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Some *Thalassiosira* species with one central process (Bacillariophyceae)

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T. nordenskiöldii
aestivalis
pacifica
angulata
allenii

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Thalassiosira nordenskiöldii Cleve, *T. aestivalis* Gran, *T. pacifica* Gran & Angst, and *T. angulata* (Greg.) comb. nov. belong to the medium-sized to larger species of the genus, while maximum measured diameter of *T. allenii* Takano is 20 μm . All 5 species have one central strutted process, one marginal ring of strutted processes, and one marginal labiate process. They are differentiated by areolae size, areola array, structure and height of valve mantle, distance between marginal processes, location and size of labiate process compared with adjacent strutted processes, and shape of external part of processes. *T. angulata* was not observed in samples from the Pacific Ocean. None of the 5 species were observed in our material from the southern hemisphere.

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Thalassiosira nordenskiöldii Cleve, the genotype, has one central strutted process, one marginal ring of strutted processes, and one marginal labiate process. The species discussed here share this process pattern. Although somewhat variable within a single species, certain similarities are encountered also in the areola array. Moreover, shape of colonies, gross morphology of frustule (Figs. 1-4), and composition and structure of the girdle are very similar. Thus, the distinctive features are size of areolae, distance between marginal strutted processes, size and location of labiate process, external shape of processes, and height and structure of valve mantle (Table I).

The species in question are marine and planktonic, and with the qualification that the geographic distribution of some of them is poorly known, they seem to have similar ecology, and may well appear in the same samples.

Detailed morphologic studies of *T. nordenskiöldii*, *T. pacifica* Gran & Angst, and *T. allenii* Takano by means of light and electron microscopy have been published (references under the individual species). However, little information on *T. aestivalis* Gran is available in the literature, and great confusion exists concerning the identity and nomenclature of *T. angulata* (Greg.) comb. nov. (the species usually identified as *T. decipiens* (Grun.) Jørg. in marine plankton). Such confusion is caused partly because type material has not been examined by modern

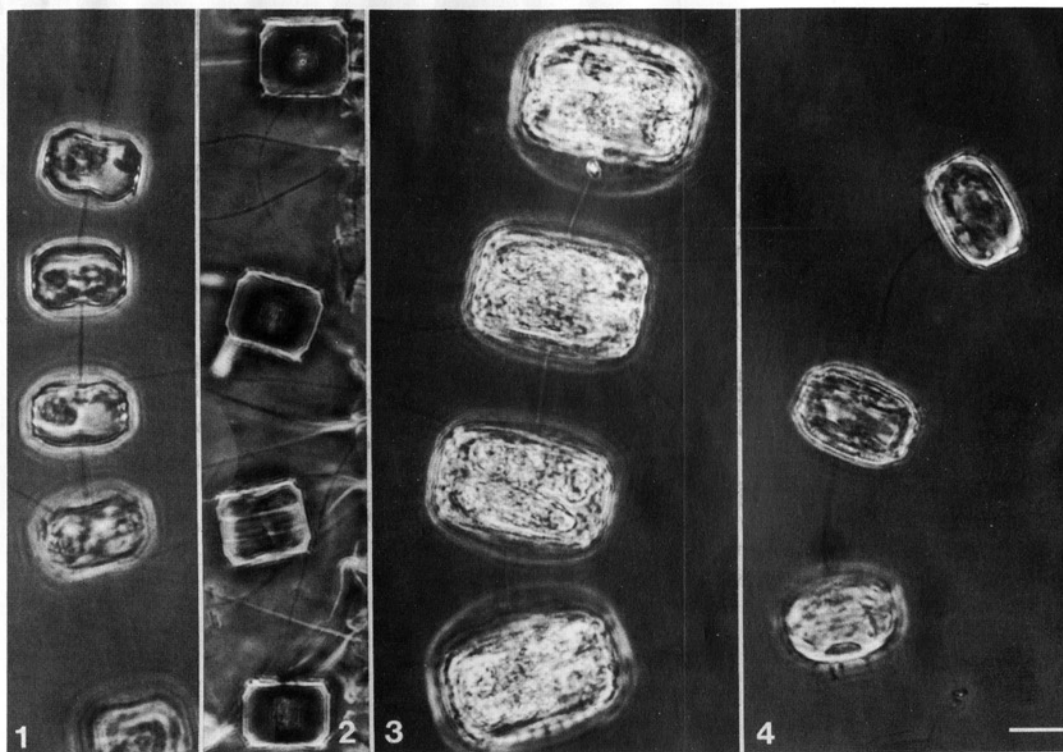
techniques, and partly because attention has been paid to unessential characters seen, for instance, on drawings of colonies.

By comparing light and electron microscope observations of type material, the present investigation attempts to clarify distinctions between species and to amplify their descriptions as was done for some other *Thalassiosira* species (Hasle & Heimdal 1968, Fryxell & Hasle 1972, Hasle 1972a, 1976a, 1978a, Fryxell 1977, Fryxell & Hasle 1977, Hasle & Fryxell 1977). This series of papers follows the same line of investigation as those by Makarova (1976a, 1977a, b) and Makarova et al. (1976), with the exception that her papers apparently do not include examination of type material.

Material and methods

Since type material in some cases did not give sufficient information, additional clonal cultures or field samples, usually net hauls, were examined. (Data on the material examined are given under the discussion of the individual species.)

Information on shape of colonies and cells in girdle view was obtained by light microscopy (LM) of raw material in water mounts or embedded in a medium. Cleaned material was examined in Hyrax mounts in LM to obtain information on valve structure. Raw material



Figs. 1-4. *Thalassiosira* colonies in LM, all the same magnification, scale = 10 μ m. Fig. 1. *T. nordenskiöldii*, resting spores and vegetative cells, clonal culture, Oslofjord, Norway (isolator E. Paasche). Fig. 2. *T. aestivalis*, Friday Harbor, Puget Sound, Washington, USA, 21 July 1930, slide IMBB No. 38. Fig. 3. *T. pacifica*, Yaquina Bay, Oregon, USA, 28 April 1974. Fig. 4. *T. angulata*, Oslofjord, 9 March 1975. Figs. 1, 3, 4. Water mounts.

Table I. Morphologic data on some *Thalassiosira* species with one marginal ring and one central strutted process (Nos. 7, 8 based on data from the literature)

Species	Diam. μ m	Valve areolae in 10 μ m		Marg.proc. in 10 μ m	Number of proc.pr. sector	Location of lab. proc.	Height of valve mantle	Marginal ribs in 10 μ m
		Face	Mantle					
1. <i>T. nordenskiöldii</i> Cleve	10-50	14-18	14-18	3	1	variable	6-8 areolae	same as mantle areolae
2. <i>T. aestivalis</i> Gran	14-56	18	>20	4(3-5)	2-3	as for a strutted	2-3 areolae	half number of valve areolae
3. <i>T. pacifica</i> Gran & Angst	7-46	10-14 (18)	>20	5(4-6)	5-6	as for a strutted	2-3 areolae	half number of valve areolae
4. <i>T. angulata</i> (Greg.) Hasle	12-39	8-18	14-24	3(2-4)	3(?)	close to one strutted	2-4 areolae	same as mantle areolae
5. <i>T. allenii</i> Takano	5-20	18-24	30(?) - 40	6(5-7)		mainly as for a strutted	3(2-4) areolae	absent
6. <i>T. decipiens</i> (Grun.) Jørg.	9-40	8-12	10-15	4-6		between two strutted	2-3 areolae	same as mantle areolae ?
7. <i>T. binata</i> G. Fryxell	4-18	30-40	30-40			close to one strutted	6 areolae	absent
8. <i>T. levanderi</i> Van Goor	8-13	20-21	23-24	?		?		
9. <i>T. muriformis</i> (Loeblich, Wight & Darley) Round	11-15	18-24	18-24	8(7-9)		between two strutted	2 areolae	absent

prepared by critical point drying was examined by transmission (TEM) and scanning electron microscopy (SEM) to obtain information on composition and structure of the girdle. Cleaned material was examined in TEM and SEM to obtain information on fine structure and nature of processes revealed when viewed in internal and external view. The methods used were summarized by Hasle (1978b).

Various types of light and electron microscopes have been used during this investigation, which has been carried out over a time interval of more than 10 years, a period of time characterized by the greatest development of techniques and instrumentation for electron microscopy.

The terminology follows that suggested by Anonymous (1975) and von Stosch (1975).

Observations

Thalassiosira nordenskiöldii Cleve - Figs. 1, 5-20, 35-37

Cleve 1873, p. 6, Pl. 1, Fig. 11, Fricke 1901, Pl. 225, Figs. 8-15, Fryxell 1975, Pl. 5, Hasle 1976b, Fig. 5, Makarova 1976a, p. 608, Pls. 4, 5, 1977a, Pl. 1, Figs. 1-5, non Helmcke & Krieger 1954, Pls. 108, 109, non Somers 1972, Figs. 3-8.

Type locality: Davis Strait Lat. 62°36' Long. 52°50', Lat. 63°30' Long. 52°40', Lat. 61°25' Long. 50°50'.

Holotype: P. T. Cleve's slide labelled 'Davis Strait, 1871' in Swedish Museum of Natural History (S), Section of Botany, Stockholm.

Numerical morphological data of *T. nordenskiöldii* were summarized from the literature by Takano (1965) and Makarova (1970). The drawings by Fricke (1901) were made on specimens from the type locality (Figs. 8-12 from the Baffin Bay, Figs. 13-15 from the Davis Strait), possibly from the type material. The LM picture (Hasle 1976b, Fig. 5) was made from the holotype slide. Fryxell (1975) made a thorough SEM examination of a *T. nordenskiöldii* clone from the Oslofjord (Paasche's clone), and Makarova (1976a, 1977a) examined the species in TEM and SEM. Besides this, EM illustrations are found scattered in the literature (e.g. Hasle 1964, 1968, 1972b) showing some particular morphological details of *T. nordenskiöldii*.

In spite of useful information already avail-

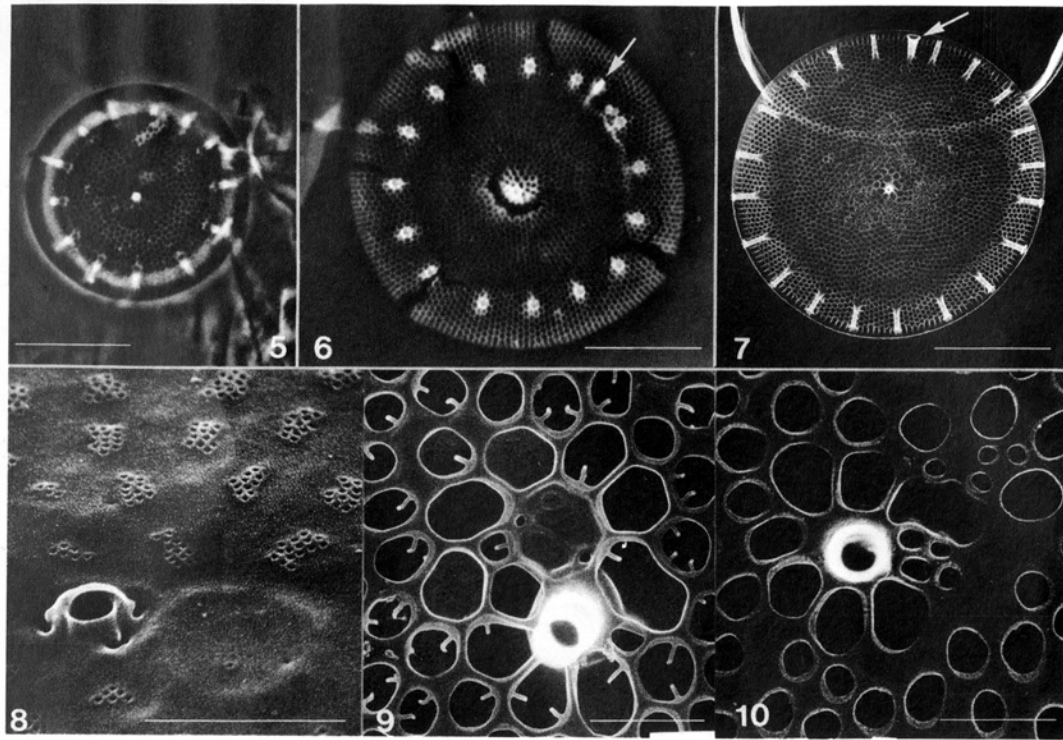
able, we feel that the morphology of *T. nordenskiöldii* as the type species of the genus deserves a detailed discussion, especially since type material has now been examined in EM. Unprepared type material was present in the P. T. Cleve Collection in the Swedish Museum of Natural History as a dry sample labelled 'Lat. 63°30', Long. 52°40', Fries, 8 June 1871', one of the samples referred to by Cleve (1873, p. 7). After the preparation for Hyrax and EM mounts valves of smaller vegetative cells and possibly also of resting spores were still intact together with fragments of larger valves.

Single valves in LM and EM were characterized by (1) a concavity in the centre, (2) one slightly eccentric strutted process adjacent to one or more larger areolae, (3) one ring of long, slender, widely separated marginal strutted processes, (4) one labiate process in the same ring, (5) a wide mantle ending in a ribbed rim, and (6) areolae on valve face and mantle of the same size, in radial rows in the smaller specimens but in more or less regular sectors of areola rows in the larger ones (Figs. 5, 11, 12, 17). The location of the labiate process varied; in some specimens it was positioned as for a strutted process, in others close to one, or about midway between two strutted processes which might be further apart than the rest of the processes in the ring (Figs. 11, 12).

Diameters of 13-30 μ m, 14-18, mainly 16-18, areolae in 10 μ m, and about 3 marginal processes in 10 μ m were measured (the holotype slide included). Measured in terms of areola size the height of valve mantle was 6-8 areolae (that is number between base of strutted processes and the ribbed mantle edge). The mantle rim had 18-20 ribs in 10 μ m corresponding to the number of areolae.

Since the type material was inappropriate for SEM and also for obtaining more informative LM pictures, observations made on other samples are included. The irregularly areolated area adjacent to the central process, depressed from the outside (Figs. 9, 10, 20), could be distinguished also when viewed from the inside of the valve. Fewer porelli and greater distance between the cribra than on the rest of the valve characterized this central area (Fig. 8).

Observations made on field samples from the Arctic (80°18'N, 28°30'E, Fig. 19), the North Atlantic (66°38'N, 14°24'W, Fig. 20), the Trondheimsfjord, Norway (Hasle 1972b, Fig. 43), the Oslofjord, Norway (Fig. 6, Hasle

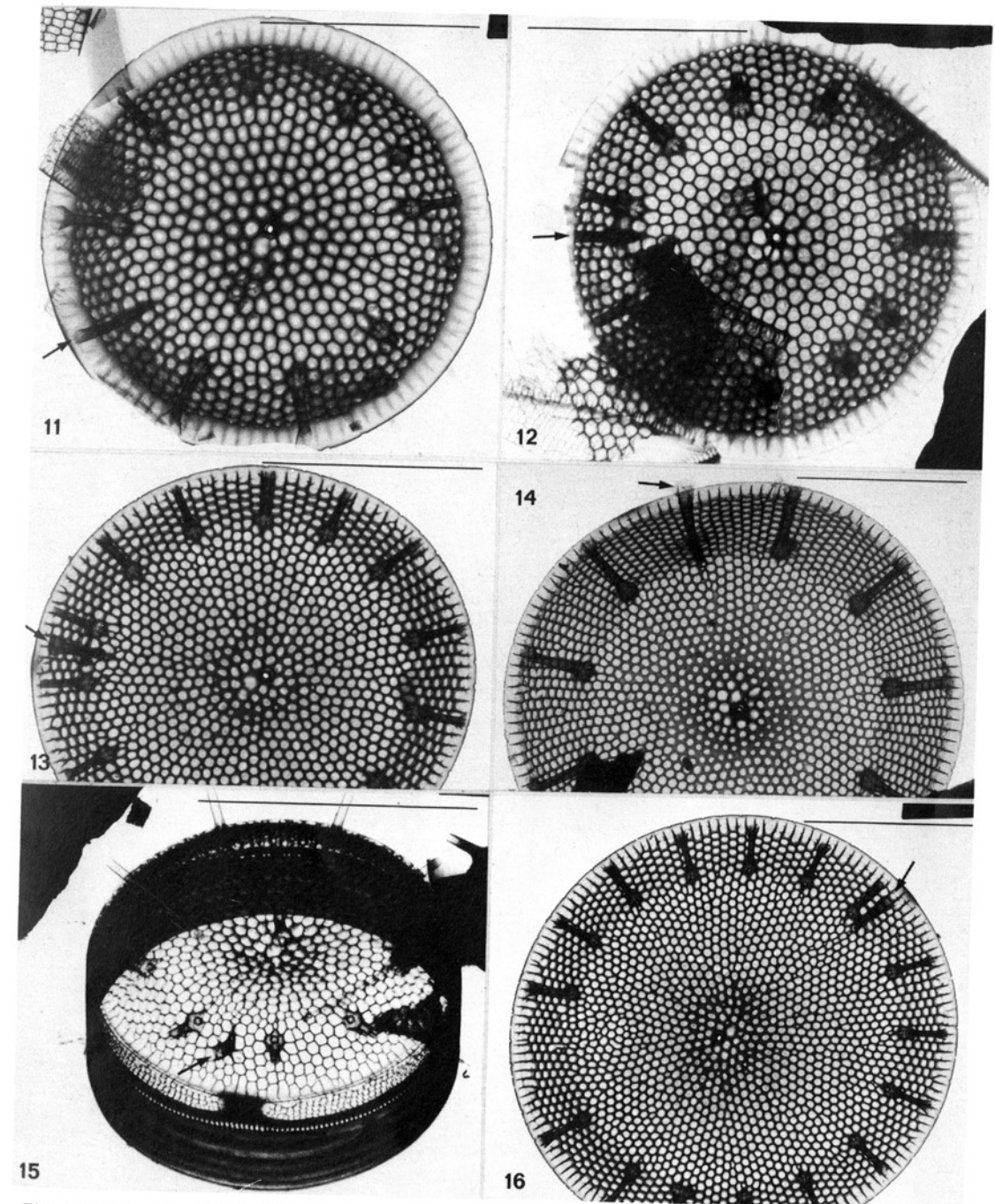


Figs. 5–10. *T. nordenskiöldii*. Fig. 5. Type material, Davis Strait, 8 June 1871, Hyrax mount, LM. Fig. 6. Drøbak, Norway, 1 April 1953, Hyrax mount, LM. Figs. 7–10. Clonal culture, Oslofjord, whole valve and central parts, SEM. Fig. 8. Internal surface, the others external surface. Scale for Figs. 5–7 = 10 μm , for Figs. 8–10 = 1 μm . Labiate process arrowed.

