# Thalassiosira punctigera (Castr.) comb. nov., a widely distributed marine planktonic diatom

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Examination of type material showed that 8 taxa must be reduced to synonomy with *Thalassiosira punctigera* (Castr.) comb. nov., an extremely variable species as to size and valve structure. Preliminary experiments indicated a certain relationship between the areola size and the temperature at which clonal cultures had been grown. While previously known from the North Pacific and the South Atlantic Oceans in addition to a single record from the Caribbean Sea it has since 1979 been recorded regularly in the Skagerrak (between Denmark and Norway).

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# To Professor, Dr. H.-A. von Stosch

This work is dedicated to Professor, Dr. H.-A. von Stosch on the occasion of his 75-years' birthday on the 4th of June 1983.

### Introduction

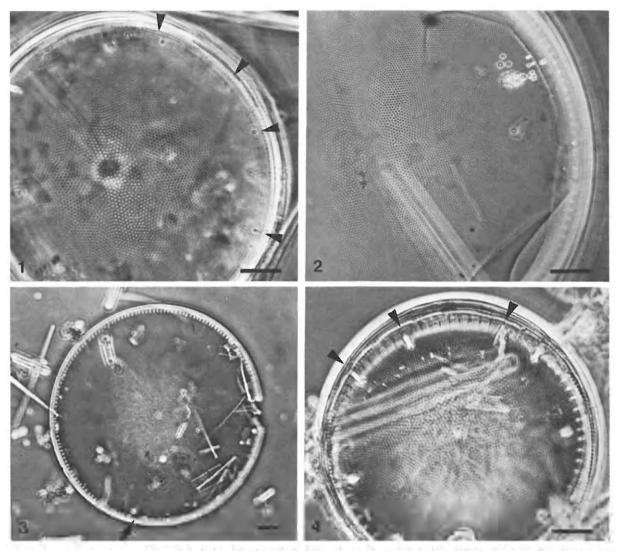
Ethmodiscus punctiger Castr. and E. japonicus Castr. were described from material collected in the Tokyo Bay by the Challenger Expedition (Castracane 1886). Peragallo in Tempère & Peragallo (1889-95: 56) proposed the combination Coscinodiscus punctiger; E. japonicus was not mentioned in this context.

Müller-Melchers (1953) compared material from coastal waters of South America and New Zealand with the type slides of *E. punctiger* and *Coscinodiscus verecundus*, the latter described by A. Mann (1907) from the Okhotsk Sea. As a conclusion Müller-Melchers stated that *E. punctiger*, *C. verecundus*, and also *Coscinodiscus angstii* var. *granulomarginatus* Gran described in Gran & Angst (1931) from Friday Harbor, Puget Sound were conspecific. The combination *Cos*-

cinodiscus punctiger was suggested for the second time (Müller-Melchers 1953: 465). The comparison included E. japonicus and C. angstii Gran var. angstii although they were not listed as synonyms of C. punctiger; Müller-Melchers' paper is somewhat ambiguous on this point, however.

Fryxell (1978) made a parallel study comparing the type material of E. japonicus (BM slides from the F. W. Payne Collection made from the Challenger material, P. A. Sims pers. com.) with some of Gran's samples of C. angstii (samples deposited in IMMB, University of Oslo) together with a clonal culture established from the type locality. She concluded that C. angstii was conspecific with E. japonicus. Makarova (1970) had already proposed the combination Thalassiosira angstii (Gran) Makarova. The affiliation to genus was verified by Fryxell (1978). By the use of electron microscopy the presence of strutted processes, one labiate process, internal cribra and external foramina, and occluded processes was demonstrated. Although E. japonicus has priority over C. angstii, Thalassiosira japonica would have been a later homonym of T. japonica Kiselev, also described from the North Pacific Ocean (Kiselev 1935). Neither Makarova nor Fryxell included Kiselev's ma-

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Figs 1–4. Thalassiosira punctigera, LM. Tokyo Bay, Japan, Challenger Expedition. Figs 1, 2. Type slide of Ethmodiscus punctiger, BM 15941. Figs 3, 4. Hyrax mounts of the corresponding loose material. – Fasciculated areolation, marginal rings of strutted processes, labiate process (Fig. 3, arrowed) and occluded processes (Figs 1, 4, arrowheads). – Scale bars = 10 µm.

terial in their investigations. Even so, the descriptions and illustrations are sufficient to prove that *C. angstii* and *T. japonica* are conspecific.

The characteristic morphological features of E. punctiger, E. japonicus and an unnamed variety of E. japonicus as interpreted from the diagnoses and illustrations (Castracane 1886: 167, 168, Pl. 3, Fig. 1, Pl. 16, Fig. 1, Pl. 22, Fig. 2) are a very delicate fasciculate areolation and a distinct marginal ring of closely spaced processes bordered by a second ring of still more closely spaced ribs. The diameter of the variety is slightly smaller than that of the two other taxa (ca. 100  $\mu$ m compared with 143 and 145  $\mu$ m).

The only information pointing to a morphological distinction between *E. punctiger* and *E. japonicus* is, 1)

the curvature of the valve which in *E. punctiger* is "very coarse" (Castracane 1886: 167), and which was not mentioned for *E. japonicus*, and 2) the density of marginal ribs, 8 in 10 µm and 11 in 10 µm for *E. punctiger* and *E. japonicus* respectively (measured on Pl. 3, Fig. 1 and Pl. 22, Fig. 2).

