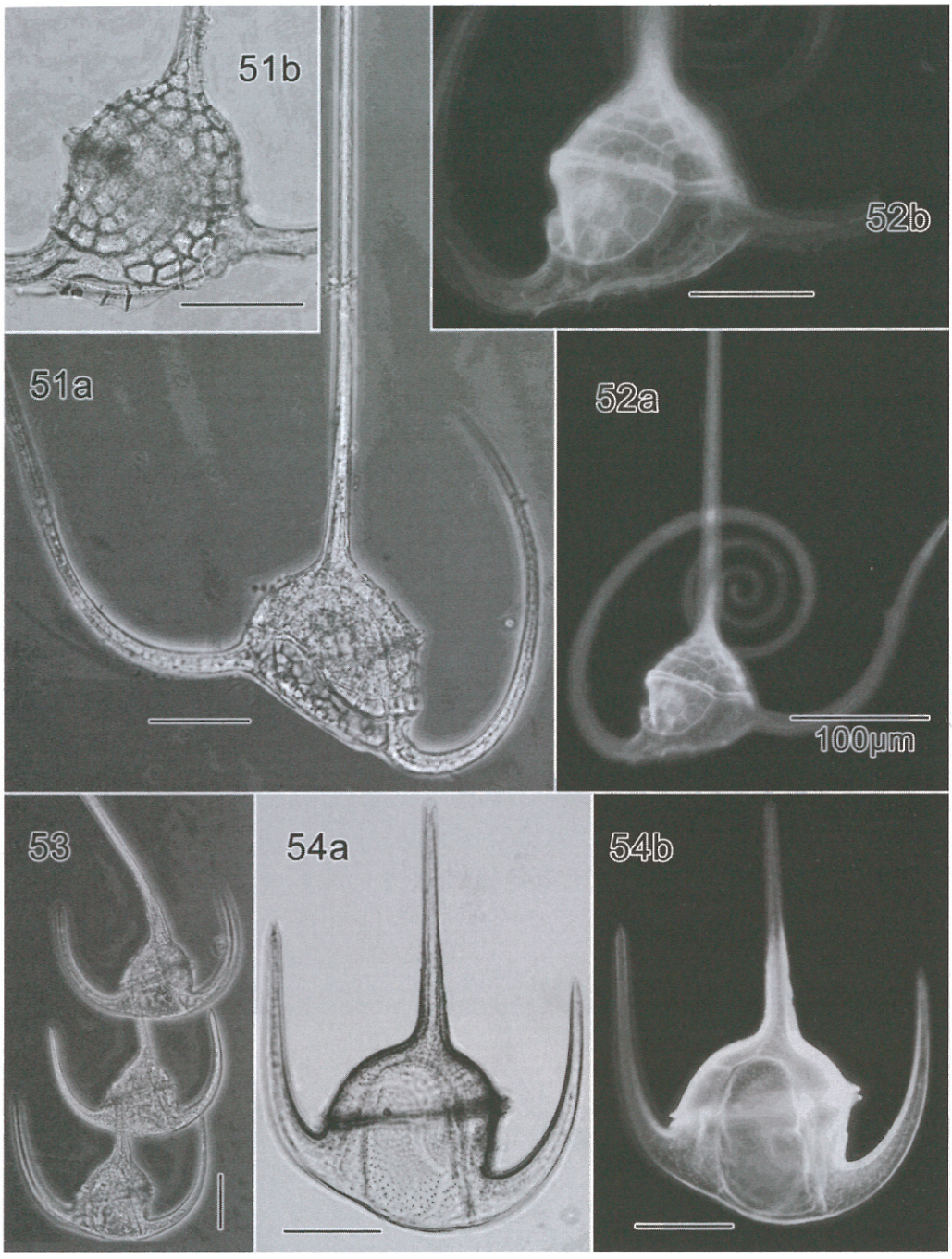
Figures 40-43. ***Tripoceratium***: - 40 a (BF) – b (Epi) – 41 (PC). Cell of *C. declinatum* in ventral view; - 42 (BF). *C. horridum* var. *molle* in ventral view; - 43 (PC). *C. horridum* var. *claviger* in ventral view. All scale bars = 50 µm.