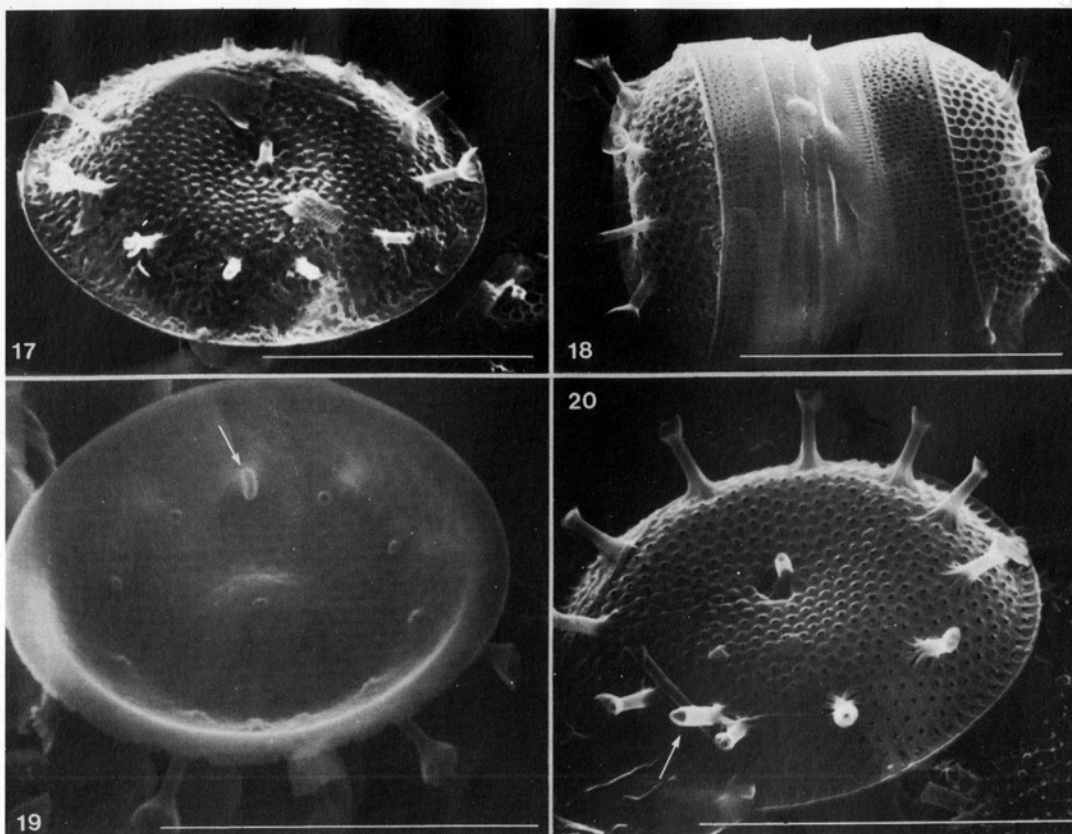
1976b, Figs. 6, 7) and British Columbia, Canada (Fig. 14), as well as on cultures from the Oslofjord (Figs. 7–10, 15, isolator E. Paasche) and Passamaquoddy Bay, USA (Figs. 13, 16, isolator A. White), showed the same variation in site of labiate process compared to the neighbouring strutted processes, the one qualification being that the site seemed to be slightly more conservative in the Oslofjord clone than in the field samples and the other culture examined. As evident from these observations, the site of the labiate process is independent of cell size as well as of geographic locality. Moreover, the distance between adjacent strutted processes is not constant in terms of number of areolae, as can be seen on pictures of specimens from the type material as well as from the other samples examined. A character which seemed to vary between, but not so much within the individual samples, is height of mantle. This variation may be size dependent, however, since the specimens from British

Columbia, which on average were larger than those measured from the type material, had 6–9 areolae between base of strutted processes and mantle edge (Fig. 14).

Our observations show clearly that the areolae on valve face and mantle have about the same size, e.g. on LM pictures of valve mantle flattened due to fractioning (Fig. 6, Hasle 1976b, Fig. 6), as mentioned above for the type material. This is in contrast to the micrograph in Helmcke & Krieger (1954, Pl. 108) cited by Takano (1965) and Makarova (1970, 1977a). (Makarova (1976a) found 20–24 areolae in 10 μm on valve face and 28 in 10 μm on valve mantle, cited in 1977 as 20–28 and 40, respectively.) At a certain level of focus the ribbed mantle edge was distinct in LM. As pointed out and illustrated by Fryxell (1975) and Makarova (1976a), there is sometimes a flared skirt around the tube of the strutted processes. This structure can be seen in LM, TEM, and SEM (Hasle 1968, 1976b) and was also seen in the type material (Figs. 11, 17).



Figs. 11–16. *T. nordenskiöldii*, TEM, scale = 10 μm . Fig. 15. Whole theca, the others single valves. Figs. 11, 12. Type material, Davis Strait, 1871. Figs. 13, 16. Culture, Passamaquoddy Bay, Canada (isolator A. White). Fig. 14. Vancouver Island, British Columbia, Canada, 48° 39.7'N, 123° 25.5'W (CEPEX), 2 June 1975. Fig. 15. Clonal culture, Oslofjord. Labiate process arrowed.



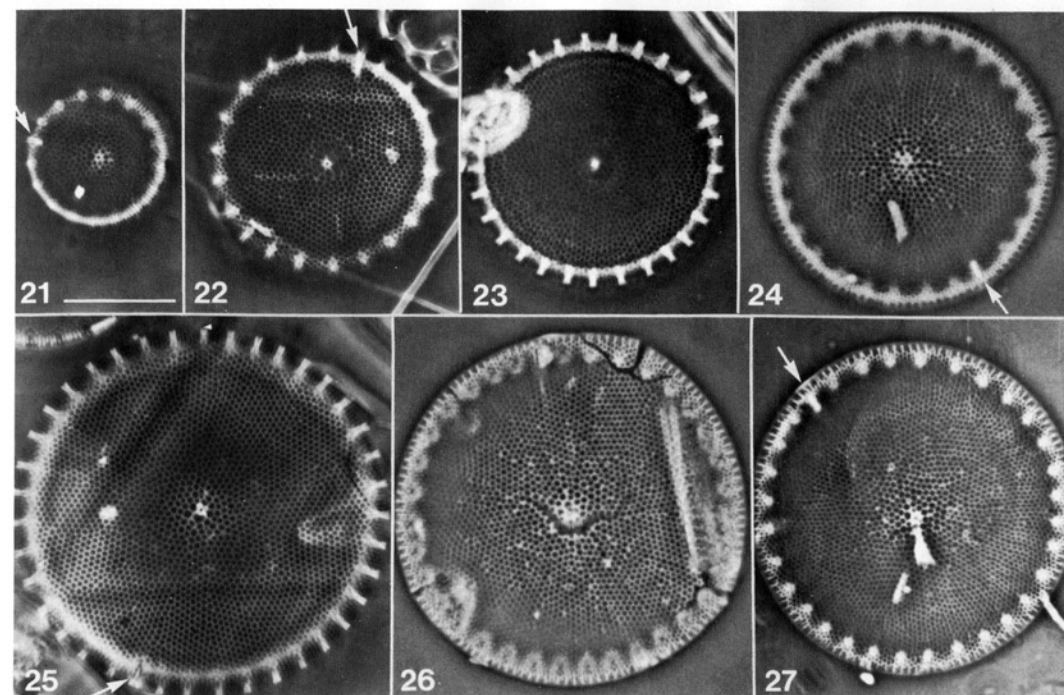
Figs. 17–20. *T. nordenskiöldii*, SEM, scale = 10 μm . Fig. 17. Single valve, external view, type material. Fig. 18. Semi-endogenous resting spore to the left, valve of vegetative valve to the right, Trondheimsfjord, Norway (photo B. R. Heimdal). Fig. 19. Single valve, internal view, Spitsbergen, 80° 18'N, 28° 30'E, 11 August 1973. Fig. 20. Single valve, external view, Iceland, 66° 38'N, 14° 24'W, 7 June 1972. Labiate process arrowed.

The external foramina varied in appearance from being widely open (Hasle 1972b, Fig. 43, Fryxell 1975, Pl. 5) to partly or almost closed (Figs. 17, 20, Fryxell 1975, Pl. 5). Resting spores and vegetative cells of *T. nordenskiöldii* can be distinguished only by denser cell content and more coarsely silicified valves with almost closed foramina (Heimdal 1974). Some of the valves pictured here could thus have been resting spore valves, although we have some evidence that valves of probable vegetative cells have smaller and larger foramina on the same specimen, particularly in the central area (Figs. 7, 10). A similar phenomenon was observed in a Recent *Actinocyclus* species (Hasle 1977) and in fossil material of representatives of several centric genera, among them also *Thalassiosira* (Mikkelsen 1977). The latter author described the

phenomenon as silica overgrowth occurring during storage of diatom material in natural sea water, and thus an artifact.

In the additional samples, diameters between about 10 to 50 μm were measured, and 15–18 areolae and about 3 marginal processes in 10 μm were seen.

Fryxell (1975) photographed whole frustules of *T. nordenskiöldii* in SEM and could thus give the first information on the morphology of the girdle of this species. The valvocopula is wide in perivalvar direction with pores in regular lines, and rimmed by an unperforated edge (Fryxell 1975, Pl. 5, c). The next band in abvalvar direction is an extremely narrow intercalary band with one row of pores (Hasle 1972b, Fig. 43; Fryxell 1975, Pl. 5, e). The bands in the middle of the cincture are unperforated,



Figs. 21–27. *T. aestivalis*, LM, single valves in Hyrax mounts, all the same magnification, scale = 10 μm . Figs. 21, 22, 25. Friday Harbor, 21 July 1930, holotype slide, IMBB No. 37. Figs. 23, 24, 26. Friday Harbor, 18 July 1930. Fig. 27. Unialgal culture, Vancouver area (isolator R. Waters). Labiate process arrowed.

being connecting bands. In this investigation, whole frustules have also been examined in SEM and furthermore in TEM after being prepared by a modified critical point drying method (Syvertsen in prep.). Our pictures (Figs. 15, 18) show the same features as just mentioned.

The girdle structure of *T. nordenskiöldii* is consistent with the one found for other *Thalassiosira* species (Fryxell 1975, von Stosch 1975, Hasle & Fryxell 1977, Syvertsen 1977).

Distribution

The records reported by Makarova (1977a) from the Aleutian Islands together with further personal records support the earlier classification of *T. nordenskiöldii* as a cold water species of the northern hemisphere (Hasle 1976b).

Thalassiosira aestivalis Gran – Figs. 2, 21–35, 38, 39

Gran & Angst 1931, p. 436, Fig. 10, Cupp 1943, p. 47, Fig. 9.

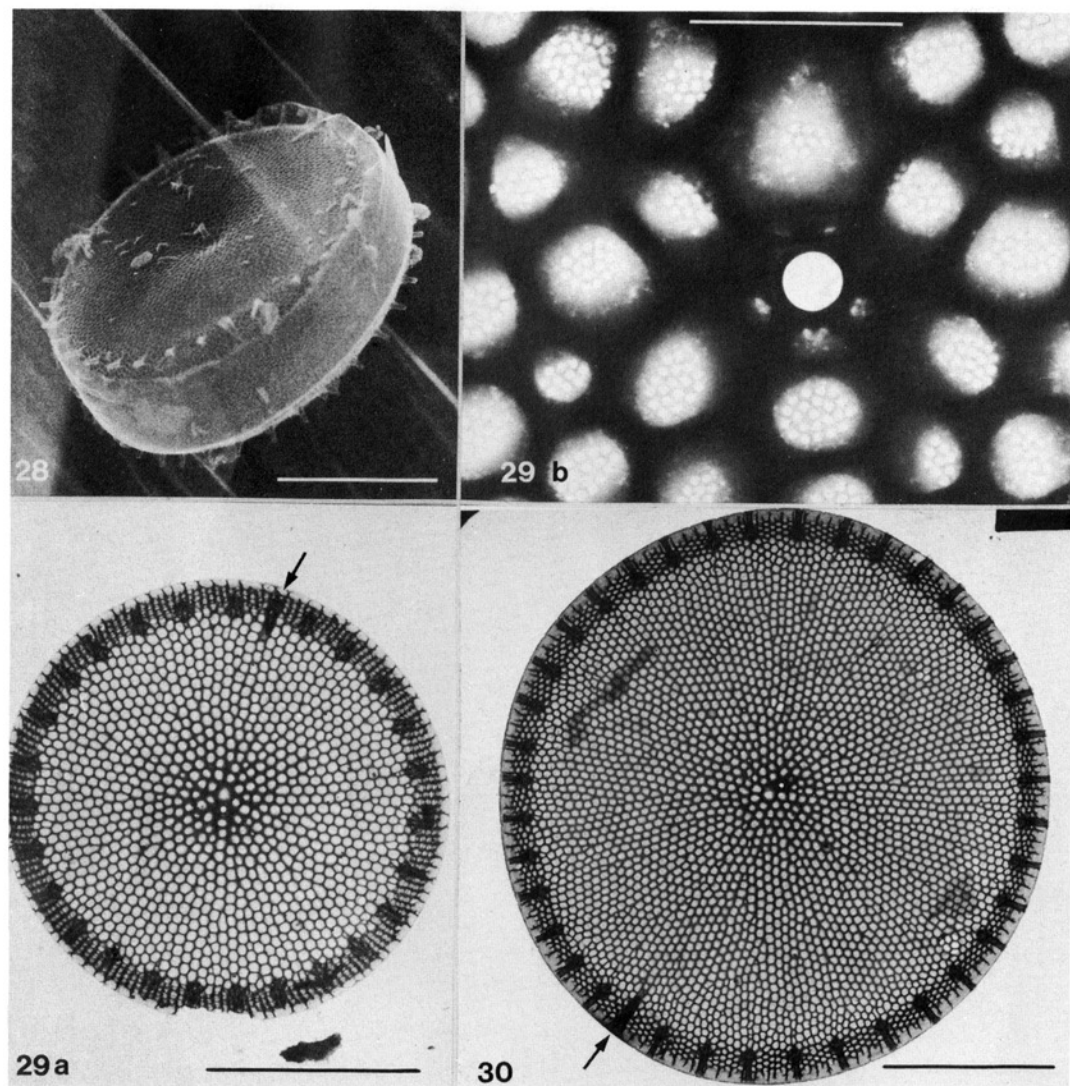
Type locality: Friday Harbor, Puget Sound, Washington, USA, July 1930.

Holotype: IMBB Univ. i Oslo slides Nos. 37 and 38 (Gran's slides labelled Friday Harbor, July 21, 1930, *Thalassiosira aestivalis*).

Thalassiosira aestivalis, in contrast to *T. nordenskiöldii*, seems to have been mentioned in the literature only occasionally, and its morphology, particularly the valve structure, is little known except for the diagnosis based on LM.

The present investigation is based on the holotype slides, the raw material used for preparation of these slides, a net haul collected in Friday Harbor July 18, 1930, a unialgal culture established in the vicinity of Vancouver, British Columbia, by R. Waters, and pump samples from *Thalassiosira* blooms during the CEPEX experiments in British Columbia (collector F. Whitney).

T. aestivalis has a slight conical depression in the valve centre (Figs. 22, 23, 38). The central strutted process is located slightly eccentrically adjacent to one or more larger areolae (Figs.

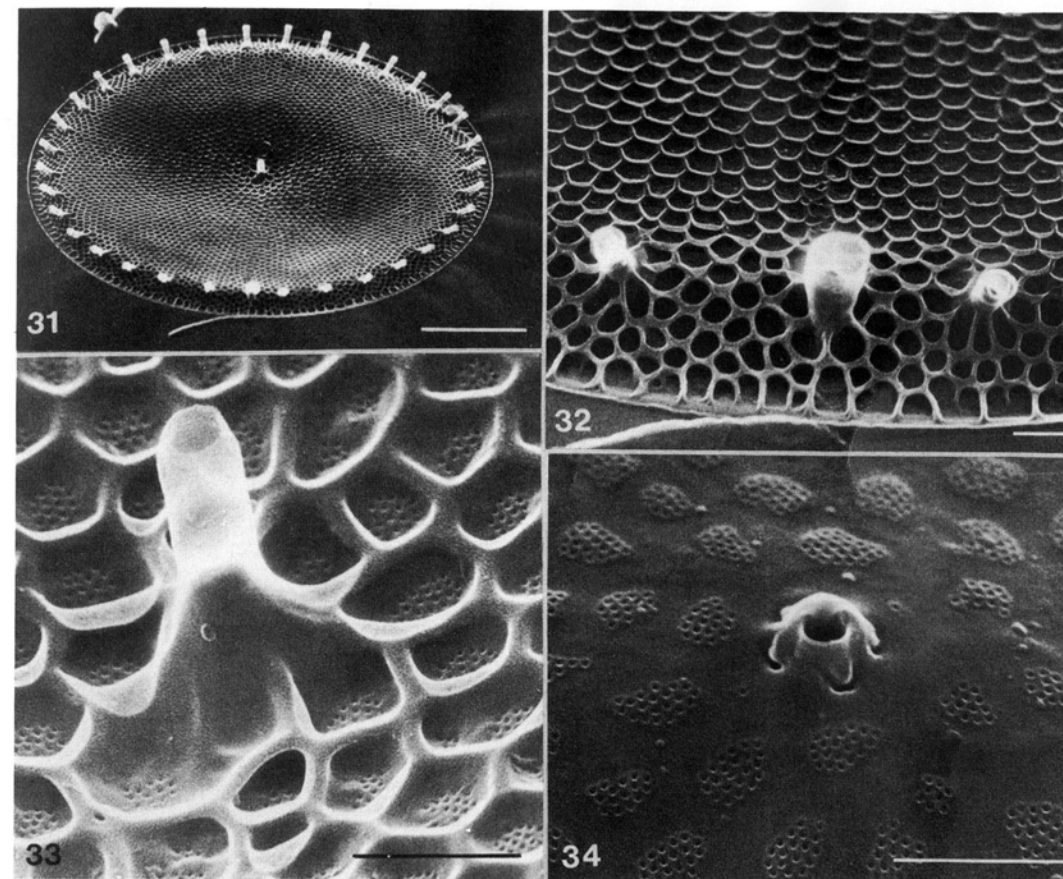


Figs. 28–30. *T. aestivalis*, TEM. Fig. 28. Whole cell, critical point dried, unialgal culture, Vancouver area. Fig. 29. Single valve, Vancouver Island (CEPEX), 10 May 1974. Fig. 30. Single valve, unialgal culture, Vancouver area. Scale for Fig. 29b = 1 μm , for the others = 10 μm . a, b, indicate same specimen photographed at different magnification. Labiate process arrowed.