Since Fryxell (1978) made a thorough examination of the slides representing the type of *E. japonicus*, the present investigation concentrates on the slide serving as the type of *E. punctiger* and on the corresponding loose material. The morphological features evident from the examination of the type will be dealt with in detail. The slides and/or loose material used for the description of *Coscinodiscus verecundus* and *C. angstii* as well as for suggesting the combination *C. punctiger* 

will be discussed shortly, mainly by light micrographs and summarized numerical data. More recently collected material from the type localities of the taxa reduced to synonymy will be dealt with in a similar way. The investigation thus represents a combination of Müller-Melchers' (1953) and Fryxell's (1978) studies with some additional information. As will be shown by comparing the collections discussed by these two authors, the essential point is that we are dealing with a taxon which during the course of time has been recorded under eight different names. If this is accepted, the correct name is *Thalassiosira punctigera* (Castr.) comb. nov. (see below), the affinity to the genus and the rejection of the name *T. japonica* already being documented (Makarova 1970, Fryxell 1978).

### Materials and methods

The loose type material and the additional samples from various localities are all net samples. They were all prepared for diatom slides and partly also for electron microscopy. The latter type of examination plays a subsidary role in the investigation since the critical morphological features could be seen with the light microscope. The measurements were with few exceptions made on light micrographs.

The terminology follows von Stosch (1975), Ross et al. (1979), Fryxell & Hasle (1979, operculate process), Syvertsen & Hasle (1982, basal chamber), and Hasle et al. 1983, maximum and minimum cells).

Tab. 1. Measurements of type material. ar = areolae, str = striae, proc = marginal strutted processes, ribs = marginal ribs, occl proc = occluded processes, + = present, - = absent, 1) from Fryxell (1978), (n) = number of specimens examined

	diam µm	ar/ 10 μm	str/ 10 μm	proc/ 10 μm	ribs/ 10 μm	occl proc
Ethmodiscus punctiger	75–126 (3)	11–13	19–20	4-5	11–12	+/-
E. japonicus 1	57-136	11-16		3-5	11 - 13	+/-
Challenger sample	55-130 (6)	12-14	14-20	4-5	11-13	+/-
Coscinodiscus punctiger	65-125 (7)	10-14	13-20	45	11-13	+/-
C. verecundus	75 (1)	11	17	4-5	11	+
C. angstii	52-120 (6)	11 - 18	16-23	4-6	11-12	+

Tab. 2. Measurements on additional material. Abbreviations as in Tab. 1.

	diam µm	ar/ 10 μm	str/ 10 µm	ргос/ 10 µm	ribs/ 10 um	occl proc
North Pacific Ocean		·				
53.39°N, 176.11°W	75 (1)	12	15-16	4-5	12	+
36.13°N, 141.21°E	57 (1)	16–17	21-22	4-5	44.46	+
35°08′N, 139°38′E	55–70 (5)	14–20	18–24	4-6	11–16	+/-
South Pacific Ocean						
Wellington, N Zealand	88-165 (4)	22-23	29-30	8	13-14	+/-
Wellington, N Zealand	78–186 (18)	16-18?	16–22?	7-11	11–14	+/?
North Atlantic Ocean						
Drøbak, Oslofjord	39-66 (4)	11-18	20-27	4-5	11-15	+
Skagerrak	40-125 (36)	10-20	17-27	4-6	11-15	+/-
Plymouth, U.K	51-80 (9)	11-12	18–20	4-5	11-12	+/-
South Atlantic Ocean						
Uhatuba, Brazil	60-110 (8)	12-14	16-19	3-5	10-11	+/-
Cananeia, Brazil	47-85 (4)	12-18	18–26	3-4	10-11	+/-
Atlantida, Uruguay	52-100 (3)	12-15	18-20	56	11	+
Quequeen, Argentina	55–110 (2)	19	24-26	4	14-16	?
Quequen, Argentina	55-120 (5)	13-18	20-24	4-6	1 <b>1</b> –14	+/-
40°49′S, 53°43′W	70–133 (14)	11-19	18–26	4–6	11–16	+/-

## Morphology

### Ethmodiscus punctiger Castr. - Figs 1-4

Examination of the type slide and the loose material from the Comber Collection demonstrated the presence of a diatom which could readily be identified as *E. punctiger*, but just as well as *E. japonicus* (Figs 1–4).

The areolation varied from fairly coarse (Fig. 1) to too fine to be resolved in the light microscope. A fasciculation with striae parallel to the median stria of the sector was more prominent in the larger than in the smaller specimens (Figs 1, 2). The areolae are hexagonal in outline with the greatest dimension along a radius. The areolae are smaller close to the margin than in the centre of the valve (Fig. 2: 12–13 areolae in 10 µm in the centre and 18 near the margin measured along a radius, 16 in 10 µm in the centre and 20 near the margin measured along a tangent).

The labiate process is usually very distinct. The marginal strutted processes are regularly spaced except the two bordering the labiate process (Fig. 3, arrowed).

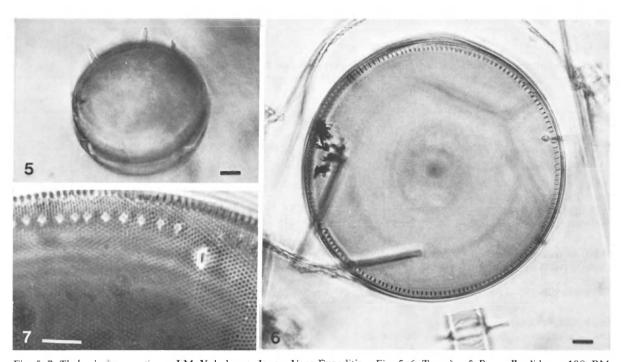
While the striation of the valve face and the marginal rings of strutted processes and ribs are evident from Castracane's (1886) diagnoses and illustrations, presence of neither a labiate nor occluded processes is indicated. Of the nine specimens measured in the type material (BM slide 15941 and loose material) four had a diameter of 55–75 µm, three of them with occluded processes (Figs 1, 4, arrowheads), whereas the five

specimens with diameter  $107-130~\mu m$  lacked occluded processes (Tab. 1). A certain correlation between presence of occluded processes and areola size was discernible, in the way that the specimens with coarser areolation had occluded processes.