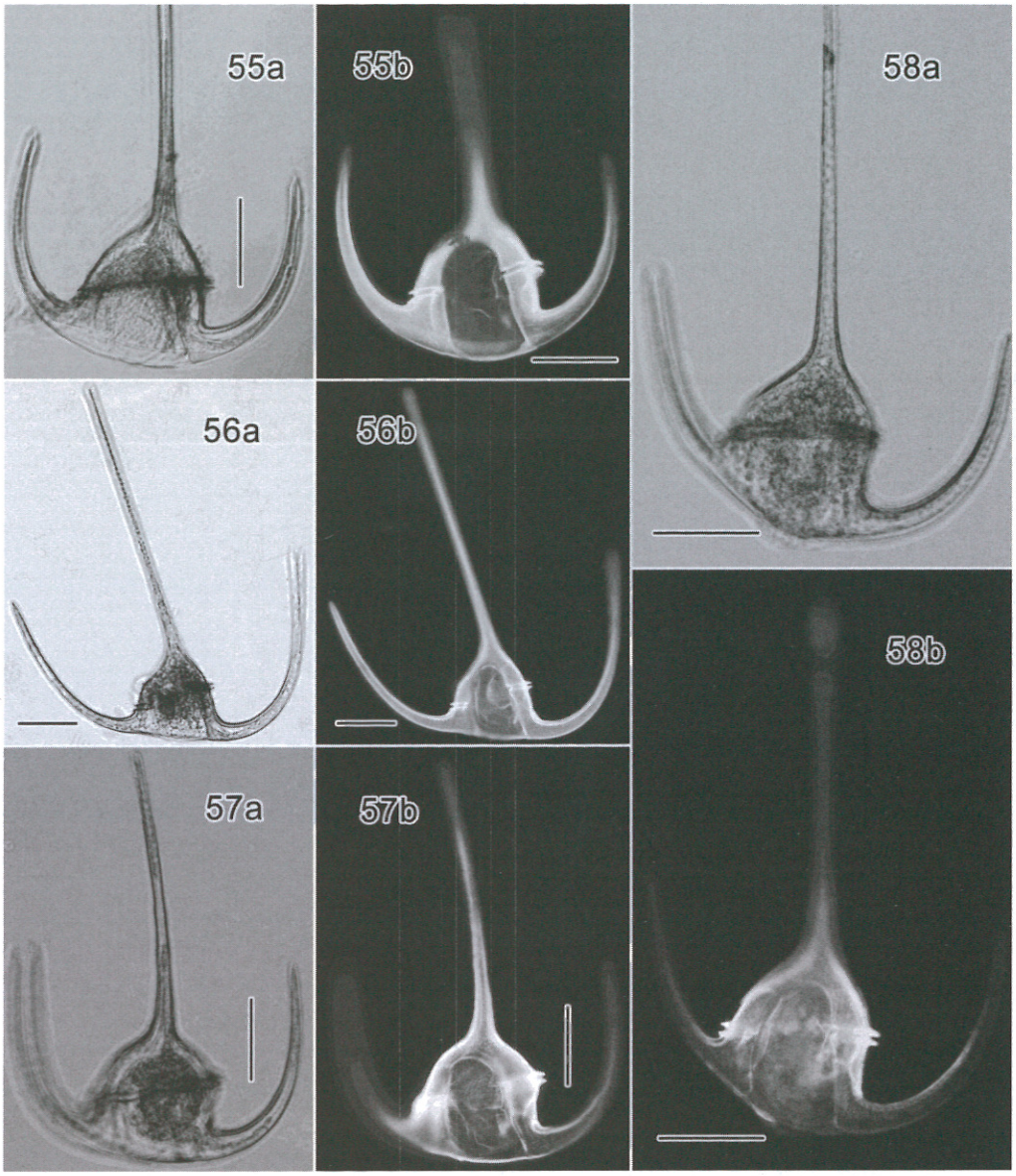
Figures 44-47. ***Tripoceratium***: - 44 a (Epi) – b (PC). Cell of *C. horridum* var. *claviger* in ventral view; - 45 a (DIC) – b (Epi). *C. gibberum* in ventral view; - 46 (BF). *C. dens* in ventral view; - 47 (PC). *C. lunula*. All scale bars = 50 µm.