25, 29, 33). The labiate process is positioned as for a strutted process (Figs. 21, 24, 30). The external part of the strutted processes has a flared skirt (Fig. 39), and while the internal part of the marginal strutted processes has four satellite pores, the central process may have more than four (Fig. 29b). The narrow valve mantle has slightly smaller areolae than those of the valve face (Figs. 26, 27, 30). The areolae are in radial rows in narrow, more or less

distinct sectors. The areolae rows are parallel to the median row of the sector, and there are two to three marginal processes per sector (Figs. 22, 25). The larger central areolae have an internal cribrum like other areolae (Figs. 29b, 33, 34). The vertical walls of the areolae are high, and the external foramina are wide (Fig. 33).

Diameters measured were 14–56 μm . There were about 18 areolae in 10 μm on valve face and slightly more than 20 in 10 μm on valve



Figs. 31–34. *T. aestivalis*, SEM, unialgal culture, Vancouver area. Fig. 31. Single valve. Fig. 32. Valve mantle, labiate process between two strutted processes. Fig. 33. Central process adjacent to irregular central areolae. Fig. 34. Central part of internal valve surface. Figs. 31–33. External valve surface. Scale for Fig. 31 = 10 μm , for the others = 1 μm .

mantle, and 3–5 (usually 4) marginal strutted processes in 10 μm . The mantle height was equivalent to 2–3 areolae. Although somewhat irregularly spaced, the usual number of marginal ribs was 14 in 10 μm .

Taxonomy

According to Gran & Angst (1931) *T. aestivalis* is distinguished from *T. nordenskiöldii* by smaller marginal processes, a narrower marginal zone (valve mantle), and a longer distance between cells in colonies. Length of connecting thread may vary considerably in *T. nordenskiöldii* colonies, although it is usually short compared with that of many other *Thalassiosira* species (e.g. Figs. 1–4). Size of marginal processes and height of valve mantle are good

distinctive characters, however (Figs. 11–16, 28–32, 35). The labiate process of *T. aestivalis* seems to have a more stable location than that of *T. nordenskiöldii*. Besides, it is also larger compared with the strutted processes, externally as well as internally (Figs. 36–39). The marginal ribs of *T. aestivalis* are continuations of the walls of almost every second mantle areola (Figs. 26, 30, 32), while in *T. nordenskiöldii* they are merely walls of the mantle areolae (Figs. 11–16). The almost closed foramina encountered in resting spores and possibly also in vegetative cells of *T. nordenskiöldii* were not seen in *T. aestivalis*, neither is resting spore formation observed in this species. But, as far as is known, the culture examined here was never exposed to conditions favouring resting spore formation in *T. nordenskiöldii*. The distinctive characters

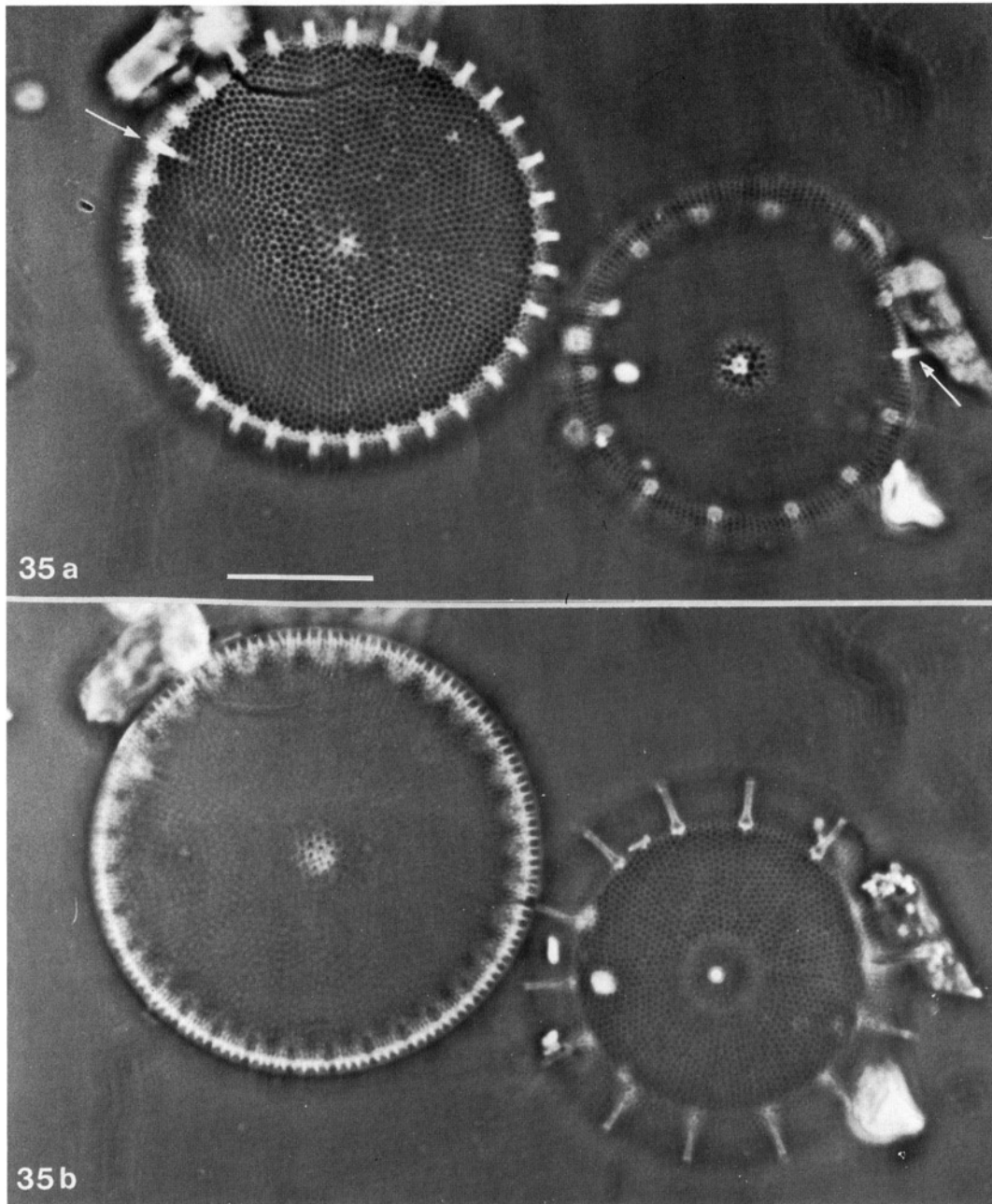
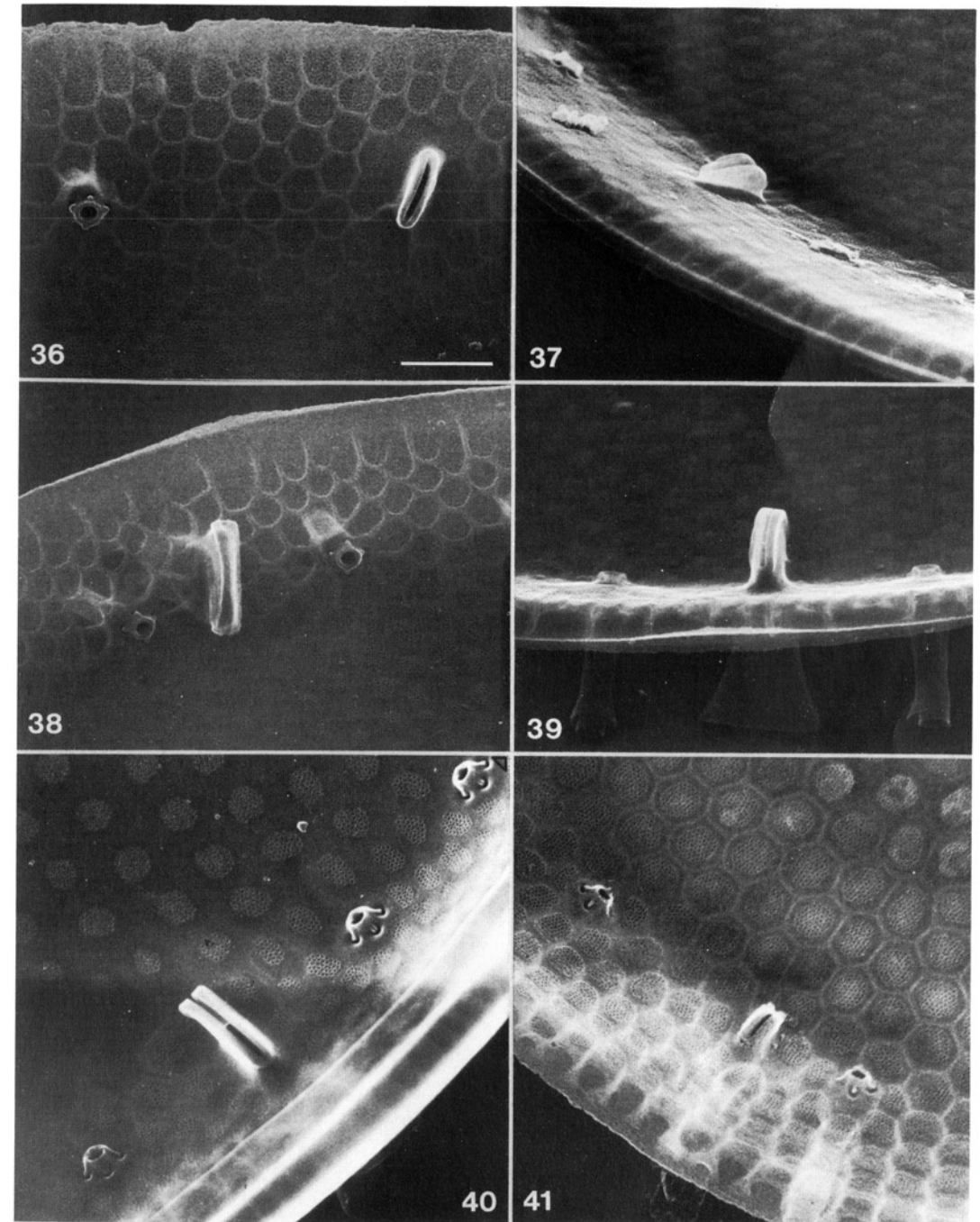


Fig. 35. *T. nordenskiöldii* (to the right) and *T. aestivalis* (to the left), Hyrax mount, LM, photographed at two different focuses. Notice difference in height of valve mantle and distance between marginal processes. Vancouver Island (CEPEX), 2 June 1975. Scale = 10 μm . Labiate process arrowed.



Figs. 36-41. Internal view of labiate and strutted processes, SEM, all the same magnification, scale = 1 μm . Figs. 36, 37. *T. nordenskiöldii*, clonal culture, Oslofjord. Figs. 38, 39. *T. aestivalis*, culture, Vancouver area. Fig. 40. *T. pacifica*, Friday Harbor, 21 March 1928, type material. Fig. 41. *T. angulata*, Botnfjord, Nordmøre, Norway, 22 March 1975.

indicate that *T. aestivalis* is a well defined species.

Distribution

In the present investigation the species was identified with certainty only from northwest American coastal waters (Puget Sd., Washington and Vancouver Is.).

Makarova (1971a) listed *T. aestivalis* from the northern Atlantic Ocean, the tropical Indian Ocean, and the northern, tropical and southern Pacific Ocean, probably mainly based on observations made by Russian scientists. Records from the Bay of Valparaiso and the Bay of Concepcion, Chile, by Avaria (1965) and Rivera (1968) were accompanied by illustrations of cells in colonies but with no information on valve structure. Records from the Gulf of Panama (Smayda 1966) and from Peruvian coastal waters (Strickland et al. 1969) included no illustrations.

It should be mentioned here that confusion with other species may easily take place if too much emphasis is laid on published drawings of colonies (Gran & Angst 1931, Cupp 1943). The threads extruded from the marginal processes so dramatically illustrated are not at all specific to *T. aestivalis*. In fact, they were most likely first shown for *T. gravida* Cleve (Mangin 1908), and they are probably more an indication of vigorous growth than a taxonomic criterion.

Diatoms similar to *T. aestivalis* from Chile, Cape Town, South Africa, Sylt, the North Sea (clonal culture established by G. Drebes) and the Oslofjord, Norway, were examined in this investigation. They had slightly smaller areolae than those of *T. aestivalis*; the marginal strutted processes were in some specimens further apart, and the labiate process was not positioned as for a marginal strutted process. Size of diameter and height of valve mantle were in accordance with *T. aestivalis*. These diatoms were also different from *T. nordenskiöldii*, although having about the same process pattern and areola size. More observations are evidently needed to decide whether diatoms from the southern hemisphere belong to a separate taxon or to *T. aestivalis*.

Thalassiosira pacifica Gran & Angst – Figs. 3, 40, 42–69

Gran & Angst 1931, p. 437, Fig. 12, Helmcke & Krieger 1954, Pl. 108 (as *T. nordenskiöldii*),

Makarova 1970, p. 17, 1976a, p. 608, Pls. 2, 3, 1977a, Pl. 2, Figs. 1–4, Schrader 1973, Pl. 14, Fig. 18 (perhaps also Figs. 19, 20), Hasle 1976b, Figs. 14–16, Kozlova & Strelnikova 1974, Pl. 1, Figs. 4, 5, non Jouse 1962, Fig. 63.3, non Schrader 1973, Pl. 14, Figs. 13, 14, Pl. 25, Figs. 18, 20, 21.

Synonym: *Thalassiosira pulchella* Takano 1963, p. 5, Fig. 1.

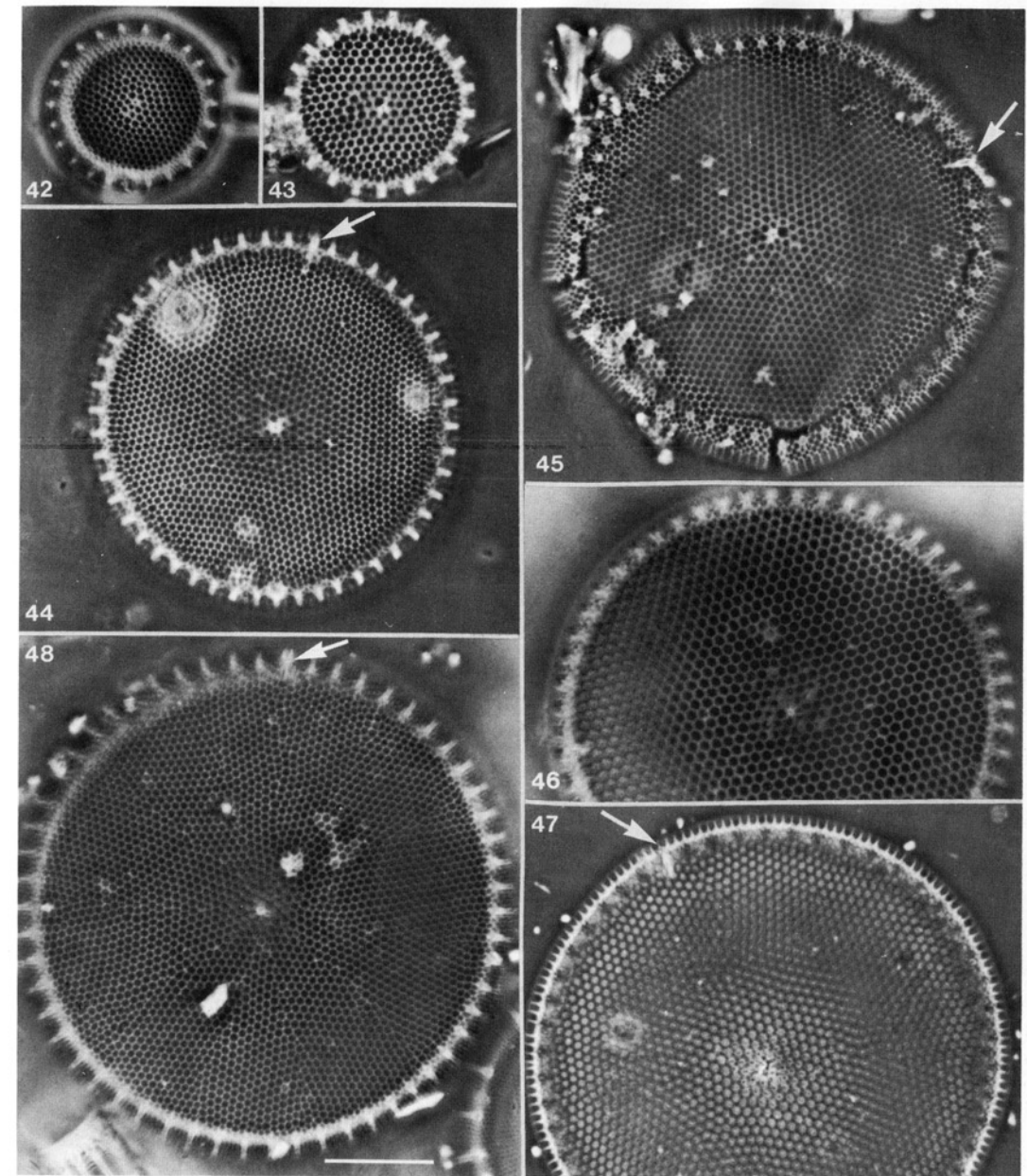
Type locality: Puget Sound, Washington, USA, March–April 1927, 1928.

