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The Diatom Genus *Eucampia*: Morphology and Taxonomy

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With 14 plates and 4 text figures

Abstract. Examination of clonal cultures and natural samples showed that *Eucampia groenlandica* Cleve is a distinct species, significantly different from *E. zodiacus* Ehrenb. The latter species appeared in two forms; *E. zodiacus* forma *zodiacus* Ehrenb. and *E. zodiacus* forma *cylindrocornis* Syvertsen forma nov., differing in overall morphology and fine structure of the valve. *E. cornuta* (Cleve) Grun. is a characteristic species distinguished from the other taxa by having a heavily silicified rib on the advalvar half of the bands, giving the girdle a transversally striated appearance. *E. groenlandica* and *E. balaustium* Castr. form straight as well as curved colonies. In *E. balaustium* curved colonies seem to be linked with the formation of exogenous resting spores whereas straight colonies form semi-endogenous resting spores.

The distal ends of the elevations of *Eucampia* Ehrenb. and the closely related *Cerataulina* H. Perag. ex Schütt include the morphological features of an ocellus as well as of a pseudocellus but differ from these structures by being furnished with silicified ribs. A special term, "costate ocellus", coordinate to ocellus and pseudocellus is suggested for the distal ends of elevations structured as in these two genera. Otherwise *Eucampia* is consistent with the diagnosis of the subfamily Hemiauloidae Jouse, Kiselev & Poretskii sensu Ross, Sims & Hasle 1977 of the family Bidulphiaceae Kütz.

Introduction

The diatom genus *Eucampia* was described by Ehrenberg (1841), at that time including a single species, *E. zodiacus* Ehrenb., from the

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North Sea. In the course of time more taxa have been referred to the genus, and five are currently listed as valid species (VanLandingham 1968). The genus is regarded as marine and planktonic (e.g. Hustedt 1930).

W. Smith (1856) was apparently the first to classify *E. zodiacus* as a diatom after it had originally been regarded as a desmid by Ehrenberg (1841) and Kützing (1844). After having been included in the family Eucampiaceae Lemmerm. (Lemmermann 1899, Lebour 1930) or Biddulphiaceae Kütz. (Hustedt 1956, Hendey 1964, 1974, Drebes 1974), Simonsen (1979) placed it in the subfamily Hemiauloideae Jouse, Kiselev & Poretskii sensu Ross, Sims & Hasle 1977 of the family Biddulphiaceae.

The species discussed here have been described as belonging to either *Eucampia* or *Moelleria* Cleve. The main diagnostic character of the generitype *M. cornuta* Cleve, and thus of the genus, was the particular structure of the girdle (“Connecting membrane with numerous costæ”, Cleve 1873, p. 7). Grunow (in Van Heurck 1883, pl. 95bis) pointed out the similarity between *E. zodiacus* and *M. cornuta* and made the combination *E. cornuta* (Cleve) Grun. At the same time *E. zodiacus* was depicted with a distinct central process (Grunow in Van Heurck 1882, pl. 95, figs 17, 18), termed a “central pseudo-nodule” by Van Heurck (1896, p. 461). Castracane (1886, p. 98) amended the diagnosis of *Moelleria* emphasizing that it did not “differ essentially from *Eucampia*, except by the presence of a nodule in the centre of the valve”. In the same paper the diagnosis of two new species appeared; *Moelleria antarctica* was described as possessing a central nodule; the other species, thought to be lacking this feature, was given the name *Eucampia balaustium*. Van Heurck (1909, p. 38) tended to regard *M. antarctica* as a summer form of *E. balaustium*, and Mangin (1914) found them in the same chain and thus proved that they were conspecific. Even so, Hoban, Fryxell & Buck (1980) were the first ones to show that the lightly silicified *M. antarctica* was the vegetative cell and the coarsely silicified *E. balaustium* the resting spore of the same species, both possessing a labiate process (= “central nodule” sensu Castracane 1886, “pore” sensu Steyaert & Bailleux 1975a). Since the only two *Moelleria* species had been transferred to *Eucampia* as the first genus described, Mangin (1915) was correct in placing *Moelleria* as a later synonym of *Eucampia*. Although not always followed in

subsequent publications (for references see Steyaert & Bailleux 1975a) this usage is now generally accepted (e.g. Hustedt 1930, VanLandingham 1968).

Eucampia is evidently more closely related to *Cerataulina* H. Perag. ex Schütt and *Hemiaulus* Ehrenb. than to any other genera of the subfamily Hemiauloideae. It lacks the linking spines present in *Cerataulina* and the similar structures found in some *Hemiaulus* species, but the principal construction of the elevation top plates is similar to that found in *Cerataulina* (Hasle & Syvertsen 1980) and comparable to the structure of one *Hemiaulus* species examined (Ross et al. 1977). Areola structure and array are similar in *Eucampia* and *Cerataulina*, while the valve outline of *Eucampia* is oval and that one of *Cerataulina* circular.

Methods and Material

The procedure of examination has been the one outlined by Hasle (1978). Culture work included batch cultures in 250 ml Erlenmeyer flasks (Pyrex) with 100 ml of the growth medium "Guillard f/2" (Guillard & Ryther 1962) or a synthetic medium after Kester et al. (1967). The cultures were grown at various temperatures and light intensities, standard conditions being 12°C and approximately 2000 lux (fluorescent tubes Philips TL32 and TL33) in a 12:12 hours dark:light cycle.

For light microscopy (LM) a Leitz Orthoplan with Zernicke condenser for phase contrast and bright field illumination was used. Electron microscopes included Siemens Elmiskope I (TEM), Jeol JEM-100C/ASID/SEG (TEM), Cambridge Stereoscan Mk IIa (SEM) and Jeol JSM-35C (SEM).

A number of permanent mounts from the British Museum (Natural History) were used during this investigation. Slides of *E. virginica* Grun. (BM 43165, Artesian Well, Atlantic City), *E. nodosa* Schmidt (BM 43164, Arafura Sea, Coll. Comber 262 and BM 43163, surface of Arafura Sea, 10.038, Nov. 13, Coll. F.W. Payne) were studied in the light microscope.

The illustrations of the different species are mainly based on preserved

net samples except where otherwise indicated, and the Figures are corresponding to the following samples:

E. zodiacus: Biloxi, Miss. U.S.A., 19 Jan. 1970; Fig. 25. Campeche Bank, Mexico, autumn 1971; Figs 5-11, 27, 28. Menai Bridge, Wales, 13 Sept. 1970; Fig. 38. Patuxent River, Maryland, U.S.A., Dec. 1974; Figs 23, 24, 26. Ubatuba, State of Sao Paulo, Brazil, 23°30' 01''S, 7 July 1978; Figs 12-21, 29, 41-47. Viksfjord, Oslofjord, Norway, clonal culture "OEz2", isolated 30 Sept. 1978; Figs 7, 22, 32-34, 36, 37 and clonal culture "OEz6", isolated 11 Nov. 1979; Figs 30, 31, 35, 39, 40.

E. groenlandica: Baffins Bay 15/VIII, Cleve's material, B.M. slide 33027; Figs 48-50. Barents Sea, Arctic, clonal culture "BEg2", isolated from 77°02'N, 33°37'E, 19 July 1979; Figs 51-53, 55-65, and clonal culture "BEg3" from 77°02'N, 33°19'E, 18 July 1979; Fig. 54.

E. cornuta: Arafura Sea, B.M. 31053, permanent slide; Fig. 74. Campeche Bay, Mexico, summer 1979; Figs 75, 76, 83. Ubatuba, State of Sao Paulo, Brazil, 7 July 1978; Figs 66-73, 77-82.

E. balaustium: Brategg Expedition, St. 28, 58°00'S, 150°05'W, Antarctic, 19 Jan. 1948; Figs 94-103, 111, 122-129. Norwegian Antarctic Expedition 78/79, St. W209, 72°20,1'S, 15°46'W, 6 Feb. 1979; Figs 84-92, 103, 105-110, 112, 113-116, and St. W218, 74°39,12'S, 34° 52,32'W, 14 Feb. 1979; Figs 104, 117-120.

The terminology follows von Stosch (1975) and Ross et al. (1979) except where otherwise stated.

Observations

***Eucampia zodiacus* f. *zodiacus* Ehrenb. (Figs 1a-d, 5-8, 22-26, 30-40).**

Ehrenberg 1841, p. 151, pl. 4, fig. 8.

Synonyms: *Eucampia britannica* W. Smith 1856, pl. 61, fig. 378.