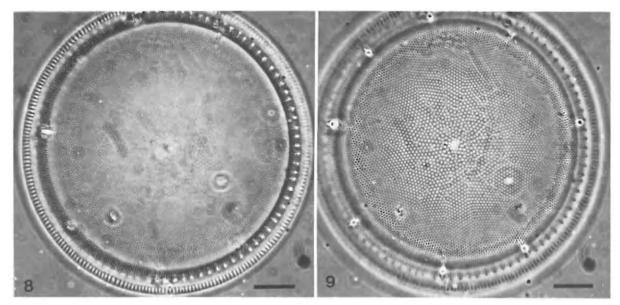
The numerical data of *E. japonicus* obtained by examination of the F. W. Payne slides (Fryxell 1978: Tab. 2) coincide with those of *E. punctiger* presented here (Tab. 1). Moreover, a possible correlation between size of valve diameter and presence of occluded processes was observed in *E. japonicus* as well (Fryxell 1978: 135). Sufficient evidence is thus provided to conclude that Castracane (1886) described the same species twice from the same material, i.e. *E. japonicus* and *E. punctiger* are conspecific.

# Coscinodiscus punctiger (Castr.) H. Perag. - Figs 5-7

Tempère & Peragallo's (1889–95) record was also from Japan ("Récolte pélagique", Yokohama, Vega-Expedition). A certain correlation between size of diameter and presence of occluded processes was noticed (Figs 5, 6, the same magnification) in the seven specimens measured on the Tempère & Peragallo slides nos 107 and 108. Three specimens with valve diameter 65–ca. 70 µm had occluded processes, and three specimens with valve diameter ca. 110–125 µm lacked occluded processes. The numerical data are consistent



Figs 5–7. Thalassiosira punctigera, LM. Yokohama, Japan, Vega Expedition. Figs 5, 6. Tempère & Peragallo slide no. 108, BM 14360. Fig. 7. Tempère & Peragallo slide no. 107, BM Adams 244 M. – Occluded processes (Fig. 5), labiate process, and marginal rings of strutted processes and ribs (Figs 6, 7). – Scale bars =  $10~\mu m$ .



Figs 8, 9. Thalassiosira punctigera, LM, the same specimen at different foci. Type slide of Coscinodiscus verecundus US Nat. Mus. 590 122. Marginal rings of strutted processes and ribs, labiate process (Fig. 8), fasciculation, labiate process and 7 occluded processes (Fig. 9). – Scale bars = 10 μm.

with those of *E. punctiger* and *E. japonicus* (Tab. 1), and the greater distance between the strutted processes adjacent to the labiate process is prominent (Fig. 7).

# Coscinodiscus verecundus A. Mann - Figs 8, 9

The single specimen on the type slide had all the morphological features of a medium-sized *Ethmodiscus* punctiger (Figs 8, 9, Tab. 1). Mann (1907: 259) characterized the areolation as "indistinct fascicles . . . irregular in width, showing the watch-milling effect of an *Actinocyclus*". The margin was also described in detail, the strutted processes (= "dim beads in a single circle") and the marginal ribs (= "transverse (radial) striae") inclusive. The structures representing the labiate process (Fig. 8) and the occluded processes (Fig. 9) were not mentioned, however.

C. verecundus thus fits nicely into the distribution as well as the morphological patterns of E. punctiger.

### Coscinodiscus angstii Gran - Figs 10-18

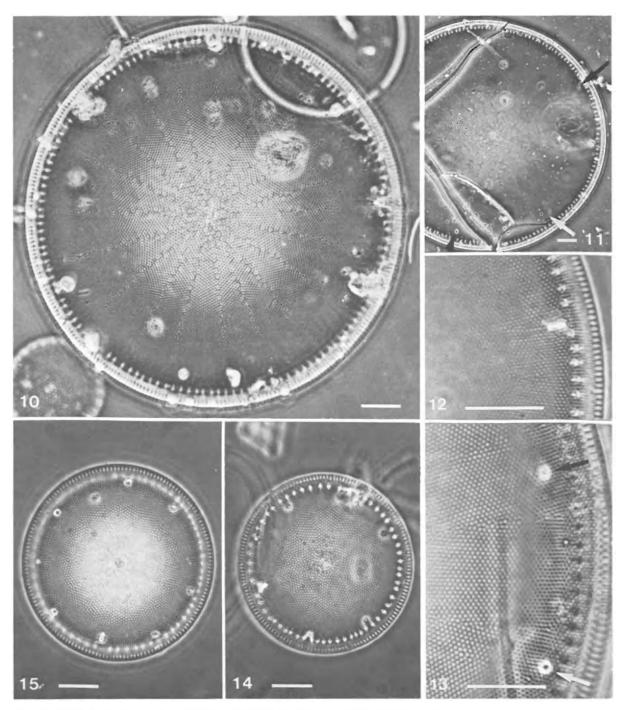
A diatom slide evidently intended to serve as a holotype of *C. angstii* does exist whilst a similar slide of *C. angstii* var. *granulomarginatus* has not been found in Gran's collection of diatom slides from Puget Sound and British Columbia.