Holotype: IMBB Univ. i Oslo slide No. 39 (Gran's slide labelled Fr. H. March 21. 1928, *Thalassiosira pacifica*, *Coscinodiscus angstii*, *excentricus*).

LM pictures of specimens on the holotype slide were published by Hasle (1976b). Makarova's (1976a, 1977a) TEM and SEM studies were based on material collected far north in the eastern and middle Pacific Ocean. According to Makarova (1970), records in some Russian publications were partly due to misidentification of *T. eccentrica* (Ehrenb.) Cleve. The diatoms pictured by Jouse (1962) and Schrader (1973) following Jouse's identification, are too coarse in structure to be *T. pacifica*.

The present investigation is based on the holotype slide, raw material of this slide, net hauls collected by or for Professor Gran in 1929 in the Puget Sound–Vancouver Island area, net hauls and pump samples (CEPEX) collected in the 1960–70s as well as a unialgal culture (isolator R. Waters) established from the same area, and net hauls from various other localities in the North Pacific and North Atlantic Oceans.

Valve face of *T. pacifica* is flattened or slightly concave in contrast to the pronounced concavity around valve centre of *T. nordenskiöldii* and *T. aestivalis* (Figs. 3, 49, 54). The slightly eccentrically located strutted process is adjacent to a larger areola with a wider foramen than elsewhere on the valve (Figs. 43, 45, 50, 52). The cribrum of the central areola is smaller than elsewhere on the valve (Figs. 52a, 56, 57). The labiate process is positioned as for a strutted process, although in some specimens the distance between the labiate and the next strutted process may be slightly smaller than between neighbour strutted processes in general (Figs. 40, 44, 45). It is easily discerned in LM (Fig. 47), being large compared with the strutted processes internally as well as externally (Figs. 51, 55). Moreover, while the marginal

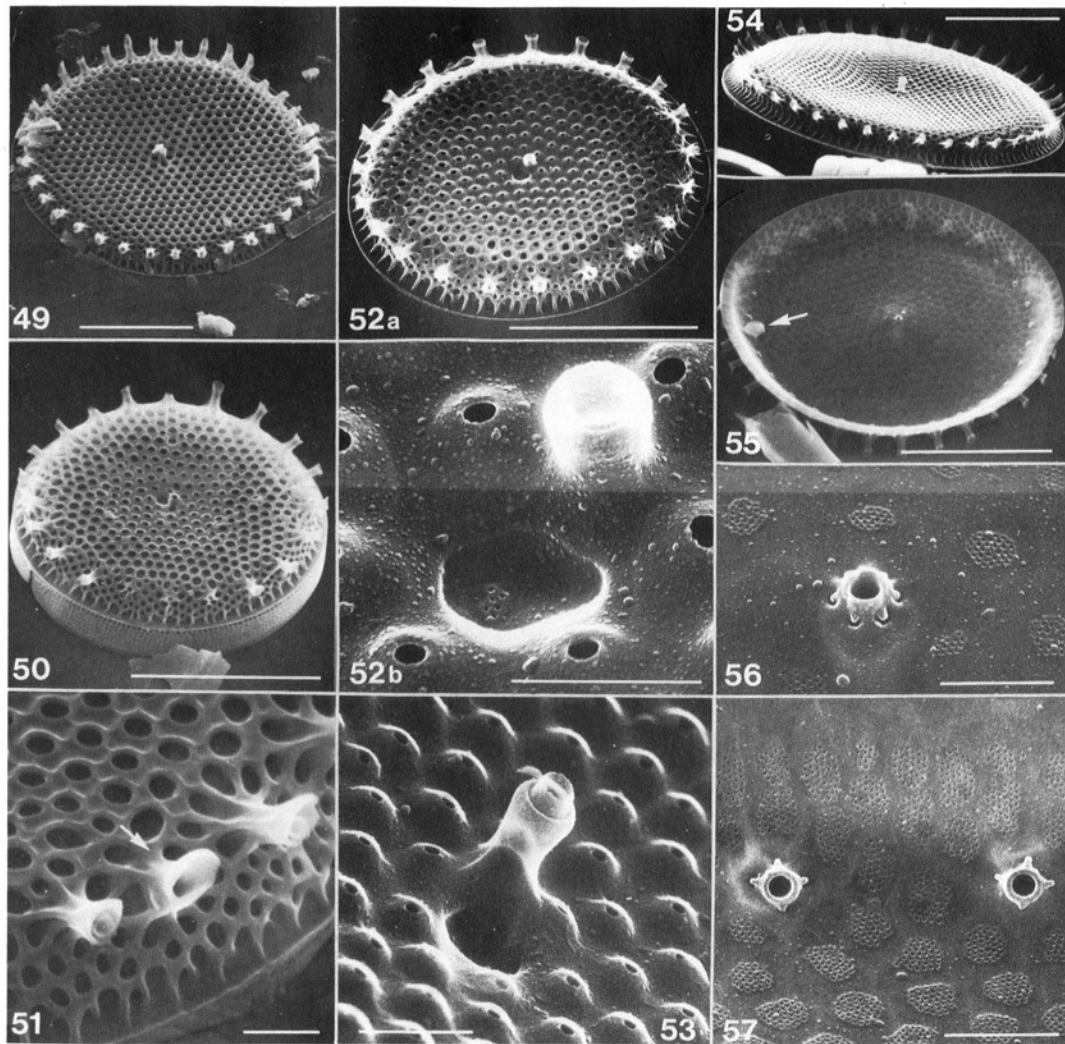


Figs. 42–48. *T. pacifica*, LM, single valves, all the same magnification, scale = 10 μm. Figs. 42–47. Friday Harbor, 21 March 1928, holotype slide IMBB No. 39. Fig. 48. Jericho, Vancouver, 5 May 1971. Labiate process arrowed.

strutted processes have an external flared skirt, the labiate process lacks it (Figs. 51, 60). The external part of the central process apparently also consists of two tubular layers. In contrast to the marginal processes the outer tube ends in a thickened or deflated rim (Fig. 53), fairly similar

to the central process of *T. hendeyi* (Hasle & Fryxell 1977). A similarly structured central process was occasionally seen in *T. nordenskiöldii*.

As in *T. aestivalis*, the central strutted process may have more satellite pores than the marginal

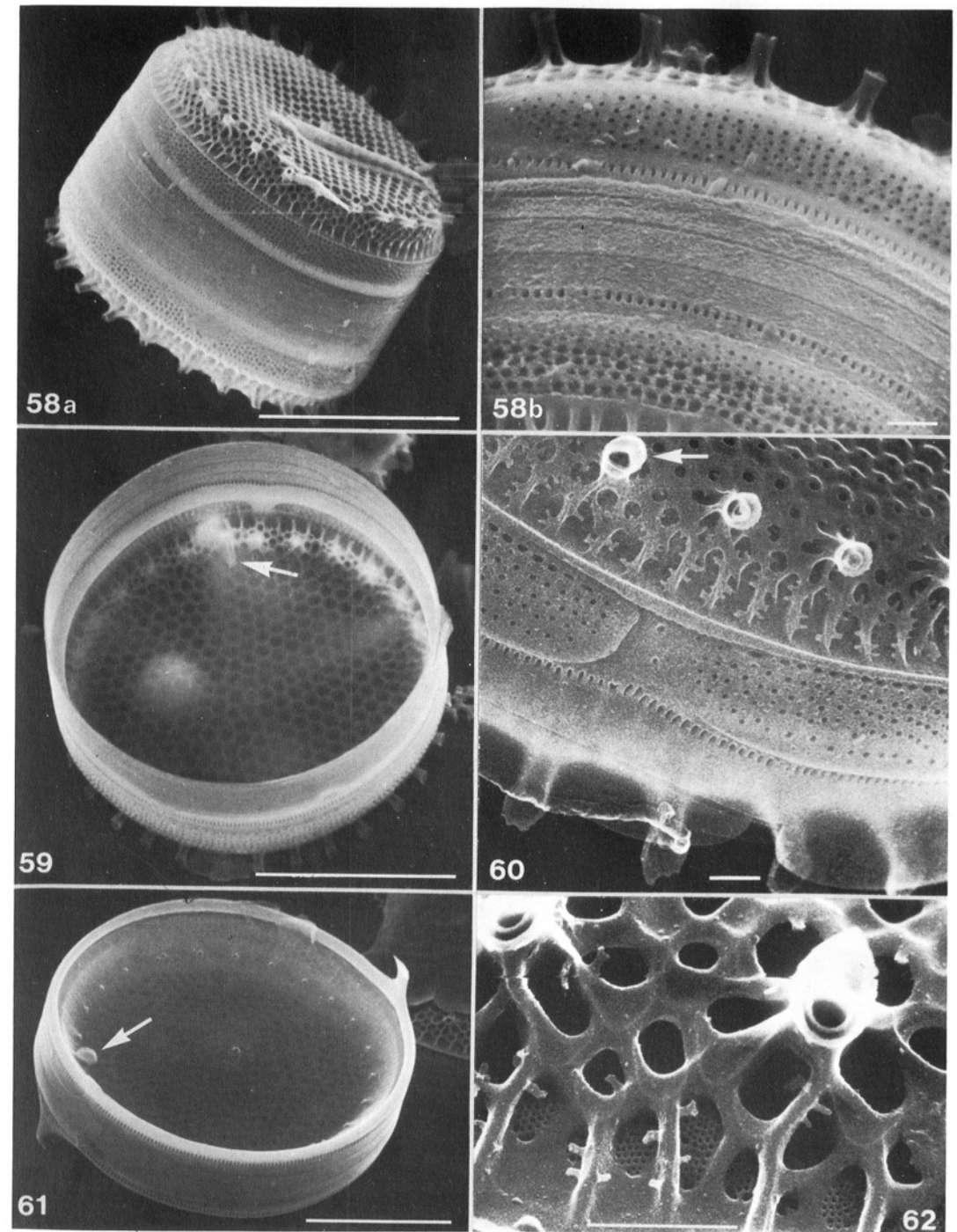


Figs. 49–57. *T. pacifica*, SEM, single valves. Figs. 49–54. External view. Figs. 55–57. Internal view. Fig. 50. Valvocopula attached to valve. Fig. 51. Labiate and two strutted processes. Figs. 52b, 53 and 56. Central process and central areolae. Fig. 57. Two marginal strutted processes. Fig. 49. Ucluelet, 2 February 1929. Figs. 50, 51, 55. Cape Beale, 25 April 1929, both localities Vancouver Island. The others, Friday Harbor, 21 March 1928, type material. Scale for Figs. 49, 50, 52a, 54, 55 = 10 μ m, for the others = 1 μ m. a, b indicate the same specimen photographed at different magnification.

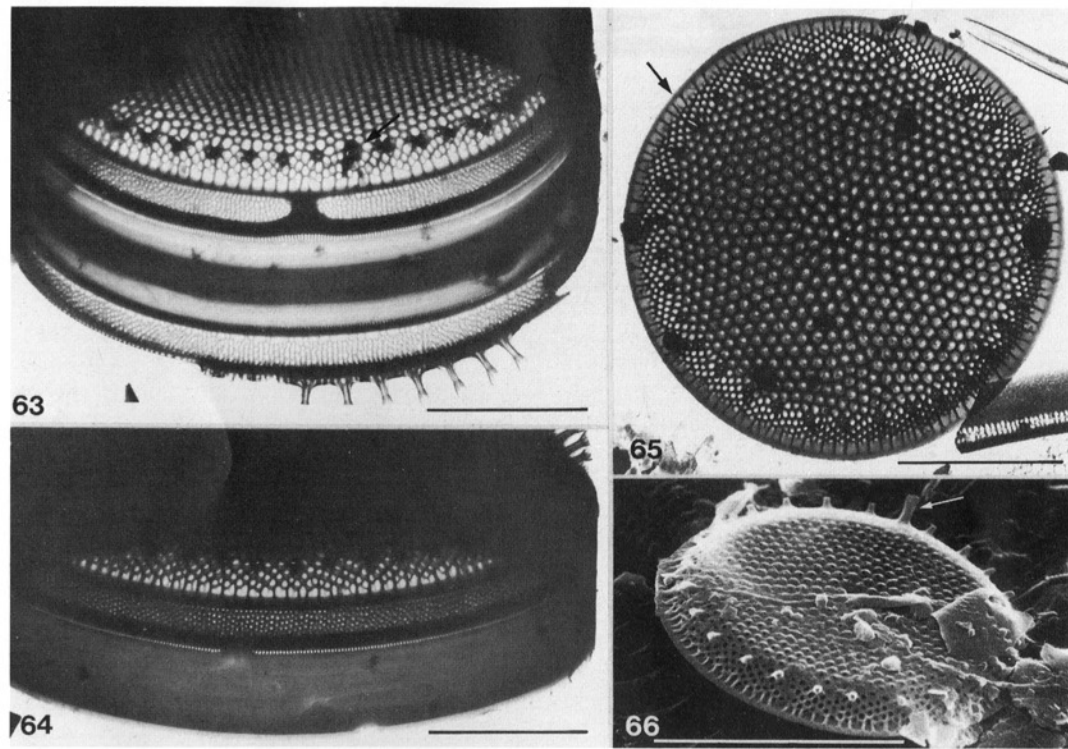
processes; all have outgrowth from the central tube into the pores (Figs. 56, 57).

As in *T. nordenskiöldii* the areolae might be almost closed externally. In the most extreme cases the external velum is highly vaulted and has a small circular opening, the only areola without a vaulted velum being the central one (Fig. 52). In less extreme cases the central part of valve face had this type of areolae (Fig. 50), while in other cases all areolae had a wide foramen (Fig. 49). This difference was best seen

in SEM but also visible in TEM (Figs. 63, 65, Makarova 1976a, Pl. 2, Figs. 5, 7, Makarova 1977a, Pl. 2, Fig. 1). The narrow valve mantle has smaller areolae than valve face (Figs. 50, 65). The cribra of the mantle areolae are more elongate in outline than those of valve face (Fig. 57). The mantle edge is distinctly ribbed (Figs. 45, 47, 49–52a, 65). The marginal ribs have some outgrowths and are raised above the regular areola walls (Figs. 60, 62). The uttermost edge of valve mantle is flattened (Fig. 54).



Figs. 58–62. *T. pacifica*, SEM. Fig. 58. Whole frustule. Fig. 59. One theca, valve and cingulum in internal view, notice intercalary band with septum. Fig. 60. Valve mantle with one labiate and two strutted processes and thickened rim, perforated valvocopula, intercalary band with ligula and one row of pores, and one connecting band. Fig. 61. Valve inside girdle of parent cell, notice intercalary bands with ligula. Fig. 62. Part of valve mantle, external view, two strutted processes, marginal ribs on top of areolae. Figs. 58, 59, 61. Cape Beale, 25 April 1929. Figs. 60, 62. Friday Harbor, 21 March 1928, type material. Scale for Figs. 58a, 59, 61 = 10 μ m, for the others = 1 μ m. a, b indicate the same specimen photographed at different magnification. Labiate process arrowed.



Figs. 63–66. *T. pacifica*. Figs. 63–65. TEM. Fig. 63. Whole frustule, notice intercalary band with ligula and septum. Fig. 64. Theca with five (?) connecting bands, two ligulae visible. Figs. 63, 64. Friday Harbor, 21 March 1928, type material. Fig. 65. Single valve, notice the smaller valve mantle areolae and the marginal ribs, Lopez Sound, Washington, 10 August 1965. Fig. 66. Single valve, external view, SEM, Saltfjord, Norway, ca. 67° 20'N, 5 April 1900. Scale = 10 μ m. Labiate process arrowed.

Although not exactly regular there seems to be one rib for every second mantle areola as in *T. aestivalis* (Figs. 50, 65, 66).

The areola array varies from linear to eccentric to fasciculated, independent of size of valve diameter (Figs. 42–50). When fasciculated, the sectors of *T. pacifica* are much wider than those of *T. nordenskiöldii* and *T. aestivalis*, usually including five to six marginal processes (Figs. 45, 48).

Diameters measured were 7–46 μ m. There are 10–18, (mostly 10–14) areolae in 10 μ m on valve face and more than 20 in 10 μ m on valve mantle, and 4–6 (mostly 5) marginal processes in 10 μ m. The mantle is 2–3 areolae high. There was a positive correlation between areola size and size of diameter, specimens larger than 25 μ m having 10–12 areolae in 10 μ m.

The girdle of *T. pacifica* is structured much the same as that of other *Thalassiosira* species investigated (e.g. Hasle & Fryxell 1977, Syvert-

sen 1977), although some variation within the genus is evident. The well perforated valvocopula is present also in *T. pacifica* (Figs. 58, 63). The single row of elongate pores belongs to the band next to valvocopula (Fig. 60). This band is thus an intercalary band, and it has a septum (Figs. 59, 61). In addition there are apparently 3–4 unperforated connecting bands per theca (Figs. 59, 64).

Taxonomy

According to Gran & Angst (1931, p. 436), *T. pacifica* is distinguished from *T. aestivalis* by three characters: (1) 'the rounded corners of the cells seen in girdle view', (2) 'the coarser structure of the valve', and (3) 'the equal thickening of all sutures in the girdle zone'. Illustrations presented here indicate that the angle between valve face and mantle of *T. pacifica* may be less sharp than in *T. aestivalis*

(Figs. 2, 3, 31, 50). Moreover, the marginal processes of *T. pacifica* seem to be located in the valve mantle while those of *T. aestivalis* are just between valve face and mantle (Figs. 32, 54). Valve areolae of *T. pacifica* are in general larger and valve wall more strongly silicified than in *T. aestivalis*, although some of the smaller *T. pacifica* specimens are thin-walled with smaller areolae. The 'four thickened sutures' of *T. pacifica* mentioned by Gran & Angst (1931, p. 438) most likely refer to the suture between valve mantle and valvocopula, and the narrow septum of the single intercalary band of each theca. Unfortunately this investigation includes no information on the structure of a possible intercalary band of *T. aestivalis* and on the possible presence of a thickened list attached to the valve mantle sometimes seen in *T. pacifica* (Figs. 60, 64).