E. nodosa A. Schmidt 1874, pl. 141, fig. 28.

E. zodiacus var. *cornigera* Grunow in Van Heurck 1883, pl. 95bis, figs 3, 4.

E. zodiacus f. Schröder 1906, p. 352, fig. 18.

Type locality: Cuxhaven, North Sea.

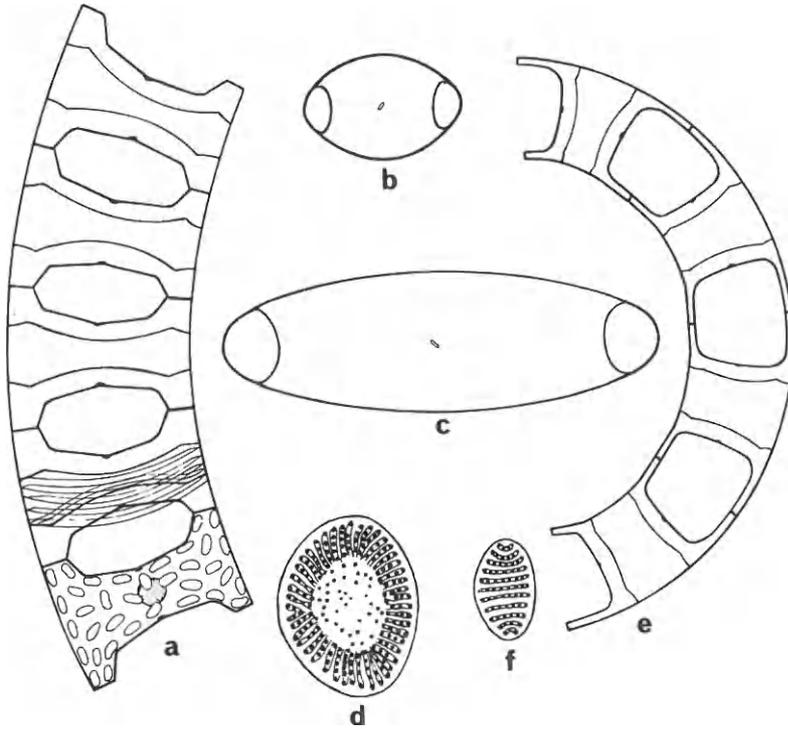


Fig. 1. *Eucampia zodiacus*. a. *E. zodiacus* f. *zodiacus*, broad girdle view. b, c. Valve outlines. d. *E. zodiacus* f. *zodiacus*, top plate. e. *E. zodiacus* f. *cylindrocornis*, broad girdle view. f. *E. zodiacus* f. *cylindrocornis*, top plate. Approximate magnifications: filaments $\times 500$, valves $\times 1000$, top plates $\times 4000$.

***Eucampia zodiacus* f. *cylindrocornis* Syvertsen f. nov.** (Figs 1e-f, 12-21, 41-47).

Long cylindrical horns at the poles, subcircular in cross section with the longer axis in transapical direction. Top of horns traversed by parallel lamellae in apical direction, ends of lamellae more or less curved towards the apices of the top plate. Valve face slightly concave in apical and strongly convex in transapical direction. Valve margin undulated, lobing down at apices, more at the convex than at the concave side as seen in broad girdle view. Apical axis 8-80 μm , transapical axis 8-15 μm . Areolae roundish poroids with a simple external velum formed by thin strands of silica, mostly in a cruciform pattern, 10-20 in 10 μm branching out from the central labiate process.

Differt a typo cornibus longioribus cylindricisque.

Subtropical to tropical. Type locality: Ubatuba, Brazil, 23°30'02''S. Holotype: IMBB slide no. 76, University of Oslo. Isotypes will be sent to the Hustedt Collection, Bremerhaven, and British Museum (Natural History).

The helically coiled chains of *E. zodiacus* are well known from numerous illustrations published. The single cells are laterally flattened, elliptical in valve view (Figs 1b, c, 23, 31, 32) and united into chains by the abutting top plates of the horns (Figs 1a, e, 5-13, 41). The length of the perivalvar axis may vary from less than half the apical length in large cells (Fig. 5) to more than five times the width in smaller specimens (Figs 13, 14, 18). The cells are slightly twisted about the perivalvar axis. Together with a curved transapical plane this brings about the typically coiled chains. The chloroplasts are numerous and parietal, and the nucleus is centrally oriented.

The girdle consists of many open bands (mostly 10-15 in a mature theca) which are slightly narrowing towards the concave side of the girdle, thus adding to the curvature of the cell (Fig. 22). The bands are finely perforated by transverse rows of pores (Figs 22, 47), 32-40 in 10 μm , and apparently lacking a distinct longitudinal rib. Ligulae and antiligulae are situated along a straight line in narrow girdle view.

The larger valves are lanceolate to elliptical in outline, rounding more off as the size diminishes (Figs 1b, c, 31, 32). The valve face is concave in broad girdle view, and the change of slope between valve face and horns is abrupt in *E. zodiacus* f. *zodiacus*, but sometimes smoother in *E. zodiacus* f. *cylindrocornis* (Figs 12-21). The valve mantle is undulated, prolonged downwards apically as well as transapically (Figs 30, 41-43). This is in accordance with Smith's (1856, pl. 60, fig. 299) and Grunow's (in Van Heurck 1882, pl. 95, figs 17, 18) illustrations, whereas Hustedt (1930, fig. 451c) depicted a straight mantle. The length of the apical axis varies from 8 to 80 μm , whereas the transapical axis may be from 10 to 70 μm long.

Starting at the central labiate process, the striae branch off towards the horns and margin, each new row of areolae usually starting from a single poroid (Figs 23, 26, 31). The areolae are rectangular or almost elliptical to square in outline, 10-20 in 10 μm , decreasing in size towards the margin and the horns. Okuno's reconstructions, based on

TEM observations, show loculate areolae, partly occluded, internally only leaving a small circular foramen, and with an external velum (Okuno 1954, p. 240, pl. 1, figs C, D, pl. 4, figs a-g). However, SEM observations show that the areolae are simple poroids, the velum being flush with the outer surface (Figs 38-40). The velum consists of narrow silica strands forming a delicate filigree pattern (Fig. 26). In *E. zodiacus* f. *cylindrocornis* the cribrum may be very simple, consisting of a few cruciform silica strands only (Figs 29, 44).

The horns of *E. zodiacus* f. *zodiacus* are low, broad and conical forming an angular elliptical aperture between adjacent valves (Figs 5, 8). The horns of *E. zodiacus* f. *cylindrocornis* are typically long, slender and subcylindrical, forming square to rectangular apertures (Figs 12, 13). The horn on the convex side of the chain is slightly longer than that on the other side, more so in *E. zodiacus* f. *cylindrocornis* than in *E. zodiacus* f. *zodiacus* (Figs 19, 22, 42).

The top plates of the horns have ribs with regular rows of pores in-between. In *E. zodiacus* f. *zodiacus* radial ribs surround a central smooth silica plate perforated by scattered pores (Figs 23-25, 35). The internal surface of the top plate is structured in a similar way (Fig. 38). With decreasing specimen size the size of the top plate also diminishes and the ribs extend further towards its centre (Fig. 36). The horns of *E. zodiacus* f. *cylindrocornis* are slightly flattened in apical direction (Figs 42, 43). The top plates accordingly have an oval outline and are normally furnished with transverse ridges which expand into small marginal teeth (Figs 45, 46) probably instrumental in chain formation. The smaller *E. zodiacus* f. *zodiacus* specimens (still with the velum typical of this taxon) may have top plates equalling those of *E. zodiacus* f. *cylindrocornis* in size and structure (Fig. 37; the same clone as in Fig. 36 after size reduction, magnification the same). Narrower horns may or may not have a narrow central siliceous plate, however, (Figs 27, 28) indicating that the structure of the top plate is unstable in this size interval.

There is one central labiate process, evident as a slit in the outer surface (Fig. 40), whereas internally it is spatulate and shallow (Fig. 39). Its orientation about the valve axes is variable, it may be transapical, apical or somewhere inbetween (Figs 23, 31, 32).

Reproduction has not been studied and resting spores have never been observed.

Whereas *E. zodiacus* f. *zodiacus* is widely distributed in temperate and subtropical waters, *E. zodiacus* f. *cylindrocornis* has only been observed in material from tropical and subtropical areas (Campeche Bank, Gulf of Mexico; Ubatuba, Brazil; Fort Pierce, Florida). The two forms appeared together only occasionally and then concurrently with chains composed of both forms. The dimorphism may be a response to particular environmental factors, and the distinction between them may thus give information of ecological significance.