The diagnosis and the illustrations of *C. angstii* reveal all the details discernible in the light microscope, including colony formation, numerous plate-like chloroplasts, and a "variable number of larger, somewhat radiating hollow spines inside the spinules" (Gran

& Angst 1931: 443) where "spines" obviously stand for occluded processes and "spinules" for strutted processes

C. angstii var. granulomarginatus was described as having no "inner spines", and compared to C. angstii var. angstii as having thinner cell walls, larger diameter (75-120 µm compared to 50-90 µm), and more delicate structure (25 areolae and 15 marginal "granules" compared to 15 rows of areolae, 12 "granules" and 7 "spinules", all in 10 µm). Number of "spinules", i.e. strutted processes, in 10 µm was not reported for C. angstii var. granulomarginatus. Judging from a poorly reproduced micrograph (Gran & Angst 1931: Fig. 20) they may be more closely spaced than in C. angstii var. angstii. The variety name granulomarginatus evidently refers to the "marginal granules", here interpreted as ribs. These structures stand out more prominently in the larger specimens of this diatom (Figs 3, 6, 11). It should be noticed however that the type slide of C. angstii var. angstii contained specimens as large as 120 µm in diameter with occluded processes, and furthermore that the most delicate specimens on this type slide had 21-23 striae in 10 µm (Tab. 1, Figs 11, 13 bases of occluded processes arrowed).

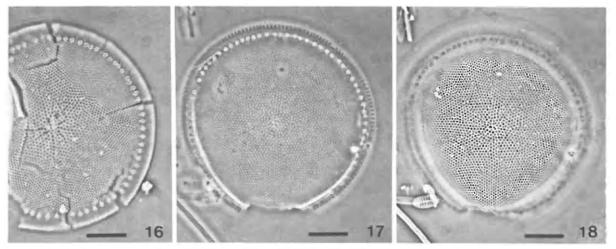
Gran & Angst (131) suggested vaguely that var. granulomarginatus might be identical with C. verecundus, and also that it might not deserve the status of a separate taxon but that it belonged to C. angstii. The reason for keeping C. angstii var. angstii and C. angstii var. granulomarginatus separate for the time being was the finding of the long hollow spines (the occluded processes) in the former but not in the latter with no finds



Figs 10–15. Thalassiosira punctigera, LM. Figs 10–13. Friday Harbor, 21 Mar 1928, type slide of Coscinodiscus angstii, IMBB no. 39. Fig. 14. Sechart Channel, British Columbia, 4 Feb 1929. Fig. 15. Ucluelet, British Columbia, 2 Feb 1928. – Morphological details as in Figs 1–9, bases of occluded processes arrowed on Figs 11 and 13. – Scale bars =  $10 \mu m$ .

of transition forms between the two types. The present investigation includes observations on specimens with diameters 44–120  $\mu m$  and occluded processes (e.g. Figs 10, 11, 13–15) as well as on specimens near the

minimum size of the species lacking occluded processes (Figs 16-19). We therefore have to reject *C. angstii* var. granulomarginatus as a separate taxon if based on absence of occluded processes. A strict linking of size of



Figs 16–18. Thalassiosira punctigera, LM. Sechart Channel, British Columbia, 4 Feb 1929, small valves lacking occluded processes. – Scale bars = 10 μm.

diameter and valve structure is evidently also lacking as documented by Fig. 18 showing a valve with diameter  $55 \mu m$  and an areolation barely visible in the light microscope, and 14 marginal ribs in  $10 \mu m$ .

The generic affinity to Coscinodiscus was questioned by Gran & Angst (1931), mainly because of the presence of occluded processes ("the hollow spines"), which were not known from this genus. A closer relationship to Thalassiosira was proposed.

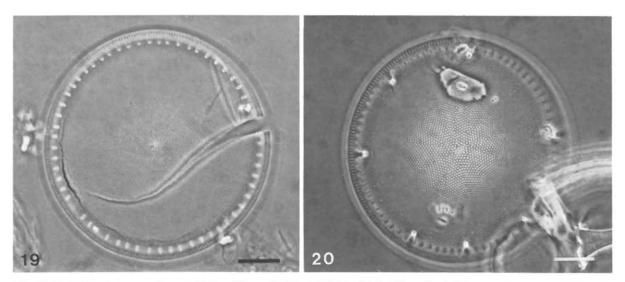
### Thalassiosira japonica Kiselev

The specimens Kiselev (1935) used for describing T.

japonica covered the same range of diameter size,  $52-126~\mu m$ , as for the diatoms listed in Tab. 1. The density of areolae, 13-16 in  $10~\mu m$ , of marginal processes, 5-6 in  $10~\mu m$ , and of marginal ribs, 10-12 in  $10~\mu m$ , is also consistent with the data in Tab. 1.

Kiselev had observed colonies, cells united by a thin thread, which was obviously the justification for the generic classification. Presence of occluded processes was described ("eine Reihe aus einigen (6–8) langen, dicken Stacheln"), and illustrated.

Kiselev's material has not been available for this investigation. The diatom in question, identical with Thalassiosira angstii (Gran) Makarova as confirmed by



Figs 19, 20. Thalassiosira punctigera, LM. Sea of Japan, 25 Oct 1980. Fig. 19. Ca. 20 areolae in  $10 \, \mu m$ , occluded processes absent. Fig. 20. Ca. 14 areolae in  $10 \, \mu m$ , occluded processes present. – Scale bars =  $10 \, \mu m$ .

Fryxell (1978), has been examined in samples collected in waters from which Kiselev had his observations, namely near the Aleutian Islands (February 1971) and in the Sea of Japan (October 1980). The most noteworthy record from these samples is documented by Figs 19 and 20 which show two valves of the same diameter but distinctly different as to fineness of areolation and presence of occluded processes.