The main distinction between *T. pacifica* and *T. aestivalis* is, however, more manifest in the areola array. The areolae of *T. aestivalis* are in straight radial rows (Figs. 21–27), mostly in a large number of fairly narrow sectors (as many as about half the number of marginal processes). In contrast, the areolae of *T. pacifica* are in straight or slightly curved tangential rows or in radial rows parallel to the median row of much wider sectors, occasionally with a mixture of curved, tangential rows and sectors (Figs. 42–47). The areola array of *T. aestivalis* is thus more similar to that of *T. nordenskiöldii* while *T. pacifica* in this respect is more similar to *T. angulata* to be discussed next.

Distribution

As indicated by Hasle (1976b), *T. pacifica* is most abundant along the coasts of the Pacific Ocean although it is also found in the open ocean and in the North Atlantic Ocean. The present investigation includes observations of *T. pacifica* as the predominant species in samples from the Vancouver Island area (CEPEX, May 1974). It was also present in samples collected in coastal waters of the Netherlands in April 1976 and along the Norwegian coast (Botnfjord, Møre, March 1975, Saltfjord, April 1900, Figs. 66, 69, Vestfjord, March 1900, Figs. 67, 69 and March 1968, Lofoten, March 1977, crude culture). The specimens from Norwegian coastal waters were fairly small and partly weakly silicified (Figs.

67–69) except those from the crude culture (Fig. 66). The southernmost records of *T. pacifica* are from about 35°N in the eastern Pacific Ocean and from about 39°N in the western Atlantic Ocean, and the northernmost records from about 50–55°N in the Pacific Ocean (the Aleutian Is., Makarova 1977a) and about 68°N in the eastern Atlantic Ocean (Vestfjord, Norway). Makarova (1971a) listed the species from the North Pacific Ocean only. The specimen photographed by Helmcke & Krieger (1954) was from Blankenberge, Belgium, and those photographed by Schrader (1973) were from the Northeast Pacific Ocean. According to present information, *T. pacifica* may therefore be classified as a cold to temperate water species restricted to the northern hemisphere.

Thalassiosira angulata (Greg.) Hasle
comb. nov. – Figs. 4, 41, 70–99

Basionym: *Orthosira angulata* Gregory 1857, p. 498, Pl. 10, Fig. 43.

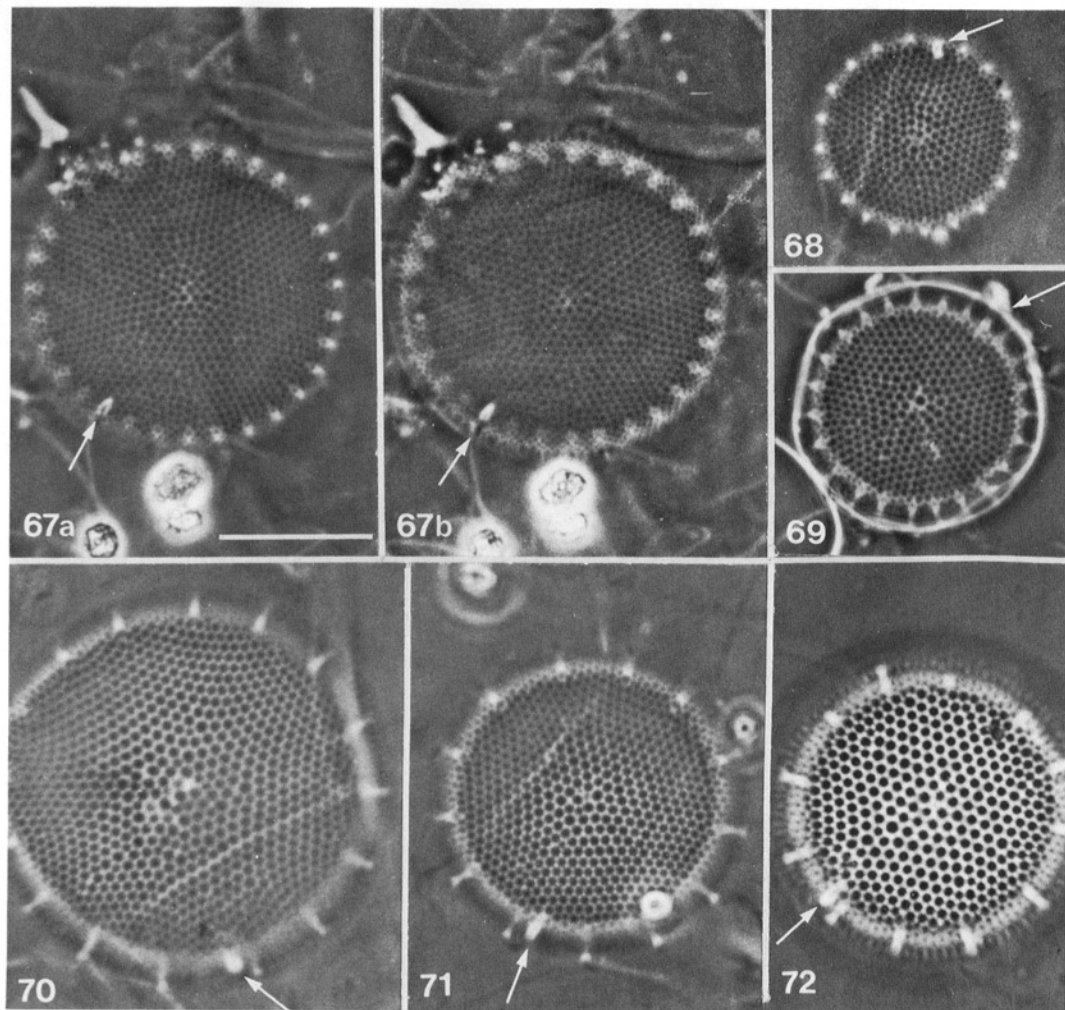
Synonyms: *Coscinodiscus decipiens* Grun. in Van Heurck 1882, Pl. 91, Fig. 10, non *Coscinodiscus eccentricus* var.? *decipiens* Grun. in Schneider 1878, p. 125, Pl. 4, Fig. 18, *Thalassiosira decipiens* Grun. in Jørgensen 1905, p. 96 pro parte, Pl. 5, Fig. 3a–e, *Thalassiosira decipiens* (Grun.) Jørg. in Hustedt 1928, p. 322, Fig. 158, Cupp 1943, p. 48, Fig. 10, Hasle et al. 1971, Figs. 44, 45, non *Thalassiosira decipiens* (Grun.) Jørg. in Hasle (1978a).

Type locality: Lamlash, Arran, Scotland.

Holotype: BM slide No. 1213 – 'Lamlash, Arran, Gregory 57 – Type of *Orthosira angulata*, S.V.'

The present investigation is based on the holotype slide and another slide, BM No. 1195 labelled 'F.V.' (=face view), prepared from the same material. Slides prepared of Jørgensen's material published in 1905 were also examined. 21 specimens on the Gregory slides were photographed and measured; a few of them were seen in girdle view and most of them in valve view. Two of Jørgensen's samples were available as unprepared material and have been used here together with material from various localities along the Norwegian coast as well as from further south in the North Atlantic Ocean for LM and EM examination.

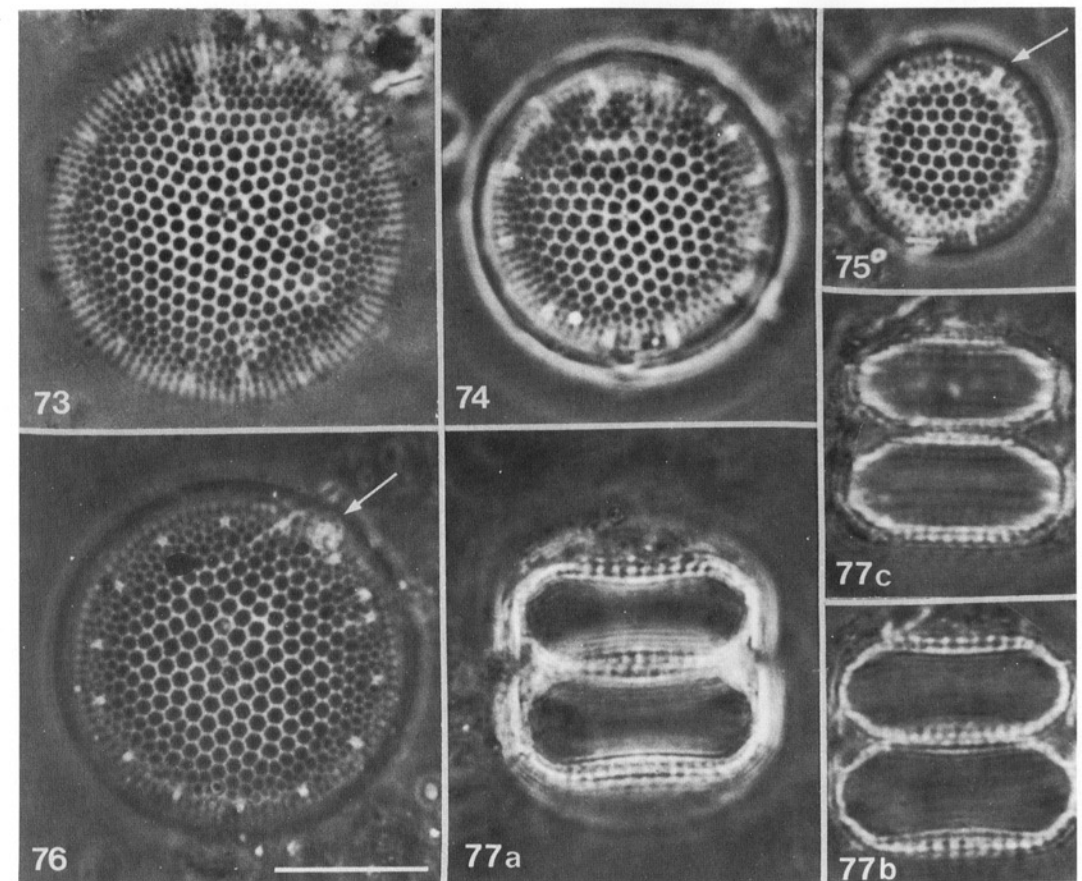
Length of perivalvar axis varied from about



Figs. 67-72. Specimens from E. Jørgensen's material, BG (= Bergen, Norway), single valves, LM, all the same magnification, scale = 10 μm . Figs. 67-69. *T. pacifica*. Figs. 70-72. *T. angulata*. Figs. 67, 68, 70, 71. BG slide labelled '30/3 1900 Vestfjord 0-25 m. Oxyd. glødet'. Figs. 69, 72. Saltfjord, 5 April 1900. a, b indicate same specimen photographed at different focuses. Labiate process arrowed.

one third to almost the whole length of the cell diameter (Figs. 4, 77-79). Although colony formation by means of a central connecting thread was the only one observed in the present marine plankton samples as well as in cultures grown in sea water media, cells connected by their valve face were present on the type slides (Fig. 77) such as depicted by Gregory (1857). However, the Gregory slides as made from cleaned material are not conclusive on this point; colony formation by a central thread might well have occurred in the original

collection but have been destroyed during the cleaning procedure. Moreover, the sharp distinction between valve and girdle is characteristic for specimens in ordinary *Thalassiosira* colonies (Figs. 4, 78, 79) as well as in the colonies on the type slides (Fig. 77), and is due to the broad flattened brim of the valve mantle to which the valvocopula is attached (Figs. 83-86). As in other *Thalassiosira* species examined, the valvocopula is well perforated while the only other perforation of the bands resolved here is between the valvocopula and the band next to it



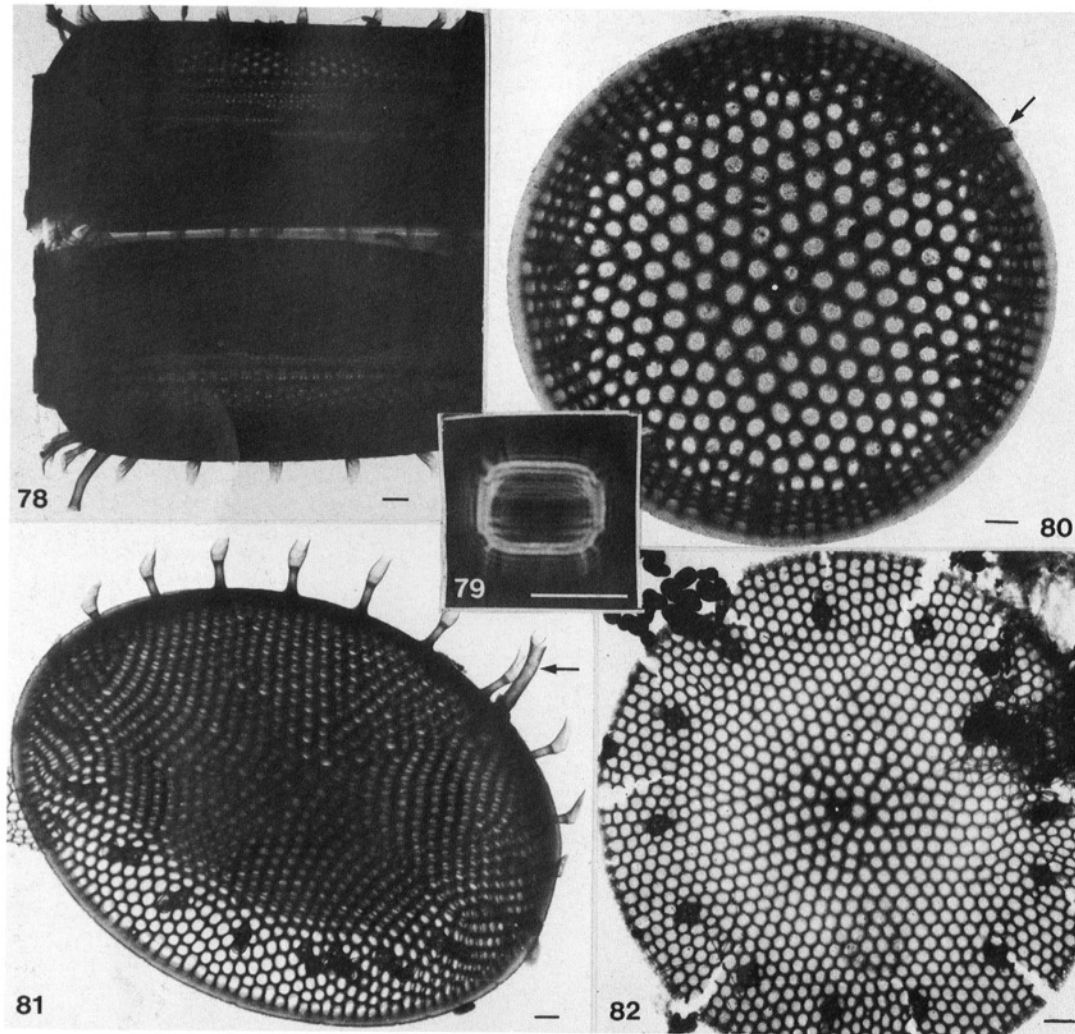
Figs. 73-77. *T. angulata*, LM, all the same magnification, scale = 10 μm . Figs. 73-76. Single valves. Fig. 77. Part of colony in girdle view. Figs. 73, 74. Lamlash, Arran, Gregory 57, Type. B.M. (= British Museum) 1213. Figs. 75-77. Arran, Gregory 57, B.M. 1195. a, b, c indicate same specimen photographed at different focuses. Labiate process arrowed.

(Figs. 78, 88). Each theca has apparently several bands.

Valve face is flattened with no pronounced concavity in the centre, and valve mantle is smoothly curved (Figs. 4, 78, 79, 83-86). Cell diameter measured was 12-39 μm , and length of pervalar axis ca. 10-15 μm .