***Eucampia groenlandica* Cleve (Figs 2, 48-65).**

Cleve 1896, p. 10, pl. 2, fig. 10.

Synonyms: *E. groenlandica* var. *typica* Cleve-Euler 1951, p. 112, fig. 237a-e.

E. groenlandica var. *atlantica* Cleve-Euler 1951, p. 99, fig. 237f.

E. groenlandica var. *recta* Kiselev 1925, p. 33, fig. 1a, b.

E. groenlandica f. *atlantica* Gran 1908, p. 99, fig. 127d.

E. recta Gran & Braarud 1935, p. 364.

Type locality: Baffin Bay and Davis Strait.

The cells of *E. groenlandica* are rectangular to square in broad girdle view, the length of the perivalvar axis being larger than or equal to the apical axis. The extremely lightly silicified cells may be curved as in *E. zodiacus* or straight when seen in broad girdle view (Figs 48-52). In the latter case they are curved in narrow girdle view (Fig. 53). According to Cleve (1896) the length of the cells should be from 32-100 μm which is well in agreement with our measurements, the perivalvar axis being 30-100 μm long.

The protoplast is characterized by a central nucleus, often displaced towards the narrow girdle side (Fig. 2a). The chloroplasts are oblong, often somewhat constricted in the middle, and numerous (Figs 2a, 51-55). Reports on few chloroplasts (e.g. Gran 1908, p. 99: 4-10 chloroplasts) most probably originate from observations on poorly preserved material.

Like in the other species of the genus the cells are united into chains by the top plates of their horns. Cleve (1896) depicted the colonies curved as seen in broad girdle view in the same way as for *E. zodiacus*, whereas Gran (1908) pointed out that they were less curved than in the

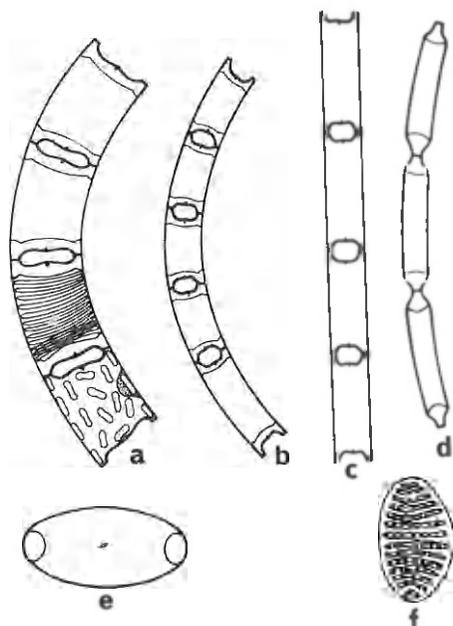


Fig. 2. *Eucampia groenlandica*. a, b. Broad girdle view of curved chains. c. "Straight" chain, broad girdle view. d. "Straight" chain, narrow girdle view. e. Valve outline. f. Structure of top plate. Approximate magnifications: filaments $\times 500$, valves $\times 1000$ and top plates $\times 5000$.

latter species. Kiselev (1925) described a new variety, *E. groenlandica* var. *recta*, based on the observations of straight colonies. Braarud (in Gran & Braarud 1935) described a new species *E. recta* from Bay of Fundy which most probably is identical to *E. groenlandica* (Braarud pers. comm.). However, one clonal culture may produce chains of both types (Figs 51, 52), the two types often dominating at different times without any obvious pattern as to size or environment. The same phenomenon has been observed in natural samples. Whereas the cells may be curved in either broad or narrow girdle view, they seldom seem to be twisted about the pervalvar axis like in *E. zodiacus*. Together with the less pronounced curvature this makes helical colonies rare.

The girdle consists of open bands with ligulae and antiligulae alternating with pointed band ends in a straight line in narrow girdle view (Fig. 65). The bands are perforated by transverse rows of fine pores,

52-56 in 10 μm , a number far higher than in the other taxa. The number of bands in a mature theca under unlimited growth conditions seems to be 15-20. The valve outline is elliptical, becoming more rounded with decreasing cell size (Fig. 2e). The horns are transapically elongated in section (Figs 59-61) with only a small variation in diameter depending on cell size. The height of the horns shows some variation, even within the same chain (Fig. 55). In broad girdle view the valve face is flattened or slightly convex (Figs 48-52, 55), never distinctly concave as in *E. zodiacus*. In transcapical section it is convex, obscuring a differentiation between valve face and mantle. The valve margin is very pronouncedly prolonged downwards apically as well as transapically (Figs 50, 56-58).

According to Cleve (1896) the apical length may vary between 13 and 20 μm . Gran (1908) described *E. groenlandica* f. *atlantica* as a large form without giving any measurements. His figure (fig. 127d), however, has dimensions covered by Cleve's measurements. In our material the apical length varied from 10-33 μm , the largest specimens being measured on Cleve's original slide (Fig. 48). The length of the transapical axis is less variable, approximately 10-12 μm regardless of apical length.

The roundish poroid areolae radiate from a central labiate process. The velum is very simple, consisting of a ring attached to the areola walls by a few strands (Fig. 62). The number of the evenly sized areolae in 10 μm is 38-42, twice the number found in the other taxa of the genus.

The top plates of the horns are perforated by rows of pores more or less parallel to the apical axis, separated by low ridges seemingly oriented towards an indistinct transapical line displaced towards the narrow girdle side (Figs 59-61). As in *E. zodiacus* the rows of pores seem to be the continuation of the valve striae, but lacking a velum (Fig. 60). There is no distinct thickened rim limiting the top plate from the rest of the horn and there are apparently only very small teeth connected with the top plates.

The single labiate process is easily seen in LM, especially when embedded in a medium of high refractive index (Figs 48-50). In SEM the external opening is seen as a mere slit (Fig. 62), whereas its inner part is long-necked and flat, it is by far the largest labiate process within *Eucampia* (Figs 63, 64).

Reproduction has not been studied in detail, although auxospores have been observed in culture. The initial cells did not differ much morphologically from the ordinary vegetative cells, although a small percentage of the largest cells had four horns per valve instead of two. However, normal bicornuate valves were formed after a few cell divisions.

Resting spores have not been reported for the species. *E. groenlandica* is a cold water species. We have found it northwards from approximately 60°N in the Norwegian and the Barents Seas, in coastal as well as oceanic waters. In culture it grows well from zero to ca. 12°C. We have not been able to grow it at temperatures above 16°C.

***Eucampia cornuta* (Cleve) Grunow (Figs 3, 66-83).**

Grunow in Van Heurck 1883, pl. 95bis, fig. 5.

Basionym: *Moelleria cornuta* Cleve 1873, p. 7, pl. 1, fig. 6.

Type locality: Sea of Java.

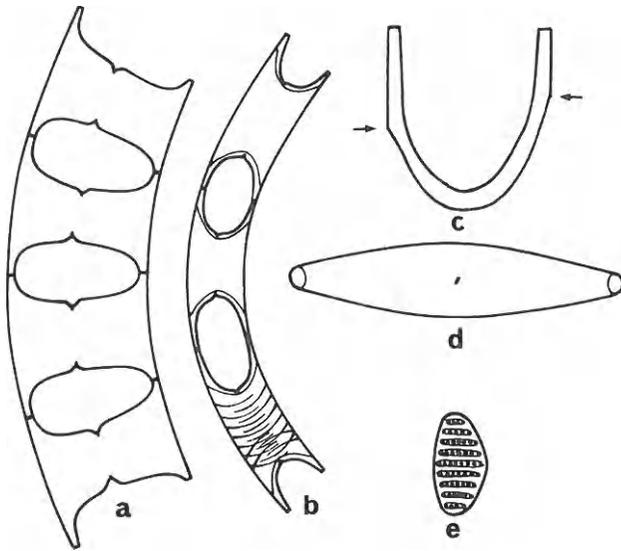


Fig. 3. *Eucampia cornuta*. a, b. Chains of different size, broad girdle view. c. Valve in broad girdle view, end of margin arrowed. d. Valve outline. e. Structure of top plate. Approximate magnifications: filaments $\times 500$, valves $\times 1000$, top plate $\times 5000$.