# Observations from areas outside the North Pacific Ocean -Figs 21-31

Müller-Melchers (1953) was the first to record the diatom in question, Coscinodiscus punctiger (Castr.) Müller-Melchers according to his use of the nomenclature, from the South Atlantic and South Pacific Oceans. In an attempt to investigate material the authors of the many names of the diatom in question had at hand, samples from the waters Müller-Melchers examined have also been included, namely from Wellington Harbour, New Zealand (Mar 1962, Aug 1981); Cananeia (Dec 1953) and Ubatuba (Jul 1978), Brazil; Atlantida, Uruguay (Feb 1949); Quequeen, Argentina (Mar and Aug 1961); and off the Argentine coast (40°49.2'S, 53°43.6'W, date unknown).

The latter sample was the one most extensively examined from the South Atlantic Ocean. Occluded processes were seen, although sparsely. Size of areolae and density of marginal ribs varied considerably (Tab. 2), these two characters being highly correlated and independent on size of valve diameter (Figs 21–23). The variability of another character, namely the number of areolae between the marginal strutted processes, was particularly well documented in the South Atlantic mat-

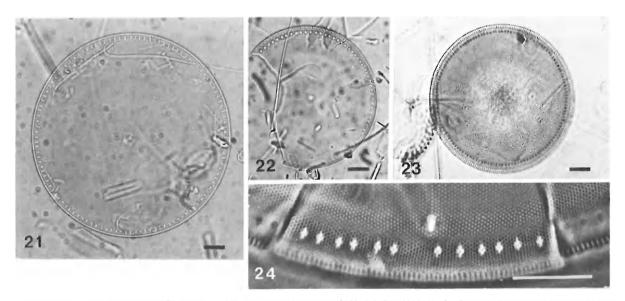
erial in general. The number varied between specimens from the same gathering as well as within the single specimen (Figs 24, 25, 28).

The specimens seen in the two collections from the Wellington Harbour were the largest ones observed (78–186  $\mu$ m in diameter, 20  $\mu$ m net used for the 1981 collection). Occluded processes were frequent, particularly in the recent collection (15 specimens with occluded processes of 18 examined, including specimens with diameters 130, 170, and 180  $\mu$ m). Most of these specimens had 20 or more areolae in 10  $\mu$ m (Figs 29–31). The most striking feature was the densely packed marginal strutted processes, 7–11 in 10  $\mu$ m, mostly separated by a single areola (Fig. 26). Compared with specimens from other geographical localities (e.g. Figs 7, 12, 24) these strutted processes are comparatively small and arranged in a zig-zag rather than in a straight ring (Fig. 30).

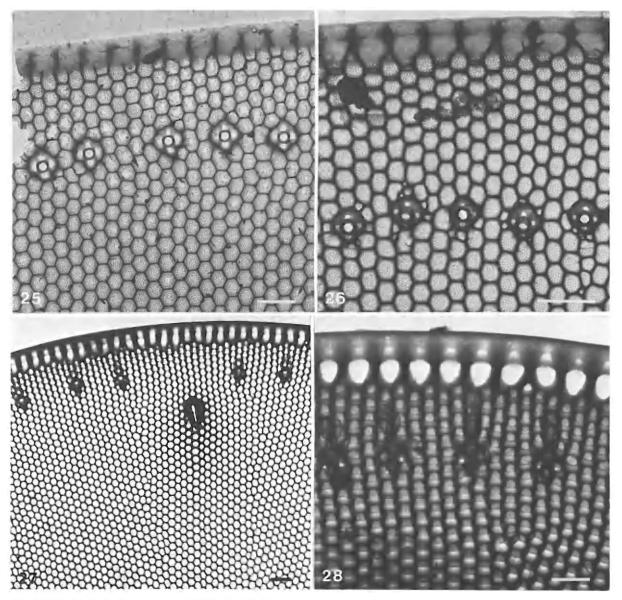
# The fine structure of the siliceous frustule - Figs 32-44

Fryxell (1978) documented by scanning electron micrographs the presence of one central operculate strutted process, one marginal ring of operculate strutted processes with urn shaped external tubes, one externally as well as internally large labiate process located inside two widely separated strutted processes, and a varying number of long occluded processes with a diameter slightly smaller than that of the external tube of the labiate process but much larger than that of a strutted process. Syvertsen & Hasle (1982) showed that the occluded processes were "occluded" towards the cell interior by cribra.

The present investigation revealed a fairly compli-



Figs 21–24. Thalassiosira punctigera, LM. Off the Argentine coast ( $40^{\circ}49.2^{\circ}S$ ,  $53^{\circ}43.6^{\circ}W$ ). Occluded processes sparse, other morphological features as above. – Scale bars =  $10 \ \mu m$ .



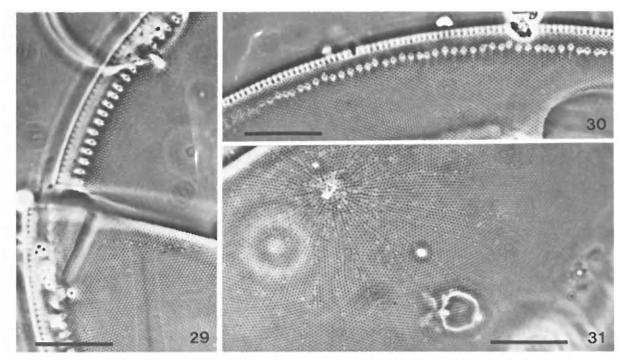
Figs 25–28. Thalassiosira punctigera, TEM. Figs 25, 28. Queqeen, Argentina, August 1961. Fig. 26. Wellington Harbour, New Zealand, 28 Mar 1962. Fig. 27. von Stosch clone 64341 (Heligoland). – Valve margins with ribs, strutted processes separated by a variable number of areolae (Fig. 25) and a labiate process (Fig. 27). – Scale bars = 1  $\mu$ m.

cated structure of the marginal strutted processes. The part raised above the external valve surface consists of the tubular extension of a wide basal chamber and a conspicuous urn shaped structure with spiral markings. The base of the latter is at some distance above the valve surface, and the pointed top is high above the end of the external tube (Figs 32, 33, 36). The central strutted process (Fig. 37, arrowed) is inconspicuous compared with the marginal ones. The difference in the width of the occluded processes and the marginal strut-

ted processes is particularly prominent when the external tubes are broken off (Fig. 34).