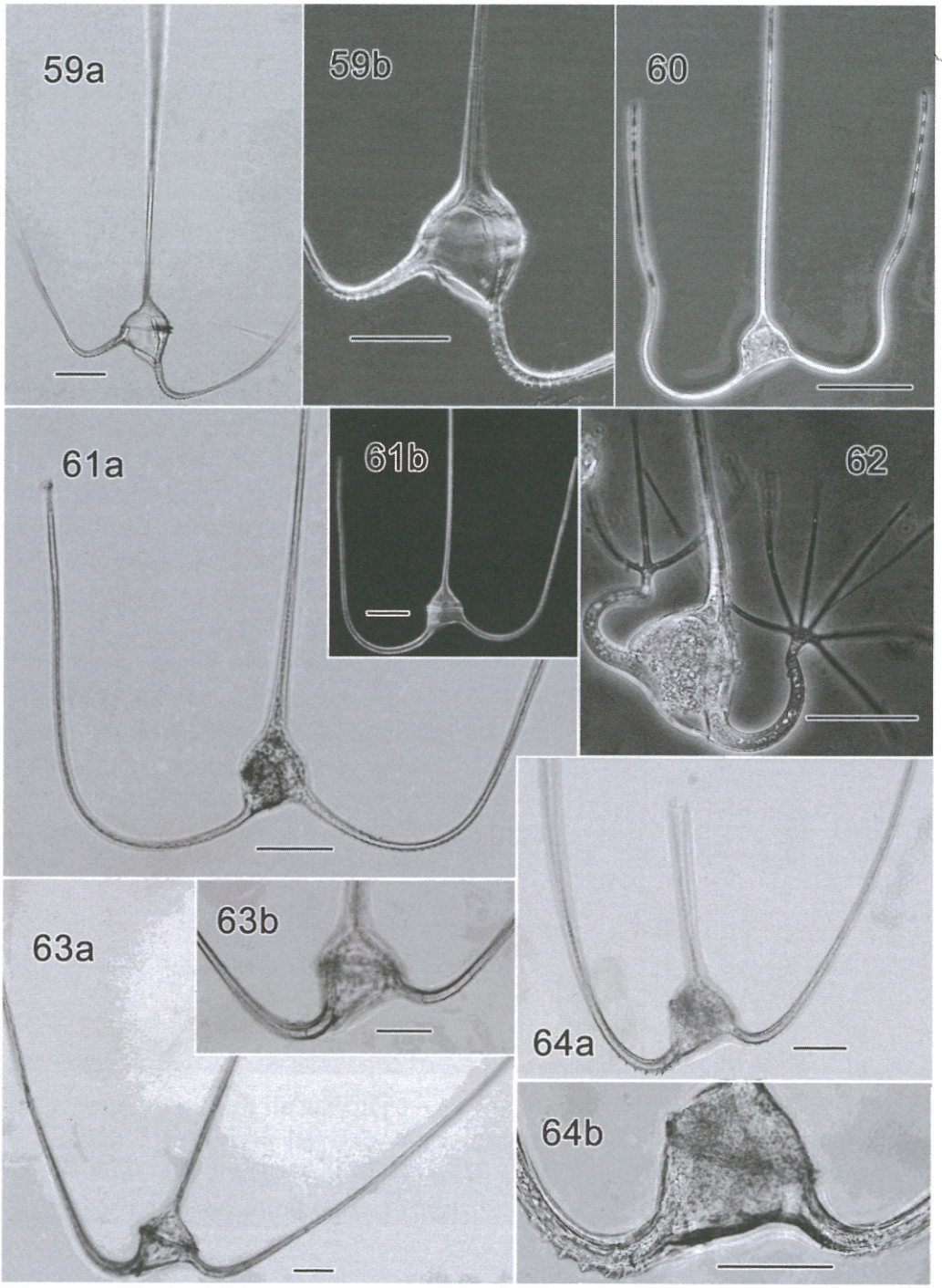
Figures 48-50. ***Tripoceratium***: - 48 a (BF) – b, c (Epi). Cell of *C. symmetricum* in ventral view; - 49 (DIC). *C. limulus* in dorsal view; - 50 a (DIC) – b, c (Epi). *C. paradoxides* in ventral view (50a-b) and in dorsal view (50c). All scale bars = 50 µm.



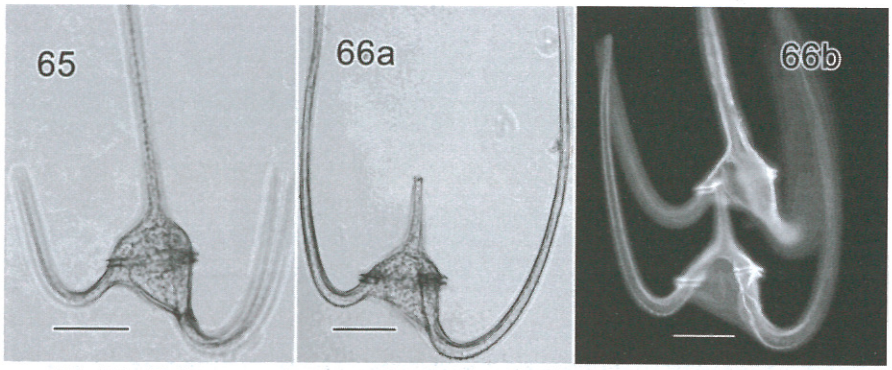
Figures 51-54. ***Tripoceratium***: - 51 a (PC) – b (DIC). Cell of *C. hexacanthum* var. *hexacanthum*; - 52a-b (Epi). *C. hexacanthum* var. *spiralis* in ventral view; - 53 (BF). *C. tripos* var.*atlanticum* in ventral view; - 54a (PC) – b(Epi). *C. tripos* var. *ponticum*. All scale bars = 50 µm.