The typical *E. cornuta* cell is slightly curved in broad girdle view, and has a peralvar axis of about twice the length of the apical axis. Features like long, narrow and tapering horns, together with an apparently heavy silicification of band “sutures”, make the species easily recognizable. Immediately after auxospore formation the cell proportions may be quite different (Fig. 69) resembling broad cells of *E. zodiacus* f. *cylindrocornis* (Fig. 12) except for the thickened bands. Cleve (1873) gives 144 μm for the total cell height. Our measurements, including both small and large cells, show a variation in the length of the peralvar axis between 20 and 90 μm .

We had no access to living material and, as the protoplast seems to break down very easily in preserved material, we are not able to give any details about its structure. It seems from the remnants we have seen, however, that the species has numerous disc-like chloroplasts and a centrally oriented nucleus.

Long chains have been extremely scarce in our material, most often single cells and short chains with up to four cells were found (Figs 66-71). Being only slightly curved, *E. cornuta* colonies resemble *E. groenlandica* in this respect. It seems evident, however, that *E. cornuta* cells are slightly twisted about the peralvar axis, making helical coiling of long chains possible. In their most typical appearance the apertures between the cells are highly elliptical (Figs 66-68), giving an impression considerably different from the other *Eucampia* taxa. The few extremely broad chains we have found differ from this, however, and the colonies look more like *E. zodiacus* except for the characteristic girdle (Fig. 69).

The band structure is undoubtedly the most easily recognizable feature of *E. cornuta*. The uneven thickenings in the girdle are readily visible in LM water mounts (Fig. 70) and even more so in permanent mounts (Fig. 71). At higher magnification the structure of the single band may be seen (Fig. 74). SEM observations manifested that the uneven thickenings of the girdle are silicified ribs on the advalvar half of the single band (Figs 78, 79). The bands are regularly perforated by transverse rows of quadratic pores. Two or three of the pores in each transversal row are found on the advalvar side of the thickened rib and five to seven on the opposite side (Fig. 79). There are approximately 26-31 rows of pores in 10 μm . The number of bands per mature cingulum seems to range from 15 to 20.

The valve outline is narrowly elliptical, somewhat more pointed apically than in the other species (Fig. 3d). The valve is U-shaped in broad girdle view, the apices extending into long, narrow horns with the polar margins drawn far up (Figs 3c, 72, 73, 75-77). The horn on the convex side of the cell is slightly longer than the other and the margin is drawn somewhat higher up on the concave side, both features adding to the curvature of the cells (Figs 75, 77). Cleve (1873) reported the length of the apical axis to be 36 μm . In our material this varied from 13 to 60 μm and that of the transapical axis from 8 to 10 μm .

The areolation is irregular and the areolae are roundish to rectangular, being smallest on the horns and mantle (Fig. 77). The number in 10 μm varied from 7 to 21. A striking feature is the apparent lack of a velum; in one instance only we have found single, very thin strands of silica crossing the areolae. In all other observations they have been quite open without a trace of any velum-like structure. As in *E. zodiacus* and *E. groenlandica* the areola array is branching out from a single, central labiate process.

The top plates of the horns are crossed by low, parallel ridges in apical direction with evenly spaced pores in between. The ribs are evidently continuations of the interstriae of the horns (Figs 81, 82). At the margins of the top plates the ridges may be drawn out into small spine-like structures, fitting into grooves on the neighbouring top plate (Fig. 80), thus possibly making linking more efficient. The central labiate process is situated in a depression on the valve face and is easily visible in LM (Figs 69, 72). The process has no outer extension, whereas on the inside it is broad and flat, having a short neck with a somewhat broader labiate part (Fig. 83).

We have no observations on reproduction. Resting spores have never been reported for the species.

E. cornuta seems to be restricted to subtropical and tropical waters.

***Eucampia balaustium* Castracane (Figs 4, 84-129).**

Castracane 1886, p. 97-99, pl. 18, figs 5, 6.

Synonyms: *Hemiaulus antarcticus* Ehrenberg 1844, p. 203, fig. 8.

Moelleria antarctica Castracane 1886, p. 98, pl. 18, fig. 8.

Eucampia antarctica (Castr.) Mangin 1914, p. 480, figs 7, 8.

E. balaustium var. *minor* Castracane 1886, p. 98, pl. 18, fig. 6.

E. balaustium f. *hiberna* Heiden in Heiden & Kolbe 1928, p. 535.

E. balaustium f. *aestiva* Heiden in Heiden & Kolbe 1928, p. 536.

Type locality: Antarctic Ocean.

As mentioned above the identity of *Eucampia balaustium* and *Moelleria antarctica* has been discussed by several authors (see Steyaert & Bailleux 1975a) until it was documented by Hoban et al. (1980) that they represent the resting spore and the vegetative cells respectively of the same species. Ross et al. (1977, p. 191), taking into account that the species had first been described as *Hemiaulus antarcticus* by Ehrenberg (1844) and that *E. balaustium* and *M. antarctica* had been described in the same paper, questioned the validity of the combination *Eucampia antarctica* (Castr.) Mangin as well as the validity of the name *E. balaustium*. They preferred, however, to follow the prevailing custom, which was also done by Hoban et al. (1980) and in this paper by naming the species *E. balaustium*.

E. balaustium resembles the other taxa of the genus in gross morphology by having bipolar valves with horns and numerous open bands. The ratio between apical and perivalvar axis may vary considerably. As we had access to preserved material only, we have no new information on the protoplast.

The illustrations accompanying the description of *M. antarctica* and *E. balaustium* showed cells curved in broad girdle view (Castracane 1886, pl. 18, figs 5, 6) like those of *E. zodiacus*. Mangin (1914, 1915) apparently overlooked this fact and stated as a specific feature of *E. antarctica* straight chains as seen in broad girdle view, but called attention to the fact that the chains were curved when seen in narrow girdle view (Mangin 1914, p. 482, fig. 6). In our investigation the majority of the colonies have been of the latter type (Figs 84, 85), whereas in one sample, dominated by very short chains and single cells, the specimens were curved as seen in broad girdle view (Figs 94, 95).

The girdle consists of numerous very thin open bands which are barely distinguished in the light microscope (Figs 85, 86). The number per epitheca varies from 10 to 20. In SEM they are seen to be perforated

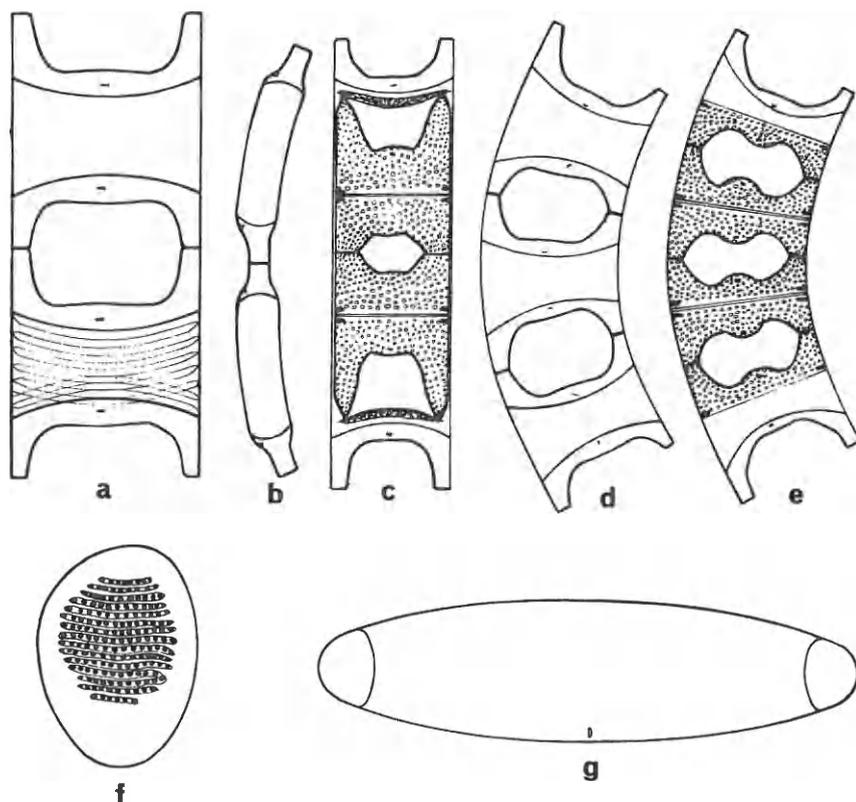


Fig. 4. *Eucampia balaustium*. a. Two cells in broad girdle view, "straight" chain. b. "Straight" chain, narrow girdle view. c. Parent cell with semi-endogenous resting spores. d. "Curved" chain, broad girdle view. e. Exogenous resting spores. f. Structure of top plate. g. Valve outline. Approximate magnifications: filaments $\times 500$, valve $\times 1000$, top plate $\times 5000$.

by transverse rows of elongate pores, approximately 10 pores per row, separated by a narrow rib two to four pores from the advalvar edge of the band (Fig. 112). The number of pores (rows) in $10 \mu\text{m}$ is 28-32.