The foramina are comparatively small and sometimes occluded by flaps extending from the areola wall towards the centre of the foramen (Fig. 32). Similar external occlusions are present also between the slightly raised marginal ribs (Figs 32–35). It should be noticed however, that well developed internal cribra are present as well (Fig. 36, Fryxell 1978: Fig. 19).

Fryxell's (1978) study included one scanning electron



Figs 29-31. Thalassiosira punctigera, LM. Wellington Harbour, 28 Mar 1962. Figs 29, 30. Valve margin with small, densely packed, 8 in 10 μm, strutted processes, one labiate and one broken occluded process (Fig. 29). Fig. 31. Central part of valve, fasciculated areolation, more than 20 areolae in 10 μm. – Scale bars = 10 μm.

micrograph of two types of bands. The present study adds information on single bands as seen in the transmission electron microscope and on a cingulum as seen in the scanning electron microscope. The cingulum had three types of bands; one fully areolated valvocopula, one copula with a single advalvar row of areolae and four hyaline pleurae (Figs 33-35). All bands are open with a broad ligula (Figs 42, 43), the valvocopula excepted. The areolae of the valvocopula as well as those of the single row of the copula had cribra (Figs 41, 42) and foramina (Figs 33-35). The areolae of the copula as well as the areolae of the valvocopula near the junction of the partes exteriores and interiores were elongated in pervalvar direction (Figs 41, 42, Fryxell 1978: Fig. 20). The pars interior of the valvocopula seemed to be slightly septate and thus well fitted to interlock with the thickened margin of the valve mantle (Figs 33-35, Fryxell 1978: Figs 17, 20), and the partes interiores of the pleurae were extremely thin-walled (Figs 43, 44).

# Thalassiosira punctigera (Castr.) Hasle comb. nov.

Basionym: Ethmodiscus punctiger Castracane 1886: 167, Pl. 3, Fig. 1. – Synonyms: Coscinodiscus punctiger (Castr.) H. Perag. in Tempére & Peragallo 1889–1895: 57, nos 107, 108. – Coscinodiscus punctiger (Castr.) Müller-Melchers 1953: 465, Fig. 2, nom. illeg. – Type material: BM 15941, surface, Yeddo [Tokyo] Bay, Japan, Challenger Exp., Deby Coll. – Note: The

slide is a strewn mount not marked for any particular species. Loose material was available from a bottle labelled "Surface diatoms, Yeddo Bay, Challenger Exp." in Comber Coll. deposited in British Museum (Natural History).

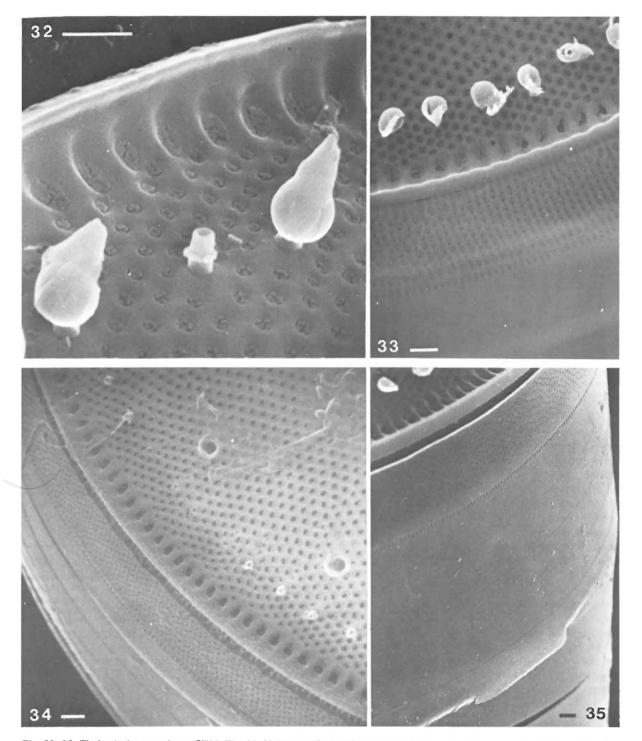
Ethmodiscus japonicus Castracane 1886: 168, Pl. 22, Fig. 2. – Type material: BM 43190, 43192, 43733, Tokyo Bay, Challenger Exp., Payne Coll. – Note: The slides are strewn mounts not marked for any particular species.

Coscinodiscus verecundus Mann 1907: 259, Pl. 50, Fig. 1. – Type: 590122 U.S. National Museum, Okhotsk Sea, August 27, 1896, 1,562 fathoms, bottom of brown mud and fine sand. (US holotype). – Note: The slide contains a single specimen.

Coscinodiscus angstii Gran in Gran & Angst 1931: 443, Fig. 19. – Thalassiosira angstii (Gran) Makarova 1970: 13. – Type material: IMBB (University of Oslo) 39, Friday Harbor, Puget Sound, March 21, 1928, Gran Coll. – Note: The slide is a strewn mount labelled in Gran's handwriting, "Fr. H. March 21.1928 – Thalassiosira pacifica, Coscinodiscus angstii, excenticus" with no marked specimens. Loose material from Friday Harbor as well as from other localities included in the collection used by Gran & Angst (1931) was available.