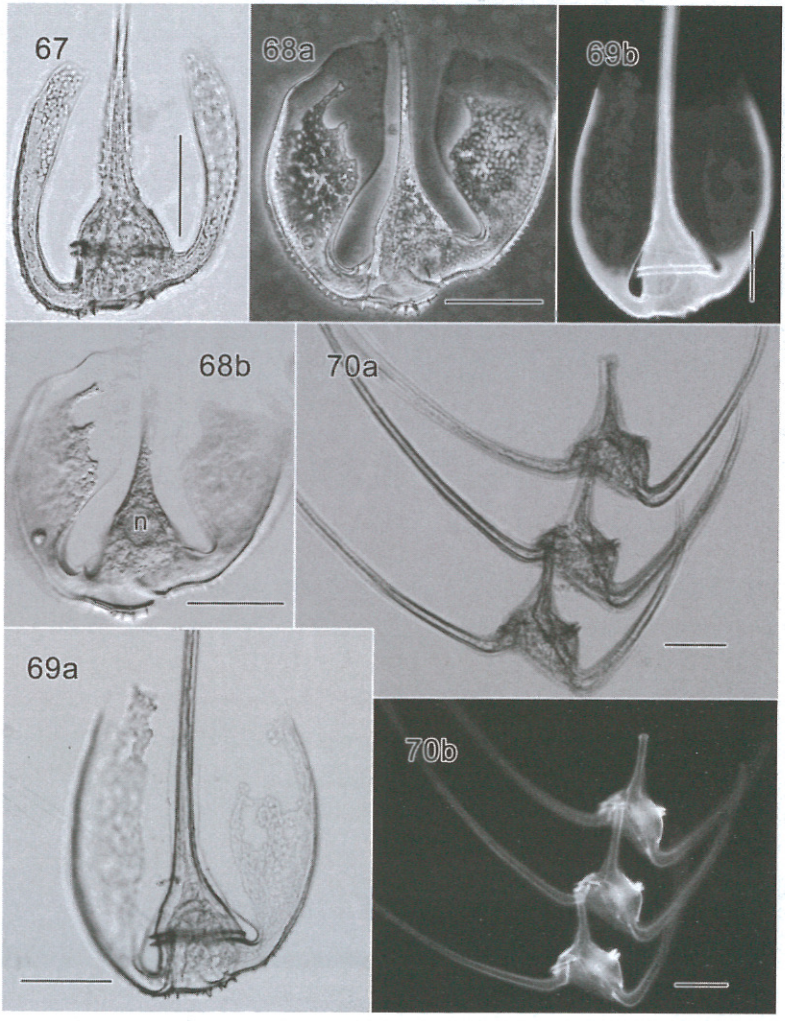
Figures 55-58. ***Tripoceratium***: - 55a (BF) – b (Epi). Cell of *C. tripos* var. *pulchellum* f. *semipulchellum* in ventral view; - 56a (BF) - b (Epi). *C. tripos* var. *atlanticum* in ventral view; - 57a (BF) – b (Epi). *C. tripos* var. *atlanticum* in ventral view; - 58a (BF) – b(Epi). *C. tripos* f. *tripodioides*. All scale bars = 50 μm.