The valve outline is elliptical, the narrower the longer the apical axis is (Fig. 4g). The valve is furnished with two horns of varying height, mostly $1/2$ to $3/4$ the length of the apical axis (Figs 84, 88). Valves with four horns appeared in a small number of especially broad cells (Fig. 102). The horns are fairly broad, mostly somewhat compressed terminally in apical direction (compare Figs 88 and 89). The valve mantle is curved smoothly downwards in broad girdle view and

rounded upwards at the apices (Fig. 105). The apical axis varied from 18 to 92 μm in length, while the transapical axis was about 15-20 μm .

Valve structure consists of large, more or less square areolae decreasing in size on the horns and valve margins (Figs 104, 105). The striae start at the single labiate process which is located close to the valve margin and which can be readily seen in water mounts (Fig. 103). As in *E. zodiacus* each stria mostly starts with a simple poroid through the valve wall (Fig. 104). The number of poroid areolae in 10 μm is mostly 3-10, the smallest number found within the genus. The velum is an externally located filigree attached to the areola walls by single strands (Figs 106-109) and is principally of the same type as in *E. zodiacus*. The top plates of the horns differ from those of the other species by not occupying the whole top area of the horn (Figs 4f, 108). The position of the top plate is somewhat eccentric and the largest part of the horn left free is often drawn out into an appendix which is sometimes strongly developed (Figs 109, 110). The development of ridges between the rows of pores is pronounced and they are interdigitating in neighbouring cells (Steyaert & Bailleux 1975b, figs 21, 22).

The marginal labiate process has no external extension (Fig. 107) and the internal part is short-necked and flattened (Fig. 106) and of the same overall structure as in the other taxa.

Resting spores were abundant in the samples. As was mentioned above, Castracane (1886) based his description of *Eucampia ba-laustium* on the resting spore. He illustrated the description with drawings of two curved chains consisting of three and four spores respectively, whereas all later investigators seem to have seen no more than *two* spores in *straight* chains (Mangin 1914, 1915, 1922; Hustedt 1958; Steyaert & Bailleux 1975a; Hoban et al. 1980). Heterovalvate construction of the resting spores was first depicted by Mangin (1915, pl. 1, fig. 1) and later demonstrated in LM and SEM by Steyaert & Bailleux (1975a, figs 10, 11; 1975b, figs 3-6) and in SEM by Hoban et al. (1980, figs 6, 8).

The formation modus of the second spore type was indicated by Mangin (1915, fig. 43, pl. 1, fig. 1). It starts with the elongation of the parent cell (Fig. 86) followed by the formation of two heavily silicified primary valves (Fig. 87) and is completed by the formation of two

secondary valves with pointed horns. Two rudimentary valves and a residual body (Fig. 88) from the terminal unequal division are left on top of the secondary valves. In the completed spores the primary valves are normally free, while the secondary valves are enclosed in the thecae of the parent cell (Figs 88, 89). According to the terminology of Ross et al. (1979) these resting spores are semi-endogenous. Eventually the resting spores may be free from the parent cell thecae (if they do not germinate before that), but the rudimentary valves are very often attached to the spores for a while (Figs 90, 113). Sooner or later they are lost (Figs 91, 114) and the spore doublets often fall apart into single spores (Fig. 115).

The long prevailing belief that resting spores do not have a girdle has been disproved for a number of species (von Stosch & Fecher 1979, Syvertsen 1979) and Hoban et al. (1980) state that a girdle is present in *E. balaustium* spores. This is evident in Fig. 92 for free primary valves. Secondary valves presumably do not develop a girdle before germination.

The primary valve of the resting spore has two blunt horns, whereas the secondary valve has pointed horns. The valve face is always convex and the number of areolae is 2-5 in 10 μm (except close to the top of the pointed horns). As in the vegetative valves the striae are radiating from the eccentric labiate process, although this pattern may be obscured by the heavy silicification (Figs 113, 115). The areolae are circular to subcircular with a velum of the same type as the vegetative cells. However, the velum is situated half-way into the deep poroid areolae of the heavily silicified spores (Figs 120, 121).

The top plates of the primary valve horns are developed with pronounced ribs between the parallel rows of pores and a broad, flat, unstructured rim limiting the top plate from the rest of the horns (Figs 116, 119). The ridges are raised above the surrounding homogeneous rim (Fig. 120) and those of sibling valves interdigitate (Fig. 121). The horns have no spine-like structures. The pointed horns of the secondary valves lack any trace of a top plate (Figs 114, 115).

The single labiate process is situated in a depression comparatively close to the valve center on the convex side of the cell which can perhaps be seen in Figs 114 and 115. The outer opening is a mere slit in the valve wall, while on the inside of the valve the process is a short heavily silicified structure with a narrow slit (Figs 117, 118).

As was shown by Steyaert & Bailleux (1975b, figs 6, 7) the spore valves have very well developed pseudosepta (Fig. 117). In LM they are seen as paired dark markings in the middle of the spores (Fig. 91) and they were in fact already indicated by Castracane in his illustration of spore chains (1886, pl. 18, figs 5, 6). Internal costae, as shown by Ross et al. (1977, fig. 62), have not been observed during this investigation.

The spores discussed until now occur in pairs; they are semi-endogenous and appear in vegetative chains which are straight in broad girdle view and curved in narrow girdle view (Figs 87-89). The resting spores in chains curved in broad girdle view, described by Castracane (1886) as *E. balaustium*, were present in majority in one of our samples. According to the definition of Ross et al. (1979) they are exogenous, being "neither completely nor partially enclosed in its parent frustule". An exception has to be made for the terminal spores of a spore chain, however, since their secondary valves will very often be enclosed in the parent cell thecae. The two valves of the exogenous spores are identical in gross morphology (Figs 98, 99, 124). In most cases the top plates of the horns seem to be less developed than in the primary valve of the semi-endogenous spore (Figs 127, 128), and the top plates of the end valves of the spore chains may be rudimentary if at all present (Figs 125, 126). The areolation, the velum and the position of the labiate process are the same in the two spore types. This is also the case with the spore girdle where the number of bands seems to be 5-7. The single bands have transversal rows of pores, 25-30 rows in 10 μm .

The demonstration of two different types of resting spore formation in *E. balaustium* is not unique as this has also been shown for *Thalassiosira* Cleve species (Syvertsen 1979). More interesting is the fact that exogenous spores in *E. balaustium* evidently are able to divide and form new spores (Figs 93, 97, 100, 101). This is clearly demonstrated by Figs 122 and 123, showing the epithecae of two spores facing each other and having completed the development of spore hypovalvae. This phenomenon raises questions about the concept of resting spore formation.

E. balaustium seems to have a strictly circumpolar subantarctic to antarctic distribution.

Discussion

The essential morphological features of the four species are shown in Figs 1-4 and Table I.

Table I. Data on *Eucampia*

	<i>Eucampia zodiacus</i>		<i>E. groenlandica</i>	<i>E. cornuta</i>	<i>E. balaustium</i>
	<i>f. zodiacus</i>	<i>f. cylindrocornis</i>			
Apical axis μm	8 - 80	18 - 44	10 - 33	13 - 60	18 - 92
Valve areolae number per 10 μm	10 - 20	10 - 16	38 - 42	7 - 21	3 - 10
Bands, number per theca	10 - 15	10 - 15	15 - 20	15 - 20	10 - 20
Bands, pores per 10 μm	34 - 40	32 - 38	52 - 56	26 - 31	28 - 32

The generitype *E. zodiacus* is a morphologically variable species appearing in two main forms. *E. zodiacus f. zodiacus* is easily distinguished from the rest of the genus by the radial ribs of the elevation top plates (Fig. 1d). *E. zodiacus f. cylindrocornis* (Fig. 1e) is more easily confused with *E. cornuta*, especially in water mounts. It may be distinguished from the latter by the difference in the shape of the valve margin and horns (Figs 1e, 3c).