Coscinodiscus angstii var granulomarginatus Gran & Angst 1931: 444, Fig. 20. – Type material: Friday Harbor, Puget Sound. – Note: No slide with reference to this taxon is present in the Gran Coll.

Thalassiosira japonica Kiselev 1935: 99, 116, Figs 17–19. – Patroklus Bay (43°03'94N, 131°57'25E), Sea of Japan. – Type material not seen.



Figs 32–35. Thalassiosira punctigera, SEM. Fig. 32. Valve margin, two intact strutted processes, the one in the middle lacking the distal external conical part, foramina with flaps. Figs 33–35. Valve margin, valvocopula, copula and pleurae. British Columbia. – Scale bars =  $1 \mu m$ .

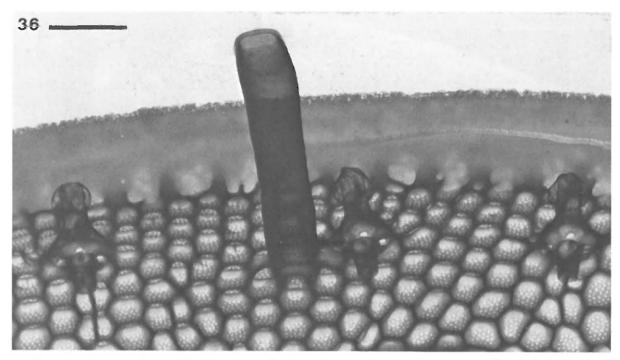


Fig. 36. Thalassiosira punctigera, TEM. Valve margin with three strutted and one occluded process. – Clonal culture, Viksfjord, Norway. – Scale bar =  $1 \mu m$ .

Cell in girdle view box shaped. Chloroplasts many, small, rounded discs. Cells in colonies united by a thin thread. Valvocopula fully areolated, one advalvar row set off from the rest. One copula with one advalvar row of elongate areolae. Four hyaline pleurae. All bands open. Valve convex with ribbed (10-16 ribs in 10 µm) flattened margin. Cell diameter 40-186 µm. Cribrum internal, external foramina partly occluded by flaps from the areola wall. Areolation fasciculated. 10-23 areolae in 10 μm measured along a radius, 15-30 striae in 10 µm measured along a tangent. One large marginal labiate process with long, tubular external extension. A varying number of long tubular occluded processes. One marginal ring of operculate strutted processes (3-11, mostly 4-5 in 10 μm) with an external pointed urn shaped part, located closer to the margin than the labiate and the occluded processes. One central strutted process with a short tubular external part.

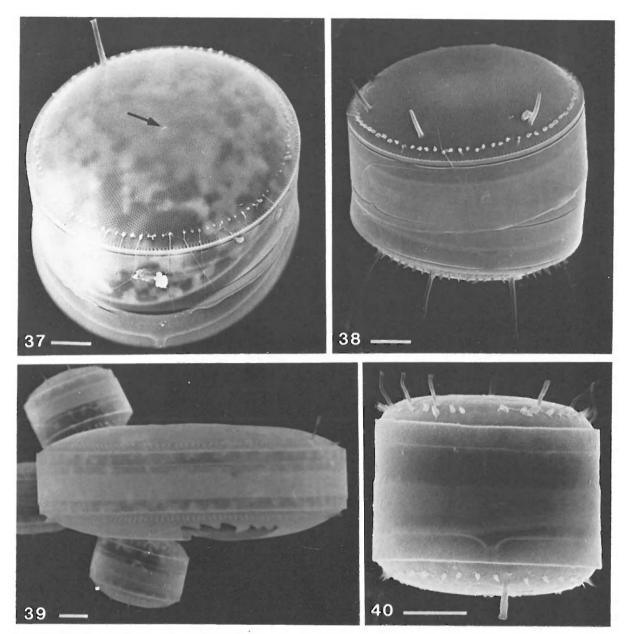
### Discussion

The taxonomic confusion here revealed is easily explained by the variable valve morphology of *T. punctigera* demonstrated by two clonal cultures isolated from the North Atlantic area (von Stosch clone 64341 from Heligoland, October 1979 and the Syvertsen clone from Viksfjord, outer Oslofjord, November 1979). The

maximum cells (after auxospore formation) had a cell diameter of  $120~\mu m$ , and the minimum cells were ca.  $30~\mu m$  in diameter (Figs 39, 45). Cells of the same size range were present in the field samples from the same area while still larger cells were measured in samples from Wellington Harbour and the Argentine coast (Tab. 2).

Presence of occluded processes is certainly no stable morphological character as also mentioned by Fryxell (1978) and shown here by one cell with occluded processes on one valve only (Fig. 40). Although the occluded processes appeared more regularly in the smaller and the medium sized specimens, it should be kept in mind that some of the largest specimens measured had occluded processes.