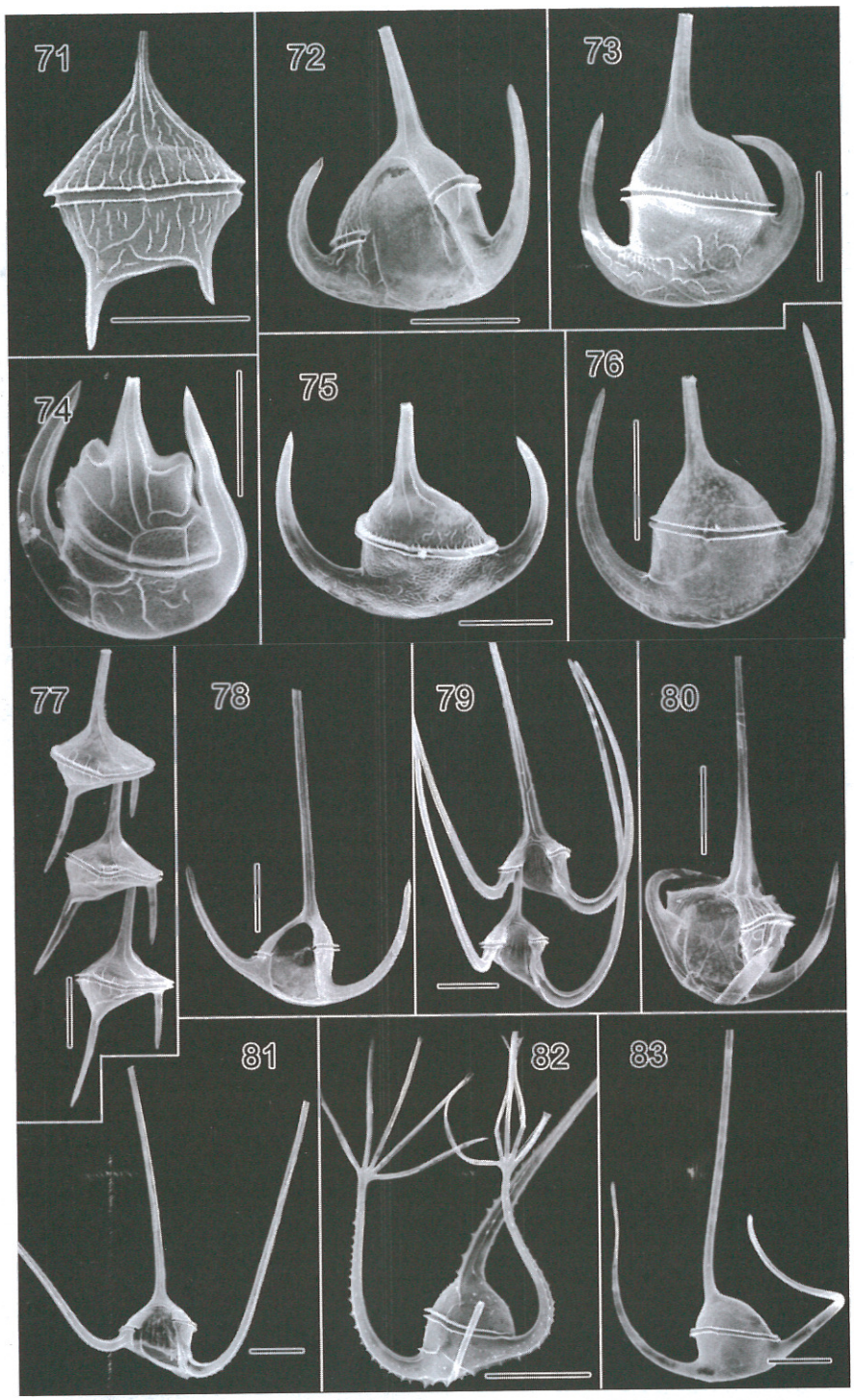
Figures 59-64. ***Tripoceratium***: - 59a (BF) – b (PC). Cell of *Ceratium macroceros* var. *gallicum* in ventral view; - 60 (PC). *C. contrarium* in dorsal view; - 61a (BF) – b (Epi). *C. trichoceros* in ventral view; - 62 (PC). *C. ranipes* in ventral view; - 63a-b (BF). *C. massiliense* f. *armatum*; 64a (BF) – b (DIC). *C. massiliense* var. *protuberans*. All scale bars = 50 µm.



Figures 65-66. *Tripoceratium*: - 65 (BF). *C. deflexum* in ventral view; - 66a (BF) – b (Epi). *C. vulture* var. *japonicum* forma *robustum*. All scale bars = 50 µm.



Figures 67-70. *Tripoceratium*: - 67 (BF). *C. platycorne* var. *dilatatum*; - 68a-b (PC). *C.platycorne* var. *platycorne*; 69a (PC) – b (Epi). *C. platycorne* var. *cuneatum*; 70a (BF) – b (Epi). *C. vultur* var. *submatranum*. All scale bars = 50 µm.



Figures 71-83: Scanning electron micrographs: - 71. *C. pentagonum,* - 72-73 & 75-76. *Ceratium breve*, - 74. *C. limulus*, - 77. *C. candelabrum*, - 78. *C. tripos*, - 79. *C. vultur* var. *japonicum* forma *robustum*, - 80. *C. gibberum*, - 81. *C. massiliense*, - 82. *C. ranipes*, - 83. *C. contortum*. All scale bars = 50 µm.

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