E. groenlandica is similar to narrow cells of *E. zodiacus*. It is distinguished from the latter in LM in broad girdle view by having a flat or convex valve face (Figs 2a-c), while that of *E. zodiacus* is concave (Fig. 1a), and secondly by the much smaller valve areolae and pores of the bands (Table 1). The small poroids and band pores are unique to *E. groenlandica*.

E. cornuta is characterized by the shape of the valve mantle and the heavy ribs on the advalvar half of the single bands (Figs 3b, c), features peculiar to this species.

E. balaustium differs from the other taxa by the specific position of the labiate process, easily visible in LM (Figs 4a-e, g). The very large valve areolae and the aberrant top plate of the horns are other specific characters.

As has been demonstrated above, the top plate morphology of the horn varies within the genus. In *E. zodiacus* f. *zodiacus* the radial striae of the top plate are continuations of the striae on the elevations (Figs 25, 38). In the narrower horns of *E. zodiacus* f. *cylindrocornis* the pattern is transformed into parallel striae which can still be regarded as continuations of the valve areola rows (Figs 27, 46). This pattern is also found in *E. groenlandica* (Figs 60, 61) and *E. cornuta* (Figs 81, 82). In *E. balaustium* the pattern is strikingly different with no apparent correspondence between the single striae of the top plates and the ones on the elevations, the distance between the parallel crossing ribs being much smaller than the width of the elevation interstriae.

Resting spore formation seems to take place in *E. balaustium* as the only species of the genus.

VanLandingham's (1968) usage of synonyms relevant to *Eucampia* has been checked and we disagree on a few points. The reason why the name *E. balaustium* is preferred to *E. antarctica* has been explained earlier. *E. groenlandica* var. *atlantica* (Gran) Cleve-Euler and *E. groenlandica* var. *recta* can hardly be recognized as separate within the range of variation of the species as is shown in this study of clonal cultures. *Eucampia payerii* Grunow (1884, p. 107, pl. 2(b), fig. 17, listed by VanLandingham 1968) is described and illustrated in a way making a reliable identification impossible. It has some resemblance to *E. groenlandica* with which it shares the habitat, being recorded from the under-surface of arctic ice.

The current terminology is inadequate for the description of the distal ends of the elevations of *Eucampia* as well as those of the closely related genus *Cerataulina*. Ross et al. (1977) suggested that the *E. balaustium* structure could be the result of an evolutionary development of the poorly developed pseudocellus with feebly developed spines present in *Hemiaulus rossicus* Pant., belonging to Hemiauloideae, or that it could be regarded as an ocellus crossed by parallel costae. Hoban et al. (1980, p. 594) reported the presence of "a ridged ocellus" in the resting spore of *E. balaustium*. Hasle & Syvertsen (1980) more or less rejected regarding the elevation ends of *Cerataulina* as pseudocelli, viz. "field of areolae decreasing in size from those of the main part of the valve" (Ross et al. 1979, p. 521). Continuing the line of reasoning of Ross et al. (1977) the development from a

poorly developed pseudocellus with feeble spines may have resulted in first producing the top plate of *Eucampia* furnished with silicified ribs (interstriae) alternating with perforated plates (striae) to end with the ribbed top plate of *Cerataulina* lacking striae. This line of development would then be specific for these two genera and differ from the one leading from the Hemiauloideae to the Biddulphioideae with true pseudocelli (see Ross et al. 1977). Since at present no other specific characters can be pointed out, *Eucampia* and *Cerataulina* may be placed in the Hemiauloideae as well as in a separate subfamily or family. The ribbed distal ends of the elevations deserve a specific term, however, and we suggest "costate ocellus" to be used co-ordinately with ocellus and pseudocellus.

The morphologies of the four species discussed in this paper show close relationship, and they are sufficiently different from the most related genera (*Cerataulina*, *Hemiaulus*) to be assigned to the separate genus *Eucampia* Ehrenb. which can be circumscribed as follows:

Cells elliptical in cross section, united into helically coiled or straight chain-formed colonies as seen in broad girdle view, adhering by the top plates of the horns at the poles. Chloroplasts numerous and disk-like. Valve lanceolate to sub-circular in outline. Areolae poroid. Distal end of horns with costate ocelli; vertical lamellae radiating out from a central silica plate, or more or less parallel in apical direction. Rows of pores between lamellae. One central or marginal labiate process per valve, lacking an outer extension. Recent, planktonic, marine or brackish water.

Key to *Eucampia*

- A. Valve face convex or flat in broad girdle view
 - I. Labiate process central. *E. groenlandica*
 - II. Labiate process marginal. *E. balaustium*
- B. Valve face concave in broad girdle view
 - I. Bands with heavily silicified rib. *E. cornuta*
 - II. Bands homogeneously silicified
 - 1. Horns short and conical. *E. zodiacus* f. *zodiacus*
 - 2. Horns long and cylindrical. *E. zodiacus* f. *cylindrocornis*

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Explanation of Plates

Plate 1

Figs. 5-11. *Eucampia zodiacus*, LM. — Figs 5, 8. Typical *E. zodiacus* f. *zodiacus* chains. — Figs 6, 7. Single cells in broad and narrow girdle view. — Figs 9-11. Transition stages between the two forms. Water mounts, $\times 500$.

Plate 2

Figs 12-21. *E. zodiacus* f. *cylindrocornis*, LM. — Figs 12, 13. Typical chains. — Figs 14, 15, 17, 18. Whole frustules. Note length of perivalvar axis. — Fig. 16. Single theca. — Figs 19-21. Valves in broad girdle view. Note horns and shape of margin. Figs 12-16. Water mounts, $\times 500$. Figs 17, 18. Pleurax mount, $\times 500$. Figs 19-21. Hyrax mounts, $\times 1000$.

Plate 3

Figs 22-26. *E. zodiacus* f. *zodiacus*, TEM. Figs 27, 28. Transition type. SEM. Fig. 29. *E. zodiacus* f. *cylindrocornis*, SEM. — Fig. 22. Whole frustule in broad girdle view. — Fig. 23. Valve. Note areola array and labiate process. — Fig. 24. Typical top plate. — Fig. 25. Top plate. Rows of diminishing areolae of the horn crossing the top plate. — Fig. 26. Detail of Fig. 23, showing typical vela. — Figs 27, 28. Top plates from transition frustules. — Fig. 29. Simple velum and labiate process. Fig. 22. Critical point dried, $\times 800$. Figs 23-29. Acid cleaned and air dried. Fig. 23. $\times 2800$. Fig. 24. $\times 5600$. Fig. 25. $\times 5400$. Fig. 26. $\times 8400$. Figs 27, 28. $\times 11,000$. Fig. 29. $\times 17,500$.

Plate 4

Figs 30-40. *E. zodiacus* f. *zodiacus*, SEM. — Fig. 30. Valve, broad girdle view, margin undulated. — Fig. 31. Valve view. — Fig. 32. Smaller valve, inside view. — Fig. 33. Smaller valve, broad girdle view. — Fig. 34. Smallest valve found in culture. — Fig. 35. Top plate of broad valve. — Fig. 36. Top plate of smaller valve. — Fig. 37. Top plate of one of the smallest valves. — Fig. 38. Inside view of horn. — Fig. 39. Labiate process, inside. — Fig. 40. Labiate process, outside. Figs 31-34. $\times 2000$. Figs 35-37. $\times 5500$. Fig. 38. $\times 10,500$. Figs 39, 40. $\times 11,000$.

Plate 5

Figs 41-47. *E. zodiacus* f. *cylindrocornis*, SEM. — Fig. 41. Sibling valves. — Figs 42, 43. Typical valve in broad and oblique narrow girdle views. — Fig. 44. Typical velum. — Figs 45, 46. Typical top plates. — Fig. 47. Part of girdle, hypocingulum on top. Fig. 41. $\times 1,300$. Figs 42, 43. $\times 2000$. Fig. 44. $\times 4400$. Figs. 45, 46. $\times 13,000$. Fig. 47. $\times 4300$.

Plate 6

Figs 48-55. *E. groenlandica*, LM. — Figs 48-51. Cells curved in broad girdle view. — Figs 52-55. Chains straight in broad girdle view and curved in narrow girdle view. Figs 48-50. Embedded in resin of unknown type. Figs 51-54. Water mounts. Fig. 55. Pleurax. All figs $\times 500$.