Areolae on valve face as well as on valve mantle have a regularly hexagonal outline when observed in LM and TEM (Figs. 73-76, 80-82, 89-95). The external foramina are fairly wide, and the curved external velum with a small central opening, occasionally seen in other species discussed here, is hardly present in *T. angulata* (Figs. 96-98). The internal cribra are fairly irregular in outline. The areolation is typically eccentric, i.e. the areolae are arranged

in curved rows (Figs. 73, 80, 85) although almost straight rows (Figs. 74-76, 91) and areola rows arranged in sectors parallel to the middle row or a mixture of two types of areolation were also seen (Figs. 70-72, 87, 94, 95). Size of areola varied considerably, 8-18 in 10 μm on valve face and 14-24 in 10 μm on valve mantle. Figs. 73-76 show specimens from the type material with about 9 areolae in 10 μm on valve face while 8, 10, and 12 areolae in 10 μm were also measured on the type slide. Thick-walled specimens with 8-10 areolae in 10 μm were otherwise observed in field samples collected off North Cape, North Norway, in May 1962, in the Oslofjord in January 1961 and February 1962, in Kiel Bay in April 1970 and November 1969, and off the coast of the Netherlands in April 1976

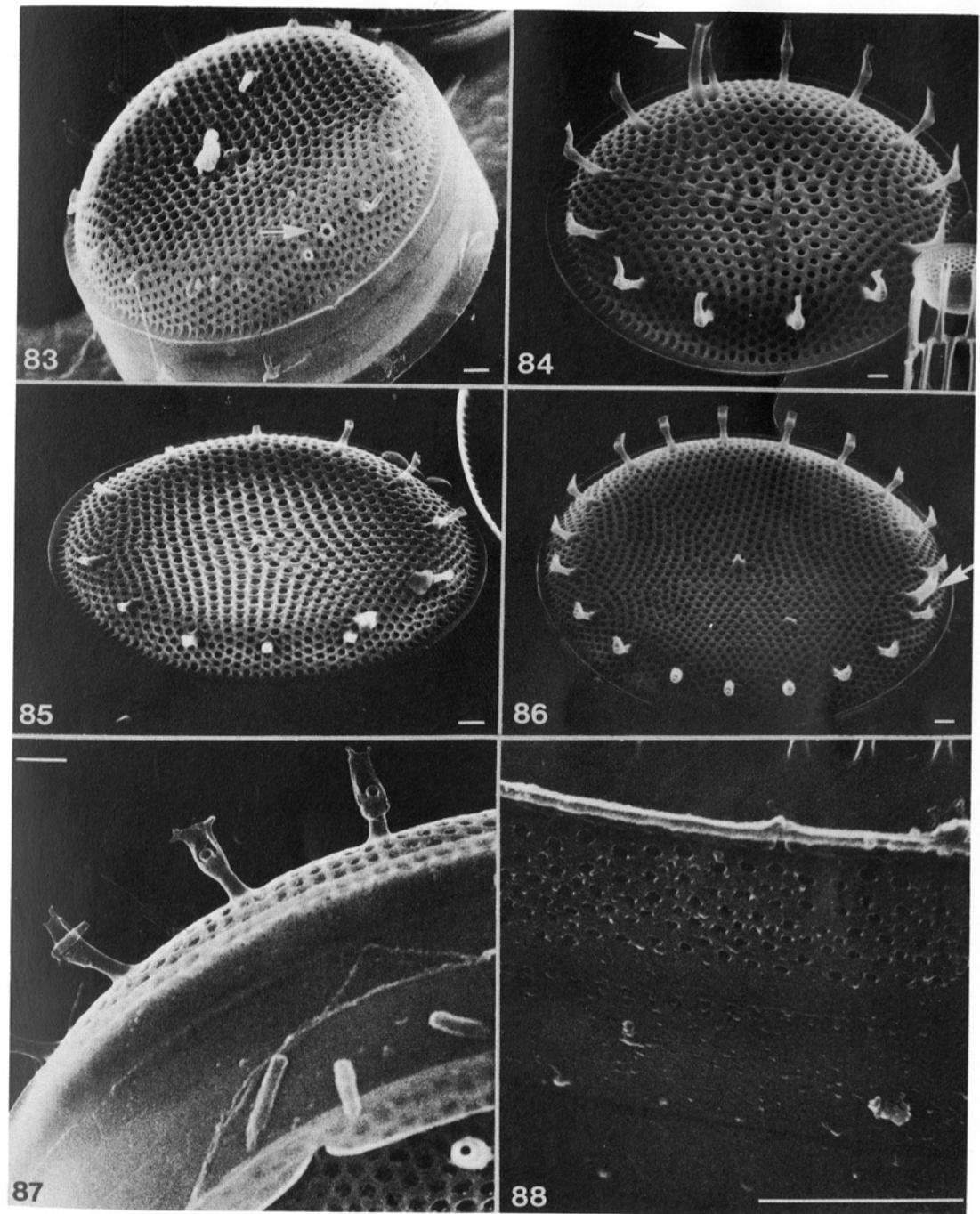


Figs. 78–82. *T. angulata*. Fig. 79. Cell in girdle view, Drøbak, 23 February 1962, LM, scale = 10 μm . Fig. 78. Two newly divided cells in girdle view, clonal culture, Oslofjord, critical point dried. Figs. 80–82. Single valves. Fig. 80. Drøbak, 23 February 1962. Fig. 81. Somers' culture SD 820, clone 11, Belgium. Fig. 82. Inner Oslofjord, 14 August 1960, crude culture. Figs. 78, 80–82. TEM, scale = 1 μm .

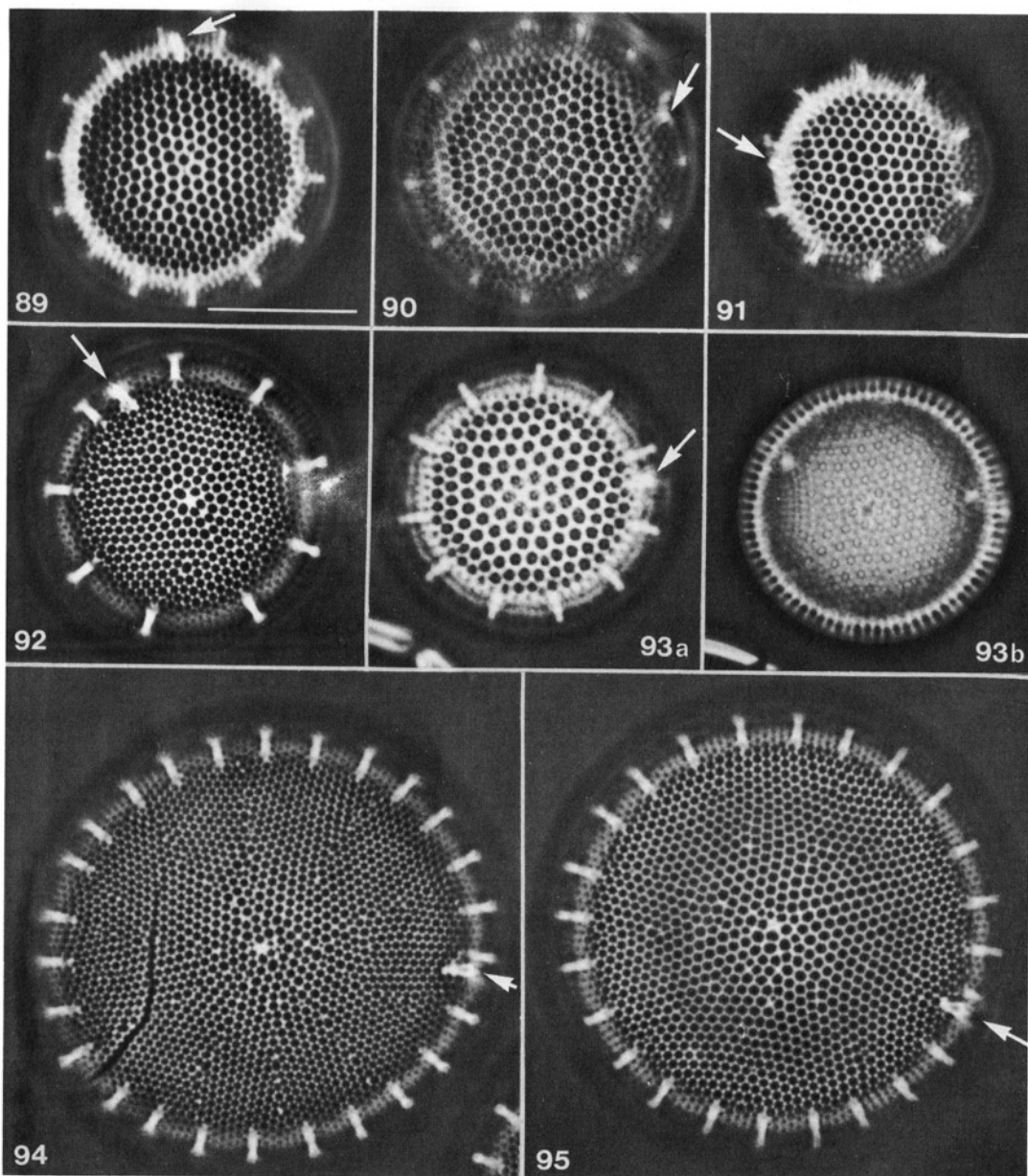
(Figs. 80, 89–91, 93). Smaller areolae, 12–16 in 10 μm , were present in specimens collected in the Botnfjord in March 1975, Saltfjord in April 1900 and Vestfjord, Norway, in March 1900 and 1968, and in the inner Oslofjord and Skagerrak in November 1976 (Figs. 70–72, 92), while the smallest areolae 14–18 in 10 μm were seen in specimens grown in cultures established from the inner Oslofjord (crude culture, August 1960, Fig. 82, Throdsen dilution culture, October 1971, Paasche's clone, Figs. 94, 95), off Heligoland (Drebes' clone), and from Belgian coastal

water (Somers SD 820, Fig. 81, SD 815). Although there is a certain trend in the Oslofjord observations for more lightly silicified specimens with smaller areolae present in summer and autumn, the present material is insufficient to give conclusive results.

There is one stout, slightly curved labiate process located close to a marginal strutted process. When not partly eroded as in the type material, it is visible on all valves photographed here in LM as well as EM. The external tube of the labiate process is easily distinguished from



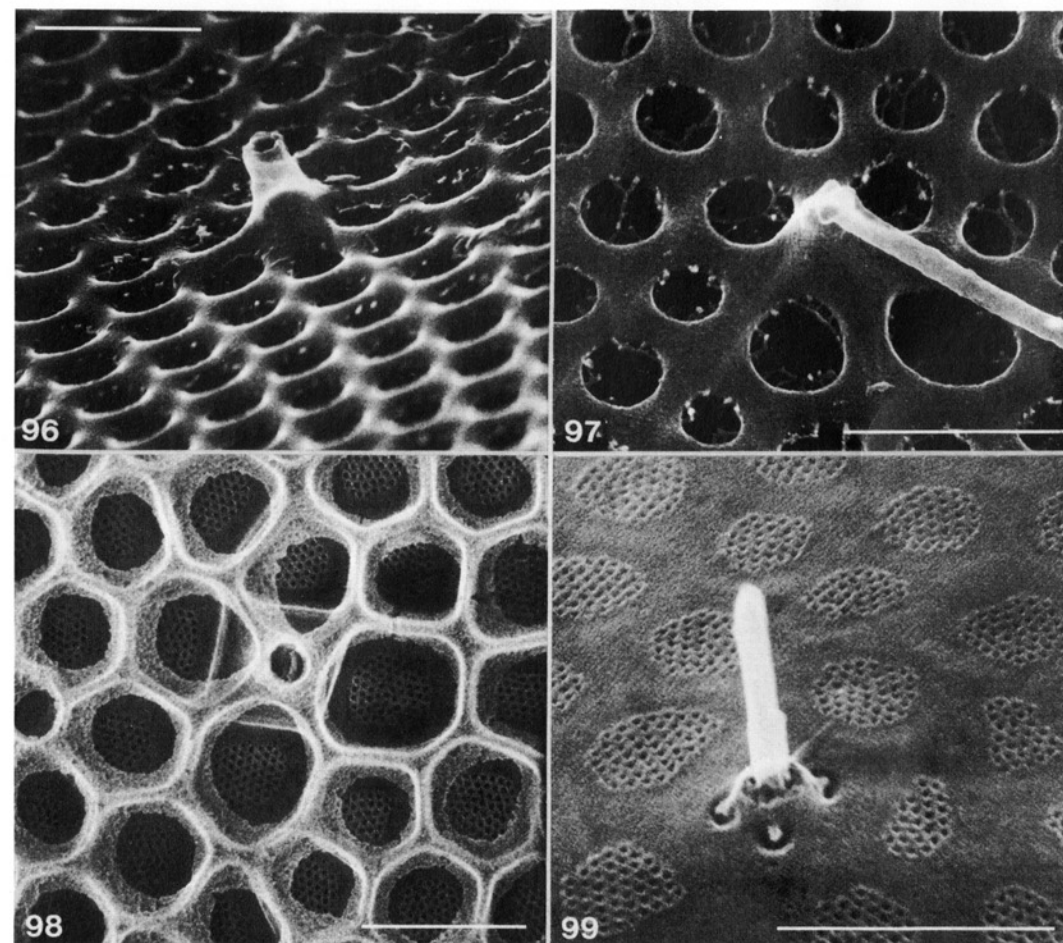
Figs. 83–88. *T. angulata*, SEM, scale = 1 μm . Fig. 83. Valve and girdle. Figs. 84–86. Single valves, external view. Fig. 87. Marginal strutted processes and epicingulum. Fig. 88. Thickened rim of valve mantle, perforated valvocopula. Figs. 83, 86–88. Clonal culture, Oslofjord. Fig. 84. Beian, Trondheimsfjord, Norway. Fig. 85. Saltfjord, 5 April 1900, E. Jørgensen's sample. Labiate process arrowed.



Figs. 89–95. *T. angulata*, single valves, Hyrax mounts, LM, all the same magnification, scale = 10 μm . Fig. 89. North of North Cape, Norway, ca. 71°N, 1 May 1962. Fig. 90. Kiel Bay, Germany, 6 April 1970. Fig. 91. Drøbak, 23 February 1962. Fig. 92. Skagerrak, 9 November 1976. Fig. 93. Off the coast of the Netherlands, 8 April 1976. Figs. 94, 95. Clonal culture, Oslofjord, grown at 18 C and 35‰. a, b indicate the same specimen photographed at different focuses. Labiate process arrowed.

those of the strutted processes by length and shape (Figs. 78, 81, 84). The internal labiate-shaped part is small compared with that of the species discussed above and with the internal part of the strutted processes (Fig. 41).

The marginal strutted processes have a very characteristic shape consisting, at least for some length, of a double tube obliquely cut distally and with the half-cylinder bent vertically (Figs. 81, 84, 87, 92). The single ring of marginal



Figs. 96–99. *T. angulata*, valve centre with strutted process, SEM, scale = 1 μm . Figs. 96–98. External view. Fig. 99. Internal view. Figs. 97, 99. Connecting thread from central tube of strutted process. Figs. 96, 97. Clonal culture, Oslofjord, grown at 15 C and 18‰, critical point dried. Figs. 98, 99. Botnfjord, Norway, 22 March 1975.

strutted processes is located at a short distance from the border between valve face and mantle (Figs. 78, 84). There are usually 3 marginal processes in 10 μm , occasionally 2 or 4 in 10 μm .

The single central strutted process is located in the geometrical centre of the valve, sometimes adjacent to a larger areola (Figs. 82, 83), while in most cases no such areola could be distinguished (e.g. Fig. 80). When present, the central areola was apparently not deeply immersed as in the species discussed above. The central process is raised on the top of crossing walls of the areolae in valve centre (Figs. 96–98) in such a way that the areolation pattern is not

disturbed (Fig. 80), and is therefore less conspicuous in LM than in the species discussed above. It has a short internal tube surrounded by four satellite pores with club-shaped outgrowths (Fig. 99). The peculiar angular structure surrounding the central process at a level below the external surface seen on Fig. 98 indicates a particular type of wall around the process in the intermediate layer. It is also noteworthy that the part of the connecting thread not dissolved during the preparation process is present not only outside the valve (Fig. 97) but also on the inside (Fig. 99).

Taxonomy

Jørgensen (1905) admitted that he had never seen the first illustration and description published of *Coscinodiscus decipiens* Grun. (Grunow in Schneider 1878). The combination *Thalassiosira decipiens* (Grun.) Jørg. was based on the illustration Grunow published in Van Heurck (1882). This depicted a diatom from Lamlash Bay which is the type locality of *Orthosira angulata* Gregory (1857), while the type locality of *C. decipiens* is the Caspian Sea. Investigations by Hasle (1978a and the present one) demonstrate that Jørgensen was right in regarding the diatom from northern Norwegian fjords as being conspecific with the one from Lamlash Bay. He gave no reason why he used the more recent specific epithet *decipiens* except that he might have followed Van Heurck (1882). Since the specific epithet *decipiens* was first used for the diatom from the Caspian Sea, which is also a *Thalassiosira* species, the combination *T. decipiens* (Grun.) Jørg. is valid for this diatom.

T. angulata may be more closely related morphologically to *T. decipiens* than to any other species, however. After having compared the holotypes Hasle (1978a) concluded that shape, length, and direction of external tubes as well as distance between adjacent marginal strutted processes formed the major distinction between the two species. Compared with *T. angulata*, *T. decipiens* has generally larger areolae, greater size difference between valve face and mantle areolae, no fasciculation as areolation pattern even in the larger valves, the labiate process usually midway between two strutted processes, and an internal larger labiate process compared with the strutted ones.

As shown here Jørgensen's samples from the northern Norwegian fjords contained *T. pacifica* as well as *T. angulata* (Figs. 67–72). In fact, he mentions himself that the species he calls *T. decipiens* (Grun.) is very variable in structure, and that 'two principal series of forms occur, the one with numerous marginal spines and a not very plain excentric structure, but plain fasciculi; the other with fewer marginal spines and plainer excentric secondary curves' (Jørgensen 1905, p. 96). The distinction between the two forms corresponds exactly to that between *T. pacifica* and *T. angulata*. Location of labiate process and structure of valve mantle are other distinct morphologic criteria (Figs. 67b, 72).

Jørgensen (1905) also lists *Thalassiosira*

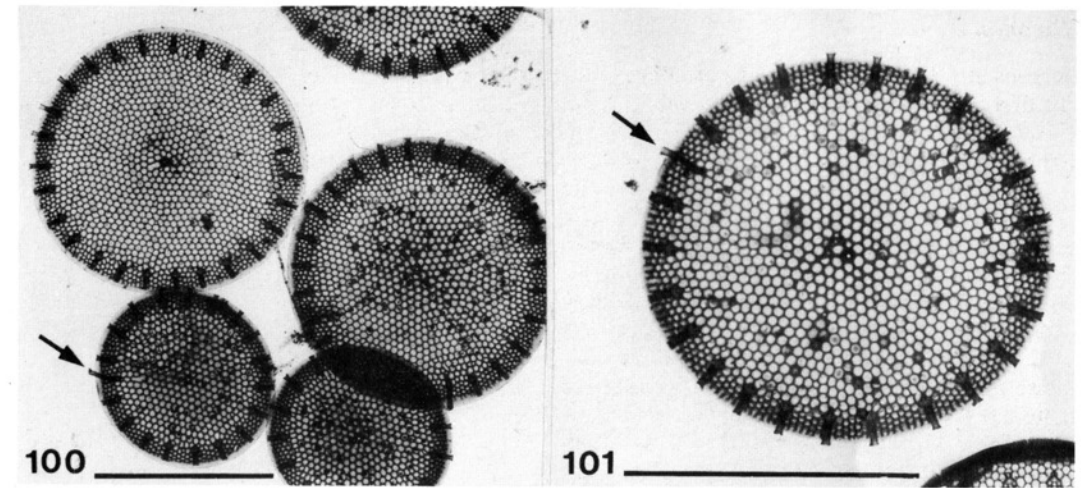
gelatinosa Hensen (1887, p. 87). This diatom was never validly published, only mentioned in this way: 'in Schleim eingebettet zu Haufen beisammen lag und in der Zahl von 2 Millionen im Ocean vorkam. Ich will dieselbe als *Thalassiosira gelatinosa* [sic!] vorläufig bezeichnen'. Lemmermann (1899, p. 377) recorded a diatom as *Coscinodiscus gelatinosus* with *T. gelatinosa* Hensen and *Coscinodiscus excentricus* var. *gelatinosa* Hensen (Cleve 1897, p. 23) as synonyms. Gran (1897, p. 30) introduced the name *Coscinodiscus excentricus* Ehrenb. var. *catenata* Gran for a diatom from the coasts of Norway. The description of this diatom indicates that Gran was dealing with *T. angulata*. Gran suggested that it should be referred to *Thalassiosira* and be separated from 'excentricus', and moreover that a diatom from the North Sea figured by Schmidt (1875, Pl. 3, Figs. 36–38) and referred to *C. excentricus* with the suggestion that it might be a *Thalassiosira* species, belonged to the variety he introduced. Since none of these collections have been examined here, these names have not been listed as synonyms of *T. angulata*, although examination of material from more or less the same localities showed that *T. angulata* is present in Kiel Bay, the North Sea, and Norwegian coastal waters.