A third variable morphological character observed particularly in field samples but also in clonal cultures, is the size of the valve areolae. Growth experiments showed that the Viksfjord clone kept at 12°C and later transferred to 3°C seemed to respond to the temperature change by an increase in the areola size (20–22 and 14–18 areolae in 10  $\mu$ m at 12°C and 3°C, respectively). The experiments are at a preliminary stage but the results correspond well with the seasonal variation of the two parameters as observed in net hauls collected in the Skagerrak from the autumn of 1979 to the spring of 1982. Unfortunately the rest of the material examined for this investigation is not fit for a systematic analysis of

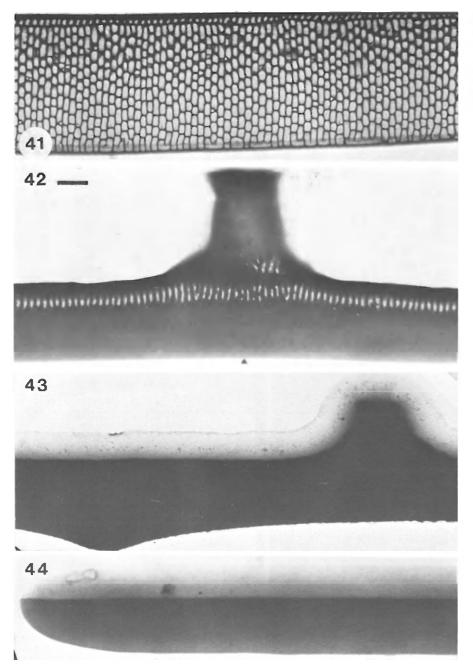


Figs 37–40. Thalassiostra punctigera, SEM. Fig. 37. Labiate process prominent,  $\beta$ -chitin threads from the marginal strutted processes, central strutted process arrowed. Fig. 38. Long occluded processes on both valves, same gathering as Fig. 37. Fig. 39. Maximum cells without occluded processes, minimum cells with occluded processes (von Stosch clone 64341). Fig. 40. One valve with labiate and occluded processes, the other with labiate process and no occluded processes (Viksfjord clone). Figs 37, 38. British Columbia. – Scale bars =  $10 \mu m$ .

the possible relationship between the valve morphology and environmental factors. The two observations from the North Pacific Ocean which included information on temperature, and the observations from Quequen, Argentina in March and August 1961 showed a similar trend, however (Tab. 2).

Whereas the number of marginal ribs seemed to vary consistently with the number of areolae in 10  $\mu m$ 

(10–17 and 11–20, respectively), the number of marginal strutted processes, 4–5 in 10  $\mu$ m, occasionally 3 or 6, seemed to be independent of the areola size. One exception from the overall picture was striking however. 18 specimens in one sample collected in Wellington Harbour, 6 Aug 1981, had diameters 78–186  $\mu$ m and 7–11 marginal strutted processes in 10  $\mu$ m, the largest cells having the most closely spaced processes. All



Figs 41–44. Thalassiosira punctigera, TEM. von Stosch clone 64341. Fig. 41. Valvocopula. Fig. 42. Copula with ligula. Fig. 43. Pleura with ligula and antiligula. Fig. 44. End of pleura. – Scale bar = 1 μm.

specimens would probably be classified as "finely areolated" (approximately 16 to more than 20 areolae in 10 µm measured under the light microscope, no micrographs). It may be questioned whether the specimens belong to the taxon now reported from so many other localities or to a separate taxon distinguished by the larger cell diameter, the densely packed, apparently also smaller strutted processes, and the delicate areolation. Examination of more samples from various seasons,

and/or clonal cultures would be the means to answer this question.

The cingulum is structured as in most *Thalassiosira* species examined until now (Syvertsen 1979, Fryxell et al. 1981). A feature that may be worthwhile mentioning is the gap between the valve mantle and the apparently horizontal pars interior of the valvocopula. The latter structure also interpreted as a narrow septum shows some similarity to a corresponding structure in the pen-

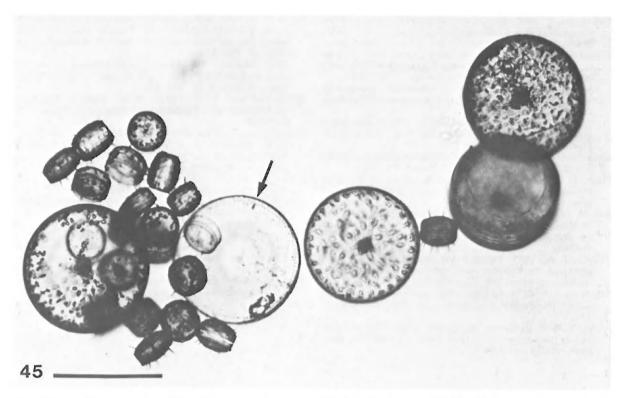


Fig. 45. Thalassiosira punctigera, LM. Maximum and minimum cells (von Stosch clone 64341). Whole cells with chloroplasts, single large valve with labiate process (arrowed) and marginal strutted processes, minimum cells with occluded processes. Water mount. – Scale bar =  $100 \ \mu m$ .

nate diatom *Rhoicosphenia curvata* (Kütz.) Grun. where the pars interior of the band adjacent to the valve fits tightly around the thickened margin of the valve (Mann 1982).

T. punctigera belongs to the group of Thalassiosira species that has typically loculate areolae with well defined cribra. The flaps extending from the areola wall are more exceptional although observed in at least one species before, T. ferelineata Hasle & Fryxell. Since the flaps evidently fit into the definition of volae, the exceptional feature is the joint occurrence of a cribrum and volae. It should be noticed however that we are dealing with an arrangement different from the cribrum-borne volae in the pores of some raphid diatoms where the flaps extend from the bars of the cribra (Mann 1981).

The world-wide distribution of *T. punctigera* is documented by the localities of the taxa suggested as synonyms (Tab. 1) as well as of the additional material examined (Tab. 2). It has been frequently recorded from the North Pacific Ocean (Makarova 1970) while judging from the literature it may be less common in the eastern North Atlantic recorded as rare in the eastern Caribbean Sea in the winter 1955–1956 (Takano 1960). The records from the North Atlantic area are of particular interest since until 1978 it had not been

observed in this part of the world (Kat 1982). These observations are even more interesting when seen in connection with the appearance of two other planktonic diatoms in the western English Channel, one observed for the first time in 1966 and the second one in 1977 (Boalch & Harbour 1977a, b).

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