Plate 7

E. groenlandica, SEM. — Figs 56, 57. Valves in broad girdle view. Note slightly convex valve face. — Fig. 58. Valve in oblique narrow girdle view. Note lobed margin. — Figs 59-61. Top plate of horns, showing orientation of ridges towards a diffuse line. — Fig. 62. Areolation of valve, velum and external slit of labiate process. — Figs 63, 64. Labiate process on valve inside. — Fig. 65. Part of girdle. Note rows of pores, ends of bands and ligulae/antiligulae. Figs 56-58. $\times 2000$. Figs 59-64. $\times 11,000$. Fig. 65. $\times 4800$.

Plate 8

E. cornuta, LM. — Figs 66-69. Typical chains. — Figs 70, 71. Single frustules. Bands. — Figs 72, 73. Valves in broad girdle view. Note margins of horns (triangles). — Fig. 74. Part of girdle. Triangles show "sutures" between bands. Figs 66-70. Water mounts. Fig. 71. Pleurax. Figs 72, 73. Hyrax mount. Fig. 74. Embedded in unknown resin. Figs 66-71. $\times 500$. Fig. 74. $\times 1500$.

Plate 9

E. cornuta, SEM. — Fig. 75. Valve, broad girdle view. Note margin on narrow band side (triangles). — Fig. 76. Valve, oblique narrow girdle side. Note valve margin on horn. — Fig. 77. Valve and advalvar part of cingulum, showing that these bands have no extra thickening of median rib. — Figs 78, 79. Parts of cingulum. In Fig. 79 arrows point to thickened median ribs and triangles to sutures between bands. Note ligula in Fig. 78. — Fig. 80. Sibling horns. — Figs 81, 82. Top plate of horns. — Fig. 83. Labiate process on inside of valve. Figs 75-77. $\times 2000$. Fig. 78. $\times 2100$. Fig. 79. $\times 2300$. Figs 80-83. $\times 11,000$.

Plate 10

E. balaustium, LM. — Fig. 84. Short “straight” chain, broad girdle view. — Fig. 85. Part of chain, narrow girdle view. — Fig. 86. Frustule. Labiate process. — Fig. 87. First step in semi-endogenous resting spore formation, resting spore different from vegetative cell in shape and silicification. — Fig. 88. Two complete semi-endogenous resting spores, inside the parental thecae, showing rudimentary valves on top of secondary spore valves. — Fig. 89. Similar to Fig. 88, narrow girdle view. — Fig. 90. Two free spores, rudimentary valves still attached. — Fig. 91. Two free resting spores, primary and secondary valves different in shape. — Fig. 92. Two free primary resting spore thecae, with extremely hyaline cingula. Water mounts, $\times 500$.

Plate 11

E. balaustium, LM. — Fig. 93. Part of chain showing formation of exogenous spores. — Figs 94, 95. Parent cell thecae with primary spore valves. — Fig. 96. End of a spore chain, showing sibling rudimentary valve. — Figs 98, 99. Single spores of exogenous type. Figs 97, 100, 101. Dividing spores, new valves with spore morphology. — Fig. 102. Deviating valves having four horns. — Fig. 103. Small, vegetative valve in valve view, showing areola array and labiate process. Water mounts, $\times 500$.

Plate 12

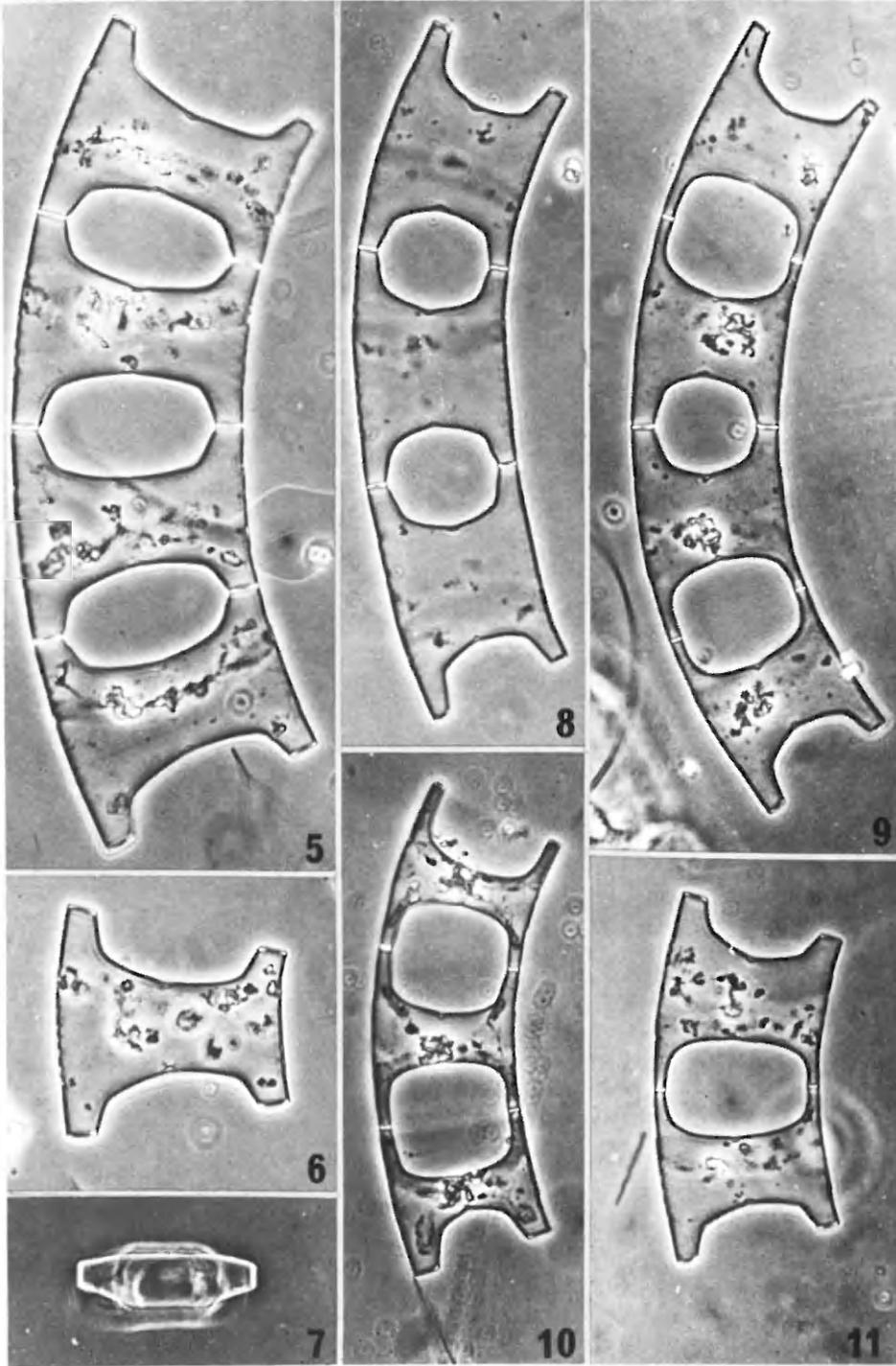
E. balaustium, vegetative cells, SEM. — Fig. 104. Valve, inside view, areola array oriented towards marginal labiate process. — Fig. 105. Valve seen from oblique narrow girdle side. Margin, position of labiate process and areola array on horns. — Fig. 106. Labiate process, inside. — Fig. 107. External opening of labiate process. — Fig. 108. Top plate of horn. — Figs 109, 110. Sibling horns, showing different development of appendices. — Fig. 111. Top plate of horn, typical of samples containing exogenous spores. — Fig. 112. Part of vegetative cell girdle, ligulae and band ends, indistinct advalvar rib. Fig. 104. $\times 1500$. Fig. 105. $\times 1000$. Figs 106, 107. $\times 11,000$. Figs 108, 109. $\times 6000$. Fig. 110. $\times 4800$. Fig. 111. $\times 6000$. Fig. 112. $\times 4800$.