The typical eccentrically areolated *T. angulata* may easily be confused with thick-walled specimens of *T. eccentrica* (Ehrenb.) Cleve, although the latter has marginal spines, two marginal rings, and strutted processes scattered on the valve face (Fryxell & Hasle 1972).

The similarity between *T. angulata* and the diatoms photographed from the Black Sea and identified as *T. coronifera* Proshkina-Lavrenko (syn. *T. coronata* Proshkina-Lavrenko) by Proshkina-Lavrenko (1955a, Pl. 1, Figs. 6, 7) and Proshkina-Lavrenko (1955b, Pl. 2, Figs. 1, 2) should also be mentioned.

Distribution

The present investigation includes records of *T. angulata* from 71°N, north of North Cape, Norway, to 41°N, off the Portuguese coast, in the eastern part of the North Atlantic Ocean. It was present in net hauls collected in Loch Etive and Loch Eive in May 1975 and July 1972 (somewhat further north along the Scottish coast than the type locality Lamlash Bay), in collections from the Grand Banks, Newfoundland, Gulf of Maine, Narragansett Bay and Ches-



Figs. 100, 101. *T. allenii*, see Takano 1965, Plate 1, Figs. 9, 10, TEM, scale = 10 μ m. Labiate process arrowed.

apeake Bay along the North American east coast, and it was sparse in collections from Saronikos Gulf, Greece, 21 January 1975. Gran & Angst (1931, p. 436) recorded *T. angulata* (as *T. decipiens*) as 'Common, but never abundant' from Puget Sound, Washington. In spite of a fairly large collection available for this investigation from Washington and British Columbia from the 1920–1930s as well as 1960–70s no records have been made of *T. angulata*. No personal records of this species from other localities in the Pacific Ocean have been made either. This may indicate that *T. angulata* has its main distribution area in the North Atlantic region.

Thalassiosira allenii Takano – Figs. 100–128

Takano 1965, p. 4, Fig. 2, Pl. 1, Figs. 9–11, Makarova 1977a, p. 31, Pls. 3, 4.

Type locality: Manozuru, Kanagawa Prefecture, Japan.

The description of *T. allenii* was based on TEM observations of cultures grown in synthetic media. The species was examined in field samples from the Adriatic Sea in TEM and SEM by Makarova (1977a).

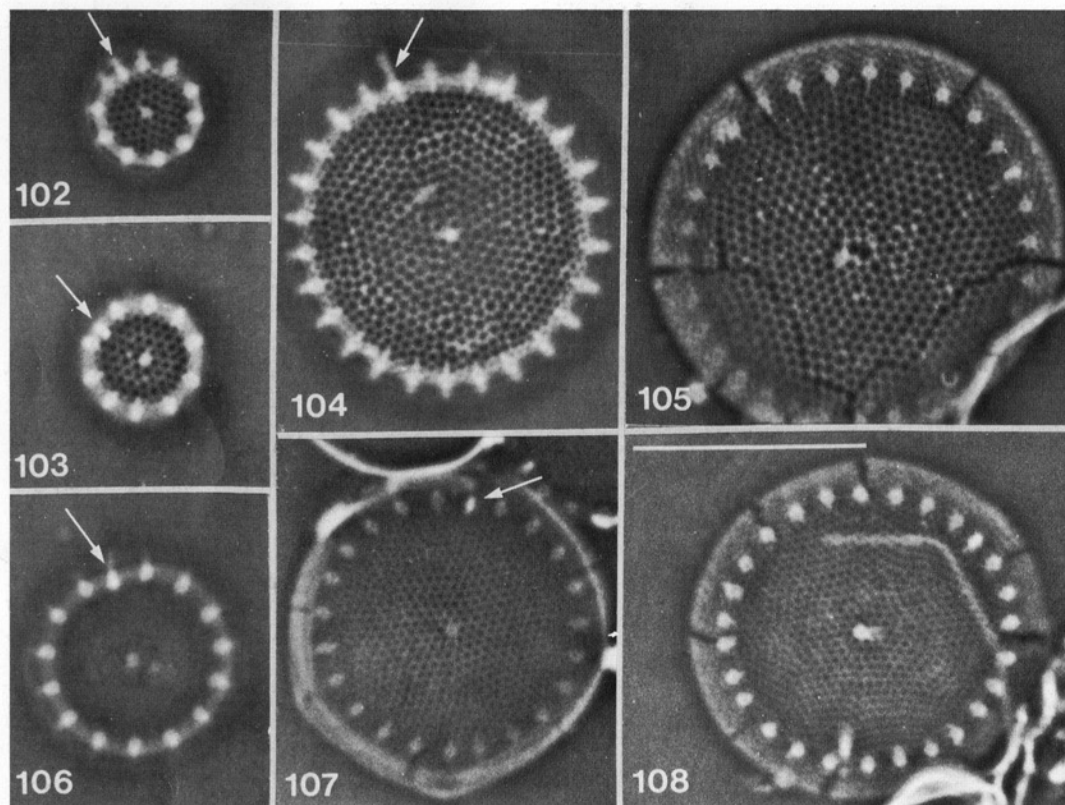
Type material was not available for this investigation. Dr. Takano kindly placed prints of electron micrographs at my disposal, and

since they can be regarded as iconotypes, they are reproduced here for comparison (Figs. 100–101). The present investigation is based mainly on two unialgal cultures, one established by Dr. E. Laws from Kaneohe Bay, Oahu, Hawaii, and clone F99 established by Dr. G. A. Fryxell from the Gulf of Mexico. Specimens from the latter culture were slightly coarser in structure (18–24 areolae in 10 μ m on valve face, probably dependent on size of valve diameter) than the one from Hawaii. Observations from some other warm water localities have been included.

The results are overall consistent with those published by Takano (1965) and Makarova (1977a). But, in contrast to these two authors' statements, valve face areolae could be seen in LM when the specimens were freed from organic material, mounted in Hyrax, and examined under phase contrast illumination (Figs. 102–108). The slightly eccentric process, the single labiate, and the marginal ring of strutted processes are readily visible in LM in specimens prepared in this way.

Takano (1965, Fig. 2a) observed *T. allenii* as single cells or in short chains. The connecting thread was slightly longer than the perivalvar axis. Makarova (1977a) found 3–6 cells in chains. Cells in girdle view are similar to *T. nordenskiöldii* (Fig. 1); however, the connecting thread of *T. allenii* is comparatively longer and cell diameter is generally smaller.

No intact theca was observed, but it is evident



Figs. 102–108. *T. allenii*, single valves, Hyrax mounts, LM, all the same magnification, scale = 10 μm . Figs. 102–105. Clonal culture, F99, Gulf of Mexico. Figs. 106–108. Clonal culture, Kaneohe Bay, Oahu, Hawaii. Labiate process arrowed.

from observations of single bands and valves with valvocopula that the advalvar and abvalvar parts of valvocopula are unperforated with a wide perforated part inbetween (Fig. 111). Moreover, the advalvar part has one row of larger pores, and it is probably curved to fit to the thickened list of valve mantle (Fig. 113).

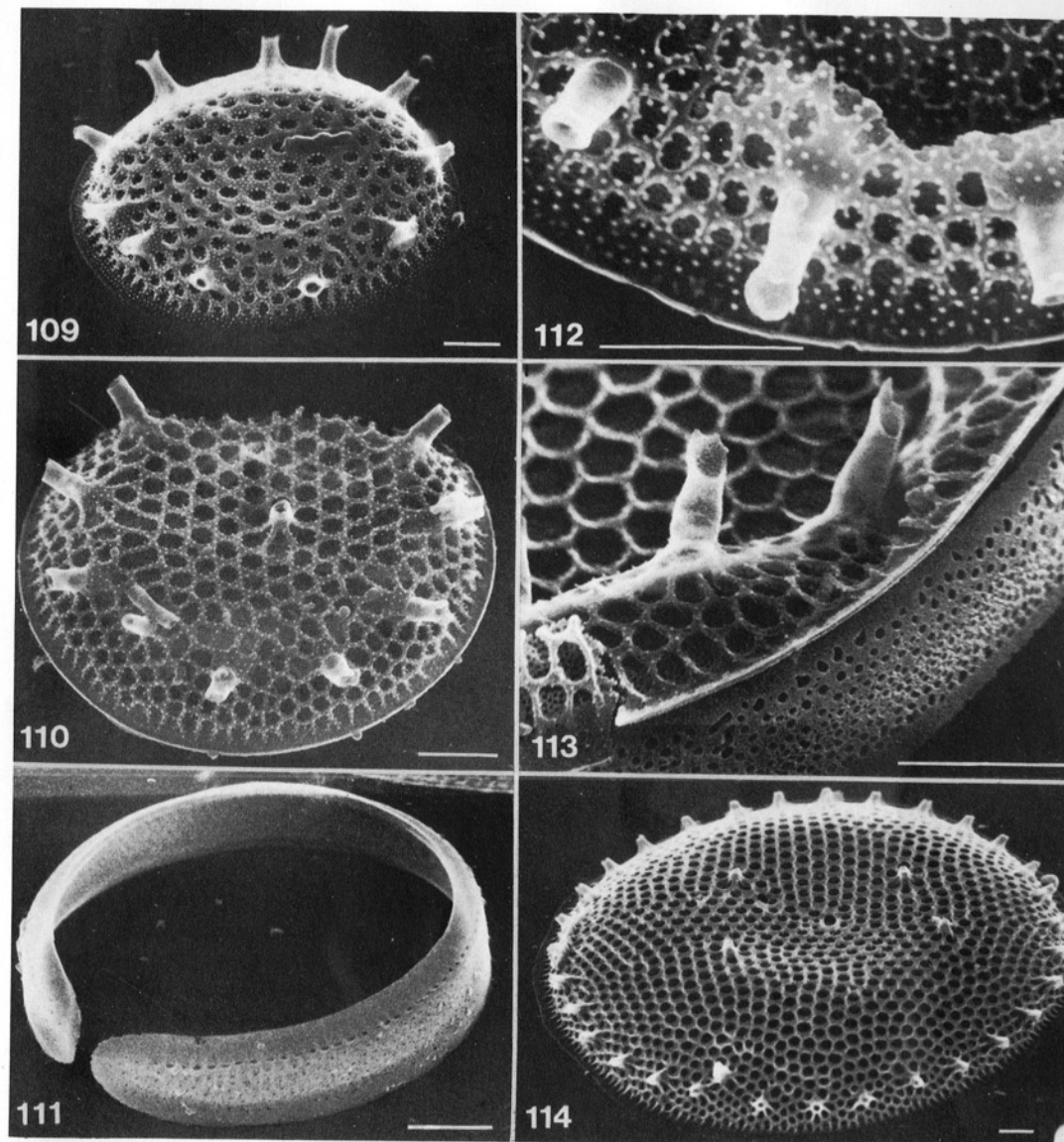
The areolae are arranged in straight or curved rows, or in radial rows with a tendency of fasciculation (Figs. 102–105, 115, 116, 121, 122) although no distinct fasciculation was observed. The most distinctive feature is the great difference between valve face and mantle areolae, about 20 and 40 in 10 μm , respectively, in addition to the generally finer structure than in the four related species discussed above (Table I).

The external valve surface is covered by siliceous granules, on the flattened brim of valve mantle (Fig. 112) as well as on the walls between foramina (Fig. 127) and on the basal part of the

processes (Figs. 112, 128). The external foramina are wide and usually circular in outline (Figs. 109, 110).

Although one or more of the areolae in valve centre is slightly larger and more irregular in outline than the others, there is no areola which can be designated a central areola. The internal cribra of areolae surrounding the single central strutted process are just as the rest (Fig. 126).

The central process takes about as much space as an areola. It has 3–5 satellite pores (Figs. 121–123, 126), while four seemed to be the constant number of satellite pores in the marginal ring (Figs. 123–125). The external tube of the central process is raised above the valve surface (Fig. 110). In the intermediate layer between the external and internal valve surface the wall of the central process seems to be widened (Figs. 126, 127) in the same way as in *T. angulata*. The external tube of the marginal

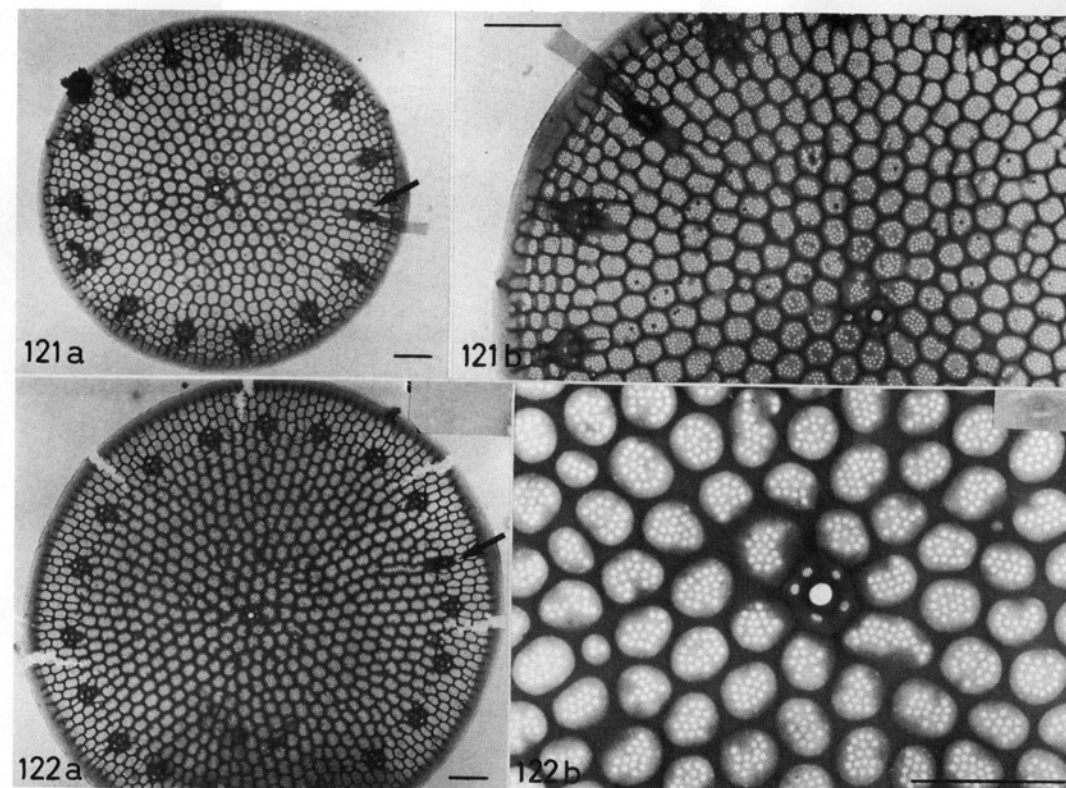
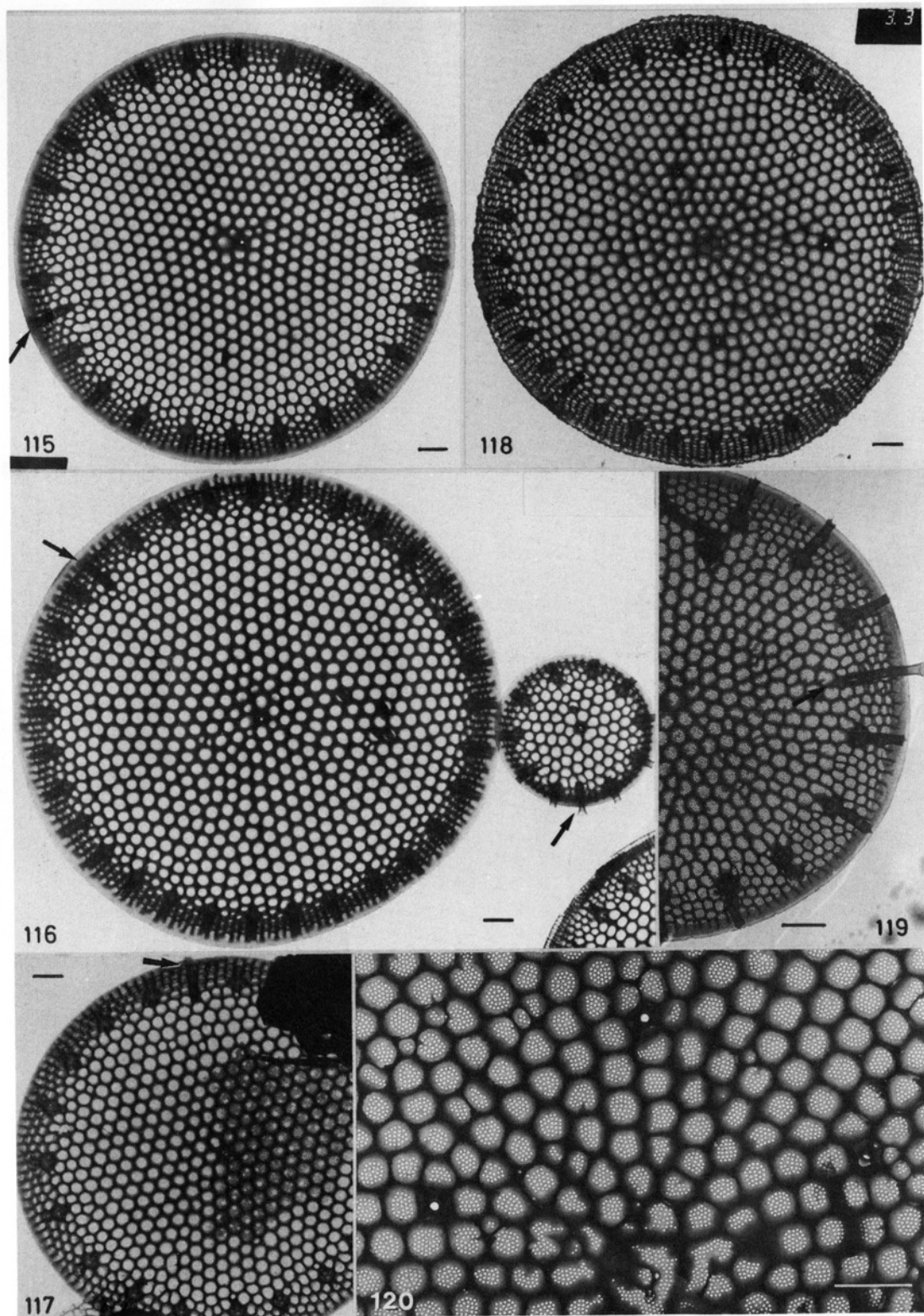