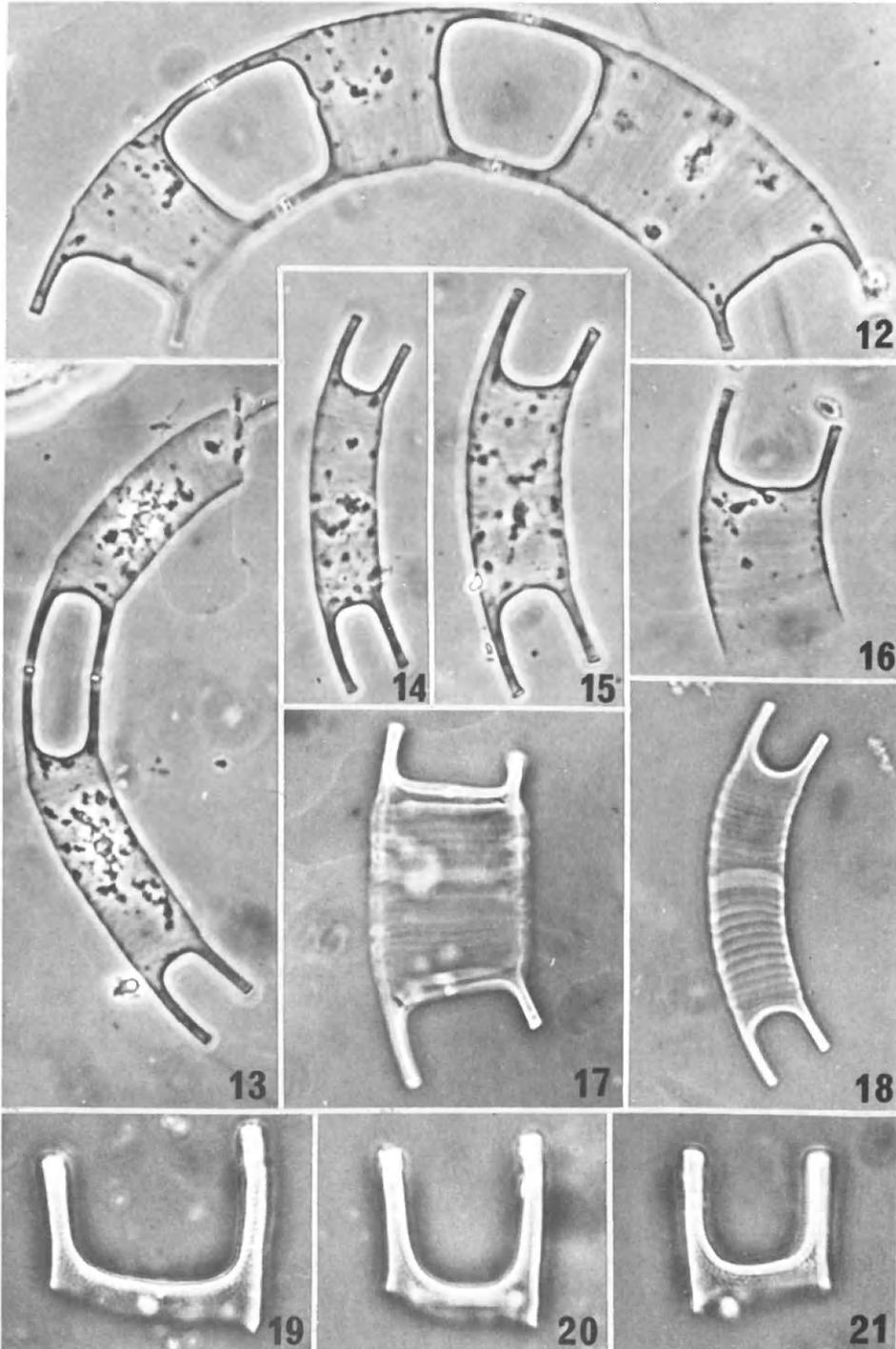
Plate 13

E. balaustium, semiendogenous resting spores, SEM. — Fig. 113. Sibling spores, broad girdle view. Attached rudimentary valves. — Fig. 114. Curved spore doublets seen in oblique narrow girdle view. — Fig. 115. Single spore, epitheca (facing downwards) and secondary valve with pointed horns. — Fig. 116. Top plate of primary valve horn. Note thickened rim. — Fig. 117. Primary valve with pseudoseptum and labiate process. — Fig. 118. Larger magnification of labiate process in Fig. 117. — Figs 119, 120. Top plates of primary valve horns at two angles. — Fig. 121. Sibling horns. Figs 113, 114. $\times 480$. Fig. 115. $\times 720$. Fig. 116. $\times 6000$. Fig. 117. $\times 1500$. Fig. 118. $\times 8600$. Figs. 119, 120. $\times 3200$. Fig. 121. $\times 2200$.

Plate 14

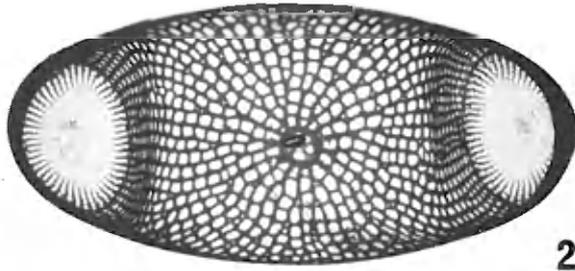
E. balaustium, exogenous spores, SEM. — Fig. 122. Two spores of a chain, sibling hypothecae, demonstrating that they are the result of spore division. Note epicingula. — Fig. 123. Narrow girdle view. — Fig. 124. Typical spore from a chain of exogenous spores, secondary valve at the bottom. — Fig. 125. Terminal spore of a chain with attached rudimentary valve and pycnotic nucleus. — Fig. 126. Top plate of elevation of the secondary valve in the preceding figure. Note extremely poorly developed top plate. — Figs 127, 128. Typical "internal" top plates of a chain of narrow spores. — Fig. 129. Epicingulum of the spore in Fig. 124, showing six bands. Figs 122-125. $\times 1000$. Fig. 126. $\times 3200$. Figs 127, 128. $\times 6000$. Fig. 129. $\times 5000$.



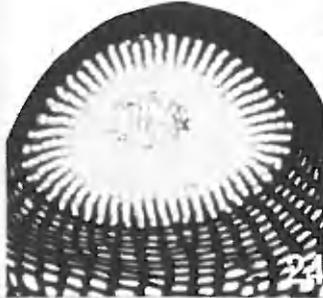




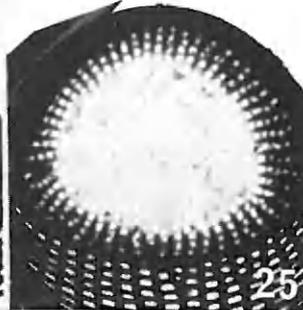
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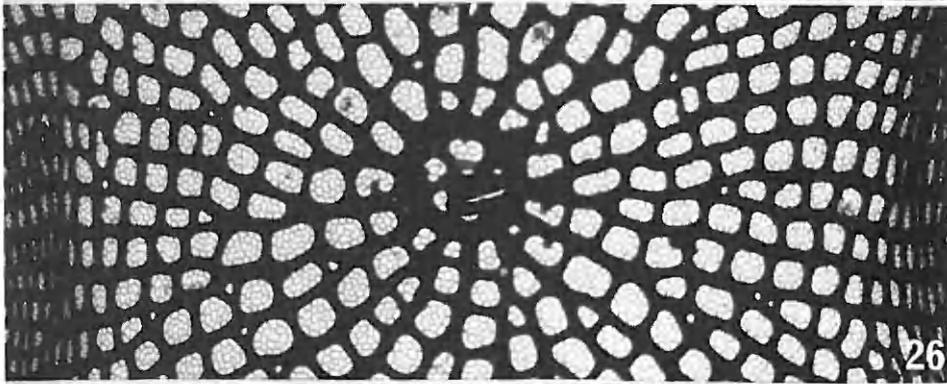
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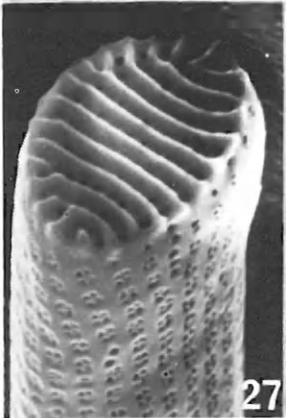
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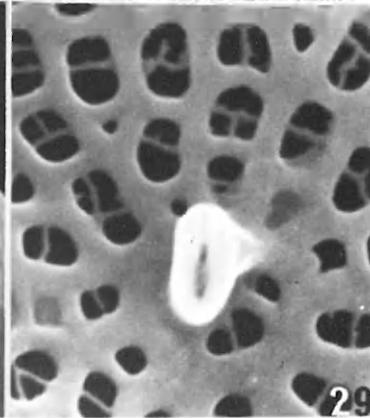
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