Figs. 109–114. *T. allenii*, SEM, external view, scale = 1 μm . Figs. 109, 110. Valves with processes. Fig. 111. Valvocopula. Fig. 112. Labiate process and two strutted processes, granules on valve surface. Fig. 113. Valvocopula attached to thickened rim of valve mantle. Fig. 114. Valve of initial cell, notice processes on valve face. Figs. 109, 111, 112, 114. F99, Gulf of Mexico. Figs. 110, 114. Kaneohe Bay.

processes may be fairly long (Figs. 102, 104, 106, 110), but except for a slight constriction and widening before its distal opening (Figs. 109, 112), it has no additional structure such as in *T. nordenskiöldii* and *T. angulata*. The marginal strutted processes, 5–7 in 10 μm in the present material, are located between the flattened valve face and the valve mantle which

is usually three, sometimes two or four areolae high (Figs. 112, 113, 122).

The bases of the labiate and the marginal strutted processes are located at about the same distance from the mantle edge (Figs. 123, 124). The labiate process is in most cases positioned as for a marginal strutted process with the qualification that distances between the labiate



Figs. 121, 122. *T. allenii*, TEM, single valves, scale = 1 μm , Kaneohe Bay. Fig. 121. Long external tube of labiate process. Fig. 122a. Broken valve mantle with smaller areolae. Fig. 122b. Central strutted process with five satellite pores. Labiate process arrowed.

process and the adjacent strutted ones may be somewhat shorter than in the rest of the ring (Figs. 115–119, 121–123). Its external tube is still longer than that of a marginal strutted process and slightly curved (Figs. 109, 112, 119, 121). The internal labiate-shaped part is somewhat larger than a strutted process; it is short-necked and radially oriented (Figs. 123, 124).

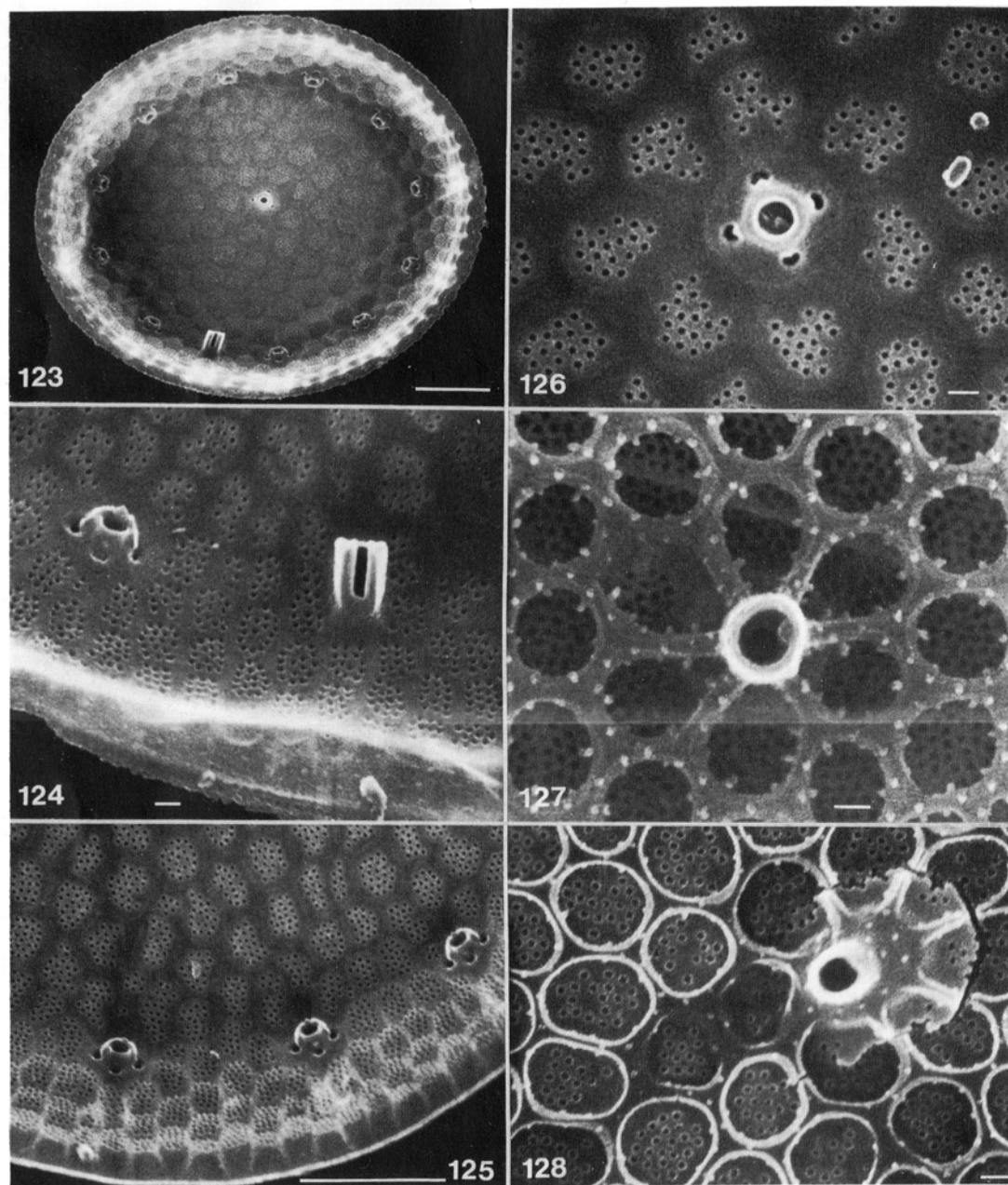
The Gulf of Mexico culture was harvested at a time when the smallest cells were about 5 μm and the largest 20 μm in diameter. Initial valves formed after auxospore formation were also present. They were distinguished by a more convex valve face, no central process, and a few strutted processes irregularly scattered on valve face (Figs. 114, 118, 120).

Taxonomy

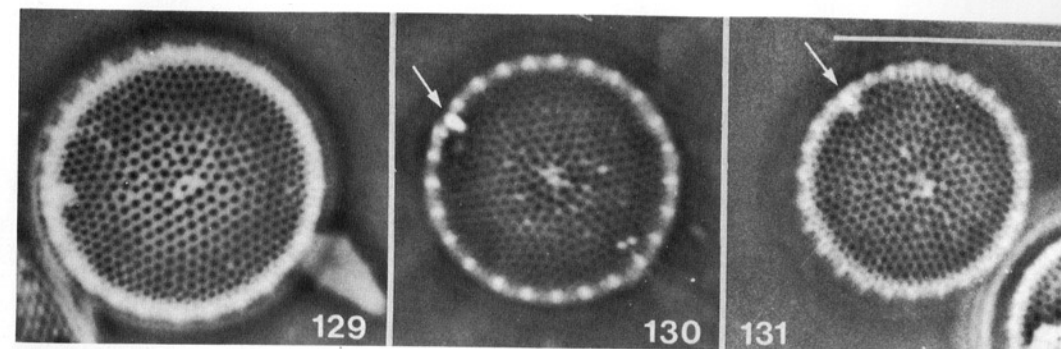
Makarova (1970) suggested that *T. allenii* was not a discrete species but belonged to *T. nordenskiöldii*. More recently this suggestion was rejected (Makarova 1977a), and *T. allenii* was classified as belonging to the section *Tangentales* Makarova, while *T. nordenskiöldii* had been placed in the section *Thalassiosira* Cleve (Makarova 1971b). This classification refers to differences in areola array. In this respect *T. allenii* is more similar to *T. pacifica* and *T. angulata* than to *T. nordenskiöldii*.

Takano (1965) compared data on *T. allenii*, *T. nordenskiöldii*, *T. aestivalis*, and *T. pacifica*. Makarova (1970) compared data on *T. allenii*

Figs. 115–120. *T. allenii*, TEM, single valves, scale = 1 μm . Figs. 118, 120. Valves of initial cells, notice strutted processes on valve face. Fig. 117. Miami Beach, Florida, USA, 14 December 1970. Fig. 119. Kaneohe Bay. The others F99. Labiate process arrowed.



Figs. 123–128. *T. allenii*, SEM, F99, Gulf of Mexico, scale for Figs. 123, 125 = 1 μm , for the others = 0.1 μm . Figs. 123–126. Internal view. Figs. 127, 128. External view of valve centre. Fig. 124. One strutted and the labiate process, internal cribra of smaller valve mantle areolae. Fig. 125. Marginal strutted processes. Fig. 126. Valve centre, strutted process with four satellite pores.



Figs. 129–131. *Planktoniella muriformis*, single valves, Hyrax mounts, LM, all the same magnification, scale = 10 μm . Lower California (collector T. J. Smayda, NSF Grant GX 33502). Figs. 129, 130. 26° 51'N, 114° 11'W, 30 March 1973. Fig. 131. 25° 55'N, 114° 02'W, 29 March 1973. Labiate process arrowed.

and *T. nordenskiöldii*, and Makarova (1977a) based a comparison of *T. allenii*, *T. nordenskiöldii*, and *T. pacifica* on her EM investigations. Except for data on areola size of *T. nordenskiöldii*, Makarova's (1977a) observations agree with the results presented in this paper (Table I).

T. allenii is thus distinguished from *T. nordenskiöldii*, *T. aestivalis*, *T. pacifica*, and *T. angulata* by being generally smaller, by having smaller areolae, and by a greater distinction between valve face and mantle areola size; from *T. nordenskiöldii* and *T. angulata* also by more densely placed marginal processes, from *T. nordenskiöldii* moreover by a more shallow valve mantle, and from *T. angulata* by the location of the labiate process. *T. allenii* is close to *T. aestivalis* and *T. pacifica* in height of valve mantle and number of marginal strutted processes in 10 μm , but lacks the distinct marginal ribs of the valve mantle of the two latter species.

T. decipiens, although a small species, has a much coarser structure than *T. allenii*, and *T. binata* G. Fryxell is characterized by a much higher valve mantle and the labiate process located close to a marginal strutted process.

T. levanderi Van Goor is included in Table I although too few data are known for a meaningful comparison with *T. allenii*.

The similarity in valve structure of *T. allenii* and *Planktoniella muriformis* (Loeblich, Wight & Darley) Round (Figs. 129–131) should be mentioned, however, even though the dissimilarity in colony shape is extreme. The investigations by Loeblich et al. (1968) and by

Round (1972) as well as the present one show that single valves of *P. muriformis* and *T. allenii* are distinguished by a still lower valve mantle of *P. muriformis* (Figs. 132–134) besides shorter distance between marginal strutted processes and a much larger labiate process. Shape and location of central strutted process and size and arrangement of areolae are much the same in the two species compared.

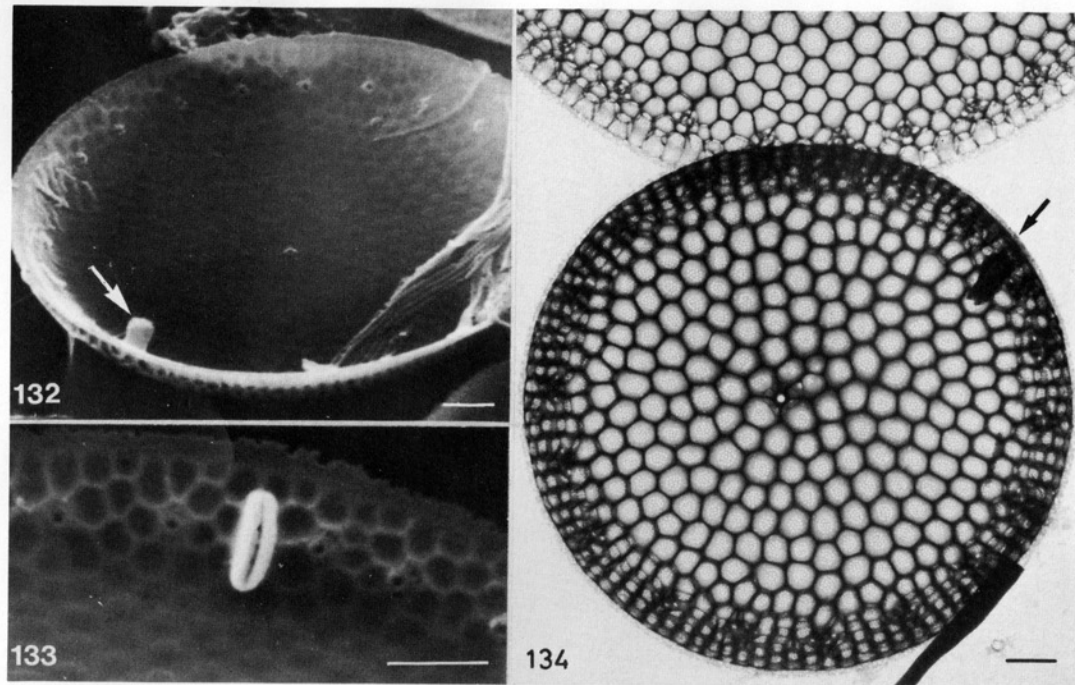
Distribution

As suggested by Makarova (1977a) *T. allenii* most likely belongs to warm waters. It was grown at 14–26°C (Takano 1965). It was recorded from the Adriatic Sea by Makarova (1977a), and in the present investigation from Hawaii, Gulf of Mexico, Miami in Florida, Tokyo Bay in Japan, Saronicos Gulf in Greece, and off West Africa.

Discussion

The *Thalassiosira* species discussed here belong to the larger or medium-sized species of the genus, except *T. allenii*. Even so, they may easily be confused when seen in girdle view as single cells or in colonies, or confused with still other species.

T. nordenskiöldii is the most characteristic one with an octangular outline and short distance between cells in colonies, although the length of the thread may vary somewhat (Fig. 1). Colonies of *T. nordenskiöldii* and *T. aestivalis* are similar, but the connecting thread is generally longer and



Figs. 132–134. *Planktoniella muriformis*, single valves, Lower California, 26° 45'N, 113° 54'W, 2 April 1973, scale = 1 μ m. Figs. 132, 133. SEM, internal view, labiate and strutted processes. Fig. 134. TEM, central strutted process, internal cribra. Labiate process arrowed.

the valve mantle lower in *T. aestivalis* (Figs. 2). *T. pacifica* in colonies (Fig. 3) may well be confused with *T. antarctica* Comber and *T. gravis* since all have flattened valve face and rounded corners. *T. angulata* with the long, thin connecting thread and the prominent distinction between valve and girdle (Fig. 4) is usually fairly easily recognized. *T. allenii* in colonies is apparently very similar to *T. floridana* (Cooper) Hasle, of the same size-group, although valve mantle of *T. floridana* is lower and forms a less sharp angle with valve face than in *T. allenii* (unpubl. obs.).

As for many other *Thalassiosira* species, a reliable identification can in most cases be made only by examination of cells in valve view. With the exception of the number of valve mantle areolae in 10 μ m, all the morphologic criteria listed in Table I are discernible in LM on cleaned valves mounted in Hyrax.

If Makarova's (1971b) classification of *Thalassiosira* is followed, *T. nordenskiöldii* and *T. aestivalis* belong to the section *Thalassiosira* Cleve, and *T. pacifica*, *T. angulata*, and *T. allenii* to *Tangentales* Makarova. The classifica-

tion into sections was based on areola array while arrangement and number of processes were used as distinctive criteria of species (Makarova 1976b). This point of view is partly in contrast to the one advocated by Hasle (1968), who estimated the variation in areola array to be greater than that of process number and arrangement. The high number of *Thalassiosira* species now known seems to require a subdivision of the genus. But, unfortunately, in spite of the many detailed *Thalassiosira* investigations published during the last decade, there seems to be still a long way to go until a generally acceptable basis for a clear-cut distinction of divisions is established.

As to distribution of the species discussed here, the results concerning *T. nordenskiöldii* and *T. pacifica* are probably reliable; they are restricted to the northern hemisphere, *T. nordenskiöldii* with a more northern distribution than *T. pacifica*. The records of *T. aestivalis* and *T. allenii* are too few to give any conclusive results, and *T. angulata* has apparently in the past been confused with too many other species for any conclusion to be drawn at all. It is

noteworthy, however, that *T. angulata* was not seen in samples available for this investigation from the Pacific Ocean, indicating that if not absent, it is most probably fairly rare in this ocean.

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